Maintien à long terme des communautés d'insectes forestiers dans un contexte de changement global : Réponses écologiques des communautés d'Orthoptères dans une succession forestière et face à la progression d'espèces invasives

Jeremy Anso

▶ **To cite this version:**

Jeremy Anso. Maintien à long terme des communautés d'insectes forestiers dans un contexte de changement global : Réponses écologiques des communautés d'Orthoptères dans une succession forestière et face à la progression d'espèces invasives. Biodiversité et Ecologie. Université de la Nouvelle-Calédonie, 2016. Français. NNT : 2016NCAL0005 . tel-02937448

HAL Id: tel-02937448
https://unc.hal.science/tel-02937448

Submitted on 14 Sep 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

UNIVERSITE DE LA NOUVELLE-CALEDONIE

ECOLE DOCTORALE DU PACIFIQUE (ED 469)

Maintien à long terme des communautés d'insectes forestiers dans un contexte de changement global : Réponses écologiques des communautés d'Orthoptères dans une succession forestière et face à la progression d'espèces invasives

THESE

Pour obtenir le grade de

DOCTEUR DE L'UNIVERSITE DE LA NOUVELLE-CALEDONIE

Discipline : Biologie des populations et écologie

IMBE UMR CNRS, IRD, UAPV / ISYEB – UMR 7205 CNRS, MNHN, UPMC, EPHE, Muséum national d'Histoire naturelle, Sorbonne Universités

Présentée et soutenue publiquement par Jérémy ANSO

Le 30 Mars 2016

Direction de thèse : Hervé Jourdan, Laure Desutter-Grandcolas et Eric Vidal

JURY

M. Olivier DANGLES	**Directeur de recherche, IRD**	**Rapporteur**
M. Bruno FOGLIANI	**Maître de conférences, IAC**	**Rapporteur**
M. Yves LETOURNEUR	**Professeur, UNC**	**Examinateur**
M. Philippe GRANDCOLAS	**Directeur de recherche, CNRS**	**Examinateur**
M. Olivier BLIGHT	**Maître de conférences, Université d'Avignon**	**Examinateur**
M. Eric VIDAL	**Directeur de recherche, IRD**	**Co-directeur**
M. Hervé JOURDAN	**Ingénieur de recherche, IRD**	**Co-directeur**
Mme. Laure DESUTTER-GRANDCOLAS	**Professeure, MNHN**	**Co-directrice**

Remerciements

Je remercie tous les membres du jury qui ont accepté d'évaluer ce travail de recherche. Merci à MM. Olivier Dangles et Bruno Fogliani, tous deux rapporteurs de ce travail, ainsi qu'à MM. Philippe Grandcolas, Yves Letourneur et Olivier Blight, tous trois examinateurs.

Je remercie Hervé Jourdan qui m'a épaulé durant tout ce travail au centre IRD de Nouméa. Merci à Hervé de m'avoir fait confiance dès le départ de cette thèse et de ce long travail que l'on sait formateur. Hervé est une véritable encyclopédie vivante sur la Nouvelle-Calédonie, et sur pratiquement tous les sujets qui s'y réfèrent. Une encyclopédie vivante, mais surtout très mobile ! Le plus difficile avec Hervé, c'est de le trouver, et de le garder sous la main pour avoir accès à son savoir ! Je n'oublierais pas les fameux « *input* » percutants et pertinents d'Hervé sur mon travail. J'ai en mémoire un excellent souvenir de cette semaine passée ensemble à Cairns pour mon deuxième congrès scientifique, un moment de partage scientifique et humain que je n'aurais surement pas apprécié à sa juste valeur sans sa présence. Un grand merci à Hervé pour m'avoir bien aidé à obtenir un studio à l'IRD (ainsi qu'Eric) et pouvoir ainsi me retrouver à bonne portée de mon ordinateur. Un énorme travail de terrain a été réalisé, et je dois remercier Hervé pour avoir obtenu les moyens financiers nécessaires pour mener à bien ce travail (notamment le GOPS et bien d'autres). Finalement, je souhaite remercier Hervé pour l'organisation de la fin de la thèse, le contact des examinateurs et des rapporteurs, gérer les différents agendas, ou encore les réservations de billets.

Je souhaite remercier Laure Desutter-Grandcolas ma co-directrice de thèse pour m'avoir fait confiance depuis mon premier stage de Master 1 à l'Université d'Angers, puis lors d'un second stage en Master 2 à l'Université de Rennes 1, toujours dans les locaux du Muséum pour commencer des travaux passionnants sur les grillons et l'acoustique. C'est à la suite de mon Master 2, et de missions inoubliables en Guyane française, qu'un sujet de thèse sur les grillons de la Nouvelle-Calédonie a été ébauché, et si j'en suis là aujourd'hui, c'est bien grâce à la volonté, aux connaissances et à la précieuse aide fournis par Laure. Le destin aussi. J'avais pris pour habitude de raconter une histoire qui me touche beaucoup à toutes les personnes qui souhaitaient l'entendre. J'aimerais sceller cette histoire dans cette thèse, car la principale intéressée le mérite amplement. C'est lors d'un cours de phylogénie à l'Université d'Angers pour mon Master 1 que nous devions choisir des sujets, avec des articles scientifiques, afin de les présenter oralement. Dans les sujets au choix, surprise, la « Nouvelle-Calédonie ». Sans plus de précision et sans attendre, je choisi ce sujet dont je

suspecte le professeur de l'époque d'avoir délibérément choisi à cause de mes origines calédonienne. Face à des articles scientifiques compliqués, des amis me conseillent de contacter les auteurs des articles afin d'avoir des explications plus claires et en français. Vous vous en doutez, l'une des personnes contactées était ma future co-directrice. Ce premier contact m'aura permis, quelques mois plus tard, de lui faire une demande spontanée de stage, d'obtenir un entretien sur Paris, et de commencer l'aventure dont vous êtes en train de lire la conclusion. Inutile de vous dire que lors de ce premier entretien, j'ai eu la surprise de voir une immense carte de la Nouvelle-Calédonie dans l'un des bureaux, et de me faire la réflexion suivante : « je suis forcément au bon endroit ! ». Plus sérieusement, Laure à été d'une aide décisive et sans faille tout au long de se travail de thèse. Sa connaissance taxonomique, phylogénétique et acoustique sur la faune des grillons a été capitale pour la réussite de ce travail de thèse. J'ai toujours été accueilli chaleureusement lors des mes missions en métropole pour réaliser des analyses complémentaires. Je la remercie pour son soutien, son franc-parler et son implication dans ce travail de thèse.

Je souhaite également remercier Eric Vidal, co-directeur de thèse et chef de notre équipe (IMBE) à Nouméa, pour m'avoir accueilli dans l'équipe et pour m'avoir fourni tout le matériel nécessaire pour mener à bien ce travail de thèse. L'environnement de travail au sein de l'équipe à Nouméa a toujours été optimal, avec un chef d'équipe qui implique l'ensemble de ces étudiants dans toutes étapes de la recherche scientifique, qui n'oublie personne et qui entretien un contact agréable avec tout le monde. Impossible de ne pas remercier Eric pour m'avoir fourni un environnement de travail idéal (du matériel informatique aux logiciels d'analyses ultra-coûteux), et de m'avoir permis de réaliser de nombreuses missions de terrain pour collecter grillons, chants et autres bébêtes.

Je tiens à remercier l'ensemble de l'administration du centre IRD pour la qualité de l'ambiance générale et le bon vivre dans le centre. Je remercie tout particulièrement Christine Hartmann et Georges De Noni pour m'avoir permis d'être héberger dans un studio du centre, qui représente une opportunité incroyable pour travailler efficacement, dont je suis extrêmement reconnaissant.

Je remercie Tony Robillard, qui travaille au Muséum de Paris sur les Eneopterinae, et qui m'a beaucoup apporté depuis que je fréquente les locaux du Muséum. Mise à part les discussions scientifiques passionnantes autour d'un café, ce sont aussi des moments super sympathiques passés à boire des grogs, ou à créer des personnes de science-fiction que nous

n’aurons malheureusement pas eu l’occasion de faire vivre. Merci à Tony pour sa collaboration active pour l’identification de nombreuses espèces de grillons dans mes parcelles, et pour sa participation dans l’un des papiers de cette thèse. Tony est je pense animé d’une bonne humeur constante et d’un réel envie d’aider ses étudiants.

Bien sûr, je remercie l’ensemble de l’équipe de l’IMBE, et toutes les personnes que j’ai pu côtoyer durant ce travail de thèse. La première personne qui me vient à l’esprit est Frédéric Rigault, avec qui j’ai partagé le bureau pendant 1 an peut-être ! Merci Fred pour tous les bons délires durant les pauses café ou les « crêpages de chignons » avec d’autres collègues. Tu m’as apporté une aide précieuse et primordiale pour obtenir des données botaniques sur l’ensemble de mes parcelles de terrain. Merci pour ton temps, ton énergie et tes vannes. Merci également pour tes compétences sur des logiciels que je ne maîtrise pas du tout (comme ArcGis), et de ta patience pour changer 25 fois de fond de carte pour que le rendu plaise à tous les auteurs ! Tu as un franc-parler qui fait plaisir, quelle tristesse ce moment où tu as quitté le bureau des « thésards » ! ;)

Un grand merci bien particulier pour Edouard Bourguet, qui m’a fortement épaulé pour mon travail de terrain, jour et nuit, que je savais très pénible. Toujours motivé, et motivant, sans Edouard je n’aurais pas acquis les résultats principaux de ma thèse et je n’en serais surement pas là aujourd’hui. Merci à lui pour son temps, son énergie et sa bonne humeur sans faille malgré les heures de voiture, parfois sous la pluie et complètement trempé, sans forcément avoir du chauffage…

Un grand merci spécial pour mes « collocs » du bureau des thésards. Je pense bien sûr à Agathe, qui a soutenu sa thèse récemment et l’a obtenue avec brio ! Félicitation à toi ! Agathe est quelque part la collègue rêvée, que tout le monde souhaiterait avoir. Discrète la plupart du temps, elle reste toujours attentive et disponible pour une brève de 15 minutes sur un sujet tendu, professionnel ou personnel. La présence d’Agathe dans ce bureau des « thésards » a été une condition majeure pour la bonne ambiance générale, à n’en point douter. Toujours prête à partager un sachet de thé pour une pause vitale, je ne compte plus nos minutes de palabres et nos échanges sur tous les sujets qui nous venaient à l’esprit. Je ne tiendrais pas rigueur à Agathe de m’avoir aspergé de glaçon lors d’une sieste sur le deck de mon studio, mais je la remercierais plutôt pour la magnifique planche à découpé en bois d’olivier offerte lors de son retour triomphale après sa soutenance de thèse ! Merciii ! Une autre collègue de bureau doit faire partie de ces remerciements, c’est Maureen ! Merci à elle

pour ses qualités humaines et professionnelles. Maureen est toujours à l'écoute de ses collègues, des problèmes, des besoins de parler. Toujours très avenante, je ne saurais remercier Maureen du nombre de fois où je suis arrivé dans mon bureau avec un café chaud qui m'attendait ! Merci également à Maureen pour les coups de main sur le terrain pour ramasser du grillon ou faire des photos de canopée ! Indéniablement, Maureen est une collègue en or, qui va probablement récupérer le flambeau de la fin de thèse après moi. Je lui souhaite donc tout le courage du monde pour finir ce travail dantesque ! Merci à ma chère collègue Quiterie, qui affronte les aléas de la thèse également ! Des échanges humains et scientifiques toujours super intéressants avec Quiterie ! Je rajoute cette ligne pour remercier Quiterie pour m'avoir relu des chapitres de thèse pour vérifier la grammaire, l'orthographe et l'organisation des idées. Merci à toi pour ton temps dans ce travail ! J'en profite pour lui souhaiter une bonne continuation pour terminer sa thèse, et beaucoup de courage pour affronter les épreuves mais surtout pour otenir le Graal du « docteur » !

Un grand merci également à tous mes collègues de l'équipe, qui sont nombreux ! Martin, Pauline, Noémie, Oriana, Mathilde, et Céline avec qui j'ai pu partager des cafés, des discussions, des apéros, ou du terrain et qui ont tous participé à cette ambiance agréable au sein du centre IRD.

Je souhaite remercier les nombreux stagiaires que j'ai eu sous ma direction pendant ma thèse. Je pense à Aurélie, Alexia, Morgane, et Fariz. J'en profite pour rendre hommage à l'une de mes étudiantes, Léa Colmas, que j'ai eu sous ma direction pendant quelques mois. Léa a été une étudiante modèle, impliquée et extrêmement intéressée par le sujet, avec une philosophie de vie admirable. Malheureusement, Léa a perdu la vie peu de temps après lors d'une randonnée en montagne à cause d'une avalanche.

Petite dédicace et remerciement pour Chloé Papaya ! Merci à elle pour son soutien rapproché, sa joie de vivre communicative mais également ses remontrances pour lâcher du lest. Merci pour tous les partages de repas maisons, toujours aussi bon les uns que les autres, ou les cadeaux occasionnels (pas assez à mon goût) déposés devant ma porte ! Je ne compte plus les petits apéros ou délires communs autour des sujets qui nous passionnent respectivement ! Ne dit-on pas qu'entres thésards, on se comprend !

Je remercie vivement et chaleureusement celle que je nomme la Grande Déesse de l'Inférence Bayésienne. Même si Laure est arrivée tardivement dans ma thèse pour une collaboration sur l'un des papiers, elle a véritablement contribué à me donner une démarche

précise et rigoureuse pour rédiger des articles scientifiques. Une démarche qui m'a été utile pour tous mes papiers de thèse, et pour les suivants très probablement ! Il fallait que je « *bullet point* » disait-elle ! Je ne compte donc plus les nombreuses fois où nous sommes allés boire une clope et fumer un café (oui, oui, vous avez bien lu !) avec une feuille de brouillon pour tisser les nouveaux plans, les nouvelles discussions et les derniers points à aborder avec les co-auteurs. Merci donc pour ta franche sympathie, ton humour virevoltant (« *hé ouais* »), ton altruisme envers les petits thésards submergés, et ta rigueur scientifique pour une belle partie de cette thèse !

Voilà les remerciements pour la Déesse suivante, Amandine, la Grande Déesse de l'acoustique passive ! Deux chapitres de cette thèse ont pu voir le jour grâce à une super collaboration entre Amandine et notre équipe de Nouméa. Amandine est venue avec son savoir-faire en acoustique passive et en analyse statistique sous R pour faire aboutir plusieurs projets scientifiques passionnants et novateurs dans le domaine. Je ne compte plus les heures passées sur le terrain, les Skype à l'autre bout du monde pour avancer les analyses, les figures et la rédaction des papiers. Au final, et malgré la somme de boulot à faire, tu as su garder ta bonne humeur et ta joie de vivre, avec une rigueur exemplaire sur le terrain (« *il ne faut faire confiance à personne d'autre* ! »)

Je tiens à remercier l'école doctorale (ED) du Pacifique, sous la direction d'Yves Letourneur, pour l'organisation des différents évènements au sein de l'université (e.g. les Doctoriales, les modules de formations, etc.). Merci également à l'ED du Pacifique pour le soutien financier accordé pour participer à deux congrès internationaux en métropole et en Australie (Ecoacoustics congress et l'IUSSI respectivement.)

Je remercie la Direction de l'Environnement de la Province Sud pour nous avoir donné les permis de collecte dans les zones dédiées à la thèse, et nous avoir permis d'accéder de jour et nuit à nos parcelles d'études dans les parcs provinciaux.

Je remercie le Gouvernement de la Nouvelle-Calédonie de m'avoir accordé la bourse d'encouragement à la recherche universitaire pour ce projet de thèse.

A ma famille et mes amis.

Table des matières

1 Introduction générale et objectifs de ce travail de thèse 2

1.1 Introduction générale 2

1.1.1 Crise mondiale de la biodiversité 2

1.1.2 Crise de biodiversité et invasions biologiques 6

1.1.2.1 Généralités, phénomènes naturels et amplifiés par l'Homme 6

1.1.2.2 Modes d'impact des espèces invasives sur la biodiversité 8

1.1.2.3 Impact des fourmis envahissantes sur la biodiversité 11

1.1.2.4 Sensibilité des écosystèmes insulaires aux invasions biologiques 12

1.1.3 Crise de biodiversité et notion de bio-indicateurs 13

1.1.3.1 Définitions et généralités 13

1.1.3.2 Les indicateurs de biodiversité 15

1.1.3.3 Le choix des indicateurs biologiques 16

1.1.4 Nouvelle-Calédonie : un archipel exceptionnel et menacé 17

1.1.4.1 Généralités sur l'archipel 17

1.1.4.2 Une histoire géologique complexe 20

1.1.4.3 Impact de la géologie sur la biodiversité et l'endémisme 21

1.1.4.4 Originalité de la biodiversité et des richesses naturelles 22

1.1.4.5 Flore et faune endémique 24

1.1.4.6 Les menaces sur la biodiversité Néo-Calédonienne 25

1.2 Objectifs de la thèse et présentation des chapitres 29

Chapitre I 35

2 Les grillons, un modèle d'intérêt en écologie 36

2.1 Présentation générale des grillons 36

2.2 Rôle des grillons dans le fonctionnement des écosystèmes 39

2.3 Les grillons en tant qu'indicateurs biologiques 41

2.3.1 Les grillons : un groupe candidat en Nouvelle-Calédonie pour la bio-indication ? 41

2.3.2 Utilisation de signaux sonores des grillons : implication dans la bio-indication 43

2.4 Les signaux acoustiques des grillons : production du signal, propagation, détection et bio-indication 44

2.4.1 Généralités 44

2.4.2 Production du signal acoustique : le mécanisme de stridulation 48

2.4.3 Propagation du signal sonore : atténuation et dégradation 49

2.4.3.1 Atténuation sonore 49

2.4.3.2 Dégradations du signal ... *50*
2.4.3.3 Les interférences acoustiques d'origine biologique ... *51*
2.4.3.4 Facteurs biologiques de sélection sur les signaux sonores ... *51*
2.4.4 Stratégies d'émission et concept de niche acoustique ... 52
2.4.4.1 Ségrégation spectrale ... *53*
2.4.4.2 Ségrégation spatiale (horizontale et verticale) ... *54*
2.4.4.3 Ségrégation temporelle ... *55*
2.4.5 Stratégie de réception du signal ... 56
2.4.5.1 Sélectivité précise pour la fréquence d'émission ... *56*
2.4.5.2 Position du receveur et mécanisme neuronal d'amplification ... *57*
2.5 Les grillons : un groupe majeur dans les écosystèmes néo-calédoniens ... 57
2.5.1 La faune de grillons de Nouvelle-Calédonie ... 57
2.5.2 Distribution et endémisme ... 58
2.5.3 Diversité des niches écologiques et des guildes fonctionnelles des grillons en Nouvelle-Calédonie 62
2.5.3.1 La diversité des niches acoustiques des grillons ... *64*
2.6 Conclusion ... 67
3 Les grillons (Insecta, Orthoptera, Grylloidea) de Nouvelle-Calédonie: description de nouvelles espèces, données écologiques et bioacoustiques ... 70
3.1 Résumé ... 71
3.2 Abstract ... 71
3.3 Introduction ... 72
3.4 Material and methods ... 73
3.4.1 Specimens ... 73
3.4.2 Morphology ... 73
3.4.3 Parcels of vegetation studied ... 73
3.4.4 Acoustic data ... 74
3.4.5 Abbreviations and symbols ... 75
3.5 Systematics ... 77
3.6 Discussion ... 201
3.7 Conclusion ... 203
3.8 Acknowledgments ... 204
Chapitre II ... 206

4 Enjeux et importance des milieux miniers à travers l'étude d'un nouveau genre de grillon endémique 207

4.1 Résumé 208

4.2 Abstract 209

4.3 Introduction 210

4.4 Material and methods 211

4.4.1 Study sites and cricket sampling 211

4.4.2 Taxon description 212

4.4.2.1 Nomenclatural Acts 212

4.4.2.2 Bioacoustic study 212

4.4.2.3 Abbreviations 213

4.4.3 Molecular phylogeny 214

4.4.3.1 Taxon sampling 214

4.4.4 Selection of DNA regions 225

4.4.5 Laboratory procedures and Preparation of datasets 225

4.4.6 Phylogenetic analyses 226

4.4.7 Bayesian divergence times estimates 227

4.4.8 Calibration point 228

4.4.9 Species richness and relative diversification rates 228

4.4.10 Ensemble species distribution modelling 228

4.5 Results 229

4.5.1 Systematics and taxon description 229

4.5.2 Acoustic description 241

4.5.3 Phylogenetic relationships of *Pixibinthus.* 241

4.5.4 Divergence time estimates 244

4.5.5 Species richness estimates and relative diversification rates 248

4.5.6 Species distribution modelling 248

4.6 Discussion 249

4.6.1 The discovery of a new original cricket genus in 'maquis minier' 249

4.6.2 Origin of the '*Pixibinthus-Agnotecous*' clade in New Caledonia 249

4.6.3 Two different ecological specializations within the '*Pixibinthus-Agnotecous*' clade 250

4.6.4 Ecological specializations suggest mutual evolution of body size and airborne signal 251

4.6.4.1 Pixibinthus: failing to diversify? 252

4.6.4.2 Impact of past climatic fluctuations? 252

4.6.5 Impact of fire regimes? 253

4.6.6 *Pixibinthus*: on the way to extinction? 253

4.7 Conclusion 254

4.8 Acknowledgments 255

4.9 Supporting information 257

5 Les communautés de grillons en tant que potential indicateurs écologiques d'une succession forestière dans un hotspot de biodiversité 265

5.1 Résumé 266

5.2 Abstract 267

5.3 Introduction 268

5.4 Material and methods 270

5.4.1 Sampling sites 270

5.4.2 Crickets sampling 272

5.4.3 Environmental variables 272

5.4.4 Analysis 273

5.5 Results 275

5.5.1 Cricket species in the succession 275

5.5.2 Beta diversity of cricket assemblages 276

5.5.3 Species co-occurrence 279

5.5.4 Environmental conditions 279

5.6 Discussion 282

5.7 Implications for conservation 284

5.8 Acknowledgments 286

5.9 Supporting information 286

6 Mesure de l'impact de deux fourmis invasives (*Wasmannia auropunctata* Roger, *Anoplolepis gracilipes* Smith) sur les communautés de grillons: implication pour la conservation dans un hotspot de biodiversité 288

6.1 Résumé 289

6.2 Abstract 290

6.3 Introduction 291

6.4 Material and methods 293

6.4.1 Sampling sites 293

6.4.2 Sampling method 295

6.4.3 Species identification 295

6.4.4 Analysis 295

6.5 Results 296
6.5.1 Non-invaded cricket communities 296
6.5.2 Singers versus mute species 297
6.5.3 Invaded plots by Wasmannia auropunctata and Anoplolepis gracilipes 297
6.6 Discussion 302
6.6.1 Contrasted responses of cricket communities toward ant invasions 302
6.6.2 Predation and competition hypothesis between ants and crickets 303
6.6.3 Implications in conservation 304
6.7 Acknowledgment 305

Chapitre III 307

7 Suivi de la biodiversité par l'analyse globale des ambiances sonores: détection d'une invasion terrestre silencieuse par la fourmi *Wasmannia auropunctata* 314
7.1 Résumé 315
7.2 Abstract 316
7.3 Introduction 317
7.4 Material and methods 319
7.4.1 Study sites 319
7.4.2 Acoustic sampling by automated sensors 319
7.4.3 Acoustic measurements on field recordings 321
7.4.4 Analyses 321
7.5 Results 322
7.5.1 Daily pattern differences in acoustic diversity 322
7.5.2 Comparison of acoustic activity between invaded and un-invaded sites. 323
7.5.3 Correlations between acoustic diversity index and calling cricket community. 324
7.6 Discussion 325
7.6.1 When soundscapes become silent 325
7.6.2 The strength of the global acoustic method 326
7.6.3 Concrete application in the field: Needs and limitations 327
7.6.4 What is next? 329
7.7 Acknowledgment 330
7.8 Supporting information 331

Chapitre IV 333

8 Etude des commnautés acoustiques de grillons en tant que bio-indicateur d'une succession forestière et d'une invasion biologique terrestre 334

8.1 Résumé 335

8.2 Abstract 336

8.3 Introduction 337

8.4 Material and methods 338

8.4.1 Study sites 338

8.4.2 Selection of sites invaded by W. auropunctata 339

8.4.3 Soundscape recording procedure 340

8.4.4 Species-specific calls recordings database 340

8.4.5 Identification of calling groups and counting of vocalizations 340

8.4.6 Analysis 342

8.5 Results 344

8.5.1 Occurrence of calling species 344

8.5.2 Calling cricket community 345

8.5.3 Species accumulation curves 347

8.5.4 NMDS and hierarchical clusters of cricket communities 347

8.5.5 Species richness and acoustic activity of crickets with Wasmannia auropunctata 349

8.6 Discussion 350

8.6.1 Acoustic signatures by habitat type 351

8.6.2 Cricket calls as a detector of *W. auropunctata* 353

8.7 Conclusion and perspectives 355

8.8 Acknowledgments 355

8.9 Supporting information 356

9 Discussion générale, applications et perspectives 358

9.1 Enrichissement de la biodiversité calédonienne 358

9.2 Les grillons sont-ils des bio-indicateurs pertinents ? 360

9.2.1 L'étude des peuplements de grillons par inventaire taxonomique 360

9.2.1.1 Dans le cadre d'une succession forestière 360

9.2.1.2 Dans le cadre d'invasions biologiques 362

9.2.2 Recommandations appliquées en conservation 364

9.3 Utilisation des signaux acoustiques pour l'évaluation de l'ambiance acoustique globale et de la communauté de grillons 366

9.3.1 Analyse globale des ambiances sonores 366

9.3.2 Analyse fine des ambiances sonores à travers les peuplements de grillons 368
9.3.3 Recommandations appliquées en conservation 370

9.4 Perspectives de recherche 371
9.4.1 Reconnaissance automatique des signaux sonores 371
9.4.2 Perspectives de bio-indication des grillons face à d'autres espèces envahissantes 374
9.4.3 Vers la détection automatique d'une invasion biologique majeure 375

9.5 Conclusions 377

10 Références 381

11 Annexes 409
11.1 Liste des publications 409
11.1.1 Articles publiés 409
11.1.2 Articles soumis 409
11.1.3 Article en préparation 410

11.2 Congrès Internationaux 410

11.3 Liste des sites sélectionnés pour l'étude, Détection de *Wasmannia auropunctata*, matériel déposé sur place et période d'enregistrement. 412

Contexte d'étude

Ce manuscrit est composé d'une introduction et d'une discussion générale en français et de plusieurs chapitres composés d'articles scientifiques (acceptés, soumis ou en préparations) en anglais. Tous les articles scientifiques présentés commencent par un résumé en français et en anglais, suivi d'une introduction, du matériel et méthode, des résultats et de la discussion en anglais..

Cette thèse s'inscrit le cadre d'un partenariat historique et renouvelé entre les équipes de l'IRD et du MNHN, au travers de la collaboration entre l'Institut Méditerranéen de Biodiversité et d'Ecologie marine et continentale (IMBE, UMR IRD 237, Aix Marseille Université, CNRS, IRD, Avignon Université) sous la direction de Thierry Tatoni et l'Institut de Systématique, Évolution, Biodiversité (ISYEB, UMR 7205 – CNRS, MNHN, UPMC, EPHE, Sorbonne Universités) du Muséum national d'Histoire naturelle (MNHN) de Paris sous la direction de Philippe Grandcolas. Plus précisément, ce travail de thèse s'articule au sein de deux équipes : l'équipe « Ecologie de la Conservation et Interactions Biotiques (ECIB) » de l'IMBE, sous la direction d'Eric Vidal et de Laurence Affre, et l'équipe « Evolution Fonctionnelle et Systématique (EvoFonct) » de l'ISYEB, sous la direction de Frédéric Legendre. L'équipe ECIB étudie la vulnérabilité des systèmes écologiques, notamment insulaires comme la Nouvelle-Calédonie, face à des pressions écologiques comme l'introduction d'espèces envahissantes. L'équipe EvoFonct étudie des caractéristiques fonctionnelles de taxons (comportement acoustique, morphologie) avec des approches comparatives et phylogénétiques.

Cette thèse a été financée par une bourse d'encouragement à la recherche universitaire du Gouvernement de la Nouvelle-Calédonie. Au cours de ce travail de thèse, plusieurs financements complémentaires ont été acquis et ont permis la réalisation des travaux tant sur le terrain qu'au laboratoire. Ainsi, les travaux phylogénétiques et moléculaires présentés dans le chapitre 3 ont été soutenus par deux « Action Transversale du Muséum » (ATM) (i) 'Biodiversité actuelle et fossile. Crises, stress, restaurations et panchronisme: le message systématique', et (ii) ATM 'Barcode', tandis que les analyses présentées dans les chapitres 4 et 5 (approche d'acoustique globale des communautés, et bioacoustique fine des communautés de grillons) ont été soutenues par le Grand Observatoire du Pacifique Sud: AAP GOPS 2013 / 'Bioacoustique des grillons de Nouvelle-Calédonie'.

1 Introduction générale et objectifs de ce travail de thèse

1.1 Introduction générale

1.1.1 Crise mondiale de la biodiversité

A l'échelle de la planète, et selon les estimations de différents auteurs (Barnosky *et al.*, 2011; Ceballos *et al.*, 2015), la biodiversité actuelle subit la crise la plus importante et la plus dramatique de son histoire, en raison de l'ampleur et de la rapidité des changements de conditions auxquels sont confrontés les écosystèmes et les espèces qui les composent, notamment par un taux d'extinction accéléré (Fig. 1.1).

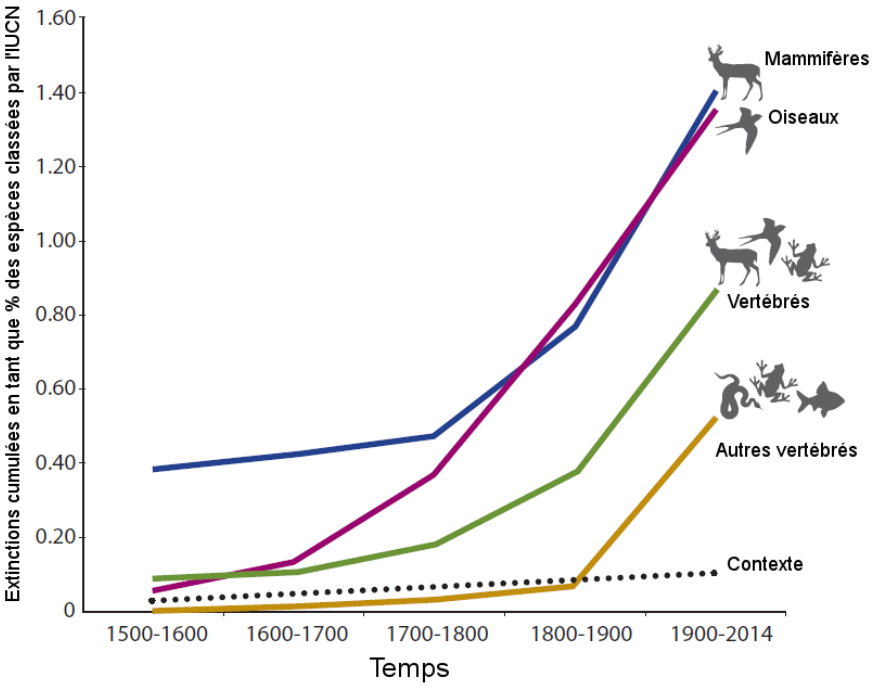

Figure 1.1. *Proportions de vertébrés éteints selon l'IUCN. Le contexte (pointillé) indique un taux d'extinction constant de l'ordre de deux espèces tous les millions d'années. Modifié d'après Ceballos et al. (2015).*

Cette « 6ème crise d'extinction » fait suite aux cinq grandes crises d'extinctions identifiées qui ont rythmé l'histoire du vivant au cours des temps géologiques (Raup, 1986; Barnosky et al., 2011; McCallum, 2015), respectivement à la fin de l'Ordovicien, puis du Dévonien, du Permien, au Trias et à la fin du Crétacé (Fig.1.2).

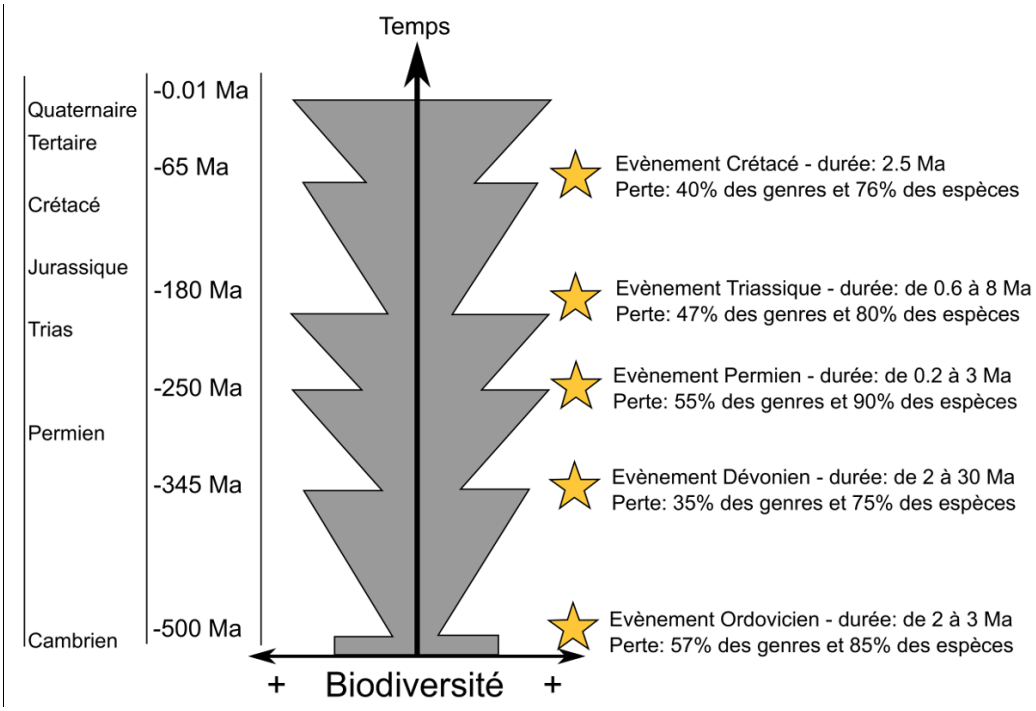

Figure 1.2. *Illustration des cinq précédentes crises d'extinction que la biodiversité a traversée au cours des temps géologiques (Modifié de Barnovsky et al. 2011)*

Ce qui caractérise la crise actuelle du vivant, c'est le rythme extrêmement rapide des changements en cours. Ainsi, les taux d'extinction des espèces seraient aujourd'hui largement supérieurs aux estimations passées, reposant sur l'analyse des fossiles (Stork, 2010; Pimm *et al.*, 2014). Ainsi, selon Pereira *et al.* (2010), les taux d'extinction actuels seraient au moins 100 fois plus importants, et dans certains cas jusqu'à 10.000 fois plus importants (selon les paramètres du modèle et des groupes animaux considérés). Si la plupart des estimations ont été réalisées sur les vertébrés (Millenium Ecosystem Assessment 2005 ; Barnovsky *et al.* 2011), des travaux récents illustrent que le phénomène est bien général pour le vivant, y compris pour les arthropodes et mollusques (Dirzo *et al.*, 2014; Régnier *et al.*, 2015). Si l'entrée dans cette 6ème crise du vivant est aujourd'hui avérée, celle-ci implique non seulement la disparition d'espèces, mais se caractérise par des conséquences qui s'étendent aux processus et au fonctionnement des écosystèmes (Valiente-Banuet *et al.*, 2015).

Par exemple, Duncan *et al.* (2013) ont mis en évidence les extinctions massives des oiseaux terrestres non passereaux dans les îles du Pacifique avec l'arrivée de l'Homme. Ainsi, d'après les modèles utilisés et les fossiles disponibles dans la région, les auteurs estiment que près de 1.000 espèces d'oiseaux terrestres auraient disparu entre la première colonisation humaine et les contacts avec les Européens (Duncan *et al.*, 2013).

Autre originalité de la crise actuelle de la biodiversité : elle se distingue de toutes les autres par son moteur d'origine anthropique, aujourd'hui reconnu et avéré (Barnovsky *et al.*, 2012). Pour certains auteurs, associent cette crise du vivant à une nouvelle ère ou époque géologique, « l'Anthropocène » (Crutzen & Stoermer, 2000; Crutzen, 2002; Meybeck, 2003; Steffen *et al.*, 2011; Zalasiewicz *et al.*, 2011). Ce concept reste toujours débattu par la communauté scientifique, notamment pour en établir la période depuis le début de l'ère industrielle ou plus anciennement à l'occasion de l'expansion de l'Homme à travers les continents (Capinha *et al.*, 2015; Kopf *et al.*, 2015; Rocha *et al.*, 2015).

Ainsi, sous la pression des activités anthropiques, la biosphère subit des changements globaux qui se matérialisent par des modifications/transformations d'habitats et des ressources, des changements de distribution d'espèces (promotion d'invasions biologiques), des effondrements de population, y compris sous la pression du changement climatique et ses conséquences (sur la température, la pluviométrie, les évènements extrêmes, le régime de houles, la montée du niveau de la mer…) (Fig. 1.3). Ainsi, parmi les activités humaines, l'exploitation des ressources naturelles, l'urbanisation, la déforestation, les pollutions ou les propagations d'espèces envahissantes participent et amplifient les changements globaux qui perturbent le fonctionnement des écosystèmes, entraînent une perte importante et irréversible de biodiversité, mais impactent également les activités, l'économie et la santé publique humaine (Millennium Ecosystem Assessment, 2005; Steffen *et al.*, 2006; Kumschick *et al.*, 2015; Miranda *et al.*, 2015). Ces changements globaux affectent négativement la biodiversité planétaire, mais aussi les services éco-systémiques majeurs associés, qui bénéficient aux sociétés humaines (la séquestration du carbone, la production de nourriture avec la pollinisation, ou encore la prévention des inondations à travers la protection des bassins versants (Millennium Ecosystem Assessment, 2005; Lewis *et al.*, 2015; Orwin *et al.*, 2015; Rocha *et al.*, 2015)). Les phénomènes sont complexes et en interactions, ce qui affectent voire altèrent les capacités de survie des espèces et le maintien des écosystèmes (Bellard *et al.*, 2012; Bellard *et al.*, 2013; Bellard *et al.*, 2016). Comme illustré par la figure 1.3, il existe de nombreuses interactions des phénomènes physiques issus du changement climatique avec la biologie/physiologie/écologie des espèces et les écosystèmes. Les conséquences s'appliquent depuis l'échelle individuelle jusqu'à l'écosystème.

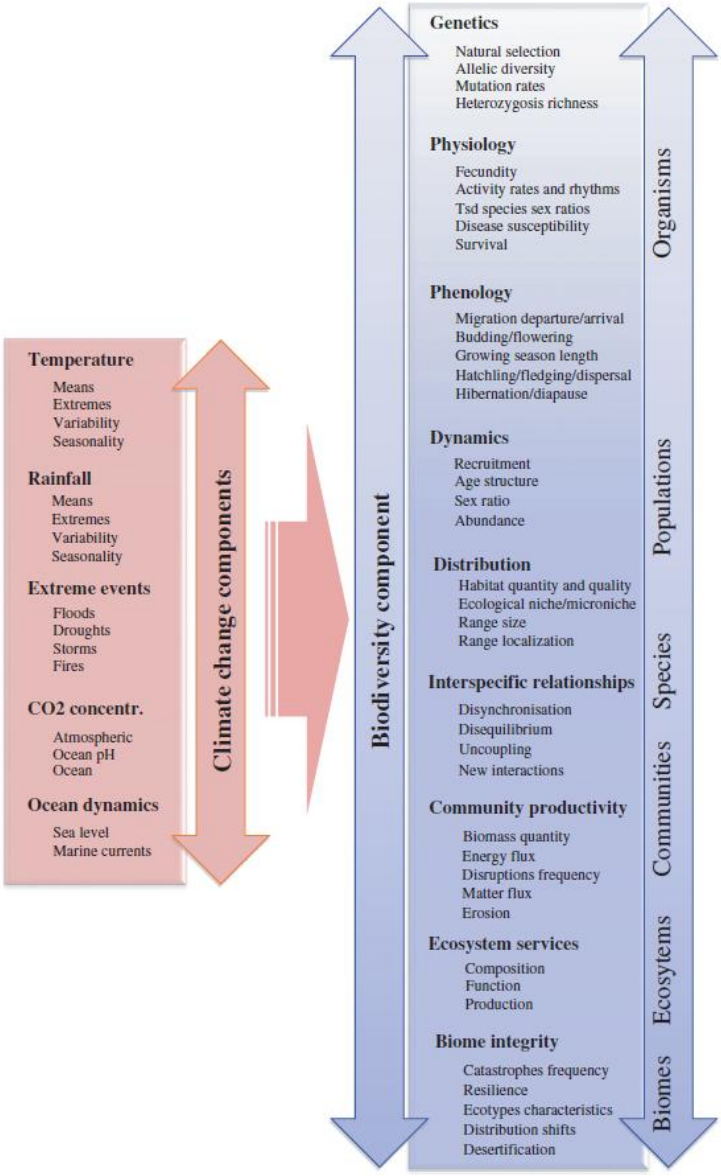

Figure 1.3. *Interactions entre les facteurs du changement climatique et les différents niveaux d'organisation du vivant. Modifié d'après Bellard et al. (2012).*

La perte et la fragmentations des habitats sont définis comme des causes majeures de la dégradation de la qualité des écosystèmes et de l'érosion biodiversité mondiale (Brooks *et al.*, 2002; Dirzo & Raven, 2003). La conversion des milieux forestiers en zone agricole ou urbaine sont des causes directes de l'activité humaine sur la biodiversité. Selon l'expertise collégiale (EM) diligentée par les Nations Unies, la déforestation et la destruction des habitats touchent 8.5 % des forêts de la planète (Millennium Ecosystem Assessment, 2005; Morales-Hidalgo *et al.*, 2015). Ainsi, les forêts tropicales qui abritent plus des 2/3 de la biodiversité mondiale sont les plus durablement touchées par les changements globaux et les activités humaines (Dirzo & Raven, 2003; FAO, 2010; Aerts & Honnay, 2011). Les feux représentent

un facteur important dans la destruction des milieux forestiers (Cochrane, 2003), avec selon la *Food and Agriculture Organisation* (FAO) des Nations Unies, près de 20 millions d'hectares de forêts tropicales brûlés tous les ans (chiffres obtenus sur 118 pays pendant quatre années). Parmi les causes indirectes d'origine anthropique qui affectent les écosystèmes, la démographie croissante de la population mondiale, les changements climatiques, l'excès de fertilisants inorganiques responsables de l'eutrophisation des milieux dulçaquicoles ou de l'hypoxie des milieux marins côtiers participent à la dégradation des conditions environnementales et aux changements globaux qui affectent les écosystèmes (Foley *et al.*, 2005; Millennium Ecosystem Assessment, 2005).

La propagation d'espèces exotiques (ou exogènes, allochtones, importées qui sont des synonymes) dans de nouveaux territoires, avec le concours direct ou indirect de l'homme, est aujourd'hui une composante majeure des changements globaux (Vitousek *et al.*, 1996). Les invasions biologiques affectent les écosystèmes terrestres et marins (Ruiz *et al.*, 1997) jouant un rôle majeur dans l'érosion de la biodiversité mondiale, et affectant fortement les activités humaines et le bien-être des populations (Vitousek *et al.*, 1997; Mack *et al.*, 2000; Simberloff, 2011; Kumschick *et al.*, 2015; Tershy *et al.*, 2015).

1.1.2 Crise de biodiversité et invasions biologiques

1.1.2.1 Généralités, phénomènes naturels et amplifiés par l'Homme

Une invasion biologique implique le déplacement d'une espèce en dehors de son aire de répartition d'origine, son installation dans un nouvel environnement, son maintien et sa propagation avec des impacts potentiellement négatifs sur les équilibres écologiques des écosystèmes, et les services éco-systémiques associés pouvant bénéficier aux sociétés humaines (IUCN, 2000; Richardson *et al.*, 2000; Pimentel *et al.*, 2001; Ricciardi, 2004; Pejchar & Mooney, 2009; Vilà *et al.*, 2011; Katsanevakis *et al.*, 2014). Les invasions biologiques sont toutefois des phénomènes naturels qui se distinguent de celles d'aujourd'hui par la différence de la magnitude des paramètres des invasions : la fréquence des invasions biologiques est plus élevée ; le nombre d'espèces transportées plus important avec une augmentation significatives des voies de dispersion, ainsi que la disparition des barrières géographiques entraînant une homogénéisation globale de la biodiversité. Les invasions

biologiques jouent également un rôle majeur en tant que cause indirecte des changements globaux (Ricciardi, 2007; Vilà *et al.*, 2011; Fagúndez, 2012).

Certains auteurs estiment que l'importance et la diversité des invasions biologiques aujourd'hui sont caractéristiques d'une nouvelle ère, celle de la « Globalisation », dont les principaux composantes sont liées aux risques croissants des invasions biologiques (Hulme, 2009). Ainsi, Hulme (2009) démontre que la croissance économique d'un pays, mesurée par le produit intérieur brut, est le principal facteur associé positivement avec le nombre d'espèces invasive à travers les régions du globe.

Aujourd'hui, la multiplication des voies de navigation à travers le globe, principalement pour le transport de marchandises et le tourisme (Anderson *et al.*, 2015), sont responsables de l'augmentation importante de propagation d'espèces en dehors de leur aire de répartition d'origine (Martin & Coetzee, 2011; Lenda *et al.*, 2014; Gotzek *et al.*, 2015). La propagation d'espèces envahissantes peut être réalisée de manière intentionnelle, avec par exemple la dispersion d'espèces pour la lutte biologique, le déplacement d'animaux domestiques (i.e. les chats ou les chiens) lors des déplacements de populations ou l'utilisation de plantes ornementales (Mack *et al.*, 2000). La dispersion d'espèces exotiques peuvent également être involontaires, notamment lors du transport de marchandises par cargo ou fret aérien contaminés par des pathogènes, ou dans les eaux de ballast (Bax *et al.*, 2003; Hulme, 2009; Vilà *et al.*, 2009; Leidenberger *et al.*, 2015).

Au niveau économique, Pimentel *et al.* (2005) ont estimé que les espèces invasives introduites aux Etats-Unis étaient responsables dégâts environnementaux et de coût d'opérations de contrôle colossaux, entraînant des coûts de l'ordre de 113 milliards d'euros par an. En Europe, Kettunen *et al.* (2009) ont estimé à 12 milliards d'euros l'impact économique des espèces envahissantes introduites. Les auteurs estiment que les dégâts économiques et les opérations de contrôle pourraient être cependant sous-estimés et dépasser les 20 milliards d'euros (Kettunen *et al.*, 2009). Au Royaume-Uni et en Irlande, les espèces invasives entraîneraient des pertes économiques de l'ordre de 2.5 milliards d'euros par an (Kelly *et al.*, 2013).

1.1.2.2 Modes d'impact des espèces invasives sur la biodiversité

Les espèces envahissantes sont une préoccupation majeure à l'échelle mondiale à cause des conséquences dramatiques sur les écosystèmes, et les menaces d'extinction des espèces natives, rares ou menacées (Donlan & Wilcox, 2008; Szabo *et al.*, 2012; Bellard *et al.*, 2016). Ainsi, Clavero & Garcia-Berthou (2005) estimaient que les invasions biologiques sont l'une des causes principales de l'extinction des espèces animales (54%), voire la seule cause impliquée dans ces phénomènes d'extinction (20%). Par exemple, le rôle prépondérant des invasions biologiques dans la perte de biodiversité chez les oiseaux est mis en avant dans de nombreuses études (Clavero *et al.*, 2009; Szabo *et al.*, 2012) ; bien que ces impacts négatifs soient activement débattus au sein de la communauté scientifique en fonction des modèles étudiés, et des conditions particulières de chaque environnement (Gurevitch & Padilla, 2004a, b; Ricciardi, 2004).

Les interactions biologiques entre les espèces natives et les espèces envahissantes sont nombreuses, et reçoivent une attention particulière de la communauté scientifique et des organismes de décision. Ainsi les espèces invasives peuvent être impliquées dans des phénomènes de prédation (Plentovich *et al.*, 2009; Marcó *et al.*, 2015), ou de compétition (par exploitation ou interférence), transmettre des parasites ou des maladies (Dunn & Hatcher, 2015; Romeo *et al.*, 2015), ou provoquer des hybridations et de l'introgression (Vuillaume *et al.*, 2015) ou des déplacements de niches écologiques (Mooney & Cleland, 2001; Mazzoni *et al.*, 2015).

Hybridation et introgression

Dans certaines situations, les espèces envahissantes peuvent s'hybrider avec des espèces natives proches (apparentées), et ainsi réaliser un transfert de gènes susceptibles de diminuer les chances de survie et de reproduction des espèces natives, y compris au travers de l'émergence d' hybrides stériles et pouvant progressivement conduire à l'extinction de ces espèces natives (Rhymer & Simberloff, 1996; Mooney & Cleland, 2001). Par exemple, le canard colvert (*Anas platyrhynchos*) qui a été introduit dans de nombreuses régions à travers le monde est responsable du déclin de plusieurs espèces de canard par hybridation, comme décrit pour les populations de canard à sourcils (*Anas superciliosa superciliosa*) en Nouvelle-Calédonie et en Nouvelle-Zélande (Pascal *et al.*, 2006) ou come observé avec le canard des

Hawaï (*Anas wyvilliana*), et le canard brun de Floride (*Anas fulvigula fulvigula*) (Rhymer & Simberloff, 1996). Dans les Petites Antilles, Vuillaume *et al.* (2015) ont mis en évidence le déplacement rapide et des extinctions localisées de l'iguane (*Iguana delicatissima*), classé comme vulnérable selon l'IUCN, du fait de l'existence d'un hybridation et d'introgression avec l'iguane invasif (*Iguana iguana*).

Prédation

La prédation des espèces natives par des espèces invasives représente l'interaction biotique la plus mise en cause dans les cas documentés d'extinction (Sax & Gaines, 2008; Veer & Nentwig, 2014). L'absence de reconnaissance des nouveaux prédateurs introduits et d'une réponse comportementale adaptée (i.e. évitement, défense) par les espèces natives sont généralement mis en cause afin d'expliquer l'importance des actes de prédation (Simberloff, 1995; Cox & Lima, 2006; Gérard, 2015). La sensibilité accrue des espèces natives est défini par le concept de naïveté, regroupé selon quatre niveaux (Banks & Dickman, 2007; Carthey & Banks, 2014), avec une sensibilité plus importante dans les milieux insulaires que dans les milieux continentaux (Gérard, 2015).

En termes d'impact, Sax & Gaines (2008) nous indique que la prédation par des espèces envahissantes est le seul facteur responsable de l'extinction de 31% d'espèces indigènes. Lorsqu'elle est cumulée avec d'autres facteurs (e.g. la pollution ou la perte des habitats), la prédation est responsable de l'extinction de 67% des espèces natives (Sax & Gaines, 2008). Par exemple, le chat sauvage (*Felis silvestris catus* Linnaeus, 1758) représente une menace sérieuse pour la survie de nombreuses espèces natives (squamates, oiseaux, ou rongeurs) dans les zones d'introduction (Medina *et al.*, 2011; Zarones *et al.*, 2015). La pression de prédation du chat haret sur les colonies de nidification du Puffin de Méditerranée (*Puffinus yelkouan* Acerbi, 1827) pourraient entraîner l'extinction rapide de cette espèce menacée (Bonnaud *et al.*, 2012). D'autres mammifères introduits, comme les rats (*Rattus rattus* Linnaeus, 1758, *R. norvegicus* Berkenhout, 1769 et *R. exulans* Peale, 1848) menacent directement un grand nombre d'espèces d'oiseaux marins, en réalisant des actes de prédation sur les œufs, les jeunes et les adultes (Jones *et al.*, 2008). Les rats sont également responsables du déclin de la régénération forestière dans plusieurs îles à cause de leur consommation des graines d'espèces forestières (McConkey *et al.*, 2003; Meyer & Butaud, 2009). Ainsi, Meyer & Butaud (2009) ont montré qu'au moins 15 espèces végétales menacées en Polynésie

Française étaient impactées par les rats, avec une forte prédation des fruits avant leur maturité. Ces auteurs indiquent des cas extrêmes de prédation sur certaines espèces végétales, avec plus de 99% des fruits mangés sur une période de surveillance de trois années (Meyer & Butaud, 2009).

Compétition

Les interactions biotiques entre les espèces d'une communauté impliquent des interactions compétitives largement documentés dans les écosystèmes du globe (Schoener, 1974, 1983). Deux principaux types de compétitions interspécifiques existent : (i) la compétition par exploitation, impliquant le partage d'une ressource (alimentaire, spatiale, etc.) entre plusieurs espèces et apportant des bénéfices pour celles qui exploitent les ressources ; (ii) la compétition par interférence qui impliquent des contacts directs entre les espèces, notamment des rapports agressifs, la production de composés chimiques entraînant l'exclusion ou le déplacement de certaines espèces (Schoener, 1983). D'une manière plus précise, Schoener (1983) définit six types de compétitions :

1. la compétition par consommation (typiquement une ressource alimentaire, l'accès à l'eau ou des nutriments particuliers) ;
2. la compétition préventive (occupation passive et préventive d'une ressource, par l'exemple l'espace) ;
3. la compétition de croissance (le développement de l'individu peut nuire celui des autres, par exemple pour l'accès à la lumière de certaines plantes) ;
4. la compétition chimique avec la production et la diffusion de composés chimiques pour limiter le développement d'autres espèces ;
5. la compétition territoriale pour la défense d'une zone importante pour l'espèce, impliquant des comportements agressifs et des interactions directes ;
6. la compétition de rencontre qui implique les espèces mobiles (vol de nourritures, blessures) pouvant aller jusqu'à de la prédation.

Si la prédation était définie précédemment comme une cause majeure dans l'extinction des espèces, il en est rarement de même de la compétition (Sax *et al.*, 2007). Cependant, lorsque la compétition est cumulée avec d'autres facteurs, comme l'arrivée d'espèces invasives par exemple, elle est impliquée dans 18% des extinctions recensées dans la littérature par des

espèces envahissantes (Sax & Gaines, 2008). Chez les plantes, l'introduction d'une espèce envahissante peut nuire au développement d'espèces natives par compétition (Gioria & Osborne, 2014). Par exemple, la Salicaire commune (*Lythrum salicaria* Linnaeus 1753) agit par compétition avec ses congénères (*L. alatum*) en monopolisant plus de pollinisateurs et réduisant ainsi la qualité et la quantité du pollen des espèces natives (Brown *et al.*, 2002). La propagation du crabe invasif (*Hemigrapsus sanguineus*) perturbe les équilibres écologiques avec d'autres espèces de crabes natives, notamment par compétition pour les abris ou pour l'accès à la nourriture (Epifanio, 2013). L'invasion du squamate *Hemidactylus frenatus* dans le Pacifique est par exemple à l'origine du déplacement des populations d'un gecko natif (*Lepidodactylus lugubris*) par compétition d'exploitation pour les ressources alimentaires (Mooney & Cleland, 2001).

Parmi les espèces exotiques et envahissantes connues pour impacter négativement et considérablement la biodiversité, les fourmis exotiques sont au cœur des investigations scientifiques et de conservation afin d'estimer la nature des préjudices écologiques sur le fonctionnement des écosystèmes, et de proposer des méthodes de contrôle efficaces pour limiter les perturbations générées.

1.1.2.3 Impact des fourmis envahissantes sur la biodiversité

Parmi les espèces envahissantes, les fourmis représentent un groupe majeur compte tenu de l'ampleur des conséquences associées à leur propagation (Holway *et al.*, 2002; Lach *et al.*, 2010). Ainsi, cinq d'entres elles (*Solenopsis invicta* Buren 1972, *Anoplolepis gracilipes* Smith 1857, *Linepithema humile* Mayr 1868, *Pheidole megacephala* Fabricius 1793, *Wasmannia auropunctata* Roger 1863) sont listées parmi les 100 espèces envahissantes les plus dommageables pour le fonctionnement des écosystèmes (Lowe *et al.*, 2000). Le succès invasif des fourmis invasives est généralement assuré par des traits biologiques, phylogénétiques et morphologiques caractéristiques : (i) une absence d'agressivité entre les colonies de la même espèce (i.e., l'unicolonialité), (ii) un développement des populations par polygynie (i.e. avec plusieurs reines), (iii) une forte agressivité et l'utilisation d'aiguillons venimeux dans les interactions interspécifiques, (iv) une capacité de recrutement massif d'ouvrières, (v) l'utilisation du miellat sucré des insectes phytophages par mutualisme, (vi) l'absence de résistance biotique des communautés envahies (Holway, 1998; Holway *et al.*, 2002; Diaz *et al.*, 2004)

Pour l'ensemble de ces caractéristiques, l'introduction d'une fourmi invasive est généralement accompagnée d'une frappante compétition pour les ressources ou les sites de nidification et d'une prédation active sur les différentes communautés d'invertébrés et vertébrés (Rowles & O'Dowd, 2007; Vonshak *et al.*, 2011). Par exemple, la fourmi de feu (*Solenopsis invicta*) serait impliquée dans l'extinction de l'escargot terrestre (*Orthalicus reses reses*) en Floride (Forys *et al.*, 2001), ainsi que dans le déclin de nombreuses espèces de fourmis natives, de mammifères, d'amphibiens et de squamates par prédation (Lubin, 1984; Wojcik *et al.*, 2001; Holway *et al.*, 2002). La fourmi folle jaune entre en compétition avec les crabes natifs des îles des Samoa en monopolisant les carcasses d'animaux morts, et en repoussant les crabes en dehors des zones envahies (McNatty *et al.*, 2009). Cette compétition par exploitation et interférence (i.e. jet d'acide formique) entraîne l'abaissement du niveau trophique des crabes, et les orientent vers une alimentation plus herbivores. Généralement, l'introduction de fourmis envahissantes entraîne la réduction voire l'éradication de nombreuses espèces qui composent la communauté (Holway, 1999; Mooney & Cleland, 2001; Holway *et al.*, 2002; Lach & Hooper-Bui, 2010).

1.1.2.4 Sensibilité des écosystèmes insulaires aux invasions biologiques

Les milieux insulaires ne représentent qu'environ 5.3% des terres émergées de la planète (Tershy *et al.*, 2015), mais abritent une biodiversité exceptionnelle, regroupant les principaux *hot spot* de biodiversité (Simberloff, 1974; Myers *et al.*, 2000). La biodiversité insulaire englobe par exemple 17% des plantes connues, 19% des oiseaux ou 17% des rongeurs, et elle présente une sensibilité plus marquée aux changements globaux, notamment aux invasions biologiques, que la biodiversité continentale (Tershy *et al.*, 2015), pouvant être en partie expliquée par un syndrome insulaire (Crespin *et al.*, 2012; Novosolov *et al.*, 2013). Généralement, les espèces insulaires forment de petites populations avec des distributions restreintes (MacArthur & Wilson, 1967) et une diversité génétique plus limitée que les espèces des milieux continentaux (Frankham, 1997). Le syndrome insulaire regroupe également tous les traits d'histoire de vie, les comportements et les attributs morphologiques des espèces qui seraient principalement inadaptés ou manquants face à la menace des espèces exotiques introduites (Bowen & Vuren, 1997; Tershy *et al.*, 2015). Ainsi, l'isolement des écosystèmes insulaires peut entraîner la perte de comportement anti-prédateur de certaines espèces (van Damme & Castilla, 1996), qui serait coûteux en énergie et non-fonctionnel,

augmentant ainsi la vulnérabilité de ces espèces insulaires aux nouveaux prédateurs (Blumstein & Daniel, 2005).

Ainsi, parmi les 35 hotspots de biodiversité identifiés à l'échelle de la planète, dix sont des régions insulaires (Myers *et al.*, 2000; Mittermeier *et al.*, 2011). Parmi ces hotspots insulaires, la Nouvelle-Calédonie est caractérisée par la plus petite taille et par l'une des flores les plus riches et endémiques du globe, avec cependant des menaces croissantes et diverses (invasions biologiques, destruction d'habitats, pollution, urbanisation) (Kier *et al.*, 2009).

1.1.3 Crise de biodiversité et notion de bio-indicateurs

Dans ce contexte de dégradation rapide de l'environnement et compte tenu du déficit actuelle de connaissances sur l'ensemble des composantes de la biodiversité, il est important pour les sociétés humaines de pouvoir établir des diagnostiques de biodiversité afin de mettre en œuvre des mesures de gestion, de conservation voire de restauration de l'environnement. Dans cette perspective, certains organismes vivants peuvent avoir des réponses indicatrices de l'état de leur environnement et des pressions subies. On parle d'organismes bio-indicateurs. Ces proxys de l'état de l'environnement subissent de manière exacerbée les changements environnementaux et leur observation permet de déclencher rapidement des plans d'action. Il s'agit d'un champ scientifique en plein développement, dont seuls les grands principes seront présentés ci-dessous, au même titre que la nécessité et l'intérêt de la recherche de nouveaux organismes bio-indicateurs.

1.1.3.1 Définitions et généralités

Le suivi et le maintien de l'état des écosystèmes sont indispensables pour comprendre et préserver les équilibres écologiques et la biodiversité actuels. Toutefois, le suivi des écosystèmes se révèle délicat du fait même de la complexité de la biodiversité et des relations entre les groupes fonctionnels, de notre manque de connaissances taxonomiques et des coûts élevés inhérents aux programmes de suivi de la biodiversité. Ainsi, dans le but de déterminer « l'état de santé » des écosystèmes, l'utilisation de groupes fonctionnels particuliers, ou bio-indicateurs, représente une alternative efficace pour détecter de manière précoce les perturbations des équilibres écologiques.

Les bio-indicateurs regroupent toutes les espèces ou groupes fonctionnels, qui peuvent traduire l'état de santé d'un milieu ou d'un écosystème, à travers l'étude de leur abondance et de leur diversité (Niemi & McDonald, 2004; Heink & Kowarik, 2010). Ces indicateurs attestent des différentes perturbations (environnementales ou écologiques) affectant les écosystèmes, et doivent permettre d'en identifier les causes (Dale & Beyeler, 2001). Une très grande variété de bio-indicateurs existe en fonction des habitats considérés et des perturbations mesurées, incluant des vertébrés (par exemple, oiseaux et mammifères) et des invertébrés (Pearce & Venier, 2005, 2006).

Les indicateurs biologiques sont répartis en trois catégories non exclusives, en fonction des perturbations et de la nature de l'information fournie : les indicateurs de biodiversité, les indicateurs environnementaux et les indicateurs écologiques (McGeoch, 1998; Niemi & McDonald, 2004; Heink & Kowarik, 2010; Gerlach *et al.*, 2013) (Fig. 2.2).

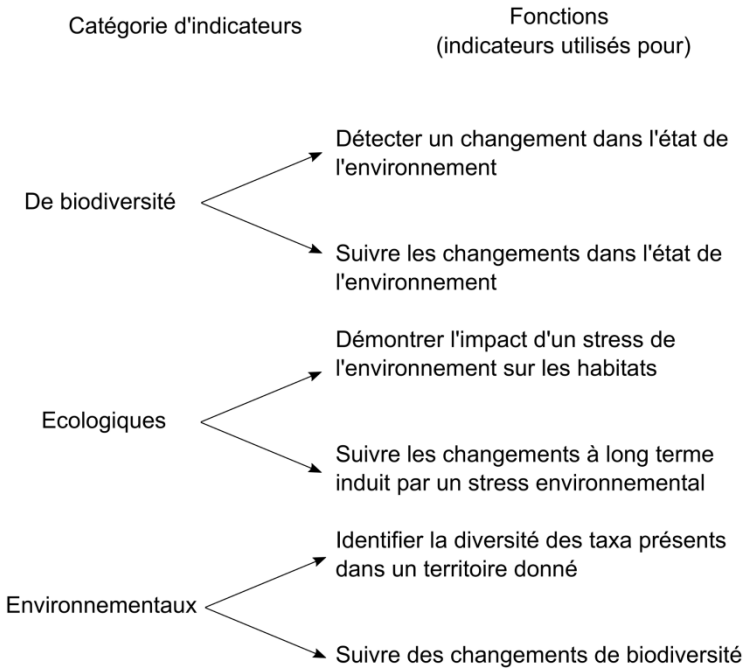

***Figure 1.3**. Catégories des bio-indicateurs et les fonctions associées. Adapté de McGeoch (1998).*

1.1.3.2 Les indicateurs de biodiversité

Ce groupe inclut toutes les espèces ou groupes d'espèces dont la présence, l'abondance ou la diversité permettent d'estimer la diversité d'autres espèces, du même ou d'autres groupes taxonomiques possédant les mêmes mécanismes de dispersion. Par exemple, des travaux réalisés sur les papillons d'Amérique du Nord ont montré que seulement 4 à 5 espèces indicatrices permettent d'expliquer la diversité de 77% à 88% du reste de la communauté de papillons (MacNally & Fleishman, 2002, 2004).

Les indicateurs environnementaux

Ce groupe inclut toutes les espèces ou groupes d'espèces qui sont sensibles à plusieurs perturbations à l'échelle de l'environnement (comme la qualité des sols ou les conditions bioclimatiques par exemple) et qui, à ce titre, peuvent servir d'indicateur de l'état de santé des écosystèmes (McBride *et al.*, 2011; Gerlach *et al.*, 2013). Par exemple, les insectes Carabidés (Coléoptères, Caraboidea) sont des indicateurs pertinents de l'influence des changements climatiques sur le fonctionnement des écosystèmes (Koivula, 2011).

Les indicateurs écologiques

Ce groupe inclut toutes les espèces ou groupes d'espèces qui reflètent les effets de perturbations écologiques précises (par exemple l'introduction d'espèces envahissantes ou le changement des conditions microclimatiques), délimitées dans le temps et dans l'espace, avec des liens avérés de cause à effet (Niemi & McDonald, 2004; Bouyer *et al.*, 2007; Gerlach *et al.*, 2013). Par exemple, la diversité des mantes religieuses (Insecta, Dictyoptera, Mantodea) est définies dans le plus grand ensemble karstique de Slovaquie comme indicatrice du taux d'humidité du sol (Gavlas *et al.*, 2007).

Les dernières catégories d'indicateurs, environnementaux et écologiques, peuvent être subdivisées en trois groupes en fonction de leur réponse aux perturbations ou changements de l'environnement : ce sont les détecteurs, les exploiteurs et les accumulateurs.

- Les détecteurs sont une composante naturelle (espèces résidentes) des écosystèmes étudiés, qui sont sensibles aux perturbations environnementales et aux stress écologiques

affectant l'habitat considéré et réagissant avec des fluctuations marquées de population (variations d'effectifs voir extinction locale). Par exemple, les communautés d'insectes (les Formicidae notamment) sont des indicateurs très sensibles d'une invasion biologique de fourmis exotiques (Bos *et al.*, 2008).

- Les exploiteurs sont des espèces dont l'abondance augmente en réponse à un stress écologique ou environnemental. Par exemple, Bianchi *et al.* (2014) ont démontré que la densité des populations de punaises (Pentatomidae) au Brésil étaient plus importante dans les milieux les plus perturbés par les activités humaines. Certains insectes phytophages suceurs de sève sont également des indicateurs de la présence d'une perturbation écologique, avec des densités pouvant être multipliées par cinq en présence d'une fourmi envahissante (*Solenopsis invicta* Buren, 1972) (Diaz *et al.*, 2004).

- Enfin, les accumulateurs ou bio-accumulateurs ont la capacité d'accumuler des produits toxiques comme les métaux lourds ; on peut les utiliser pour mesurer le niveau de toxicité et de pollution d'un environnement (Badiou-Bénéteau *et al.*, 2013; Fahmy *et al.*, 2014). Par exemple, une espèce de moule (*Mytilus galloprovincialis* Lamarck, 1819) a révélé son efficacité et sa sensibilité face à l'accumulation de certains métaux lourds en relation avec des perturbations naturelles ou anthropiques (Gorbi *et al.*, 2008).

1.1.3.3 Le choix des indicateurs biologiques

Plusieurs auteurs (Dale & Beyeler, 2001; Niemi & McDonald, 2004; Samways *et al.*, 2010; Gerlach *et al.*, 2013) ont défini les critères de sélection pour choisir des espèces ou des taxons supra spécifiques en tant que bio-indicateurs :

• Les bio-indicateurs doivent être facilement échantillonnés, sans poser de problème conséquent en coût et en temps, et avoir des abondances relativement importantes permettant des analyses statistiques rigoureuses.

• Ils doivent être sensibles à des stress ou des perturbations clairement définis, avec des liens de cause à effet avérés, et des réponses prévisibles en fonction du stress considéré (cf. détecteurs, accumulateurs ou exploiteurs). Si plusieurs taxons sont étudiés, ils doivent avoir des sensibilités contrastées aux perturbations, afin d'interpréter les variations spécifiques de chaque espèce. Dans l'idéal, les espèces choisies doivent posséder des capacités de dispersion différentes, ce qui permet de distinguer les colonisations rapides, indiquant une première

restauration de l'environnement, des colonisations lentes qui indiquent des stades avancées du rétablissement de l'environnement.

- Le groupe étudié en tant que bio-indicateur doit bénéficier d'une expertise taxonomique suffisante.

- Les fluctuations naturelles d'abondances doivent être connues et différentiées des fluctuations observées en réponse à des perturbations de l'environnement.

- Les bio-indicateurs doivent être en mesure d'alerter rapidement sur les changements écologiques des écosystèmes, c'est-à-dire qu'ils doivent réagir très rapidement aux perturbations et pressions subies par l'écosystème surveillé.

- Finalement, ils doivent permettre d'anticiper de futures perturbations écologiques., notamment sur les services écosystémique (Harrington *et al.*, 2010).

Selon Niemi & McDonald (2004), les bio-indicateurs jouent également un rôle majeur pour évaluer la performance des programmes de protection des écosystèmes et les choix réglementaires environnementaux par les gestionnaires. Les indicateurs biologiques doivent également être compris du public (Schiller *et al.*, 2001).

1.1.4 Nouvelle-Calédonie : un archipel exceptionnel et menacé

1.1.4.1 Généralités sur l'archipel

La Nouvelle-Calédonie est un archipel situé dans le sud-ouest de l'océan Pacifique, entre les 18e et 23e parallèles, à quelques degrés au nord du tropique du Capricorne. Les îles les plus proches sont distantes de plusieurs centaines de kilomètres (Vanuatu : 800 km, Australie et Fidji : 1500 km et la Nouvelle-Zélande : 1700 km), ce qui en fait l'un des archipels les plus isolés au monde (Fig. 1.4).

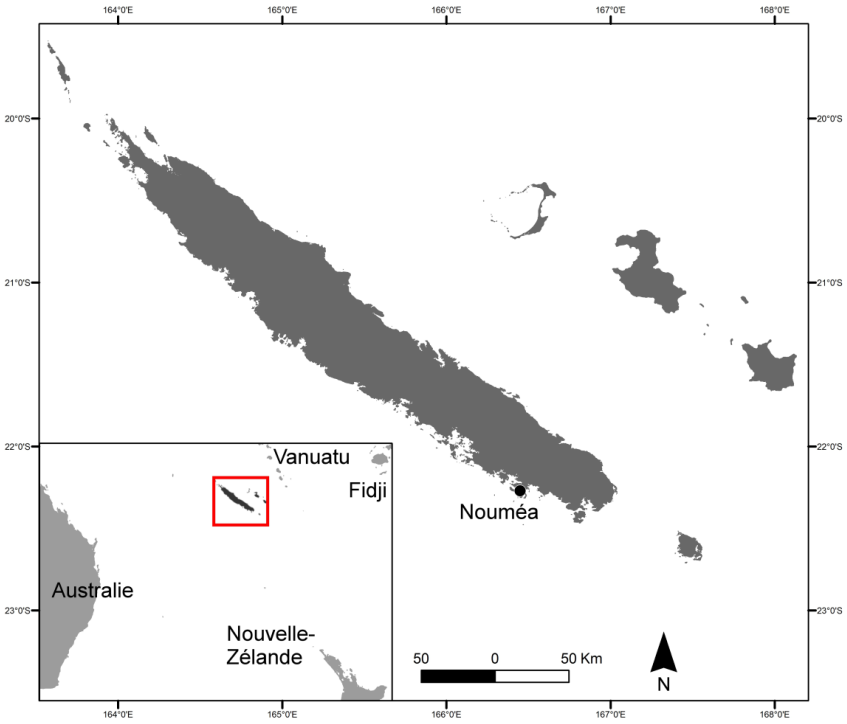

Figure 1.4. *Carte du monde indiquant la localisation de la Nouvelle-Calédonie dans l'océan Pacifique, avec le détail de l'archipel et des Iles Loyautés.*

L'île principale, appelée Grande Terre, a une forme allongée selon un axe Nord-Ouest / Sud-Est et s'étend sur une longueur de 400 km et une largeur de 50 km pour une superficie d'environ deux fois la Corse (16400 km²), ce qui en fait la troisième plus grande île du Pacifique sud-ouest, après la Papouasie Nouvelle-Guinée et la Nouvelle-Zélande. La Grande Terre se prolonge au Nord par l'archipel des Belep et au Sud par l'île des Pins, et forme deux provinces administratives : la province Nord et la province Sud. Une troisième province est constituée des Iles Loyautés (Lifou, Maré et Ouvéa), situées à 100 km au Nord-Est de la Grande Terre. L'altitude de la Grande Terre est modérée et essentiellement constituée d'une chaîne centrale avec comme plus hauts sommets le Mont Panié (1628 m) au Nord et le Mont Humboldt (1618 m) au Sud. Cette chaîne centrale est située davantage à l'Est, le versant ouest de l'île a donc un relief plus adouci et une bande côtière plus large que son versant est (Fig. 1.5).

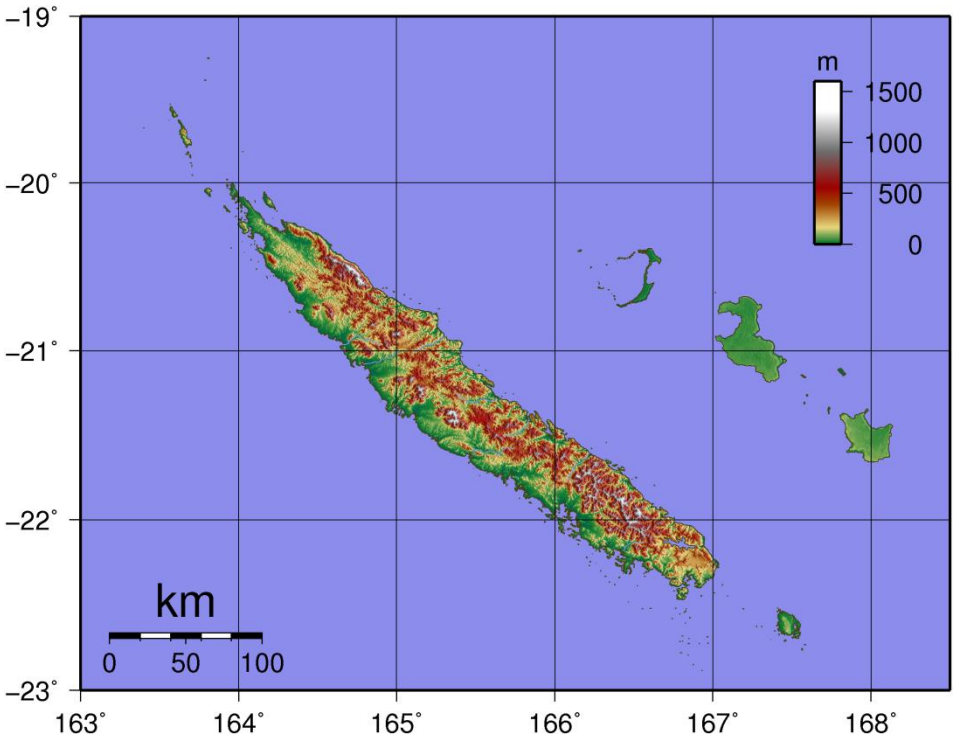

Figure 1.5. *Aperçu du relief général de la Nouvelle-Calédonie (source Atlas IRD, 2014).*

Pour le climat, la position géographique de la Nouvelle-Calédonie, dans le courant des Alizés, lui confère un climat tempéré, qualifié de « tropical océanique ». Les variations interannuelles de la ceinture anticyclonique subtropicale au Sud, et de la Zone Intertropicale de Convergence (ZIC) au Nord, déterminent quatre saisons. Une saison chaude de mi-novembre à mi-avril, durant laquelle les dépressions tropicales évoluent parfois en cyclones et abordent les côtes calédoniennes. Celle-ci est suivie par une saison de transition, de mi-avril à mi-mai, où les perturbations tropicales (dépressions et cyclones) sont moins fréquentes ; la température de l'air décroît sensiblement et la pluviométrie diminue sur le territoire. La troisième saison dure cinq mois, de mi-mai à mi-septembre, c'est la saison dite fraîche ; la température de l'air passe par son minimum annuel ; la ZIC est dans l'hémisphère Nord. Des perturbations d'origine polaire traversent fréquemment la mer de Tasman pouvant atteindre régulièrement le territoire calédonien, y provoquant des pluies parfois fortes. Finalement, de mi-septembre à mi-novembre, c'est une saison de transition ou la « belle saison ». Malgré un retour de la ZIC vers l'hémisphère Sud, la ceinture subtropicale de hautes pressions a atteint son développement maximal et protège donc le territoire des perturbations polaires. Pendant cette saison la température augmente graduellement et la pluviométrie enregistrée est la plus basse de l'année (source Atlas IRD, 2014).

1.1.4.2 Une histoire géologique complexe

La géologie de la Nouvelle-Calédonie est le résultat d'une histoire complexe marquée par une série de longs processus tectoniques, sédimentaires, volcaniques et d'accrétions. Cela est responsable d'une grande variété de types de roches ou « unités » qui composent le sous-sol de l'archipel (Pelletier, 2006; Cluzel *et al.*, 2012). Cette histoire géologique complexe est marquée par plusieurs grandes phases qui ont donné naissance à la diversité des unités géologiques actuelles (Fig. 1.6).

La première phase Gondwanienne du Crétacé moyen à l'Eocène inférieur (-120 à -55 Ma) est marquée par une subduction de la marge orientale du Gondwana. Après la dislocation d'une partie continentale australienne entre -88 et -83 Ma, qui formera le noyau de la Nouvelle-Calédonie (Brothers & Lillie, 1988; Neall & Trewick, 2008), plusieurs événements géologiques, notamment des expansions et des extensions de la croûte océanique, entraîneront la formation de plusieurs fragments de croûte continentale (i.e. la ride de Lord Howe, la ride de Norfolk et l'arc des Loyautés) et au moins de trois bassins océaniques : celui de la mer de Tasmanie, de la Nouvelle-Calédonie et des Loyautés. Ensuite, des roches sédimentaires se mettront en place au cours du Paléocène (-65 à -55 Ma) (i.e. des calcaires et des phtanites), à la suite d'une subduction et d'une immersion de ce fragment continental australien.

La seconde phase se déroule au cours de l'Eocène (-55 à -34 Ma) durant laquelle se produit une convergence des marges orientales Gondwaniennes fragmentées. Cette convergence a débuté par une subduction côté Est le long du bassin sud Loyauté, qui a été ensuite bloquée par la pointe nord de la ride de Norfolk. L'obduction subséquente entraîne la mise en place d'une couche de lithosphère océanique ou nappe ophiolitique d'unités mafiques et ultramafiques sur le noyau Néo-Calédonien. Finalement, une extension lithosphérique entraîne la ré-émergence définitive de la Nouvelle-Calédonie.

La dernière phase de l'Oligocène à l'actuel (-34 Ma à aujourd'hui) se traduit par plusieurs événements géologiques, tels qu'un rééquilibrage isostatique post-obduction (Lagabrielle *et al.*, 2005), une transgression marine, mais également une pénéplanation, des mouvements de tectoniques « cassants », une subsidence et du volcanisme.

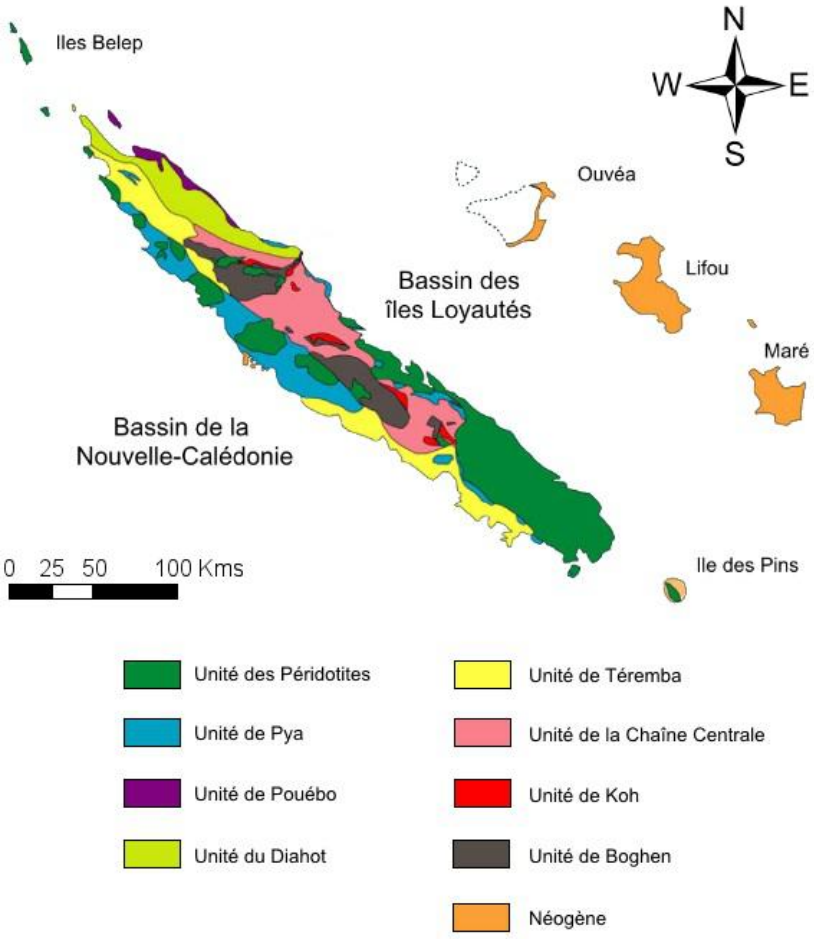

Figure 1.6. *Carte géologique simplifiée de la Nouvelle-Calédonie représentant les principales unités géologiques (source Atlas IRD, 2014).*

1.1.4.3 Impact de la géologie sur la biodiversité et l'endémisme

L'analyse des sous-sols Néo-Calédoniens nous indique que la Nouvelle-Calédonie portée par la ride de Norfolk est restée immergée pendant au moins 20 Ma, entre -65 à -45 et -34 Ma. Les dépôts sédimentaires composés de calcaires mais également de cherts (ou phtanites) témoignent ainsi d'une immersion en profondeur. La longue immersion de la Nouvelle-Calédonie impliquerait donc une colonisation de l'île par la faune et la flore seulement après sa ré-émersion (Murienne *et al.*, 2005; Grandcolas *et al.*, 2008; Nattier *et al.*, 2011; Pillon, 2012), cette réalité géologique rend délicate l'hypothèse de biotes d'origine gondwanienne, sauf à considérer que ceux-ci sont restés sur d'autres terres émergées, aujourd'hui disparues, jusqu'à réémergence de la Nouvelle-Calédonie (Heads, 2010, 2011).

De plus, l'histoire géologique de la Nouvelle-Calédonie qui a conduit un important recouvrement de sa surface par une couche ophiolitique est une caractéristique majeure de l'archipel, avec des conséquences sur l'évolution de la biodiversité de l'île (Grandcolas *et al.*, 2008). Les sols métallifères sont actuellement représentés par un important massif ultramafique (1/3 de la Grande Terre) dans la partie méridionale avec des patchs de petite taille au centre et au nord de l'île. Ces sols dérivent de l'altération de la roche mère ophiolitique et présentent la particularité d'être pauvres en nutriments favorisant la croissance des plantes (phosphore, potassium, calcium) (Jaffré, 1980), tandis que ces sols sont riches en métaux lourds (nickel, cuivre) pouvant fortement contraindre la croissance de la végétation (Proctor, 2003).

1.1.4.4 Originalité de la biodiversité et des richesses naturelles

La Nouvelle-Calédonie présente une diversité marquée de paysages et d'écosystèmes en du fait de la diversité du relief (plaine et chaîne centrale), du gradient de température, de la diversité des sols (sol ultramafiques, volcano-sédimentaires) et de la pression des activités humaines (Jaffré, 1993; Jaffré *et al.*, 2009).

Cette diversité est principalement regroupée en six catégories d'habitats natifs de l'archipel : (i) les forêts denses humides, (ii) les forêts sèches, (iii) les maquis de basse et moyenne altitude (< 900m), (iv) les maquis de haute altitude (> 900m), (v) les habitats secondaires tels que les savanes à niaoulis (*Melaleuca quinquenervia*), les fourrés à gaïac (*Acacia spirorbis*) ou à faux-mimosa (*Leucaena leucocephala*), et (vi) les mangroves des zones humides (Morat, 1993; Jaffré *et al.*, 1998a) (Fig. 1.7).

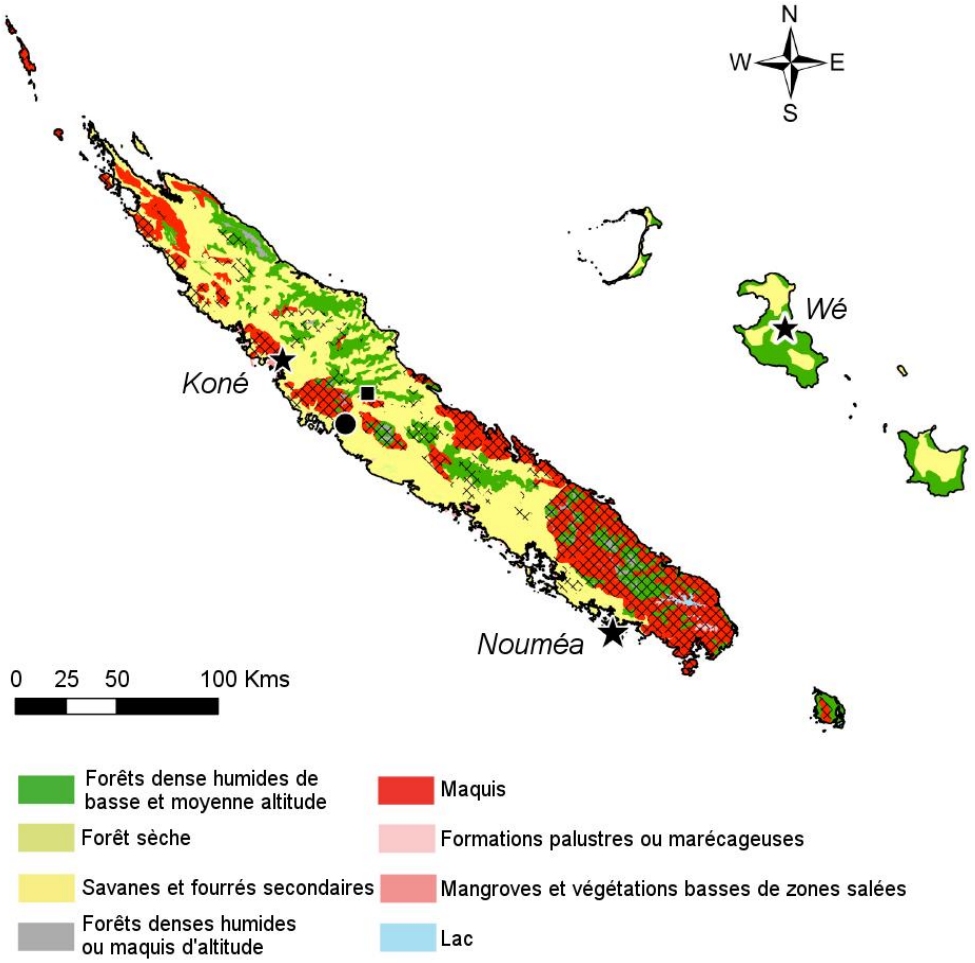

Figure 1.7. *Carte simplifié des principales formations végétales de la Nouvelle-Calédonie et des Iles Loyautés, les zones hachurées représentent les roches ultramafiques. Modifié d'après Ibanez (2012).*

Le statut de *hotspot* ou point chaud de la biodiversité définit les régions avec des concentrations exceptionnelles d'espèces endémiques qui subissent des dégradations et des pertes d'habitats majeurs, et qui de fait sont des régions prioritaires pour la conservation de la biodiversité. La Nouvelle-Calédonie a été identifiée parmi les dix premiers *hotspot* de biodiversité (Myers, 1988), puis dans la liste des 25 actualisés (Myers *et al.*, 2000), et finalement parmi celle des 35 *hotspot* de biodiversité à travers le globe (Mittermeier *et al.*, 2011).

1.1.4.5 Flore et faune endémiques

L'archipel néo-calédonien abrite ainsi une flore et une faune très riche et fortement endémique, avec des particularités uniques au monde. Les forêts tropicales humides abritent plus de 2000 espèces végétales avec un taux d'endémisme supérieur à 82%, tandis que les maquis abritent plus de 1150 espèces végétales avec un taux d'endémisme plus marqué, de l'ordre de 90% (Jaffré *et al.*, 2001; Pillon *et al.*, 2010; Morat *et al.*, 2012). A titre d'illustration, la Nouvelle-Calédonie possède le seul représentant de la famille des Amborellaceae : *Amborella trichopoda*, qui serait, selon les études..., une espèce relique et le groupe frère de toutes les plantes à fleurs (Jansen *et al.*, 2007; Albert *et al.*, 2013). Au total, la Nouvelle-Calédonie compte cinq familles de plantes endémiques, au moins 108 genres et 2500 espèces endémiques soit un taux d'endémisme de 76% (Wulff *et al.*, 2013).

La faune néo-calédonienne présente également une grande originalité avec des taux d'endémisme importants. Ainsi, plus de 92% des 105 espèces de squamates connues de Nouvelle-Calédonie sont endémiques de l'archipel (Bauer & Jackman, 2006). Chez les oiseaux, la faune néo-calédonienne présente 20% d'endémisme (24 espèces ou sous espèces) parmi près de 100 espèces connues de l'archipel (Barré *et al.*, 2010). Parmi les espèces d'oiseaux terrestres menacées, nous signalons le cagou, (*Rhynochetos jubatus* Verreaux & DesMurs, 1860), espèce emblématique de l'archipel. Cette espèce est le seul représentant actuel de la famille Rhynochetidae. Ce oiseau terrestre, incapable de voler, est classé parmi les 10 espèces d'oiseaux les plus en danger d'extinction (Ekstrom *et al.*, 2002). Les menaces sont principalement la prédation par les mamifères introduits en particulier les chiens (Hunt *et al.*, 1996) et de la compétition (Letocart & Salas, 1997). Aujourd'hui, les populations de cagou sont stables comprenant sans doute près de 1500 individus. Pour ce qui concerne les mammifères, seuls des chiroptères ont colonisé naturellement l'île avec un total de 9 espèces, dont 5 endémiques (Pascal *et al.* 2006).

Chez les invertébrés, près de 6000 espèces sont déjà été décrites (Chazeau, 1993), avec certains groupes qui démontrent des taux d'endémismes records, comme les cigales dont l'intégralité des espèces sont endémiques du territoire (Boulard, 1992, 1993, 1997; Delorme *et al.*, 2015) ou les éphéméroptères (Peters, 2001). A titre d'exemple, la faune néo-calédonienne est également composée d'un groupe particulier, les grillons (Ensifères, Orthoptères) avec un taux d'endémisme supérieur à 90% (Chopard, 1915; Otte *et al.*, 1987; Desutter-Grandcolas, 1997c, 2002; Robillard *et al.*, 2010), détaillé dans la chapitre suivant. Toutefois, cette faune

reste principalement méconnue, surtout des milieux contraignants sur substrat ultramafique (Barré *et al.*, 2010).

1.1.4.6 Les menaces sur la biodiversité Néo-Calédonienne

Bien que les écosystèmes naturels et la biodiversité de la Nouvelle-Calédonie soient reconnus pour leur originalité et leur unicité, ils demeurent néanmoins exposés à des menaces de plus en plus importantes. Ainsi, les activités minières liées principalement à l'exploitation des gisements de nickel (et à moindre mesures de cobalt et de chrome), les feux de brousse (Jaffré *et al.*, 1998b; Ibanez, 2012; Curt *et al.*, 2015; Gomez *et al.*, 2015) et l'introduction d'espèces invasives (Beauvais *et al.*, 2006; Jourdan & Mille, 2006) sont les trois menaces les plus sérieuses sur l'archipel Néo-Calédonien (Pascal *et al.*, 2008; Pellens & Grandcolas, 2009) (Fig. 1.8).

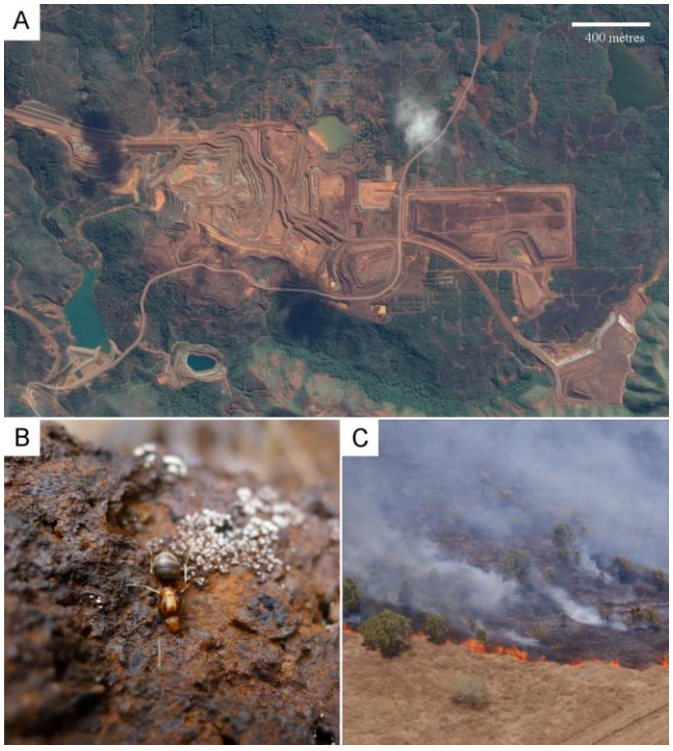

Figure 1.8. (A) Zone d'exploitation minière de la mine de Goro dans le sud de la Grande Terre ; (B) une reine de la fourmi invasive Anoplolepis gracilipes dans un maquis arbustif dans le sud de la Grande Terre (© J. Anso) ; (C) feu de brousse ravageant des savanes (© Ministère de la Défense et des anciens combattants).

Les feux qui se déclarent en Nouvelle-Calédonie ravagent annuellement des milliers d'hectares (i.e. 10.000 hectares par an ; Curt et al. 2015.), principalement les milieux les plus inflammables (i.e. maquis, savanes, pâturages ; voir Fig. 1.7) et les plus proches des

habitations ou des routes, soutenant une origine majoritairement anthropique (Curt *et al.*, 2015). Ces feux de brousse entraînent des perturbations profondes sur la structure des écosystèmes, avec par exemple le développement et l'envahissement de la fougère aigle (*Pteridium esculentum*) dans les maquis brûlés à répétition (Jaffré *et al.*, 1998b). Plusieurs espèces de conifères endémiques sont actuellement menacées par les feux et leur intensification (Perry & Enright, 2002; Jaffré *et al.*, 2010), ainsi que des espèces caractéristiques des forêts sèches (Bocquet *et al.*, 2007). Les travaux d'Ibanez *et al.* (2013) avancent une faible adaptation de certaines espèces végétales aux feux, résultant sur des mortalités post-feux élevées. Les forêts sèches, qui représentent un écosystème remarquable et protégé de Nouvelle-Calédonie, sont fortement sensibles et menacées par les feux de brousse. Aujourd'hui, cette formation est restreinte à des lambeaux de petites tailles, couvrant environ 1% de sa surface initiale (Jaffré *et al.*, 1998a; Bocquet *et al.*, 2007). Couplé avec l'impact des feux de brousse, les activités industrielles liées à l'exploitation des ressources minières et forestières sont responsables d'une destruction importante des habitats Néo-Calédonien, et de la biodiversité résidente (Pascal *et al.*, 2008; Pellens & Grandcolas, 2009).

La biodiversité néo-calédonienne est également menacée par de nombreuses espèces exotiques envahissantes (Beauvais *et al.*, 2006). En effet, la Nouvelle-Calédonie réalise des échanges commerciaux avec de nombreux pays et bénéficie d'un flux touristique constant tous les ans (environ 200.000 touristes par an) (Beauvais *et al.*, 2006). De plus, le développement économique de l'archipel entraîne l'importation de nombreuses marchandises (e.g. plantes ornementales, provisions alimentaires, semences ou graines) facilitant l'introduction d'espèces exotiques. En conséquence, l'archipel de Nouvelle-Calédonie abrite de nombreuses espèces terrestres et d'eaux douces invasives, avec des impacts négatifs relativement important au regard de l'espèce considérée sur la biodiversité, l'économie du territoire et le bien être des populations.

Chez les vertébrés, près d'une quarantaine d'espèces introduites sont présentes sur le territoire avec notamment des mammifères, des oiseaux, des squamates, des amphibiens ou encore des poissons dont la plupart n'ont pas encore fait l'objet d'une évaluation de leurs impacts (Pascal *et al.*, 2006). Le cerf rusa (*Cervus timorensis*, Blainville, 1822) est un exemple emblématique puisqu'il a été introduit sur la Grande Terre dans les années 1870 avec seulement une dizaine d'individus, et représente aujourd'hui une menace très sérieuse d'au moins 200.000 individus pour de nombreuses plantes endémiques des forêts sèches et humides menacées d'extinction (Bel *et al.*, 1997; de Garine-Wichatitsky *et al.*, 2005;

Beauvais *et al.*, 2006; Spaggiari & de Garine-Wichatitsky, 2006). Le rat du pacifique (*R. exulans*, Peale, 1848), le rat noir (*Rattus rattus*, Linnaeus, 1758), et le rat surmulot (*R. norvegicus*, Berkenhout, 1769) et le chat haret (*Felis silvestris catus* Linneaus, 1758) sont présents en Nouvelle-Calédonie, avec des impacts documentés sur la faune et la flore dans la région Pacifique (Robinet *et al.*, 1998; Medina *et al.*, 2011).

Parmi les invertébrés, la Nouvelle-Calédonie est soumise également à une forte pression. Aujourd'hui près de 500 espèces d'invertébrés sont considérés comme exotiques (Jourdan et Mille 2006). Ainsi, plusieurs espèces exotiques hautement nuisibles pour la biodiversité, appartenant aux 100 espèces les plus néfastes pour la biodiversité et le fonctionnement des écosystèmes (Lowe *et al.*, 2000) sont présentes sur le territoire, telles que l'escargot géant d'Afrique (*Achatina fulica*), l'euglandine rose (*Euglandina rosea*), l'aleurode (*Bemisia tabaci*), et plusieurs fourmis envahissantes (Jourdan & Mille, 2006). Plusieurs espèces de fourmis envahissantes, dont la petite fourmi de feu (*Wasmannia auropunctata*), la fourmi folle jaune (*Anoplolepis gracilipes*) et la fourmi à grosse tête (*Pheidole megacephala*). La petite fourmi de feu (native des régions néotropicales) et la fourmi à grosse tête (native d'Afrique de l'Ouest voire de la région malgache) ont été introduite en Nouvelle-Calédonie au cours des années 1960 (Jourdan & Mille, 2006). La fourmi folle jaune, dont la distribution d'origine n'est pas connue (vraisemblablement en Asie du Sud est), et la fourmi de feu tropical (*Solenopsis geminata*) ont été introduites en Nouvelle-Calédonie à la fin du XIXème siècle (Emery, 1883; Jourdan & Mille, 2006). La fourmi de feu tropical est également native d'Amérique du sud.

Parmi ces quatre espèces de fourmis envahissantes, la petite fourmi de feu représente la menace la plus sérieuse pour la biodiversité néo-calédonienne (Jourdan, 1999; Le Breton *et al.*, 2003; Le Breton *et al.*, 2005; Jourdan & Mille, 2006), puisque cette espèce est virtuellement présente dans tous les habitats, perturbés (maquis arbustifs, fourrés à gaïacs) ou non (forêts denses humides) (Berman *et al.*, 2013a). Cette fourmi est la plus étudiée sur le territoire car elle cumule les impacts négatifs sur les communautés animales et végétales de l'île, mais également sur les sociétés humaines à travers les dégâts économiques (e.g. la culture de café, le maraîchage ou l'élevage) et l'atteinte à la santé publique (i.e. piqûres, blessures) (Jourdan, 1997; Jourdan, 1999; Jourdan *et al.*, 2001; Chazeau *et al.*, 2002; Le Breton *et al.*, 2003; Le Breton *et al.*, 2005; Orivel *et al.*, 2009; Berman *et al.*, 2013a; Berman *et al.*, 2013b). Le succès invasif de la petite fourmi de feu repose notamment sur l'absence de comportement agressif entre les colonies de l'île (Le Breton *et al.*, 2004), sur sa capacité à

exploiter efficacement les niches vacantes et les ressources des écosystèmes néo-calédoniens (e.g. alimentaire, site de nidification) (Le Breton *et al.*, 2005), mais également sur le comportement défensif inadapté de certaines espèces de fourmis natives (Le Breton *et al.*, 2007). Ainsi, les communautés natives et endémiques de fourmis sont les premières négativement touchées par l'invasion de *Wasmannia auropunctata*, avec une chute dramatique de la diversité dans les habitats où elle se propage (Le Breton *et al.*, 2003; Berman *et al.*, 2013a; Berman *et al.*, 2013b). L'herpétofaune est également une composante de la biodiversité fortement menacée par l'introduction de *W. auropunctata*. Jourdan et al. (2000) indiquaient que l'abondance deux espèces de squamates dominantes, *Bavayia cyclura* (Günther, 1872) et *Caledoniscincus austrocaledonicus* (Bavay, 1869) était fortement réduite en présence de la petite fourmi de feu. Le mécanisme implique probablement de la prédation et de la compétition, notamment à cause de la réduction potentielle des proies disponibles pour les communautés de squamates (Jourdan *et al.*, 2000).

Les fourmis invasives introduites restantes, *Pheidole megacephala*, *Anoplolepis gracilipes* et *Solenopsis geminata* ne bénéficient en revanche que d'une attention limitée de la part de la communauté scientifique, avec peu d'études conduites sur elles. *A. gracilipes* est retrouvée principalement dans les milieux ouverts ou perturbés de Nouvelle-Calédonie, tandis que les milieux forestiers sont généralement préservés de cette fourmi (Berman *et al.*, 2013a). D'après Jourdan & Mille (2006), la fourmi folle jaune pourrait être en Nouvelle-Calédonie dans une phase de latence, caractérisée par des populations peu denses et ne monopolisant pas dramatiquement les ressources des écosystèmes naturels. Cette situation de latence aurait été observée sur l'île de Christmas où les populations d'*A. gracilipes* sont restées faibles durant 60 ans après son introduction approximativement (Jourdan & Mille, 2006). Ce ne serait qu'après l'arrivée d'une cochenille, avec laquelle la fourmi peut entretenir une relation mutualiste pour récupérer du miellat sucré (en échange de la protection par les fourmis) que les populations auraient explosé, avec des conséquences graves pour la biodiversité de l'île et le fonctionnement des écosystèmes (Lester & Tavite, 2004; Abbott, 2006; Thomas *et al.*, 2010; Misso & West, 2014). De récentes études ont permis de confirmer le statut probablement latent de la fourmi folle jaune en Nouvelle-Calédonie, avec des impacts modérés sur les écosystèmes, principalement sur les communautés natives de fourmis (Berman *et al.*, 2013a; Berman *et al.*, 2013b). L'invasion de *Pheidole megacephala* entraîne généralement le déclin des communautés natives de fourmis (Hoffmann *et al.*, 1999; Vanderwoude *et al.*, 2000; Hoffmann & Parr, 2007; Wetterer, 2007). En Nouvelle-Calédonie,

Il semblerait que la fourmi à grosse tête soit négativement associée avec les communautés natives de fourmis (Berman *et al.*, 2013a). *S. geminata* ne bénéfice quant à elle d'aucune étude d'impact en Nouvelle-Calédonie, et ne semble pas poser de problème majeur pour les écosystèmes et la biodiversité calédonienne à ce jour (Jourdan & Mille, 2006). A notre connaissance, une seule étude réalisée sur l'archipel des Galápagos montre le potentiel impact négatif d'une telle invasion sur la faune native (vertébrés et invertébrés) (Wauters *et al.*, 2014).

1.2 Objectifs de la thèse et présentation des chapitres

Ces travaux de thèse s'inscrivent dans le contexte actuel de crise de la biodiversité, avec le besoin urgent de développer de nouvelles approches innovantes et de tester de nouveaux modèles d'études à destination des gestionnaires et des scientifiques pour mesurer le plus efficacement et rapidement possible l'état de santé des écosystèmes qui traversent des perturbations (i.e. des invasions biologiques ou des fragmentations des habitats). Pour répondre à cette problématique, nous avons choisi d'étudier les communautés de grillons (Ensifères, Orthoptères) de Nouvelle-Calédonie dans une gamme définie d'habitats (en forêt, en maquis paraforestier et arbustif), représentant les grandes étapes d'une succession forestière sur sol métallifère. L'impact d'une fourmi invasive majeure, *Wasmannia auropunctata* (Hyménoptère, Formicidé), a également été mesuré à travers la réponse des communautés de grillons, dans tous les habitats considérés.

La réponse des communautés de grillons a donc été mesurée dans le sud de la Grande Terre à travers des échantillonnages taxonomiques (capture et identification des espèces ; chapitre III) et acoustiques (enregistrement et identification des espèces émettrices ; chapitre V) en fonction de l'habitat et de la présence de *Wasmannia auropunctata* (voir Fig 1.9). Une approche novatrice a été mise en place sur les parcelles d'études, avec l'analyse globale des signaux sonores (méta-acoustique des communautés émettrices ; chapitre IV).

Chapitre I : Ce premier chapitre propose de faire un état des connaissances sur les grillons d'une manière générale, avec la description générale du groupe, la phylogénie des différents groupes, le régime alimentaire et leur rôle dans le fonctionnement des écosystèmes. Un point majeur abordera le domaine de la bio-indication avec les grillons, mais également le

mode de production de signaux sonores par les mâles et leurs utilisations en écologie. Finalement, une partie de ce chapitre présentera les nouvelles espèces et nouveaux genres de ce travail de thèse, avec des données nouvelles sur l'écologie, la distribution et les productions sonores de la faune néo-calédonienne.

Chapitre II : La faune de grillons néo-calédonienne est très riche, avec au moins 180 espèces décrites, très diversifiée et fortement endémique (supérieur à 90%). A notre connaissance, aucune étude de cette ampleur n'a été réalisée sur cette faune particulière en Nouvelle-Calédonie à l'échelle des communautés, dans une succession forestière incluant les emblématiques maquis minier et couplée avec la présence d'une fourmi invasive majeure. Ce chapitre de thèse se divise en trois sections, et permet d'évaluer le rôle de cette faune en tant que bio-indicateur de la qualité des habitats de Nouvelle-Calédonie.

La première section fait état de la découverte d'un taxon inédit et original dans les maquis minier du sud de la Grande Terre. La distribution et la position phylogénétique de ce dernier au sein des clades déjà présents en Nouvelle-Calédonie a permis de mettre en évidence le rôle majeur des maquis bas en tant qu'hôte d'une biodiversité originale, et de mieux appréhender des mécanismes complexes de dynamiques paysagères. Ce nouveau taxon se place comme un prometteur modèle d'étude des anciennes dynamiques paysagères qui ont affectés les formations forestières de Nouvelle-Calédonie. Le rôle spécifique du régime des feux naturels et anthropiques et de la nature de la végétation sur la distribution et la faible diversité de ce nouveau taxon sont discutés.

La seconde section de ce chapitre propose d'étudier la structure des communautés de grillons dans le sud de la Grande Terre (richesse spécifique, abondance relative) en fonction des formations forestières, au sein d'un continuum composé de trois habitats caractéristiques : les forêts denses humides, les maquis paraforestiers et les maquis arbustifs. La réponse des communautés de grillons a été mesurée selon l'abondance et la diversité des espèces, mais également selon la structure et la composition de ces communautés en fonction des habitats, et de variables environnementales (ouverture de la canopée, nombre de troncs larges, etc.) La sensibilité probable des grillons aux conditions bioclimatiques des milieux nous permettent de proposer comme hypothèse de travail que nos communautés devraient se distinguer selon les habitats considérés.

La troisième et dernière section de ce chapitre mesure l'impact d'une invasion biologique sur les communautés de grillons du sud de la Grande Terre. L'espèce invasive choisie est la petite fourmi de feu, *Wasmannia auropunctata*, Roger, 1863, décrite comme l'une des espèces envahissantes les plus dommageables pour la biodiversité et comme la plus grande menace pour la Nouvelle-Calédonie. Des communautés de grillons en présence de la fourmi envahissantes ont été comparées avec des communautés indemnes dans les trois habitats qui composent le continuum. A la lumière des impacts négatifs dramatiques de la petite fourmi de feu sur les arthropodes terrestres, nous attendons que nos communautés de grillons en présence de la fourmi invasive soient significativement et négativement impactées par cette espèce exotique.

Chapitre III : L'utilisation des bio-indicateurs pour réaliser des mesures rapides de la qualité des écosystèmes, ou pour détecter des perturbations environnementales ou écologiques (cf. des espèces envahissantes) est indispensable pour prendre des décisions rapides sur les mesures de gestion des habitats naturels. Cependant, l'utilisation des bio-indicateurs est fortement limitée dans les milieux tropicaux par les connaissances taxonomiques épars. Pour répondre à ce problème, le suivi de la biodiversité à travers l'analyse de l'ensemble des signaux sonores d'une communauté sans identification pourrait être une réponse adaptée et efficace pour ce type de milieu. Ainsi, au cours de ce chapitre, toutes les ambiances sonores émises par les communautés animales ont été enregistrées, puis analysées en relation avec l'habitat (cf. succession forestière) et la pression d'une espèce invasive majeure (cf. *Wasmannia auropunctata*). L'objectif de cette étude est de pouvoir distinguer les différents habitats, avec ou sans la présence de Wasmannia, à l'aide d'indice acoustique (i.e. indice d'analyse de pic fréquentiel), permettant de mesurer indirectement la biodiversité des milieux.

Chapitre IV : Dans le chapitre précédent, nous avons exploré les possibilités d'un suivi de la biodiversité à l'aide d'enregistreurs automatiques et du traitement global des données acoustiques, afin de distinguer des sites à différents stades de développement (restauration écologique) avec ou sans la présence d'une fourmi invasive majeure (pression écologique). Au cours de ce chapitre, nous avons réalisé des analyses plus approfondies des fichiers sonores collectés. En effet, à l'écoute afin de déterminer toutes les espèces chanteuses des communautés, et de comptabiliser leur vocalisations, dans le but de connaître la

composition de nos communautés acoustiques. Les identifications des espèces chanteuses ont été réalisées de jour et de nuit, à l'aide d'une base de données acoustiques conséquente et de la visualisation des spectrogrammes de fréquence. Une attention particulière a été portée sur l'identification des grillons, qui possèdent des chants hautement spécifiques et très stéréotypés, car jouant un rôle clé dans la biologie de ces espèces. Il en résulte une base de données inédite pour chaque site, et chaque modalité (par habitat et par état d'invasion), qui décrit la composition et la structure de la communauté acoustique (rythme d'activité, richesse spécifique, abondance des chants, etc.). Ces résultats nous permettent (i) de déterminer qui sont les groupes chanteurs de la biophonie néo-calédonienne, et (ii) de vérifier la pertinence de l'utilisation des chants de grillons en tant que bio-indicateurs de la qualité des habitats.

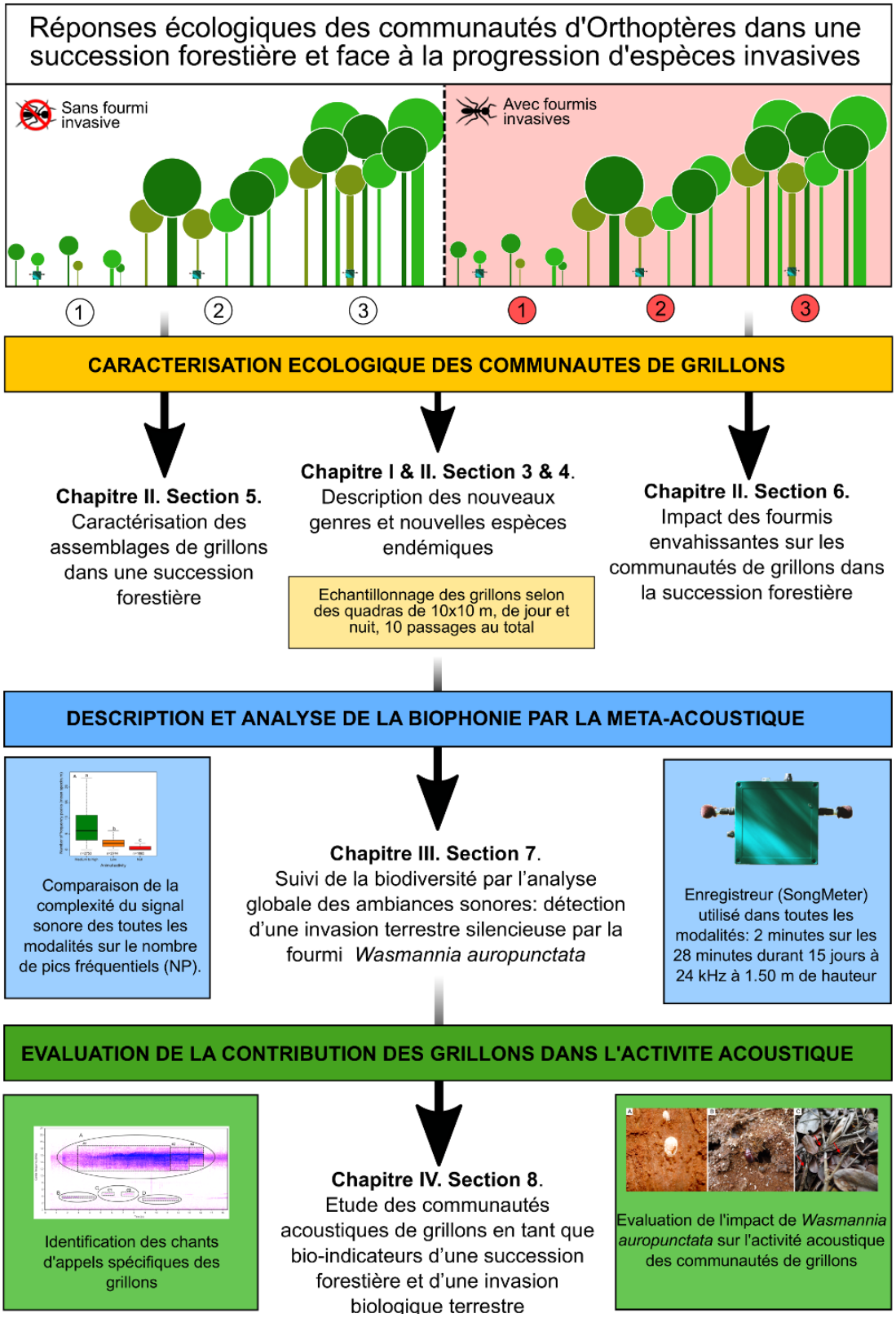

Figure 1.9. *Synthèse générale des grands volets de recherche développés au cours de ce travail de thèse. Abbreviation : 1, maquis arbustif ; 2, maquis paraforestier et 3, Forêt dense mixte.*

Chapitre I

2 Les grillons, un modèle d'intérêt en écologie

2.1 Présentation générale des grillons

Au sein des hexapodes, les grillons appartiennent à l'ordre des Orthoptères, plus précisément à l'infraordre des Gryllidea Laicharting, 1781. Ce groupe d'insectes comprend plus de 5500 espèces, réparties au sein de deux superfamilles : les Grylloidea Laicharting, 1781 et les Gryllotalpoidea Leach, 1815, selon la nouvelle classification dérivée d'une phylogénie à large échelle des grillons (Chintauan-Marquier *et al.*, 2016) (Fig. 2.1). Les grillons sont très largement répartis sur la surface du globe. On les rencontre dans tous les milieux tropicaux et tempérés, y compris les déserts, et ils sont particulièrement diversifiés dans les écosystèmes insulaires, tel que Hawaii (Otte, 1994) et les Grandes Antilles (Desutter-Grandcolas, 1993; Otte & Pérez-Gelabert, 2009). Les distributions géographiques diffèrent fortement selon les groupes et les espèces étudiés, avec des cas de très large répartition ou au contraire de répartition très restreinte (i.e. micro-endémisme). Par exemple *Lepidogryllus comparatus* (Walker, 1869) ou *Teleogryllus marini* (Otte & Alexander, 1983) sont présent dans tout le Pacifique (Otte & Alexander, 1983), et quelques espèces anthropophiles ont une répartition mondiale (e.g., *Acheta domestica* Linnaeus, 1758) ou pantropicale (*Gryllodes sigillatus* Walker, 1869). A l'inverse, la grande majorité des espèces ont une distribution très réduite. Ainsi, le genre *Laupala* Otte, 1994 est endémique de l'archipel d'Hawaii mais comprend 35 espèces (Otte, 1994; Shaw, 1996). De même, le genre *Agnotecous* Saussure, 1878, endémique de Nouvelle-Calédonie, présente des espèces qui ne sont actuellement connues que d'une seule localité, ou d'un seul massif montagneux (i.e. *A. meridionalis*, *A. minoris*, *A. pinsula*, *A. brachypterus*, *A. doensis*), alors que d'autres espèces possèdent des répartitions plus vastes sur l'archipel (i.e. *A. yahoue*, *A. clarus*, *A. obscurus*, *A. robustus*) (Robillard *et al.*, 2010; Nattier *et al.*, 2011; Nattier *et al.*, 2012).

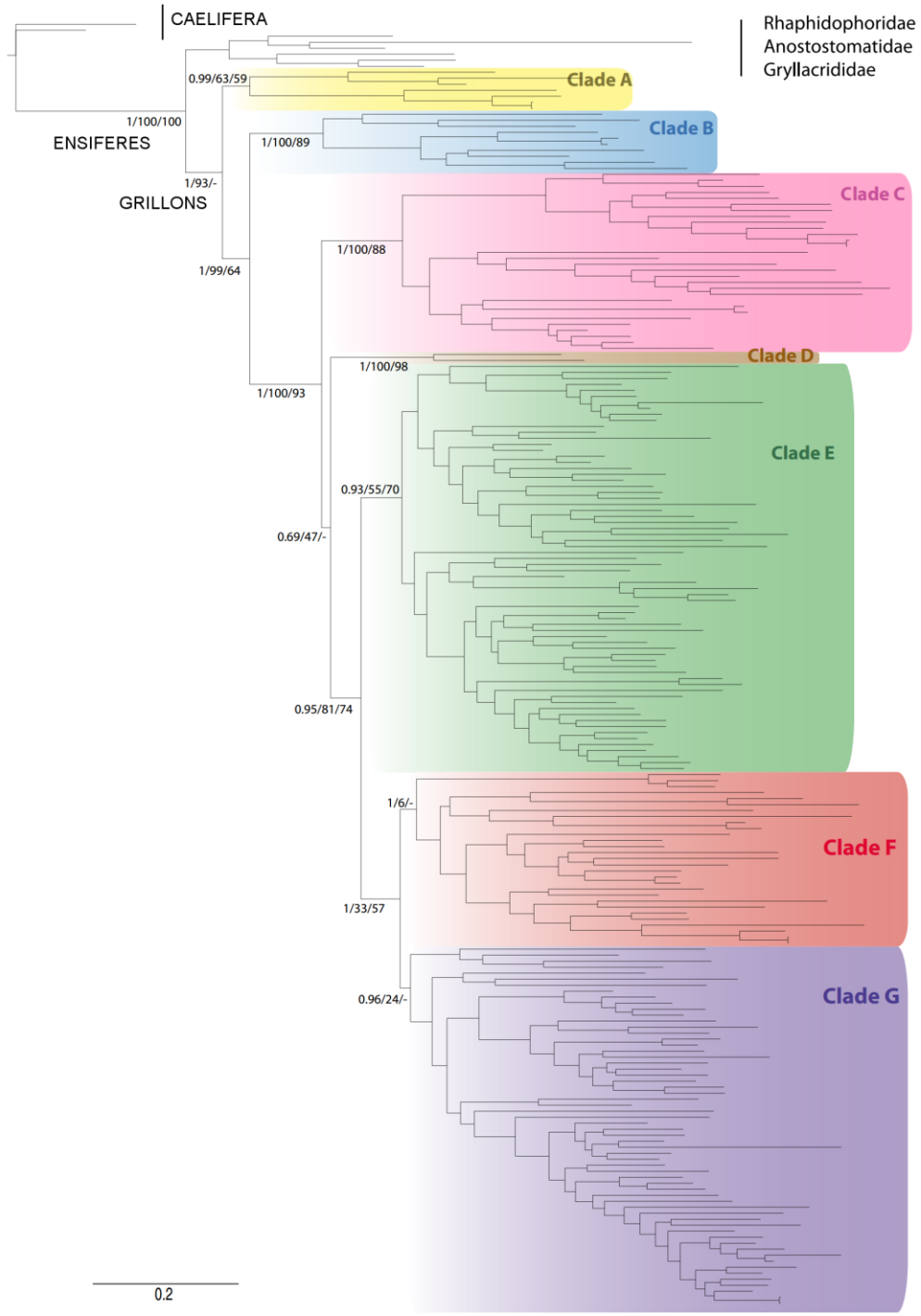

Figure 2.1. *Phylogénie générale des grillons en inférence Bayésienne basée sept marqueurs moléculaires. Le clade A représente les grillons myrmécophyles ; le clade B représente les Mogoplistidae (« grillons à écailles ») ; le clade C représente les Trigonidiinae et les Nemobiinae ; le clade D comprend les Pteroplistini ; le clade E représente principalement les Phalangopsinae ; le clade F représente globalement la sous-famille des Podocirtinae ; le clade G comprend des Gryllinae et quelques Podocirtinae. Adapté de Chintauan-Marquier et al. (2016).*

Parmi les Gryllidea, les Grylloidea ou les « grillons vrais » constitue le groupe le plus riche, avec plus de 4900 espèces décrites. Ainsi, ils sont répartis en quatre familles, elles-mêmes composées d'un certain nombre de sous-familles, dont la monophylie n'est pas encore avérée (Chintauan-Marquier *et al.* 2015; Desutter-Grandcolas *et al.*, in prep). Les Grylloidea comprennent les familles des Mogoplistidae, Phalangopsidae, Trigonidiidae et Gryllidae. En Nouvelle-Calédonie, les sous-familles suivantes sont représentées: au sein des Gryllidae, nous comptons les Eneopterinae Saussure, 1893, les Euscyrtinae Gorochov, 1985, les Gryllinae, les Oecanthinae Blanchard, 1845 et les Podoscirtinae Saussure, 1878; au sein des Trigonidiidae, sont présents les Nemobiinae Saussure, 1877 et les Trigonidiinae Saussure, 1874. Pour ce qui est des Phalangopsidae, les sous-familles sont en cours d'évaluation phylogénétique et de redéfinition. Les Gryllinae, Nemobiinae, Trigonidiinae et Oecanthinae possèdent une répartition mondiale, alors que les Phalangopsidae, Euscyrtinae et Podoscirtinae sont distribués sous les tropiques uniquement, avec une large radiation circum-méditerranéenne pour les premiers (Chintauan-Marquier *et al.* 2015). D'un point de vue écologie, les Grylloidea ont colonisé et occupent une très large diversité d'habitats : la famille des Phalangopsidae occupent par exemple principalement les milieux forestiers, où ils sont généralement observés actifs pendant la nuit sur des troncs, des rochers ou des racines de taille moyenne à grande (Desutter-Grandcolas, 1992, 2002) ; à l'opposé, d'autres Grylloidea occupent des milieux plus ouverts et plus anthropisés, avec par exemple la sous-famille des Oecanthinae Blanchard, 1845 (Collins *et al.*, 2014); la famille des Trigonidiidae quant à elle possède une répartition mondiale avec des espèces actives de jour comme de nuit dans la litière forestière ou en lisière (Desutter, 1990).

Leurs régimes alimentaires pourraient également être très variés, même si les observations dans le milieu naturel sont peu fréquentes à ce sujet : ils sont considérés généralement comme omnivores (Huber, 1989). Leurs régimes pourraient inclure des champignons (L. Desutter-Grandcolas, comm. pers.), ou varier d'un régime exclusivement herbivores à base de débris végétaux, de feuilles, de spores ou de pollen, à un régime fortement « carné » composé d'œufs de mantes, de termites et d'invertébrés (Smith, 1959; Gangwere, 1961). Ainsi, plusieurs observations *in situ* font état d'acte de prédation de la part de certains Grylloidea à l'encontre des coléoptères et des nymphes de diptères (Monteith, 1971; Burgess & Hinks, 1987). Dans le sud de la Nouvelle-Calédonie, des observations dans

le milieu naturel ont permis de montrer que des Nemobiinae de la litière pouvaient capturer des petits diptères (Anso J., obs. pers.).

Les Mogoplistidae ou les « grillons à écailles » comptent plus de 380 espèces décrites aujourd'hui. Cette famille est également très largement répartie dans tous les écosystèmes de la planète, y compris dans des milieux stressant comme les mangroves ou les déserts. Les grillons à écailles sont généralement de petite taille, le plus souvent aptères, mais quand ils chantent, ils émettent des chants d'appels très doux et de faible intensité, parfois très difficiles à localiser dans la végétation.

Outre les Grylloidea, les Gryllidea comprennent la superfamille des Gryllotalpoidea, séparés en deux familles, Gryllotalpidae et Myrmecophilidae. Les Gryllotalpidae (ou courtilières) sont représentés de par le monde par plus de 120 espèces, qui vivent essentiellement dans des terriers d'où les mâles produisent leurs émissions acoustiques.

Les Myrmecophilidae comprennent quant à eux plus de 70 espèces, et sont présents sur tous les continents, dans les régions tropicales et tempérées. Ils sont répartis en deux tribus regroupés dans la sous-famille des Myrmecophilinae : les Bothriophylacini, inféodés aux déserts de l'Ancien Monde, et les Myrmecophilini, qui ont la particularité de vivre exclusivement avec différentes espèces de fourmis. De très petite taille, les Myrmecophilini sont aptères et ne possèdent pas d'appareil stridulatoire ni de tympan. Ces grillons myrmécophiles sont souvent décrits comme des parasites sociaux ou des klepto-parasites (Wheeler 1900, Henderson et Akre 1986, Hölldobler et Wilson 1990). Par exemple, *Myrmecophilus pallidithorax* (Chopard, 1930) est un petit grillon myrmécophile vivant au sein des colonies d'une fourmi invasive *Anoploleplis gracilipes* Smith, 1857. L'agilité de ce grillon serait le critère principal lui permettant de prospérer au sein des colonies (Wheeler, 1900; Henderson & Akre, 1986; Drescher, 2011).

2.2 Rôle des grillons dans le fonctionnement des écosystèmes

Les écosystèmes sont composés de nombreux groupes taxonomiques (e.g., les insectes, les oiseaux, les squamates) susceptibles d'interagir entre eux, à travers divers processus écologiques. Toutes les espèces qui exploitent le même type de ressource et de la même manière au sein des écosystèmes sont définies comme appartenant à la même guilde écologique (Root, 1967; Simberloff & Dayan, 1991). Ces guildes sont généralement décrites

comme des groupes fonctionnels (Cummins, 1974; Hawkins & MacMahon, 1989), avec par exemple, les autotrophes et les hétérotrophes qui interagissent entre eux en tant que producteurs et consommateurs. Les groupes fonctionnels intègrent ainsi des niveaux trophiques spécifiques qui régissent les interactions entre les groupes, et qui sont généralement représentés dans une chaîne alimentaire intégrée à l'écosystème (Capinera, 2011).

Au sein de ces écosystèmes, les insectes représentent un groupe fonctionnel majeur principalement composés de consommateurs primaires et secondaires. Les consommateurs primaires se nourrissent généralement des producteurs primaires (les plantes), tandis que les consommateurs secondaires se nourrissent des consommateurs primaires. Les insectes occupent ainsi les rôles de détritivores et de décomposeurs en dégradant la matière organique d'origine végétale et animale, respectivement (Capinera, 2011).

En tant qu'organisme à sans froid (ectothermes), les insectes font partie des organismes qui transforment le plus efficacement les ressources alimentaires en énergie pour leur développement (productivité secondaire). D'après Capinera (2011), les insectes peuvent allouer jusqu'à 20% de l'énergie produite pour la croissance et le développement des individus, alors que les oiseaux ou les mammifères n'allouent que 2% de cette productivité secondaire pour la croissance. Cette différence est principalement dû au fait que les animaux à sang chaud doivent allouer de l'énergie supplémentaire pour maintenir des fonctions vitales, notamment la température corporelle (endothermes).

De par leurs régimes alimentaires dans les milieux naturels, ainsi que leur diversité, leur richesse et leur abondance, les grillons sont des espèces clés dans le fonctionnement naturel des écosystèmes (Capinera, 2011; McGeoch *et al.*, 2011; Wellstein *et al.*, 2011). Comme mentionné plus haut, les grillons sont principalement détritivores et herbivores (avec quelques espèces prédatrices et au moins partiellement fongivores), et participent donc activement à transformer la production primaire (issus principalement des végétaux) en ressource et en énergie pour tous les niveaux trophiques supérieurs (Hairston *et al.*, 1960; Polis & Strong, 1996). Ils agissent directement sur la décomposition de la matière organique, en mettant par exemple plus facilement à disposition les déchets organiques pour les microorganismes (Swift *et al.*, 1979), mais également en enrichissant la qualité des nutriments détritiques avec leurs excréments (Belovsky & Slade, 2000).

Enfin, les grillons jouent également un rôle majeur dans les écosystèmes en permettant la remise en circulation des nutriments dans les réseaux trophiques des écosystèmes considérés (Prather *et al.*, 2013). Les orthoptères en général, et les grillons en particulier, sont des ressources majeures dans de nombreux réseaux trophiques supérieurs, principalement en tant que proies. Les grillons sont largement présents dans le régime alimentaire de certains batraciens (Pyke & White, 2001), oiseaux (Ostrand & Bollinger, 2012) et chauve-souris (Pereira *et al.*, 2002). Malheureusement, la grande majorité des études portant sur le régime alimentaire des espèces prédatrices d'insectes limitent l'identification aux grands ordres, les Orthoptères dans notre situation. D'une manière plus ou moins formelle, les Orthoptères, et donc très probablement des grillons, sont présents abondamment dans le régime alimentaire des araignées (Tahir *et al.*, 2009; Kumar & Yashkamal, 2011; Salomon, 2011), et de différents squamates (Cappellari *et al.*, 2007; Shea *et al.*, 2009; Maia *et al.*, 2011; Garda *et al.*, 2012).

2.3 Les grillons en tant qu'indicateurs biologiques

2.3.1 Les grillons : un groupe candidat en Nouvelle-Calédonie pour la bio-indication ?

D'une manière générale, les grillons ont été l'objet de peu d'études scientifiques dans le contexte du développement d'indicateurs biologiques, pour identifier les réponses de ces insectes face à différentes perturbations ou pour la gestion des habitats (Gerlach *et al.*, 2013). Hoffmann *et al.* (2002) ont étudié la réponse des communautés de grillons dans le nord de l'Australie en fonction d'une pollution de dioxyde de souffre d'origine minière ; ils ont montré que trois genres, *Eurepella* Otte & Alexander, 1983, *Salmanites* Chopard, 1951 et *Endacusta* Brunner von Wattenwyl, 1873, avaient une sensibilité marquée à la pollution par le dioxyde de souffre. Selon ces auteurs, la pollution agirait indirectement sur la diversité des grillons, en réduisant la diversité de la végétation, entraînant une perte d'habitats favorables, et une baisse des ressources alimentaires disponibles. La pollution accumulée dans l'organisme des grillons pourrait également entraîner des dysfonctionnements physiologiques en perturbant des réactions biochimiques.

Malheureusement, Hoffmann *et al.* (2002) ont été dans l'incapacité de mettre leurs résultats en perspective avec d'autres données recueillis sur ce groupe. Ils mettent ainsi en exergue que les études sur les Orthoptères sont principalement basées sur les criquets (sous-

ordre des Caelifera) ou les sauterelles (O'Neill *et al.*, 2003; Marini *et al.*, 2009; Fartmann *et al.*, 2012). Ainsi, très peu d'espèces de grillons sont ainsi prises en compte, ce qui correspond de fait à la faible diversité du clade en zone tempérée et en milieu ouvert (Marini *et al.*, 2009; Alignan *et al.*, 2014). Par exemple, dans les steppes du Nord-est de l'Allemagne, Fartmann *et al.* (2012) ont montré que les communautés d'Orthoptères acridiens sont composées d'espèces spécialisées dans ce type de milieux ouverts, caractérisant les premiers stades d'une succession forestière. La seule espèce de grillon collectée dans cette étude, *Gryllus campestris* Linnaeus, 1758, a été exclue de l'étude parce qu'elle vit principalement dans des terriers.

Jana *et al.* (2006) ont étudié la diversité de plusieurs ordres d'insectes en réponse à l'industrialisation de l'environnement, prenant comme référence des habitats non industrialisés. Parmi les espèces étudiées, trois espèces étaient des grillons et l'une d'entre elle, *Modicogryllus confirmatus* Walker, 1859, s'est révélée très sensible à la perturbation de l'environnement provoquée par l'industrialisation, allant jusqu'à disparaitre du milieu.

Dans le Nord-est du Brésil, Araújo *et al.* (2015) ont étudié la réponse de quatre groupes taxonomiques différents, les coléoptères, les araignées, les fourmis et les grillons, en fonction de l'état de dégradation des habitats : (i) dans des milieux naturels forestiers, (ii) dans des milieux restaurés plus ouvert, et dans des milieux (iii) modérément à (iv) fortement dégradés avec peu de végétation et beaucoup de sol nu. Si les auteurs ont pu démontrer un effet négatif de la dégradation de l'environnement sur les coléoptères, les araignées et les fourmis, ils n'ont pu observer d'effet de la qualité des habitats sur les grillons, justifiant cette observation de par le régime alimentaire principalement omnivore et opportuniste des grillons. Cependant, les résultats obtenus dans cette étude ne permettent pas de conclure sur le rôle des grillons en tant que bio-indicateur, car le mode d'échantillonnage utilisé, des pièges semi-enterrés dans le sol (pitfall), est notoirement peu efficace pour piéger les grillons qui résident dans la végétation, occupent des micro-habitats très localisés ou bien se déplacent peu. Comme seules les abondances ont été prises en compte pour mesurer l'impact de l'habitat, les nombres d'individus se sont révélés très faibles pour les grillons, avec en moyenne quatre individus par site, mais ils ne reflètent pas forcément l'abondance des espèces échantillonnées.

Ce constat est à nuancer pour les habitats forestiers en milieux tropicaux, qui abritent une faune très diversifiée tant pour les acridiens que pour les grillons : les deux groupes ont en effet été utilisés comme bio-indicateurs efficaces pour caractériser les habitats lors d'une

succession forestière après culture sur brûlis en Amazonie péruvienne (Amédégnato & Descamps, 1980a, b; Desutter, 1990; Desutter-Grandcolas, 1992; Amedegnato, 1997) : pour les grillons comme pour les acridiens, des assemblages distincts d'espèces caractérisaient les différents âges de la régénération forestière, avec des périodes de transition marquées par un appauvrissement en espèces.

Les grillons demeurent malgré tout un groupe relativement peu étudié dans un contexte de conservation et de restauration des habitats. Ils n'en demeurent pas moins des potentiels marqueurs de la qualité des habitats, avec un statut qui doit encore être exploré et validé par la communauté scientifique. De plus, les grillons ont la particularité d'émettre des signaux acoustiques dans l'environnement, un point majeur discuté dans le paragraphe suivant.

2.3.2 Utilisation de signaux sonores des grillons : implication dans la bio-indication

L'utilisation des productions acoustiques des grillons en tant qu'alternative aux méthodes d'échantillonnages classiques et souvent lourdes, surtout dans les milieux tropicaux (Lawton *et al.*, 1998), représente une option prometteuse suivant les caractéristiques de ce groupe d'intérêt. En effet, les grillons représentent un large groupe d'espèces réparti à travers le globe, et présent dans une gamme diversifiée d'habitats (Otte *et al.*, 1987; Desutter, 1990; Otte, 1994; Nischk & Riede, 2001; Desutter-Grandcolas, 2014, 2015) ; Les grillons représentent également un groupe d'intérêt en tant qu'indicateur biologique de la condition des écosystèmes. Les grillons sont sensibles aux perturbations de l'environnement, notamment aux changements de structures de végétation au cours d'une succession forestière (Desutter, 1990; Desutter-Grandcolas, 1992), et aux changements écologiques pouvant affecter les écosystèmes. Finalement, ils produisent des chants facilement identifiables, à l'oreille (Diwakar *et al.*, 2007) ou visuellement sur des logiciels d'analyses acoustiques (Diwakar & Balakrishnan, 2007a), et ces chants constituent des caractéristiques propres à chaque espèce.

Malheureusement, les recherches scientifiques s'appuyant sur les signaux sonores des grillons en tant qu'indicateurs de la qualité des habitats n'ont à ce jour pratiquement jamais été conduites. Toutes les études mêlant l'acoustique et les grillons portent sur la biodiversité des communautés en fonction des habitats (Riede, 1997; Nischk & Riede, 2001; Diwakar & Balakrishnan, 2007a; Jain *et al.*, 2014), sur le partitionnement dans la niche acoustique

(Diwakar & Balakrishnan, 2007b; Jain & Balakrishnan, 2012; Schmidt *et al.*, 2013) ou bien sur l'évolution de la communication dans un cadre phylogénétique (Desutter-Grandcolas & Robillard, 2004; Robillard & Desutter-Grandcolas, 2011). Toutefois, une étude conduite sur l'île de Rodrigues apporte des éléments pour valider l'utilisation des chants des grillons en tant que bio-indicateur de l'état de l'environnement. Pour quantifier l'effet de la restauration de milieux sur les communautés d'insectes, Hugel (2012) a utilisé l'acoustique pour compter le nombre d'espèces et estimer la densité des chanteurs de chaque espèce pour contraster deux modalités environnementales, i.e. des zones envahies et dominées par plusieurs plantes exotiques et des zones restaurées où toutes les plantes exotiques avaient été enlevées du milieu. Même avec une communauté de grillons réduite, ne comprenant que deux espèces endémiques du genre *Ornebius* Guérin-Méneville, 1844 (Mogoplistidae), Hugel (op. cit.) a pu démontré que les aires restaurées abritaient un nombre d'espèces et une densité d'individus plus importants que les milieux envahis. Les fortes abondances des grillons dans les zones restaurées pourraient d'ailleurs expliquer le repeuplement de ces zones par la fauvette de Rodrigues (*Acrocephalus rodericanus* Newton, 1865).

L'utilisation de la bioacoustique pour estimer des perturbations environnementales est également validée par le suivi des communautés de sauterelles réalisé par Penone *et al.* (2013) sur des routes françaises. La richesse spécifique, la diversité et l'abondance des communautés de sauterelles ont été mesurées lors d'un suivi acoustique en bord de route le long d'un gradient d'urbanisation. Les auteurs ont montré que tous ces paramètres étaient négativement corrélés avec l'urbanisation, entrainant une perte de diversité et des moindres effectifs en zone urbanisée (Penone *et al.*, 2013).

2.4 Les signaux acoustiques des grillons : production du signal, propagation, détection et bio-indication

2.4.1 Généralités

Les grillons émettent des signaux acoustiques pour accomplir différentes fonctions biologiques essentielles (Alexander, 1962). Dans le cadre de la reproduction, les mâles émettent des chants d'appel à longue distance pour la recherche d'un partenaire sexuel ; également avant l'accouplement lors des parades copulatoires (chants de cour) et après l'accouplement (chant post- ou inter-copulatoire) (Alexander, 1962). Lors d'affrontements

entre mâles, ces derniers peuvent émettre des chants très courts et intenses afin d'engager des comportements agressifs (Alexander, 1961). Les chants d'agression sont principalement documentés chez les espèces vivant dans des milieux confinés comme des espèces cavernicoles ou cavicoles et chez des grillons des champs (Alexander, 1961, 1962).

Les chants d'appel émis par les mâles adultes pour attirer une partenaire sexuelle sont classiquement utilisés dans les descriptions intégratives des espèces (Dayrat, 2005), car ils sont généralement caractéristiques d'une espèce (Huber, 1989; Gerhardt & Huber, 2002) : on connait effectivement très peu d'espèces différentes ayant un chant identique. Les propriétés temporelles du chant, comme le nombre et la longueur des syllabes ou la durée des silences entre les motifs, avec les propriétés spectrales (fréquence minimale, maximale ou dominante), représentent des critères de base dans la description du chant d'appel (Fig. 2.3). De plus, les chants des grillons, contrairement à ceux des sauterelles et des criquets, sont émis avec des fréquences dominantes comprises dans une bande très étroite de fréquences grâce à un système de production acoustique entretenu empêchant des vibrations désordonnées des résonateurs (Montealegre-Z *et al.*, 2011).

Les caractéristiques temporelles et spectrales du chant d'appel sont indispensables dans la reconnaissance du signal par les femelles dans l'environnement (Schmidt *et al.*, 2011; Simmons, 2013), soulignant ainsi la spécificité des chants des grillons. L'importance de la fréquence du chant d'appel a été mis en évidence lors d'études portant sur la réponse et la sélectivité des neurones auditifs des femelles adultes pour certaines fréquences : les résultats indiquent que les femelles possèdent une sensibilité et une sélectivité très fines pour les fréquences de leur espèce (Pollack, 2000; Schmidt & Römer, 2011; Schmidt & Balakrishnan, 2015).

Dans ce contexte, il est alors possible de distinguer aisément les différentes espèces de grillons émettrices de signaux sonores qui composent les communautés acoustiques (Nischk & Riede, 2001; Diwakar & Balakrishnan, 2007a), et cela est valable même pour les espèces cryptiques (Walker, 1964). Ainsi, David *et al.* (2003) ont pu distinguer trois espèces cryptiques de *Gryllus* à Rio Claro sur la base du chant d'appel et de la structure des dents de la râpe stridulatoire, confirmant à une échelle locale les résultats obtenus par Desutter (1990) à l'échelle du continent américain. Diwakar *et al.* (2007) ont montré que des expérimentateurs entraînés étaient capables d'identifier avec précision les différentes espèces de grillons qui

composent une communauté forestière : les résultats obtenus par les expérimentateurs ont été meilleurs que ceux des logiciels informatiques pour les chants basses fréquences.

Les grillons font partie des insectes chanteurs les plus étudiés par la communauté scientifique, que ce soit pour les mécanismes de production du signal sonore, les processus auditifs de réception ou les réactions comportementales (phonotaxie et prédation) (Gerhardt & Huber, 2002; Dangles *et al.*, 2006; Dangles *et al.*, 2007; Hedwig, 2014). La dimension acoustique est donc un outil important pour l'identification et la description des espèces capables de chanter. On retrouve cette relation chez tous les groupes communiquant par l'acoustique, comme les amphibiens (Angulo & Reichle, 2008; Glaw *et al.*, 2010; De Carvalho & Giaretta, 2013), les sauterelles (Orci *et al.*, 2010; Iorgu, 2012) ou les acridiens (López *et al.*, 2013). Dans de rares cas, certaines espèces possèdent des chants identiques, comme le montre Alexander & Bigelow (1960) lors d'événements de spéciation allochroniques en Amérique du Nord.

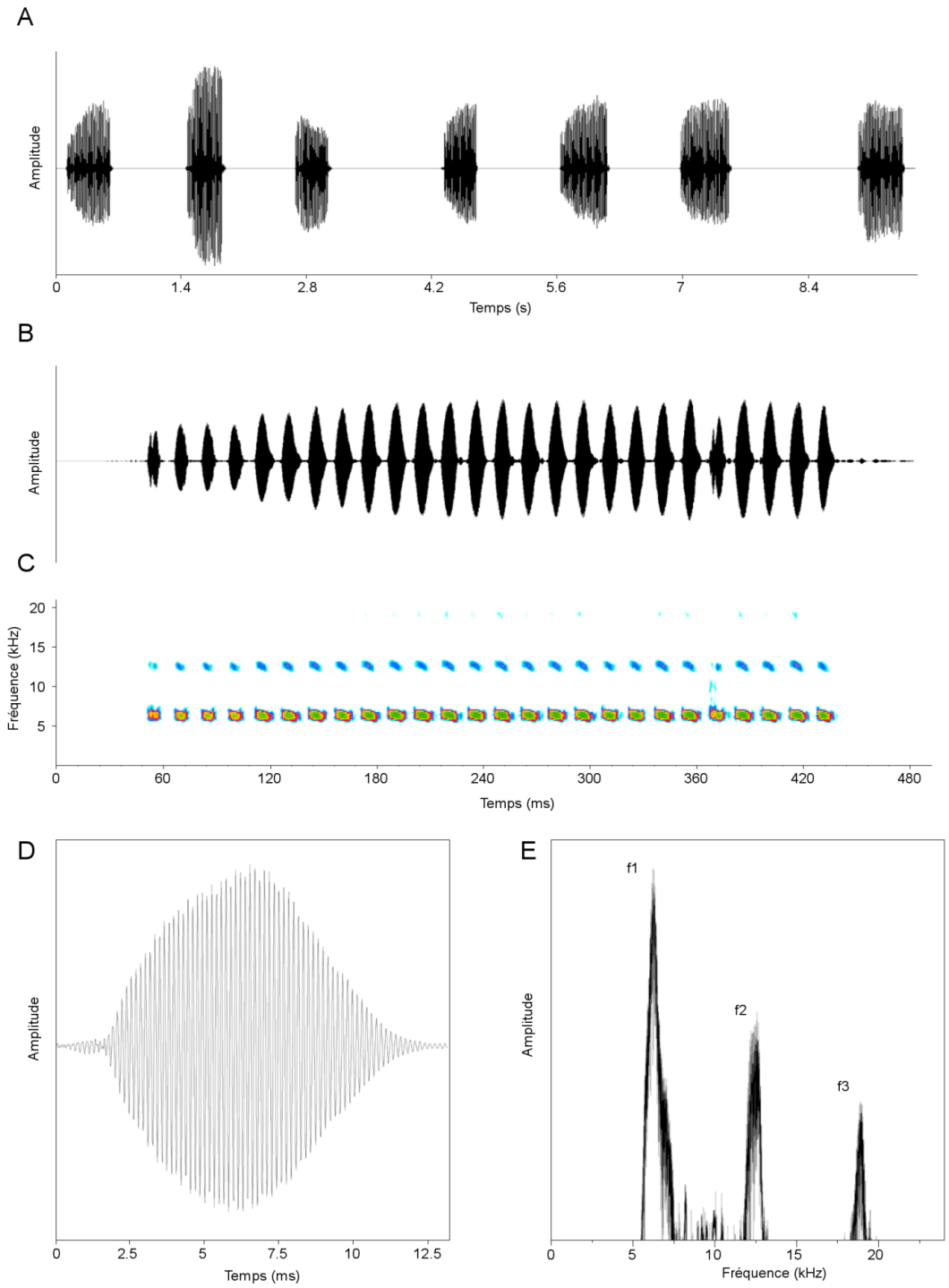

Figure 2.2. *Description du chant d'appel de Bullita obscura Anso et Desutter-Grandcolas n. sp. ; comprenant (A) l'oscillogramme du chant d'appel composé de sept motifs ; (B) le détail d'un motif composés 26 syllabes, l'unité élémentaire du chant produite lors de la stridulation ; (C) le sonagramme du motif ; avec (D) le détail de l'oscillogramme d'une syllabe ; et (E) le spectrogramme du motif représenté, dans lequel on peut identifier 3 fréquences, la fréquence fondamentale et dominante (f1) et les deux harmoniques (f2 et f3).*

2.4.2 Production du signal acoustique : le mécanisme de stridulation

Les grillons chantent par stridulation, en frottant leurs élytres l'un contre l'autre. Chez les grillons, les deux élytres sont symétriques ou presque (Simmons & Ritchie, 1996). L'appareil stridulatoire est composé de deux parties majeures: une partie comprenant la râpe stridulatoire de l'élytre droit et le plectrum de l'élytre gauche, est impliquée dans la production de sons (Koch *et al.*, 1988) (Fig.2.4). La seconde partie, comprenant essentiellement la harpe des deux élytres, et quelques aires connexes, amplifie le son produit en modifiant son spectre de fréquences (Bennet-Clark, 1999; Bennet-Clark, 2003). Le son est en effet produit à une fréquence correspondant à la fréquence des contractions musculaires (i.e., à la fréquence du mouvement de fermeture des élytres), relativement faible et autour de quelques dizaines ou centaines de Hz (de 30 Hz par exemple pour *Gryllus campestris* Linnaeus, 1758), tandis que la fréquence dominante du signal, qui porte le maximum d'énergie, est multipliée par les structures spécialisées et généralement comprise entre 2 et 8 kHz (entre 4.5 et 5 kHz pour *Gryllus campestris*) (Bennet-Clark, 1999). Pendant la stridulation, les élytres s'ouvrent et se ferment alternativement: le son est produit durant la fermeture, l'ouverture étant généralement silencieuse (Bennet-Clark, 1998, 1999).

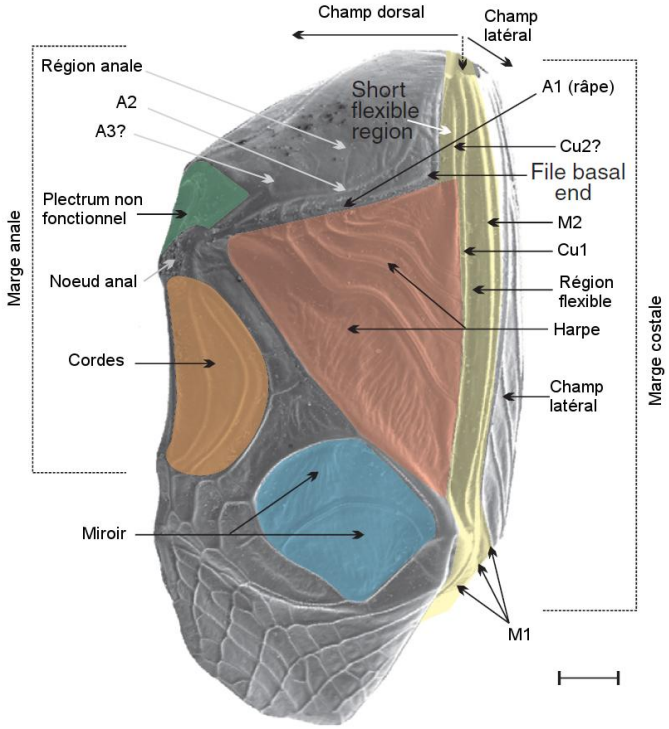

***Figure 2.3**. Elytre droit de Gryllus bimaculatus montrant les principales aires impliquées dans la stridulation. La nomenclature des veines de l'élytre suit Desutter-Grandcolas & Robillard (2003), celle des cellules de l'élytre suit Bennet-Clark (2003). M, veine médiane ; A, veines anales ; Cu, veines cubitales. Echelle, 1mm. Modifié d'après Montealegre-Z et al. (2011).*

Lors de la stridulation, les élytres sont dressés d'environ 30° à 90° par rapport au corps, l'élytre droit au dessus du gauche ; au cours d'une fermeture d'élytre, le système « plectrum-râpe » commence une série d'engagement et désengagement entre les deux élytres. Ce système habituellement comparé à une horloge (Elliott & Koch, 1985; Bennet-Clark & Bailey, 2002) excite la harpe (résonateur) via la râpe après le détachement du plectrum. Une oscillation élémentaire de son est produite par chaque impact d'une dent contre le plectrum ; le système étant parfaitement entretenu chez le grillon, il n'existe pas d'oscillation « parasite » qui serait produite par l'amortissement de la vibration des résonateurs (sauf en fin de motif), contrairement à ce qui se passe chez les sauterelles. L'émission d'un signal cohérent provient de l'interaction mécanique des deux élytres, nécessitant qu'ils vibrent à la même fréquence et en phase (Montealegre-Z *et al.,* 2009). D'étroites relations fonctionnelles existent ainsi entre les élytres pour la production et l'émission du signal (Simmons & Ritchie, 1996). La stridulation chez les grillons permet la production d'un signal sonore très harmonieux émis dans une gamme de fréquences étroite et constante au cours du temps (Koch *et al.,* 1988). Les femelles ne possèdent jamais d'appareil stridulatoire, malgré la présence d'élytres plus ou moins développés selon les espèces.

D'une manière générale, la présence, le développement et la structure des élytres chez les deux sexes sont autant de critères aidant à distinguer des espèces morphologiquement proches, le chant d'appel constituant un autre caractère de reconnaissance pour les espèces communiquant par voie acoustique.

2.4.3 Propagation du signal sonore : atténuation et dégradation

Une fois le signal produit par l'individu, ce dernier traverse l'environnement ambiant de l'animal émetteur. Cette environnement est susceptible d'affecter les propriétés et l'intégrité du signal émis (e.g. végétation, couches d'air à différentes températures, point d'eau) en fonction à la fois des propriétés du signal sonore et des caractéristiques de l'environnement (Marten & Marler, 1977; Marten *et al.*, 1977).

2.4.3.1 Atténuation sonore

Tout signal subit une atténuation sonore lors de sa propagation, qui sera d'autant plus forte que le receveur s'éloigne de la source. L'intensité sonore diminue de 6 dB en doublant la distance entre la source et le receveur. L'atténuation du signal sonore dépend également des

phénomènes d'absorption atmosphérique, de la dispersion du signal par des phénomènes de réflexion ou réfraction (végétation ou turbulence atmosphérique), et des interférences avec le sol (Wiley & Richards, 1978).

2.4.3.2 Dégradations du signal

Le signal sonore subit également des phénomènes de dégradation, principalement du fait de la réverbération et des variations d'amplitudes, qui modifient la structure temporelle et spectrale du signal (Richards & Wiley, 1980). La réverbération résulte de multiples réflexions et dispersions du son durant sa propagation. Elle est fonction de la fréquence du signal, de la foliation de l'environnement et de la directivité de la source : les hautes fréquences souffrent des taux de dégradation les plus forts, et les milieux les plus feuillus (forêt dense tropicale) réverbèrent le plus fortement le signal ; ce phénomène est de fait quasi-absent dans les milieux ouverts de types plaine ou savane, mais caractéristique des milieux forestiers. Enfin, la directionnalité de la source influence les niveaux de réverbération, un chant émis de manière omnidirectionnelle est davantage dégradé que les émissions très directionnelles (Richards & Wiley, 1980). Les trilles, signaux constitués par la répétition rapide d'une seule syllabe, subissent des dégradations spécifiques par réverbération ; les modifications les plus intenses interviennent sur les trilles les plus rapides et sur les syllabes émises en fin de trille (Wiley & Richards, 1982; Naguib, 2003).

Un signal acoustique qui se propage dans un milieu turbulent (gradient de vent) subit des variations d'amplitude, qui sont fonctions de la turbulence atmosphérique (vitesse du vent), de la fréquence du signal et de la distance parcourue. Richards et Wiley (1980) ont montré que les fluctuations d'amplitude augmentaient avec la fréquence et la distance entre la source et le receveur dans un milieu turbulent, à midi et pendant les forts vents. A l'inverse, lors de périodes plus calmes, à l'aube et au crépuscule, les fluctuations d'amplitude sont les plus faibles, et elles ne sont pas corrélées à la fréquence du signal et la distance source-receveur. Les fluctuations irrégulières d'amplitude n'affectent pas la structure spectrale du signal mais sa signature temporelle.

2.4.3.3 Les interférences acoustiques d'origine biologique

Dans les milieux naturels, les grillons qui utilisent les signaux acoustiques pour trouver des partenaires sexuels entrent en compétition avec les mâles de leur propre espèce et avec toutes les autres espèces chanteuses qui composent la communauté, principalement d'autres grillons, des sauterelles, des cigales, ainsi que les vertébrés (oiseaux, batraciens, mammifères) : on parle alors d'espace sonore et de niches acoustiques. Toutes les productions sonores abiotiques résultant d'un processus physique (le vent et la pluie par exemple) ou d'origine anthropique (pollution sonore) interagissent également avec les signaux des espèces. La détection et la reconnaissance des transmissions acoustiques par les femelles sont donc fortement contraintes et brouillées par l'intensité et la diversité de l'ambiance sonore (Schmidt & Römer, 2011). Cependant, les émetteurs et les receveurs ont développé différentes stratégies qui minimisent l'impact des émissions sonores présentes dans le même environnement et rendent la communication acoustique efficace dans le milieu naturel (Endler, 1992; Römer, 2013).

2.4.3.4 Facteurs biologiques de sélection sur les signaux sonores

Lorsqu'ils émettent des signaux acoustiques, les mâles adultes, seuls capables de chanter chez les grillons, s'exposent à de nombreux prédateurs et parasites tels que les mammifères (chauves-souris et chats), les oiseaux, les batraciens, les lézards (Sakaluk & Belwood, 1984), les mouches parasitoïdes (Zuk & Kolluru, 1998) ou les guêpes chasseresses (Gnatzy & Heusslein, 1986; Gnatzy & Kämper, 1990; Gnatzy & Otto, 1996).

Les mouches Tachinaires et les guêpes parasitoïdes localisent des insectes chanteurs afin d'y pondre leurs larves (Sabrosky, 1953a, b), entraînant la mort de l'hôte parasité (Cade, 1975). La présence de ces parasites acoustiques est de fait une pression de sélection importante chez les espèces chanteuses, qui entraînent des modifications du comportement acoustique. Ainsi, Zuk *et al.* (1993) ont montré à Hawaii que les populations de *Teleogryllus oceanicus* Le Guillou, 1841, sous la pression de la mouche parasite *Ormia ochracea* Bigot, 1889, émettaient des chants plus courts que les mêmes populations non parasitées. La pression des mouches parasitoïdes entraînent également un changement de l'heure de l'activité de certaines espèces de grillons vers les heures de la journée où les mouches parasites sont les moins actives (Cade *et al.*, 1996). Finalement, les mâles adultes peuvent rester muets à

proximité de mâles chanteurs et développer un comportement dit « de satellite », leur permettant de limiter la pression de prédation tout en ayant la possibilité d'intercepter les femelles attirées par les chanteurs (Cade, 1984; Walker, 1986). Au-delà des mouches parasitoïdes, Hedrick (2000) a démontré que les grillons qui possèdent des chants « extravagants » sont également les plus prudents face à la pression de prédation : ils cessent de chanter et restent abriter plus longtemps après avoir été dérangé par un potentiel prédateur que les grillons avec des chants moins détectables.

Le contexte socio-sexuel a montré son importance sur l'évolution de la structure des signaux acoustiques, notamment chez deux espèces de grillons des champs, *Gryllus veletis* Alexander & Bigelow, 1960, et *G. pennsylvanicus* Burmeister, 1838 (Bertram *et al.*, 2013). Ces travaux indiquent que selon le contexte socio-sexuel, les signaux acoustiques des mâles adultes varient et deviennent plus attractifs pendant les périodes de la journée où l'activité sexuelle est la plus intense. Ainsi, durant ces périodes les chants des mâles sont plus intenses, avec moins de silences entre les motifs, et une fréquence dominante légèrement plus basse.

2.4.4 Stratégies d'émission et concept de niche acoustique

Dans une communauté acoustique, toutes les espèces qui émettent des signaux sonores doivent se partager des canaux de transmission acoustique, pouvant être assimilés à des ressources écologiques particulières, de la même manière qu'en écologie des communautés traditionnelle où les espèces animales doivent coexister en fonction des ressources présentes dans le milieu (Schoener, 1974; Roughgarden, 1976). Ces canaux de transmission acoustique comprennent la dimension spectrale et temporelle du signal sonore, de même que la période de l'émission sonore (saison, nycthémère) et le lieu (poste de chant) (Pollack, 2000). Ainsi, les espèces chanteuses qui composent une communauté acoustique entrent en compétition pour ces ressources que l'on peut visualiser au sein d'une niche acoustique à plusieurs dimensions, traduisant un partitionnement des ressources disponibles (Duellman & Pyles, 1983; Luther, 2008).

2.4.4.1 Ségrégation spectrale

Selon l'hypothèse de niche acoustique, nous devrions attendre une ségrégation spectrale des espèces chanteuses pour limiter les interférences, comme cela a été proposé chez les amphibiens (Chek *et al.*, 2003; Nityananda & Bee, 2011) ou les cigales (Shieh *et al.*, 2015). Ces interférences acoustiques, représentées par le chevauchement de la fréquence des chants d'appel destinés à la reproduction, entraînent des confusions chez les femelles pour distinguer les signaux d'intérêts conspécifiques au milieu des signaux acoustiques hétérospécifiques, et pour choisir entre les différents mâles chanteurs (Wiley, 1994; Amézquita *et al.*, 2006). Chez les grillons, la fréquence du chant d'appel est un paramètre important dans la détection, la reconnaissance et la sélection des mâles par les femelles dans l'environnement (Gerhardt & Huber, 2002; Hirtenlehner & Römer, 2014). De plus, les grillons émettent dans des bandes de fréquences relativement étroites (grâce à un système de production et d'amplification particulier, cf. supra), comparées aux sauterelles et aux criquets (Riede, 1993, 1997; Diwakar & Balakrishnan, 2007a). A ce titre, et dans les communautés tropicales ou tempérées composées de nombreuses espèces, nous devrions être en mesure d'attendre une ségrégation de la fréquence dominante des signaux sonores en tant que ressource acoustique, limitant ainsi les interférences acoustiques.

Riede (1993, 1998) apporte une première évidence soutenant la répartition spectrale des grillons dans l'espace acoustique et de la partition des ressources acoustiques, notamment la bande de fréquence des mâles chanteurs. Au cours d'une description des propriétés acoustiques des espèces chanteuses d'une forêt dense d'Amazonie, les spectrogrammes indiquent de manière qualitative une possible séparation des espèces en fonction de la fréquence dominante (Riede, 1998). En Inde, les travaux de Diwakar & Balakrishnan (2007a) dans une forêt tropical supportent l'idée d'une ségrégation des fréquences des 17 espèces qui composent la communauté, entre 1.7 et 14 kHz, bien qu'aucune analyse quantitative n'a été réalisée. Ces résultats ont été confortés par Schmidt *et al.* (2013) et Jain *et al.* (2014) sur des assemblages de grillons et de sauterelles au Panama et en Inde, respectivement. Ainsi, Schmidt *et al.* (2013) indiquent que les 18 espèces prises en compte dans cette étude présentent peu de chevauchement de la fréquence dominante.

In fine, l'hypothèse adaptative selon laquelle la compétition acoustique dans une communauté diversifiée de grillons entraînerait des pressions de sélection sur les émetteurs, et que ces pressions tendraient à répartir les chanteurs dans l'espace acoustique disponible

(suivant les dimensions temporelle, spatiale et spectrale) afin de limiter les interférences, n'est pas toujours vérifiée au sein des communautés de grillons. Ainsi, Schmidt *et al.* (2015) en forêt dense humide au Panama n'ont trouvé aucune évidence d'une ségrégation des espèces dans l'espace acoustique, selon la structure temporelle et spectrale du signal, l'heure d'émission et le poste de chant. Ces travaux semblent indiquer que les processus de sélection des signaux acoustiques touchent également les femelles (réceptrices des signaux), qui doivent ultimement réussir à détecter le signal d'intérêt et décrypter l'information qu'il contient. De fait, dans le milieu naturel, les femelles sont également confrontées à une ambiante sonore plus ou moins forte et de nombreuses interférences peuvent diminuer les capacités de détection et de reconnaissance des signaux d'intérêts. Les femelles possèdent également plusieurs stratégies, d'ordres physiologiques, pour diminuer l'impact des bruits ambiants sur la réception d'un signal sonore et la reconnaissance des signaux d'intérêts.

2.4.4.2 Ségrégation spatiale (horizontale et verticale)

Dans la niche acoustique, les espèces qui émettent des signaux sonores peuvent se séparer selon l'axe spatial, horizontalement ou verticalement, permettant ainsi de limiter les interférences acoustiques en augmentant la distance entre les émetteurs et donc l'atténuation et la dégradation des signaux entre eux. L'hypothèse de la stratification spatiale comme facteur limitant la compétition acoustique est en partie soutenue pour la stratification verticale des milieux (limitée par la hauteur de la canopée), tandis que la stratification horizontale semble être structurée de manière aléatoire (limitée par la diversité des habitats et des micro-habitats, par la densité des populations, et par les comportements notamment territoriaux des individus émetteurs) (Jain *et al.*, 2014). Sans mesures et tests statistiques précis, Nischk & Otte (2000) montre une ségrégation verticale selon le poste de chant dans un assemblage de grillons Phalangopsidae en Equateur. Diwakar & Balakrishnan (2007b) ont pu vérifier cette hypothèse et confirmer une structuration verticale des chanteurs pour une communauté composée de grillons et de sauterelles : elles ont ainsi mis en évidence six strates allant du sol jusqu'à la canopée (supérieure à 12 m). L'hypothèse du recouvrement spatial a également été testée sur l'assemblage de grillons néotropicaux au Panama (Schmidt *et al.*, 2013) : aucune organisation selon l'axe horizontale n'a été mise en évidence, mais l'assemblage présentait

une structuration verticale en fonction de la hauteur des chanteurs dans les strates de végétation.

Cette stratification verticale pourrait être la résultante d'une compétition acoustique, permettant ainsi de limiter les interférences entre chanteurs, mais elle pourrait aussi résulter de la répartition écologique des chanteurs selon d'autres critères, comme l'habitat ou la tolérance à l'ensoleillement par exemple. Jain & Balakrishnan (2012) ont testé l'hypothèse d'adaptation acoustique en mesurant la dégradation du signal sonore de 12 espèces de grillons et de sauterelles dans le parc national de Kudremukh en Inde : Elles ont montré que les mesures de dégradation du signal (atténuation, rapport signal-bruit et la distorsion de l'enveloppe) ne soutenaient pas une ségrégation verticale des espèces selon une compétition acoustique, sauf pour une seule des espèces présentes. Il faut noter cependant que cette étude a été réalisée sans cadre phylogénétique, ce qui de toute façon interdisait un test d'une hypothèse d'adaptation.

2.4.4.3 Ségrégation temporelle

Les insectes chanteurs ont la possibilité de répartir leurs productions acoustiques au cours du temps pour limiter les chevauchements et les interférences sonores. Cette ségrégation peut se répartir sur des échelles de temps différentes : très large au niveau des cycles annuels ou des saisons ; plus court au niveau des cycles nycthéméraux ; ou bien très finement, se jouant à l'échelle d'un chant (la minute ou la seconde). Les études sur les communautés acoustiques de grillons ne semblent pas montrer de ségrégation temporelle des chants d'appels (Diwakar & Balakrishnan, 2007b; Schmidt *et al.*, 2013). Au Panama, Schmidt *et al.* (2013) ont montré que les communautés de grillons concentrent leur chant d'appel selon l'heure de la journée, avec un chevauchement significatif de la niche supérieur à celui attendu par hasard (selon un modèle nul).

Cependant, à l'échelle des groupes taxonomiques (grillons, sauterelles, cigales, oiseaux, grenouilles, etc.), les études semblent indiquer des fenêtres temporelles réduites occupées par certains groupes (Gogala & Riede, 1995; Riede, 1997; Sueur, 2002). Des études complémentaires plus fines au niveau des espèces doivent cependant être réalisées pour mesurer la répartition des chants au cours du temps. Schmidt & Balakrishnan (2015) indiquent que les espèces acoustiques tendent à concentrer leurs émissions acoustiques durant les mêmes périodes, notamment durant les cœurs à l'aube et au crépuscule, et émettent

l'hypothèse que les bénéfices d'un tel comportement seraient supérieurs au coût du chevauchement des signaux sonores. Les conditions environnementales particulièrement favorables pour les transmissions sonores expliqueraient cette concentration temporelle (Wiley & Richards, 1978).

Toutefois, l'apparent chevauchement temporel des signaux acoustiques de grillons pourraient être remis en question lors d'analyses plus fines, à des échelles temporelles réduites de l'ordre de la minute. En effet, les chants d'appels sont composés d'un nombre réduit de syllabes, souvent courtes, avec un rapport signal-bruit généralement élevé. On peut donc émettre l'hypothèse que des espèces émettant au même moment éviteraient un chevauchement trop important de leurs signaux grâce à la structure même des signaux. Jain *et al.* (2014) apportent des résultats en ce sens sur les communautés acoustiques des forêts tropicales d'Inde, où les signaux des espèces chanteuses ne se chevauchent que très peu sur des échelles de temps très courtes, de l'ordre de la minute.

2.4.5 Stratégie de réception du signal

Chez le receveur, des modifications physiologiques peuvent intervenir pour améliorer la détection et la reconnaissance des signaux d'intérêts par les femelles dans les environnements bruyants (Römer & Bailey, 1998; Schmidt & Römer, 2011). Ainsi, les receveurs sont capables de modifier les caractéristiques des filtres du système auditif central ou périphérique (Langemann *et al.*, 1998; Witte *et al.*, 2005; Amézquita *et al.*, 2006; Schmidt *et al.*, 2011), en modifiant par exemple la fréquence idéale de ces filtres en fonction des paramètres de l'ambiance sonore (Römer & Bailey, 1998). La position du receveur dans l'espace, ainsi qu'un contrôle neuronal particulier sont également observé pour réduire les problèmes d'interférences (Römer & Krusch, 2000).

2.4.5.1 Sélectivité précise pour la fréquence d'émission

Les études en neurophysiologie indiquent que le système auditif des femelles est particulièrement sensible et sélectif pour les fréquences des conspécifiques, entraînant une forte suppression du bruit ambiant proche des fréquences cibles et une augmentation du rapport « signal – bruit » (Schmidt & Römer, 2011). Schmidt *et al.* (2011) ont démontré expérimentalement la concordance quasi-identique des filtres auditifs pour une fréquence précise (i.e., celle du chant d'appel du mâle) et l'intérêt de cette sélectivité fine pour réduire

les interférences avec le bruit ambiant, et permettre l'extraction des informations du signal sonore (i.e., structure temporelle, spectrale). Les auteurs indiquent que le système auditif des femelles serait plus sélectif pour des fréquences particulières dans les milieux tropicaux où le bruit ambiant serait plus riche et dense que dans des milieux moins sonores (e.g. pour le grillon des champs *Gryllus campestris*) (Schmidt *et al.*, 2011)

2.4.5.2 Position du receveur et mécanisme neuronal d'amplification

La position du receveur dans l'espace sonore représente une stratégie intéressante pour améliorer la détection des signaux sonores d'intérêts. Ainsi, les signaux acoustiques séparés dans l'espace permettent un traitement différencié par la femelle réceptrice, permettant dans certains cas d'améliorer le seuil de détection du chant d'appel (Römer & Krusch, 2000).

Finalement, le receveur peut également filtrer les signaux acoustiques non pertinents du bruit de fond, à travers un mécanisme automatique de contrôle nerveux visant à supprimer les signaux acoustique les moins intenses (i.e. généralement associés au bruit de fond), afin d'améliorer la détection et la reconnaissance des signaux d'intérêts les plus intenses (Römer & Krusch, 2000; Schmidt & Römer, 2011). Chez certaines espèces, ce mécanisme spécifique, qui implique une hyperpolarisation de la membrane des cellules nerveuses, peut réduire efficacement jusqu'à 60% la perception du bruit de fond par le receveur (Schmidt & Römer, 2011).

2.5 Les grillons : un groupe majeur dans les écosystèmes néo-calédoniens

2.5.1 La faune de grillons de Nouvelle-Calédonie

Parmi les groupes d'invertébrés qui composent la biodiversité néo-calédonienne, les coléoptères sont les plus diversifiés avec environ 1500 espèces, suivi des lépidoptères (524), des diptères (410), des hémiptères (350), des hyménoptères (250) et des Araneae (185). Les orthoptères sont représentés par plus de 27.000 espèces connues à ce jour, dont 180 sont des grillons (Anso *et al.* 2015a, b). Les nombreux travaux de description de la faune de grillon en Nouvelle-Calédonie ont commencé avec Chopard (1915), puis se sont poursuivis et intensifiés dans les trois dernières décennies (Gorochov 1986, Otte *et al.* 1987, Desutter-Grandcolas 1997a, b, 2002, Desutter-Grandcolas & Robillard 2006, Robillard & Desutter-Grandcolas

2009, Robillard *et al.* 2010, Desutter-Grandcolas *et al.* 2014), jusqu'à récemment (Anso *et al.* 2015a).

2.5.2 Distribution et endémisme

Les grillons de Nouvelle-Calédonie sont présents sur l'ensemble de l'archipel, incluant la Grande Terre, les îles Loyautés (Lifou, Maré et Ouvéa) ainsi que les îles de Bélép et l'île des Pins. Ils démontrent une très forte diversité et sont représentés au sein de cinq familles regroupées en deux superfamilles, les Mogoplistidae, Gryllidae, Trigonidiidae et Phalangopsidae dans les Grylloidea, et les Myrmecophilidae dans les Gryllotalpoidea ; 40 genres sont actuellement décrits. Ce groupe de macro-arthropodes présente un taux d'endémisme global très élevé, supérieur à 90%, et constitue une composante très caractéristique de la faune calédonienne (Lowry, 1998; Myers *et al.*, 2000).

La distribution des espèces présentent en Nouvelle-Calédonie reste relativement peu connue, du fait d'un déficit d'échantillonnages intégrés. Toutefois, l'archipel néo-calédonien héberge des espèces à vaste répartition, présentes principalement dans les milieux ouverts ou anthropisés tel que *Oecanthus rufescens* Serville, 1838 ; mais la très grande majorité des espèces ont une aire de répartition restreinte, avec de nombreux cas documentés de micro-endémisme. Le genre endémique *Agnotecous* qui comprend 19 espèces illustre les différents patrons de distribution retrouvés en Nouvelle-Calédonie : *A. doensis* Desutter-Grandcolas, 2006 n'est connue que d'une seule localité, la forêt humide du Mt Do; plus au nord de la Grande Terre, *A. obscurus* Chopard, 1970 occupe quand à elle un espace géographique d'environ 90 km de long sur la côte Est, incluant des zones côtières et des forêts humides (Nattier *et al.*, 2012).

A l'échelle des habitats, les grillons occupent des gammes d'habitat variées avec des conditions bioclimatiques particulières. Les forêts denses humides caractérisées par des canopées entièrement couvrantes, des plantes forestières, et une litière épaisse abritent une faune spécialisées de grillon, avec par exemple les Phalangopsidae *Protathra* Desutter-Grandcolas, 1997, *Caltathra* Otte, 1987 et *Pseudotrigonidium* Chopard, 1915 et les Gryllidae *Notosciobia* Chopard, 1915 qui sont inféodés à ces milieux fermés et forestiers (Fig. 2.5). Dans le continuum forestier, des espèces quant à elles se retrouvent à la fois dans des milieux moins fermés à tendance forestières (les maquis paraforestiers par exemple) mais également dans les milieux ouverts avec peu de végétation et de litière dans les maquis arbustifs bas.

C'est le cas notamment du grillon *Koghiella flammea* Anso et Desutter-Grandcolas, n. sp., de plusieurs espèces de la famille des Mogoplistidae, ainsi que du genre *Pixibinthus* Robillard & Anso, 2015. A l'opposé des milieux forestiers, les milieux ouverts et dégradés de type maquis arbustifs bas abritent également une faune de grillons spécialisée. Ces milieux sont principalement définis comme des successions post-incendie (Jaffré *et al.*, 1998b), caractérisés par l'absence de canopée, une litière plus fine et très localisée au niveau des patchs de végétation, et une partie significative de sol nu. Toutefois, et malgré un sous-échantillonnage de ces milieux perturbés par la communauté scientifique, des travaux récents réalisés dans ces habitats ont permis d'identifier un genre endémique de ces maquis, *Pixipterus* Desutter-Grandcolas, 2015, ainsi qu'une espèce de Mogoplistidae.

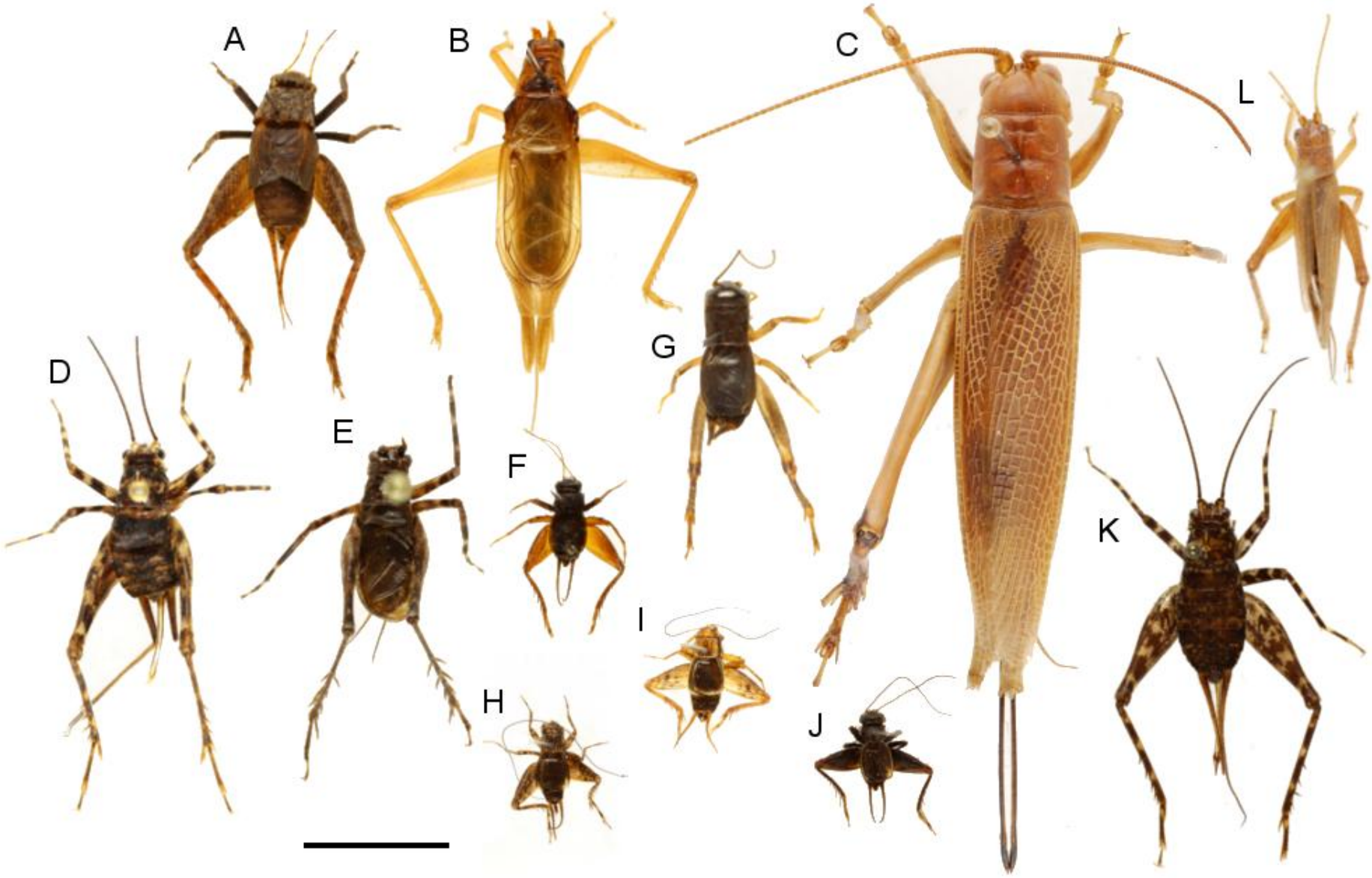
A
B
C
L
D
G
E
F
I
H
J
K

Figure 2.4. *Diversité des tailles, morphologies, colorations et niches écologiques chez les grillons de Nouvelle-Calédonie. A, Agnotecous azurensis Desutter-Grandcolas, 2006 (Gryllidae, Eneopterinae), espèce dominante dans les sous-bois forestier du sud de la Grande Terre; B, Archenopterus bouensis Otte, 1987 (Gryllidae, Podoscitinae), espèce de canopée; C, Calscirtus magnus Anso & Desutter-Grandcolas, 2015 (Gryllidae, Podoscitinae), espèce principalement inféodée aux milieux forestiers; D, Caltathra balmessae Anso & Desutter-Grandcolas, 2015 (Phalangospsidae), espèce de forêt dense humide. ; E, Pseudotrigonidium caledonica (Otte, 1987), espèce de forêts denses humides; F, Bullita mouirangensis Anso & Desutter-Grandcolas, 2015 (Trigonodiidae, Nemobiinae), espèce de litière que l'on retrouve uniquement en forêt dense humide; G, Notosciobia minoris Anso & Desutter-Grandcolas, 2015 (Gryllidae, Gryllinae), espèce de milieu forestier, vivant dans un terrier ; H, Koghiella nigris Anso et Desutter-Grandcolas, 2015 (Trigonidiidae, Nemobiinae), espèce de forêts denses humides recherchant des micro-habitats de sol nu; I, Koghiella flammea Anso et Desutter-Grandcolas, 2015 (Trigonidiidae, Nemobiinae), espèce de litière en maquis miniers proches d'un milieu forestier ; J, Bullita obscura Anso et Desutter-Grandcolas, 2015 (Trigonidiidae, Nemobiinae), petit grillon de litière présent uniquement dans les maquis paraforestiers du sud de la Grande Terre ; K, Caltathra meunieri Anso & Desutter-Grandcolas, espèce de milieu forestier, active de nuit sur des troncs, des rochers ou des racines ; L, Pixipterus punctulatus Desutter-Grandcolas & Anso, une espèce de milieu ouvert vivant dans les maquis sur la végétation. Echelle 1cm.*

2.5.3 Diversité des niches écologiques et des guildes fonctionnelles des grillons en Nouvelle-Calédonie

En Nouvelle-Calédonie, la faune de grillon est présente dans tous les milieux (forêts sclérophylles ou denses humides, milieux côtiers, grottes, maquis, etc.) avec des spécialisations écologiques propres à chaque espèce ou groupe d'espèces (Fig. 2.6).

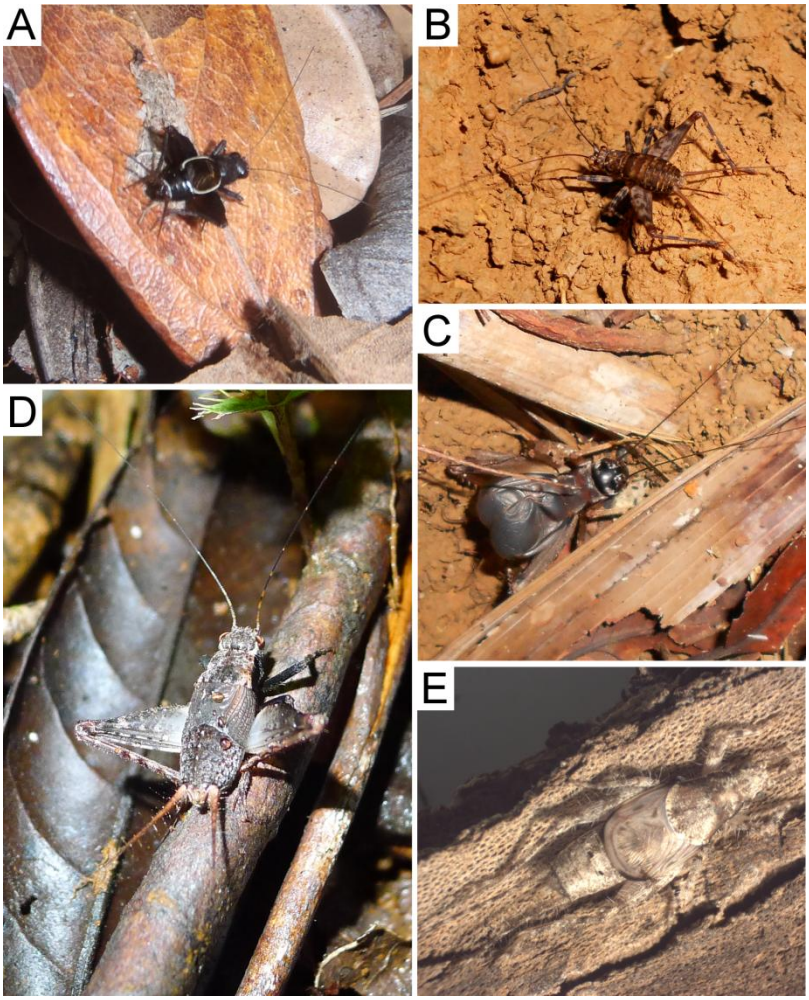

Figure 2.5. *Diversité des niches écologiques de plusieurs espèces de grillons de Nouvelle-Calédonie. Un mâle adulte de Bullita obscura actif de jour dans la litière (A) ; une femelle adulte de la famille des Phalangopsidae active de nuit dans les ravines (B) ; un mâle adulte de Notosciobia en train de chanter de nuit sur le sol (C) ; un mâle adulte d'Agnotecous azurensis actif de nuit sur des supports dans la litière (D) ; et un mâle adulte de Mogoplistidae sp1 actif de nuit sur la végétation (E).*

Les espèces de grillons se répartissent selon l'occupation de l'espace (litière, végétation basse ou haute, rochers ou grottes) et le type d'activité (repos, chant, reproduction, fourragement et déplacement), définissant ainsi des guildes écologiques. Ainsi, Desutter-Grandcolas (1997d) a défini, lors d'une étude des peuplements de sous-bois de grillons au col d'Amieu, quatre guildes principales, regroupant toutes les espèces en fonction de l'heure d'activité (jour vs nuit), de l'habitat d'activité et de l'habitat refuge (occupé pendant la phase d'inactivité).

1. Espèces strictement straminicoles, vivant exclusivement dans la litière, diurnes et nocturnes. Les genres concernés par cette guilde sont les *Bullita*, *Koghiella*, et *Notosciobia*, qui creuse des terriers (Otte *et al.* 1987 ; obs. pers.).

2. Espèces nocturnes perchées de nuit sur divers supports (branches, structures saillantes) et se réfugiant de jour dans la litière. Ces espèces de litière se perchent de nuit sur divers supports, tels que des branches, des bois morts, des troncs d'arbres ou sur la végétation basse environnante. Les espèces du genre *Agnotecous* intègrent cette guilde. Le comportement de perchage a été observé chez plusieurs espèces, en association avec le chant des mâles (branchages et structures saillantes dans la litière) mais également lors de mue ou durant la prise de nourriture (Desutter-Grandcolas & Robillard, 2006; Robillard *et al.*, 2010).

3. Espèces nocturnes perchées sur la végétation du sous-bois. Ces espèces nocturnes se perchent la nuit sur les plantes du sous-bois et se cachent pendant la journée dans différentes structures végétales. Plusieurs espèces ont été identifiées appartenant à ce groupe (*Pseudotrigonidium noctifolia* Desutter-Grandcolas, 1997, *Calcirtus amoa* Otte, 1987) ainsi que des genres tels qu'*Adenopterus* Chopard, 1951 et *Matuanus* Gorochov, 1986.

4. Espèces nocturnes cavicoles, actives sur des troncs d'arbres. Les Phalangopsidae, avec notamment les genres *Protathra* et *Caltathra*, appartiennent à cette guilde. On retrouve ces espèces actives de nuit sur les troncs morts ou vivants, debouts ou couchés, mais également sur des rochers ou des racines de tailles moyennes (Desutter-Grandcolas, 2002). Elles se cachent pendant la journée dans des cavités (troncs creux, interstices entre troncs et racines, troncs et souches, etc).

En plus de ces quatre guildes, nous pourrions en définir une cinquième pour affiner la troisième guilde identifiée par Desutter-Grandcolas (1997d). Cette nouvelle guilde inclut les espèces nocturnes de canopée. Ces espèces se cachent durant la journée ou descendent dans les strates inférieures tandis qu'elles demeurent actives de nuit (émission de signaux acoustiques). Les espèces telles que *Calscirtus magnus* Desutter-Grandcolas & Anso, 2015, *Calscirtus toroensis* Desutter-Grandcolas & Anso, 2015 et *Archenopterus bouensis* Otte, 1987 sont essentiellement retrouvées actives durant la nuit dans les plus hautes strates de la végétation, avec la production importante de signaux acoustiques de haute intensité (Anso, obs, pers). Toutefois, ces milieux restent difficiles à échantillonner à cause de l'accès restreint à la canopée, ou seules les échantillonnages de type 'fogging' d'insecticides ou les collectes ciblées avec des grimpeurs permettent d'estimer cette biodiversité.

2.5.3.1 La diversité des niches acoustiques des grillons

Les grillons de Nouvelle-Calédonie occupent une large gamme de niches acoustiques. Les mâles chanteurs se retrouvent majoritairement au sol, émettant depuis la litière alors que ce type de milieu est considéré comme l'un des pires environnements pour les transmissions sonores (Marten & Marler, 1977; Marten *et al.*, 1977; Schmidt & Balakrishnan, 2015). Une petite fraction de la faune néo-calédonienne émet dans les strates arbustive et arborée supérieure, avec une séparation un peu artificielle en deux catégories : la strate arbustive, plus basse, entre 50cm et 5m, et la strate arborée, haute, où les chanteurs émettent depuis la canopée (Fig. 8). Plus finement, des espèces émettent leurs signaux d'appel sur des sites de chant spécialisés. Par exemple, *Koghiella nigris* (Nemobiinae) a été retrouvé et enregistré exclusivement en forêt dans des micro-patchs de sol nu.

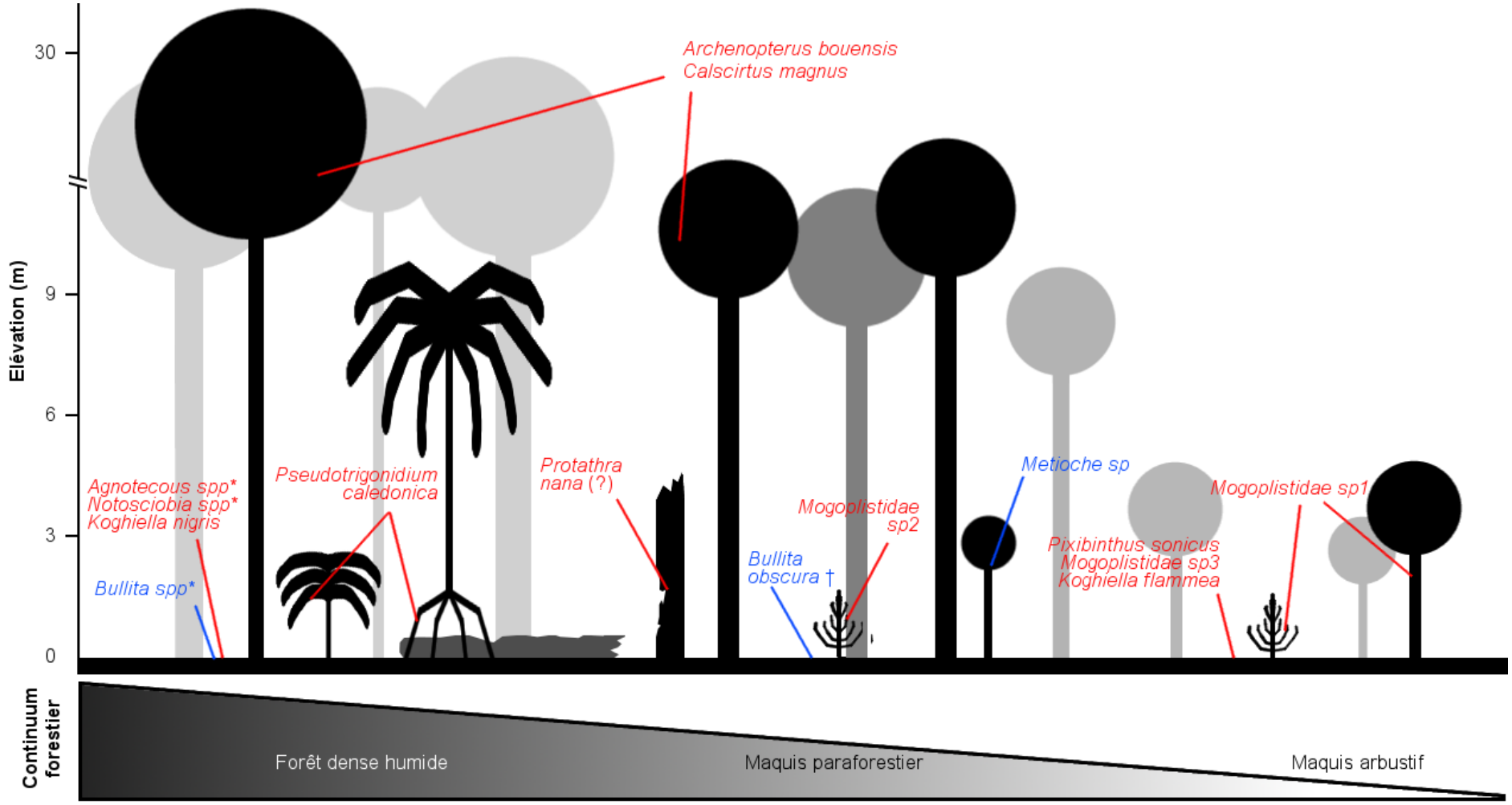

Figure 2.6. *Habitat et période d'activité acoustique de quelques espèces de grillons retrouvées dans le sud de la Grande Terre. Les espèces en rouge sont actives durant la nuit, tandis que les espèces en bleu sont actives pendant la journée.*

Sur l'axe spectral, les grillons néocalédoniens émettent principalement une fréquence dominante comprise entre 2 et 10 kHz, suivant en cela les tendances générales des grillons (Riede, 1993, 1997; Bennet-Clark, 1998). Toutefois, la faune de grillon néo-calédonienne comprend également deux genres endémiques de la Grande Terre, *Agnotecous* et *Pixibinthus* (Anso *et al.* 2016), plus un genre à vaste répartition, *Cardiodactylus*, qui émettent des chants d'appels très largement au-delà du domaine habituel. Les *Agnotecous* émettent des signaux acoustiques avec des structures stridulatoires modifiées, leur permettant d'utiliser des fréquences dominantes entre 11 et 20 kHz (Desutter-Grandcolas, 1997c; Desutter-Grandcolas & Robillard, 2006; Robillard *et al.*, 2010). L'espèce *Lebinthus lifouensis* Desutter-Grandcolas, 1997, décrite de l'île Loyautés de Lifou possède un chant d'appel avec une fréquence dominante de 12 kHz (Desutter-Grandcolas, 1997c). Quant à *Pixibinthus* Robillard et Anso, 2016, inféodé aux maquis arbustifs hautement emblématiques de la Nouvelle-Calédonie il n'est connu que par une seule espèce, *Pixibinthus sonicus* Anso & Robillard, 2016, qui émet un chant d'appel dans les ultrasons à 28.5 kHz, faisant de lui le grillon avec la plus haute fréquence jamais documentée dans le clade (Anso *et al.* 2015). Cette découverte taxonomique et acoustique conforte la place des grillons dans le domaine des ultrasons (Robillard *et al.*, 2007). Inaudibles, les espèces émettrices d'ultrason sont certainement sous échantillonnées.

Au niveau du rythme circadien, les grillons néo-calédoniens répartissent leurs émissions acoustiques au cours de la journée, avec comme nous l'avons vu, une présence marquée durant la nuit. Trois groupes peuvent être identifiés selon le rythme d'activité circadien : (i) les espèces strictement nocturnes ; (ii) les espèces strictement diurnes et (iii) les espèces mixtes, qui peuvent émettre de manière indifférenciée de jour et de nuit (par exemple avec *Bullita obscura*) ou bien émettre principalement durant une partie du nycthémère (la journée par exemple) en chevauchant la seconde partie (durant la nuit dans cet exemple). Toutefois, il est courant d'entendre des espèces de Phalangopsidae ou d'*Agnotecous* chanter la nuit et émettre leur chant d'appel, et d'entendre de jour des chants de cour émis dans des habitats de refuge, où on trouve toujours les mâles et les femelles ensemble (L. Desutter-Grandcolas comm pers.).

Bien que l'on dispose de nombreuses données sur la description des chants, les sites d'émission et les habitats des espèces, aucune étude quantitative n'a été menée pour tester l'hypothèse de partition acoustique des communautés de grillons néo-calédoniennes. Quoi qu'il en soit, des travaux récents réalisés par Gasc *et al.* (2013) dans plusieurs forêts dense

humide de Nouvelle-Calédonie semblent indiquer une succession structurée de groupes d'espèces acoustique dans le temps ; l'identification des groupes chanteurs (oiseaux, grillons, sauterelles, etc.) n'avait cependant pas pu être faite, les connaissances nécessaires en termes de systématique et de bioacoustique n'étant pas disponibles ; pour les grillons notamment, les localités enregistrées n'avaient jamais été échantillonnées auparavant pour les grillons. Qualitativement, la faune de grillons de Nouvelle-Calédonie présente des indices d'une ségrégation de la niche acoustique, à des niveaux et des degrés divers. Ainsi, deux espèces de Mogoplistidae possèdent des chants très proches pratiquement indissociables à l'oreille, composés d'une répétition de motifs dissyllabiques émis avec une fréquence dominante proche (6.4 et 6.7 kHz), mais ne se retrouvent jamais dans le même habitat. D'autres espèces font montre d'une possible stratification verticale : par exemple, deux grillons émettent avec une fréquence de 4.1 kHz, mais vivent l'un dans la litière (*Notosciobia minoris* Robillard, 2010), l'autre dans la canopée (*Calscirtus magnus* Desutter-Grandcolas & Anso, 2015) ; leurs chants diffèrent également fortement par leur rythme. Ces observations renforçent l'idée qu'une analyse rigoureuse du partitionnement de la niche acoustique dans les communautés de grillons de Nouvelle-Calédonie doit intégrer toutes les dimensions possibles de la niche acoustique et écologique des espèces.

2.6 Conclusion

En Nouvelle-Calédonie, les grillons représentent l'un des groupes d'insectes les plus abondants des écosystèmes ; ils sont très diversifiés et fortement endémiques. Les grillons sont distribués sur l'ensemble du territoire et occupent une gamme variée d'habitats. Les grillons sont des macro-arthropodes importants dans le fonctionnement des écosystèmes (en tant que proies et aussi en fonction de leur régime alimentaire majoritairement détritivore pour la plupart des espèces) ; ils sont sensibles aux conditions bioclimatiques de l'environnement, à la structure de la végétation et à différents régimes de perturbations (espèces invasives, pollutions, successions forestières). Finalement, ce groupe est très actif pour la production de signaux acoustiques hautement spécifiques, permettant des identifications taxonomiques de bonne qualité que l'on peut lier avec la biodiversité globale des habitats (Sueur *et al.*, 2008). L'ensemble de ces caractéristiques sont autant de critères pour considérer les grillons comme un groupe prometteur en tant qu'indicateurs de biodiversité et indicateurs écologiques de l'état des écosystèmes.

Ce rôle possible de bio-indicateur est particulièrement étudié dans les chapitre 2 à 4 du présent travail: la réponse des communautés de grillons à des perturbations de l'environnement a été mesurée lors d'échantillonnages *in situ* en fonction de deux modalités, (i) selon un continuum forestier représentant une succession forestière dans le sud de la Grande Terre (section 2), et (ii) selon la présence de plusieurs invasions biologiques majeures par la fourmi électrique *Wasmannia auropunctata* Roger, 1863 (section 3) et la fourmi folle jaune *Anoplolepis gracilipes* Smith, 1857. La première section de ce chapitre met l'accent sur la découverte inédite de *Pixibinthus sonicus* Robillard & Anso, 2015, dans les maquis arbustifs : ce taxon pourrait représenter un modèle de référence pour étudier les dynamiques paysagères (notamment les feux naturels et anthropiques) ; cette section met également l'accent sur les maquis bas qui peuvent abriter une faune d'Orthoptères originale et inédite, pouvant apporter des connaissances majeures pour comprendre l'origine de la biodiversité de l'archipel de Nouvelle-Calédonie.

.

3 Les grillons (Insecta, Orthoptera, Grylloidea) de Nouvelle-Calédonie: description de nouvelles espèces, données écologiques et bioacoustiques

Cette section a été l'objet d'un article de recherche accepté à *Zootaxa*, sous la forme suivante :

Anso, J., Jourdan, H., Desutter-Grandcolas, L. (2016). Crickets (Insecta, Orthoptera, Grylloidea) from Southern New Caledonia, with descriptions of new taxa. *Zootaxa*.

3.1 Résumé

Un échantillonnage poussé des communautés de grillon a été réalisé dans le sud de la Nouvelle-Calédonie, dans des types de végétation spécifiques, i.e. des forêts tropicales, des formations préforestières et des maquis arbustifs. Les échantillonnages ont permis la découverte de nombreux nouveaux taxons décrits dans cet article de recherche, regroupés avec les espèces des régions avoisininantes. Les descriptions sont réalisées sur la morphologie générale et les caractéristiques des génitalias. Les chants d'appels sont également décrits pour toutes les nouvelles espèces chanteuses, excepté pour deux espèces, ainsi que les observations sur les habitats. Au total, 32 espèces appartenant à 13 genres sont étudiés, dont 21 et deux sont nouveaux pour la science, respectivement.

Mots-clés: Taxonomie, Océanie, Trigonidiidae, Nemobiinae, Gryllidae, Gryllinae, Podoscirtinae, Phalangopsidae, Nouvelles espèces, Nouveaux genres, Bioacoustique

3.2 Abstract

Intensive sampling of cricket communities has been undertaken in southern New Caledonia in selected plots of vegetation, i.e. rain forest, preforest and maquis shrubland. This leads to the discovery of many new taxa, which are described in the present paper, together with closely related species from nearby areas. Descriptions are based on general morphology and characters of genitalia. Calling songs are described for all acoustic taxa but two, and observations about species habitats are given. In total, 32 species belonging to 13 genera are studied, including 21 new species and two new genera.

Key words: Taxonomy, Oceania, Trigonidiidae, Nemobiinae, Gryllidae, Gryllinae, Podoscirtinae, Phalangopsidae, New genera, New species, Bioacoustics

3.3 Introduction

Following the pioneering work of Chopard (1915), the cricket fauna from New Caledonia has been well-studied during these last decades (Gorochov, 1986; Otte *et al.*, 1987; Desutter-Grandcolas, 1997b, d, e, c, 2002; Desutter-Grandcolas & Robillard, 2006; Robillard & Desutter-Grandcolas, 2008; Robillard *et al.*, 2010; Desutter-Grandcolas *et al.*, 2014) and more than 150 species are presently known from the Archipelago.

Despite all this taxonomic work, New Caledonian crickets are still badly known as far as their distributions, habitats and behaviours are concerned. Yet, crickets are one of the main groups of arthropods in the natural habitats of New Caledonia (Anso *et al.* 2015, in prep) They also prove an interesting model to test hypotheses about the origin and evolution of New Caledonian fauna, because of their diversity, high macro- and micro- endemism and original biological traits (Desutter-Grandcolas, 1997d; Desutter-Grandcolas & Robillard, 2006; Grandcolas *et al.*, 2008; Nattier *et al.*, 2011; Nattier *et al.*, 2012).

In this context, intensive sampling of cricket communities has been undertaken by one of us (JA) in southern New Caledonia, in order to 1/ characterize cricket communities from the point of view of their species composition and structure; 2/ check the influence of forest regeneration on the presence and abundance of cricket species, 3/ test the resilience of cricket community to invasive ants, and finally 4/ check the value of the cricket model as bioindicators to evaluate ecological disturbance in New Caledonia (Anso *et al.* 2015, submitted).

In the present paper, we describe the new cricket species (Gryllidea, Grylloidea: Gryllidae, Trigonidiidae, Phalangopsidae) collected during this sampling effort or found in near-by areas. We also propose the biological information, in terms of habitats and advertisement calls, gathered on some already known species we found during field work. In total, 34 species are discussed, 21 of which are new to science and described. They belong to the genera *Adenopterus* Chopard, 1951, *Archenopterus* Otte, 1987, *Bullita* Gorochov, 1986, *Calscirtus* Otte, 1987, *Caltathra* Otte, 1987, *Kanakinemobius* Desutter-Grandcolas, n. gen., *Koghiella* Otte, Alexander & Cade, 1987, *Matuanus* Gorochov, 1986, *Notosciobia* Chopard, 1915, *Paniella* Otte, Alexander & Cade, 1987, *Pixipterus* Desutter-Grandcolas, n. gen., *Protathra* Desutter-Grandcolas, 1997 and *Pseudotrigonidium* Chopard, 1915. One new genus and species of Eneopterinae crickets, *Pixibinthus sonicus* Anso & Robillard, 2015, from low

shrubland vegetation, has been described elsewhere (Anso *et al.* submit_a), and new species and data on scaly crickets (Gryllidea, Grylloidea, Mogoplistoidae, Mogoplistidae) will be published separately (Anso *et al.* unpublished data) as will be new data about ant-loving crickets, only recently recorded in New Caledonia but actually quite diverse (unpublished data). Finally, generic diagnoses and a key to identify cricket genera of New Caledonia will be proposed in a forthcoming paper (Desutter-Grandcolas & Anso submitted).

3.4 Material and methods

3.4.1 Specimens

Most studied specimens have been collected in the field in southern New Caledonia by J. Anso to study cricket community in several patches of forest at different regeneration steps (Anso *et al.* 2015, submitted). Each specimen is given a field reference number (fn), with the following information: VEGETATION TYPE (abbreviation, see below) parcel number - unique specimen number. Type specimens are deposited in the collections of the Muséum national d'Histoire naturelle, Paris (MNHN) and reference specimens are deposited in the Institut de Recherche et de Développement, Nouméa (OMNC).

3.4.2 Morphology

Male phallic complexes were removed, cleaned with cold 10% KOH and kept in glycerine with the specimens. Observations were performed using a Leica MZ12 stereomicroscope. Drawings were made under a camera lucida. Photos of male genitalia were taken with a Canon EOS 60D camera with an macro lens Canon MP-E 65mm mounted on a Leica stereomicroscope and controlled by the software Helicon Remote. Photos were combined using the stacking option of Helicon Focus software v. 6.2.2 lite (© 2000-2014 Helicon Soft. Ldt.). Genitalia were tinted with a drop of Punktol product.

3.4.3 Parcels of vegetation studied

Most crickets were collected in specific types of vegetation along a succession gradient from maquis to rainforest in the southern part of Grande Terre, between 22.15142° S 166.68643° E in the North and 22.34820° S 166.97343° E in the South, and between 22.31902° S 166.80473° E in the West and 22.27103° S 166.96355° E in the East. Three different types of

vegetation were studied (Fig. 39): low shrubland (called "maquis"), preforest formation (called "paraforestier") and rainforest (called "rainforest"). The description of the vegetation found in the parcels, and the list of dominant plant species, are given elsewhere (Anso *et al.* 2015, submitted).

3.4.4 Acoustic data

Calling songs were recorded from several males in the field and at the laboratory, up to 5 specimens for a single species. In the field, calling songs were recorded with a microphone (Seinnheiser K6/ME62, frequency range: 20 - 20 kHz ± 2.5 dB), placed at 40 cm from the calling male, connected to a Field memory recorder Fostex FR-2LE (48 kHz sampling frequency, stereo). At the lab, males were placed in round boxes covered by a mosquito net, and then, recorded as in the field with the same audio materials. Time of day, temperature and calling perch were noted for every calling male. In one specific case, collected crickets from the field were recorded with a modified condenser microphone (CM16 Avisoft Bioacoustics, Berlin, frequency range: 3 - 150 kHz ± 6 dB, R. Specht pers. comm.), placed at 30 cm from the calling male, in a sound-attenuated room controlled for temperature in the MNHN. One insect was placed all night long in a cage made of mosquito net to avoid echoes. This specific protocol was made for one species that emit a calling song above 24 kHz. Songs were recorded under the "*.wav"* format, and deposited in the Sound Libraries of the MNHN (where they can be found using their unique reference number: MNHN-SO-XXXX).

Calling songs were analyzed with the computer software Avisoft-SASLab Pro (version 4.40. Specht 2008). Automatic analyses were performed under human supervision to avoid aberrant measurement. Temporal characteristics (syllable lengths, intra-syllable silences) and spectral characteristic (dominant frequency) were collected with "automatic train". Songs were described and analyzed according to the terminology from Ragge & Reynolds (1998). One syllable is the elementary unit of the singing call and corresponds to one opening-closure cycle of the male forewings. A repeated group of syllables is called an echeme, and a group of echemes is called an echeme sequence.

When several individuals have been recorded at different temperatures, original data are given for each temperature.

3.4.5 Abbreviations and symbols

Specimens. fn, field number.

Female genitalia. c.p., copulatory papilla; sp., spermatheca.

Male genitalia. Membranous parts figured with dots. In the legends, structures seen through the membranes designated with dotted lines. Named after Desutter (1987) and Desutter-Grandcolas (2003): arc, ectophallic arc; d. cav., dorsal cavity; d. v., ectophallic dorsal valves; ec. a., ectophallic apodeme; ec. f., ectophallic fold; ec. f. m., ectophallic fold ventral margins; en. a., endophallic apodeme; en. s., endophallic sclerite; l. pr. ps., left dorsal process of pseudepiphallus; l. ps., lower part of pseudepiphallic sclerite; m.l., median lobe; pr. ps., dorsal processes of pseudepiphallus; ps., pseudepiphallic sclerite; ps. a., pseudepiphallic apodeme; ps.l.1, 2, pseudepiphallic lateral lobe, 1, 2; ps. m., pseudepiphallic median lobe; ps. m., pseudepiphallus distal margin; ps. p., pseudepiphallic parameres; r., ramus; r. pr. ps., right dorsal process of pseudepiphallus; t. p., transverse plate between pseudepiphallus and the ectophallic fold (Gryllidae, Podoscirtinae); u. ap., apodeme of the upper part of pseudepiphallus; u. ps., upper part of pseudepiphallic sclerite; v. ps., ventral sclerotization of pseudepiphallus; v. v., ventral valves.

General morphology. I, II, III, anterior, median, posterior (leg, tarsomere); A1, first anal vein (bearing the stridulatory file); DD, LL, dorsal disc, lateral lobe of pronotum; FW, forewing; HW, hindwing. Wing venation named after Desutter-Grandcolas (2003) and Robillard & Desutter-Grandcolas (2004b).

Repositories. ANSP, Academy of Natural Sciences, Philadelphia; BPBM, Bishop Museum, Honolulu, HI (formerly, Bernice Pauahi Bishop Museum); HNHM, Hungarian Museum, Budapest; MNHN, Muséum national d'Histoire naturelle, Paris; NHM, Naturhistorisches Museum, Vienna; OMNC, Institut de Recherche et de Développement, Nouméa; UMMZ, University of Michigan Museum of Zoology, Ann Arbor.

Data base. OSF, Orthoptera Species File online (http:www.orthoptera.speciesfile.org). Specimens deposited in the MNHN collections have a unique inventory number, MNHN-EO-ENSIF-XXXXX, and can be found in the collection data base of the MNHN at the following address, https://science.mnhn.fr/institution/mnhn/collection/eo/search

Measurements (in mm). iod, intra-ocular distance; LFIII, length of hind femur; LFW,

forewing length; Lpron, pronotum length; LTIII, length of hind tibia; OL, ovipositor length; wFIII, width of hind femur; wFW, median forewing width, at the level of mirror anterior angle; wpron, pronotum width.

Vegetation parcels. Parcelle codes include two letters for the type of vegetation (MA, maquis; PA, paraforestier; FO, rainforest), and two or three letters for the location of the parcelles (BDS, Bois du Sud, Col de Ouénaru; FN, Forêt Nord; GK, Grand Kaori; MAD, Les Chutes de la Madeleine; MOU, CM, Col de Mouiranges; PEP, Pépinière; PDP, Pic du Pin; RIV, Rivière Bleue). For the geographic location of the parcelles, see Anso *et al.* (submitted).

List of studied taxa

Adenopterus sp. affinis crouensis Otte, 1987

Adenopterus meridionalis Desutter-Grandcolas & Anso, n. sp.

Adenopterus octolineatus Desutter-Grandcolas & Anso, n. sp.

Archenopterus bouensis Otte, 1987

Bullita fusca (Gorochov, 1986)

Bullita mouirangensis Anso & Desutter-Grandcolas, n. sp.

Bullita obscura Anso & Desutter-Grandcolas, n. sp.

Bullita sp.

Calscirtus amoa Otte, 1987

Calscirtus magnus Desutter-Grandcolas & Anso, n. sp.

Calscirtus toroensis Desutter-Grandcolas & Anso, n. sp.

Caltathra balmesae Anso & Desutter-Grandcolas, n. sp.

Caltathra meunieri Anso & Desutter-Grandcolas, n. sp

Kanakinemobius Desutter-Grandcolas, n. gen.

Kanakinemobius mandjelia Desutter-Grandcolas, n. sp.

Kanakinemobius sp.

Koghiella flammea Anso & Desutter-Grandcolas, n. sp.

Koghiella nigris Anso & Desutter-Grandcolas, n. sp.

Matuanus sp. *affinis mirabilis* Desutter-Grandcolas, 1997

Matuanus kaorensis Desutter-Grandcolas & Anso, n. sp.

Notosciobia sp. *affinis paranola* Otte, 1987

Notosciobia minoris Anso & Desutter-Grandcolas, n. sp.

Notosciobia farino Anso & Desutter-Grandcolas, n. sp.

Notosciobia sp. 1

Notosciobia sp. 2 (calling song only)

Paniella bipunctatus Desutter-Grandcolas & Anso, n. sp.

Paniella sp.

Pixipterus Desutter-Grandcolas, n. gen.

Pixipterus fusculus Desutter-Grandcolas & Anso, n. sp.

Pixipterus minutus Desutter-Grandcolas & Anso, n. sp.

Pixipterus mou Desutter-Grandcolas, n. sp.

Pixipterus punctulatus Desutter-Grandcolas & Anso, n. sp.

Protathra nana Anso & Desutter-Grandcolas, n. sp.

Pseudotrigonidium ana Anso & Desutter-Grandcolas, n. sp.

Pseudotrigonidium aptera (Desutter-Grandcolas, 1997)

Pseudotrigonidium caledonica (Otte, 1987)

3.5 Systematics

Grylloidea Laicharting, 1781

Phalangopsidae Blanchard, 1845

Four genera of Phalangopsidae are currently known in New Caledonia, *Parendacustes* Chopard, 1924, *Caltathra* Otte, 1987, *Protathra* Desutter-Grandcolas, 1997 and *Pseudotrigonidium* Chopard, 1915. *Pseudotrigonidium* belongs to the subfamily Phaloriinae Gorochov, 1985, as proposed by Gorochov (2010), and supported by molecular evidence (Chintauan-Marquier *et al.*, 2016). The positions of the other three genera are more confused, because the subfamilial divisions in Phalangopsidae need be redefined deeply in a phylogenetic context (see Desutter-Grandcolas *et al.* in prep.); the only supported hypothesis is the close relationship between *Caltathra* and *Protathra*, proposed from morphological observations (Desutter-Grandcolas, 1997e, 2002), and confirmed by molecular analysis (Chintauan-Marquier *et al.*, 2016).

Genus Caltathra Otte, 1987

Caltathra Otte in Otte *et al.* 1987: 414.

Type species. *Caltathra panaki* Otte, 1987.

Emended diagnosis. See Desutter-Grandcolas & Anso (submit.).

Distribution. *Caltathra* is known from New Caledonia only, where it has been found in the Central mountain chain in Col d'Amieu (*C. amiensis* Desutter-Grandcolas, 1997, *C. chopardi* Desutter-Grandcolas, 1997, *C. areto* Desutter-Grandcolas, 1997), in the northeast area, close to Mont Panié (*C. paniensis* Desutter-Grandcolas, 2002, *C. doensis* Desutter-Grandcolas, 2002, *C. paniki* Otte, 1987), and in the southern part of the Grande Terre (*Endotaria steinmanni* Gorochov, 1986 in the Mont Koghis, *C. minuta* Desutter-Grandcolas, 2002, *C. balmessae* Anso & Desutter-Grandcolas, n.sp., *C. meunieri* Anso & Desutter-Grandcolas, n. sp., *Endacusta dubia* Chopard, 1915 in southeastern New Caledonia).

Remark. The definition, species composition and habitat of *Caltathra* Otte, 1987 have been reviewed in previous papers (Otte *et al.* 1987; Desutter-Grandcolas 1997d). On this occasion, two species groups, the *chopardi* species group and the *amiensis* species group, have been defined on the basis of the presence versus absence of small inner tympanum on TI, the presence versus absence of a pair of hook-like lateral sclerites on epiphallic median processus, and the number of TIII inner subapical apurs. Observations of *Caltathra balmessae* Anso & Desutter-Grandcolas, n.sp. show that the definition of the *chopardi* species group must be

amended to keep only the genitalic characters and the number of TIII spurs, as *C. balmessae* Anso & Desutter-Grandcolas, n. sp., which belongs clearly to the *chopardi* group, is lacking an inner tympanum.

Caltathra balmessae Anso and Desutter-Grandcolas, n. sp.

(Figs 3.1A-F, 3.2A-C)

Type locality. New Caledonia, Grande Terre, Rivière bleue.

Type material. Holotype: New Caledonia, Grande Terre, Rivière blanche, rainforest, 22.15142° S 166.68643° E, 19.iii.2014, at night, 1 male, fn FORIV2-36, on trunk 40 cm high, J. Anso (MNHN-EO-ENSIF3749). **Allotype:** Same locality as the holotype, 12.iii.2014, at night, 1 female, fn FORIV2-18, on roots above ground 5 cm high, J. Anso (MNHN-EO-ENSIF3750).

Additional material. New Caledonia, Grande Terre, Rivière blanche, paraforestier, 22.15280° S 166.68033° E, 10.xii.2013, at night, 2 juveniles, fn PARIV2-3, 5, on trunk, J. Anso (MNHN).

Etymology. Named after the maiden name of Monique Anso.

Distribution. New Caledonia, Grande Terre, Rivière blanche.

Diagnosis. Species of the *chopardi* group, according to TIII spurs and male genitalia. Size small compare to other species of the group; close to *C. chopardi* from which it differs by the absence of the small inner tympanum on TI, by the shape of dorsal valves and the length of lateral sclerites on epiphallic median processus in male genitalia, and by female copulatory papilla and ovipositor length. *C. balmessae* Anso & Desutter-Grandcolas, n. sp. can also be recognized by its black antennae, and by the coloration of its scapes, face, cheeks and coxae I (see infra). *C. balmessae* Anso & Desutter-Grandcolas, n. sp. could be close to *C. dubia* (Chopard, 1915) from Yaté, as shown by the coloration of the scapes (no distal dorsal brown ring) and metanotum (white line behind pronotum), and by ovipositor length (about 9 mm); details of coloration (yellow spot under the antennal pit, yellow lines on head dorsum) and size (compare pronotum length and width) differ however, and the hindlegs and genitalia of *C. dubia* are not known.

Description. In addition to the characters of the genus and species group (Otte *et al.* 1987, Desutter-Grandcolas 1997d). Size small for the species group. TIII inner serrulation: no spine between the apical and the first subapical spur and between subapical spurs 1 and 2, and between spurs 2 and 3; 0-1 spine between subapical spurs 3 and 4; 3 spines above subapical spur 4. TIII outer serrulation: no spine between apical and subapical spurs, and between subapical spurs 1 and 2; 1 (male) and 1-2 (female, mean 1.5) spines between subapical spurs 2 and 3; 3 (male) and 2 (female) spines between subapical spurs 3 and 4; 9-10 (male, mean 9.5) and 10-11 (female, mean 10.5) spines above subapical spur 4. Tarsomeres III-1: 6-8 (male, mean 7) and 5-7 (female, mean 6) outer and 3 (male) and 2-3 (female, mean 2.5) inner spines, in addition to apical spines.

Coloration. Slightly contrasted, mostly dark brown with yellowish parts on legs. Head dorsum light brown between the eyes with 4 lighter cone-shaped longitudinal bands; occiput dark brown (Fig. 3.2C); cheeks light yellow behind the eye, the posterior margin brown, with a short light band from the lower angle of the eye down to subgenal suture (Fig. 3.2B); face dark brown, with a whitish bottle-shaped median band from median ocellus down to epistemal suture, prolonged on preclypeus, and a small yellowish dot under each antennal pit (Fig. 2A); antennae black with few, small yellow articles; scapes light yellow with dark lateral sides ventrally, and one dark line along outer margin margin dorsally. Maxillary palpi: articles 3-5 black brown with a thin dorsal yellow line. Pronotum black brown, with dark anterior margin and light brown posterior margin (Fig. 3.2C); DD homogeneously dark brown, with a yellow longitudinal band on anterior two third, widened distally but not reaching DD distal margin, 2 yellowish pyriform inscriptions and a short yellow line on each anterior angle; LL dark brown, with a more or less distinct yellow dot in anterior angle; DD and LL separated by a short concave yellow line. Legs: TI, TII and TIII yellow, with 4 irregular dark dorsal flecks, ventral margins yellow; FI, FII yellow with two black rings in apical half, a more irregular one in basal half and a short one at base, ventral margins marked with dark brown; FIII with two irregular dark apical rings, and a more basal irregular one; outer basal part of FIII only lightly marked with brown. Abdomen dark brown, marked with black and yellow in female at hand. Cerci yellow brown, lighter at base.

Male. Subgenital plate strongly transverse; moderately elongate. Abdomen mostly brown black with yellowish transversal bands for the 3 first segments. Cerci getting slightly darker toward the apex on their whole length.

Male genitalia. Fig. 3.1A-C. Lateral sclerites on epiphallic median processus longer than those of the species group *chopardi* (Fig. 3.1A, B). In lateral view, pseudepiphallic median lophi more elongate and raised than in *C. chopardi* and *C doensis* (Fig. 3.1C). Sclerotisation of the inner margin of dorsal valves slightly concave compared to that of *C. areto* and *C. doensis*. Endophallic sclerite U-shaped as in *C. doensis*, its margins slightly larger than in *C. chopardi* (see Desutter-Grandcolas 2002, Fig. 10 and 12).

Female. Subgenital plate distal margin slightly bisinuous, the median part acute. Ovipositor as long as TIII (see measurements). Abdomen mostly dark brown without specific forms and coloration. Cerci darker than in male holotype, almost black brown.

Female genitalia. Fig. 3.1D-F. Copulatory papilla very small, with open basal ring; apex thinner but not sinuous as in *C. chopardi* (see Desutter-Grandcolas 1997c, Fig. 25).

Juvenile. Juveniles can be identified and more specifically separated from sympatric *C. balmessae* Anso & Desutter-Grandcolas, n. sp. by the number of TIII subapical spurs and details of coloration (especially scapes, coxa 1, to a lesser extend cheeks).

Measurements (in mm).

	PronL	PronW	FIIIL	FIIIW	TIIIL	OL
Male holotype	2.6	3.1	11.1	2.6	8.5	-
Female allotype	2.6	3.1	11.8	3	9.3	9.3

Habitat and life history traits. *C. balmessae* Anso & Desutter-Grandcolas, n. sp. is a nocturnal species, who lives in mixed rainforest, on trunks and large roots.

Caltathra meunieri Anso and Desutter-Grandcolas, n. sp.

(Figs 3.1G-I, 3.2 D-F)

Type locality. New Caledonia, Grande Terre, Pic du Grand Kaori, 22.28535° S 166.89674° E.

Type material. Holotype: New Caledonia, Grande Terre, Pic du Grand Kaori, rainforest, 22.28535° S 166.89674° E, 03.vi.2013, at night, 1 male, fn PGK2-42, on dead trunk, J. Anso (MNHN-EO-ENSIF3751). **Allotype:** New Caledonia, Grande Terre, Col de Mouirange, rainforest, 22.20416° S 166.68086° E, 25.vii.2012, at night, 1 female, fn LD67, L. Desutter-Grandcolas (MNHN-EO-ENSIF3752). **Paratypes: 6 males, 3 females.** New Caledonia, Grande Terre, same data as the allotype, 1 male, J. Anso (MNHN-EO-ENSIF3613); 25.vii. 2012, at night, 1 male, fn LD62, on trunk, L. Desutter-Grandcolas (MNHN-EO-ENSIF3612); 14.viii.2013, at night, 1 male, fn FOMOU2-4, on trunk, J. Anso (MNHN-EO-ENSIF3753); 21.viii.2013, at night, 4 males, fn PCM1-69, 74, 75, 85, on trunk, J. Anso (MNHN-EO-ENSIF3754, 3755, 3609, 3610). Same locality as the holotype, 28.xii.2012, at night, 1 female, fn FOGK1-37, on litter; 09.vii.2012, at night, 1 female, fn PGK3-11, on trunk; 11.vii.2012, at night, 1 female, fn PGK3-12, on trunk, J. Anso (MNHN-EO-ENSIF3611, 3614-3615).

Additional material. New Caledonia, Grande Terre, Col de Mouirange, rainforest, 22.20416° S 166.68086° E, 20.viii.2013, by day, 1 female, fn FOMOU1-14; 22.viii.2013, by night, 1 juvenile, fn FOMOU1-36; 29.viii.2013, by day, 2 juveniles, fn FOMOU1-46-47; 14.viii.2013, by night, 1 juvenile, fn FOMOU2-6; 24.viii.2013, by day, 1 juvenile, fn FOMOU2-22, J. Anso, MNHN.

New Caledonia, Grande Terre, Pic du Grand Kaori, rainforest, 22.28535° S 166.89674° E, 11.xii.2012, by night, 1 juvenile, fn FOGK1-2, leaf litter; 17.xii.2012, by night, 1 juvenile, fn FOGK2-28. Same locality as the allotype, 21.viii.2013, by night, 4 juveniles, fn PCM1-70-73, J. Anso, MNHN.

New Caledonia, Grande Terre, Rivière blanche, rainforest, 22.15142° S 166.68643° E, 11.iii.2014, by night,1 juvenile, fn FORIV1-26, on trunk; 10.xii.2013, by night, 1 juvenile, fn FORIV2-5, J. Anso. MNHN.

New Caledonia, Grande Terre, Pic du Pin, rainforest, 22.24680° S 166.82715° E, 12.ii.2014, by night, 1 juvenile, fn FOPDP1-42, J. Anso, MNHN.

New Caledonia, Grande Terre, Pic du Grand Kaori, paraforestier, 22.28000° S 166.89383° E, 22.viii.2013, by night, 1 juvenile, fn PAGK2-26, J. Anso, MNHN.

New Caledonia, Grande Terre, Rivière Blanche, paraforestier, 22.15280° S 166.68033° E, 10.xii.2013, by night, 1 male, fn PARIV2-2, J. Anso, MNHN.

Etymology. Named in honor of Jean-Yves Meunier, who greatly helped one of the author for field work.

Distribution. New Caledonia, Grande Terre, Col de Mouirange and Pic du Grand Kaori.

Diagnosis. Species of the *amiensis* species group. From *C. minuta, C. meunieri* Anso & Desutter-Grandcolas, n. sp. can be separated by its larger size (compare FIII and TIII length), the shape of the median processus in male genitalia (more raised in *C. meunieri* Anso & Desutter-Grandcolas, n. sp.), the shape of female copulatory papilla (lateral margins almost straight, not sinuous as in *C. minuta*), and its darker coloration. From *C. paniensis*, *C. meunieri* Anso & Desutter-Grandcolas, n. sp. can be separated by its smaller size, and by the larger dorsal valves and the longer and thinner lateral sclerites of median process in male genitalia.

Description. In addition to the characters of the genus and species group (Otte *et al.* 1987, Desutter-Grandcolas 1997d). Size medium for the species group. TIII inner serrulation: no spine between apical and subapical spurs and between subapical spurs 1 and 2; 0-1 (mean 0.3) between spurs 2 and 3; 11-14 (males, mean 11.5) and 6-10 (female, mean 8.3) spines above subapical spur 4. TIII outer serrulation: no spine between apical and subapical spurs; 0-1 (males, mean 0.5; females, mean 0.3) between subapical spurs 1 and 2; 2-3 (males, mean 2.5) and 1-2 (females, mean 1.5) spines between subapical spurs 2 and 3; 2-3 (males, mean 2.7) and 1-3 (females, mean 1.8) spines between subapical spurs 3 and 4; 11-14 (males, mean 13) and 9-13 (females, mean 10.7) spines above subapical spur 4. Tarsomeres III-1: 6-7 (males, mean 6.5) and 3-7 (females, mean 5) outer, and 3-5 (males, mean 4.2) and 2-5 (females, mean 3.2) inner spines, in addition to apical spines.

Coloration. Mostly dark brown with yellowish flecks. Head dorsum black brown with 4 light yellow cone-shaped bands (Fig. 3.2F); cheeks black brown along their distal margins, the dark part covering part of the subgenal suture, and in direct contact with a dark line under the lower angle of the eyes (Fig. 3.2E); antennae brown (not black), with few, small yellow rings; scapes light yellow, with an apical ring and a dark fleck along each margin in dorsal view, a thin dark line along dorsal outer margin, and a wide, rounded black fleck along dorsal inner margin. Face black with a median, bottle-shaped whitish band prolonged on part of the clypeus only; no yellow spots under the antennal pits (Fig. 3.2D). Maxillary palpi: articles 3-5 black brown, yellow dorsally. DD homogeneously black brown, with 2 brown pyriform flecks, and a yellow longitudinal median line reaching, or almost reaching, distal margin; LL

dark brown with one brown dot on the half; DD and LL separate by a short and thin, curved, median yellow line. Legs: FI, FII brown with 3 black flecks; FIII brown with 2 large black and irregulars flecks, with 2 ringed black fleck on apical part. TI, TII and TIII almost entirely black with 3 small whitish dots. Abdomen almost homogeneously black brown. Cerci brown dorsally, and black brown laterally.

Male. Subgenital plate not elongate; a median slightly incurved furrow along its whole length; depressed in its apical half.

Male genitalia. Fig. 3.1G-H. Very similar to that of *C. minuta* (see Desutter-Grancolas 2002, Figs. 4-6). In ventral view, dorsal valves less angular than in *C. minuta*. Epiphallic sclerite more flat that of in *C. paniensis* in lateral view (see Desutter-Grandcolas 2002, Fig. 3). Basal part of endophallic sclerite more angular than in *C. minuta*. Membraneous part between the endophallic sclerite and the ectophallic fold more extended than in *C. minuta*. Ectophallic fold lower than in *C. minuta*.

Female. Subgenital plate as in *C. balmessae* Anso & Desutter-Grandcolas, n. sp., its apex perhaps slightly less sinuous (Fig. 3.1I). Ovipositor shorter than cerci, FIII and TIII (see measurements).

Female genitalia. Copulatory papilla very small. Lateral margins almost straight, not sinuous as in *C. minuta* (see Desutter-Grandcolas 2002, Fig. 7); in lateral view, papilla very similar to that of *C. minuta*, but more flat.

Juvenile. Unknown

Measurements (in mm).

	PronL	PronW	FIIIL	FIIIW	TIIIL	OL
Male holotype	2.5	2.7	10.7	2.9	9.5	-
Female allotype	3.2	3.6	9.9	2.9	8.0	6.1
Male paratypes (n=6)	2.2-2.8 (2.5)	2.7-3.5 (3.3)	9.8-11.5 (10.6)	3.1-2.4 (2.7)	8.6-10.3 (9.5)	-
Female paratypes (n=4)	2.4-3.2 (2.6)	3.3-3.8 (3.6)	9.9-10.6 (10.3)	2.7-3.3 (3)	6.5-9 (8.2)	6.1-7.3 (7)

Habitat and life history traits. *C. meunieri* Anso & Desutter-Grandcolas, n. sp. is a nocturnal species, who lives in mixed rainforest, on trunks.

Remark. *Caltathra balmessae* Anso & Desutter-Grandcolas, n. sp. and *C. meunieri* Anso & Desutter-Grandcolas, n. sp. are very similar, although they can be readily separated by the characters of the species group (TIII subapical spurs, and male and female genitalia). They can also be recognized by details in coloration, such as the presence / absence of a small yellow dot under each antennal pit, the shape of the dark coloration on the cheek (reaching or not the subgenual suture and the lower angle of the eye), the coloration of antennae (black versus brown), that of the scapes (presence / absence of a dark distal ring dorsally, size and shape of black fleck along the ventral inner margin), and that of the pronotum (median longitudinal line on DD, and yellow line separating DD and LL).

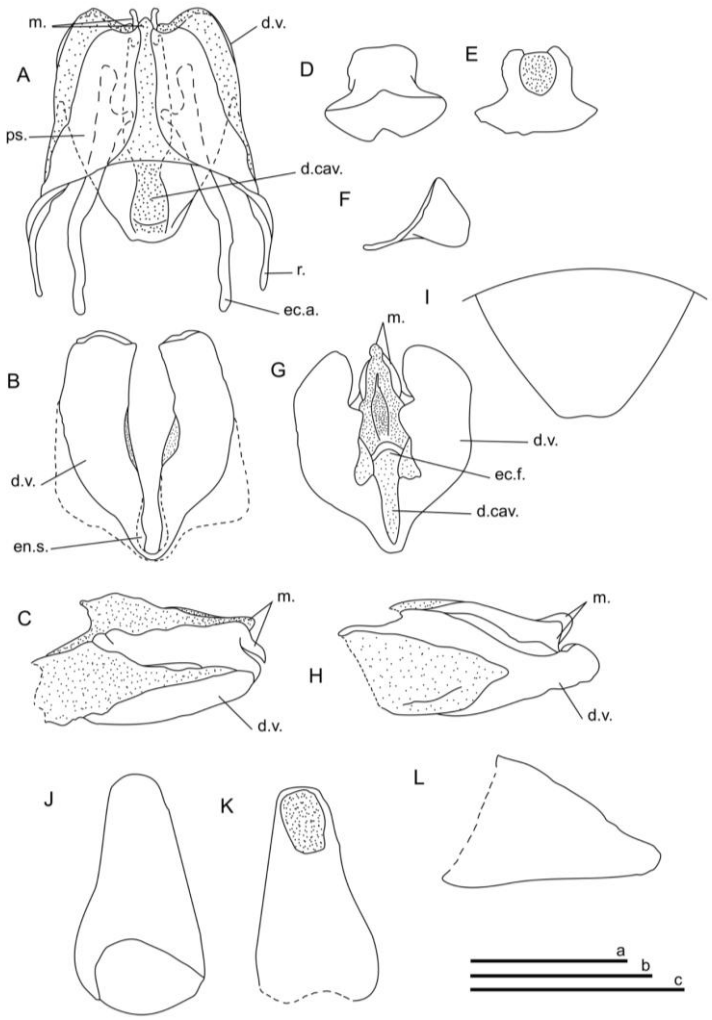

Figure 3.1. *Caltathra Otte, 1987 and Protathra Desutter-Grandcolas, 1997. Caltathra balmessae Anso & Desutter-Grandcolas, n. sp. (A-F), C. meunieri Anso & Desutter-Grandcolas, n. sp. (G-I) and Protathra nana Anso & Desutter-Grandcolas, n. sp. (J-L): male genitalia, dorsal (A), ventral (B, G) and lateral (C, H); female copulatory papilla, dorsal (D, J), ventral (E, K), lateral (F, L); female subgenital plate, ventral (I). Scales 1 mm. Abbreviations: see Material and methods.*

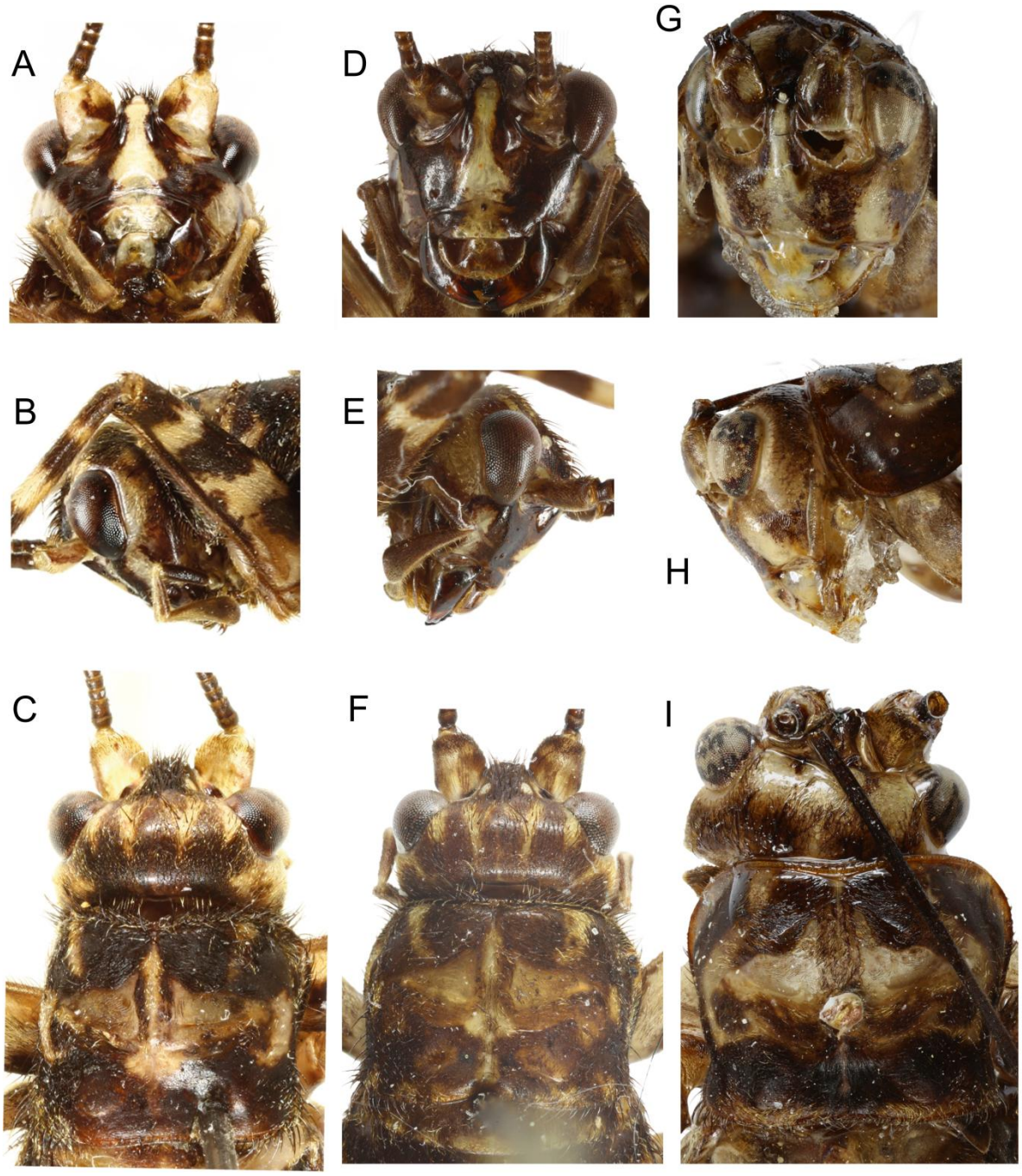

Figure 3.2. *Caltathra Otte, 1987 and Protathra Desutter-Grandcolas, 1997. Caltathra balmessae Anso & Desutter-Grandcolas, n. sp. (A-C, male holotype, DD length 3.1mm), C. meunieri Anso & Desutter-Grandcolas, n. sp. (D-F, female allotype, DD length 3.6mm) and Protathra nana Anso & Desutter-Grandcolas, n. sp. (G-I, female holotype, DD length 3.9mm): Face (A, D, G); head, lateral (B, E, H), lateral head and pronotum, dorsal (C, F, I).*

Genus *Protathra* Desutter-Grandcolas, 1997

Protathra Desutter-Grandcolas, 1997b: 150.

Type species. *Protathra gigantea* Desutter-Grandcolas, 1997b.

Emended diagnosis. See Desutter-Grandcolas *et al.* (2014) and Desutter-Grandcolas & Anso (submitted).

Distribution. *Protathra* is known from New Caledonia only, where it has been found in the Aoupinié mountain (*P. centralis* Desutter-Grandcolas, 2014) and in Col d'Amieu (*P. gigantea* Desutter-Grandcolas, 1997d).

Protathra nana Anso and Desutter-Grandcolas, n. sp.

(Figs 3.1J-L, 3.2G-I)

Type locality. New Caledonia, Grande Terre, Rivière bleue.

Type material. Holotype: New Caledonia, Grande Terre, Rivière blanche, rainforest, 22.15142° S 166.68643° E, 10.xii.2013, at night, 1 female, fn FORIV2-1, on tree 50 cm high, J. Anso (MNHN-EO-ENSIF3616).

Etymology. Named after the small size of the species within the genus.

Distribution. New Caledonia, Grande Terre, Parc de la Rivière bleue, Rivière blanche.

Diagnosis. Very similar to the other species of the genus, from which it can be readily separated by the small size of its ovipositor, shorter than TIII.

Description. In addition to the characters of the genus (Desutter-Grandcolas 1997b, Desutter-Grandcolas *et al.* 2014, Desutter-Grandcolas & Anso submit.). TIII inner serrulation: no spine between apical and subapical spurs, and between subapical spurs 1 and 2; 3-4 (mean 3.5) spines between subapical spurs 2 and 3; 20-22 (mean 21) spines above subapical spur 3. TIII outer serrulation: no spine between apical and subapical spurs; 1 spine between subapical spurs 1 and 2; 3-5 (mean 4) spines between subapical spurs 2 and 3; 5 spines between subapical spurs 3 and 4; 15-16 (mean 15.5) spines above subapical spur 4. Tarsomeres III-1: 5-7 (mean 6) outer and 5 inner spines, in addition to apical spines.

Coloration. Face brown with 3 whitish median bands (Fig. 3.2G), one under the median ocellus, growing wider toward the epistemal suture and prolonged onto the clypeus, and one under the apex of each eye, straight, slightly widened along the lower margin of the cheek and prolonged onto the mandibula. Cheeks otherwise light brown, except for a light yellow line around the eye (Fig. 3.2H). Vertex brown, with a median light yellow part. Head dorsum (Fig. 3.2I) light yellow between the eyes, crossed by two thin longitudinal brown lines in addition to a pair of thin and short brown lines arriving along the eyes inner margin; head vertew brown, connected to these four brown lines. Scapes light yellow with a brown distal ring and a large brown fleck on anterior side; antennae black brown with few short yellow rings. Palpi lacking. Pronotum (Fig. 3.2H, I) black brown with yellow marks, the anterior margin yellow, the lateral margins light brown, the distal margin yellow except for the brown median part; DD black brown with a very thin longitudinal yellow line, yellowish pyriform inscriptions, a pair of yellow transverse lines in distal half; limit between DD and LL marked with yellow and brown; LL dark brown, except for a yellow fleck along the anterior yellow margin. Abdomen brown, black brown and yellow; tergites 3-5 black along their anterior margin, with a black 3-prong median fleck, these bordered with yellowish; other tergites more uniformly brown. Legs light yellow with black brown flecks and rings. FI with 3 almost complet black rings, in addition to a basal black fleck; FII with 2 black rings in distal half and an elongate black fleck on inner side; FIII with 2 black rings in distal half, two black flecks in basal half on inner side, and two additional elongated flecks, one dorsal and one on outer side. TI, TII with 3 dorsal black flecks, ventral margin yellow; TIII with 3 long black flecks, and a very small one close to the knee, ventral margin yellow. Cerci dark brown homogeneously.

Male. Unknown

Female. Subgenital plate very similar to that of *P. centralis* (see Desutter-Grandcolas *et al.* 2014), transverse, distal margin largely sinuate. Ovipositor shorter than TIII.

Female genitalia. Fig. 3.1J-L. Copulatory papilla dorsally cone-shaped form, the ventral membranous part ovoid.

Juvenile: Unknown

Measurements (in mm).

	PronL	PronW	FIIIL	FIIIW	TIIIL	OL
Female holotype	4	3.9	18.3	4	17.3	17

Habitat and life history traits. *P.nana* Anso & Desutter-Grandcolas, n. sp. is a nocturnal species, who lives in mixed rainforest, on trunks.

Calling song. Unknown.

Genus *Pseudotrigonidium* Chopard, 1915

Pseudotrigonidium Chopard, 1915: 152.

Type species. *Pseudotrigonidium sarasini* Chopard, 1915.

Diagnosis. See Desutter-Grandcolas & Anso (submit.).

Distribution. *Pseudotrigonidium* has long been considered endemic to New Caledonia under the name *Tremellia* Stål, 1877 (Otte *et al.* 1987; Desutter-Grandcolas 1997d, c). It has been removed from the synonymy with *Tremellia* by Gorochov (1996). *Pseudotrigonidium* is currently recorded from New Caledonia, Australia, Papua New Guinea, Malaysia and the Solomon islands in the OSF data base.

Remark. Gorochov (1996) defined two subgenera, according to the shape of male genitalia, *Pseudotrigonidium* (*Pseudotrigonidium*) Chopard, 1915, with relatively long and narrow genitalia, and *Pseudotrigonidium* (*Tripsegonium*) Gorochov, 1996, with relatively short and wide genitalia. They will have to be checked for their monophyly.

Pseudotrigonidium caledonica (Otte, 1987)

(Fig. 3.3)

Tremellia caledonica Otte in Otte *et al.*, 1987: 420.

Pseudotrigonidium caledonica, Desutter-Grandcolas 2009: 623.

Type locality. New Caledonia, Mt. Koghi, west side of Mt Bouo, tall forest.

Type material. Holotype: New Caledonia, Mt. Koghi, west side of Mt Bouo, tall forest, 27.ii.1983, 1 male, Alexander, Otte and Cade (ANSP).

Examined material. New Caledonia, Grande Terre, Rivière blanche, rainforest, 22.15142° S 166.68643° E, 14.iii.2014, by day, 1 male, fn FORIV1-38, in leaf litter, J. Anso (MNHN-EO-ENSIF3623). New Caledonia, Grande Terre, Pic du Pin, 22.14525 S 166.49426 E, 26.vii.2015, 1 male, by night, in *Nothophagus* forest, singing on a low branch of Pandanacae, J. Anso & L. Desutter-Grandcolas (OMNC); same locality, habitat and collectors, 31.vii.2015, by night, 1 male, fn 2015-20, recorded in the field by J. Anso (MNHN-EO-ENSIF3918).

Diagnosis. Within the genus, *Pseudotrigonidium* (*Pseudotrigonidium*) *caledonica* is characterized by its male genitalia, especially the shape of pseudepiphallic parameres: parameres deeply bifidous, with a short ventral part, regularly narrowed toward apex and thus broadly triangular; dorsal part very long and thin, plicated at right angle at mid length, its arcuate apex making a thin hook turned outwardly (see Otte *et al.* 1987, Fig. 24E); the parameres crossed each other at mid length (see Remark below). Other characters: lower third of pronotum LL yellow, the lower limit of coloration prolonged on the cheeks (black brown behing the eyes) and on the face, under the eyes; a wide longitudinal dark brown band from the fastigium to the tip of the labrum; vertex and occiput dark brown, with three short, longitudinal yellow lines; palpi light yellow, the tip of joint 5 dark brown. FWs longer than abdomen in male; stridulatory apparatus as in Otte *et al.* (1987)'s Fig. 23B.

Habitat and life history traits. *P.* (*Pseudotrigonidium*) *caledonica* (Otte, 1987) lives in tropical forests. Males were found in mixed rainforest perched on leaves and dead branches at night, or hidding in leaf litter close to tree trinks during the day. They start singing few minutes after dusk usually perched on vegetation, such as *Pandanus* or tree ferns, or large roots; on plants, they are usually under the leaves while singing.

Calling song. Fig. 3.3. One specimen has been recorded in the field (four song bouts, 11 echemes, 1044 syllables) and collected. At 16°C, the calling song of *Pseudotrigonidium caledonica* (Otte, 1987) consists of a repetition of echemes of 3.2 ± 0.5 s; each echeme is made of 95 ± 16 syllables, with the following characteristics: syllable duration = 16.8 ± 3.7 ms; syllable period = 33.5 ± 5 ms; syllable duty cycle = 49.6 %; the dominant frequency is 2.8 kHz. Inventory number MNHN-SO-2016-1.

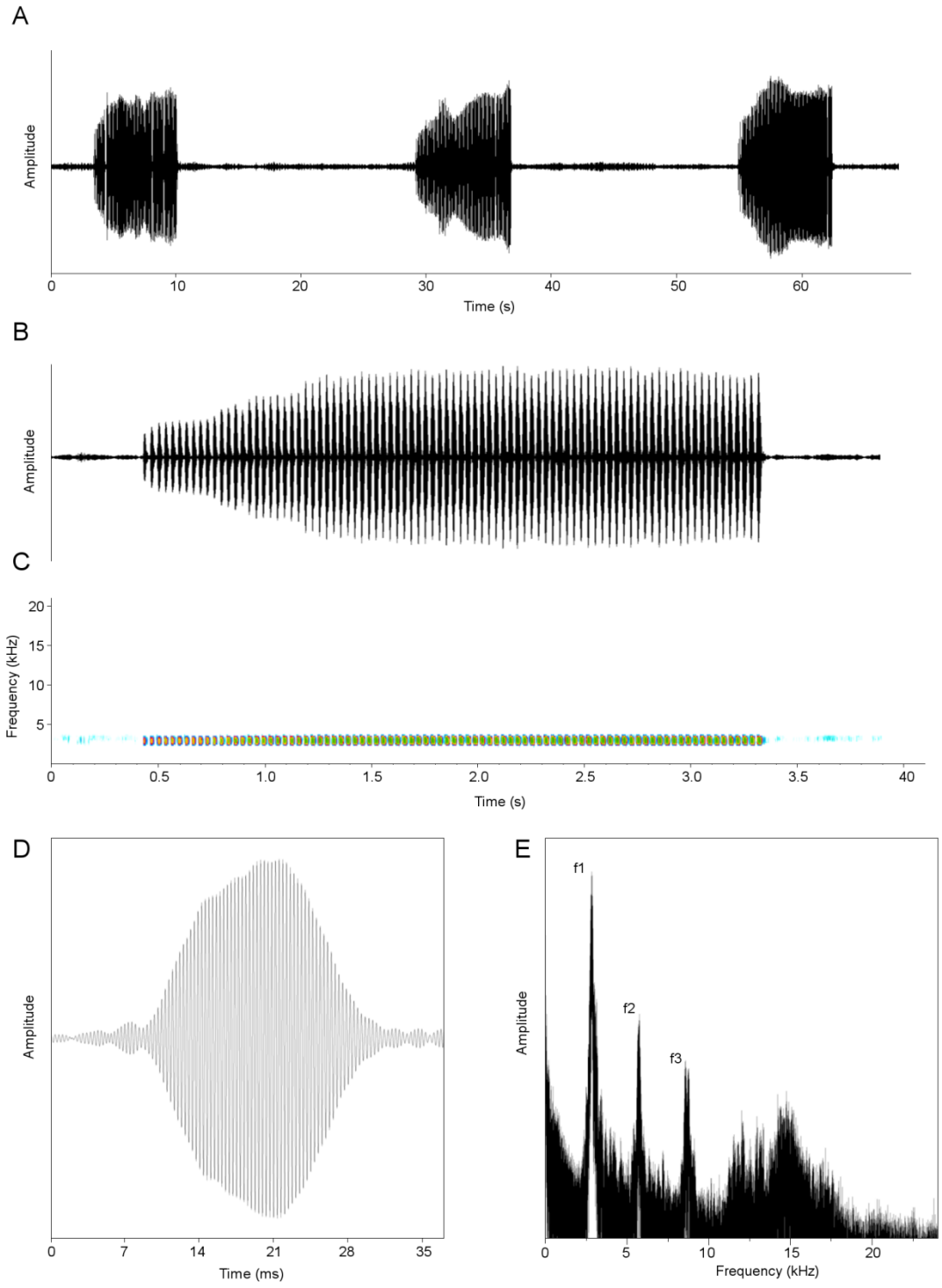

Figure 3.3. *Calling song of Pseudotrigonidium caledonica (Otte, 1987). Oscillogram of three successive echemes (A); detailed oscillogram (B) and sonogram (C) of one echeme; oscillogram of one syllable (D); logarithmic spectrogram of one syllable (E). Symbols: f1-f3, first (fundamental) to third harmonic frequencies.*

Remark. In the male examined, the left and right parts of the male phallic complex cross each other in mid line, while on the figure of by Otte *et al.* (1987), the parameres are widely apart.

Pseudotrigonidium aptera (Desutter-Grandcolas, 1997)

(Fig. 4A, B)

Tremellia aptera Desutter-Grandcolas, 1997c: 174.

Pseudotrigonidium aptera, Desutter-Grandcolas 2009: 174.

Type locality. New Caledonia, Province Sud, Rivière bleue.

Type material. Holotype: New Caledonia, Province Sud, Rivière bleue, 25 km NE Nouméa, 20m, forêt sempervirente sur roche ultrabasique, 12-25.xi.1986, 1 male, L. Bonnet de Larbogne, J. Chazeau & S. Tillier, MNHN-EO-ENSIF3626.

Additional material examined. New Caledonia, Grande Terre, Col de Mouirange, rainforest, 22.20416° S 166.68086° E, 9.vii.2012, at night, 1 male, PCM1-25, on leaf litter, J. Anso (MNHN-EO-ENSIF3907).

Distribution. The newly observed specimen extend the distribution of the species westward in the South of New Caledonia.

Pseudotrigonidium ana Anso and Desutter-Grandcolas, n. sp.

(Figs 3.4C-I, 3.5)

Type locality. New Caledonia, Grande Terre, Pic du Grand Kaori.

Type material. Holotype: New Caledonia, Grande Terre, Pic du Grand Kaori, rainforest, 22.28535° S 166.89674° E, 30.i.2013, by night, 1 male, fn FOGK1-54, in leaf litter, J. Anso (MNHN-EO-ENSIF3617). **Allotype.** New Caledonia, Grande Terre, Pic du Grand Kaori, rainforest, 22.28535° S 166.89674° E, 10.vii.2013, by day, 1 female, fn NOU38-PG4, on trunk, 10 cm high, J. Anso (MNHN-EO-ENSIF3618). **Paratypes. 2 females.** New Caledonia,

Grande Terre, Goro, Le Trou, Pépinière, paraforestier, 22.27103° S 166.96355° E, 11.ii.2014, by night, 1 female, fn PAPEP1-27, on vegetation, 50cm high, J. Anso.

New Caledonia, Grande Terre, Rivière blanche, paraforestier, 22.15280° S 166.68033° E, 19.iii.2014, by day, 1 female, fn PARIV1-47, leaf litter, J. Anso (MNHN-EO-ENSIF3619-3620).

Additional material. 2 females, 3 juveniles. New Caledonia, Pic du Grand Kaori, paraforestier, 22.28000° S 166.89383° E, 21.viii.2013, by night, 1 female (without PIII), fn PAGK2-18, on vegetation, J. Anso (MNHN).

New Caledonia, Rivière blanche, paraforestier, 22.15280° S 166.68033° E, 20.iii.2014, by night,1 female, fn PARIV2-65, on trunk, J. Anso (MNHN).

New Caledonia, Grande Terre, Goro, Le Trou, Pépinière, paraforestier, 22.27103° S 166.96355° E, 11.ii.2014, by night,1 juvenile, fn PAPEP1-28, on vegetation, 50cm high, J. Anso (MNHN).

New Caledonia, Pic du Pin, rainforest, 22.24680° S 166.82715° E, 10.ii.2013, by night, 1 juvenile, FOPDP2-17, on vegetation, 1m high, J. Anso; 13.ii.2013, by night, 1 juvenile, FOPDP2-49, on vegetation, 1m high, J. Anso (MNHN).

Etymology. Named after the kanak word "ana" for the snake *Laticauda colubrina* called "tricot rayé" in French, because of its striped coloration.

Diagnosis. Within the genus, *Pseudotrigonidium* (*Pseudotrigonidium*) *ana* Anso and Desutter-Grandcolas, n. sp. is close to *P.* (*P.*) *aptera* (Desutter-Grandcolas, 1997c) by its small size, its very short FWs, in both males and females, the lack of tympanum, its striped coloration (head, pronotum and abdomen lightly coloured with yellow longitudinal bands, legs ringed with black brown), and its male genitalia. It can be separated from *P. aptera* by detailed shape of pseudepiphallic sclerite and parameres, the lack of a lateral "projection" (not shown in Desutter-Grandcolas 1997c, Fig. 20, but see Fig. 3.4A, B and compare with Fig. 3.4C, D), thin ectophophallic apodemes and arc (thick and wide in *P.* (*P.*) *aptera*), and the size and shape of the rami, widely separated from the pseudepiphallic sclerite and short (long and connected to pseudepiphallic sclerite in *P.* (*P.*) *aptera*). The female, unknown in *P.* (*P.*) *aptera*, is characterized by its ovipositor, much shorter than FIII, its copulatory papilla, made of a ventral sclerite only, more or less oval in shape (Fig. 3.4F-I).

Description. In addition to the characters indicated for the genus by Desutter-Grandcolas (1997c): Body with many long and strong setae; abdomen setose. Eyes highly protruding; separated from the subgenual suture by a distance greater than eye width. Fastigium longer than wide, wide on its whole length and only slightly wider at its base than at apex; not separated from the vertex by a transverse furrow. Median ocellus almost apical in position. Maxillary palpi short; article 3 much shorter than article 4, shorter than article 5; article 5 slightly widened, apically truncated. Scapes large, longer than wide. Pronotum slightly longer than wide; anterior margin slightly concave; posterior margin convex; LL narrowed posteriorly. TIII inner serrulation: no spine between the apical and the first subapical spur, 0-1 (females, mean 0.4) or 0 spine (male) between subapical spurs 1 and 2; 1-3 (females, mean 2) and 0 spine (male) between spurs 2 and 3; 2-5 (females, mean 3.6) and 3-4 (male, mean 3.5) spines between subapical spurs 3 and 4; 7-11 (females, mean 10) and 10-11 (male, mean 10.5) spines above subapical spur 4. TIII outer serrulation: no spine between apical and subapical spurs; 3-4 (females, mean 3.4) and 3 (male) spines between subapical spurs 1 and 2; 3-5 (females, mean 4.6) and 4 (male) spines between subapical spurs 2 and 3; 3-6 (females, mean 5) and 3 (male) spines between subapical spurs 3 and 4; 10-13 (females, mean 12) and 9 (male) spines above subapical spur 4. Tarsomeres III-1: 2-4 (females, mean 3.2) and 4 (male) outer and no inner spines, in addition to apical spines.

Coloration. Body and FIII striped yellow and brown, legs 1 and 2, and TIII ringed yellow and black (Fig. 3.5A). Head dorsum (Fig. 3.5C) light yellow with 4 longitudinal light brown lines, 2 median, wider ones extending anteriorly to fastigium tip, and narrowed before occiput, and 2 lateral ones bordering the inner margins on the eyes; antennal pits circled with black, separated from the inner angle of the eyes by a black spot prolonging a thick black line on antennal membrane; median ocellus circled with black. Face, cheeks and mouthparts ivory; the cheeks separated from the head dorsum by a wide brown band (Fig. 3.5D); face with a pair of wide, rounded black brown lines prolonged dorsally along the antennal pits and toward the median ocellus (Fig. 3.5B). Scapes light yellow with 2 longitudinal brown lines dorsally, the outer one slightly prolonged laterally and connected to a wide ventral brown fleck (Fig. 3.5B, C). Antennae light brown. Palpi light yellow with indistinct brown spots on outer sides of articles 3-5. Pronotum variegated yellow and brown; DD with a thin, yellow median line, variously prolonged on metanotum and abdominal tergites, and two thicker lateral ones not reaching posterior margin; anterior margin yellow, posterior margin light brown (Fig. 3.5C); LL dark brown with a yellow margin and a yellow spot in anterior angle (Fig. 3.5D); DD and

LL separated by a thin yellow curved line. FWs dark grey and whitish. PI, II light yellow with dark brown marks; FI, FII with two brown rings in distal half, in addition to a small apical one; TI, TII with 4 black brown rings separated by yellow basally and white apically; tarsomeres 1and 3 brown with white anterior half, except for black ventral margin; tarsomeres 2 dark brown; claws whitish. FIII striped yellow and brown on inner and outer sides; 2 longitudinal brown lines on outer side (Fig. 3.5E); TIII with 5 brown dorsal flecks and a black distal ring; spurs brown with whitish base and apex. Abdomen variegated yellow and brown, with 3 indistinct yellow lines dorsally; black laterally. Cerci light brown.

Male. Metanotum and tergites not glandular. FWs very short, not reaching metanotum posterior margin, and lateral only. Subgenital plate very long and wide, with a deep distal furrow; light yellow with brown dorsal margin.

Male genitalia. Fig. 3.4C, D. Size smaller than in *P.* (*P.*) *aptera*. General shape of phallic complex similar, but rami small, thin and not connected to pseudepiphallic sclerite; pseudepiphallic sclerite paired, each sclerite distinctly rounded on inner side and with a rounded apex about as wide along its whole length (Fig. 3.4D); no lateral projection (Fig. 3.4C); pseudepiphallic paramere bifid, but outer lobe straight and its apex acute (Fig. 3.4C).

Female. FWs as in the males. Subgenital plate wider than long; distal margin slightly concave (Fig. 3.4E). Ovipositor very short, a little more than half TIII length; apex as on Figure 3.5F.

Female genitalia. Copulatory papilla made of one ventral sclerite only (Fig. 3.4F). Spermathecal duct very wide basally, then abruptly very thin (Fig. 3.4G).

Juveniles. Young juveniles are very pale in coloration, with whitish stripes on the head and pronotum, and a white median line on the abdomen; their TIII are not serrulated.

Measurements (in mm).

	PronL	PronW	FWL	FIIIL	TIIIL	OL
Male holotype	1.7	1.7	0.3	7	6.5	-
Female allotype	2.1	1.9	0.5	8.1	7.5	4.2
Female paratypes	1.8-2.2	1.7-2	0.4-0.5	6.8-7.8	6.2-7.5	3.8-4.5
(mean, n=4)	(2.1)	(1.9)	(0.5)	(7.6, n=3)	(7.1, n=3)	(4.2)

Variation. The female PARIV2-65 is not identified for sure. It is somewhat bigger than the other females (PronL 2.2, PronW 2.1, FWL 0.5, FIIIL 8.3, TIIIL 7.9, OL 4.5). Its serrulation fits that of the other females (0, 2, 4 and 9 inner spines, and 3, 4, 5 and 10 outer spines respectively), but it has no inner spine, and 4 outer spines on tarsomere 1-III. Its FWs reach the metanotum distal margin. Also, its copulatory papilla has a slightly different shape, being more quadrate and deeply concave on median part; its spermathecal duct is thinner close to the papilla than in other individuals, between the papilla and the wider duct part (Fig. 3.4I). For comparison, the papillas of the females PAPE1-27 (Fig. 3.4H) and PGK4 (Fig. 3.4F) are much more similar.

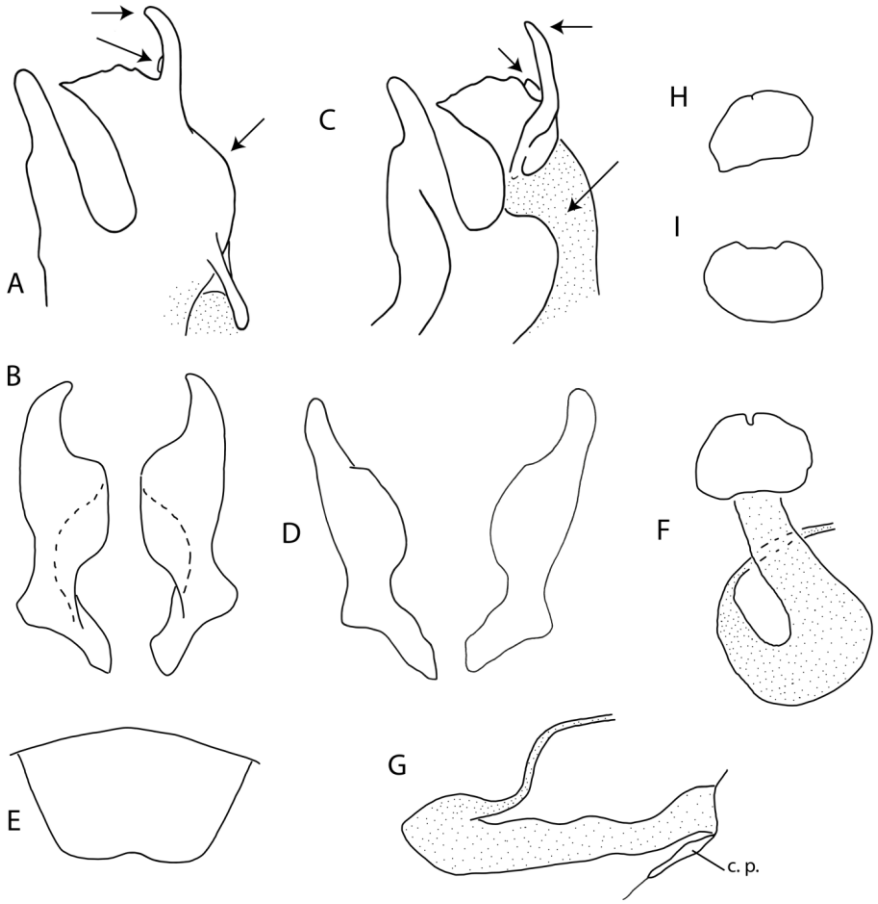

Figure 3.4. *Pseudotrigonidium Chopard, 1915. Pseudotrigonidium aptera Desutter-Grandcolas, 1997 (A, B) and Pseudotrigonidium ana Anso & Desutter-Grandcolas, n. sp. (C-I): male genitalia, pseudepiphallus in lateral view (A, C), dorsal valves in ventral view (B, D); female subgenital plate (E); female copulatory papilla, ventral (F, H, I), lateral (G), in females PGK-4 (F, G), PAPEP1-27 (H) and PARIV2-65 (I). Scales 1 mm. Abbreviations: see Material and methods.*

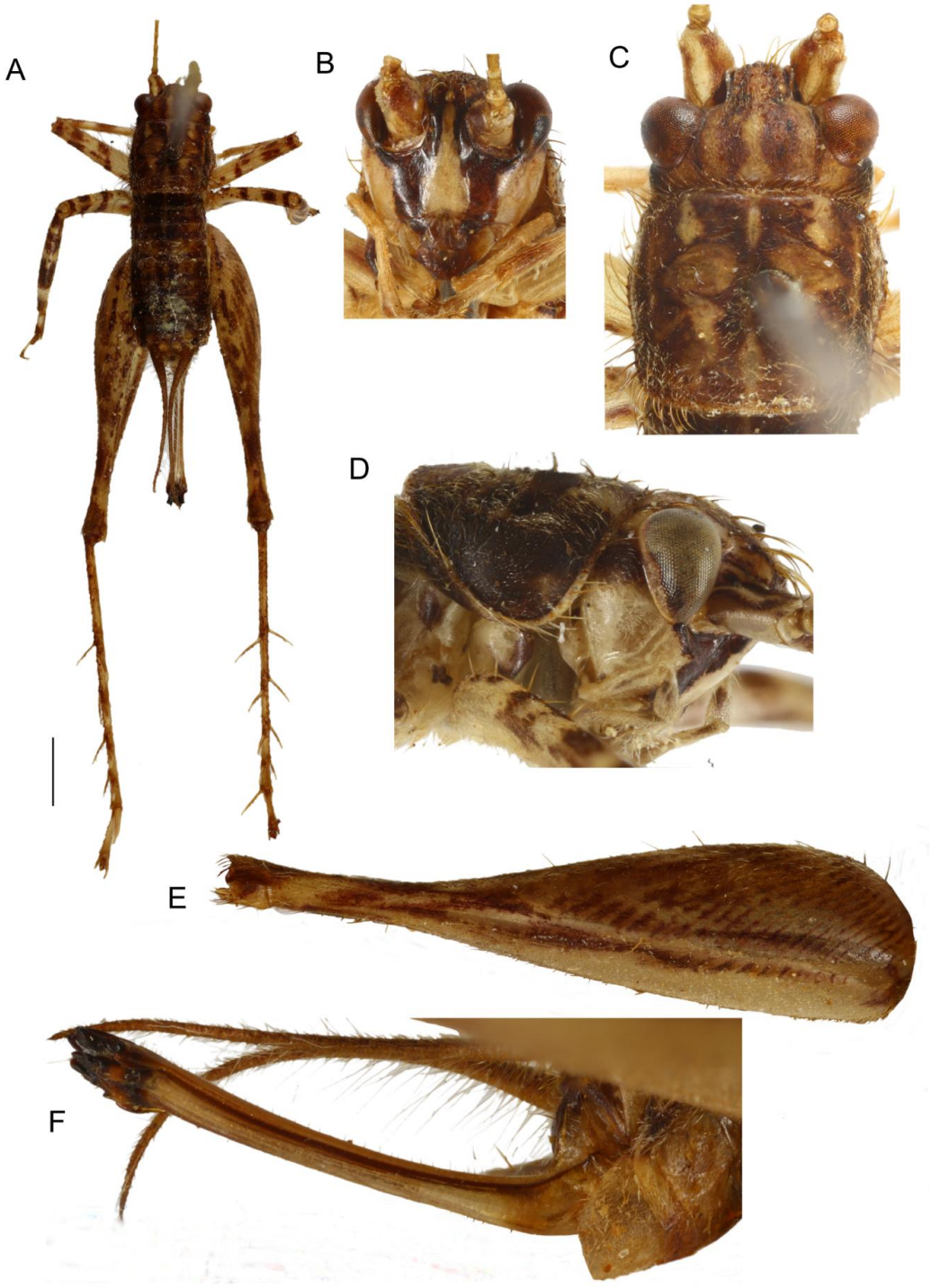

Figure 3.5. *Pseudotrigonidium ana Anso & Desutter-Grandcolas, n. sp., holotype (D) and allotype (A-C, E, F): body, dorsal view (A); face (B); head and pronotum in dorsal (C) and lateral (D) views; hind femur, outer side (E); ovipositor in lateral view (F). Scale 2mm.*

Family Gryllidae Laicharting, 1781

We use this family according to the phylogeny of Chintauan-Marquier *et al.* (2015), and the definition of Desutter-Grandcolas *et al.* (in prep.). Here, only the subfamilies Gryllinae Laicharting, 1781 and Podoscirtinae Saussure, 1878 are represented in the species at hand.

Subfamily Gryllinae Laicharting, 1781

Genus *Notosciobia* Chopard, 1915

Notosciobia Chopard, 1915: 140. Otte *et al.* 1987: 385.

Type species. *Notosciobia rouxi* Chopard, 1915.

Emended diagnosis. See Desutter-Grandcolas & Anso (submit.).

Distribution. Endemic to New Caledonia.

Remark. Three species group, the *nola*, *fausta* and *poya* groups, have been defined by Otte *et al.* (1987) according to male genitalia (dorsal cavity large in *nola* group, versus short in *fausta* and *poya* groups; pseudepiphallic parameres very long in *poya* group, inwardly turning apically in *fausta* group; pseudepiphallic sclerite distal margin V-shaped in *fausta* group, more roundly curved in the other two groups: see Otte *et al.*, 1987, Figs 7-11).

Notosciobia sp. affinis *paranola* Otte, 1987

(Figs 3.6A, B, 3.7)

Type locality. New Caledonia, Mt Koghi, west slope of Mt Bouo, tall forest.

Type material. Holotype: New Caledonia, Mt Koghi, west slope of Mt Bouo, tall forest, 1 male, 27.ii.1983, Alexander, Cade & Otte (ANSP).

Examined material. New Caledonia, Grande Terre, Goro, Le Trou, Pépinière, 22.27103° S 166.96355° E, paraforestier, 12.ii.2014, 1 male, fn PAPEP1-21, J. Anso (MNHN-EO-ENSIF3910), specimen without PIII, genitalia damaged.

Remark. The material examined resembles *N. paranola* Otte, 1987 by its large size and very dark coloration, the shape of male genitalia (pseudepiphallic sclerite with a rounded, very

shallow indentation apically; pseudepiphallic parameres not bifid: see Otte *et al.* 1987, Fig. 7) and male FW venation (see Otte *et al.* 1987, Fig 6I). Its differs from that species by its smaller size (see measurements), and details in coloration (head and antennae entirely black brown) and in male FW venation (fewer harp veins, mirror shape, stridulatory file with 195 teeth: see Fig. 3.6A, B). Whatever these characters, material at hand is not sufficient to describe a new species.

Measurements (in mm).

	PronL	PronW	FWL	FWw	TIIIL	File
Male examined	3.8	5.7	10.9	7.5	--	195

Calling song. Fig. 3.7. One specimen has been recorded, but could not be collected; one song bout was analyzed, and measurements were made on 11 eschemes (85 syllabes). At 24°C, the calling song of *Notosciobia sp. affinis paranola* consists of a repetition of echemes of 186.7 ± 7.6 s; each echeme is made of 4 syllables, with the following characteristics: syllable duration = 18.1 ± 3.1 ms; syllable period = 55.8 ± 26.1 ms; syllable duty cycle = 35.9 %; the dominant frequency is 4.9 ± 0.1 kHz. Song deposited in MNHN sound library (inventory number MNHN-SO-2016-2).

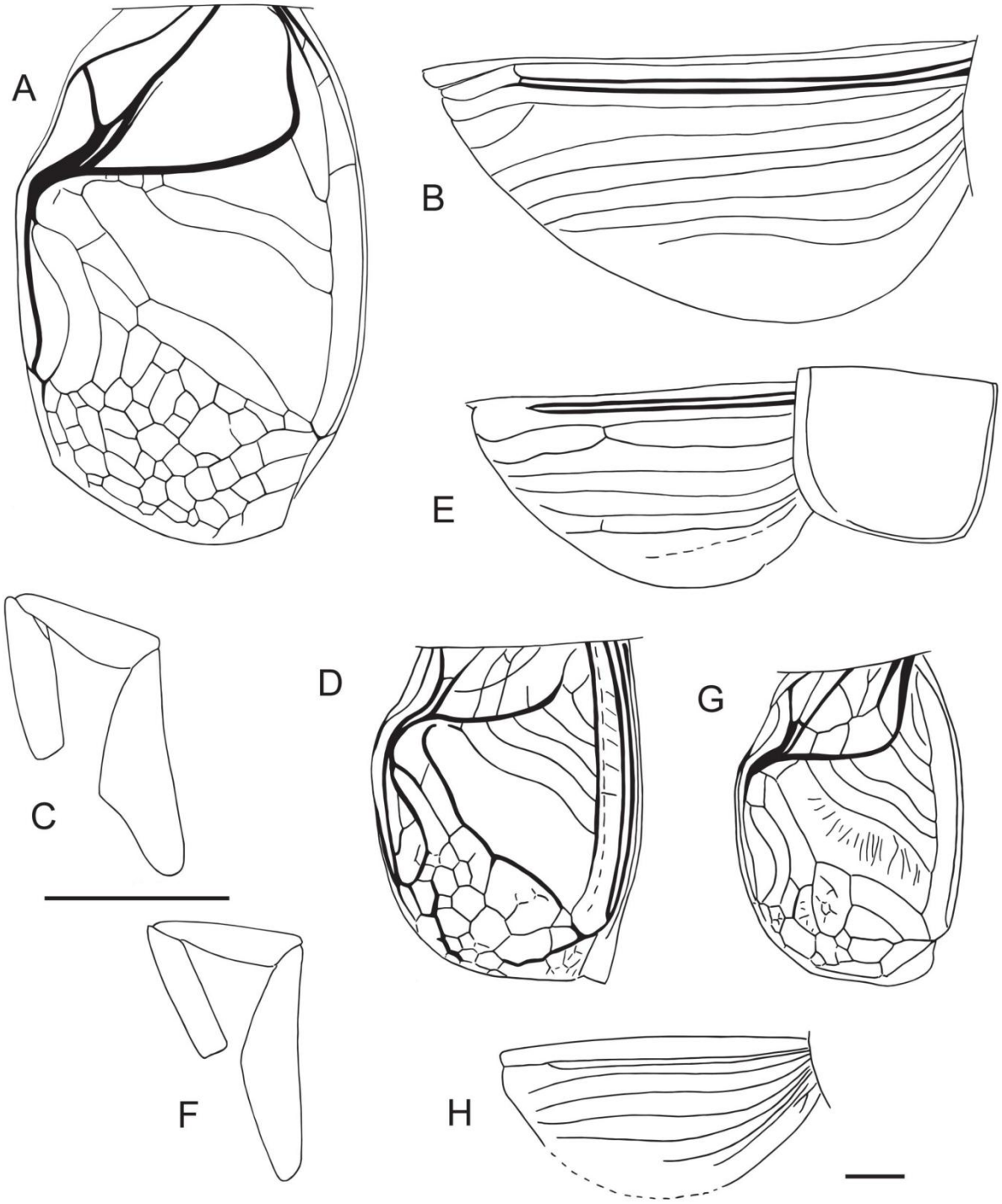

Figure 3.6. *Notosciobia Chopard, 1915. Notosciobia sp. affinis paranola Otte, 1987 (A, B), Notosciobia farino Anso & Desutter-Grandcolas, n. sp. (C-E) and Notosciobia minoris Anso & Desutter-Grandcolas, n. sp. (F-H): male FW, dorsal (A, D, G) and lateral (B, E, H) fields; maxillary palpus (C, F). Scales 1 mm.*

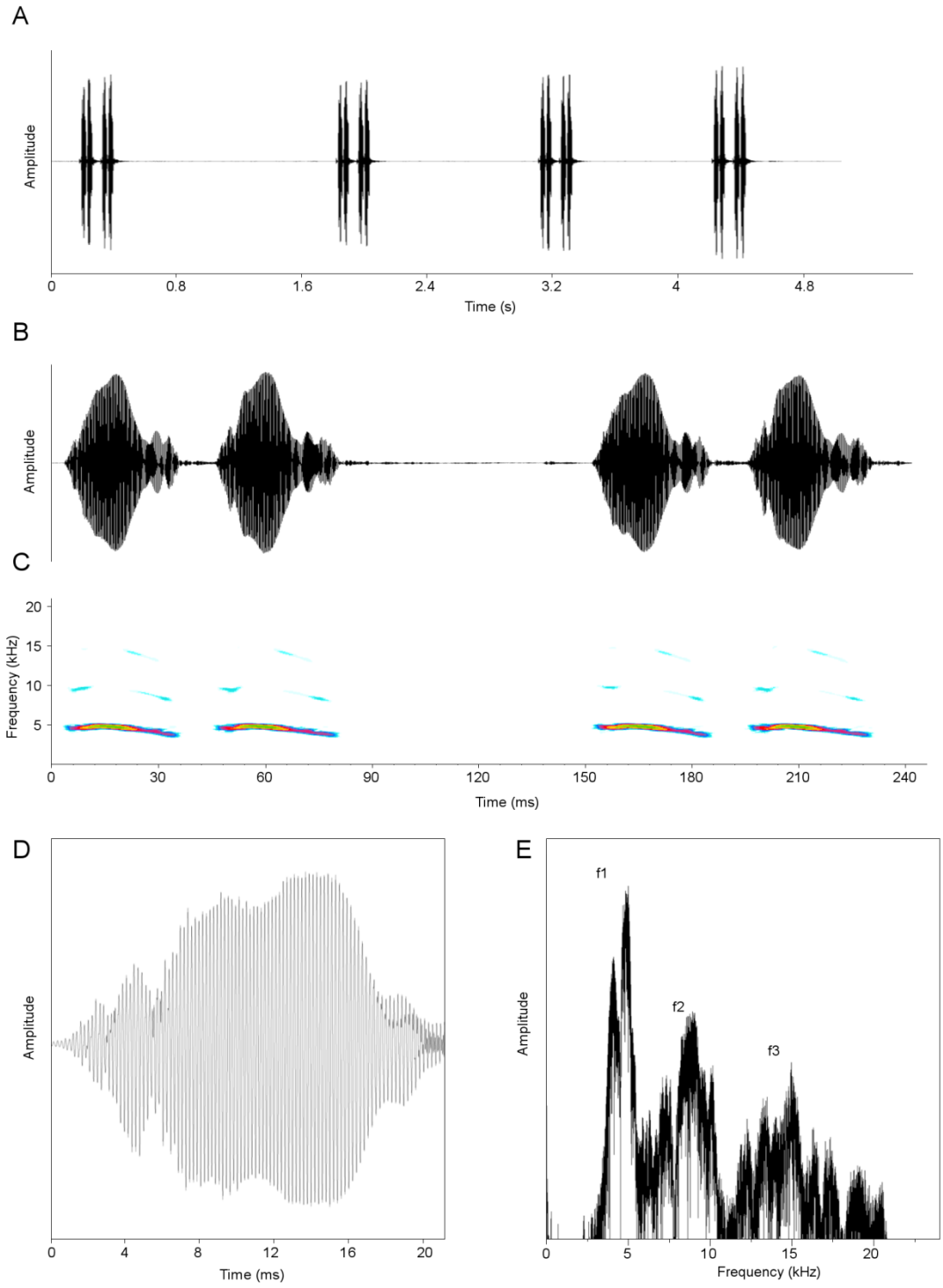

Figure 3.7. *Calling song of Notosciobia sp. affinis paranola Otte, 1987. Oscillogram of four successive echemes (A); detailed oscillogram (B) and sonogram (C) of two echemes; oscillogram of one syllable (D); logarithmic spectrogram of one syllable (E). Symbols: f1-f3, first (fundamental) to third harmonic frequencies.*

Notosciobia farino Anso and Desutter-Grandcolas, n. sp.

(Figs 3.6C-E, 3.8A-D, 3.9)

Type locality. New Caledonia, Farino.

Type material. Holotype: New Caledonia, Grande Terre, Farino, secondary forest, 21.65239° S 165.77844° E, 17.i.2013, by night, 1 male, fn NOU41-Fari1, leaf litter, recorded, J. Anso, MNHN-EO-ENSIF3628.

Etymology. Species named after type locality.

Distribution. Known from type locality only.

Diagnosis. *N. farino* Anso & Desutter-Grandcolas, n. sp. can be easily separated from other species of *Notosciobia* by its male genitalia (dorsal cavity small, as in *poya* and *fausta* group of species; pseudepiphallic sclerite very long compared to other species and raised dorsally before apex, its distal margin V-shaped as in *fausta* group; pseudepiphallic parameres very long, bifid at apex, with a ventral lobe directed inwardly as in the *fausta* group, and a dorsal lobe longer and straight: Fig. 3.6A, B). Other distinctive characters: size small for the genus, FW venation: harp with 3 sinuous, parallel veins, and two smaller additional ones, distributed regularly over file length; file with 65 stridulatory file (n=1).

Description. Species relatively small for the genus. In addition to the characters of the genus (Chopard 1915, Otte *et al.* 1987): Maxillary palpi: joint 4 slightly smaller than joint 3; joint 5 the longest, its apex very obliquely truncate at about one third of its lenght (Fig. 3.6C). DD anterior margin deeply concave. Tympana as in the genus (outer only, large, longer than wide). TI, TII apical spurs as in the genus (3 and 4 respectively, quite long). TIII apical spurs short and thick, the inner slightly longer; the median the longer on outer side; the dorsal the longer on inner side. TIII with 4 / 5 pairs of subapical spurs; not serrulated. Basitarsomere III long, squared; 3 – 5 (mean 4) inner and 4 outer dorsal spines, in additional to apical ones; spines larger toward basitarsus apex.

Coloration. Head, pronotum and FWs dark reddish brown, legs light yellowish, with golden setae. Head dorsum reddish brown, with a very thin light yellow line between the lateral ocelli, and then back to the occiput; scape yellow and brown; antennae brown; lateral ocelli

light yellow; face reddish brown, lighter around the eyes and along the subgenal and epistemal sutures; mouth parts yellowish and brown; palpi light yellow. Pronotum reddish brown, the pyriform inscriptions lighter and a thin longitudinal median furrow lighter; anterior margin black; lateral lobes reddish brown, widely lighter along anterior, ventral and posterior margins. Legs I and II light yellow, TI somewhat darker. Leg III light yellow, a brown fleck near the knee, longer on inner side than on dorsal side; TIII brown on ventral side. Spurs and spines yellow with black apex. Cerci light yellow.

Male. FWs short, not covering the whole abdomen; light brown, the lateral field darker, its lower margin widely borderd with white; veins brown, MA and MP yellow. Venation as on Fig. 3.6D; harp with 3 main veins, parallel and sinuous, and 2 smaller ones, all distributed regularly over file length; mirror separated from distal reticulation; apical field very short; lateral field (Fig. 6E) with 4 parallel, longitudinal veins, in addition to the two most dorsal ones, briefly anastomosed at about mid length. File with 65 small and rounded stridulatory teeth. Subgenital plate long and high, as in other species of the genus, going beyond FWs. Sternites and subgenital plate yellowish, darker on distal margin, the latter may be with brown basally. Supra anal plate distal part very narrow compared to its base; its base brown, its apex yellowish.

Male genitalia. Fig. 3.8A-D. Relatively small, especially the dorsal cavity, very low and not reaching rami mid length. Pseudepiphallic sclerite elongate distally, narrowed abruptly distally to the rami and then slightly and regularly toward the apex; lateral parts of apical margin elongate and raised dorsally, the median part of pseudepiphallus membranous and deep; apex raised dorsally, its distal margin shallow and V-shaped; pseudepiphallic parameres elongate, their outer margin thicker than their inner margin, their apex bifid, with a ventral lobe turned inwardly and a dorsal lobe longer and straight. Rami circular, nearly connected distally; distal part bifurcate, the dorsal branch much shorter than the ventral one.

Female. Unknown.

Measurements (in mm).

	PronL	PronW	FWL	FWw	FIIIL	FIIIw	TIIIL	tar1-IIIL	File
Male holotype	3.4	4.7	6.1	4.3	9.9	3.7	4.9	3.1	65

Habitat and life history traits. *Notosciobia farino* Anso & Desutter-Grandcolas, n. sp. lives in slightly open woodland. Males emit calling song on the ground during the night.

Calling song. Fig. 3.9. One specimen has been recorded and collected; one song bout was analyzed, and measurements made on 119 eschemes and 944 syllables. At 26.9°C, the calling song of *Notosciobia farino* Anso & Desutter-Grandcolas, n. sp. consists of a repetition of echemes of 120.2 ± 15.4 ms emitted every 753.1 ± 72.6 ms, with a duty cycle of 6.6 %; each echeme is made of 7.9 ± 1.6 syllables, with the following characteristics: syllable duration = 7 ± 1 ms; syllable period = 16.2 ± 8.1 ms; syllable duty cycle = 47.4 %; the dominant frequency is 4.1 ± 0.2 kHz and correspond to the fundamental frequency. Song deposited in MNHN sound library (inventory number MNHN-SO-2016-3).

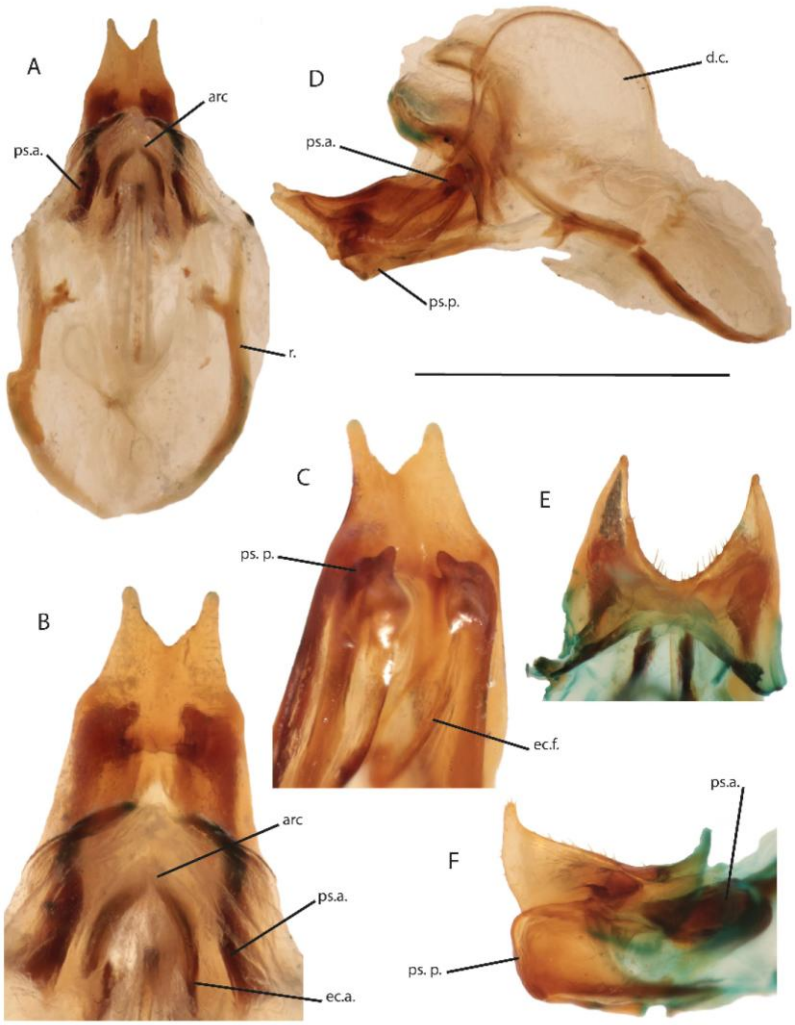

Figure 3.8. *Notosciobia Chopard, 1915. Notosciobia farino Anso & Desutter-Grandcolas, n. sp. (A-D) and Notosciobia minoris Anso & Desutter-Grandcolas, n. sp. (E-F): male genitalia, dorsal (A, B, E), ventral (C), lateral (D, F). Scale 0.5 mm (A, D); other figures magnified 1.75x bigger. Abbreviations: see Material and methods.*

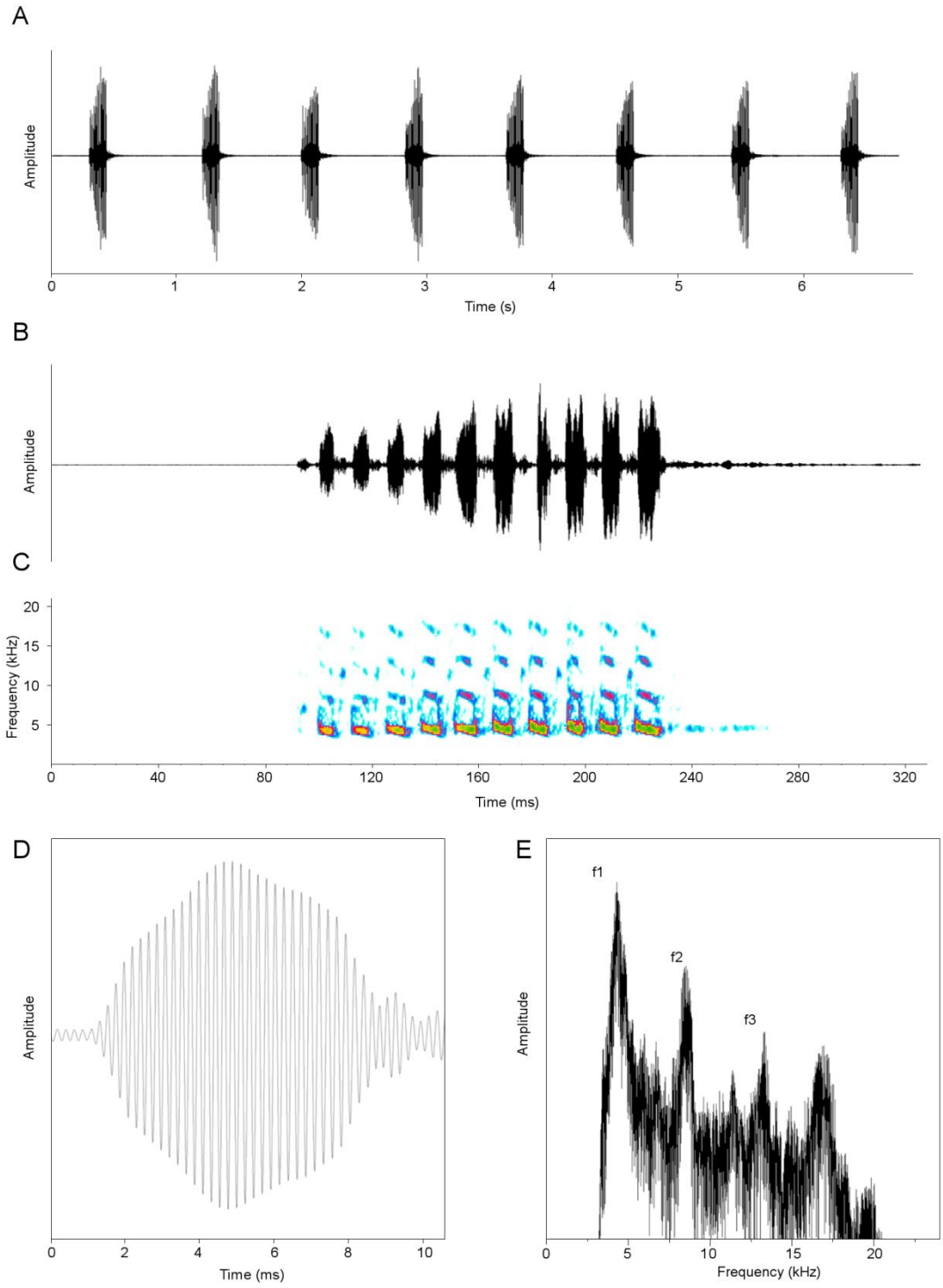

Figure 3.9. *Calling song of Notosciobia farino Anso & Desutter-Grandcolas, n. sp. Oscillogram of eight successive echemes (A); detailed oscillogram (B) and sonogram (C) of one echeme; oscillogram of one syllable (D); logarithmic spectrogram of one syllable (E). Symbols: f1-f3, first (fundamental) to third harmonic frequencies.*

Notosciobia minoris Anso and Desutter-Grandcolas, n. sp.

(Figs 3.6F-H, 3.8E-F, 3.10)

Type locality. New Caledonia, Grande Terre, Rivière bleue.

Type material. Holotype: New Caledonia, Grande Terre, Rivière blanche, paraforestier, 22.15280° S 166.68033° E, 19.iii.2014, by day, 1 male, fn PARIV1-54, leaf litter, J. Anso (MNHN-EO-ENSIF3627).

Other material. New Caledonia, Grande Terre, Rivière blanche, rainforest, 22.15142° S 166.68643° E, 17.iii.2014, at night, 1 juvenile, fn FORIV2-15, in leaf litter, J. Anso, MNHN.

Etymology. Species named after its very small size for the genus.

Distribution. New Caledonia, Grande Terre, Rivière bleue.

Diagnosis. *N. minoris* Anso & Desutter-Grandcolas, n. sp. resembles *N. hirsuta* (Otte, 1987) by the small size of its body and FIII, and by the numbers of inner and outer TIII subapical spurs. It differs however from *N. hirsuta* by its male genitalia, with a U-shaped pseudepiphallus more similar to *N. canala* Otte, 1987 (see Otte *et al.* 1987, Fig. 9, *nola* species group), and hook-like lateral sclerite close to *N. rex* Otte, 1987 (see Otte *et al.* 1987, Fig. 11).

Description. In addition to the characters of the genus (Chopard 1915, Otte *et al.* 1987). Size small for the genus. Maxillary palpi: thin; joint 4 slightly smaller than joint 3; joint 5 the longest, its apex very obliquely truncate at about half of its lengh (Fig. 3.6F). DD anterior margin deeply concave; pronotum narrowed distally. Tympana as in the genus (outer only, large, longer than wide). TI, TII apical spurs as in the genus (3 and 4 respectively, quite long). TIII apical spurs short and thick, the inner slightly longer; the median the longer on outer side; the dorsal the longer on inner side. TIII with 5 inner and 4 outer subapical spurs; not serrulated. Basitarsomere III long, squared; 4 – 5 (mean 4.5) inner and 5 – 6 (mean 5.5) outer dorsal spines, in additional to apical ones; spines larger toward basitarsus apex.

Coloration. Head, pronotum and FWs dark brown, legs dark yellowish, with brown setae. Head dorsum dark brown, with a very faint light yellow line between the lateral ocelli, and then back to the occiput; scape light brown and yellowish brown; antennae brown; lateral

ocelli light yellow; face brown, lighter under the eyes and the antennal pits; mouth parts light brown and yellowish brown; palpi yellowish, joint darker. Pronotum dark brown, including the pyriform inscriptions, the anterior margin and the lateral lobes. Legs yellowish, the tibiae and the knees darker. Femur III with a brown fleck near the knee, longer on inner side than on dorsal side, as in *N. farino* Anso & Desutter-Grandcolas, n. sp., and with dark oblique lines on outer sides; a distinct yellowish dorsal spot close to the knee. Spurs and spines yellowish with black apex. Cerci light dark yellowish.

Male. FWs covering almost completely the abdomen; dorsal field dark brown; lateral field darker, its lower margin widely borderd with white; veins brown, MA and MP somewhat lighter. Venation as on Fig. 3.6G; harp with 3 main veins, parallel and sinuous, and 2 smaller ones, clearly separated into two groups over file length, as in *N. hirsuta* Otte, 1987; mirror separated from distal reticulation; apical field almost lacking; lateral field with 5 parallel, longitudinal veins (Fig. 3.6H). File with about 81 small and rounded stridulatory teeth. Subgenital plate long and high, as in other species of the genus. Sternites and subgenital plate brown. Supra anal plate brown.

Male genitalia. Fig. 3.8E, F. Pseudepiphallic sclerite short; its distal margin U-shaped, deeply but roundly curved, compared to species of the *nola* group. Pseudepiphallic parameres very thick in lateral view; in ventral view, their inner margin extended innerly as in the *fausta* group.

Female. Unknown

Measurements (in mm).

	PronL	PronW	FIIIL	FIIIW	TIIIL	FWL
Male holotype	2.4	3.4	8.2	2.9	4.2	5.4

Habitat and life history traits. *N. minoris* Anso & Desutter-Grandcolas, n. sp. is a nocturnal species, who lives in a preforest vegetation, on litter.

Calling song. Fig. 3.10. One specimen has been recorded and collected; 69 echemes and 600 syllables from one song bout have been analyzed. At 26.5°C, the calling song of *N. minoris* consists of a repetition of echemes of 144 ± 8.5 ms emitted every 461.3 ± 49.3 ms, with a duty cycle of 12 %; each echeme is made of 8.7 ± 0.5 syllables, with the following characteristics:

syllable duration = 8.3 ± 1.1 ms; syllable period = 17.6 ± 1.8 ms; syllable duty cycle = 50.9 %; the dominant frequency is 4.1 kHz and correspond to the fundamental frequency. Song deposited in MNHN sound library (inventory number MNHN-SO-2016-4).

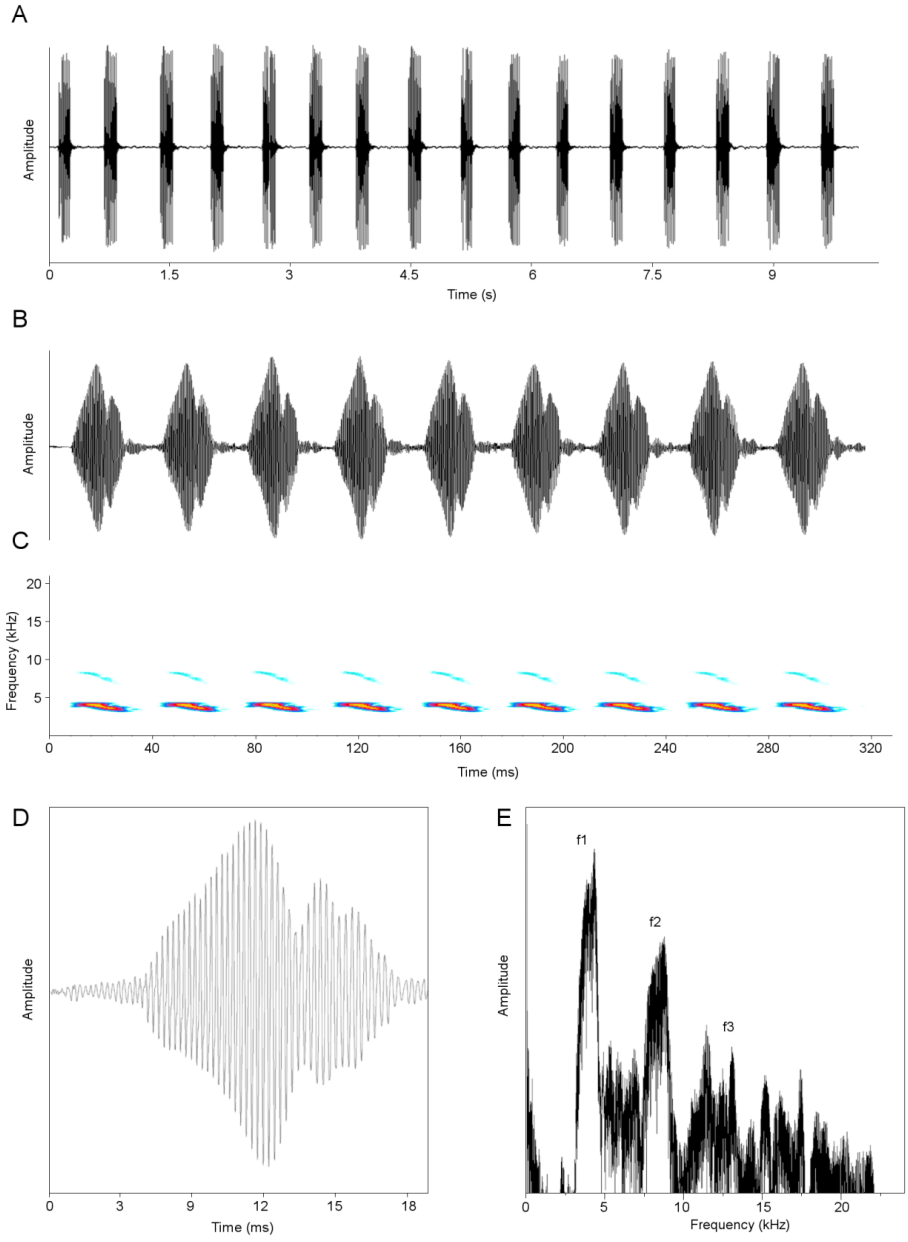

Figure 3.10. *Calling song of Notosciobia minoris Anso & Desutter-Grandcolas, n. sp. Oscillogram of 16 successive echemes (A); detailed oscillogram (B) and sonogram (C) of one echeme; oscillogram of one syllable (D); logarithmic spectrogram of one syllable (E). Symbols: f1-f3, first (fundamental) to third harmonic frequencies.*

Notosciobia sp. 1

Material examined: New Caledonia, Grande Terre, Pic du Grand Kaori, rainforest, 22.28535° S 166.89674° E, 12.ii.2013, 1 female, fn FOGK2-60, under dead trunk, J. Anso (MNHN). PI and II both missing.

We separate here one large female which coloration is quite dark (head, DD, abdomen), except for a light yellow band along LL dark margins and yellowish FIII (with brown knees and light brown oblique lines on outer and inner sides). Maxillary palpi with joint 4 shorter than joint 3; joint 5 the longest, very slightly widened distally and truncated at about one apical third. TIII have 5 inner and 5 outer subapical spurs, growing longer toward TIII apex; no subapical spines; 3 inner and 3 outer apical spurs, the dorsal the longest on inner side, the median slightly longer than the dorsal on outer sides; basitarsomere III with 4-5 inner and 5 outer dorsal spines, in addition to apica ones. female subgenital plate transverse, rounded distally; brown with light yellowish on its sides and along basal margin.

Measurements (in mm).

	PronL	PronW	FWL	FIIIL	FIIIw	TIIIL	tar1-IIIL	ovip
Female	4.2	5.1	0.6	12.8	4.2	7.5	3.8	3

Remark. Another juvenile of *Notosciobia* was found in the same place (FOGK1-36): it was found by day in a gallery under a stone, close to a scorpion that was in another gallery. Its coloration does not fit well that of the female of *Notosciobia* sp. 1.

Notosciobia sp. 2

(Fig. 3.11)

Locality. New Caledonia, Forêt Nord, paraforestier, 22.32259° S 166.93134° E, 5.x.2013, 1 male, recorded but not collected, J. Anso.

One of us (JA) recorded that species in one of our forest plot, but did not manage to catch it. We consequently describe its song without formally naming it to attest its presence in the

sampled locality. As the song significantly differs from all other known species of *Notosciobia* (JA, pers. obs.), it certainly represents a new species to be described later when specimens are collected.

Calling song. Fig. 3.11. Only one song of *Notosciobia* sp. 2 could be recorded in the field through ambient recording. At 16.3°C, it consists of a repetition of several echemes, with the following characteristics: syllable duration = 116.8 ± 21.6 ms; syllable period = 305.7 ± 57.7 ms; syllable duty cycle = 38.8%; the dominant frequency is 3.6 ± 0.2 kHz. The song file is not deposited in the MNHN sound library, as no specimen can be unambiguously associated to it.

Subfamily Podoscirtinae Saussure, 1878

Several genera of Podoscirtinae have been described for New Caledonia, i.e. *Adenopterus* Chopard, 1951, *Peltia* Gorochov, 1986, *Matuanus* Gorochov, 1986, *Archenopterus* Otte, 1987 and *Calscirtus* Otte, 1987. The genus *Aphonoides* Chopard, 1940 has also been mentioned for one species originating from the Loyalty islands (Otte *et al.* 1987), which has been transferred in the genus *Mistshenkoana* Gorochov, 1990 by Gorochov (2003).

Otte *et al.* (1987) synonymized *Peltia* with *Adenopterus*, while Gorochov (2003) considered *Archenopterus* and *Peltia* as subgenera of *Adenopterus*. None of these groups are in fact clearly monophyletic, as they are defined on male characters interpreted without a phylogenetic frame as "possible symplesiomorphy", or "resultant from parallel evolution", such as the presence/absence of the stridulum, the relative width of the FWs, partial fusion of tegminal veins, the presence/absence of tegminal glands, the width of pseudepiphallic parameres, etc, without exclusive combinations. The most obvious characters to separate these taxa, i.e. the stridulatory apparatus and tegminal glands, may be particularly labile, so that the supposed subgenera of *Adenopterus* may represent artefactual cuts within one widely diversified clade, and so be misleading. By contrast, the evolution of these characters, and of implicit behaviours, within one monophyletic entity may prove particularly interesting in a phylogenetic frame. A phylogenetic analysis of New Caledonian podoscirtines is then necessary to analyse the evolution of these structures, and settle their classification.

Meanwhile, from a taxonomic point of view, we will consider *Adenopterus* and *Archenopterus* as valid genera, as downgrading them as subgenera would just move the problem of their monophyly from one taxonomic level to another. We accept however the

synonymy of *Peltia* with *Adenopterus*, as the male genitalia of *Peltia roseola* Gorochov, 1986 are very similar to those of *Adenopterus* species.

Available molecular evidence (Chintauan-Marquier *et al.*, 2015) clearly separate *Calscirtus* from (*Matuanus* – (*Adenopterus* – *Archenopterus*)), attesting the distinctiveness of *Calscirtus* on one hand, and the close relationship between *Adenopterus* and *Archenopterus* on the other.

From the point of view of acoutic communication, *Calscirtus* and *Archenopterus* have a stridulatory apparatus and emit powerfull calling songs, while most *Adenopterus* do not. *Matuanus* has no complete stridulum, but some species, as *M. mirabilis* Desutter-Grandcolas, 1997, show a functional file and could produce an acoustic signal. To our knowledge, however, *Matuanus* behaviour has not been documented so far.

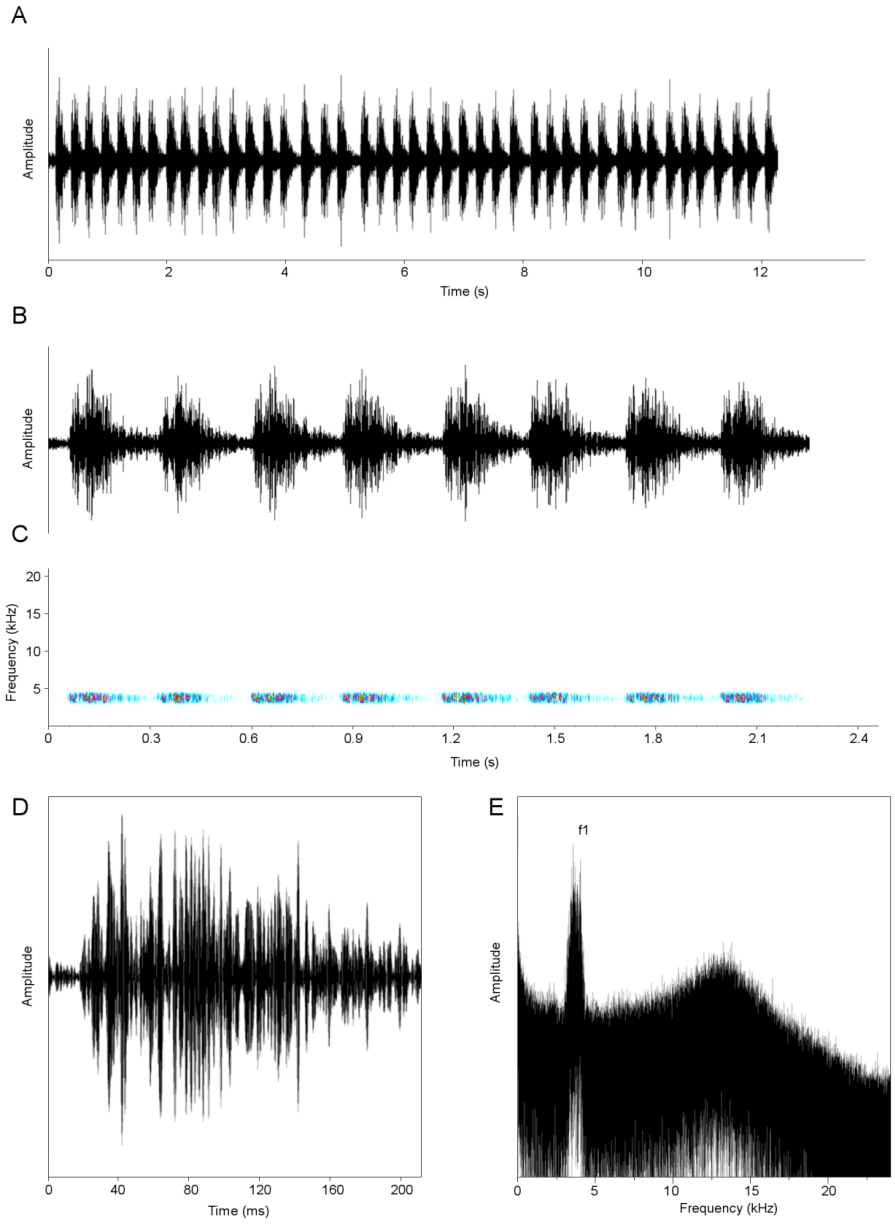

Figure 3.11. *Calling song of Notosciobia sp. 2. Oscillogram showing successive echemes (A); detailed oscillogram (B) and sonogram (C) of height echemes; oscillogram of one syllable (D); logarithmic spectrogram of one syllable (E). Symbols: f1, first (fundamental) harmonic frequency.*

Genus *Calscirtus* Otte, 1987

Calscirtus Otte in Otte *et al.*, 1987: 444.

Type species. *Calscirtus amoa* Otte, 1987.

Emended diagnosis. See Desutter-Grandcolas & Anso (submit.).

Distribution. Endemic to New Caledonia, with only three species known, from the Amoa river (*C. amoa* Otte, 1987), Oubatché in the North (*C. paniensis* Otte, 1987) and Timbia in the Southwest (*C. timbiensis* Otte, 1987). It is mentioned here for the first time from the east part of southern New Caledonia, and one new species is present in MNHN collections from Rivière bleue, close to *C. amoa*.

Remark. Using the shape of pseudepiphallus, Gorochov (2003) defined two subgenera: 1/ *Calscirtus Calscirtus*, with a long and narrow pseudepiphallic sclerite; this group includes *C. amoa* Otte, 1987; 2/ *Calscirtus Trellescirtus*, with a short and rounded pseudepiphallic sclerite, for all the other species of the genus. These groups will have to be checked for their monophyly.

Calscirtus (Calscirtus) amoa Otte, 1987

(Figs 3.12, 3.13)

Calscirtus amoa Otte in Otte *et al*., 1987: 444.

Calscirtus (*Calscirtus*) *amoa*, Gorochov 2003: 301.

Type locality. New Caledonia, Amoa river, 3 km west of main road, near Poindimié.

Type material. Holotype: New Caledonia, Amoa river, 3 km west of main road, near Poindimié, 3.iii.1983, 1 male, Alexander, Cade & Otte (ANSP).

Examined material. New Caledonia, Grande Terre, Rivière blanche, rainforest, 22.15142° S 166.68643° E, 19.iii.2014, at night, 1 male, fn FORIV2-40, on vegetation, 150 cm high, J. Anso rec., L. Desutter-Grandcolas det., MNHN.

New Caledonia, Grande Terre, Mont Panié, 20.62012° S 164.78020° E, 650 m, 20-27-v.2014, 1 male, on leaf, E. Bourguet rec., L. Desutter-Grandcolas det., MNHN.

New Caledonia, Grande Terre, Pic Grand Kaori, paraforestier, 22.28000° S 166.89383° E, 10.vii.2013, by night, 1 female, NOU25, on vegetation, 70cm high, J. Anso rec., L. Desutter-Grandcolas det., MNHN.

New Caledonia, Pic Ninga, 3.vi.2009, jour, 1 male, fn RN248, branche morte en forêt, diam. 3 cm, T. Robillard rec. and det.

New Caledonia, 4 km W Col d'Amieu, N La Foa, 690m, Mé Aréto, S21°36'14,8" E165°46'26,6", 1.i.1997, nuit, 1 male, fn15, sur plante, forêt sempervirente, Echantillon moléculaire LDG 219; id., 27.iii.1994, 1 male, 1 female, dans branche morte, L. Desutter-Grandcolas rec. and det. MNHN.

New Caledonia, Nouméa, Monts Koghis, 500m, forêt sempervirente, 10.ii.1994, nuit, 1 male, fn 69, sur plante, L. Desutter-Grandcolas rec. and det. MNHN.

Emended diagnosis. According to Otte *et al.* (1987), and in addition to the characters of the genus, TIII outer subapical spurs set into TIII apical half; basitarsomere III with 2 inner and 3 outer spines (including apical spines); HW equal to FW length plus half pronotum length; coloration: face and cheeks very pale, DD variegated pale and ivory, LL entirely pale, FIII with numerous pale brown oblique strips. **Male.** FW apical field shorter than mirror length; subgenital plate emarginate at distal end. Male genitalia: pseudepiphallus deeply grooved at apex.

Other characters: *C. amoa* is the smallest known species of the genus. Male stridulatory file with 109 to 128 teeth, mean 119 (one male from Koghis, with 135 teeth). Male and female subgenital plates yellow along dorso lateral margins. Females: Subgenital plate with an oval glandular area on each lateral flap (Fig. 3.13). Ovipositor longer than FIII in all but one examined specimen. Female genitalia: copulatory papilla small, with a sclerotized ring and a short ventral, sclerotized plate (see Desutter-Grandcolas 1997d, Fig. 38).

Complements of description. We give here a complete description of male genitalia and TIII serrulation in examined specimens.

TIII serrulated on inner and outer sides; outer spines small, especially those above the subapical spurs; inner spines somewhat bigger, but always small compared to subapical spurs,

the spine just above each subapical spur somewhat larger than the other spines, less than one third the size of the spurs. TIII inner serrulation: no spine between apical and subapical spurs; 1 spine in males, 0 – 1 spine (mean 0.7) in females between subapical spurs 1 and 2; 1-2 spines (mean 1.5 in males, 1.1 in females) between subapical spurs 2 and 3; 2 spines in males, 1 - 2 spines (mean 1.2) in females between subapical spurs 3 and 4; 1-2 (mean 1.9) spines in males, 2 spines in female between subapical spurs 4 and 5; 7 - 10 spines (mean 8.3) in males, 4 – 10 spines (mean 6.8) in females above subapical spur 5. TIII outer serrulation: no spine between apical and subapical spurs; 1 - 2 spines (mean 1.1) in males, 0-1 (mean 0.9) in females between subapical spurs 1 and 2; 2 (in males), 1 – 2 spines (mean 1.4) in females between subapical spurs 2 and 3; 2 – 3 spines (mean 2.3) in males, 2 spines in females between subapical spurs 3 and 4; 2 - 3 spines (mean 2.5) in males, 2 spines in females between subapical spurs 4 and 5; 9-13 spines (mean 10.8) in males, 8 - 11 spines (mean 9.4) in female above subapical spur 3. Tarsomeres III-1: 2 - 3 outer spines (mean 2.1) in males, 2 outer spines in females, and 1 – 2 inner spines (mean 1.1) in males, 0 – 1 spine (mean 0.9) in females, in addition to apical spines.

Male genitalia. Fig. 12. Pseudepiphallic sclerite very long and relatively narrowed; its apex deeply spilt into two flat lobes, which apex is protruding dorsally as a short, bifid hook; ventral ornementation as a pair of spiny membranous lobes located on each side of ectophallic fold apex; pseudepiphallic sclerite well-prolonged anteriorly, reaching and being articulated with the rami; rami short, but with a very long apodeme, connected to the dorsal proximal margin of pseudepiphallic sclerite; pseudepiphallic parameres asymmetrical, the right one produced as a flat, bifid lamella, and the left one almost the same width over its whole length; ectophallic fold not as long and thin as in the *paniensis* group of species, not reaching the pseudepiphallic sclerite distal margin, but with well-developed, partly sclerotized margins; fold apex thin and membranous; fold basis surrounded by ectophallic sclerotization; ectophallic apodemes short but wide, "foliaceous"; endophallic sclerite asymmetrical, connected to a long crest-like apodeme.

Variation. The males at hand cannot be separated with certainty from *C. amoa* by size, coloration, TIII spurs and serrulation, although some specimens look paler (part of Me Aréto specimens), but they show characters that could be either intraspecific variation, or characters of one or several new species close to *C. amoa*: first, their subgenital plates are longitudinally furrowed over their distal half (and not only "distally" as mentioned by Otte *et al.* (1987) in *C. amoa* description); second, while their male genitalia have the same general structure (see

above), they show variation in the shape of the right pseudepiphallic paramere, and in the shape of distal pseudepiphallic structures (see Fig. 3.13A-J). No data are available about their calling songs, but the status of these specimens will have to be reconsidered with additional information, acoustic or molecular, to precise the definition and distribution of *C. amoa*.

Measurements (in mm).

	iod	PronL	PronWa	PronWp	FWL	FWw	HWL	FIIIL	FIIIw	TIIIL	File
Male FORIV2n°40	1.6	4	3.3	4.6	12.4	4.5	13.5	12.3	3.3	10.6	109
Male Mé Aréto	1.7	3.9	3.1	4.5	13.5	4.4	14.5	11.8	3.2	9.6	121
Male Panié	1.6	3.9	3	4.2	15.2	4.3	16.2	11.3	3.3	9.7	128
Male fn15	1.5	4	3.3	4.5	14.8	4.2	15.6	11	3.7	9.3	121
Male Pic Ninga	1.7	3.8	3.1	4.1	14.5	4.2	15.2	12	3.4	9.8	116
mean (n=5)	1.6	3.9	3.2	4.4	14.1	4.3	15	11.7	3.4	9.8	119
Male Koghis	1.6	4	3.4	4.3	15.6	4.4	16.8	11.8	3.4	10	135
											OL
Female Mé Aréto 2703	1.9	4.7	3.6	4.2	15.8	--	16.6	12.3	3.6	10.6	13.7
Female Me Areto 0101, fn11	1.9	4.4	3.8	5	17.2	--	18.2	13.2	3.9	10.8	14.8
Female Me Areto 0101, fn8	1.9	4.7	3.8	4.9	17	--	17.5	13.4	3.9	10.6	14.5
Female Col Amieu	1.8	4.7	3.5	4.9	16.1	--	17.1	13.3	3.8	11.3	15.1
mean (n=4)	1.9	4.6	3.7	4.8	16.5	--	17.4	13.1	3.8	10.8	14.5
Female Grand Kaori	2	4.6	4.2	5.2	17.5	--	18.7	13.7	4.1	11.7	12.1

Habitat and life history traits. *Calscirtus amoa* Otte, 1987 lives in forested habitat. Males and females were found in rainforest and open forest, usually on vegetation at night. One male and one female juveniles were found together sheltering in a hollow branch laying on the ground in forest, and raised to adulhood in laboratory.

Calling song. Unknown.

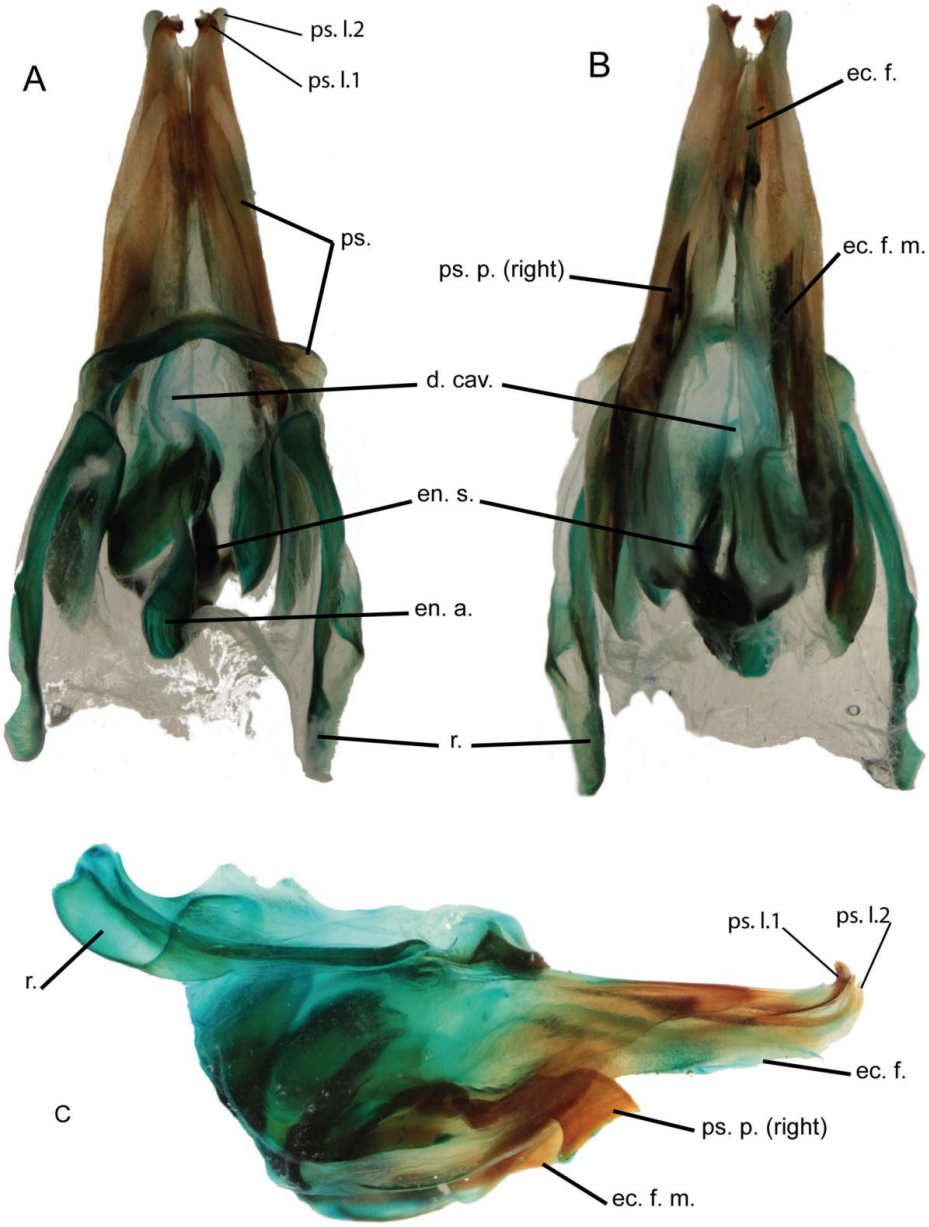

Figure 3.12. *Calscirtus amoa Otte, 1987. Specimen FORIV2-40 from Rivière bleue: male genitalia, dorsal (A), ventral (B), lateral (C). Abbreviations: see Material and methods.*

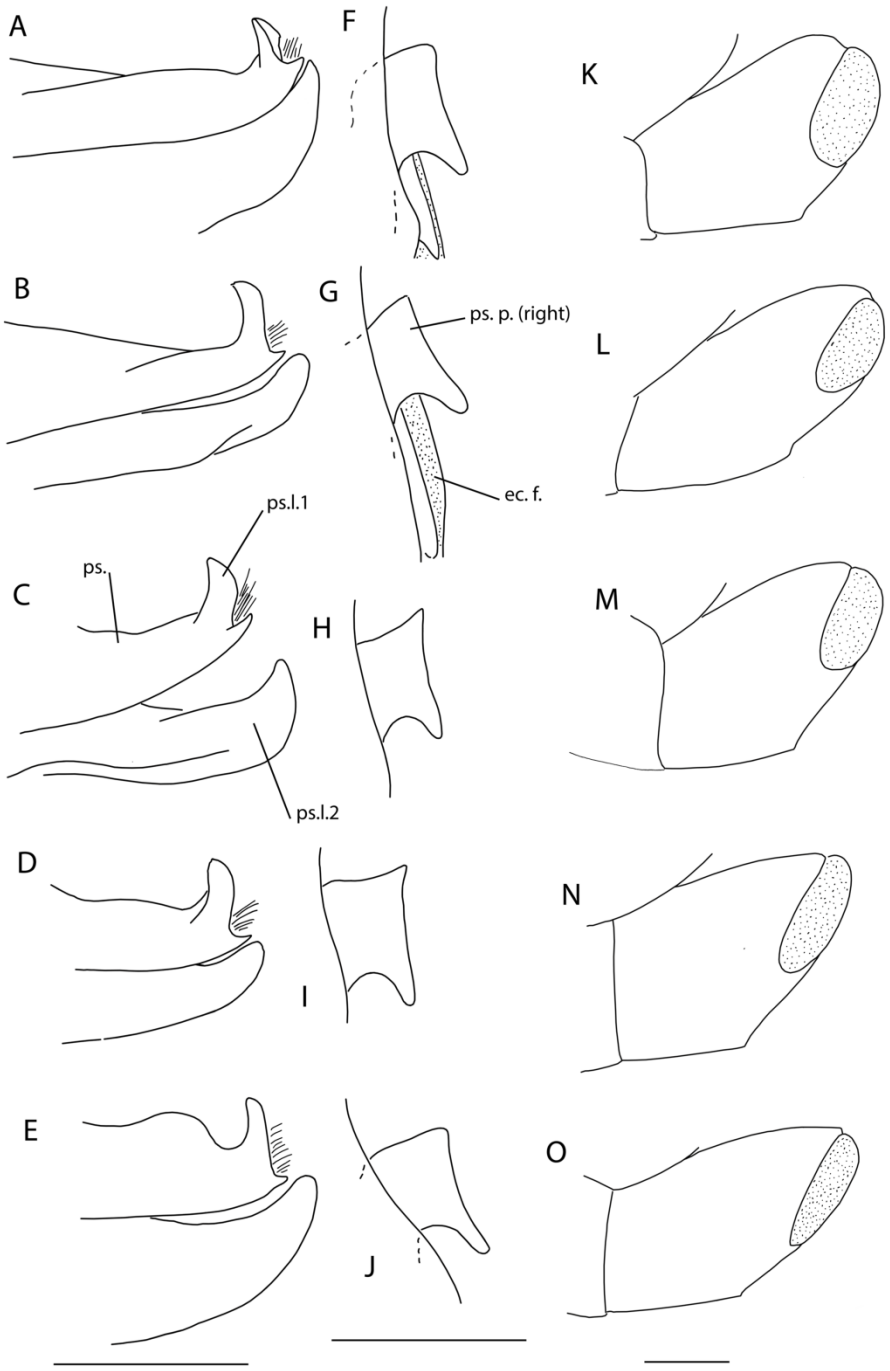

Figure 3.13. *Calscirtus amoa Otte, 1987. Variation in male (A-J) and female (K-O) genitalia: lateral view of pseudepiphallic apex (A-E) and right pseudepiphallic paramere (F-J), and female subgenital plate, lateral (K-O). Examined specimens: males from Rivière bleue (A, F), Me Areto (B, G), Mont Panié (C, H), Col d'Amieu (D, I), Pic Ninga (E, J); females from Pic du Grand Kaori (K), Me areto 27.iii (L), 0101 fn 11 (M), 0101 fn 8 (N) and Col d'Amieu (O). Scales 0.5 mm (A-E), 1 mm (F-O). Abbreviations: see Material and methods.*

Calscirtus (*Trellescirtus*) *magnus* Desutter-Grandcolas & Anso, n. sp.

(Figs 14A-H, 15A-E, 16)

Type locality. New Caledonia, Grande Terre, Pic du Grand Kaori.

Type material. Holotype: New Caledonia, Grande Terre, Pic du Grand Kaori, maquis close to rainforest, 22.28460° S 166.89436° E, 10.vii.2013, by day, 1 male, fn NOU32, on vegetation, hors parcelle GK1, J. Anso (MNHN-EO-ENSIF3629). **Allotype**: New Caledonia, Grande Terre, Rivière blanche, rainforest, 22.15142° S 166.68643° E, 19.iii.2014, at night, 1 female, fn FORIV2-39, on trunk, 150 cm high, J. Anso (MNHN-EO-ENSIF3630).

Diagnosis. Within the genus, species characterized by its very big size, coloration, female subgenital plate, and male and female genitalia. Its resembles *C. paniensis* Otte, 1987 by the number of outer subapical spurs on TIII (only 3, see Otte *et al.* 1987, Fig. 48C which represent the TIII outer side as shown by the apical spurs, *contra* Otte *et al.* 1987, p. 444) and its large size (FIII, 17mm in *C. paniensis*), and it resembles both *C. paniensis* and *C. timbiensis* Otte, 1987 by its male genitalia (pseudepiphallic sclerite very wide, rounded, pseudepiphallic parameres symmetrical). It can be separated from both species by details of male genitalia (shape of paramere apex and pseudepiphallic distal lobes: compare Fig. 14 and Otte *et al.* 1987, Fig. 49; perhaps, ventral ornementation of pseudepiphallic sclerite (not shown in *C. paniensis* and *C. timbiensis*). Stridulatory file with 80 teeth. Female (unknown in *C. paniensis* and *C. timbiensis*): FWs very long; subgenital plate with a disto-apical area greatly inflated and with numerous short setae; ovipositor longer than FIII; copulatory papilla with a narrow ring-shaped distal part.

Description.

In addition to the characters listed above. Head dorsum rounded behind the eyes, more flat between the eyes; fastigium slightly below the level of head dorsum, without a distinct limit. Fastigium long and very narrow, less than half scape width; with a longitudinal furrow over nearly its whole length. Ocelli in almost an equilateral triangle; lateral ocelli very large; median ocelli tiny, located at the base of fastigium furrow, far from fastigium apex. Scapes large, somewhat longer than wide. Antennae thick, their articles in proximal length very short. Eyes slightly protruding. Maxillary palpi very short (Fig. 14A); joint 4 smaller than joint 3;

joint 5 the longest, truncated on almost its whole inner side; thicker along its upper margin. Pronotum cylindrical, but slightly wider than long; anterior margin deeply concave. **Legs.** TI with one inner and one outer tympanum, small, dejected ventrally; TI distinctly inflated and squared from the upper limit of the tympana toward tibia distal third; three small apical spurs, set in a triangle; FI greatly widened. TII with four very short apical spurs, the dorsal ones migrated toward the ventral ones; TII somewhat inflated, but less than TI, and rounded; FII not widened. FIII not particularly widened, without a distal filiform part. TIII flattened dorsally; with three inner and three outer, short, apical spurs; dorsal the longest on inner side; median the longest on outer side. TIII (Fig. 14B, C) with three outer and five inner subapical spurs, the outer located close to TIII apex, the inner distributed over more than TIII half length; outer subapical spurs 2 and 3 distinctly longer than all other subapical spurs. TIII serrulated on inner and outer sides; outer spines small, especially those above the subapical spurs; inner spines bigger, the spine just above each subapical spur very large, about half the size of the spurs. TIII inner serrulation: no spine between apical and subapical spurs; 1 spine between subapical spurs 1 and 2; 2 spines between subapical spurs 2 and 3; 3 spines in male, 2 spines in female between subapical spurs 3 and 4; 2 -3 (mean 2.5) spines in male, 2 spines in female between subapical spurs 4 and 5; 8 spines above subapical spur 5. TIII outer serrulation: no spine between apical and subapical spurs; 1 spine between subapical spurs 1 and 2; 2 (in male), 1 (in female) spine(s) between subapical spurs 2 and 3; 24-26 spines (mean 25) in male, 23 spines in female above subapical spur 3. Tarsomeres III-1: 1 outer spine and no inner spine, in both male and female, in addition to apical spines. FWs longer than the abdomen in both males and females; HWs shortly longer than HWs, extending beyond FWs by more (male) or less (female) than half pronotum length. Cerci not very long, shorter than FIII.

Coloration. Yellowish brown, uniform; more light ochre brown and homogeneous in female allotype than in male holotype; shiny. Head dorsum yellowish brown, with indistinct short yellow lines; fastigium brown basally, with light yellow ocelli, and dark brown furrow. Eyes grey, their inner margin light yellow. Face and cheeks lighter, mouthparts partly ivory. Antennae brown, each article with a yellow upper limit. Maxillary palpi light yellowish. Pronotum light yellowish brown, the lateral lobe light yellow along its lower and anterior margins. Legs all light yellowish brown, except hind knees and TIII, dark brown; apical and subapical spurs all yellowish brown; TIII and its serrulation dark brown, making a clear contrast with the spurs. Cerci light yellowish brown.

Male. Metanotum and tergites without distinct glandular structures. FWs very long and narrow; light yellowish brown, the veins yellow, except for the veins of the stridulum, light brown. Stridulatory apparatus complete: harp with 9 oblique veins, distributed irregularly over file length (Fig. 14D); mirror long and narrow, its anterior part narrow and long (Fig. 14D), its crossing vein more straight, and less curved basally. Stridulatory file with 80 teeth (n=1). Subgenital plate long, distinctly and regularly narrowed toward apex; a short medio-longitudinal furrow on apical part and a short crest on each apical margin.

Male genitalia. Fig. 15A-E. Genitalia that can be evaginated, as in many Podoscirtinae. Pseudepiphallic sclerite anterior margin plicated dorsally (Fig. 15C); pseudepiphallic sclerite distal part elongate, wide and rounded, with a strong crest on each side (Fig. 15C); apex (Fig. 15A) narrow, subdivided into two long, flat and sclerotized lobes, hardly separated along their whole length, and each bearing a subdistal dorsal tooth (Fig. 15C); both teeth close together dorsally; apex ventral side with a pair of distal areas ornemented with many, strong teeth (Fig. 15D, E). Rami made of two structures: a short and wide, true "ramal sclerite", well-separated from the pseudepiphallic sclerite, and a long apodeme that runs along this ramal-sclerite and is prolonged toward the pseudepiphallic sclerite (Fig. 15C). Pseudepiphallic parameres symmetrical, elongate, extending beyong pseudepiphallic sclerite (Fig. 15A, B); parameres having the shape of a long and narrow plate, with a lateral tooth at about mid length. Epi-ectophallic invagination without arc (Fig. 15A). Ectophallic apodemes short, hardly extending beyong pseudepiphallic sclerite apical margin. Ectophallic fold long and thin, extending beyond pseudepiphallic sclerite (Fig. 15A, B); sclerotized ventrally with a pair of long and thin sclerites; dorsally connected to the pseudepiphallus by a strongly sclerotized plate (Fig. 15D). Endophallic sclerite 3-prongs (Fig. 15B), raised as a strongly sclerotized structure; on each side, endophallic sclerite connected to a pair of long sclerites, one directed backwards that stops before the ventral sclerotization of the ectophallic fold, and one more apical and more lateral that stops before the base of the pseudepiphallic parameres and is covered by a membranous fold (Fig. 15B). Endophallic apodeme crest like. Dorsal cavity shallow if any. Ventral valves dejected at the level of the rami (Fig. 15B).

Female. Larger than male. FWs longer than abdomen; venation with 13 longitudinal, parallel veins, separated by many transverse veins delimiting squared cells. HWs longer than FWs by less than pronotum half length. FWs light ochre brown, veins yellow. Subgenital plate deeply emarginate, surrounding the ovipositor (Fig. 14E, F); distal part greatly inflating and with

many short setae, probably glandular. Ovipositor longer than FIII, strongly curved; apex very slightly widened ventrally, with several longitudinal, parallel crests.

Female genitalia. Copulatory papilla very small and flat; with a distal circular sclerite extended by a short sclerotized plate; spermathecal duct emerging from the membrane inside the distal ring (Fig. 14G, H).

Habitat and life history traits. *Calscirtus magnus* Desutter-Grandcolas & Anso, n. sp. lives in forested habitat. Males emit their calling song at night in the highest strata of rainforest and preforest vegetation. During the day, males remain silent, as attested by soundscape recording. The male collected could have fallen from near-by trees in lower vegetation because of high wind.

Calling song. Fig. 16. *Calscirtus (Trellescirtus) magnus* Desutter-Grandcolas & Anso, n. sp. is one of the dominant singer in the canopy with *Archenopterus bouensis* Otte 1987 (see infra), as attested by soundscape recordings. It is difficult to catch, even though it can be observed sometimes during full moon or in forest edges lower on trees. One song could be isolated from soundscape recording at Pic du Grand Kaori and analyzed. At 18.7°C, the calling song of *Calscirtus* (*Trellescirtus*) *magnus* Desutter-Grandcolas & Anso, n. sp. consists of a repetition of echemes of 0.62 s; each echeme is made of 12 syllables, with the following characteristics: syllable duration = 38.5 ± 4.2 ms; syllable period = 52.5 ± 7 ms; syllable duty cycle = 76.9%; the dominant frequency is 3.2 kHz. Song deposited in MNHN sound library (inventory number MNHN-SO-2016-5).

Measurements (in mm).

	iod	PronL	PronWa	PronWp	FWL
Male holotype	1.7	5.2	4.8	5.8	23.6
Female allotype	2	6.9	6.5	7.2	33.2

	FWW	HWL	FIIIL	FIIIw	TIIIL	OL
Male holotype	5.2	26.4	16.6	4.1	14.1	-
Female allotype	6.4	35.6	22.7	5.3	18.7	25.8

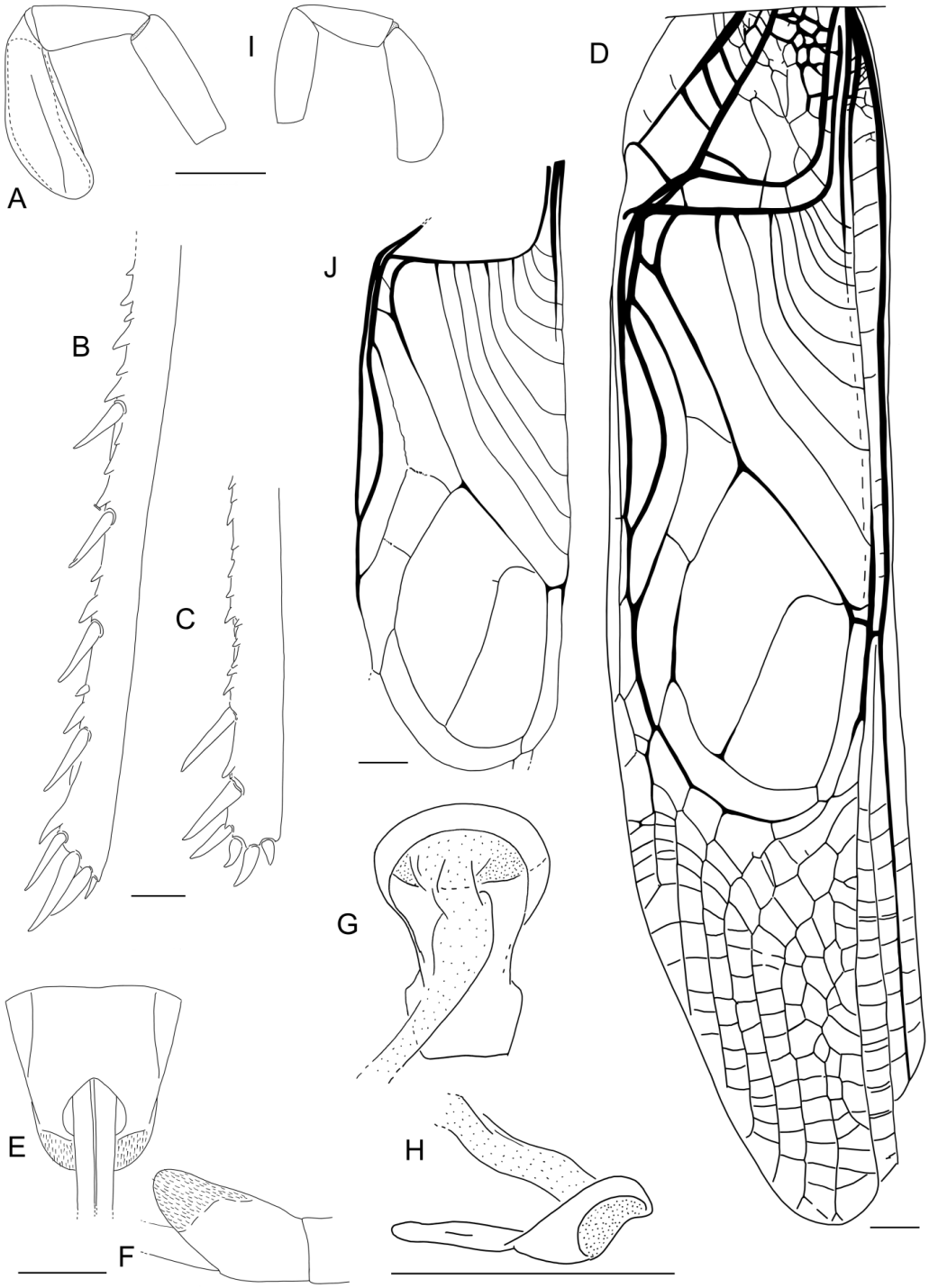

Figure 3.14. *Calscirtus Otte, 1987. Calscirtus magnus Anso & Desutter-Grandcolas, n. sp. (A-H) and Calscirtus toroensis Anso & Desutter-Grandcolas, n. sp. (I, J): maxillary palpus (A, I); hind tibia spurs and spines, inner (B) and outer (C) sides; male forewing, dorsal field (D, J); female subgenital plate, lateral (E), ventral (F); female copulatory papilla, dorsal (G), lateral (H). Scales 1 mm.*

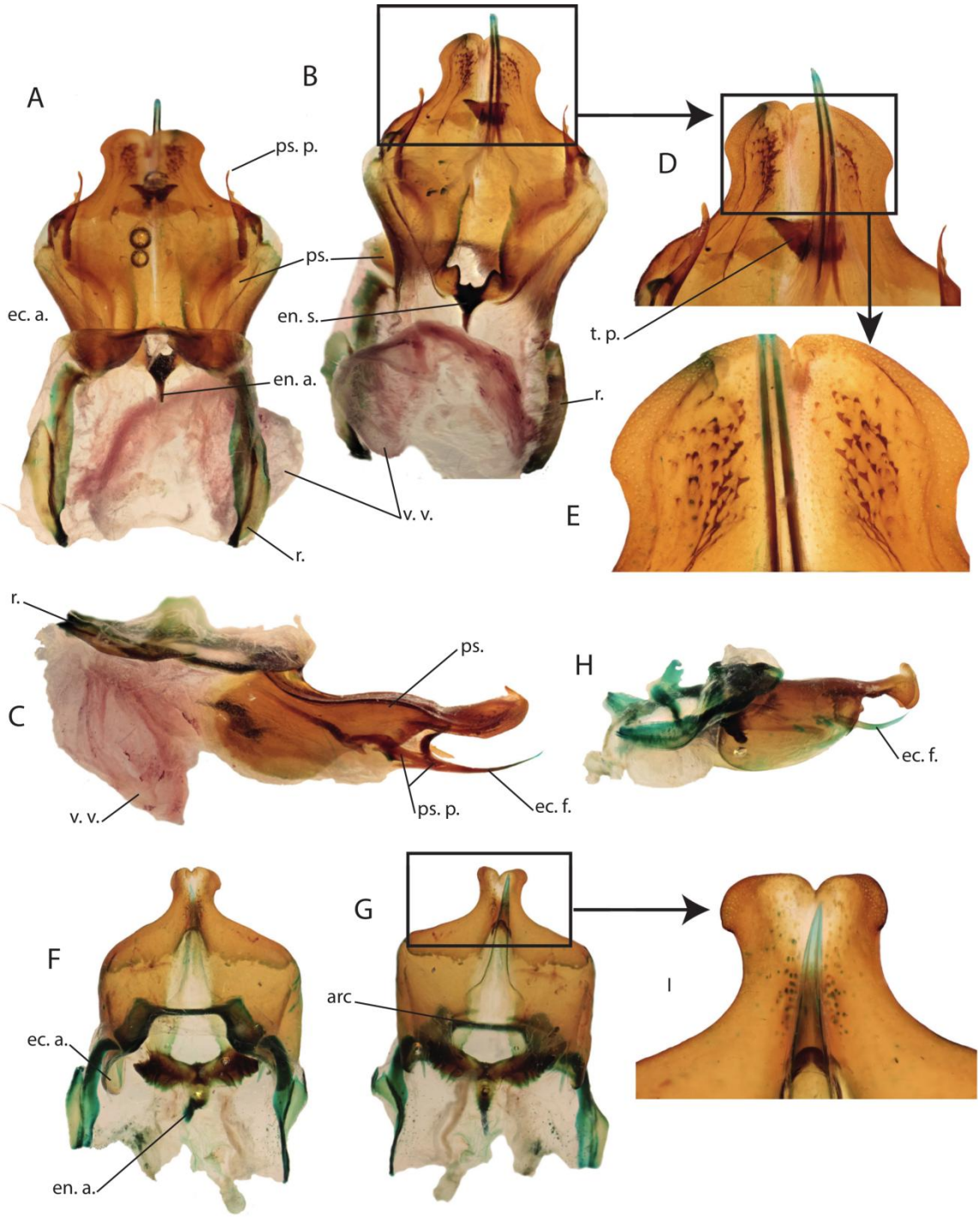

Figure 3.15. *Calscirtus Otte, 1987. Calscirtus magnus Anso & Desutter-Grandcolas, n. sp. (A-H) and Calscirtus toroensis Anso & Desutter-Grandcolas, n. sp. (I, J): male genitalia, dorsal (A, F), ventral (B, G), lateral (C, H), details of pseudepiphallic sclerite in ventral view (D, E, I). Abbreviations: see Material and methods.*

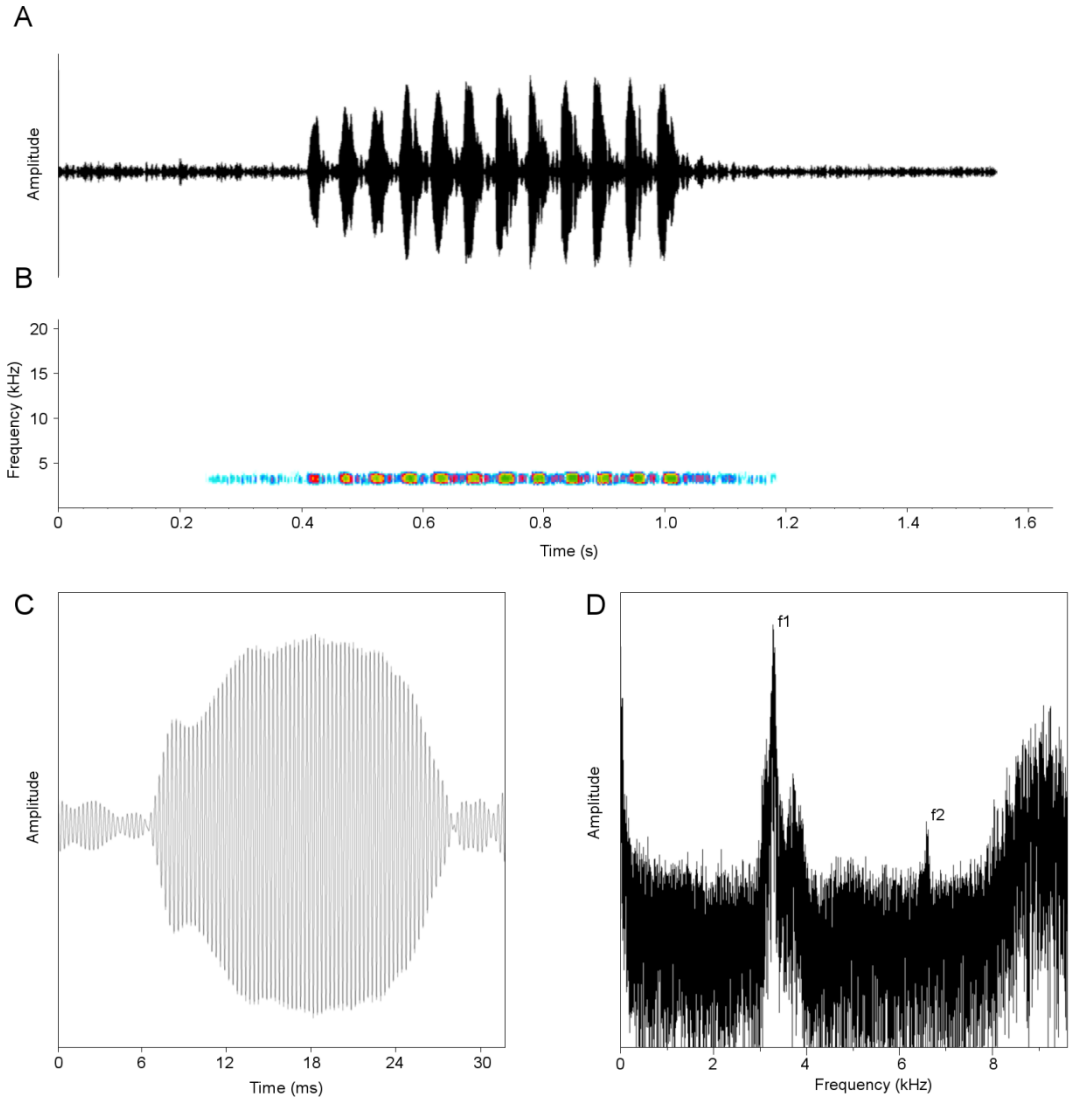

Figure 3.16. *Calling song of Calscirtus magnus Anso & Desutter-Grandcolas, n. sp. Detailed oscillogram (A) and sonogram (B) of one echeme; oscillogram of one syllable (C); logarithmic spectrogram of one syllable (D). Symbols: f1-f2, first (fundamental) to second harmonic frequencies.*

Calscirtus (*Trellescirtus*) *toroensis* Desutter-Grandcolas & Anso, n. sp.

(Figs 14I, J, 15F-I, 17)

Type locality. New Caledonia, Grande Terre, Ouen Toro, 22.30977° S 166.45309° E.

Type material. Holotype: New Caledonia, Grande Terre, Ouen Toro, sclerophyllous forest, 22.30977° S 166.45309° E, 23.x.2012, at night, 1 male, fn NOU22, on vegetation, J. Anso (MNHN-EO-ENSIF3819).

Diagnosis. Within the genus, species characterized by its coloration and male genitalia. Its resembles *C. paniensis*, *C. timbiensis* and *C. magnus* Desutter-Grandcolas & Anso, n. sp. by its male genitalia (pseudepiphallic sclerite wide and rounded), but its can be separated from these species by the subapical spurs of its TIII (as in genus diagnosis, *contra C. paniensis* and *C. magnus* Desutter-Grandcolas & Anso, n. sp.) and details in male genitalia (pseudepiphallic parameres lacking, *contra* all three species; ectophallic apodemes short and very thin, arc thin and almost complete; pseudepiphallic sclerite with rounded distal lobes and few ventral ornementation: compare Fig. 15I with Fig. 15E and Otte *et al.* 1987, Fig. 49A). Stridulatory file with 103 teeth. Female unknown.

Description. In addition to the characters of the genus: Head dorsum, fastigium, ocelli, scapes, antennae, eyes, maxillary palpi (Fig. 14I) and pronotum as in *C. magnus* Desutter-Grandcolas & Anso, n. sp.

Legs. TI shape, tympana and apical spurs, FI shape, TII apical spurs, TII, FII and FIII shape as in *C. magnus* Desutter-Grandcolas & Anso, n. sp. in *C. magnus* Desutter-Grandcolas & Anso, n. sp. TIII with five outer and five inner subapical spurs, the outer located within TIII distal half, the inner distributed over more than TIII half length; outer subapical spurs 2 to 4 slightly longer than the outer subapical spurs 1 and 5; inner subapical spurs slightly longer toward TIII apex; no striking difference in length between the inner and outer subapical spurs. TIII serrulated on inner and outer sides; outer spines small, especially those above the subapical spurs; inner spines bigger, the spine just above each subapical spur bigger, but less so than in *C. magnus* Desutter-Grandcolas & Anso, n. sp. TIII inner serrulation: no spine between apical and subapical spurs; 2 spines between subapical spurs 1 and 2; 2-3 (mean 2.5) spines between subapical spurs 2 and 3; 2-3 (mean 2.5) spines between subapical spurs 3 and

4; 2 spines between subapical spurs 4 and 5; 8 spines above subapical spur 5. TIII outer serrulation: no spine between apical and subapical spurs; 2 spines between subapical spurs 1 and 2; 2 spines between subapical spurs 2 and 3; 3 spines between subapical spurs 3 and 4; 3 spines between subapical spurs 4 and 5; 14-16 spines (mean 15) spines above subapical spur 5. Tarsomeres III-1: 1 outer spine and 1 inner spine, in addition to apical spines. FWs longer than the abdomen; HWs shortly longer than HWs, extending beyond FWs by more than half pronotum length. Cerci not very long, shorter than FIII.

Coloration. Light yellowish, uniform; shiny. Head light yellow, with indistinct whitish lines and areas; lateral ocelli ivory, with a dark brown fleck between them; fastigium furrow shortly brown basally. Eyes yellowish grey circled with brown; their inner margin whitish. Basal articles of antennae light yellowish brown basally, and light yellow distally; articles progressively darker, finally brown. Maxillary palpi light yellowish. Pronotum light yellowish and whitish, without a distinct pattern. Legs all yellowish, but hind knees marked with brown and TIII progressively brown distally; apical and subapical spurs all yellowish brown; TIII serrulation dark brown, making a clear contrast with the spurs. Cerci light yellowish brown.

Male. Metanotum and tergites without distinct glandular structures. FWs long and narrow; very light yellowish brown, some of the veins (MA, very thick, base of MP, CuP, CuA shortly, Anal veins) whitish yellow. Stridulatory apparatus complete: harp with 9 slightly oblique veins, distributed regularly over file length, the three longest harp veins almost parallel (Fig. 14J); mirror long and narrow, its anterior part narrow and long (Fig. 14J), its crossing vein somewhat curved. Stridulatory file with 103 teeth (n=1). Subgenital plate with only a very short medio-longitudinal furrow distally; subgenital plate brown, the lateral sides yellow.

Male genitalia. Fig. 15F-I. Basal part of pseudepiphallic sclerite more plicate than in *C. magnus* Desutter-Grandcolas & Anso, n. sp. (compare Fig. 15C, and Fig. 15H). Pseudepiphallic sclerite short, wide and rounded (Fig. 15F); greatly curved and elongate laterally (Fig. 15H); no dorso-lateral longitudinal crests (Fig. 15H); median part largely membranous (Fig. 15F); apical part more narrow than in *C. magnus* Desutter-Grandcolas & Anso, n. sp. and *C. paniensis*, the lobes more separated dorsally from each other, wider in lateral view, and bearing a larger dorsal tooth (compare Fig. 15C and Fig. 15H). Rami similar to those of *C. magnus* Desutter-Grandcolas & Anso, n. sp., but relatively longer. Pseudepiphallic parameres lacking. Epi-ectophallic invagination wide and shallow;

ectophallic apodemes short and thin; ectophallic arc very thin and almost complete. Ectophallic fold short, not going beyond the distal margin of pseudepiphallic sclerite (Fig. 15G); separated from the ventral side of pseudepiphallic sclerite by a sclerite having the shape of a reverse-U (Fig. 15I). Endophallic sclerite much more developped than in *C. magnus* Desutter-Grandcolas & Anso, n. sp.; no longitudinal sclerite close to the endophallic sclerite.

Female . Unknown.

Measurements (in mm).

	iod	PronL	PronWa	PronWp	FWL	FWw	HWL	FIIIL	FIIIW	TIIIL	tar 1-III
Male holotype	1.1	4.2	3.4	4.5	20	4.3	23.2	13.4	3.4	10.6	2.5

Habitat and life history traits. *Calscirtus toroensis* Desutter-Grandcolas & Anso, n. sp. lives in dry and open forested area. Males emit their calling song at night in vegetation, especially in monospecific formation of *Guaiacum officinale*.

Calling song. Fig. 17. One male has been recorded (three song bouts, 154 syllables). At 23°C the calling song of *Calcirtus toroensis* Desutter-Grandcolas & Anso, n. sp. consist of a repetition of echemes of 206.7 ± 19.6 ms; each echeme is made of 7 ± 1 syllables, with the following characteristics: syllable duration = 15.1 ± 6.3 ms; syllable period = 31.9 ± 1.9 ms; syllable duty cycle = 42.9%; the dominant frequency is 4.6 ± 0.1 kHz. Songs deposited in MNHN sound library (inventory number MNHN-SO-2016-6).

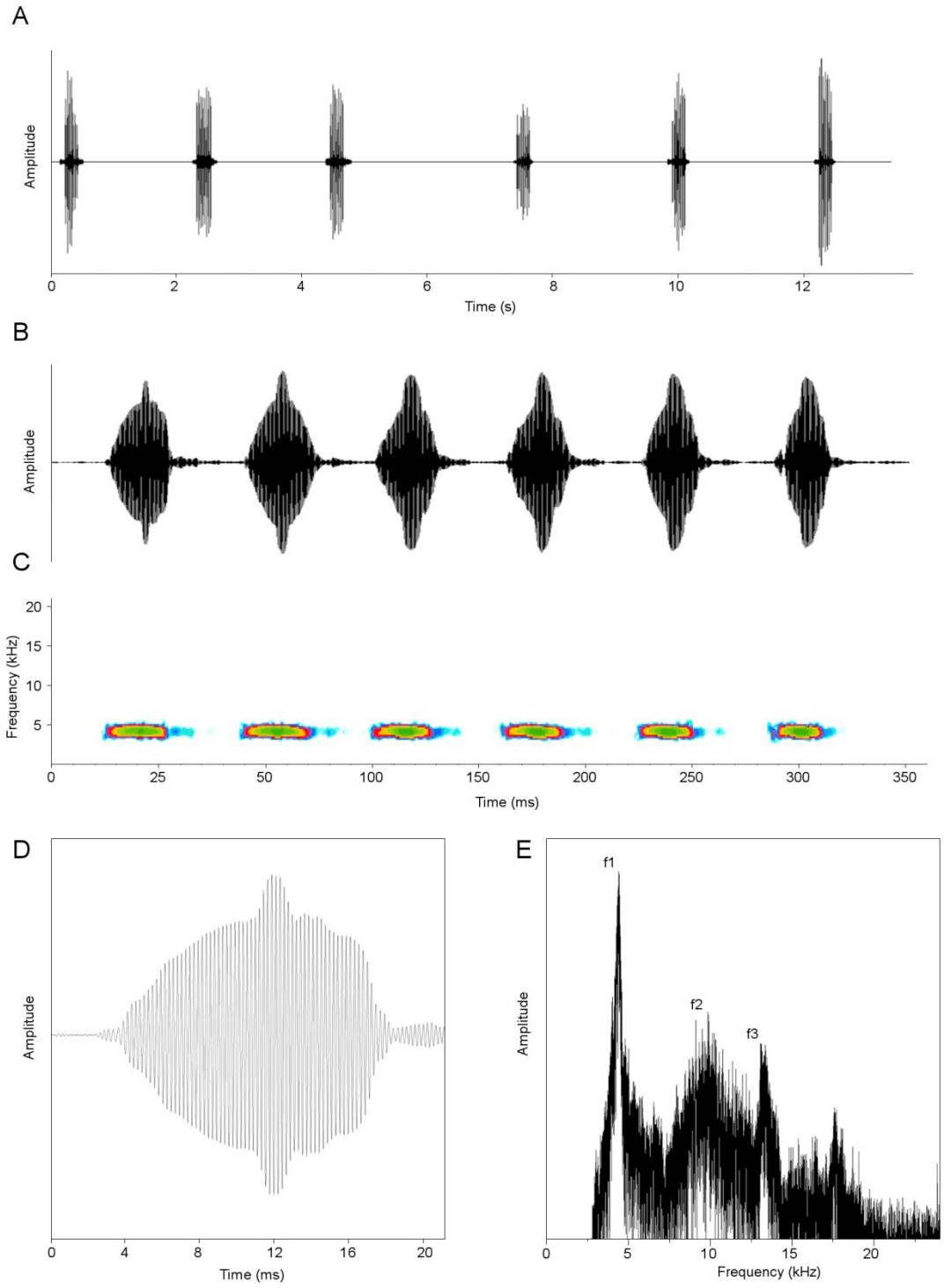

Figure 3.17. *Calling song of Calscirtus toroensis Desutter-Grandcolas & Anso, n. sp. Oscillogram of six successive echemes (A); detailed oscillogram (B) and sonogram (C) of one echeme; oscillogram of one syllable (D); logarithmic spectrogram of one syllable (E). Symbols: f1-f3, first (fundamental) to third harmonic frequencies.*

Genus *Matuanus* Gorochov, 1986

Matuanus Gorochov, 1986: 705. Otte *et al.* 1987: 447. Desutter-Grandcolas 1997b: 154. Robillard & Desutter-Grandcolas 2008: 276 (key to species, p. 275).

Type species. *Matuanus priapus* Saussure, 1878.

Emended diagnosis. See Desutter-Grandcolas & Anso (submit.).

Distribution. *Matuanus* is diversified mostly in New Caledonia, but it is recorded also in Papua New Guinea and Java (Robillard & Desutter-Grandcolas, 2008).

Matuanus sp. *affinis mirabilis* Desutter-Grandcolas, 1997

(Fig. 18A-F)

Matuanus mirabilis Desutter-Grandcolas, 1997d: 155.

Type material. Holotype: New Caledonia, 3 km WNW Col d'Amieu, N La Foa, 450 - 550 m, forêt sempervirente, 18-ii-1994, 1 male, jour, L. Desutter-Grandcolas, MNHN-EO-ENSIF1091. **Allotype:** Same locality and collector as the holotype, 17-ii-1994, 1 female, nuit, à terre, sous le rebord d'un talus. MNHN-EO-ENSIF1092.

Additional material examined. In addition to type material. New Caledonia, Grande Terre, Pic du Grand Kaori, rainforest, 22.28535° S 166.89674° E, 30.i.2013, by night, male, FOGK2-58, on vegetation, J. Anso (MNHN).

New Caledonia, Grande Terre, Pic du Grand Kaori, paraforestier, 22.28000° S 166.89383° E, 10.vii.2013, by day, 1 female, fn NOU24-PARA2, on vegetation, J. Anso (MNHN).

New Caledonia, Grande Terre, Pic du Grand Kaori, rainforest, 22.28226° S 166.89601° E, parcel invaded by *Wasmannia auropunctata*, 17.x.2012, by day, 1 male, fn FOGKW1-1, on trunk at 1m, J. Anso (MNHN).

We gather here 3 specimens which are close to *M. mirabilis* by their general shape (wide and fusiform), and by their coloration, i.e. face brown with 4 median, yellow flecks, legs I and II yellow with brown dots, TIII yellow except for brown knee, FW dorsal and lateral fields brown grey, the limit between them largely dark brown. Other characters: Female subgenital

plate deeply indented, with a pair of lateral glandular areas, as in *Calscirtus*. Male FWs: stridulatory file present, harp with 5 parallel oblique veins.

They differ by the coloration of FIII (Fig. 18C), yellowish brown with brown oblique lines (red brown in *M. mirabilis*) and a yellow ventro distal margin, light brown occiput (Fig. 18A; head dorsum brown with a thin yellow H-shaped fleck in *M. mirabilis*), light brown lateral lobes of pronotum (Fig. 18B; yellow with light brown margin in *M. mirabilis*), among others. Also, the ovipositor is shorter (12.2mm against 14.1mm in *M. mirabilis*), and smaller than FIII (slightly longer in *M. mirabilis*, with FIII length 13.5mm against 14 respectively). Finally, the male genitalia (Fig. 18D-F) are very similar to those of *M. mirabilis* (Desutter-Grandcolas 1997d, Figs 36, 37), but smaller, with comparatively longer pseudepiphallic parameres (Fig. 18C); ectophallic fold widely sclerotized dorsally, but the sclerotized part shorter than the pseudepiphallic parameres.

Measurements (in mm).

	iod	PronL	PronWa	PronWp	FWL	FWW	HWL	FIIIL	FIIIw	TIIIL	OL
Male NOU20	1.9	4	4.4	5.2	19.5	--	23.2	16.6	4.1	14.1	-
Male FOGK2-58	1.6	--	--	--	--	--	--	12.8	3.7	10.4	-
Female NOU24	1.7	3.7	3.6	5.6	17.7	--	20.9	14	4.1	12	12.2

Habitat and life history traits. *Matuanus* sp. *affinis mirabilis* Desutter-Grandcolas, 1997 lives in rainforest and paraforestier vegetation. Males and females were found on vegetation and trunk, mostly during the night when they remain active.

Acoustic behaviour. Unknown.

Matuanus kaorensis Desutter-Grandcolas & Anso, n. sp.

(Figs 18G, 19)

Type locality. New Caledonia, Grande Terre, Pic du Grand Kaori, 22.28000° S 166.89383° E.

Type material. Holotype: New Caledonia, Grande Terre, Pic du Grand Kaori, paraforestier, 22.28000° S 166.89383° E, 10.vii.2013, by night, 1 female, fn NOU21-PARA1, J. Anso (MNHN-EO-ENSIF1108).

Diagnosis. Medium size species, resembling *M. neoplumus* Otte, 1987 by its pattern of coloration (pronotum uniformally brown, femora brown, tibiae light yellow not ringed, head dorsum black from ocelli to vertex, a small yellow line behind each eye) and very long HWs, but much bigger in size (body length 14 mm, after Otte *et al.* 1987). This species can be separated from other *Matuanus* species by its pattern of coloration: FW lateral margin without a line of white spots (*contra M. elegans* Otte, 1987, *M. priapus* (Saussure, 1878), *M. rectinervis* Robillard, 2008); pronotum lateral lobe not yellow in lower half (*contra M. mirabilis* Desutter-Grandcolas, 1997, *M. rufidulus* (Saussure, 1878)); pronotum dorsal field without colored lines on lateral margins (contra *M. bicolor* Robillard, 2008); black spot on head dorsum extending from ocelli to occiput, beyond the small yellow line behind each eye (contra *M. azurensis* Robillard, 2008, *M. flavomaculatus* Gorochov, 1986, *M. bruneonervus* Robillard, 2008, *M. flavomaculatus* Gorochov, 1986) (see Robillard & Desutter-Grandcolas, 2008 for identification key). Other characters: ovipositor slightly longer than FIII (see measurements); subgenital plate wider than long, its distal margin almost straight, not deeply concave (Fig. 19B, C). Female genitalia: copulatory papilla as in the other species of the genus, but very small (Fig. 19D-F). Male unknown.

Description. In addition to the characters of the genus (Otte *et al.* 1987, Desutter-Grandcolas 1997d). Head dorsum slightly rounded between the eyes, flattened at fastigium level; fastigium long and triangular, its apex more narrow than the scape, furrowed from median ocellus to apex; ocelli settled in a flat triangle, the distance between the lateral ocelli nearly twice the distance between one lateral and the median ocelli; lateral ocelli large, median ocellus about one third the lateral ocelli, at about fastigium mid length; scapes longer than wide; eyes small but protruding anteriorly; maxillary palpi small, joints 3 and 5 abour equal in size, joint 5 truncate over more than half its length (Fig. 19A). Pronotum transverse; DD anterior margin almost straight, posterior margin slightly bisinuate.

Legs. TI widened laterally at the level of the tympana, and somewhat flat dorsally; inner tympanum the biggest, outer tympanum oval, smaller. FI not widened. TIII with five outer

and five inner subapical spurs, all located within TIII distal half; outer subapical spurs 1 to 3 very close to each other and to TIII apex; inner subapical spurs slightly longer than outer subapical spurs. TIII serrulated on inner and outer sides; spines small on both inner and outer sides, and very small compared to subapical spurs. TIII inner serrulation: no spine between apical and subapical spurs, between subapical spurs 1 and 2, and between subapical spurs 2 and 3; 1 spine between subapical spurs 3 and 4; 3 spines between subapical spurs 4 and 5; 11-13 (mean 12) spines above subapical spur 5. TIII outer serrulation: no spine between apical and subapical spurs; no spine between subapical spurs 1 and 2; 1 spine between subapical spurs 2 and 3; 2 spines between subapical spurs 3 and 4; 3 spines between subapical spurs 4 and 5; 16 spines spines above subapical spur 5. Tarsomeres III-1: no inner spine and 2 outer spines, in addition to apical spines. FWs longer than the abdomen; HWs extending beyond FWs by more than twice pronotum length (HWL / PronL 2.3). Cerci shorter than ovipositor.

Coloration. Uniform, except for head dorsum and light yellow tibiae. Head dorsum (Fig. Fig. 18G) black between ocelli and occiput; a short curved yellow line behind each eye; ocelli ivory; fastigium furrow shortly brown basally. Eyes brown circled with grey. Face and cheeks light ochre brown, the face maybe more yellowish; a pair of short yellow lines below the lower margin of each eye, and below the tip of the fastigium between the antennal pits. Scapes and base of antennae brown, antennae lighter distally; no yellow articles along the flagellum. Maxillary palpi light yellowish. Pronotum light brown, without a distinct pattern. Femora I and III uniformly light brown (legs II lacking); tibiae and tarsomeres I and III light yellow; spurs and spines light yellowish with brown apex. Cerci very light yellowish brown, darker distally.

Male . Unknown.

Female. FWs long and narrow; very light brown grey, with many very short whitish setae; dorsal field venation brown, with some yellow veins (basal third of CuP, distal two third of CuA, base of anal veins); transverse veins between MA and MP thick and yellowish. Subgenital plate wider than long, its distal margin straight, not concave as in some other *Matuanus* species and not extended around ovipositor basis (Fig. 19B, C); subgenital plate light yellowish brown, the lateral sides lighter.

Female genitalia. Fig. 19D-F. Copulatory papilla small and very short, with a short, distally bisinous dorsal part (Fig. 19D), and a short, triangular ventral plate (Fig. 19E, F); spermathecal duct very thin from the start.

Measurements (in mm).

	iod	PronL	PronWa	PronWp	FWL	FWW	HWL	FIIIL	FIIIw	TIIIL	OL
Holotype	1.6	2.2	3.2	4.1	20.6	--	25.6	12.4	3	11.5	12.6

Habitat and life history traits. *Matuanus kaorensis* Desutter-Grandcolas & Anso, n. sp. lives in preforest formation in the southern part of New Caledonia. One female was found on vegetation during the night.

Acoustic behaviour. Unknown.

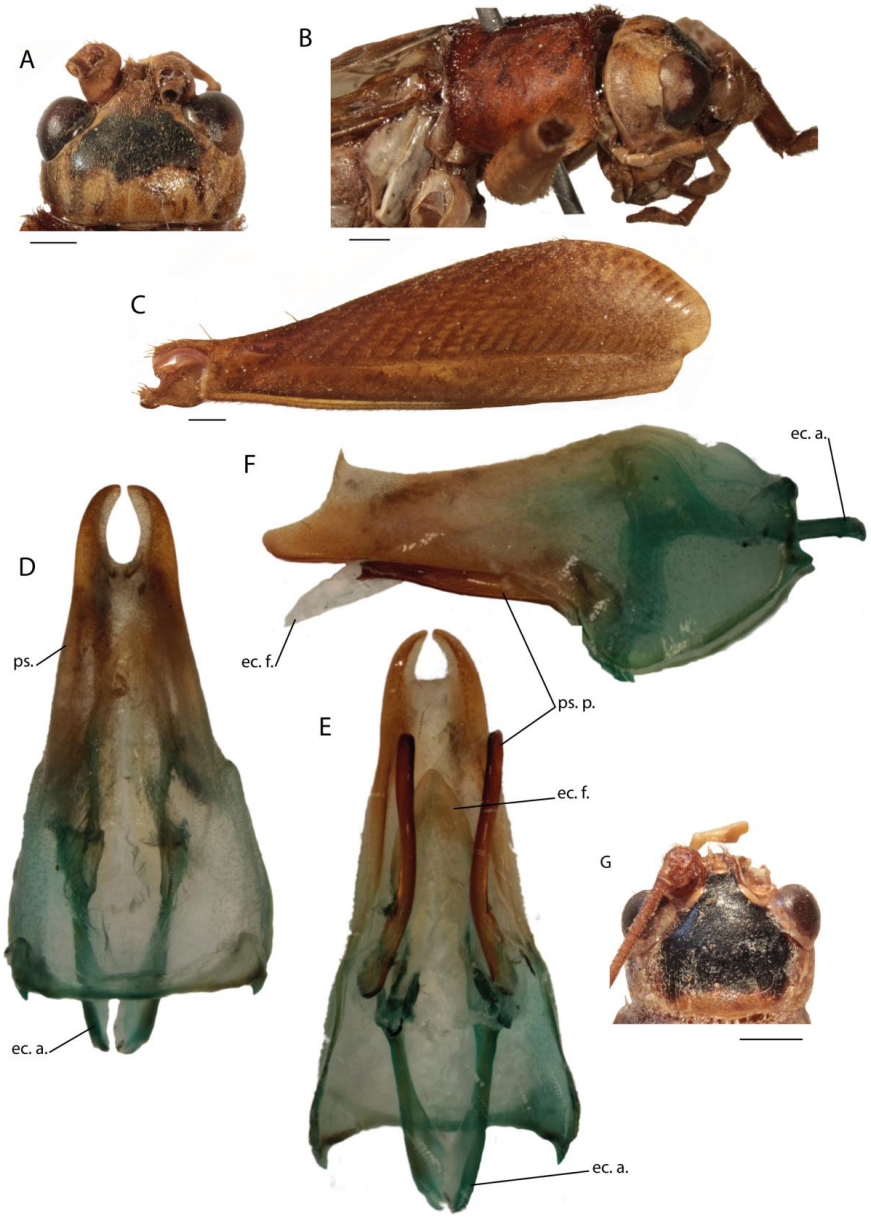

Figure 3.18. *Matuanus Gorochov, 1986. Matuanus sp. affinis mirabilis Desutter-Grandcolas, 1997 (A-F) and Matuanus kaorensis Desutter-Grandcolas & Anso, n. sp. (G): head dorsum coloration (A, G); head and pronotum, lateral (B); hind femur, outer side (C); male genitalia, dorsal (D), ventral (E), lateral (F). Abbreviations: see Material and methods.*

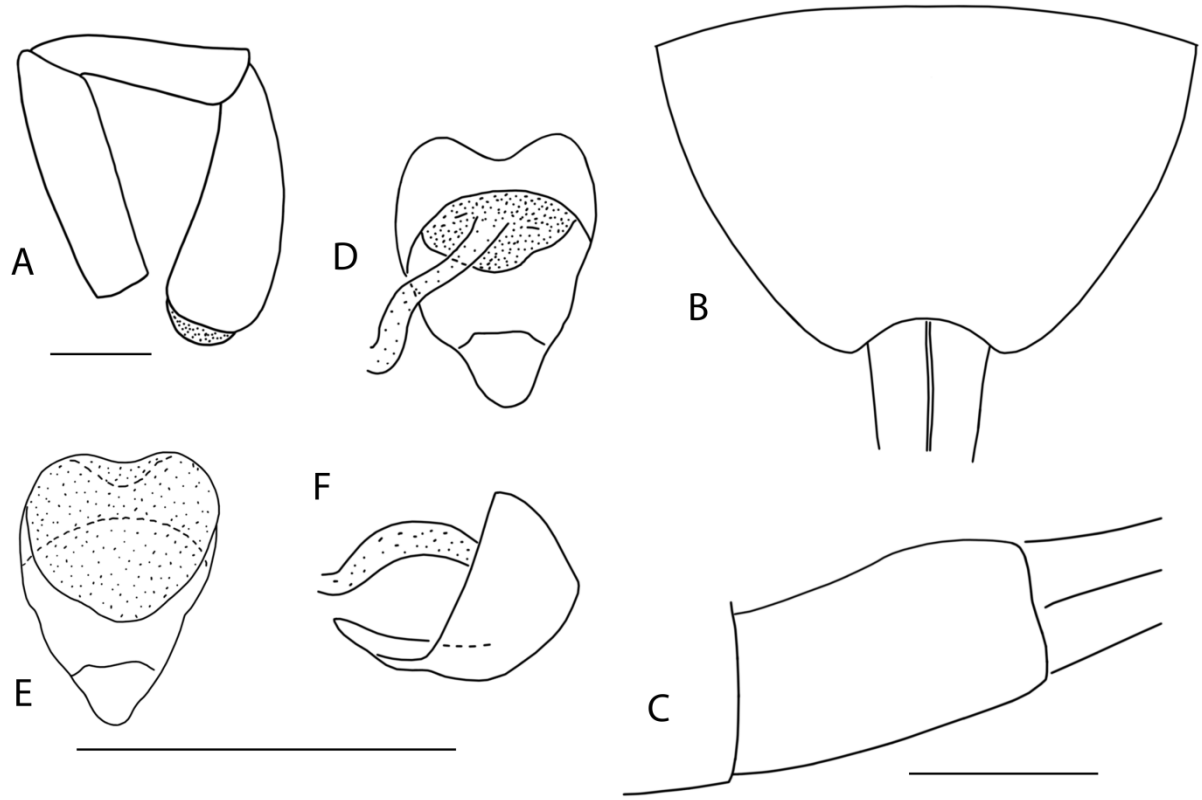

Figure 3.19. *Matuanus kaorensis Desutter-Grandcolas & Anso, n. sp.: maxillary palpus (A), female subgenital plate, ventral (B), lateral (C); female copulatory papilla, dorsal (D), ventral (E), lateral (F). Scales 1 mm. Abbreviations: see Material and methods.*

Genus *Adenopterus* Chopard, 1951

Adenopterus Chopard, 1951: 511. Otte *et al.* 1987: 425.

Adenopterus Adenopterus, Gorochov 2003: 299.

Type species. *Adenopterus norfolkensis* Chopard, 1951.

Emended diagnosis. See Desutter-Grandcolas & Anso (submit.) for New Caledonian species.

Distribution. South-eastern Oceania.

Adenopterus sp. affinis crouensis Otte, 1987

Adenopterus crouensis Otte in Otte *et al.*, 1987: 438.

Type locality. New Caledonia, La Crouen, 150-250m.

Type material. Holotype: New Caledonia, La Crouen, 150-250 m, 1 male, ii-1973, Krauss, BPBM. **Paratypes, 7 males, 9 females:** New Caledonia without precision, 1 female, syntype of Podoscirtus insularis Saussure, 1878, Coll. Brunner von Wattenwyl No. 4734, NHM.

New Caledonia, Yahoué, iii.1978, Krauss, 2 males (BPBM, ANSP).

New Caledonia, Oua Tom, 20.ix.1940, FXW, 1 male (BPBM).

New Caledonia, 2 km SE of Timbia, Noué 0-5m, 20.ix.1979, Gagné, 2 males, 2 females (BPBM).

New Caledonia, Nouméa, i.1962, Gagné, 1 female (BPBM); vii.1950, Krauss, 1 male (BPBM).

New Caledonia, forêt de Thi, 100-200m, 10.iii.1961, Sedlacek, 1 female (BPBM).

New Caledonia, La Crouen, 31.i.1963, Yoshimoto & Krauss, 1 male (BPBM); 20.iii.1968, Gressitt & Maa, 1 female (ANSP).

New Caledonia, Dumbéa valley, vi.1950, Krauss, 1 female (BPBM).

New Calednia, La Coulée, 23.i.1963, Yoshimoto, 1 female (BPBM).

New Caledonia, La Foa, 20.i.1945, Milliron, 1 female (BPBM).

Examined material. New Caledonia, Grande Terre, Forêt Nord, maquis, 22.32277° S 166.93501° E, 30.i.2014, at night, 1 female, fn MAFN2-7, at 15 cm high on vegetation, J.Anso (MNHN-EO-ENSIF3911).

New Caledonia, Bois du Sud, Col de Ouénaru, maquis, 22.17321° S 166.76.093° E, 28vii2012, 1 juvenile female, fn LD69bis, on vegetation, L. Desutter-Grandcolas, raised to adulthood in laboratory (MNHN-EO-ENSIF3912).

Distribution. Species distributed largely in the South of Grande Terre, with specimens known from Yahoué, Oua Tom, Ngoué, 2 km SE Timbia, Nouméa, Forêt de Thi, La Crouen, Dumbéa valley, La Coulée, and La Foa (specimens in BPBM, ANSP). If identification is confirmed, the specimens examined here will attest the presence of the species in the southern shrubland.

Diagnosis. The species can be recognized by its distinctive pattern of coloration (Otte *et al.* 1987): Body color dark reddish brown to purple, with rows of white spots on FWs, between all veins. Head dorsum dark reddish brown, shiny; face and cheeks shiny black. Pronotum entirely dark reddish brown with long silvery pubescence. FW membrane grey, veins dark reddish brown, transverse veins white and oval. Legs reddish brown. Other characters: ocelli not large; HWs extending nearly 2 pronotum length beyond FWs. Males: FWs with a large and deep gland, with a high process (See Otte et al. 1987, Fig. 32A). Male genitalia as in Otte *et al.* 1987, Fig. 37A. Females: Ovipositor length 9.5 – 11.2 mm (mean 10.4).

Remarks. The two females examined here have a pattern of coloration broadly similar to that of *A.crouensis*, but lighter (more yellowish brown than reddish brown, especially for pronotum and head dorsum). The female from Forêt Nord also differs from *A. crouensis* by its shorter HWs (extending less than one pronotum length beyond FWs) and a clear dark spot on TI at the level of the tympana. The female from Bois du Sud differs from *A. crouensis* by the coloration of its legs (femora light brown, tibiae yellowish), its HWs extending nearly 2 pronotum length beyond FWs. Both females may belong to two different species close to *A. crouensis*, but new to science.

Measurements (in mm).

	iod	PronL	PronWa	PronWp	FWL	HWL	FIIIL	FIIIW	TIIIL	OL
Female MAFN2-7	0.9	2	2.1	2.5	10.5	11.3	8.1	2.1	7.6	9.6
Female BDS, LD69bis	0.7	1.7	1.9	2.5	9.5	12.7	7.5	--	7.5	9

Habitat and life history traits. *Adenopterus* sp. *affinis crouensis* Otte, 1987 lives in open habitats, in low sclerophyllous shrubland mainly in the southern part of New Caledonia.

Adenopterus meridionalis Desutter-Grandcolas & Anso, n. sp.

(Figs 20A-D, 21)

Type locality. New Caledonia, Rivière blanche, 22°15'142’’S 166°68'643’’E.

Type material. Holotype: New Caledonia, Grande Terre, Rivière blanche, rainforest, 22.15142° S 166.68643° E, 11.iii.2014, by night, 1 male, fn FORIV1-25, leaf litter, J. Anso (MNHN-EO-ENSIF1109).

Diagnosis. Within *Adenopterus*, small species similar to *A. sylvaticus* Otte, 1987 by the shape of last tergite in male, extended above supra anal plate (Fig. 20D). HWs extended less than pronotum length FWs. Pattern of coloration: Head distinctly bicolor : face, mouthparts, maxillary palpi and cheeks pale yellow, head dorsum light brown between ocelli and eye midlength. **Male.** No glandular pit on FW (Fig. 21B). FW dorsal field with 7 longitudinal veins. Male genitalia: symmetrical; pseudepiphallic sclerite large, with a very small paired apex; pseudepiphallic parameres very long, thin and sinuate, with an apical hook (Fig. 21D); ectophallic fold extremely long, sclerotized and very thin (Fig. 21E); dorsal cavity low, twisted (Fig. 21E). Female unknown.

Description. Within the genus, small species. Ocelli small, the lateral ones separated by a distance greater than the distance between the median and one lateral ocelli. Maxillary palpi very short; joints 3 and 5 subequal, joint 4 smaller; joint 5 truncated over three quarter of its length (Fig. 20A). TII with 2 apical, ventral spurs; inner and outer tympana both present, equal in size; TI not inflated at tympanum level. TII with 3 apical spurs, the outer dorsal lacking. TIII with 5 inner and 5 outer subapical spurs, located in TIII distal half; subapical spurs all small and equal in length; 3 outer and 3 inner apical spurs, as in other species of the genus. TIII serrulation strong and abundant, the spines flat, located on the lateral margins of TIII, somewhat flattened dorsally and carinated laterally; TIII inner serrulation: no spine between apical and subapical spurs, between subapical spurs 1 and 2, and between subapical spurs 2 and 3; 1 spine between subapical spurs 3 and 4, and between subapical spurs 4 and 5; 14-16 (mean 15) spines above subapical spur 5. TIII outer serrulation: no spine between apical and subapical spurs; no spine between subapical spurs 1 and 2; 1-2 (mean 1.5) spines between subapical spurs 2 and 3; 3 spines between subapical spurs 3 and 4, and between subapical spurs 4 and 5; 24-25 (mean 24.5) spines above subapical spur 5. Tarsomeres III-1: no inner spine and 3 outer spines, in addition to apical spines. Cerci very long.

Coloration. Head bicolor (Fig. 21B): face below the fastigium and the cheeks pale yellow; head dorsum (Fig. 21A) light brown between ocelli and eye midlength, pale yellow toward occiput and with one Y-shaped line between each eye, the inner branch of the Y prolonged along the inner margin of the eye; fastigium light brown dorsally, light brown and pale yellow

on the face, with a clear brown line along its whole margin; eyes black, inner dorsal margin yellow; scapes light yellow, inner and outer dorsal margins very light brown. Pronotum light reddish brown without a clear pattern, anterior margin yellow; no distinct coloured line on DD and LL (Fig. 21B). Legs light yellow, FI and FII with brown dots dorsally, FIII with numerous light brown lines; TIII light brown, the dorsal side darker; tarsi light yellowMany golden and brown setae. Cerci pale yellow, with a longitudinal brown line on outer side. Sternites yellow, anterior margins marked with brown.

Male. FWs without a stridulum; dorsal field with 7 longitudinal parallel veins (Fig. 20B). FWs light yellowish brown, more reddish on latero-basal parts; dorsal field venation light brown, thicker veins yellowish basally. FW without a glandular structure, just a slightly modified venation pattern (Fig. 20C). HWs extending less than pronotum length beyond FWs. Tergite IX greatly extended distally, entirelly covering the epiproct. Subgenital plate very long, narrowed and plicated at one third of its length; apex very narrow (Fig. 20D).

Male genitalia. Fig. 21C-E. Similar to other species of the genus (see Otte *et al.* 1987, Figs 34 - 38). Symmetrical. Pseudepiphallus (Fig. 21C, D) large, with a very small paired apex; pseudepiphallic parameres (Fig. 21E) very long, as long as two third pseudepiphallic sclerite length, sinuate and very thin, their apex with a small hook; ectophallic fold (Fig. 21D) extremely long, sclerotized over its whole length, and filiform over about one third of its length; ectophallic apodemes (Fig. 21D) short; arc lacking (Fig. 21D); dorsal cavity (Fig. 21C) long but not very high, very narrow and twisted.

Female. Unknown.

Measurements (in mm).

	iod	PronL	PronWp	FWL	HWL	FIIIL	FIIIw	TIIIL
Holotype	0.8	2.1	2.3	8.6	10.4	7.5	2	6.8

Habitat and life history traits. *Adenopterus meridionalis* Desutter-Grandcolas & Anso, n. sp lives in dense forests in the southern part of New Caledonia.

Adenopterus (?) octolineatus Desutter-Grandcolas & Anso, n. sp.

(Figs 20E-J, 22)

Type locality. New Caledonia, Grande Terre, Pic du Grand Kaori, 22.28535° S 166.89674° E.

Type material. Holotype: New Caledonia, Pic du Grand Kaori, rainforest, 22.28535° S 166.89674° E, Transect 1, 17.vii.2012, 1 male, fn11, J. Anso & L. Desutter-Grandcolas (MNHN-EO-ENSIF3636). **Allotype:** New Caledonia, Grande Terre, Col de Mouirange, rainforest, 22.20416° S 166.68086° E, 11.vii.2012, at night, 1 female, fn NOU18-PCM2-18, on vegetation, J. Anso (MNHN-EO-ENSIF3637).

Etymology. Species named after the coloration of its head dorsum (pale with eight light brown lines).

Distribution. South of Province Sud (Pic du Grand Kaori, Col de Mouiranges).

Diagnosis. We describe this species in the genus *Adenopterus*, although it lacks tympana (as *Adenopterus dumbea* Otte, 1987), has four apical spurs on TII, and short, truncate HWs, because it fits the definition of the genus for TIII subapical spurs (five inner and five outer) and male subgenital plate (elongate and acute), lacks a stridulum but has a tegminal gland in males, and has similar male genitalia (Fig. 22D-H). This species also resembles *Adenopterus sylvaticus* Otte, 1987 and *A. meridionalis* Desutter-Grandcolas & Anso, n. sp. by the development of last tergite in males (Fig. 20D). It is characterized by its pale coloration, with eight light brown longitudinal lines on head dorsum (Fig. 22A), not extended on the pronotum; female subgenital plate only slightly wider than long, its distal margin straight (Fig. 20H).

Description. In addition to the characters of the genus: Maxillary palpi very short; joint 5 slightly shorter than joint 3, truncated over three quarter of its length (Fig. 20E). Lateral ocelli larger than median ocellus. Pronotum lateral lobes longer than high. TI without a tympanum on both inner and outer sides; only 2 apical spurs. TII with 4 small apical spurs. TIII with 3 inner and 3 outer apical spurs; 5 outer and 5 inner subapical spurs. TIII serrulation regular in size, the spines tightly set. TIII inner serrulation: no spine between apical and subapical spurs, between subapical spurs 1 and 2, and between subapical spurs 2 and 3; 1 spine in male, 0-1 (mean 0.5) spine in female between subapical spurs 3 and 4; 1-2 (mean 1.5) spines between subapical spurs 4 and 5; 17-18 (mean 17.5) spines in male, 14 spines in female above subapical spur 5. TIII outer serrulation: no spine between apical and subapical spurs, and

between subapical spurs 1 and 2; 1-2 (mean 1.5) spines between subapical spurs 2 and 3; 4 spines in male, 3 spines in female between subapical spurs 3 and 4, and between subapical spurs 4 and 5; 22-25 (mean 23.5) spines in male, 20-23 (mean 21.5) in female above subapical spur 5. Tarsomeres III-1: no inner spine and 2 outer spines, in addition to apical spines. Cerci very long. Cerci very long when not broken.

Coloration. Very light yellow in dry specimens. Head dorsum, scapes dorsal sides and pronotum light golden yellow. Head dorsum (Fig. 22A) with eight very light brown longitudinal lines: the median ones connected between the eyes, the next pair coming close to the inner margins of the eyes and extending toward median ocellus; the next pair short behind the eyes; the last pair made of wider lines, located at about eye midlength. Face and palpi very light yellow (Fig. 22B), antennae somewhat more light brown. Pronotum DD (Fig. 22A) with a medio-longitudinal light brown line, including a thin yellow area in its anterior half; anterior margin light golden yellow; posterior margin darker; LL yellowish (Fig. 22B). Legs all light yellow; tip of spines and spurs brown.

Male. FWs with a lateral gland (Fig. 22C); dorsal field with seven longitudinal veins. HWs truncated, extending beyond FWs less than one pronotum length. FWs light yellow, densely covered with very short light setae; veins light yellow. Last tergite extended distally, coming over supra anal plate and covering it almost completely, as in *A. sylvaticus* (Otte *et al.* 1987, Fig. 33K, L) and in *A. meridionalis* Desutter-Grandcolas & Anso, n. sp. Subgenital plate very long, its wide base less than half the plate total length; apex narrowed at three successive levels, without longitudinal furrow (Fig. 20F, G).

Male genitalia. Fig. 22D-H. Pseudepiphallic sclerite as the other species of the genus, symmetrical (Fig. 22D); pseudepiphallic parameres short but thin, symmetrical, their apex with both a short, blunt projection and an acute, half circular spine (Fig. 22E, H); no ornementation on pseudepiphallic sclerite ventral side (Fig. 22H). Ectophallic fold very long and narrow, extending well beyond pseudepiphallic distal margin (Fig. 22D, F, G); arc not complete, but base of ectophallic fold below a short sclerotized "cap". Dorsal cavity well-developed and twisted several times (Fig. 22D, F). Endophallic sclerite and apodeme very well developed (Fig. 22E).

Female. FWs and HWs as in male, but without a tegminal gland. Subgenital plate almost squared, only slightly wider than long; distal margin straight (Fig. 20H). Ovipositor straight, longer than TIII; apex as on Fig. 22I.

Female genitalia. Copulatory papilla very short, as a small sclerotized plate ventral to the spermathecal duct aperture, but interrupted dorsally to the aperture (Fig. 20I, J); duct very wide in the allotype female, but may be because of the presence of a spermatophore filament.

Measurements (in mm).

	iod	PronL	PronWp	FWL	HWL	FIIIL	FIIIW	TIIIL	OL
Male holotype	1	2.5	2.6	11	12.6	9.4	2.4	8.4	---
Female allotype	1	2.1	2.8	11.1	13	10	2.4	9	10.8

Variation. The female has an additional inner subapical spur, between spurs 2 and 3, on one TIII. It also has dark brown coloration on FIII, which seems the result of bad preservation.

Habitat and life history traits. *Adenopterus (?) octolineatus* Desutter-Grandcolas & Anso, n. sp. lives in rainforest in the southern part of New Caledonia. Specimens were found on vegetation at night.

Remark. When describing *Adenopterus dumbeus*, Otte *et al.* (1987) mentioned that this species lacks tympana, a feature which is uncommon in winged species (Otte, 1992), and related this trait to potential problems in moulting. As *Adenopterus octolineatus* Desutter-Grandcolas & Anso, n. sp. presents the same combination of characters, this explanation may not hold, and the occurrence of winged but deaf species in crickets must be acknowledged. It would now be interesting to document the life habits of *A. dumbeus* and *A. octolineatus* Desutter-Grandcolas & Anso, n. sp. to check if these species can fly and if so, how they escape predators without hearing.

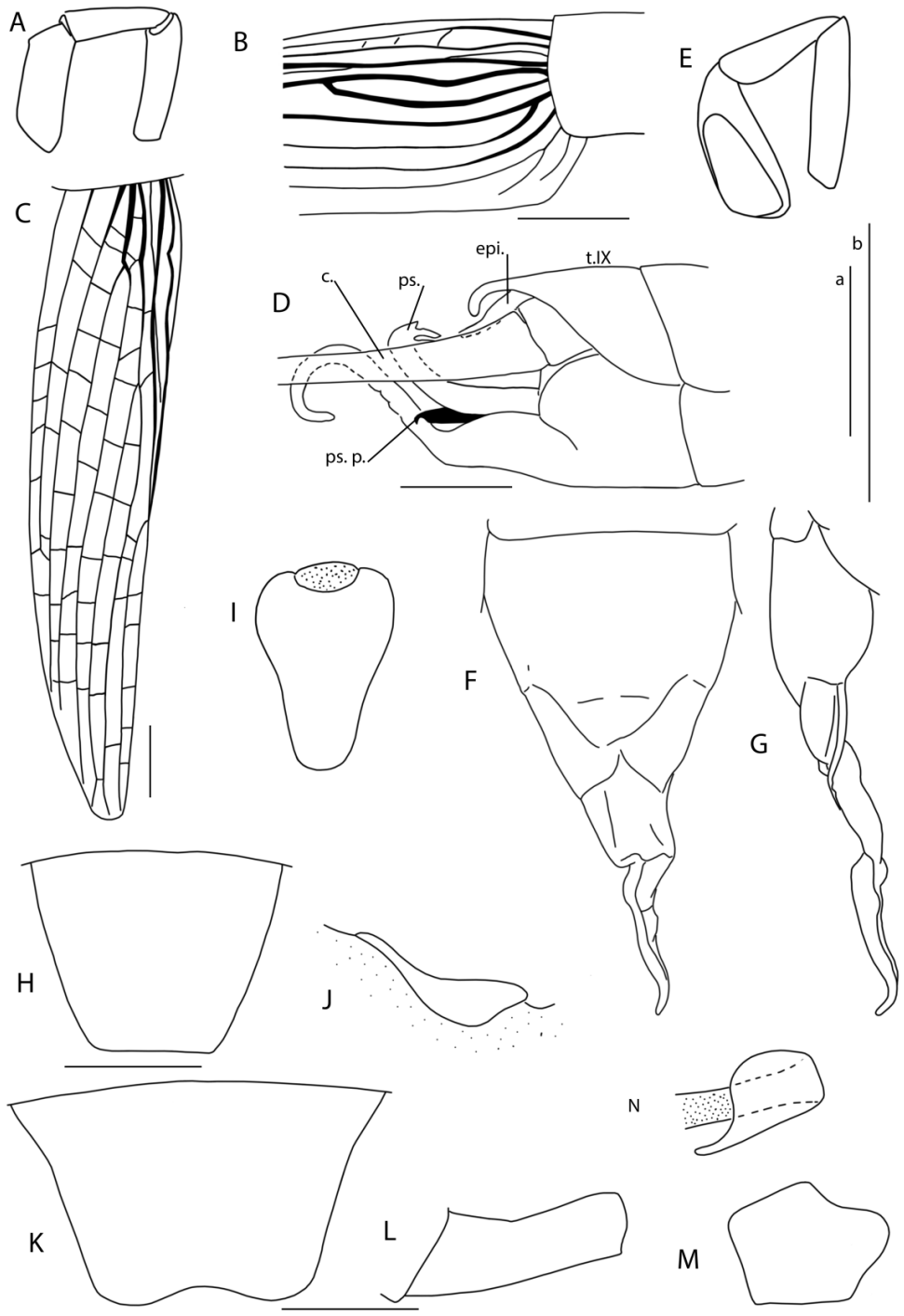

Figure 3.20. *Adenopterus Chopard, 1951 and Archenopterus Otte, 1987. Adenopterus meridionalis Desutter-Grandcolas & Anso, n. sp. (A-D), Adenopterus octolineatus Desutter-Grandcolas & Anso, n. sp. (E-J) and Archenopterus bouensis Otte, 1987 (K-N): maxillary palpus (A, E, scale a); male FW, lateral (B), dorsal (C); male terminalia (D); male subgenital plate, ventral (F), lateral (G); female subgenital plate, ventral (H, K); female copulatory papilla, ventral (I, M), lateral (J, N), scale b. Scales 1 mm. Abbreviations: see Material and methods.*

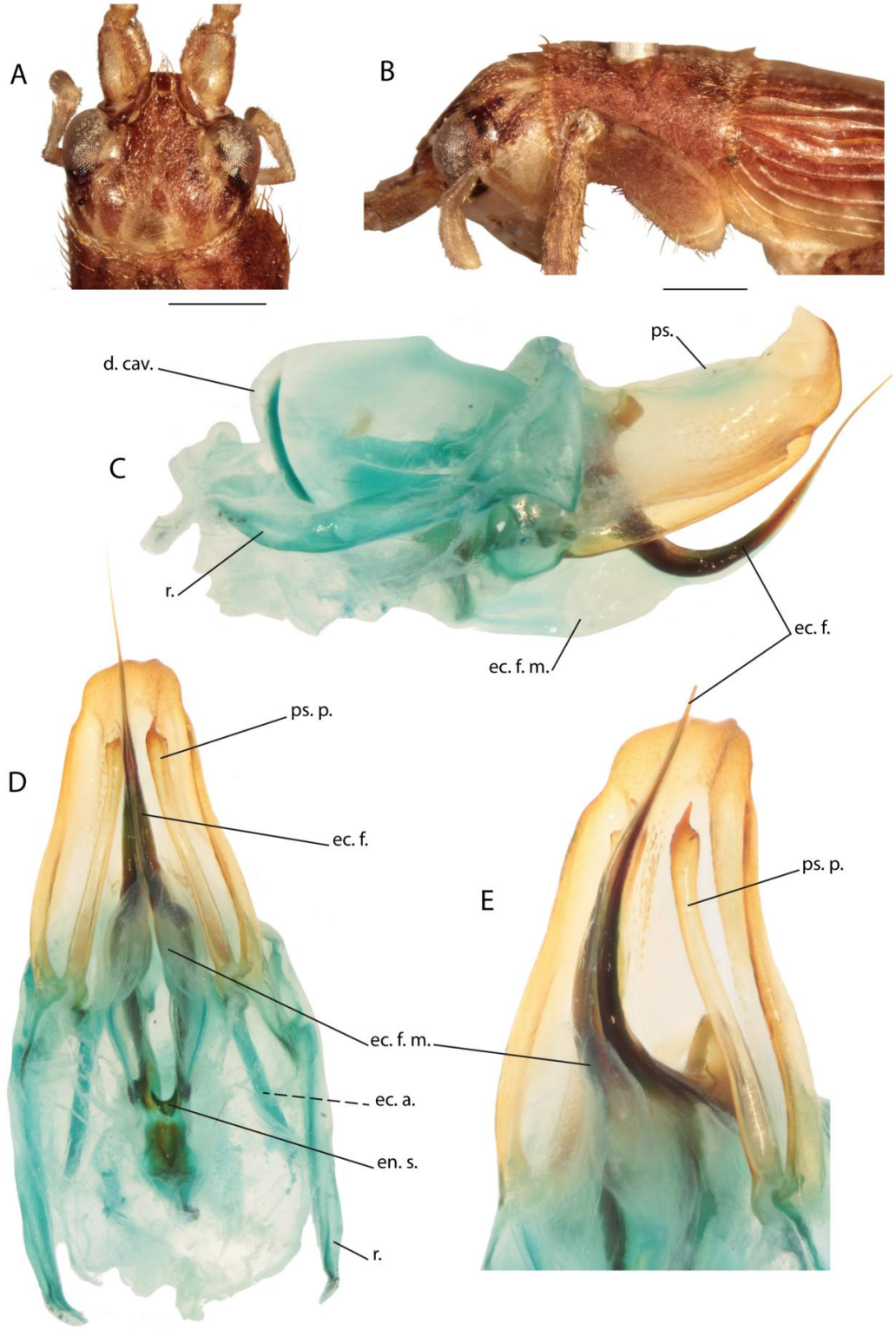

Figure 3.21. *Adenopterus meridionalis Desutter-Grandcolas & Anso, n. sp. A, head dorsum; B, head and pronotum, lateral; C-E, male genitalia, lateral (C), ventral (D), detail of ventral view (E). Scales 1 mm. Abbreviations: see Material and methods.*

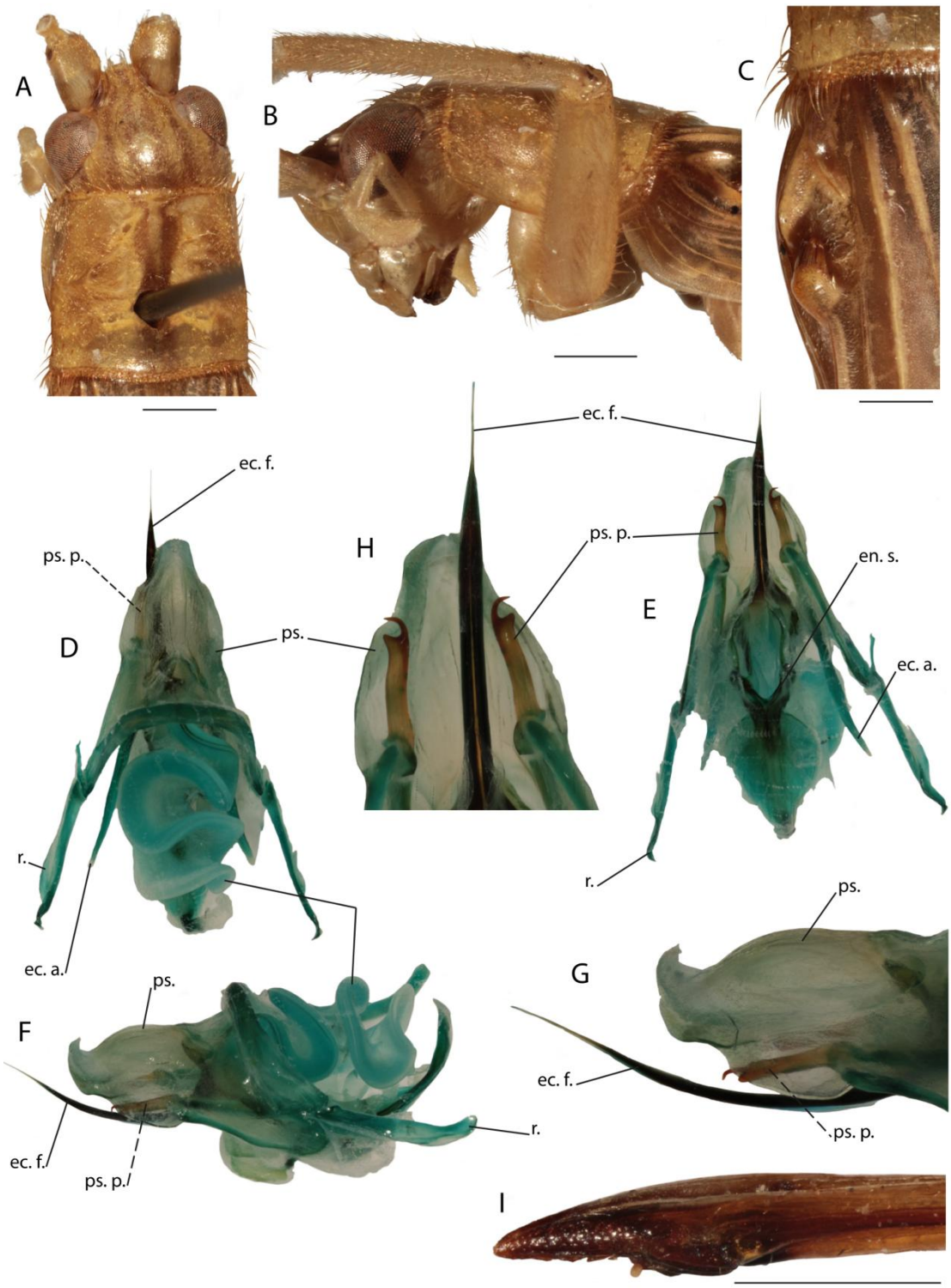

Figure 3.22. *Adenopterus octolineatus Desutter-Grandcolas & Anso, n. sp. A, B, head and pronotum, dorsal (A), lateral (B), scales 1 mm; C, male left tegminal gland, scale 0.5 mm; D-H, male genitalia, dorsal (D), ventral (E, H), lateral (F, G); I, apex of female ovipositor, scale 0.5 mm. Abbreviations: see Material and methods.*

Genus *Archenopterus* Otte, 1987

Archenopterus Otte in Otte *et al.*, 1987: 439.

Adenopterus Archenopterus, Gorochov 2003: 299.

Type species. *Archenopterus gressitti* Otte, 1987

Diagnosis. See Desutter-Grandcolas & Anso (submit.).

Distribution. *Archenopterus* is known from New Caledonia only, where it has been found in the central mountain in Col d'Amieu (*A. hemiphonus* Otte, 1987), in the northern part in high mountain (*A. hemipteroides* Otte, 1987), in Amoa Valley (*A. amoensis* Otte, 1987), and in the South, in Mont Bouo (*A. bouensis* Otte, 1987) and Mont Koghis (*A. gressitti* Otte, 1987 and *A. maai* Otte, 1987). It is reported here for the first time from southern New Caledonia.

Archenopterus bouensis Otte, 1987

(Figs 20K-N, 23)

Archenopterus bouensis Otte in Otte *et al.*, 1987: 441.

Type locality. New Caledonia, Grande Terre, Mt. Koghi.

Type material. Holotype: New Caledonia, Grande Terre, Mt. Koghi, forest on west slope of Mt. Bouo, 1 male, 26.ii.1983, Alexander, Cade & Otte (UMMZ).

Examined material. New Caledonia, Grande Terre, Rivière blanche, rainforest, 22.15142° S 166.68643° E, 20.iii.2014, by night, 1 male, on plant, 1 m high, recorded in the field at 22H09 at 20°C, J. Anso (MNHN-EO-ENSIF3935); 20.iii.2014, by night, 1 male, on plant, recorded in the lab on 27.iii.2014 à 26.5°C, J. Anso (MNHN-EO-ENSIF3936); 20.iii.2014, by night, 1 male, J. Anso (MNHN)

New Caledonia, Pic du Grand Kaori, rainforest, 22.28535° S 166.89674° E, 9.vii.2012, by night, 1 female, transect 1 n°10, L. Desutter-Grandcolas & J. Anso (MNHN).

New Caledonia, Rivière bleue, 25 km NE Nouméa, 200m, forêt sempervirente sur roches ultrabasiques, 1.iii.1994, nuit, 1 male, fn LD33, sur plante, L. Desutter-Grandcolas (MNHN).

New Caledonia, Pic du Pin, 22.14525 S 166.49426 E, 290m, 21.iv.2009, nuit, enregistrement appel DV-NC09-1(4), 18.1°C, sur arbuste 2mH, 1 male, fn TR25, T. Robillard (MNHN-EO-ENSIF3937); id, 21.iv.2009, nuit, 1 male, fn TR26, sur Pandanus, 2.2mH, T. Robillard (MNHN).

Distribution. New Caledonia, Grande Terre, Rivière bleue.

Emended diagnosis (female characters). Size large compare to other species of the genus, characterized by its pattern of coloration (face light yellow; head dorsum and fastigium ochre brown, eyes grey and ocelli ivory; pronotum margins light yellowish brown; lateral lobes ivory in distal third, brown otherwise; dorsal disc with two wide yellow bands converging anteriorly, brown with yellow spots in median part. Legs all light yellow. Male with a complete stridulum, mirror wider than long, harp with 4 long veins, the first three parallel, the fourth slightly diverging, and with 6 – 7 shorter, half circular veins in upper outer part. Stridulatory file with 298 (Otte *et al.* 2007) to 308 (male MNHN-EO-ENSIF3935) teeth. Male genitalia: pseudepiphallic parameres relatively short and somewhat inflated. Female subgenital plate (Fig. 20K, L) wider than long, narrowed before mid length, distal apex sinuate but not concave; ovipositor shorter than FIII. Female genitalia: copulatory papilla very small and hardly sclerotized, cylindrical (Fig. 20M, N).

Emended description. In addition to the characters of the genus (Otte *et al.* 1987): Size large for the genus. Hindwings longer than FWs, extending between 1.1 – 1.5 (mean 1.3) pronotum length beyond FWs. TIII inner serrulation: no spine between apical and subapical spurs; 0 spine between subapical spurs 1 and 2; 0 spine in males, 0-1 (mean 0.5) in female between subapical spurs 2 and 3; 0-1 (mean 0.8) spines in males, 1 spine in female between subapical spurs 3 and 4; 1-2 (mean 1.2) spines in males, 2 spines in female between subapical spurs 4 and 5; 15 - 22 spines (mean 17.8) in males, 20 – 22 spines (mean 21) in female above subapical spur 5. TIII outer serrulation: no spine between apical and subapical spurs; 0 spine in males, 0-1 (mean 0.5) in females between subapical spurs 1 and 2; 0-1 (mean 0.5) in males, 1 – 2 spines (mean 1.5) in female between subapical spurs 2 and 3; 2 – 3 spines (mean 2.3) in males, 3 spines in female between subapical spurs 3 and 4; 2 - 4 spines (mean 3) in males, 3-4 (mean 3.5) spines in female between subapical spurs 4 and 5; 22-25 spines (mean 23.7) in males, 23-24 spines (mean 23.5) in female above subapical spur 5. Tarsomeres III-1: 2 outer spines and 0 inner spine, in addition to apical spines.

Female. Wings longer than FWs by 1.3 pronotum length; FWs light yellowish grey, with brown veins. Legs all light yellow, but femora very light yellowish brown, FIII darker. Subgenital plate (Fig. 20K, L) rectangular, wider than long, narrowed before mid length; distal margin not concave, but sinuate; light yellow, ivory along lateral margins. Ovipositor shorter than FIII.

Female genitalia. Fig. 20M, N. Copulatory papilla small and hardly sclerotized; cylindrical, truncated apically, the aperture of spermathecal duct apical.

Measurements (in mm).

	iod	PronL	PronWa	PronWp	FWL	FWW	HWL	FIIIL	FIIIW	TIIIL	OL
Female	1.3	3.2	2.9	4	18,4	--	22.8	12.1	3	11.4	11.5
Males	1.2	2.8-3.2	2.6-2.7	4.1-4.5	16.2-17.4	6-6.2	20.2-22	11.4-12.7	2.8_3	10.5-11.8	
mean (n=3)		3.1	2.6	4.4	16.8	6.1	21.2	12.2	2.9	11.1	

Habitat and life history traits. *A. bouensis* is a nocturnal species who lives in rainforest canopy, from where males emit their calling song at night. Males can sing in lower stratifications, near the ground, during full moon (J. Anso, pers. obs.).

Calling song. Fig. 23. The specimens MNHN-EO-ENSIF3935 and ENSIF3936 were recorded, at 20°C and 26°C, representing two song bouts, five eschemes and 393 syllabes, all analyzed. At 20°C (26°C in brackets), the calling song of *A. bouensis* consists of a repetition of echemes of 2.45 ± 1.54 s (2.36 ± 0.43 s); each echeme is made of 33 ± 20 syllables (42 ± 8), with the following characteristics: syllable duration = 51.2 ± 6.4 ms (38.9 ± 1.7 ms); syllable period = 79.2 ± 2.3 ms (60 ± 1.5 ms); syllable duty cycle = 66.8% (65.5%); the dominant frequency is 4.2 ± 0.1 kHz (4.5 kHz). Songs are deposited in MNHN sound library (inventory number MNHN-SO-2016-7, MNHN-SO-2016-9, MNHN-SO-2016-10).

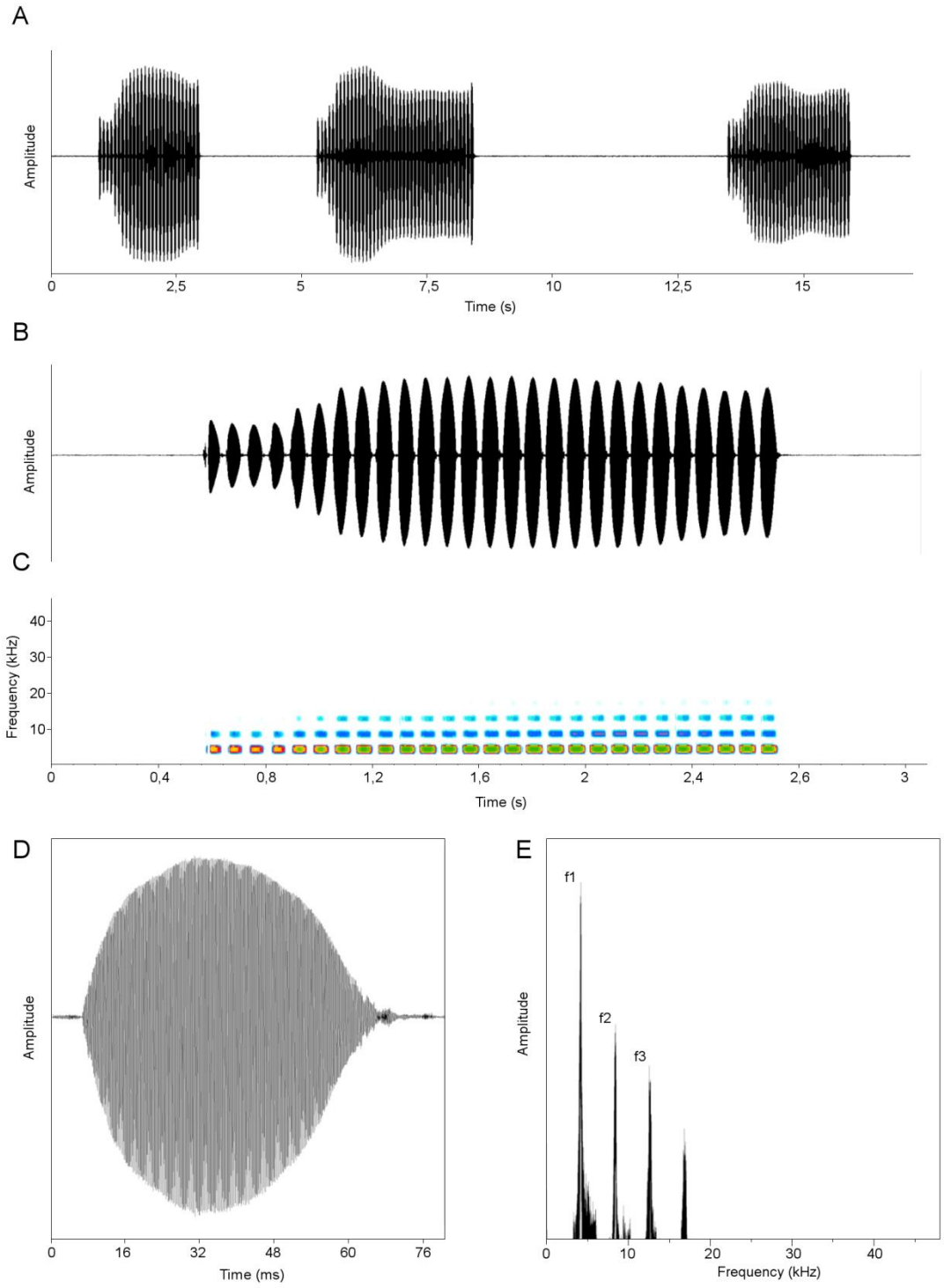

Figure 3.23. *Calling song of Archenopterus bouensis Otte, 1987. Oscillogram showing 3 successive echemes (A); detailed oscillogram (B) and sonogram (C) of one echeme; oscillogram of one syllable (D); logarithmic spectrogram of one syllable (E). Symbols: f1-f3, first (fundamental) to third harmonic frequencies.*

Genus *Pixipterus* Desutter-Grandcolas, n. gen.

(Figs 24, 25, 26)

Type species. *Pixipterus punctulatus* Desutter-Grandcolas & Anso, n. sp.

Etymology. Named after its ecological similarity with the eneopterine genus *Pixibinthus* Anso & Robillard, 2015, both genera occurring in shrubland vegetation only (see Anso *et al.* submit.a), and its close relationship to *Adenopterus*.

Diagnosis. Small, elongate species without a tympanum on both TI sides, and without a stridulum or even a file in males. General coloration homogeneous, without highly coloured spots or lines. TIII with 6 (rarely 7) inner and 6 outer subapical spurs; serrulation regular and numerous; 3 inner and 3 outer apical spurs, as in other New Caledonian genera. HWs longer than FWs in males and females. **Male.** Subgenital plate elongate, but not acute; with a transverse furrow at mid length, its distal part narrowed from the furrow toward the apex, broadly triangular and with a longitudinal furrow (Fig. 25B). Male tergite IX furrowed (Fig. 24C). Male genitalia with the same structure as *Adenopterus*, but the pseudepiphallic sclerite very long and narrow, somewhat oval; pseudepiphallic apex impair, raised and more or less flattened toward pseudepiphallic sclerite; with a pair of lateral lobes raised dorsally, one on each side of pseudepiphallic apex; pseudepiphallic anterior margin raised dorsally, but not plicated, and widened laterally ; ectophallic fold and pseudepiphallic parameres very small, located close to pseudepiphallic sclerite distal margin. **Female.** Subgenital plate concave distally, as in *Calscirtus*. Ovipositor somewhat flattened dorso-ventrally, the apex not widened but with numerous, parallel striae (Fig. 24H-J). Female genitalia having the shape of a small ring (Fig. 25H, I).

Description. Small species with narrow FWs and short HWs extended beyond FWs, in both males and females. Head dorsum flat, but very slightly rounded; eyes not protruding; ocelli all of the same size, the distance between one lateral and the median ocelli greater than the distance between the two lateral ocelli; median ocellus far from fastigium apex, from which is is separated by a short longitudinal furrow. Fastigium triangular, its apex not as wide as the scapes; scapes longer than wide. Maxillary palpi (Fig. 25A) short, joint 4 distinctly shorter than joints 3 and 5, joint 5 truncated over half of its length. Pronotum transverse; DD anterior margin concave, posterior margin sinuate; LL quandrangular. TI without a tympanum on both

inner and outer sides; 3 very small apical spurs. TII with 4 very small apical spurs. TIII with 3 inner and 3 outer apical spurs; outer apical spurs very small, the median the longest; inner apical spurs longer, the dorsal the longest, as long as basitarsomere III. TIII with 6 outer and 6 (sometimes 7) inner subapical spurs; spurs all of a similar size, alternate except for the first (most apical) ones. TIII flattened dorsally, its lateral margins somewhat higher and with many large and regular-sized teeth on both inner and outer margins, between and above subapical spurs. Basitarsomeres III with 1 outer spine only (no inner spine), in addition to apical spines.

Coloration. Homogeneous, without highly coloured spots or lines. Legs yellowish or yellow brown. FWs grey.

Male. Metanotum and tergites without glandular structures. FWs longer than the body. HWs extended beyond the FWs. No stridulum, not even a stridulatory file. FW venation with few longitudinal parallel veins separated by transverse veins, all as strong. Tergite IX deeply furrowed along median line, this furrow extended by a crest on tergte VIII (in all species ? see Fig. 24C). Supra anal plate squared. Subgenital plate (Fig. 25B) elongate, with a transverse furrow at mid length; distal part triangular, not acute, with a longitudinal median furrow.

Male genitalia. Figs 24D-G, 26D-H). Symmetrical. Pseudepiphallic sclerite long and narrow, regularly narrowed toward apex after mid length; anterior margin raised dorsally but straight, extended laterally as a squared plate connected to long and thin rami. Pseudepiphallic apex with one pair of lateral lobes, located on each side of pseudepiphallic median lobe. Pseudepiphallic parameres cylindrical, thin, with one apical hook. Ectophallic fold short, not reaching pseudepiphallic distal margin, simple (no developed margins); ectophallic apodemes not extending beyond pseudepiphallic anterior margin; no ectophallic arc. Endophallic sclerite long and paired. Dorsal cavity lacking.

Female. FWs and HWs as in male. Subgenital plate well-developed, its apical margin concave surrounding the base of the ovipositor (Fig. 25F, G). Ovipositor straight, somewhat flattened dorso-ventrally and not widened laterally before apex; ornementation as on Figure H-J, with numerous, parallel longitudinal striae (Fig. 24J).

Female genitalia. Fig. 25H-I. Copulatory papilla very small and little sclerotized, having the shape of a low ring.

Distribution. Known from material originating from the maquis vegetation of the South of Province Sud (*Pixipterus punctulatus* Desutter-Grandcolas & Anso, n. sp., *Pixipterus* sp., *Pixipterus fusculus* Desutter-Grandcolas & Anso, n. sp., *Pixipterus minutus* Desutter-Grandcolas & Anso, n. sp.) and at Mont Mou (*Pixipterus mou* Desutter-Grandcolas, n. sp.). Two specimens were collected in maquis plots invaded by the little fire ant, *Wasmannia auropunctata*.

Pixipterus punctulatus Desutter-Grandcolas & Anso, n. sp. (sp 3)

(Figs 24A-G, 25A-D)

Type locality. New Caledonia, Grande Terre, Pic du Grand Kaori, 22.28226° S 166.89601° E.

Type material. Holotype: New Caledonia, Grande Terre, Pic du Grand Kaori, maquis, 22.28460° S 166.89436° E, 10.vii.2013, by day, 1 male, fn NOU39-PGKW3-6, parcel with *Wasmannia auropunctata*, on low vegetation, J. Anso (MNHN-EO-ENSIF1107). **Paratype, 1 male:** New Caledonia, Grande Terre, Chutes de la Madeleine, maquis, 22.23568° S 166.85268° E, 20.ii.2014, at night, 1 male, fn MAMAD2-18, on vegetation, J. Anso (MNHN-EO-ENSIF1100).

Etymology. Species named after its pattern of coloration (coloration generally light yellowish brown, with many brown dots and setae on pronotum).

Diagnosis. Within the genus, small, lightly coloured species. Head dorsum very light yellowish brown, with a wide median, longitudinal darker band including a thin yellow line, and diffuse ones behind the eyes; fastigium not dark brown between the ocelli (*contra P. fusculus* Desutter-Grandcolas & Anso, n. sp.); ocelli light yellow, with a small dark spot, the median ocellus connected to each lateral ocellus by a yellow line running along the fastigium lateral side; cheeks and face light yellowish, with a wide lighter band under each eye, a thin line under the median ocellus, a pair of small dark spots above epistemal suture, and a short dark line under the corner of each eye; pronotum light yellowish brown with many dark brown spots (setae); legs light yellowish brown, except light yellow FI and brown TIII. Male genitalia small; pseudepiphallic latero-apical lobes straight, not curved; ectophallic fold straight, not widened before apex.

Description. In addition to the characters of the genus: Maxillary palpi as on Fig. 25A. TIII inner serrulation: no spine between apical and subapical spurs, and between subapical spurs 1 and 2; 0 – 1 (mean 0.3) spine between subapical spurs 2 and 3; 1-2 (mean 1.3) spines between subapical spurs 3 and 4; 2 spines between subapical spurs 4 and 5; 2-3 (mean 2.8) spines between subapical spurs 5 and 6; 10-12 (mean 11.3) spines above subapical spur 6. TIII outer serrulation: no spine between apical and subapical spurs, and between subapical spurs 1 and 2; 1 spines between subapical spurs 2 and 3; 2 spines between subapical spurs 3 and 4; 2-3 (mean 2.5) spines between subapical spurs 4 and 5; 3-4 (mean 3.3) spines between subapical spurs 5 and 6; 15-18 (mean 16) spines above subapical spur 6.

Coloration. Head and pronotum light yellowish brown, without a dark brown on fastigium; setae bases marked with dark brown spots, especially on pronotum; head dorsum with a faint longitudinal darker band and a thin light yellow median line; face and cheeks light yellow, with two brown dots above epistemal suture and a broken brown line under each eye. Maxillary palpi light yellow; joint 5 brown on distal half. Scapes light yellow, the inner margins light brown. Legs light yellowish brown, FI light yellow and TIII brown except for yellow spurs. FWs grey with brown veins and many white setae.

Male. FW dorsal field with seven longitudinal veins; lateral field with parallel oblique veins. Subgenital plate with the distal part wide and foliaceous (Fig. 25B).

Male genitalia. Figs 24D-G, 25C, D. Smaller, compared to *Pixipterus mou* Desutter-Grandcolas & Anso, n. sp. Lateral lobes of pseudepiphallic sclerite straight, not curved (Figs 24D, 25C). Ectophallic fold hardly curved laterally, without widened margins (Fig. 24E, F).

Female. Unknown.

Variation. The male paratype has 7 inner subapical spur on one TIII, with 2 spines between subapical spurs 6 and 7, and 9 spines above spur 7. Its male genitalia slightly differs from those of the holotype (compare Fig. 25C and Fig. 25D).

Measurements (in mm).

	iod	PronL	PronWp	FWL	HWL	FIIIL	FIIIW	TIIIL
Holotype	1.1	1.9	2.5	8.4	10.6	7.3	1.9	6.9
Paratype	1.1	1.9	2.6	9.3	11.6	7.8	2	7

Habitat and life history traits. *Pixipterus punctulatus* Desutter-Grandcolas & Anso, n. sp. lives in low sclerophylous shrubland, where it is found on low trees.

Pixipterus sp. Desutter-Grandcolas

(Figs 24H-J 25H, I)

Examined material. Holotype: New Caledonia, Grande Terre, Col de Mouiranges, S22.225432 E166.655077, 25.vii.2015, jour, 1 female, fn 2015-3, maquis, dry litter under small tree, L. Desutter-Grandcolas (MNHN-EO-ENSIF3941). Molecular sample 2015-LDG 543.

We separate here one female of *Pixipterus* sp. which has been collected as a juvenile in a maquis vegetation close to Bois du Sud and raised to adulthood in laboratory: this is the only female in good condition we have for the genus and it allows to describe and illustrate the ovipositor and female genitalia. It does not belong to the species described within the genus.

In addition to its relatively large size for the genus (see measurements), the female of *Pixipterus* sp. could be characterized by its coloration (unfortunately not enough preserved to allow the formal description of the species): FWs light grey-brown with brown veins; legs more light yellowish brown, with perhaps brown marks on femora; face with perhaps four brown longitudinal lines under the antennal pits and a brown spot under the lower angle of the eyes; head dorsum yellowish brown, without a brown spot at fastigium base; cheeks, maxillary palpi and antennae light yellowish; pronotum yellowish brown, its margins marked with brown (thin line on anterior margin, wide line on distal margin); cerci light yellowish. TIII inner serrulation: no spine between apical and subapical spurs, and between subapical spurs 1 and 2, and spurs 2 and 3; 1-2 spines between subapical spurs 3 and 4; 2 spines between subapical spurs 4 and 5; 2-4 spines between subapical spurs 5 and 6; 12-15 spines above subapical spur 6. TIII outer serrulation: no spine between apical and subapical spurs, and between subapical spurs 1 and 2, and spurs 2 and 3; 2 spines between subapical spurs 3 and 4; 3 spines between subapical spurs 4 and 5, and between spurs 5 and 6; 16-17 spines above subapical spur 6. The subgenital plate is deeply concave distally, surrounding the base of ovipositor as in *P. fusculus* Desutter-Grandcolas & Anso, n. sp. Its ovipositor is straight, and not widened at apex; apex ornementation as in Fig. 24H-J, with many parallel,

longitudinal striae (Fig. 24J). As to female genitalia (Fig. 25H, I), the copulatory papilla is very small and little sclerotized, having the shape of a low ring.

Measurements (in mm).

	iod	PronL	PronWp	FWL	HWL	FIIIL	FIIIW	TIIIL	ovip.
female	1.3	2.3	2.9	10.7	12.9	8.2	2.3	7.6	7.8

Habitat and life history traits. *Pixipterus sp.* lives in open habitat, on the vegetation in low sclerophyllous maquis. It has been found hidding in dry leaf litter under a low tree (Fig. 39).

Pixipterus minutus Desutter-Grandcolas & Anso, n. sp.

(Fig. 25E)

Type locality. New Caledonia, Bois du Sud, Col de Ouénaru, maquis, 22.17321° S 166.76093° E.

Type material. Holotype: New Caledonia, Bois du Sud, Col de Ouénaru, maquis, 22.17321° S 166.76093° E, 23.iv.2013, by day, 1 male, fn BDS3-9, on vegetation, parcel with *Anoplolepis gracilipes*, J. Anso (MNHN-EO-ENSIF1113). Bad condition.

Diagnosis. We separate here a male specimen which differ from the other species of *Pixipterus* Desutter-Grandcolas & Anso, n. gen. by its smaller size (compare measurements), male genitalia (pseudepiphallic sclerite very long and thin, apex as on Fig. 25E) and coloration (see below).

Description. In addition to the characters of the genus: Maxillary palpi as in *P. punctulatus* Desutter-Grandcolas & Anso, n. sp., but joint 4 shorter. TIII inner serrulation: no spine between apical and subapical spurs, and between subapical spurs 1 and 2; 1 spine between subapical spurs 2 and 3, and between subapical spurs 3 and 4; 1-2 spines (mean 1.5) between subapical spurs 4 and 5; 2 spines between subapical spurs 5 and 6; 13-14 (mean 13.5) spines above subapical spur 6. TIII outer serrulation: no spine between apical and subapical spurs, and between subapical spurs 1 and 2; 1 spine between subapical spurs 2 and 3, and between

subapical spurs 3 and 4; 2 spines between subapical spurs 4 and 5; 3 spines between subapical spurs 5 and 6; 16-18 (mean 17) spines above subapical spur 6.

Coloration. Close to that of *P. punctulatus* Desutter-Grandcolas & Anso, n. sp., but head somewhat darker.

Male genitalia. Fig. 25E. Pseudepiphallic sclerite longer and more narrow than in the other species, and distinctly narrower near its base; lateral lobes longer and more narrow; median lobes bent over the pseudepiphallic sclerite, not straight as in the other species. Pseudepiphallic parameres as in the other species of the genus. Ectophallic fold as in *P. punctulatus* Desutter-Grandcolas & Anso, n. sp., but with extended lateral margins.

Female. Unknown.

Measurements (in mm).

	iod	PronL	PronWp	FWL	HWL	FIIIL	FIIIW	TIIIL
Holotype	1.1	1.9	2.5	7.5	__	6.8	1.8	6.7

Habitat and life history traits. *Pixipterus minutus* Desutter-Grandcolas & Anso, n. sp. lives in open habitat, low sclerophyllous shrubland, in the southern part of New Caledonia.

Pixipterus fusculus Desutter-Grandcolas & Anso, n. sp.

(Figs 25F, G, 26A-C)

Type locality. New Caledonia, Grande Terre, Pic du Grand Kaori, 22.28226° S 166.89601° E.

Type material. Holotype: New Caledonia, Grande Terre, Pic du Grand Kaori, maquis, 22.28460° S 166.89436° E, 10.vii.2013, by day, 1 female, fn PGKW3-7, parcel with *Weismannia auropunctata*, on vegetation, J. Anso (MNHN-EO-ENSIF1110), ovipositor broken.

Etymology. Species named after the coloration of its head, with a dark spot on the fastigium, between the ocelli.

Diagnosis. Within the genus, species somewhat larger with a dark spot on head dorsum, at the level of the fastigium. Male unknown. Female. Subgenital plate concave distally, surrounding ovipositor basis (Fig. 25F, G).

Description.

Within the genus, species somewhat wider than the other species (provided width is not associated with sex). Maxillary palpi as in *P. punctulatus* Desutter-Grandcolas & Anso, n. sp. TIII inner serrulation: no spine between apical and subapical spurs, and between subapical spurs 1 and 2; 1 spine between subapical spurs 2 and 3; 2 spines between subapical spurs 3 and 4; serrulation damaged between subapical spurs 4 and 5; 2 spines between subapical spurs 5 and 6; 12 spines above subapical spur 6. TIII outer serrulation: no spine between apical and subapical spurs; 1 spine between subapical spurs 1 and 2; 2 spines between subapical spurs 2 and 3; 3 spines between subapical spurs 3 and 4, 4 and 5, and 5 and 6; 16 spines above subapical spur 6.

Coloration. Head dorsum yellowish, with darker lines on the occiput; fastigium distinctly dark brown (Fig. 26A, B). Cheeks yellowish with a dark brown spot below the eye corner (Fig. 26C). Face dark brown, with yelowish under the antennal pits. Maxillary palpi dark brown, the bases of joints 3 and 4 yellowish. Scapes and antennae yellowish brown. Legs all light brown, the knees and distal part of tibiae I, II darker; TIII brown, spurs and spines yellow with dark tips. Sternites and cerci light yellow; tergites brown (?).

Female. FWs longer than the abdomen; HWs extended beyond FWs by less than one pronotum length; FW venation as in males. FWs grey, with many short whitish setae; veins brown. Subgenital plate distal margin deeply concave, extending on each side of ovipositor basis; each lobe with a large area without long setae and probably glandular (Fig. 25F, G). Ovipositor broken close to its base.

Female genitalia. Copulatory papilla not observed.

Measurements (in mm).

	iod	PronL	PronWa	PronWp	FWL	FWW	HWL	FIIIL	FIIIw	TIIIL	OL
Holotype	1.3	2.3	2.5	3	9.9	--	11.8	8.2	2.4	7.7	broken

Habitat and life history traits. *Pixipterus fusculus* Desutter-Grandcolas & Anso, n. sp. lives in the southern part of New Caledonia in maquis vegetation.

Pixipterus mou Desutter-Grandcolas, n. sp.

(Fig. 26D-H)

Type locality. New Caledonia, Grande Terre, Mont Mou, maquis.

Type material. Holotype: New Caledonia, Grande Terre, Mont Mou, 550 m, S22°04'34.2" E166°20'9.9", 14.xii.1996, jour, 1 male, fn1, maquis, L. Desutter-Grandcolas (MNHN-EO-ENSIF3631). **Paratype, 1 male.** New Caledonia, Grande Terre, Mont Mou, maquis intermédiaire, 22°03'57.1"S 166°20'35.5"E, 1047m, 26.iv.2009, jour, 1 male, TR73, herbes hautes en bord de piste, T. Robillard (MNHN-EO-ENSIF3632).

Etymology. Species named its place of origin.

Diagnosis. Within the genus, species characterized by its coloration pattern (head and pronotum reddish brown; a wide yellow band below the eyes; posterior margin of the cheeks yellow; maxillary palpi light yellow, joint 5 dark brown with lighter base; FI and FII yellow, TI, TII and hindleg darker), and its male genitalia (pseudepiphallic sclerite wider than in *P. punctulatus* Desutter-Grandcolas & Anso, n. sp. and *P. minutus* Desutter-Grandcolas & Anso, n. sp.) and not narrowed close to its base (*contra P. minutus* Desutter-Grandcolas & Anso, n. sp.); lateral lobes of pseudepiphallic sclerite as on Fig. 26H (compare with Fig. 24G); ectophallic fold widened laterally at the level of pseudepiphallic parameres). Female unknown.

Description. In addition to the characters of the genus: Maxillari palpi as in *P. punctulatus* Desutter-Grandcolas & Anso, n. sp. TIII inner serrulation: no spine between apical and subapical spurs, and between subapical spurs 1 and 2; 0-1 spine (mean 0.3) between subapical spurs 2 and 3; 1 spine between subapical spurs 3 and 4, and between subapical spurs 4 and 5; 3-2 spines (mean 2.3) between subapical spurs 5 and 6; 11-12 (mean 11.3) spines above subapical spur 6. TIII outer serrulation: no spine between apical and subapical spurs, and between subapical spurs 1 and 2; 0-1 spine (mean 0.3) between subapical spurs 2 and 3; 1-2

spines (mean 1.8) between subapical spurs 3 and 4; 2-3 spines (mean 2.3) between subpical spurs 4 and 5, and between subapical spurs 5 and 6; 15-17 (mean 16) spines above subapical spur 6.

Coloration. Head dorsum reddish brown, with a very thin, irregular, longitudinal and median yellow line toward the occiput; fastigium reddish brown, the apical furrow dark brown. Ocelli light yellow, not connected by yellow lines. Cheeks light reddish brown, the lower margins and a wide band below the eyes light yellow. Face reddish brown, somewhat lighter below antennal pits and along epistemal suture; with a thin yellow line between antennal pits. Mouthparts light yellow, the anteclypeus brown laterally, the postclypeus with two short brown lines. Maxillary palpi light yellow, joint 5 dark brown with lighter base. Scapes reddish brown, with yellow outer margins. Antennae yellowish. FI and FII yellowish, TI, TII and FIII darker; FIII with faint brown lines on dorsal side; TIII darker than FIII, including spines; spurs yellow; tips of spurs and spines dark brown. Sternites yellowish, cerci darker.

Male. HWs longer than FWs by more than one pronotum length. FWs grey, with many shork, whitish setae; veins dark brown.

Male genitalia. Fig. 26D-H. Wider than the male genitalia of the other species of the genus; as long as those of *P. minutus* Desutter-Grandcolas & Anso, n. sp., but not narrowed close to its base as in the latter species; pseudepiphallic lateral lobes bent as in *P. minutus* Desutter-Grandcolas & Anso, n. sp., but triangular in shape, and acute apically; median lobe as in *P. minutus* Desutter-Grandcolas & Anso, n. sp. Ectophallic fold short, not extending beyond distal margin of pseudepiphallic sclerite, as in other species of the genus, but distinctly widened laterally, at the level of pseudepiphallic parameres (Fig. 26F, G). Endophallic sclerite long, but more distal than in *P. punctulatus* Desutter-Grandcolas & Anso, n. sp. and *P. minutus* Desutter-Grandcolas & Anso, n. sp.

Female. Unknown.

Measurements (in mm).

	iod	PronL	PronWp	FWL	HWL	FIIIL	FIIIW	TIIIL
Holotype	1.2	2	2.5	9.2	11.5	7.8	2.2	7.1
Paratype	1.1	2	2.7	8.9	11	7.4	2.2	7.2

Variation. The male paratype has 7 inner subapical spurs on one TIII, with 1 spine between subapical spurs 6 and 7, and 11 spines above spur 7.

Habitat and life history traits. *Pixipterus mou* Desutter-Grandcolas, n. sp lives preferentially in open habitat, on the vegetation in low sclerophyllous maquis.

Family Trigonidiidae Saussure, 1874

We use this family according to the phylogeny of Chintauan-Marquier *et al.* (2015), and the diagnosis of Desutter-Grandcolas *et al.* (in prep.). Two subfamilies are recognized in the Trigonidiidae, the Trigonidiinae Saussure, 1874 and the Nemobiinae Saussure, 1877. While the former poorly occurs in New Caledonia, the latter is highly diversified and abundant in the leaf litter of all forested areas and along river banks.

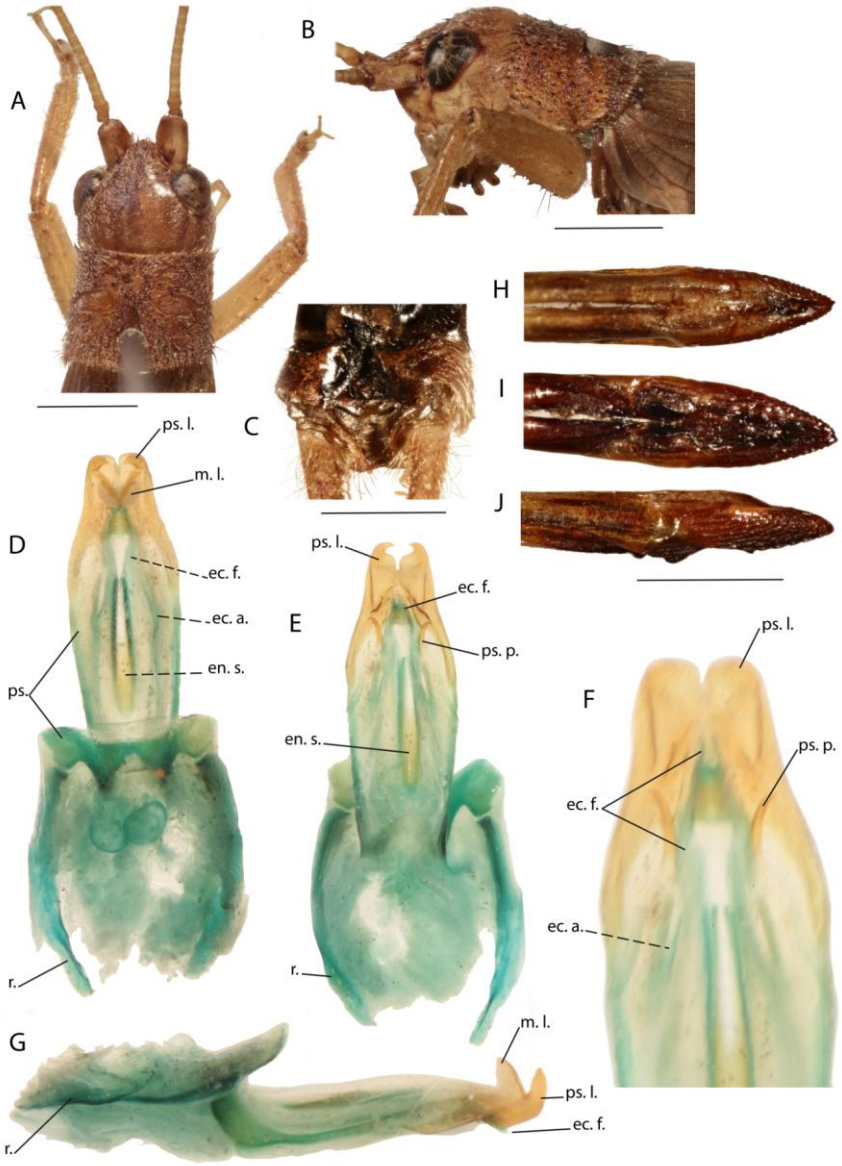

Figure 3.24. *Pixipterus Desutter-Grandcolas, n. gen. Pixipterus punctulatus Desutter-Grandcolas & Anso, n. sp. (A-G) and Pixipterus sp. (H-J): A, B, head and pronotum, dorsal (A), lateral (B); C, male supranal plate and tergite IX; D-G, male genitalia, dorsal (D), ventral (E, F), lateral (G); H, I, J, female ovipositor, dorsal (H), ventral (I), lateral (J). Scales 1 mm. Abbreviations: see Material and methods.*

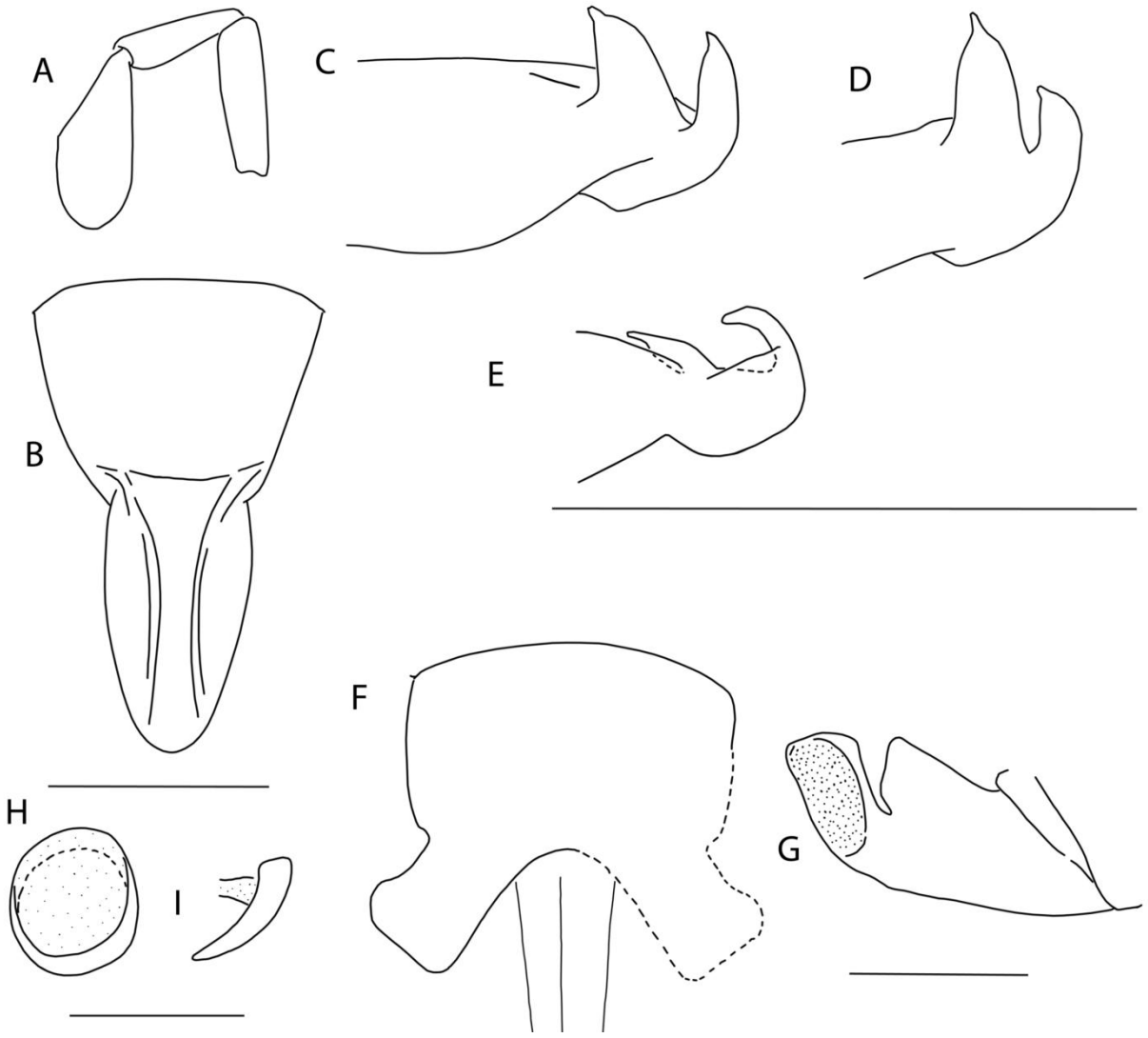

Figure 3.25. *Pixipterus Desutter-Grandcolas, n. gen. Pixipterus punctulatus Desutter-Grandcolas & Anso, n. sp. (A-D), P. minutus Desutter-Grandcolas & Anso, n. sp. (E), Pixipterus fusculus Desutter-Grandcolas & Anso, n. sp. (F, G) and Pixipterus sp. (H, I): A, maxillary palpus; B, male subgenital plate, ventral; C-E, male genitalia, lateral (C, male holotype, D, male paratype MAMAD); F, G, female subgenital plate, ventral (F), lateral (G); H-I, female copulatory papilla, ventral (H), lateral (I). Scales 0.5 mm for H, I; 1 mm otherwise.*

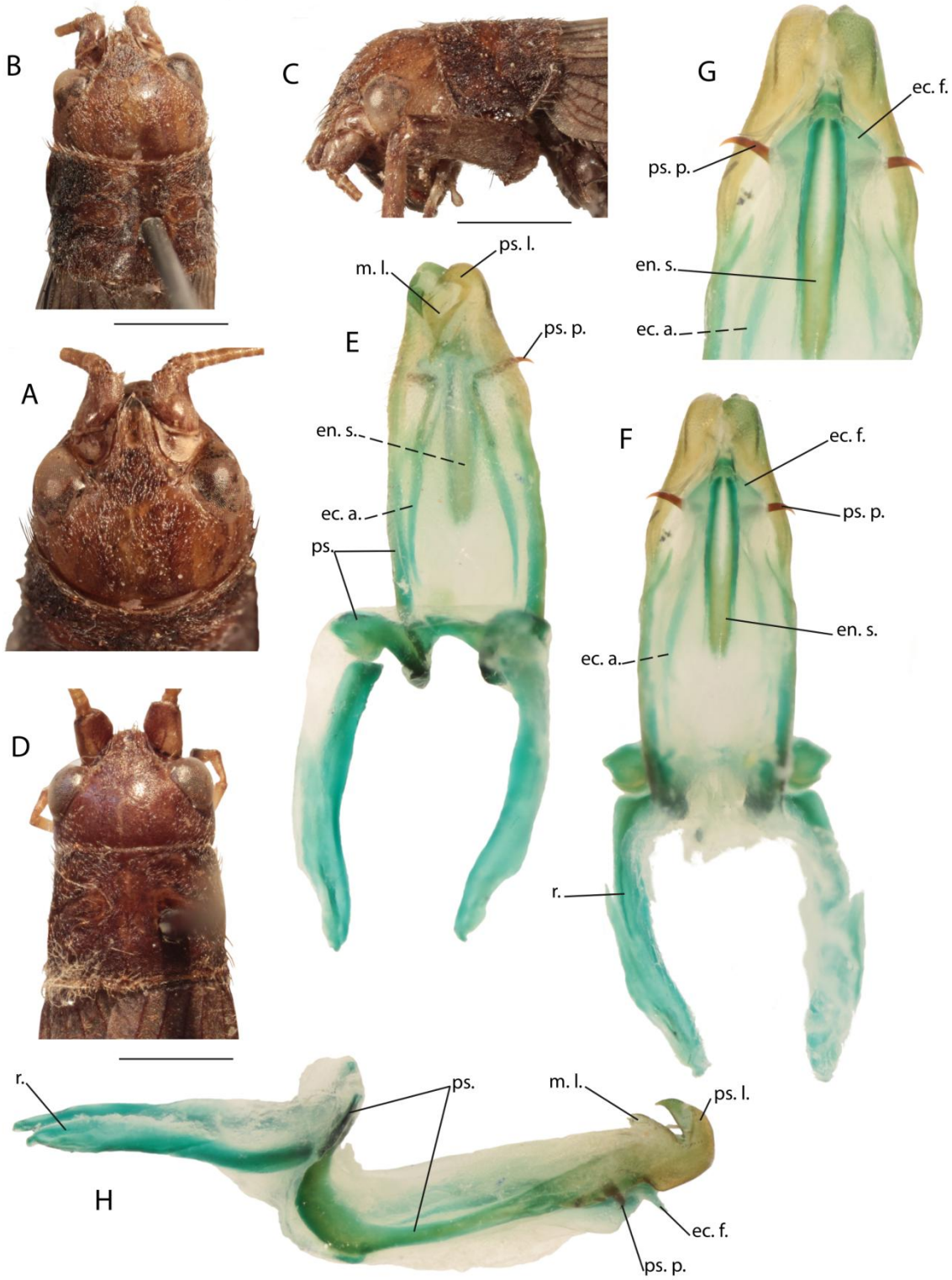

Figure 3.26. *Pixipterus Desutter-Grandcolas, n. gen. Pixipterus fusculus Desutter-Grandcolas & Anso, n. sp. (A-C) and Pixipterus mou Desutter-Grandcolas, n. sp. (D-H): A, head, dorsal; B- D, head and pronotum, dorsal (B, D), lateral (C); D-H, male genitalia, dorsal (E), ventral (F, G), lateral (H). Scales 1 mm. Abbreviations: see Material and methods.*

Subfamily Nemobiinae Saussure, 1877

Genus *Bullita* Gorochov, 1986

Bullita Gorochov, 1986: 693.

= *Bobilla* Otte and Alexander, 1983. Type species *Bobilla bivittata* (Walker, 1869) (Otte *et al.* 1987). Synonymy invalidated by Desutter-Grandcolas (1997d).

= *Fikola* Gorochov, 1986. Type species *Fikola fusca* Gorochov, 1986 (Desutter-Grandcolas 1997d).

Type species. *Bullita pacifica* Gorochov, 1986.

Distribution. Endemic to New Caledonia, with species described from the Monts Koghis (*Bullita fusca* Gorochov, 1986, *Bullita avita* Otte, 1987) and the Col d'Amieu (*B. transversa* Desutter-Grandcolas, 1997, *B. unicolor* Desutter-Grandcolas, 1997). *Bullita pacifica* Gorochov, 1986 is from New Caledonia without precision. We report here for the first time this genus from southern New Caledonia.

Diagnosis. See Desutter-Grandcolas & Anso (submitted).

Bullita fusca (Gorochov, 1986)

(Figs 27A-C, 28A-C, 29)

Fikola fusca Gorochov, 1986: 694.

Bullita fusca, Desutter-Grandcolas 1997b: 167.

Type locality. New Caledonia, Noumea, Mont Koghis.

Type material. New Caledonia, Noumea, Mt. Koghis, 1 female holotype, 14.x.1977, J. Balogh (HNHM).

Material examined. In addition to the material mentioned in Desutter-Grandcolas (1997d): New Caledonia, Grande Terre, Rivière Blanche, rainforest, 22.15142° S 166.68643° E, 10.xii.2013, by night, 3 females, fn FORIV1-6-8, 2 females, fn FORIV2-7, 8; 17.xii.2013, by day, 2 males, fn FORIV1-21, 22, 8 females, fn FORIV1-10, 11, 13, 15-19, 1 male, FORIV2-

12, 2 females, fn FORIV2-13, 14; 17.xii.2013, by night, 1 female, fn FORIV2-10; 11.iii.2014, by night, 1 male, fn FORIV1-24bis; 11.iii.2014, by day, 2 males, fn FORIV2-16, 17; 12.iii.2014, by night, 1 male, fn FORIV1-31; 12.iii.2014, by day, 2 males, fn FORIV2-24, 26, 1 female, fn FORIV2-25; 14.iii.2014, by day, 1 female, fn FORIV1-33, 2 males, fn FORIV1-34, 35, 1 juvenile, fn FORIV1-36, 2 males, fn FORIV2-30, 33, 1 female, fn FORIV2-31; 19.iii.2014, by night, 1 male, fn FORIV1-42, 1 male, FORIV2-37, 1 female, fn FORIV2-38; 19.iii.2014, by day, 1 male, fn FORIV1-49, 1 female, fn FORIV1-50, 2 females, fn FORIV2-34, 35; 20.iii.2014, by night, 2 juveniles, fn FORIV1-56, 61, 5 females, fn FORIV2-43, 44, 45, 46, 49; 26.iii.2014, by day, 1 male, fn FORIV1-63, 3 females, fn FORIV1-62, 64, FORIV2-55, 3 juveniles, fn FORIV1-66, 67, 70, in leaf litter, J. Anso (MNHN).

New Caledonia, Grande Terre, rainforest, Pic du Grand Kaori, 22.28535° S 166.89674° E, 11.xii.2012, by night, 1 female, fn FOGK1-5, 2 males, FOGK1-6, 7, 1 juvenile, fn FOGK1-8, 4 males, fn FOGK2-13-16, 2 females, fn FOGK2-17, 18; 17.xii.2012, by night, 4 males, fn FOGK1-18-21, 4 females, FOGK1-22-25, 3 juveniles, fn FOGK1-26-28, 1 male, fn FOGK2-23, 3 females, fn FOGK2-24-26; 19.xii.2012, by day, 1 male, fn FOGK1-34, 1 juvenile, fn FOGK1-35; 28.xii.2012, by night, 1 female, FOGK2-39, 2 males, fn FOGK1-40, 41; 23.i.2013, by day, 4 females, fn FOGK1-44, 45, FOGK2-47, 48, 3 males, fn FOGK1-46, 47, FOGK2-49, 1 juvenile, fn FOGK1-49; 30.i.2013, by night, 4 males, FOGK2-51-54, 3 females, fn FOGK2-55-57; 12.ii.2013, by day, 1 female, fn FOGK1-67, 1 male, fn FOGK2-62, 1 juvenile, fn FOGK2-61; 23.iv.2013, by day, 1 male, fn FOGK1-71, 1 female, fn FOGK1-70, 1 juvenile, fn FOGK2-67, leaf litter, J. Anso (MNHN).

New Caledonia, Grande Terre, Pic du Pin, rainforest, 22.24680° S 166.82715° E, 16.xii.2013, by night, 3 males, fn FOPDP1-9, 10, 12, 2 females, fn FOPDP1-8, 14, 4 males, fn FOPDP2-1, 4-6, 2 females, fn FOPDP2-2, 3, 2 juveniles, fn FOPDP2-7, 8; 10.ii.2014, by night, 1 male, fn FOPDP1-18, 1 female, fn FOPDP1-19, 3 juveniles, fn FOPDP1-20, 21, 23; 10.ii.2014, by day, 1 male, fn FOPDP2-19, 1 juvenile, fn FOPDP2-20; 10.ii.2014, by night, 2 males, FOPDP2-13, 14, 1 female, fn FOPDP2-15, 1 male, fn FOPDP2-24; 11.ii.2014, by night, 2 males, FOPDP1-29, 30, 4 females, fn FOPDP1-24-27, 3 juveniles, fn FOPDP1-33-35

; 11.ii.2014, by day, 1 male, fn FOPDP1-38, 2 females, fn FOPDP1-39, 40, 1 juvenile, fn FOPDP1-41; 12.ii.2014, by night, 2 males, fn FOPDP1-43, 44, 1 male, FOPDP2-32, 2 juveniles, fn FOPDP1-47, 48; 12.ii.2014, by day, 1 female, FOPDP2-35, 1 juvenile, FOPDP2-37, 3 females, fn FOPDP1-54-56; 13.ii.2014, by day, 1 male, fn FOPDP1-69, 2 females, fn

FOPDP2-38, 39, 3 males, fn FOPDP2-40-42, 3 juveniles, FOPDP2-43-45; 13.ii.2014, by night, 2 juveniles, fn FOPDP1-66, 67, 2 males, fn FOPDP2-46, 47, 1 female, fn FOPDP2-48, 2 juveniles, fn FOPDP2-51, 52, 1 male, fn FOPDP1-65, 5 females, fn FOPDP1-60-64; 10.iii.2114, by day, 2 juveniles, FOPDP1-71, 72; 11.iii.2014, by day, 1 juvenile, fn FOPDP2-54, leaf litter, J. Anso (MNHN).

New Caledonia, Grande Terre, Rivière Blanche, Paraforestier, 22.15280° S 166.68033° E, 10.xii.2013, by night, 2 males, fn PARIV1-7, 9, 1 female, fn PARIV1-6, 1 male, fn PARIV2-6, 1 juvenile, fn PARIV2-7; 11.iii.2014, by day, 1 male, fn PARIV2-20, 1 female, fn PARIV2-21, 1 juvenile, fn PARIV2-24; 11.iii.2014, by night, 2 males, fn PARIV1-13, 14, 1 male, fn PARIV2-35; 12.iii.2014, by night, 1 male, fn PARIV1-28, 1 juvenile, fn PARIV1-30; 12.iii.2014, by day, 2 females, fn PARIV1-35, 36, 2 juveniles, fn PARIV1-37, 38; 14.iii.2014, by day, 2 females, fn PARIV1-39, 40, 1 male, fn PARIV2-42, 2 females, fn PARIV2-43, 44, 1 juvenile, fn PARIV2-45; 17.xii.2013, by day, 2 females, fn PARIV2-11, 12, 3 males, fn PARIV2-13-15; 19.iii.2014, by day, 1 male, fn PARIV2-47, 1 female, fn PARIV2-48, 2 juveniles, fn PARIV2-49, 50, 2 females, fn PARIV1-48, 52, 2 males, fn PARIV1-49, 50, 1 juvenile, fn PARIV1-53; 20.iii.2014, by night, 1 male, fn PARIV1-67, 3 juveniles, fn PARIV1-64-66, leaf litter, J. Anso (MNHN)

Nouvelle Calédonie, Grande Terre, Forêt Nord, paraforestier, 22.32259° S 166.93134° E, 4.xii.2013, by day, 1 female, fn PAFN1-2, 1 male, fn PAFN2-8, 2 females, fn PAFN2-6, 7; 9.xii.2013, by night, 2 males, fn PAFN1-11, 12, 1 female, fn PAFN2-10; 10.xii.2013, by day, 2 males, fn PAFN1-17, 18; 10.xii.2013, by night, 1 male, fn PAFN2-16, 1 female, fn PAFN2-17, 1 juvenile, fn PAFN2-18; 16.xii.2013, by day, 1 male, fn PAFN1-25; 1 male, fn PAFN2-19, 1 female, fn PAFN2-20, 1 juvenile, fn PAFN2-21; 17.xii.2013, by day, 1 male, fn PAFN2-27, 1 female, fn PAFN2-26, 1 juvenile, fn PAFN2-28; 17.xii.2013, by night, 3 males, fn PAFN1-29, 30, 33, 4 females, fn PAFN1-27, 28, 31, 32; 20.i.2014, by night, 1 female, fn PAFN2-37; 11.ii.2014, by day, 1 female, fn PAFN2-50; 12.ii.2014, by night, 1 juvenile, fn PAFN2-55, leaf litter, J. Anso (MNHN).

New Caledonia, Grande Terre, Pic du Grand Kaori, paraforestier, 22.28000° S 166.89383° E,

31.xii.2012, by day, 1 male, fn PAGK1-7, 1 male, fn PAGK2-5, 3 juveniles, fn PAGK2-8-10; 13.viii.2013, by day, 1 female, fn PAGK1-11, 1 juvenile, fn PAGK1-12, 1 female, fn PAGK2-12; 14.viii.2013, by night, 1 female, fn PAGK1-16; 20.viii.2013, by day, 1 female, fn PAGK1-17; 21.viii.2013, by night, 2 females, fn PAGK1-23, 24; 22.viii.2013, by night, 1

male, fn PAGK2-25, 2 females, fn PAGK2-23, 24; 29.viii.2013, by night, 2 females, fn PAGK2-28, 29, leaf litter, J. Anso (MNHN).

New Caledonia, Grande Terre, Pic du Grand Kaori, rainforest, 22.28535° S 166.89674° E, 17.vii.2012, by night, 1 male, fn TGK1-19, 1 female, fn TGK1-20, leaf litter, J. Anso (MNHN).

Diagnosis. Within the genus, *Bullita fusca* is characterized by its male genitalia and coloration (body coloration dark ochre brown to black, with white patterns on tergites 2 to 5: see Fig. 27A, B; legs light ochre; FIII as on Fig. 27C). **Male.** FWs shorter than abdomen, covering about up to tergite 5 (Fig. 27A); ochre, MP yellow over its whole length, with an additional yellowish line along its inner margin. Stridulatory file with 81 - 109 teeth (mean 100, n = 10). Male genitalia (Fig. 28A-C): pseudepiphallic sclerite narrow, its lateral margin almost parallel along its whole length and hardly widened anteriorly (*contra Bullita mourangensis* Anso & Desutter-Grandcolas, n. sp. and *B. obscura* Anso & Desutter-Grandcolas, n. sp.); apical lobes very short and well-separate from one another (contra *B. unicolor* Desutter-Grandcolas, 1997 and *B. transversa* Desutter-Grandcolas, 1997). **Female.** FWs very short, not covering tergite 1 midlength; white. Tergites black; tergites 2 to 5 (rarely only 2 to 4) with a dorsolateral white spot (Fig. 27B; contra *B. unicolor* Desutter-Grandcolas, 1997 and *B. transversa* Desutter-Grandcolas, 1997), most often connected by a white band along tergite distal margin (but see variation paragraphe). Ovipositor size 3.1 – 3.2 mm (mean 3.1, n = 5).

Remark. The material examined is very similar to *Bullita fusca* from the Koghis by its male genitalia (although with longer ectophallic apodemes, extending beyond the rami) and size. Male coloration is also very similar, but FWs are darker (which highlights the ochre MP bordered with light yellow along FW inner margin), as are the legs, with the hind legs light ochre and the legs I and II (especially FI and FII) more brown.

Habitat and life history traits. *Bullita fusca* (Gorochov, 1986) lives mainly in forested area, such as tall maquis to dense forests, and they remain active during the day in the leaf litter. Males emit their calling song during the day in the leaf litter, while they stay static. Calling song starts at sunrise until the dusk. Males and females are abundant in the leaf litter all year round.

Calling song. Fig. 29. Three specimens were collected and recorded in the laboratory, one at

25°C (one song bout) and two at 27°C (three song bouts, mean values given), with a total of 240 echemes and 5500 syllables. At 27°C (25°C in parentheses), the calling song of *Bullita fusca* consists of a repetition of echemes of 0.49 ± 0.04 s (0.55 ± 0.14 s); each echeme is made of 23 ± 1 syllables (26 ± 6), with the following characteristics: syllable duration = 9.9 ± 0.9 ms (10.2 ± 1.2 ms); syllable period = 21.6 ± 1.9 ms (21.2 ± 1.6 ms); syllable duty cycle = 49.8% (49.9%) ; the dominant frequency is 6.1 ± 0.1 kHz (5.9 kHz). Song deposited in MNHN sound library (inventory number MNHN-SO-2016-11, MNHN-SO-2016-12, MNHN-SO-2016-13).

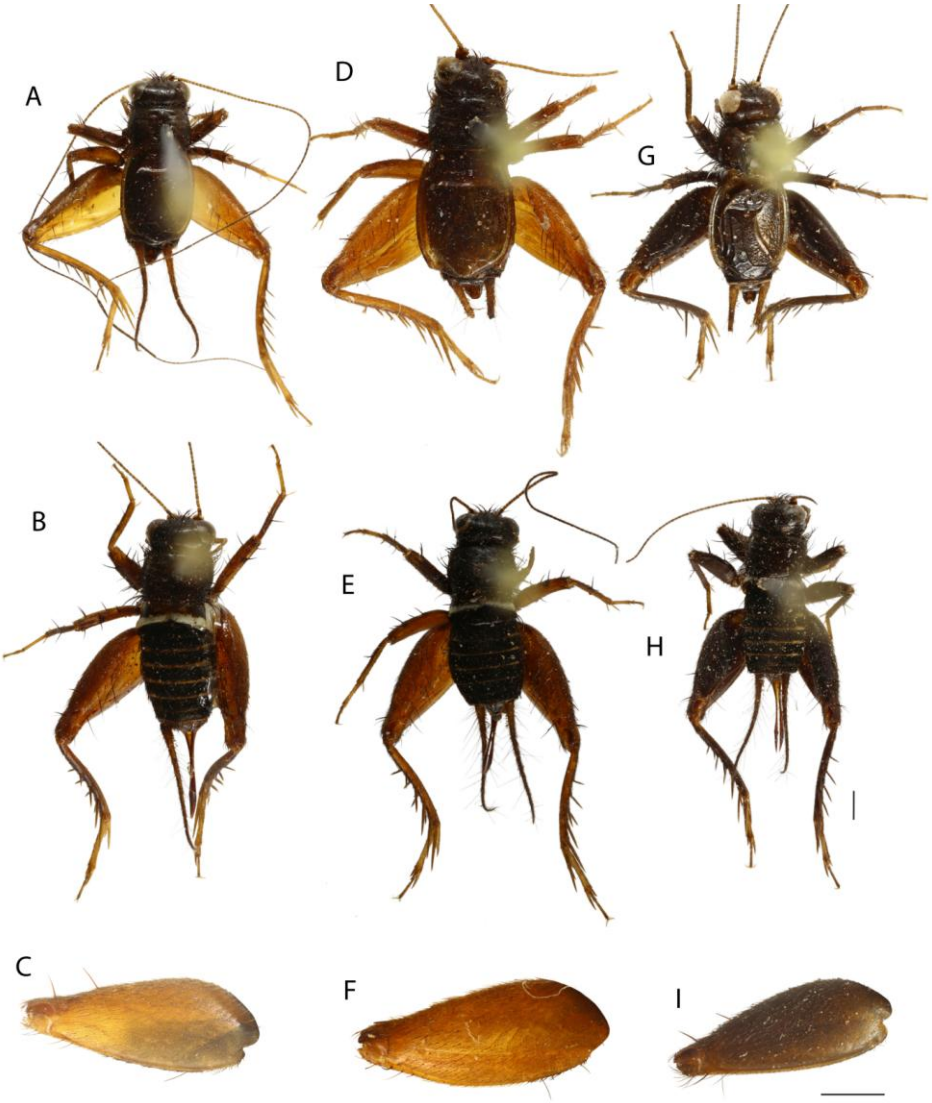

Figure 3.27. *Bullita Gorochov, 1986. Bullita fusca (Gorochov, 1986) (A-C), Bullita mouirangensis Anso & Desutter-Grandcolas, n. sp. (D-F), Bullita obscura Anso & Desutter-Grandcolas, n. sp. (G – I) and Bullita sp. (J): A, D, G, male habitus; B, E, H, female habitus; C, F, I, FIII outer side; J, juvenile. Scales 1 mm.*

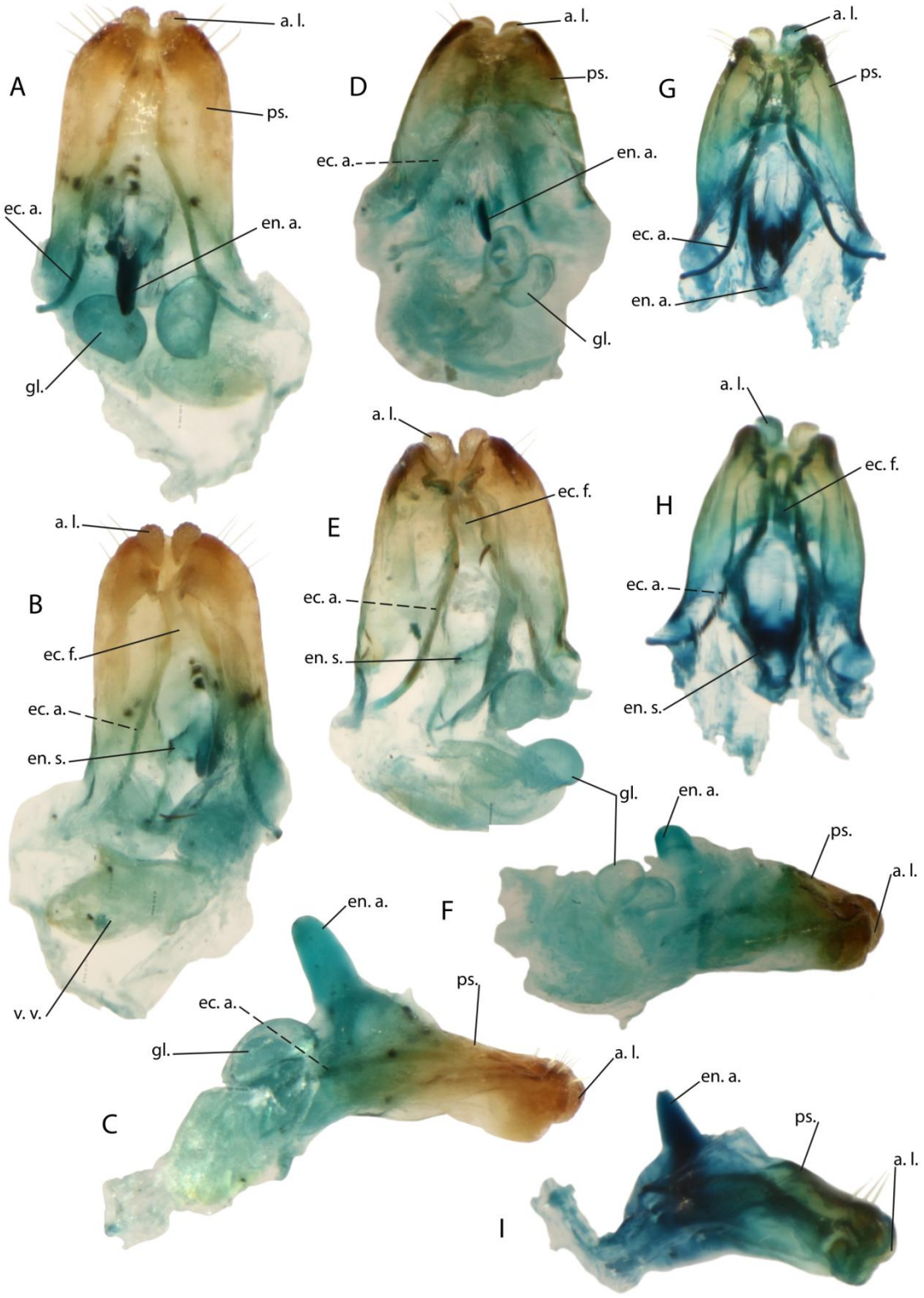

Figure 3.28. *Bullita Gorochov, 1986. Bullita fusca (Gorochov, 1986) (A-B), Bullita mouirangensis Anso & Desutter-Grandcolas, n. sp. (C-D) and Bullita obscura Anso & Desutter-Grandcolas, n. sp. (E - F): male genitalia, dorsal (A, C, E), lateral (B, D, F). Scales 1 mm. Abbreviations: see Material and methods.*

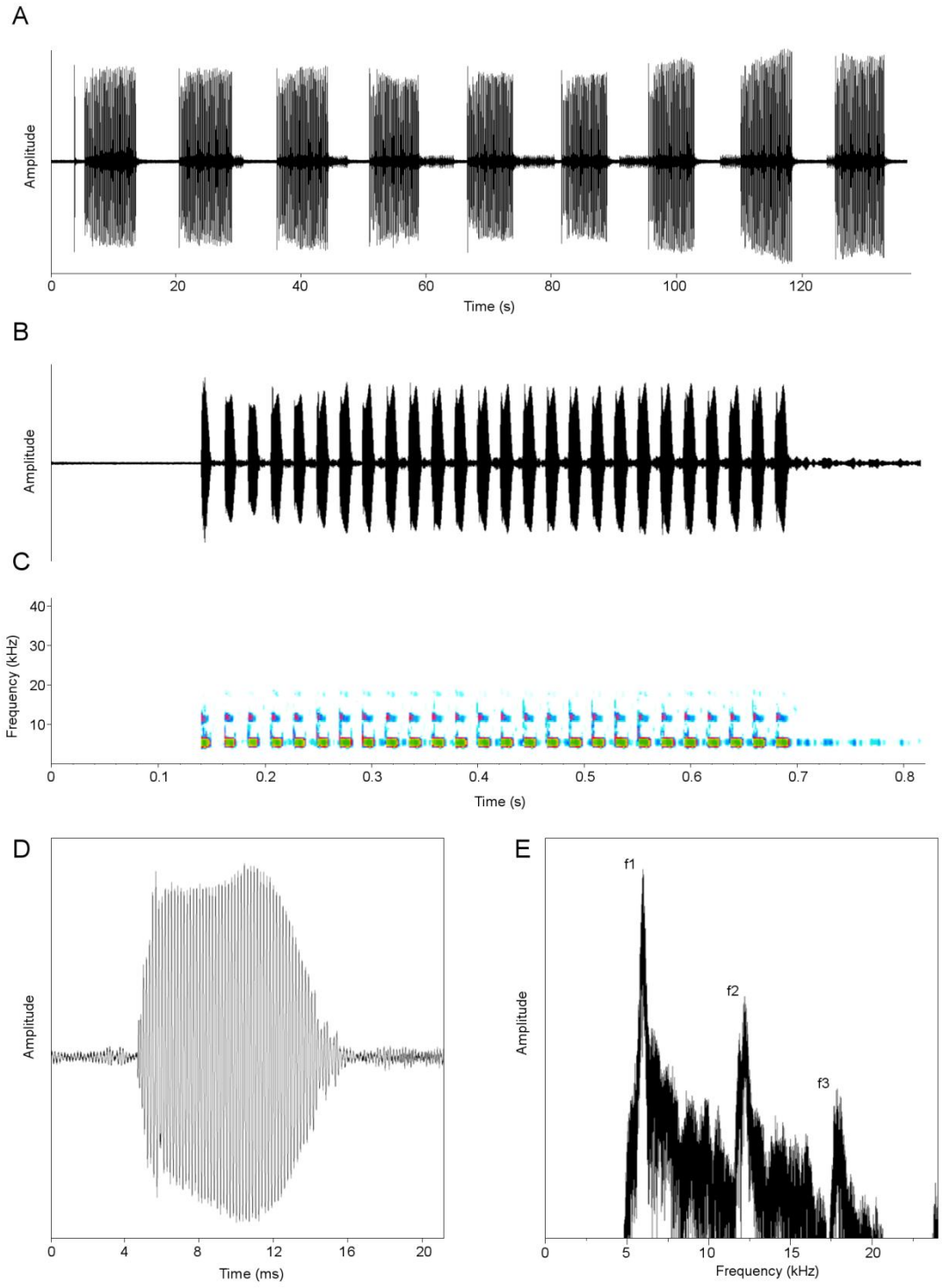

Figure 3.29. *Calling song of Bullita fusca (Gorochov, 1986). Oscillogram showing 9 successive echemes (A); detailed oscillogram (B) and sonogram (C) of one echeme; oscillogram of one syllable (D); logarithmic spectrogram of one syllable (E). Symbols: f1-f3, first (fundamental) to third harmonic frequencies.*

Bullita mouirangensis Anso & Desutter-Grandcolas, n. sp.

(Figs 27D-F, 28D-F, 30)

Type locality. New Caledonia, Grande Terre, Col de Mouiranges, tall forest.

Type material. Holotype. New Caledonia, Grande Terre, Col de Mouiranges, rainforest, 22.20416° S 166.68086° E, 29.viii.2013, by day,1 male, fn FOMOU1-45, J. Anso (MNHN-EO-ENSIF3640). **Allotype.** Same locality as the holotype, 29.viii.2013, by day, 1 female, fn FOMOU2-27 (MNHN-EO-ENSIF3641). **Paratypes, 7 males, 5 females.** Same locality as the holotype, 25.vii.2013, by day, 1 male, fn FOMOU1-4; 13.viii.2013, by night, 1 male, fn FOMOU1-13; 21.viii.2013, by night, 2 males, fn FOMOU1-32 (photo JA), 33; 21.viii.2013, by day, 1 female, fn FOMOU1-20; 22.viii.2013, by night, 1 male, fn FOMOU1-39, 1 female, fn FOMOU1-40; 29.viii.2013, by day, 1 male, fn FOMOU2-26 (photo), 2 females, fn FOMOU1-43, 44; 31.vii.2013, by day, 1 male, fn FOMOU2-1, 1 female, fn FOMOU2-2 (MNHN-EO-ENSIF3642-3648, 3821-3824).

Additional material examined. Same locality as the holotype, 21.viii.2013, by night, 1 male (without PIII), fn FOMOU2-12, 1 juvenile, FOMOU1-35; 21.viii.2013, by day, 1 juvenile, fn FOMOU1-19; 29.viii.2013, by day, 2 juveniles, fn FOMOU1-41, 42. MNHN.

Diagnosis. Size large for the genus, but coloration similar to the other species of the genus (head and pronotum black, legs ochre, tergites black with withish spots in females, see Fig. 27D, E; FIII as on Fig. 27F). **Male.** FWs quite long, covering almost the whole abdomen, only the last tergite and subgenital plate visible dorsally; yellowish brown, shining, the vein separating the dorsal and lateral fields light yellow; stridulatory file with 97 – 101 teeth (mean 99 teeth, n=2). Male genitalia: Pseudepiphallic sclerite (Fig. 28D) clearly short and wide, triangular, narrowed only apically; lateral margins convex in dorsal view; apical lobes comparatively small, not pedunculated, but well separate and not as short as in *B. obscura* Anso & Desutter-Grandcolas, n. sp. **Females.** FWs quite long, reaching tergite I, widely bordered dorsally with white. Abdomen black with pairs of small and narrow, white laterodorsal bands on tergites 2 to 5, fainter toward abdomen tip, the lateral bands on each tergite united by a very thin, median and fainter whitish color (Fig. 27E).

Description. In addition to the characters of the genus (Desutter-Grandcolas & Anso submit.):

Coloration. Fig. 27D-F. Head and pronotum entirely black, the pronotum shining. Eyes grey. Scapes and first article of antennae black brown; distal margin of dorsal side of the scapes white; antennae other wise light ochre or yellowish brown. Maxillary palpi brown; joints 3 and 4 lighter. Legs light ochre, FI and TIII light brown; FIII as on Fig. 27F. Cerci light brown.

Male. Fig. 27D. FWs covering almost the whole abdomen, except for the very last tergites; dorsal field ochre brown, lateral and apical fields darker; longitudinal vein separating dorsal and lateral fields yellow; stridualory file with 97 – 101 teeth (mean 99, n=2). Tergite IX lighter. Subgenital plate entirely black.

Male genitalia. Fig. 28D-F. Pseudepiphallic sclerite distinctly convex laterally (Fig. 28D), not narrowed before apex; distal lobes short, not pedunculated and well apart from each other.

Female. Fig. 27E. Pronotum narrowed distally. FWs quite long for the genus, reaching tergite I; often hidden under the pronotum, only the white distal margin then visible; dorsal field widely bordered with white distally. Abdomen black with pairs of small and narrow, white laterodorsal bands on tergites 2 to 5, fainter toward abdomen tip, the lateral bands on each tergite united by a very thin, median and fainter whitish color. Tergite 8 distal margin white dorsally. Ovipositor straight, shorter than TIII (see measurements below).

Measurements (in mm).

	iod	PronL	PronWp	FWL	FWW	FIIIL	FIIIW	TIIIL	OL
Male holotype	0.8	1.5	2.2	3.2	2.5	4.5	2	3.6	---
Male paratypes	0.8-0.9	1.5-1.6	2.2-2.4	3.4-3.5	2.3-2.4	4.5-4.7	1.9-2.1	3.5-3.7	---
mean (n=3)	0.8	1.5	2.3	3.4	2.4	4.6	2	3.6	---
Female allotype	1.1	1.8	2.1	0.6	---	4.8	2.1	3.7	3.3
Female paratypes	0.9-1.1	1.6	1.8-2.1	0.8	---	4.3-4.5	1.8-2	3.3-3.5	3.3-3.5
mean (n=3)	1	1.7	2	0.7	---	4.5	2	3.5	3.4

Habitat and life history traits. *Bullita mouirangensis* Anso & Desutter-Grandcolas, n. sp. lives in mixed rainforest in the southern part of New Caledonia, where they remain active during the day. Males emit their calling song in the leaf litter during the day: they start at dawn until dusk.

Calling song. Fig. 30. One specimen has been observed while singing and recorded, but not collected; 18 echemes of one song bout were analyzed. At 21°C, the calling song of *Bullita mouirangensis* Anso & Desutter-Grandcolas, *n. sp.* consists of a repetition of echemes of 0.71 ± 0.18 s; each echeme is made of 37.9 ± 9.8 syllables, with the following characteristics: syllable duration = 8.8 ± 1.3 ms; syllable period = 19.1 ± 8.7 ms; syllable duty cycle = 47.6 %; the dominant frequency is 4.96 ± 0.41 kHz. Song deposited in MNHN sound library (inventory number MNHN-SO-2016-14).

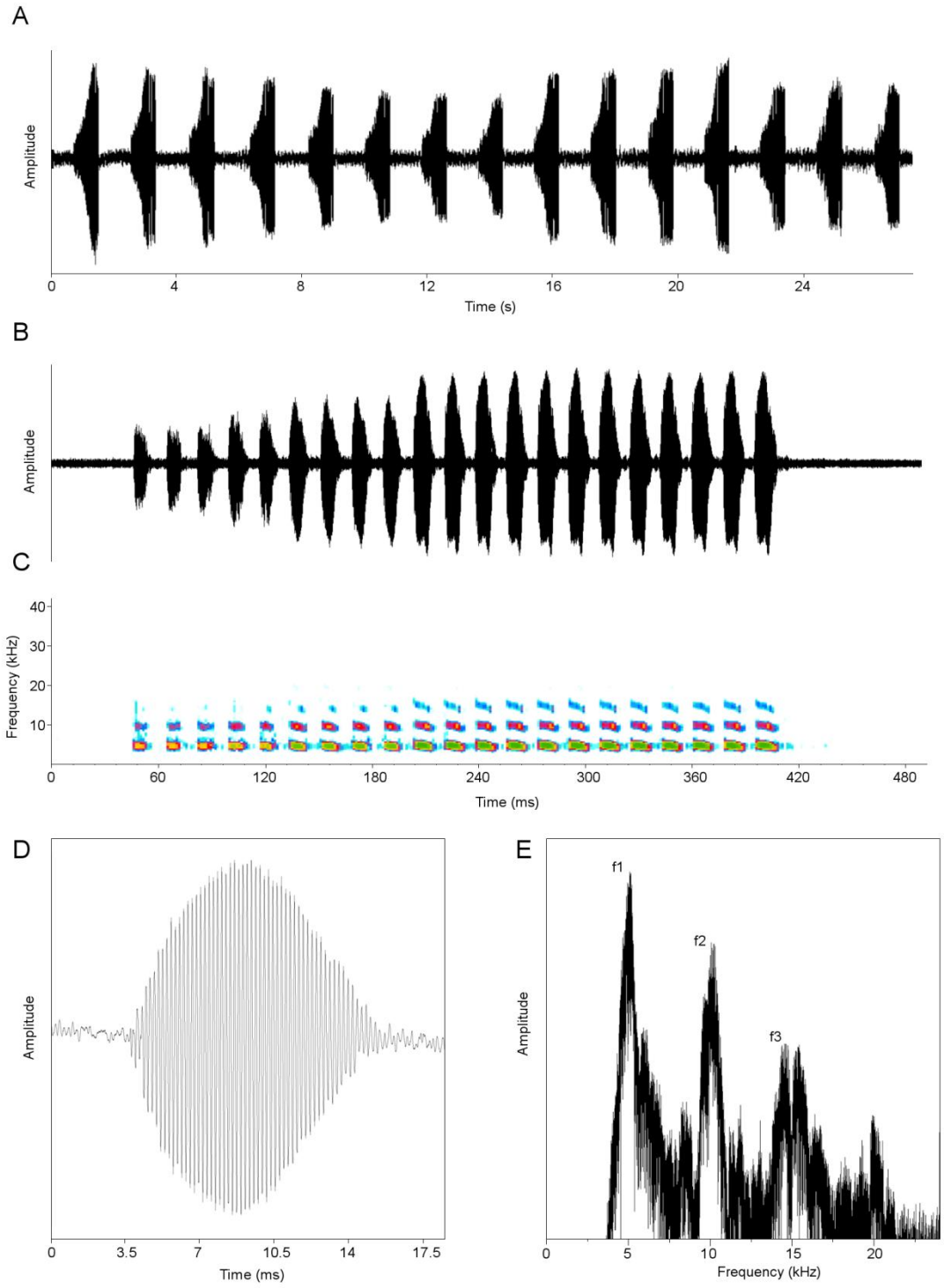

Figure 3.30. *Calling song of Bullita mouirangensis Anso & Desutter-Grandcolas, n. sp. Oscillogram showing 15 successive echemes (A); detailed oscillogram (B) and sonogram (C) of one echeme; oscillogram of one syllable (D); logarithmic spectrogram of one syllable (E). Symbols: f1-f3, first (fundamental) to third harmonic frequencies.*

Bullita obscura Anso & Desutter-Grandcolas, n. sp.

(Figs 27G-I, 28G-I, 31)

Type locality. New Caledonia, Grande Terre, Pépinière de Goro, formation préforestière.

Type material. Holotype. New Caledonia, Grande Terre, Goro, Le Trou, Pépinière, paraforestier, 22.27103° S 166.96355° E, 30.i.2014, by night, 1 male, PAPEP1-16, J. Anso (MNHN-EO-ENSIF3825). **Allotype.** Same locality as the holotype, 13.ii.2014, by day, 1 female, fn PAPEP1-43, in leaf litter, J. Anso (MNHN-EO-ENSIF3826).

Paratypes, 21 males, 23 females. Same locality as the holotype: 9.xii.2013, by day, 2 males, fn PAPEP1-9, 11; 30.i.2014, by night, 1 male, fn PAPEP1-15 (molecular sample LDG 475); 10.ii.2014, by night, 1 male, fn PAPEP1-20; 11.ii.2014, by night, 3 males, fn PAPEP1-22, 24, 25; 12.ii.2014, by night, 1 male, fn PAPEP1-37; 13.ii.2014, by day, 2 males, fn PAPEP1-45, 46; 13.ii.2014, by night, 1 male, fn PAPEP1-49; 10.iii.2014, by night, 2 males, fn PAPEP1-52, 53, leaf litter, J. Anso (MNHN-EO-ENSIF3827-3839).

Same locality as the holotype: 11.ii.2014, by day, 1 male, fn PAPEP2-16; 11.ii.2014, by night, 1 male, fn PAPEP2-24; 13.ii.2014, by day, 1 male, fn PAPEP2-31; 13.ii.2014, by night, 2 males, fn PAPEP2-36, 37; 10.iii.2014, 1 male, fn PAPEP2-47, leaf litter, J. Anso (MNHN-EO-ENSIF3840-3845). Same locality as the holotype: 9.xii.2013, by day, 3 females, fn PAPEP1-4-6; 30.i.2014, by night, 1 female, fn PAPEP1-14; 11.ii.2014, by night, 2 females, fn PAPEP1-23, 29;12.ii.2014, by night, 1 female, fn PAPEP1-36; 13.ii.2014, by day, 3 females, fn PAPEP1-40, 42, 44; 13.ii.2014, by night, 2 females, fn PAPEP1-48, 51; 10.iii.2014, by day, fn PAPEP1-56, leaf litter, J. Anso (MNHN-EO-ENSIF3846-3858). Same locality as the holotype: 11.ii.2014, by day, 1 female, fn PAPEP2-17; 11.ii.2014, by night, 1 female, fn PAPEP2-22;13.ii.2014, by day, 1 female, fn PAPEP2-32; 13.ii.2014, by night, 2 females, fn PAPEP2-38, 39; 10.iii.2014, by day, 5 females, fn PAPEP2-41, 42, 44-46, leaf litter, J. Anso (MNHN-EO-ENSIF3859-3869).

Same locality as the holotype: 26.vii.2015, by day, 2 males, fn Bo1, 2, recorded by J. Anso in laboratory, leaf-litter, J. Anso & L. Desutter-Grandcolas (MNHN-EO-ENSIF3942, 3943).

Additional specimens. Same data as the holotype, 9.xii.2013, by day, 2 males, fn PAPEP1-7, 8 (bad condition); 13.xii.2013, by day, 1 male, fn PAPEP1-41 (no hind leg); 30.i.2014, by night, 2 males, fn PAPEP2-7, 8; 10.ii.2014, by night, 1 male, fn PAPEP2-10 (no genitalia);

12.ii.2014, by night, 1 female, fn PAPEP1-35 (no head and pronotum); 11.ii.2014, by day, 1 female, fn PAPEP2-18 (no hind leg); 11.ii.2014, by night, 3 females, fn PAPEP2-23, 25, 26 (very bad condition); 9.xii.2013, by day, 1 juvenile, fn PAPEP1-12; 10.iii.2014, by day, 2 juveniles, fn PAPEP1-54, 55; 30.i.2014, by night, 1 juvenile, fn PAPEP2-6; 11.ii.2014, by day, 1 juvenile, fn PAPEP2-19; 12.ii.2014, by night, 2 juveniles, fn PAPEP2-28, 29; 13.ii.2014, by day, 1 juvenile, fn PAPEP2-33; 10.iii.2014, by day, 1 juvenile, fn PAPEP2-48, leaf litter, J. Anso, MNHN.

Diagnosis. Very small and darkly colored species (Fig. 27G-I), compared to the other species of the genus: legs black brown, as dark as the body, the tarsomeres and tibia tips somewhat lighter.

Male. FWs black brown; a wide, ivory to yellowish brown line along the outer lateral margin of dorsal field, except at its base. Male genitalia: pseudepiphallic sclerite short, quite wide basally, but distinctly narrowed before the apical lobes; ectophallic apodemes very long and thin, extending well beyond the rami.

Females. FWs short, most often hidden under the pronotum, except for the contrasting and wide white distal margin. Distal margins of tergites 2 to 5, and less distinctly tergite 6, light yellow dorsally, this coloured band wider dorso-laterally. Ovipositor size 2.7 – 2.8 mm (mean 2.7, n=3).

Description. In addition to the characters of the genus (Desutter-Grandcolas & Anso submit.):

Coloration. Fig. 27G-I. Head, pronotum and legs almost entirely shining black; eyes grey to black; scapes and antennae brown, except for a thin ivory line along the dorsal distal margin of the scapes; maxillary palpi light black brown, joint 4 lighter. FIII as on Fig. 27I.

Male. Fig. 27G. FWs covering the abdomen up to tergite IX, except for its white distal margin. Stridulatory file with 83-93 teeth (mean 89, n=3).

Male genitalia. Fig. 28G-I. Small. Pseudepiphallic sclerite narrowed before apex; lateral margins otherwise convex in dorsal view, not parallel, even anteriorly; apical lobes very small, well-apart from one another and not pedunculate.

Female. Fig. 27H. FWs short, distinctly shorter dorsally and longer laterally; dorsally not reaching tergite 1 mid length; distal margin dorsally with a wide white band, interrupted laterally by a short longitudinal vein; lateral field with four longitudinal veins, strongly arcuate, the first and second veins more widely separate, and the Second, third and fourth (more distal) veins parallel and closely set. Tergites 2 to 5 distal margins light yellow dorsally; this coloration fainter on tergite 6. Tergite 8 distal margin white, most often hidden under previous tergites. Ovipositor shorter than TIII, very short (less than 3 mm long).

Measurements (in mm).

	iod	PronL	PronWp	FWL	FWW	FIIIL	FIIIW	TIIIL	OL
Male holotype	0.7	1.3	1.7	2.7	2	3.7	1.7	2.9	---
Males paratypes	0.9	1.3	1.7	3-3.1	2.1-2.2	3.9-4.2	1.6-1.8	3-3.1	---
mean (n=3)	0.8	1.3	1.7	2.9	2.1	3.9	1.7	3	---
Female allotype	0.9	1.5	1.8	0.4	---	3.9	1.7	3	2.7
Female paratypes	0.7-0.9	1.5	1.5-1.7	0.5-0.7	---	4-4.1	1.8	3.1	2.7-2.8
mean (n=3)	0.8	1.5	1.7	0.5	---	4	1.8	3.1	2.7

Habitat and life history traits. *Bullita obscura* Anso & Desutter-Grandcolas, n. sp. lives in leaf litter in tall sclerophyllous maquis. Males emit their calling song in the leaf litter during the day, and remain silent at night.

Calling song. Fig. 31. Two males were collected and recorded in laboratory conditions. Two song bouts were analyzed per specimen, representing 34 echemes and 687 syllables. At 23°C, the calling song of *Bullita obscura* Anso & Desutter-Grandcolas, n. sp. consists of a repetition of echemes of 0.30 ± 0.08 s; each echeme is made of 19 ± 5 syllables, with the following characteristics: syllable duration = 6.9 ± 1.1 ms; syllable period = 15.1 ± 1.9 ms; syllable duty

cycle = 49.3%; the dominant frequency is 6.1 ± 0.1 kHz. Song deposited in MNHN sound library (inventory number MNHN-SO-2016-15, MNHN-SO-2016-16).

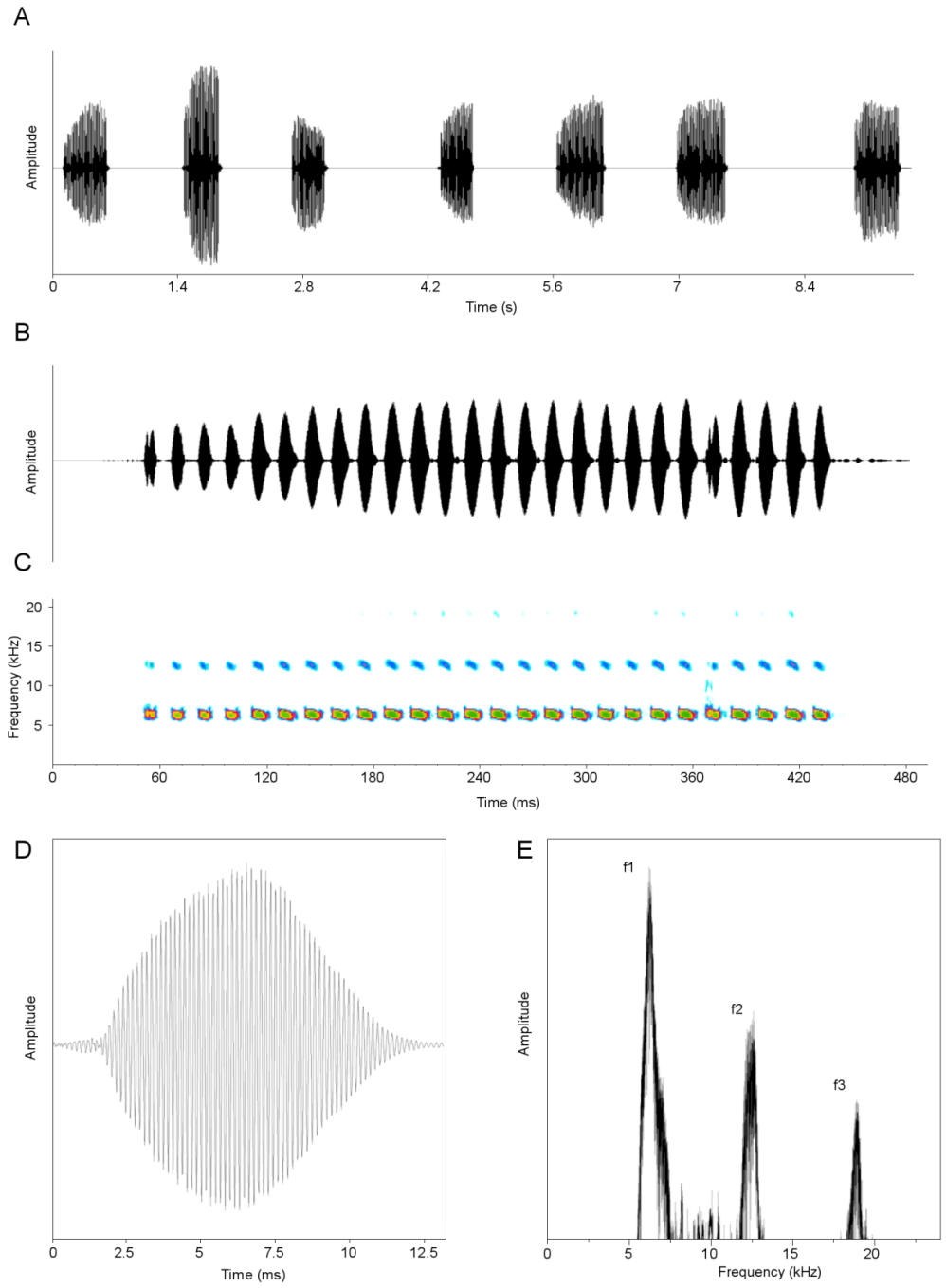

Figure 3.31. *Calling song of Bullita obscura Anso & Desutter-Grandcolas, n. sp. Oscillogram showing 7 successive echemes (A); detailed oscillogram (B) and sonogram (C) of one echeme; oscillogram of one syllable (D); logarithmic spectrogram of one syllable (E). Symbols: f1-f3, first (fundamental) to third harmonic frequencies.*

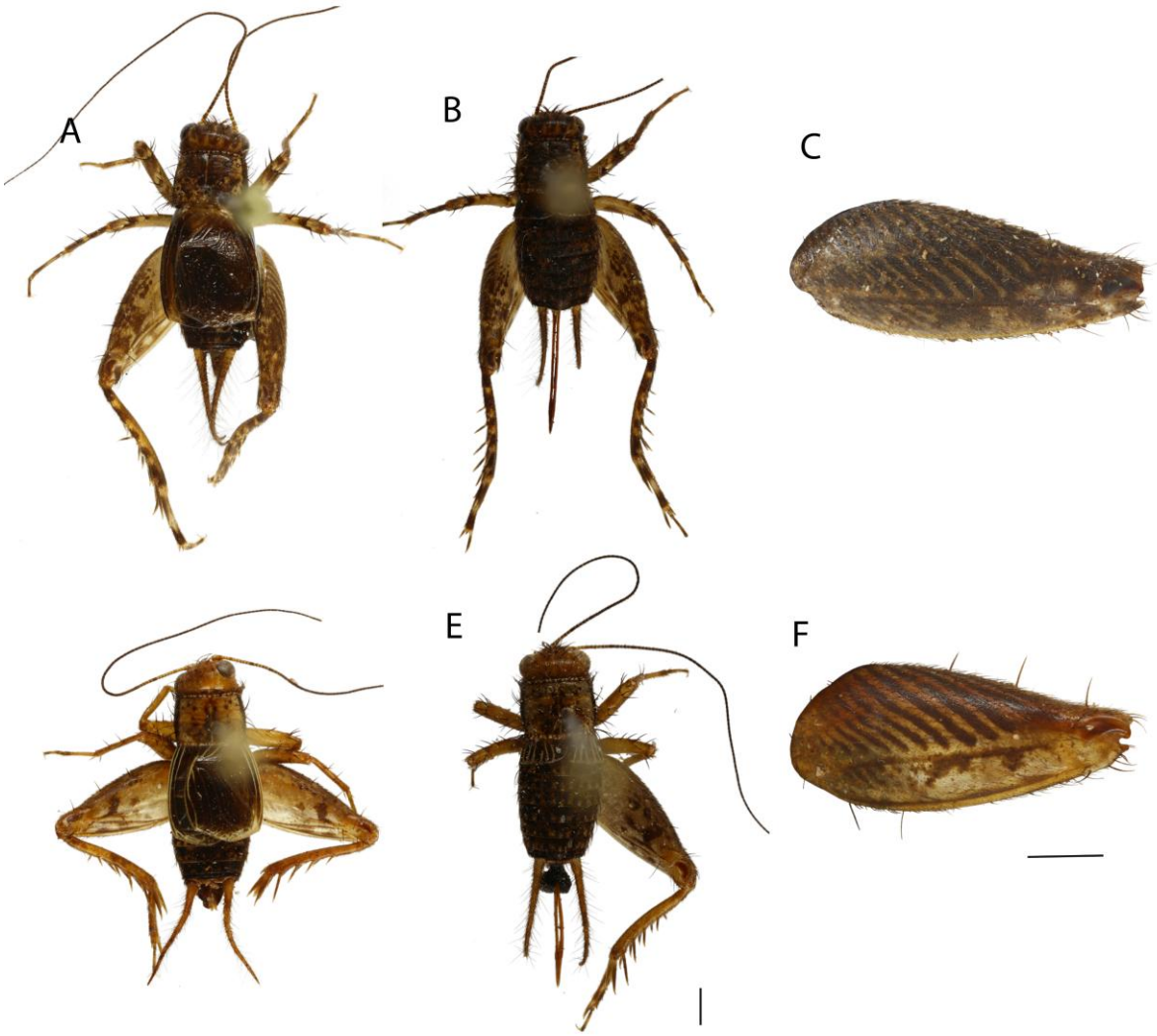

Figure 3.32. *Koghiella Otte, Alexander & Cade, 1987. Koghiella nigris Anso & Desutter-Grandcolas, n. sp. (A-C) and Koghiella flammea Anso & Desutter-Grandcolas, n. sp. (D - F): A, D, male habitus; B, E, female habitus; C, F, FIII outer side. Scales 1 mm.*

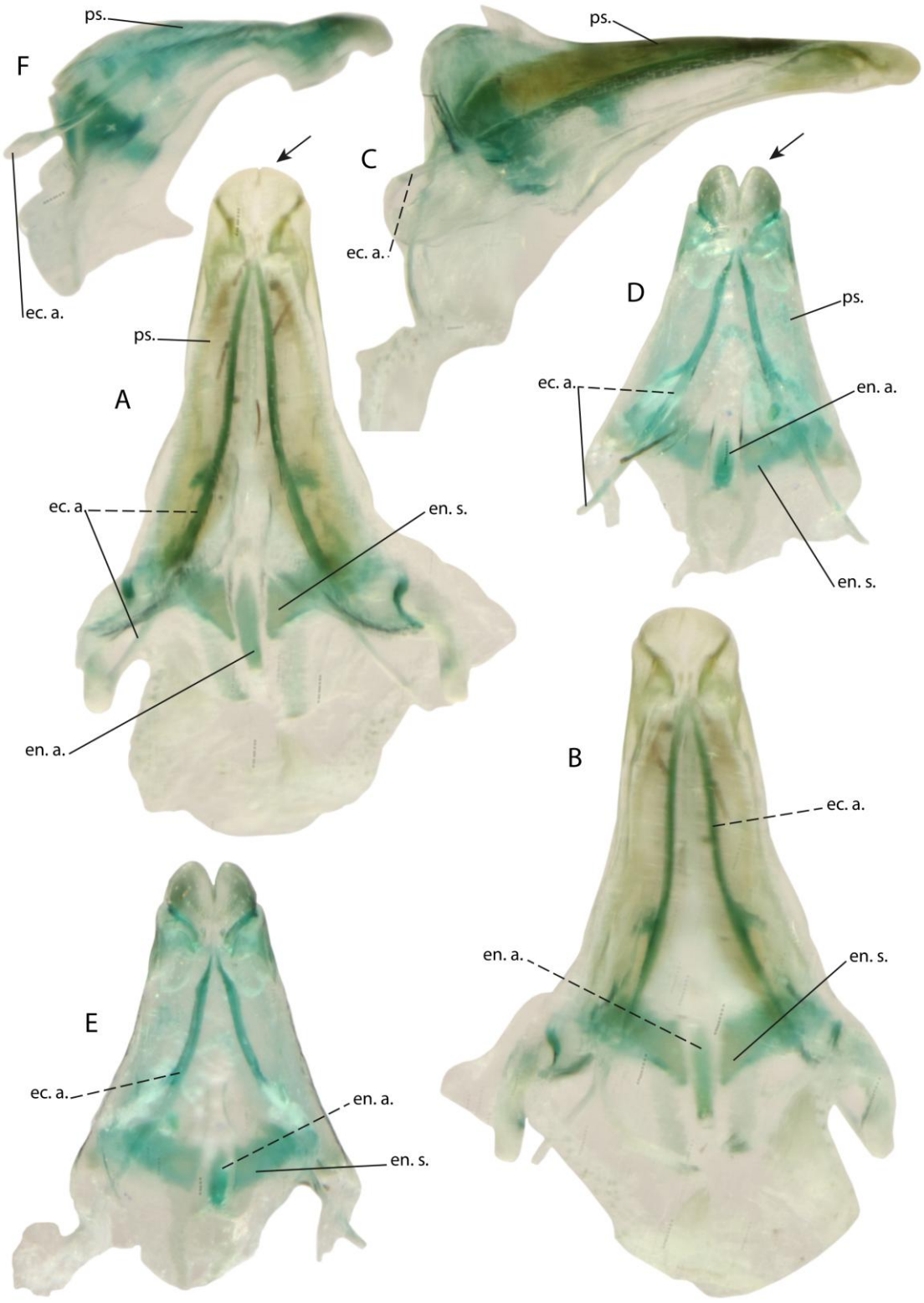

Figure 3.33. *Koghiella Otte, Alexander & Cade, 1987. Koghiella nigris Anso & Desutter-Grandcolas, n. sp. (A-B) and Koghiella flammea Anso & Desutter-Grandcolas, n. sp. (C - D): male genitalia, dorsal (A, C), lateral (B, D). Scale 1 mm. Abbreviations: see Material and methods.*

Bullita sp.

(Fig. 27J)

Examined material. New Caledonia, Grande Terre, chutes de la Madeleine, maquis, 22.23568° S 166.85268° E, 20.ii.2014, by night, 1 juvenile, fn MAMAD2-19, leaf litter, J. Anso (MNHN).

We separate here one juvenile which clearly belongs to the genus *Bullita* by its general morphology and coloration (Fig. 27J), but cannot be attributed to the species presently separated within the genus. It may represent an additional new species, but no adult has been collected in this locality to support a formal description.

Genus *Koghiella* Otte, Alexander & Cade, 1987

Koghiella Otte, Alexander & Cade, 1987: 406. Desutter-Grandcolas 1997d: 142.

Type species. *Khogiella bouo* Otte, 1987.

Diagnosis. See Desutter-Grandcolas & Anso (submit.).

Distribution. *Koghiella* is endemic to New Caledonia, where it is known from the Province Nord (Hienghene: *K. caledonica* (Chopard, 1970), Thio: *K. thio* Otte, 1987), and the Province Sud (Mt. Koghis: *K. bouo* Otte, 1987, *K. parabouo* Otte, 1987, *K. semibouo* Otte, 1987; Col d'Amieu: *K. bouleti* Desutter-Grandcolas, 1997 and *K. grandis* Desutter-Grandcolas, 1997). We document here for the first time the presence of *Koghiella* in the southern part of Province Sud.

Koghiella nigris Anso & Desutter-Grandcolas, n. sp.

(Figs 32A-C, 33A-C, 34)

Type locality. New Caledonia, Grande Terre, Rivière Blanche, rainforest.

Type material. Holotype. New Caledonia, Grande Terre, Rivière Blanche, rainforest, 22.15142° S 166.68643° E, 11.iii.2014, by night, 1 male, FORIV1-27, leaf litter, J. Anso

(MNHN-EO-ENSIF3870). **Allotype.** Same data as holotype, 12.iii.2014, by night, 1 female, fn FORIV2-21 (MNHN-EO-ENSIF3871).

Paratypes, 6 males, 5 females. New Caledonia, Grande Terre, Pic du Pin, rainforest, 22.24680° S 166.82715° E, 16.xii.2013, by night, 1 male, fn FOPDP1-11 (OMNC). Same locality, 13.ii.2014, by day, 1 female, fn FOPDP1-70; 12.ii.2014, by day, 1 male, fn FOPDP1-57 (MNHN-EO-ENSIF3881, 3876); 26.vii.2015, by day, 1 male, fn 2015-JA01, male recorded, leaf litter, J. Anso (MNHN-EO-ENSIF3931). Same locality, 26.vii.2015, by night, 1 male, fn 2015-21, leaf litter, J. Anso & L. Desutter-Grandcolas (MNHN-EO-ENSIF3944).

New Caledonia, Grande Terre, Rivière Blanche, rainforest, 22.15142° S 166.68643° E, 17.xii.2013, by day, 2 males, fn FORIV1-12, FORIV2-11, 2 females, fn FORIV1-9, 23; 12.iii.2014, by night, 1 male, fn FORIV2-23, 1 female, fn FORIV2-20; 19.iii.2014, by night, 1 male, fn FORIV1-47, 1 female, fn FORIV1-40, leaf litter, J. Anso (MNHN-EO-ENSIF3872-3875, 3877-3880).

New Caledonia, Grande Terre, rainforest, Pic du Grand Kaori, 22.28535° S 166.89674° E, 25.vii.2015, by night, 1 male, fn 2015-5, in leaf litter, recorded, J. Anso & L. Desutter-Grandcolas (MNHN-EO-ENSIF3919).

Other specimens examined. Same data as the holotype: 10.xii.2013, by night, 3 males, fn FORIV1-2 (broken genitalia), FORIV1-4 (bad condition), FORIV1-5 (no genitalia), 1 female, fn FORIV2-6 (bad condition); 11.iii.2014, by night, 1 juvenile, fn FORIV1-30; 12.iii.2014, by night, 3 juveniles, fn FORIV2-22, 27, 28; 14.iii.2014, 1 female, fn FORIV2-32 (bad condition); 19.iii.2014, by night, 2 juveniles, fn FORIV1-41, 44; 19.iii.2014, by day, 5 juveniles, fn FORIV1-48, 51-54; 20.iii.2014, by night, 5 juveniles, fn FORIV1-57, 58, 60, FORIV2-48, 51; 26.iii.2014, by day, 5 juveniles, fn FORIV1-65, 68, 69, 71, FORIV2-56, all collected in the leaf litter, J. Anso (MNHN). Same data as the holotype, 10.xii.2013, by night, 1 female, fn FORIV1-1; 11.iii.2014, by night, 2 females, fn FORIV1-28, 29; 19.iii.2014, by night, 1 male, fn FORIV1-46, leaf litter, J. Anso (OMNC).

New Caledonia, Grande Terre, Pic du Pin, rainforest, 22.24680° S 166.82715° E, 16.xii.2013, by night, 1 juvenile, fn FOPDP1-13; 10.ii.2014, by night, 2 juveniles, fn FOPDP2-12, 26; 11.iii.2014, by day, 2 juveniles, fn FOPDP2-55, 56; 12.ii.2014, by night, 1 juvenile, fn FOPDP1-32; 13.ii.2014, by night, 1 male, fn FOPDP1-59 (no genitalia), J. Anso (MNHN).

New Caledonia, Grande Terre, Rivière Blanche, paraforestier, 22.15280° S 166.68033° E, 11.iii.2014, by night, 4 juveniles, fn PARIV1-19, 20, 23, PARIV2-23; 12.iii.2014, by night, 1 juvenile, fn PARIV1-29; 19.iii.2014, by day, 1 juvenile, fn PARIV1-51; all collected in the leaf litter, J. Anso (MNHN).

Diagnosis. Within the genus, species characterized by its very dark coloration on head dorsum and pronotum, abdomen and legs; pronotum LL wholly black (Fig. 32A-C). Body narrow. **Male.** FWs short, not reaching tergite 7 distal margin. Male genitalia: Pseudepiphallic sclerite very long and narrow, the apical lobes very short and very little separate, making the distal margin almost continuous; pseudepiphallic sclerite ventrally consolidated distally by a pair of thin carinae; pseudepiphallic parameres flap-like, little sclerotized (Fig. 33A-C). **Female.** FWs overlapping, not reaching tergite 2 posterior margin. Tergites dark yellowish with many black spots; sternites brown, except for yellowish sides; subgenital plate dark brown on median part and along distal margin, yellowish otherwise. Ovipositor longer than TIII, between 4.1 and 4.3 mm long.

Description. In addition to the characters of the genus (Otte *et al.* 1987, Desutter-Grandcolas & Anso submit.):

Coloration. Fig. 32A-C. Head dorsum light brown, with several longitudinal yellow lines: one median and very thin, one behind each eye, and four very short ones on occiput; fastigium yellowish with a median black line; cheeks and lateral parts of the face brown; a central part of the face light yellow, separated from the lateral brown part with a clear oblique limit, and with a reverse-V shaped line and a median dot brown. Mouths parts extending the brown and light yellow coloration of the face and cheeks, making a V-shaped light yellow area surrounded with dark brown, except for clear median clypeus and labrum. Scapes yellowish, inner and outer margins brown. Antennae brown, the articles separated with white. Maxillary palpi brown, articles 3 and 4 varied with yellowish, article 5 dark brown. Pronotum: LL black, without yellow spots; DD light brown with light yellow anterior and posterior margins, and light yellow diffuse lateral band; posterior third variously light yellow and brown. Femora I and II light yellow and brown, the dark spots mostly in distal half. Tibiae I and II dark brown with few yellowish spots or areas. FIII (Fig. 32C) with many brown oblique lines on their outer sides, except in lower distal part, entirelery light brown with three large yellow spots sometimes partly fused; inner side more yellow than brown, especially at the base, without thin brown lines. TIII alternatively black brown and yellowish dorsally, the ventral side more

yellowish; spurs largely dark brown, shortly yellow at base and before apex, and with a brown tip. Basitarsomeres black with a median yellow spots; other tarsomeres mostly dark, but sometimes with a yellow spot. Tergites darkly coloured, making the abdomen very dark. Cerci light brown with a wide yellow ring at their base.

Male. Fig. 32A. FWs short, not reaching tergite 7 distal margin; truncated; harp with one vein, joining the file at file mid length; diagonal connected to the first chord near the chord base and close to the file, its most basal part parallel to the file; chords 2 and 3 fused basally, well apart from chord 1; lateral field with four longitudinal parallel veins, the two most distal ones more largely separated from the most basal ones. Stridulatory file with 90 - 92 teeth (mean 91, n=2). FW dorsal field dark brown with a faint yellowish or reddish tint; lateral, basal and distal veins yellowish; lateral field black, including the veins. Last tergites black brown with rows of yellowish dots. Sternites whitish with diffuse black brown. Subgenital plate long and thin, protruding between the cerci; black.

Male genitalia. Fig. 33A-C. Slightly convex. Pseudepiphallic sclerite very long and thin; apical margin rounded, and almost continous, the apical lobes being very short and very little separate (i.e., very short and tightly close); apex of pseudepiphallic sclerite ventrally consolidated by a pair of thin carinae. Pseudepiphallic parameres flap-like, little sclerotized. Ectophallic apodemes very long and thin. Endophallic sclerite with a long and thin median sclerite, and a pair of lateral wide and short ones; endophallic apodeme as a low median crest.

Female. Fig. 32B. FWs overlapping, not reaching tergite 2 posterior margin. Lateral field not going beyond dorsal field; with three distal longitudinal veins, closely set and parallel to each other and to distal margin, in addition to one or two most often incomplete veins close to the limit of dorsal field; black. Dorsal field with faint veins, visible mostly in FW distal part; brown with yellowish veins, the limit with lateral field yellowish. Tergites dark yellowish with many black spots. Sternites brown, except for yellowish sides. Subgenital plate dark brown on median part and along distal margin, yellowish otherwise. Ovipositor longer than TIII (see measurements).

Juveniles. Coloration lighter, with yellowish cheek distal margin and irregular yellowish spots on pronotum LL.

Variation. In most coloured females, the last tergite shows a large yellow spot, surrounded with brown. Also, one female from Col de Mouiranges (fn FOMOU2-3) looks very close to

females of *Koghiella nigris* Anso & Desutter-Grandcolas, n. sp. by its coloration pattern and size, but has a distinctly wider body and shorter FWs.

Measurements (in mm).

	iod	PronL	PronWp	FWL	FWW	FIIIL	FIIIW	TIIIL	OL
Male holotype	1	1.4	2	3.1	2.3	4.7	1.9	3.5	---
Males paratypes	1	14-1..6	1.9	2.9-3.1	2.2	4.2-4.7	1.7-1.8	3.1-3.5	---
mean (n=3)	1	1.5	1.9	3	2.2	4.5	1.8	3.4	---
Female allotype	1.2	1.9	2.1	0.8	---	5.1	2.2	3.8	4.4
Female paratypes	1.1-1.2	1.7-1.8	2-2.2	0.6-0.8	---	4.7-4.9	1.9-2.1	3.6-3.9	4.1-4.4
mean (n=3)	1.2	1.8	2.1	0.7	---	4.9	2.1	3.8	4.3

Habitat and life history traits. *Koghiella nigris* Anso & Desutter-Grandcolas, n. sp. lives mainly in dense forested area, and to a lesser extent in paraforestier vegetation. Males are active during the day, while they emit their calling song. Both males and females are preferentially found on bare soil in rain forest.

Calling song. Fig. 34. One specimen has been collected and recorded (one song bout, 15 echemes, 1217 syllabes). The call is made of short echemes separated by very long silences. At 23°C, the calling song of *Koghiella nigris* Anso & Desutter-Grandcolas, n. sp. consists of a repetition of echemes of 1.15 ± 0.04 s; echeme period = 16.2 ± 8.8 s; each echeme is made of 81 ± 9 syllables, with the following characteristics: syllable duration = 8.5 ± 1.6 ms; syllable period = 15.1 ± 7.3 ms; syllable duty cycle = 58.5 %; the dominant frequency is 4.72 ± 0.09 kHz. Song deposited in MNHN sound library (inventory number MNHN-SO-2016-18).

The song of *K. nigris* Anso & Desutter-Grandcolas, n. sp. resembles the song of *K. flammea* Anso & Desutter-Grandcolas, n. sp., but the echeme periode is very long in the former (about 16 s), and very short in the latter (about 2 s).

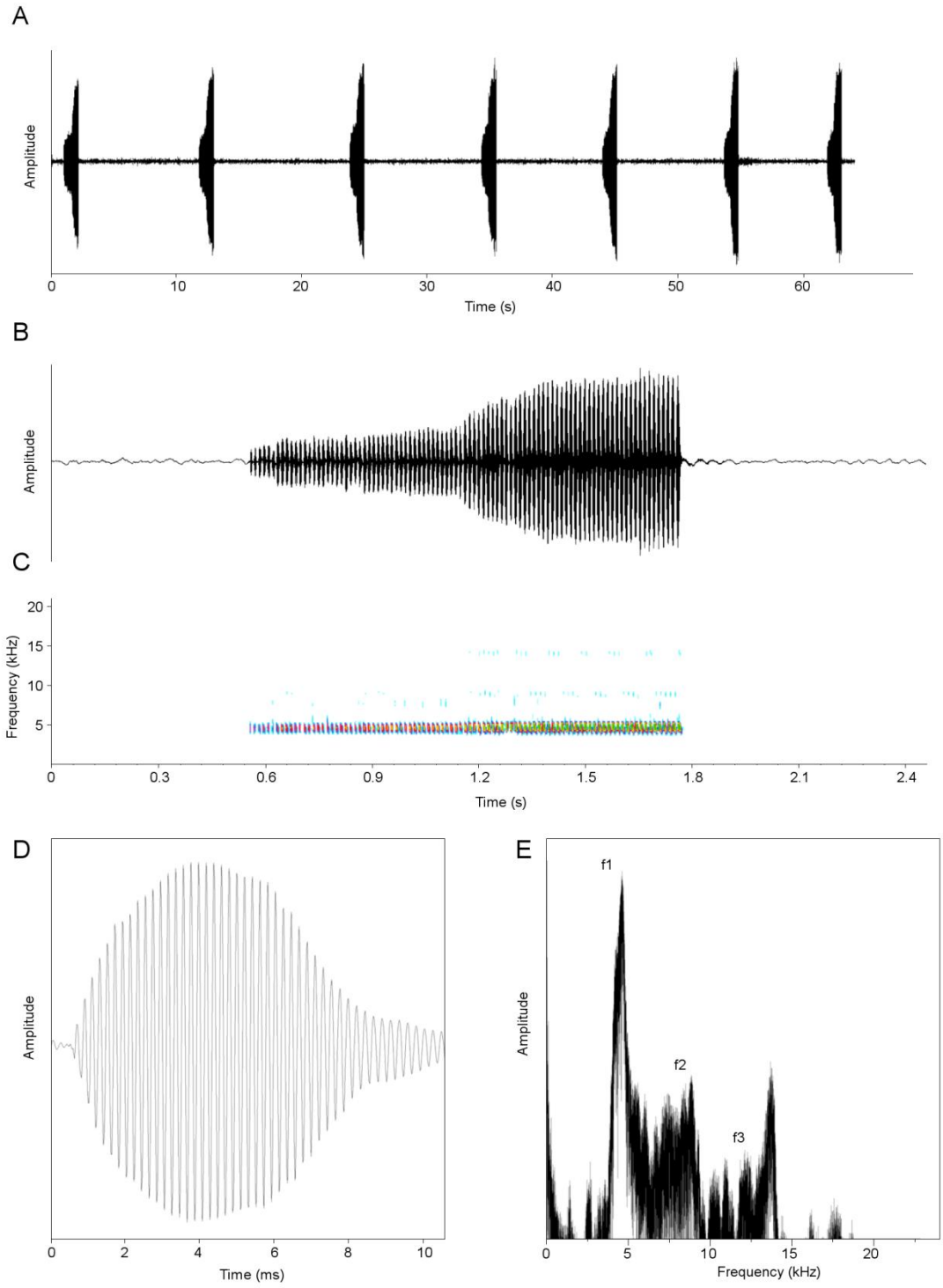

Figure 3.34. *Calling song of Koghiella nigris Anso & Desutter-Grandcolas, n. sp. Oscillogram of seven successive echemes (A); detailed oscillogram (B) and sonogram (C) of one echeme; oscillogram of one syllable (D); logarithmic spectrogram of one syllable (E). Symbols: f1-f3, first (fundamental) to third harmonic frequencies.*

Koghiella flammea Anso & Desutter-Grandcolas, n. sp.

(Figs 32D-F, 33D-F, 35, 39X)

Type locality. New Caledonia, Grande Terre, Chutes de la Madeleine, low sclerophyllous shrubland, 22.23568° S 166.85268° E.

Etymology. Species named after its orange coloration.

Type material. Holotype. New Caledonia, Grande Terre, Chutes de la Madeleine, maquis, 22.23568° S 166.85268° E, 11.ii.2014, by day, 1 male, fn MAMAD1-4, leaf litter, J. Anso (MNHN-EO-ENSIF3882). **Allotype.** Same locality as the holotype, 13.ii.2014, 1 female, fn MAMAD1-17, leaf litter, J. Anso (MNHN-EO-ENSIF3883).

Paratypes, 24 males, 6 females. New Caledonia, Col de Ouénaru, Bois du Sud, maquis, 22.17321° S 166.76093° E, 18.vii.2012, by night, 1 male, 1 female, BDS2-NOU16, 17, in leaf litter, J. Anso (MNHN-EO-ENSIF3884, ENSIF3903); 17.vii.2012, by day, 1 male, 1 female (molecular sampling LDG 309), fn 2, 3, in leaf litter, J. Anso & L. Desutter-Grandcolas (MNHN-EO-ENSIF3913-3914); 25.vii.2015, by day, 1 male, fn 2015-6, recorded, in leaf litter, J. Anso & L. Desutter-Grandcolas (MNHN-EO-ENSIF3920).

Same locality as the holotype, 10.ii.2014, by day, 1 male, MAMAD2-5; 11.ii.2014, by day, 1 male, MAMAD1-6; 11.ii.2014, by night, 1 male, MAMAD1-12; 12.ii.2014, by day, 1 male, MAMAD2-11; 13.ii.2014, by day, 2 males, MAMAD1-16, 19; 20.ii.2014, by night, 1 male, MAMAD2-21, in leaf litter, J. Anso (MNHN-EO-ENSIF3885-3891). Same locality as the holotype, 13.ii.2014, by day, 1 male, MAMAD1-18, in leaf litter, J. Anso (OMNC). Same locality as the holotype, 25.vii.2015, by day, 3 males, fn 2015-13-15, in leaf litter, J. Anso & L. Desutter-Grandcolas (MNHN-EO-ENSIF3945-3947).

New Caledonia, Grande Terre, Rivière blanche, maquis, 22.13625° S 166.70796° E, 11.iii.2014, by day, 1 male, MARIV1-4, leaf litter; 19.iii.3014, by night, 1 male, MARIV2-5, J. Anso (OMNC); 14.iii.2014, by day, 1 male, MARIV1-10; 20.iii.2014, by night, 2 males, MARIV1-16, 17, leaf litter, J. Anso (MNHN-EO-ENSIF3892-3894).

New Caledonia, Grande Terre, Forêt Nord, maquis, 22.32277° S 166.93501° E, 9.xii.2013, by night, 2 females, MAFN1-1, 7; 17.xii.2013, by night, 1 female, MAFN1-15; 12.ii.2014, by

night, 1 male, MAFN1-24, 1 female, MAFN1-23; 10.iii.2014, by day, 2 males, MAFN1-27, 28; 11.iii.2014, by day, 1 male, MAFN2-19, leaf litter, J. Anso (MNHN-EO-ENSIF3895-3902); 12.ii.2014, by night, 1 female, MAFN1-22; 16.ii.2014, by day, 1 female, MAFN2-4, in leaf litter, J. Anso (OMNC).

Other specimens examined. New Caledonia, Grande Terre, Chutes de la Madeleine, maquis, 22.23568° S 166.85268° E, 12.ii.2014, by day, 1 juvenile, MAMAD1-10; 12.ii.2014, by night, 3 juveniles, MAMAD1-12, 13, 15; 13.ii.2014, by day, 1 male, MAMAD1-20, 2 juveniles, MAMAD2-13, 14; 19.ii.2014, by night, 1 male, MAMAD2-16, 1 juvenile, MAMAD2-17; 20.ii.2014, by night, 1 male, MAMAD2-21, 4 juveniles, MAMAD1-22, 23, 25, MAMAD2-20, leaf litter, J. Anso, MNHN. Same locality as the holotype, 19.ii.2014, by night, 1 male, MAMAD2-15, leaf litter, J. Anso (OMNC).

New Caledonia, Grande Terre, Forêt Nord, maquis, 22.32277° S 166.93501° E, 9.xii.2013, by night, 4 males, MAFN1-2-5, 4 juveniles, MAFN1-6, 8, MAFN2-1, 2; 10.xii.2013, by day, 2 males, MAFN1-9, 10, 1 juvenile, MAFN2-3; 11.ii.2014, by day, 1 juvenile, MAFN1-21; 16.xii.2013, by day, 2 juveniles, MAFN1-14, MAFN2-5; 17.xii.2013, by night, 1 male, MAFN1-16, 4 juveniles, MAFN1-17-20; 30.i.2014, by night, 4 males, MAFN2-8-11, 3 juveniles, MAFN2-12-14; 12.ii.2014, by night, 1 male, MAFN2-18; 20.ii.2014, by night, 2 juveniles, MAFN1-25, 26; 20.ii.2014, by night, 1 male, fn MAMAD1-21; 10.iii.2014, by day, 1 juvenile, MAFN1-29; 11.iii.2014, by day, 1 juvenile, MAFN1-30, leaf litter, J. Anso (MNHN).

New Caledonia, Grande Terre, Rivière blanche, 22.13625° S 166.70796° E, 12.iii.2014, by day, 1 juvenile, MARIV2-1; 19.iii.2014, by night, 1 juvenile, MARIV2-6, leaf litter, J. Anso (MNHN).

New Caledonia, Grande Terre, Rivière blanche, paraforestier, 22.15280° S 166.68033° E, 10.xii.2013, by night, 1 male, PARIV1-5; 11.iii.2014, by day, 1 male, PARIV2-22, 1 female, fn PARIV2-19; all collected in the leaf litter, J. Anso (MNHN).

Diagnosis. Species close to *K. bouleti* Desutter-Grandcolas, 1997 by its small size and its lightly, almost orange, coloration. It can be separate from this species by its male genitalia (pseudepiphallic sclerite not as wide anteriorly; apical lobes much more separates from each other, with a V-shaped space between them; pseudepiphallic lateral margin of pseudepiphallic sclerite with a shallower concavity: compare Fig. 33C-D and Desutter-Grandcolas 1997b Fig.

7, 8). Other characters: joints 4 and 5 of maxillary palpi dark brown (lightly coloured in *K. bouleti*); face without a distinct ivory-coloured pattern (present in *K. bouleti*). **Male.** Stridulatory files with 82 – 85 teeth (mean 85, n=2) (against 89 – 93, mean 91, n=2, in *K. bouleti*). Male genitalia (Fig. 33C-E) lightly convex; seudepiphallic sclerite short and wide; apical lobes darkly coloured, inflated and slightly convex dorsally, well-separate dorsally from one another as a deep V-shaped margin, and laterally from the pseudepiphallic sclerite; a clear wide notch , lateral. **Female.** FWs quite long for the genus, reaching tergite 2 midlength; overlapping; lateral field and three to four curved, black veins; dorsal field dark brown with five ivory-coloured veins. Tergites black laterally, yellowish dorsally, with lines of black dots from tergite 2 to tergite 8; tergite 8 and 9 dark, supra anal plate yellowish; sternites dark yellowish, sternite 7 and subgenital plate dark brown. Ovipositor longer than TIII; 3.7-3.8 mm (mean 3.8, n=3).

Description.

In addition to the characters of the genus (see Otte *et al.* 1987, Desutter-Grandcolas & Anso submit.):

Coloration. Fig. 32D-F. Head light orange; head dorsum with indistinct longitudinal light brown lines between the eyes and a very thin, irregular, median yellow line whitish yellow, this coloration extended on the lateral margins of the fastigium down to the face; face light orange and whitish with two half-circle light brown lines, each one going from mid antennal pit to mid face, extenting between the antennal pits but not reacing the median ocellus; epistemal suture and and the limit between pre and post clypeus marked with a light brown line. Scapes and base of antennae light orange; antennae otherwise light brown. Maxillary palpi light brown, joints 4 and 5 brown. Pronotum DD light orange, with several dark brown dots and a pair of short brown lines on each side of a light yellow medio-longitudinal line ; DD anterior and postrior margins marked with ivory; LL black. Legs I and II light orange brown; tip of basitarsomeres I and II and tarsomeres 2 and 3 brown. FIII (Fig. 32F) light yellowish brown; outer side with black brown oblique lines, thick even on FIII dorsal part; a longitudinal black brown line in FIII outer lower third, linked to few large dark brown spots, and an additional one along lower margin; FIII inner sides lighter, with distal black brown and whitish elongate spots. TIII and tarses III light ochre brown; spurs brown with ochre bases and tips. Cerci light orange brown with a yellow basal ring and black brown setae.

Male. Fig. 32D. FWs covering the whole abdomen, except the last three tergites; dark reddish brown, with some yellow veins (thick base of A2 and A3, A3 at the plectrum level, and to a lesser extent on third chord, CUP and media veins); apical field very short, yellowish; lateral field black brown, with 5 – 6 longitudinal parallel veins. Stridulatory file with 82 – 88 teeth (mean 85, n=2). Tergites dark brown with yellowish distal margin; last three tergites before supra anal plate brown with a row of yellowish spots; supra anal plate yellowish. Sternites yellowish with two longitudinal brown lines; subgenital plate brown.

Male genitalia. Fig. 33D-F. Slightly convex. Pseudepiphallic sclerite short and wide (Fig. 33D). Apical lobes darkly coloured, inflated and slightly convex dorsally; well-separate dorsally from one another as a deep V-shaped margin (Fig. 33D), and laterally from the pseudepiphallic sclerite (Fig. 33F); a clear, lateral, wide notch on the apical lobes; a pair of thin oblique sclerites, running along apical lobe anterior margins. Pseudepiphallic parameres very short, flap-like and little sclerotized. Ectophallic apodemes long and thin, parallel in their basal third, then abruptly divergent . Endophallic sclerite with a long and thin median sclerite, and a pair of lateral wide and short ones; endophallic apodeme as a low median crest.

Female. Fig. 32E. FWs reaching tergite 2 midlength, partly overlapping; lateral field slightly longer than dorsal field. Venation thick; dorsal field with five straight, longitudinal veins, lateral field with 3-4 curved, parallel veins; lateral field and veins black; dorsal field dark brown with ivory-coloured veins. Tergites black laterally, this coloration extending that of the pronotum and FW lateral field; yellowish dorsally, with black dots close to distal margins, the black dots of all tergites more or less aligned , from one tergite to another, and the two median ones longer, almost making a pair of black lines from tergite 2 to tergite 8; tergite 8 dark, with few yellowish parts; tergite 9 dark. Supra anal plate yellowish, at least distally. Sternites dark yellowish, except sternite 7 and subgenital plate, dark brown. Ovipositor light ochre; longer than TIII.

Measurements (in mm).

	iod	PronL	PronWp	FWL	FWW	FIIIL	FIIIW	TIIIL	OL
Male holotype	1	1.4	1.8	2.9	2.3	4.3	1.9	3	---
Males paratypes	0.9-1.1	1.4-1.5	1.8	2.6-2.8	2. 2	3.9-4.1	1.6-1.7	2.9-3.1	---
mean (n=4)	1	1.4	1.8	2.8	2.3	4.1	1.7	3	---

Female allotype	1	1.6	1.9	0.8	---	4.3	1.8	3.2	3.8
Female paratypes	0.9	1.4-1.5	1.8	0.6	---	4-4.1	1.6-1.7	2.8-3	3.7-3.8
mean (n=3)	0.9	1.5	1.8	0.7	---	4.1	1.7	3	3.8

Habitat and life history traits. *Koghiella flammea* Anso & Desutter-Grandcolas, n. sp. lives in open habitat, such as low sclerophyllous maquis and preforest formations in the southern part of New Caledonia. Males emit their calling song during the day in the litter, while their remain silent during the night.

Calling song. Fig. 35. Two specimens could be collected and recorded in the field at 24°C and 24.6°C; 1453 syllables and 30 echemes were analyzed. At 24°C, the calling song of *Koghiella flammea* Anso & Desutter-Grandcolas, n. sp. consists of a repetition of echemes of 0.59 ± 0.07 s; each echeme is made of 46 ± 6 syllables, with the following characteristics: syllable duration = 6.9 ± 1 ms; syllable period = 13 ± 9.5 ms; syllable duty cycle = 64.3%; the dominant frequency is 6.0 ± 0.4 kHz. Song deposited in MNHN sound library (inventory number MNHN-SO-2016-17).

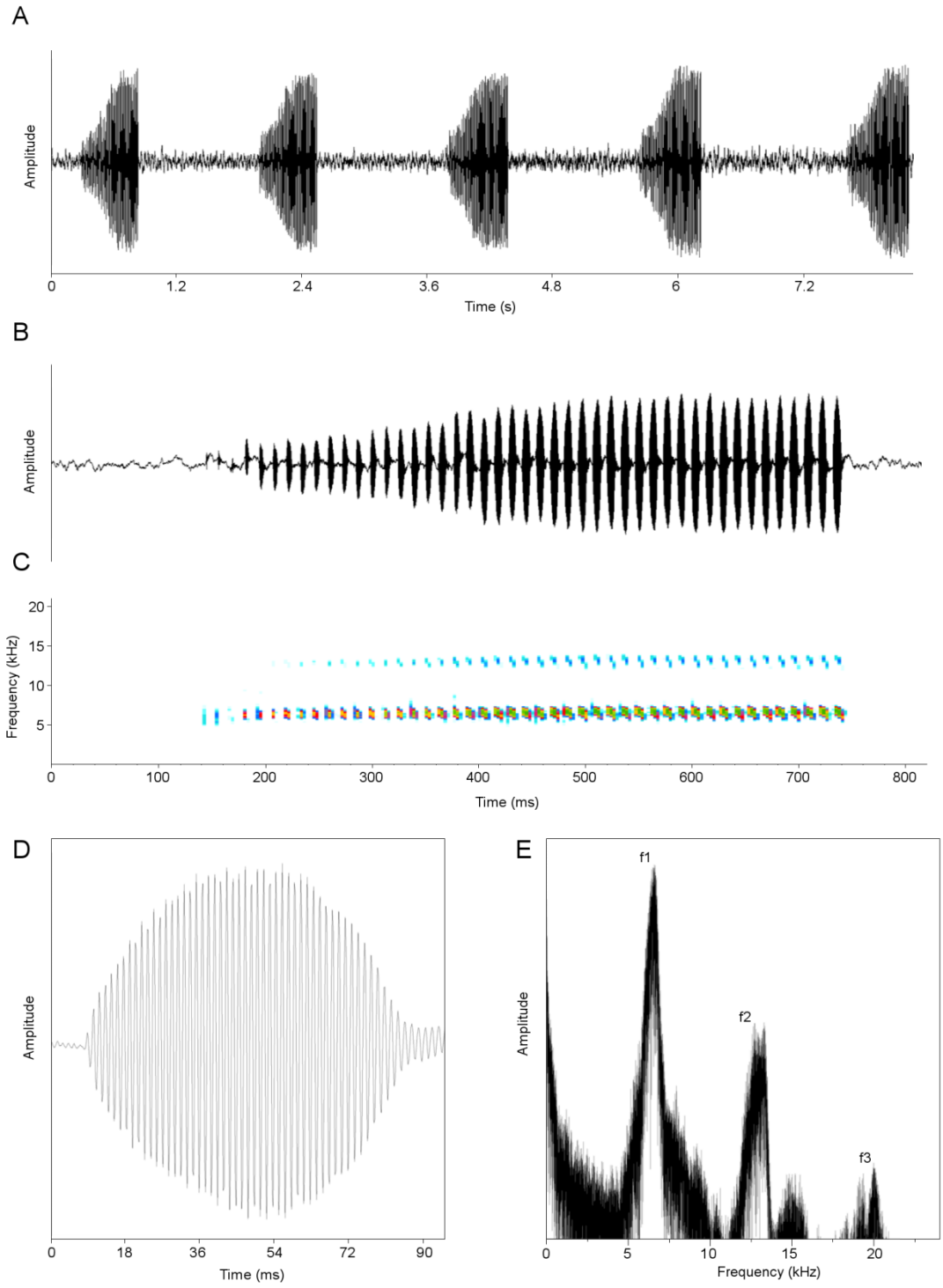

Figure 3.35. *Calling song of Koghiella flammea Anso & Desutter-Grandcolas, n. sp. Oscillogram of five successive echemes (A); detailed oscillogram (B) and sonogram (C) of one echeme; oscillogram of one syllable (D); logarithmic spectrogram of one syllable (E). Symbols: f1-f3, first (fundamental) to third harmonic frequencies.*

Variation. Males from maquis plots (fn PARIV) are bigger in size and slightly differ in coloration. Their identification should be checked with calling song analysis.

Genus *Paniella* Otte, Alexander & Cade, 1987

Paniella Otte, Alexander & Cade, 1987: 411.

Type species. *Pronemobius apterus* Chopard, 1915.

Emended diagnosis. See Desutter-Grandcolas & Anso (submit.).

Distribution. *Paniella* is endemic to New Caledonia, where it is known by only one species, *Paniella apterus* (Chopard, 1915) from the Province Nord (summit of Mont Panié, 1600 m). We document here for the first time the presence of *Paniella* in the southern part of Province Sud, but not determined material attest its presence throughout the whole Grande Terre, at both high and low elevations.

Paniella bipuntatus Desutter-Grandcolas & Anso, n. sp.

(Fig. 36A-E)

Type locality. New Caledonia, Pic du Grand Kaori, rainforest.

Etymology. Species named after the pairs of black dots present on its abdomen, and the dorsal disc of its pronotum.

Type material. Holotype. New Caledonia, [Grande Terre, Province Sud], Pic du Grand Kaori, 22°17'S 166°53'E, 250m, 22-24.xi.2004, 1 female, pyrethrum, rainforest, Monteith & Burwell (MNHN-EO-ENSIF3904). **Paratypes, 2 females.** Same data as the holotype, 1 female (MNHN-EO-ENSIF3905). New Caledonia, Grande Terre, Pic du Grand Kaori, rainforest, 22.28535° S 166.89674° E, 23.i.2014, by day, 1 female, fn FOGK1-50, sur écorce chêne à 1.50 m, J. Anso (MNHN-EO-ENSIF3906).

Diagnosis. Within the genus, species characterized by its small size and coloration pattern (see below and Fig. 36A). Male unknown. **Female.** Apterous. Ovipositor straight, longer than TIII.

Description. In addition to the characters of the genus. TIII outer subapical spurs quite long, about as long as the second inner subapical spur; inner subapical spurs longer toward TIII apex, the spur 3 (the most dorsal) the smaller, the first (the most distal) spur the longest and as long as the dorsal inner apical spur. TIII much shorter than FIII.

Coloration. Fig. 36A-C. Face and cheeks shining black, the very small ocelli yellow; head dorsum brown to yellowish brown; eyes brown. Scapes light yellowish brown; first two antennal articles light yellow, antennae otherwise brown. Maxillary palpi brown, joint 4 and joint 3 apex light yellow. Pronotum: LL black brown, shining; DD yellowish in anterior two thirds (including anterior margin), with a pair of black dots close to anterior margin; DD distal margin brown. Meso, metanotum and tergites 1 and 2 light orange basally, light yellow distally, with 2 brown small dots on each side of a small median light yellow dot; lateral parts of meso, metanotum and tergites 1 and 2 light orange, that of more distal tergites brown; tergite 3 to 6 darker, with a wide, brown median dot in adition to the small median yellow dot, and a wider black spot on each side (these much smaller on tergite 4, continuous on tergites 5 and 6). Last tergites and supra anal plate light brown. Sternites light yellow and light brown. Cerci light yellow basally, light brown more distally. Legs light yellowish brown, with yellow, brown and black colour pattern: FI and FII dark dorso-distally; TI and TII with two wide rings. FIII with few brown, oblique stripes and a wide longitudinal brown band on outer side; inner side widel light yellow, with a short brown band in distal dorsal half; knee brown on both sides. Tarsomeres 1 and 3 brown, with yellow mid length.

Male. Unknown.

Female. Ovipositor straight, shorter than FIII; apical margins of dorsal valves feebly crenulated (Fig. 3.36D, E). Subgenital plate short, transverse.

Measurements (in mm).

	iod	PronL	PronWp	FIIIL	FIIIW	TIIIL	OL
Female holotype	0.9	1.3	1.5	4	--	2.8	3.1
Females paratypes	0.9-1	1.2-1.3	1.5-1.6	4	1.6	2.8-3	3.1-3.3
mean (n=3)	0.9	1.3	1.5	4	1.6	2.9	3.2

Habitat and life history traits. *Paniella bipuntatus* Desutter-Grandcolas & Anso, n. sp. lives in dense rainforest in the southerpart of New Caledonia. According to our observation, it could live on large tree trunk covered by moss.

Paniella sp.

Examined material. New Caledonia, Grande Terre, Rivière blanche, paraforestier, 22.15280 S 166.68033 E, 20.iii.2014, by night, 1 juvenile, fn PARIV2-67, in leaf litter, J. Anso (MNHN).

We separate here a juvenile that probably belongs to *Paniella*, as attested by the small size, shape and coloration of its maxillary palpi (joint 5 short and very wide, joint 4 and distal part of joint 3 ivory, joint 5 light orange), the coloration of its antennae (scape and first two articles ivory, antennae otherwide black with articles limit white) and head (labrum, face and head dorsum ivory, occiput brown), its short legs annulated yellow and black, and the number and size of TIII subapical spurs (three short spurs on each side). This species is characterized also by its black pronotum with a yellow spot in LL distal half.

Genus *Kanakinemobius* Desutter-Grandcolas, n. gen.

(Figs 3.37, 38)

Type species. *Kanakinemobius mandjelia* Desutter-Grandcolas, n. sp.

Etymology. Genus named after the origin of the specimens within the Nemobiinae.

Diagnosis. Small to median nemobiines with a distinct coloration pattern (body quite uniformly brown to dark brown, with black head and pronotum, except for two transverse, light yellow bands on pronotum, Fig. 37A-C). Pronotum rounded, longer dorsally than laterally; distal part of lateral lobe directed inwardly. FWs very short in both males and females. TI without a tympanum, on inner and outer sides. TIII short; with 4 pairs of short, subapical spurs. **Males.** FWs only slightly overlapping; venation very reduced, but with an impressed file. Subgenital plate long and narrow. Male genitalia elongate; pseudepiphallic sclerite narrow, almost of the same width over its whole length; apical lobes very long, flat and wide. **Females.** FWs very short, most often hardly visible beneath the pronotum, widely

separate. Subgenital plate very short, transverse, its distal margin V-shaped. Ovipositor not widened distally. Female genitalia: copulatory papilla having the shape of a thick plate.

Description.

Size small to median for Nemobiinae; body resembling that of a Mogoplistidae in shape. Head narrow compared to pronotum: head dorsum quite flat; ocelli small, set in a low and wide triangle. Antennae distinctly setose. Eyes small and not protruding. Maxillary palpi (Fig. 38A) short; joint 3 slightly longer than joint 4; joint 5 the longest, regularly widened toward apex, its posterior margin convex. Pronotum rounded, as long, or longer than wide; anterior margin concave, posterior margin clearly convex; lateral lobe very short, its anterior two thirds rounded, its posterior third directed inwardly, not divergent. TI with two, ventral, apical spurs; no tympanum on inner and outer sides. TII with three long apical spurs, outer dorsal spur lacking. TIII short and widened ventrally; with 3 apical spurs on both inner and outer sides; outer spurs shorter, but the median longer than the others and quite long; inner spurs long, the dorsal the longest, only slightly longer than the median spur. TIII with four pairs of subapical spurs, longer toward TIII apex; subapical spurs all shorter than the longest apical spurs, and regularly alternate; inner spurs longer than outer spurs, the first (most distal) spur almost as long as the dorsal inner apical spur. Cerci quite long for a Nemobiinae.

Coloration. Fig. 3.37A-C. Quite uniformly brown, lighter on abdomen, the posterior margins of tergites sometimes lighter (only in adults ?); head black brown; scape and first two articles of antennae black brown, antennae otherwise light brown; pronotum dark brown with light yellow margins and with a wide light yellow band along posterior dorsal margin; legs I and II dark brown brown, FIII lighter, TIII black brown, tarsi all yellowish brown. Cerci yellowish.

Male. FWs short, not reaching metanotum half length, very little overlapping; venation almost lacking, but with an impressed file (Fig. 3.37D, 38B). Metanotum and tergites without clear glandular structures. Subgenital plate long and narrow (Fig. 3.37B).

Male genitalia. Fig. 3.37H-J. Elongate; pseudepiphallic sclerite very narrow, almost of the same width over its whole length; apical lobes very long, flat and wide; pseudepiphallic parameres shorter; ectophallic apodemes long, almost parallel.

Female. FWs (Fig. 3.37C) very short and widely separate, not reaching one third of metanotum length, and most often hardly visible from beneath the pronotum. When present, venation only lateral, faint and irregular. Subgenital plate short and transverse; distal margin

V-shaped (Fig. 38C). Ovipositor short, shorter than cerci; valves not widened before apex, but regularly thinner; dorsal valve with a variable longitudinal crest close to lower margin.

Female genitalia. Copulatory papilla having the shape of a thick squared plate, connected to spermathecal duct (at least in K. mandjelia Desutter-Grandcolas, n. sp.).

Distribution. In addition to the Mandjelia summit (750m asl), genus known from the area near Poro (600m asl), Touho area (400m asl) and, in the South, near the Grand Kaori and Rivière blanche (undescribed material in MNHN collections).

Kanakinemobius mandjelia Desutter-Grandcolas, n. sp.

(Figs 37, 38)

Type locality. New Caledonia, Mandjelia summit, 20°24'S 166°32'E.

Type specimens. Holotype: New Caledonia, Mandjelia summit, 20°24'S 166°32'E, 750m, 20.xi.2003 – 31.i.2004, 1 male, G. Monteith, flight int[erception] trap (MNHN-EO-ENSIF3948). **Allotype:** Same locality, 780m, 12.xii.2004, 1 female, G. Monteith, Berlesate, sieved litter, RF (MNHN-EO-ENSIF3949). **Paratypes, 2 males, 2 females.** Same locality and collector as the holotype, 2 males, 1 female (molecular sample LDG 402) (MNHN-EO-ENSIF3950-3952). Same locality and collector as the allotype, 1 female (MNHN-EO-ENSIF3953).

Diagnosis. Species large for the genus, according to the material at hand. Male genitalia as on Figure 37H-J.

Description. In addition to the characters of the genus: Size large, compared to the other undescribed species available. Body somewhat rounded, making the resemblance with a mogoplistid stronger. Head punctuated (Fig. 37D). Pronotum DD distinctly longer than LL in lateral view (Fig. 37E).

Coloration. Head smoky black, not shining. Maxillary palpi dark brown, the distal margin of each joint marked with light yellow. First two antennal articles black brown; others light brown, the membrane between articles light yellow in the material at hand (artefact ?). Pronotum dark brown, shining; anterior margin light yellow; posterior margin also light yellow, except for its most lateral part, black brown; DD distal part with a wide light yellow

band along the margin. Legs I and II darker than legs III, except for light brown tarsi and posterior side of FII. Outer side of FIII dark ochre brown dorsally, yellowish brown ventrally, the two coloration separated by a blackish line; TIII black brown, the spurs ochre brown with yellowish base; hindtarsi light brown. Cerci yellowish.

Male. FWs not overlapping but close to each other; dark reddish brown, the yellowish base hidden under pronotum; venation discreet, but the file vein impressed (Fig. 37D, E). Tergites and sternites brown, the membrane separating them yellowish (artefact ?); tergites IX and X black brown. Subgenital plate as on Fig. 37B.

Male genitalia. Fig. 37H-J. Apical lobes well-separate the one from the other.

Female. FWs flap-like, widely separate; dark reddish brown, the yellowish base hidden under pronotum; some undistinct lateral veins. Tergites and sternites as in males.

Female genitalia. Copulatory papilla having the shape of a thick squared plate, connected to spermathecal duct.

Measurements (in mm).

	iod	PronL	PronWa	PronWp	FIIIL	FIIIW	TIIIL	Tar1-III	OL
Male holotype	1	2	1.9	2.1	4.6	1.9	3	1.4	---
Males paratypes	1-1.1	2.1-2.2	2	2.1	4.7	1.9-2	3.1-3.2	1.5	---
mean (n=3)	1	2.1	1.9	2.1	4.7	1.9	3.1	1.5	---
Female allotype	1.2	2.4	2.3	2.3	4.9	2.1	3.1	1.5	4.2
Female paratypes	1.1-1.2	2-2.1	2-2.1	2-2.2	4.6-4.8	1.9-2	3.2-3.5	1.5-1.7	3.7-4.1
mean (n=3)	1.2	2.2	2.1	2.2	4.8	2	3.3	1.6	4

Kanakinemonius sp.

Examined specimens. New Caledonia, Grande Terre, Pic du Grand Kaori, rainforest, 22.28535° S 166.89674° E, 11.xii.2012, by night, 2 juveniles, fn FOGK2-11, 12, in leaf litter, J. Anso (MNHN).

We separate here two juvenile specimens collected in the rainforest at Grand Kaori that clearly belong to *Kanakinemobius* Desutter-Grandcolas, n. gen. They may belong to a new species, to be described with supplementary material.

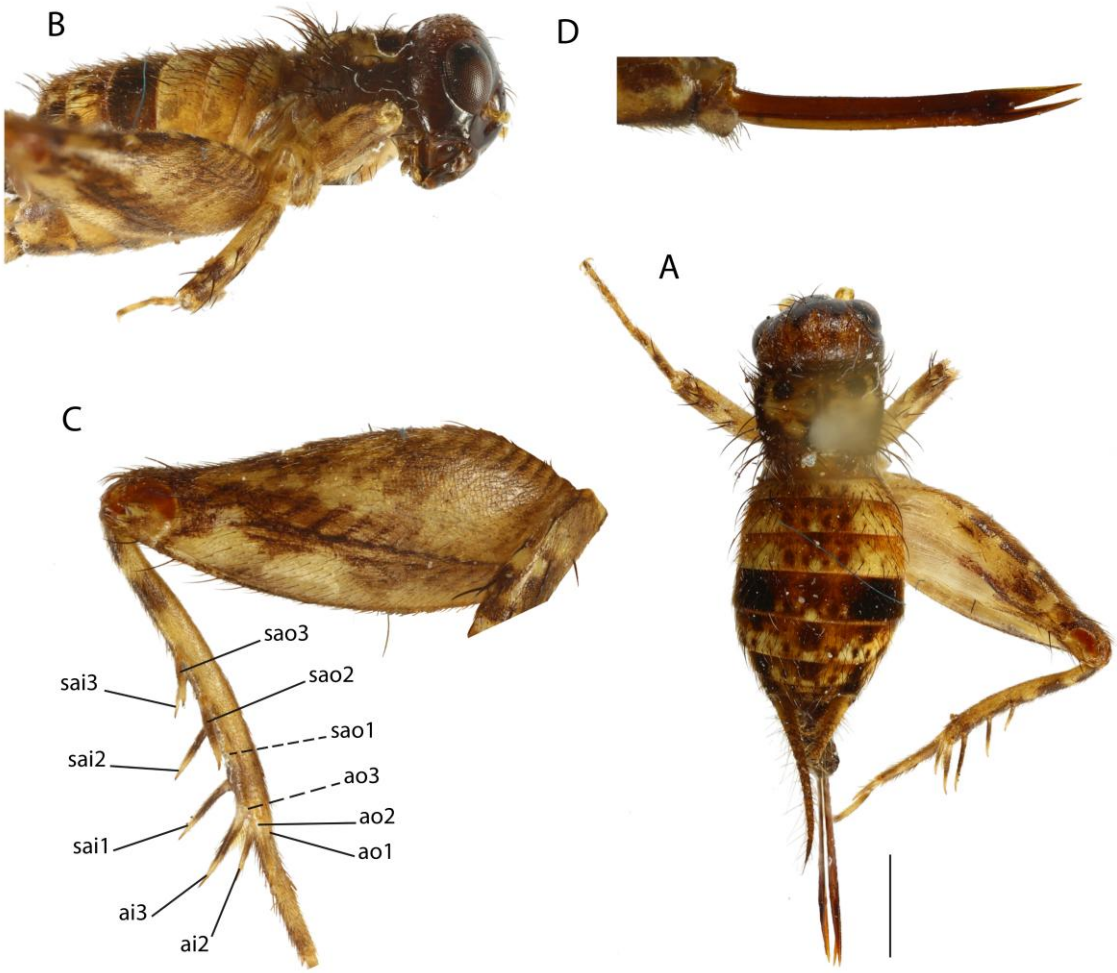

Figure 3.36. *Paniella bipuntatus Desutter-Grandcolas & Anso, n. sp. A, female habitus, dorsal, scale 1 mm; B, head and pronotum, lateral; C, leg III outer side, showing FIII outer pattern of coloration and TIII apical and subapical spurs; D, female ovipositor.*

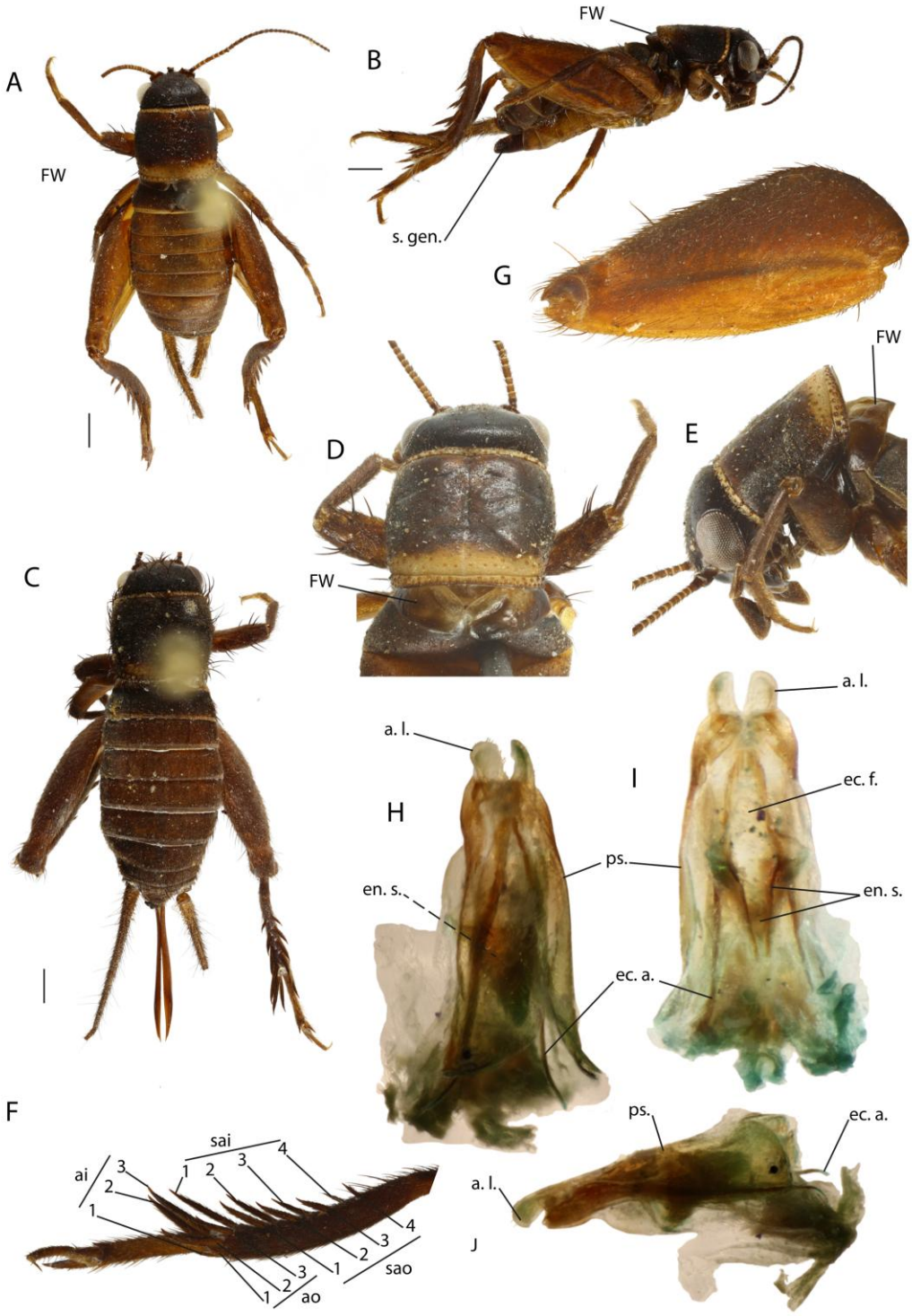

Figure 3.37. *Kanakinemobius mandjelia Desutter-Grandcolas, n. sp. A, B, habitus male, dorsal (A), lateral (B); C, female habitus, dorsal; D, E, male head, pronotum and forewings, dorsal (D), lateral (E); F, FIII, outer side, showing apical and subapical spurs; G, FIII outer side coloration; H-J, male genitalia, dorsal (H), ventral (I), lateral (J). Scales 1 mm. Abbreviations: see Material and methods.*

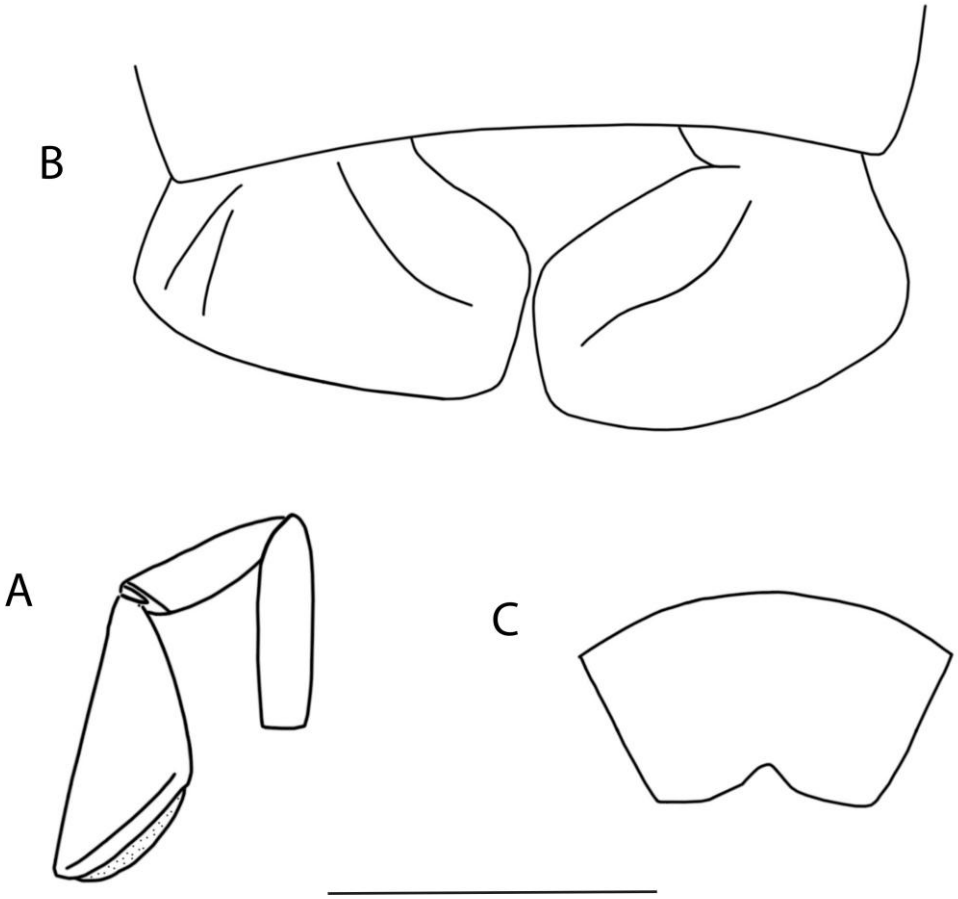

Figure 3.38. *Kanakinemobius mandjelia Desutter-Grandcolas, n. sp. A, maxillary palpi; B, male subgenital plate; C, female subgenital plate. Scales 1 mm.*

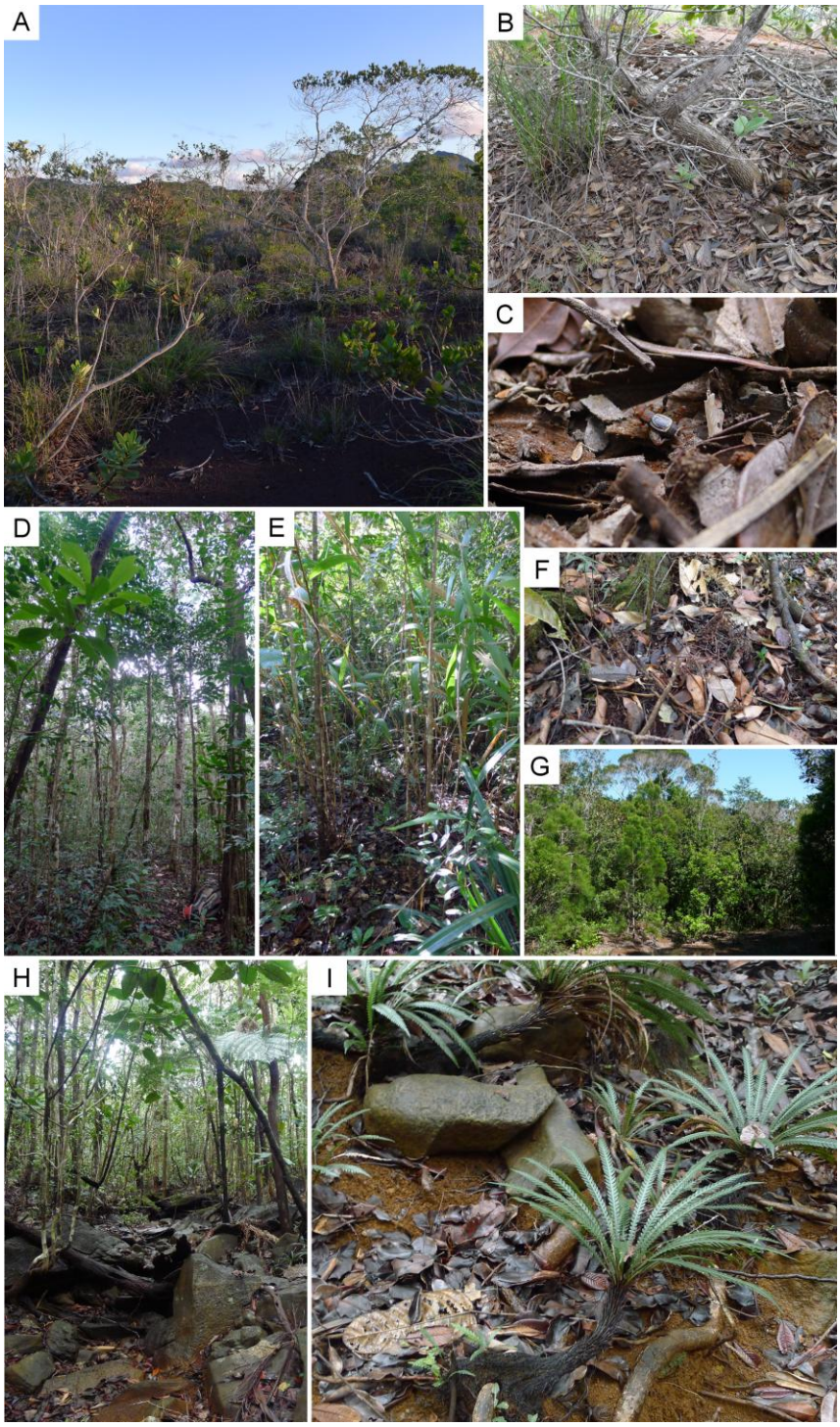

Figure 3.39. *Some cricket habitats in Southern New Caledonia: (A) open shrubland at the Col de Ouénaru where Pixipterus punctulatus Desutter-Grandcolas & Anso, n. sp. was found, 104 with (B) details of leaf litter and (C) one male of Koghiella flammea Anso & DesutterGrandcolas, n. sp.; (D) preforest formation at Grand Kaori with (E) details of the understorey and (F) leaf litter; (G) preforest maquis at Pic du Grand Kaori; (H) rainforest at Forêt Nord, with details (I) of leaf litter and bear ground where Koghiella nigris Anso & DesutterGrandcolas, n. sp. was usually found.*

3.6 Discussion

Although New Caledonian crickets have been sampled for several tens of years (dated back to first descriptions by Henri de Saussure in 1878 and Ignacio Bolivar in 1882), recent continuous and intensive sampling of selected parcels of varied vegetation in the context of a detailed ecological survey in southern part of New Caledonia (an area comprised between the perimeter south of a virtual line linking Noumea to Goro) revealed an unsuspected pattern of specific diversity, which lead to new species descriptions as pointed out in this paper.

Many taxa have been discovered, including three new genera and 21 new species, which appear to the best of our knowledge all endemic to New Caledonia. This is rather a surprising discovery, as the sampled plots are located in the southern part of New Caledonia, either on ultramafic substrates, which have been depicted as less favorable for crickets in terms of environmental conditions, or in areas close to well-sampled spots (Ouen Toro in the vicinity of Nouméa; Farino near Col d'Amieu). Anyway, this leads to a significant increase of New Caledonian biodiversity, and reinforces the high endemism rate of the archipelago (Grandcolas *et al.*, 2008).

Among these taxa, several species are specialized on open vegetation. Most of the newly described species have been discovered in the context of a study of the cricket communities along an ecological gradient from low maquis shrubland to rain forest. It especially have revealed that a specific group of species are asscociated to maquis shrubland and preforest (our "paraforestier") habitats and do not dwell the putative "most favorable" habitats represented by nearby rain forest patches (Anso *et al.* submit_b). Though some of these taxa are the sister group of forest-dwelling taxa; for example the eneopterine genus *Pixibinthus* Robillard & Anso, 2015 is the sister group of the speciose, forest-living genus *Agnotecous* Saussure, 1878, and the specialization of both taxa for maquis shrubland on one hand, and forest on the other may date back from the very colonization of New Caledonia by ancestral eneopterine crickets (Anso *et al.* submitted). In the same way, the podoscirtine genus *Pixipterus* Desutter-Grandcolas n. gen. and the nemobiine species *Koghiella flammea* Anso & Desutter-Grandcolas, n. sp. are only found in maquis shrubland and preforest plots. Although the lack of phylogeny precludes to check the origin of their specialization, both Podoscirtinae and Nemobiinae are mainly diversified in forests, which lends support to a hypothesis of habitat specialization at a generic, or specific level respectively. These original taxa are different from the widespread species which currently occurs in degraded shrubland plots and

along roadsides, such as *Oecanthus rufescens* Serville, 1838, described from India to south-western Pacific, the trigonidiines *Metioche vittaticolis* (Stål, 1861) or *Trigonidomorpha sjostedti* (Chopard, 1925), or even the grylline *Lepidogryllus comparatus* (Walker, 1869), *Teleogryllus marini* Otte & Alexander, 1983 and *T. oceanicus* (Le Guillou, 1841) distributed in the large Australasian region (Otte & Alexander, 1983). These two groups of species strongly differ by their distribution (putative endemic versus widespread) and their occurrence in the turnover of natural environments: the first ones are native specific components of New Caledonian communities, while the latter ones are supertramp "outsiders" that may have spread more recently to New Caledonia by both natural spread or promoted by human activities, which should be checked by future phylogenetic studies (Ricklefs & Bermingham, 2002). Both groups may be however considered specialized taxa, with a different range of potential habitats.

The sampling effort conducted in forest plots confirmed the real specialization of several genera for closed forest conditions. This is especially the case for the following genera: the phalangopsid *Caltathra* Otte, 1987, *Protathra* Desutter-Grandcolas, 1997 and *Pseudotrigonidium* Chopard, 1915, the grylline *Notosciobia* Chopard, 1915 and potentially the nemobiine *Kanakinemobius* Desutter-Grandcolas, n. gen. and *Paniella* Otte, 1987, which live mostly in forests but may occur in preforest plots. Within the Nemobiinae, *Bullita* spp occur mostly, or exclusively, in closed forests, while *Koghiella* is encountered in both closed forest and maquis shrubland conditions. The status of most Podoscirtinae remains less clear-cut relatively to forest versus maquis shrubland specialization, as these species live in the canopy and could colonize any plot as soon as some kind of trees (given species? given height?) are present; this may be the case in particular of *Adenopterus*, but *Matuanus* and *Archenopterus* genera, and some species of *Calsirtus*, who may seek day-time refuges in hollow twigs and/or similar habitats (Desutter-Grandcolas, 1997d), should be more restricted to forests. As often pinpointed for closed-forest dwelling species, these taxa appear well-specialized for their habitats: *Caltathra* and *Protathra* are mostly active on tree trunks, large roots and rocks, *Pseudotrigonidium* is active on understorey plants, and often found singing at night and hidding during the day on treeferns or Pandanaceae, while *Notosciobia* inhabits burrows in the ground; *Kanakinemobius* Desutter-Grandcolas, n. gen. and *Paniella* may live on mossy trunks or aerial leaf litter, but observations are too few to establish their habitat requierements.

Anyway, in southern New Caledonia both the maquis community and the forest community of crickets are composed of specialized species, and present a given ecological and phylogenetic structure as far as the habitats and relationships of the species are concerned.

Available data of forest communities from the Col d'Amieu, located toward North from the area sampled in the present paper, shows that the community is similar in composition and structure to that sampled in the South (Desutter-Grandcolas 1997c), but with a lower richness and diversity, which could result from a lower sampling effort (see Anso *et al.* submitted).

Finally, the recent discovery of maquis shrubland endemics, i.e. *Pixibinthus* Anso & Robillard, 2015 and *Pixipterus* Desutter-Grandcolas, n. gen., and of forest specialists, i.e. *Kanakinemobius* Desutter-Grandcolas, n. gen., calls for intensive field work focusing on original habitats. These observations parallel the discovery of rare and most often endangered, endemic species in the SWIO islands, related to specific habitats and ancient adaptation (Hugel, 2012)

3.7 Conclusion

Among Arthropoda, crickets appear as one of the best known clade in New Caledonia, thanks to intensive studies since more than twenty years. More than 150 species are now known from the territory, more than 95% of which being endemic.

However, except for detailed ecologically studied localities by Desutter-Grandcolas (1997c) and Anso *et al.* (submitted_b), most of already sampled sites have been visited by orthopterists in context of classical taxonomic investigations, and are known for most of them by only one species and never exceed 5 species (Gorochov 1986, Otte *et al.* 1987, Desutter-Grandcolas 1997b, 2002, Desutter-Grandcolas & Robillard 2006, Robillard & Desutter-Grandcolas 2008, Robillard *et al.* 2010, Nattier *et al.* 2012; Desutter-Grandcolas, pers. obs.). As restricted range endemism (microendemism) is a general pattern in Grande Terre (Grandcolas *et al.*, 2008; Nattier *et al.*, 2011; Nattier *et al.*, 2012; Barrabé *et al.*, 2014), local cricket communities may be composed of many yet undescribed cricket species, including in abundant clades such as Nemobiinae, as already pointed out by the discovery of these 22 taxa through ecological directed research on the basis of intensive sampling in various habitat conditions. More detailed sampling toward associated ecological and conservation questions should be promoted to better assess the huge original cricket fauna of this archipelago. Such

effort could also lead to nice models to be tested in the context of putative scenario aimed at explaining the origin and evolution of such high biodiversity.

3.8 Acknowledgments

This study was partly funded by a PhD grant, 'Bourse d'encouragement à la recherche universitaire', attributed to J. Anso by the Government of New Caledonia. Field work was partly supported by a grant from the Grand Observatoire du Pacifique Sud: AAP GOPS 2013 / 'Bioacoustique des grillons de Nouvelle-Calédonie' and by Action Transversale du Muséum (ATM 'Biodiversité actuelle et fossile. Crises, stress, restaurations et panchronisme: le message systématique'). J. Anso was also supported for visiting the MNHN collections by funding from LABex and Gops.

We thank Joseph Manauté and Joël Delafenêtre from the Parc provincial de la Rivière Bleue who grants us access to rainforest, preforest formation and shrubland vegetation in the park. We also thanks all the Bs and Ms students involved in this project, respectively Audrey Espalieu, Léa Colmas, Alexia Omont, who provide a great effort on field work. Edouard Bourguet, Martin Thibault and Fréderic Rigault also provide helpful support for field work.

Chapitre II

4 Enjeux et importance des milieux miniers à travers l'étude d'un nouveau genre de grillon endémique

Cette section a été l'objet d'un article de recherche accepté à *PloS ONE*, sous la forme suivante :

Anso, J., Barrabé, L., Desutter-Grandcolas, L., Jourdan, H., Grandcolas, P., Dong, J., and Robillard, T. (2016). Old lineage on an old island: *Pixibinthus*, a new cricket genus endemic from New Caledonia shed light on Gryllid diversification in a hotspot of biodiversity. *PloS ONE*.

4.1 Résumé

Peu d'études ont été conduites sur les premiers événements de colonisation de la Nouvelle-Calédonie par les insectes, après la réémergence de l'île principale (la Grande Terre) il y a 37 Ma. Dans ce papier, nous étudions le mode et le tempo de l'évolution d'un nouveau de grillon endémique, *Pixibinthus*, récemment découvert dans la partie la plus méridionale de la Grande Terre. Premièrement, nous décrivons ce nouveau genre monotypique retrouvé exclusivement dans les végétations ouvertes de maquis bas sur sols métallifères, couramment appelées « maquis minier » et unique de la Nouvelle-Calédonie. Ensuite nous avons réalisé une phylogénie et une datation moléculaire basée sur cinq locus mitochondriaux et quatre locus nucléaires, dans le but d'établir les relations de parentés de Pixibinthus avec les représentants des Eneopterinae ainsi que les temps de divergence. *Pixibinthus* est décrit comme le nouveau groupe frère du genre endémique *Agnotecous*, composé principalement d'espèces forestières. Les résultats de datation indiquent que la colonisation de l'archipel par l'ancêtre commun des deux groupes frères remonte à 34.7 Ma, relativement peu de temps après la réémergence de la Nouvelle-Calédonie, plaçant ainsi *Pixibinthus* et *Agnotecous* comme les plus anciennes lignées d'insectes documentées en Nouvelle-Calédonie. Ces travaux mettent l'accent pour la première fois de deux spécialisations écologiques très différentes et très marquées, la première en forêt pour les *Agnotecous* composé de 19 espèces, et la seconde en milieu ouvert pour *Pixibinthus*, avec une seule espèce documenté jusqu'alors. A titre d'hypothèse, la très faible diversité du genre *Pixibinthus* pourrait être expliquée par l'évolution des dynamiques paysagères de la Nouvelle-Calédonie, et notamment par les événements climatiques majeurs et les régimes d'incendies. De plus, les préférences contrastées pour les milieux ouverts pour Pixibinthus, et pour les milieux fermés pour Agnotecous s'observent dans la spécialisation acoustique des espèces chanteuses, avec des fréquences dominantes plus hautes en milieu ouvert et plus basses en milieu fermé. Finalement, l'histoire évolutive hors du commun de cette vieille lignée néo-calédonienne nous invite à renforcer nos connaissances sur la biodiversité faunistique des « maquis minier », dans le but d'améliorer notre compréhension de l'origine de la biodiversité de Nouvelle-Calédonie et les anciennes dynamiques qui l'ont influencée.

Mots clés: Nouvelle-Calédonie; dynamiques paysagères; *Pixibinthus*; Lignée relique; grillons; *Agnotecous.*

4.2 Abstract

Few studies have focused on the early colonization of New Caledonia by insects, after the re-emergence of the main island, 37 Myr ago. Here we investigate the mode and tempo of evolution of a new endemic cricket genus, *Pixibinthus*, recently discovered in southern New Caledonia. First we formally describe this new monotypic genus found exclusively in the open shrubby vegetation on metalliferous soils, named 'maquis minier', unique to New Caledonia. We then reconstruct a dated molecular phylogeny based on five mitochondrial and four nuclear loci in order to establish relationships of *Pixibinthus* within Eneopterinae crickets. *Pixibinthus* is recovered as the sister clade of the endemic genus *Agnotecous*, mostly rainforest-dwellers. Dating results show that the island colonization by their common ancestor occurred around 34.7 Myr, shortly after New Caledonia re-emergence. *Pixibinthus* and *Agnotecous* are then one of the oldest insect lineages documented so far for New Caledonia. This discovery highlights for the first time two clear-cut ecological specializations between sister clades, as *Agnotecous* is mainly found in rainforests with 19 species, whereas *Pixibinthus* is found in open habitats with a single documented species. The preference of *Pixibinthus* for open habitats and of *Agnotecous* for forest habitats nicely fits an acoustic specialization, either explained by differences in body size or in acoustic properties of their respective habitats. We hypothesize that landscape dynamics, linked to major past climatic events and recent change in fire regimes are possible causes for both present-day low diversity and rarity in genus *Pixibinthus*. The unique evolutionary history of this old New Caledonian lineage stresses the importance to increase our knowledge on the faunal biodiversity of 'maquis minier', in order to better understand the origin and past dynamics of New Caledonian biota.

Keywords: New Caledonia; landscape dynamics; *Pixibinthus*; relict lineage; cricket; *Agnotecous*

4.3 Introduction

Understanding the origin of island biota requires that the evolutionary history of clades is reconstructed in details and linked to the evolution of local environments (Carlquist, 1965; Whittaker & Fernández-Palacios, 2007). This task is both especially interesting and demanding in hotspots of biodiversity, such as New Caledonia in the Southwest Pacific, where richness and endemism reach outstanding levels (Myers *et al.*, 2000; Grandcolas *et al.*, 2008; Kier *et al.*, 2009). New Caledonia has a long and complex environmental history since the main island re-emerged 37 ± 2 Myr ago (Pelletier, 2006; Schellart *et al.*, 2006), after having been largely covered with an ophiolithic layer during its obduction under the Pacific plate (Pelletier, 2006; Cluzel *et al.*, 2012). This layer has been progressively reduced to only one third of the island surface after several intense weathering events under climate control. These geological and climatic events led to the establishment of a mosaic of soils, including metalliferous soils (rich in heavy metals such as magnesium, manganese and nickel), habitats and landscapes (e.g., (Chevillotte *et al.*, 2006)). The present-day vegetation on metalliferous soils is constituted by two main native types, rainforest and open shrubby vegetation named 'maquis minier', both harboring many endemic species (Jaffré, 1980; Morat *et al.*, 1986). Many studies refer to the interaction between metalliferous soils and the corresponding vegetation as a peculiar and original system dating back to the first ages of the island colonization. Pre-adaptation or adaptation to these specific soils on ultramafic rocks would have been an early engine of diversification of endemism for at least a major part of New Caledonian biota with the subsequent prediction that island old groups have narrow relationships to metalliferous soils (Morat *et al.*, 1986; Pillon *et al.*, 2010; Paun *et al.*, 2015). This theory has both been corroborated and refuted depending on group of organism studied (e.g., (Espeland *et al.*, 2008; Murienne *et al.*, 2008; Nattier *et al.*, 2013; Pouteau *et al.*, 2015)) and a dated phylogenetic framework is now clearly required to clarify this subject. The present-day vegetation dynamics can also obscure the reconstruction of past processes. The balance between 'maquis minier' and forest is controlled by climatic variations, fire regimes and human influences leading to a present increase and over-representation of this open vegetation type (Delcourt & Delcourt, 1983; Prentice, 1986; Byrne *et al.*, 2011). Therefore, 'maquis minier' is often seen as a secondary and disturbed vegetation type when it is actually a rich original endemic formation potentially indicative of early New Caledonian ecosystems (Jaffré *et al.*, 1998b; Morat *et al.*, 2012).

Our study is aimed at unraveling the evolution of an insect lineage endemic to ‘maquis minier’, to date its origin, to emphasize on its adaptation to the habitat and to suggest future research directions for better understanding its relationships to landscape dynamics and human disturbance. We focused on the insect group of crickets (Orthoptera, Grylloidea) that gained increasing attention from the scientific community as they both play a significant role in ecosystem functioning (Wellstein *et al.*, 2011)and are relatively sensitive to environmental disturbances (Gerlach *et al.*, 2013). In New Caledonia, the cricket fauna is rich and has been recently studied, providing some insights on the dynamics of the micro-endemism and of the adaptation to the environment (Desutter-Grandcolas, 1997c; Desutter-Grandcolas & Robillard, 2006; Nattier *et al.*, 2012; Robillard *et al.*, 2013). This fauna was still insufficiently known in ‘maquis minier’ where we concentrated our efforts, permitting the discovery and description of a new genus, *Pixibinthus*Robillard and Anso, gen. nov., that was used to ask the present questions.

4.4 Material and methods

4.4.1 Study sites and cricket sampling

Intensive cricket samplings were performed from October 2013 to March 2014 to study the composition of cricket species along a gradient from ‘maquis minier’ to rainforest (S5 Table). We selected our study sites on the uniform metalliferous soil located in the southern part of Grande Terre. We subsequently recorded for each sampling site the absence / presence of each cricket species. For each cricket sampled in the field, time of day and habitats were noted. Crickets were identified as morphospecies at the Institut de Recherche pour le Développement (IRD) in Noumea, and identifications were checked by comparisons with the collections of the Muséum national d’Histoire naturelle, Paris (MNHN). Specimens were deposited in the collections of the MNHN, and in collections of the IRD, Noumea (ONNC), and in collection of the Institut Agronomique néo-Calédonien, Pocquereux (CXMNC). Field Permit: the Province Sud Environment Office (DENV- Direction de l’Environnement de la Province Sud)

S5 Table. List of localites for the cricket sampling with geographical coordinates.

4.4.2 Taxon description

Morphological descriptions follow the pattern and terminology of recent publications (e.g., (Robillard *et al.*, 2014; Vicente *et al.*, 2015)). Direct observations and dissections have been made using a binocular microscope Leica MZ16 at magnifications up to 115×. Male tegminal veins and cells follow terminology of Ragge (1955) and Robillard & Desutter-Grandcolas (2004b). Male and female genitalia have been dissected in softened or fresh specimens. Male genitalia were dissected by cutting the membranes between the paraprocts and the subgenital plate; in females, copulatory papilla were dissected by cutting the membranes between the ovipositor and the subgenital plate. Genitalia have been cleared with cold KOH and preserved in glycerine in vials pinned under specimens. Male genitalia terminology follows Desutter (Desutter, 1987), modified in Desutter-Grandcolas (Desutter-Grandcolas, 2003) and Robillard & Desutter-Grandcolas (Robillard & Desutter-Grandcolas, 2004b). Photographs of male genitalia were obtained using an AmScope MU1000 digital camera (www.Amscope.com). Genitalia were stained with a drop of Punktol (JLB, Germany).

4.4.2.1 Nomenclatural Acts

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature, and hence the new names contained herein are available under that Code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix "http://zoobank.org/". The LSID for this publication is: urn:lsid:zoobank.org:pub: AFAE2A4F-7161-4100-A1DB-D420FA5C0435. The electronic edition of this work was published in a journal with an ISSN, and has been archived and is available from the following digital repositories: PubMed Central, LOCKSS.

4.4.2.2 Bioacoustic study

Collected crickets from the field were recorded with a modified condenser microphone (CM16 Avisoft Bioacoustics, Berlin, frequency range: 3 - 150 kHz ± 6 dB, R. Specht pers.

comm.) in a sound attenuated room controlled for temperature in the MNHN. The insects were placed over night alone in a cage made of mosquito net to avoid echoes. The microphone was placed 30 cm from the cage. Automatic recordings were made using the program Avisoft Triggering Harddisk Recorder version 2.97 and a 8-Pre MOTU sound card at a sampling frequency of 96 kilo-samples per second (16 bit). The temporal acoustic activity of crickets was obtained in the field by ambient acoustic recordings with a SongMeter SM2 Bat sensor (Wildlife Acoustics, concord, NY, U.S.A.) at Pic du Grand Kaori during 72 hours.

Cricket song terminology follows Ragge & Reynolds (Ragge & Reynolds, 1998): one song unit is called a syllable and corresponds to one opening-closing cycle of the male forewings; a group of syllables forming a cricket call is named an echeme. We used the computer software Avisoft-SASLab pro V. 5.2.06 (Avisoft bioacoustics; Specht 2012) to automatically analyze cricket calls. We used automatic analyses to calculate syllable duration and period, number of syllable per echeme, duty-cycle, and dominant frequency. Eight calling songs from 4 different males were used for the analysis (two per male). Measurements acquired from automatic analyses were verified manually in order to avoid errors or aberrant values. Sound tracks were deposited in the Sound Library of the MNHN, Paris (MNHN‑SO‑2015-9, 10, 11, 12, 13, 14).

4.4.2.3 Abbreviations

General morphology: FW: forewing; Tarsomere III-1: basal segment of hind leg tarsomere; T: tibiae.

Male genitalia: ect ap: ectophallic apodeme; ect arc: ectophallic arc; ect f: ectophallic fold; ect lat exp: ectophallic lateral expansion; end ap: endophallic apodeme; end s: endophallic sclerite; pse p: pseudepiphallic paramere.

Tegminal venation: 1A-4A: first to fourth anal veins; CuA: anterior cubitus; CuP: posterior cubitus; M: median vein; Sc: subcostal vein; R: radial vein; di: diagonal vein; ob: oblique veins, c1-3: first to third cells of C alignment; d1 cell (mirror): first cell(s) of D alignment; d2: second cell of D alignment; e1: first cell of E alignment.

Morphological measurements: FIIIL: length of hind femora; FIIIW: width of hind femora; FWL: forewing length; FWW: forewing width (at the level of maximal width); Ias: inner spines on TIII dorsal side, above the spurs; Ibs: inner spines on TIII dorsal side, between the spurs; Oas: outer spines on TIII dorsal side, above the spurs; Obs: outer spines on TIII dorsal side, between the spurs; OL: ovipositor length; PronL: pronotum length; PronW: pronotum width; TIIIL: length of hind tibiae; TaIIIs: spines on outer edge of third hind tarsomere, not including the apical spine.

Acoustics: fd: dominant frequency; TSR: tooth-strike rate.

4.4.3 Molecular phylogeny

4.4.3.1 Taxon sampling

Two molecular datasets were built aiming both to investigate the phylogenetic placement of *Pixibinthus* within crickets (= dataset 1), and to generate a molecular dating to estimate divergence times of *Pixibinthus* and its close relatives (= dataset 2).

The molecular sampling of dataset 1 comprised six individuals of *Pixibinthus* (from three different locations). As *Pixibinthus* shares the typical morphology of the Lebinthini tribe within the subfamily Eneopterinae (see below), a special emphasis has been put on the taxonomical sampling of this tribe, by incorporating representatives of the genera *Agnotecous* Saussure, 1878 (nine species; 14 samples), *Lebinthus* Stål, 1877 (six species; seven samples), *Cardiodactylus* Saussure, 1878 (four species; five samples), and *Swezwilderia* Chopard, 1929 (one species). The sampling was then completed with other species belonging to the other four current tribes of the Eneopterinae subfamily (sensu (Robillard & Desutter-Grandcolas, 2008)): Eurepini (one species), Eneopterini (one species), Nisitrini (two species; three samples), and Xenogryllini (one species). A total of 26 species were then used in the ingroup sampling of dataset 1 (corresponding to 39 samples; Table 4.1). Two species from a different cricket subfamily (Gryllinae: *Achetadomesticus* (Linnaeus, 1758) and *Gryllusbimaculatus* De Geer, 1773) were finally used as most external outgroups.

Table 4.1. *List of taxa investigated in the molecular study, with voucher information, molecular dataset, country and locality origin of samples, taxonomical classification, and genbank accession numbers. Newly generated sequences are indicated with an asterisk (and would be very soon referred to a genbank accession number). The superscript numbers refer to the publication where the sequences were first published: [1](Nattier et al., 2012), [2](Huang et al., 2000), [3](Regier et al., 2010), [4](Nattier et al., 2011), [5](Robillard & Desutter-Grandcolas, 2006), [6](Jost & Shaw, 2006), [7](Jaiswara et al., 2012), [8](Chintauan-Marquier et al., 2016), [9](Flook et al., 1999). The phylogeny-based taxonomies of Chintauan-Marquier et al. (Chintauan-Marquier et al., 2016) for Gryllidea and Robillard & Desutter-Grandcolas (Robillard & Desutter-Grandcolas, 2008) for Eneopterinae were used; superfamilies and families are indicated for all taxa, and subfamilies and tribes for ingroup taxa only. Abbreviations used for subfamilies: ENEO = Eneopterinae, GRYL = Gryllinae; Tribes: Ene = Eneopterini, Eur = Eurepini, Gry = Gryllini, Leb = Lebinthini, Nis = Nisitrini, Xen=Xenogryllini.N/A corresponds to non-available data.*

Species	Superfamily / Family	Ingroup: subfamily / tribe	Country	Locality	Vouchers	dataset 1	dataset 2	16S	12S	Cytb
Acheta domesticus (Linnaeus, 1758)	GRYLLOIDEA Gryllidae	/ GRYL / Gry	France	Laboratory strain	MNHN-EO-ENSIF3523	x	x	AF248698 [2]	Z97611 [9]	AF248682 [2]
Afrophaloria amani Desutter-Grandcolas, 2015	GRYLLOIDEA Phalangopsidae	/	Tanzania	Amani	MNHN-EO-ENSIF3341		x	KR903696 [8]	KR903858 [8]	KR903353 [8]
Agnotecous albifrons Desutter-Grandcolas, 1997 CT	GRYLLOIDEA Gryllidae	/ ENEO/ Leb	New Caledonia	Col Toma	MNHN-EO-ENSIF2767	x	x	JX897353 [1]	JX897394 [1]	JX897314 [1]
Agnotecous albifrons Desutter-Grandcolas, 1997 Ge	GRYLLOIDEA Gryllidae	/ ENEO/ Leb	New Caledonia	Gelima	MNHN-EO-ENSIF1771	x		JX897354 [1]	JX897396 [1]	JX897316 [1]
Agnotecous azurensis Desutter-Grancolas, 2006 GK	GRYLLOIDEA Gryllidae	/ ENEO/ Leb	New Caledonia	Grand Kaori	MNHN-EO-ENSIF2777	x		JX897360 [1]	JX897389 [1]	JX897331 [1]

Agnotecous azurensis Desutter-Grancolas, 2006 RB	GRYLLOIDEA Gryllidae	/	ENEO/ Leb	New Caledonia	Rivière Bleue (Pourina)	MNHN-EO-ENSIF2780	x	x	JX897358	1	JX897376	1	JX897329	1
Agnotecous clarus Desutter-Grandcolas, 2006	GRYLLOIDEA Gryllidae	/	ENEO/ Leb	New Caledonia	Pic du Pin	MNHN-EO-ENSIF2788	x	x	JX897347	1	JX897400	1	JX897324	1
Agnotecous meridionalis Desutter-Grandcolas, 2006 IDP	GRYLLOIDEA Gryllidae	/	ENEO/ Leb	New Caledonia	Ile des Pins	MNHN-EO-ENSIF2772	x		JX897349	1	JX897401	1	JX897311	1
Agnotecous meridionalis Desutter-Grandcolas, 2006 PB	GRYLLOIDEA Gryllidae	/	ENEO/ Leb	New Caledonia	Port Boisé	MNHN-EO-ENSIF2771	x	x	JX897350	1	JX897402	1	JX897313	1
Agnotecous obscurus (Chopard, 1970) Ao	GRYLLOIDEA Gryllidae	/	ENEO/ Leb	New Caledonia	Aoupinié	MNHN-EO-ENSIF2786	x		JX897356	1	JX897398	1	JX897319	1
Agnotecous obscurus (Chopard, 1970) Ma	GRYLLOIDEA Gryllidae	/	ENEO/ Leb	New Caledonia	Mandjélia	MNHN-EO-ENSIF2785	x	x	JX897357	1	JX897393	1	JX897320	1
Agnotecous occidentalis Desutter-Grandcolas, 2006	GRYLLOIDEA Gryllidae	/	ENEO/ Leb	New Caledonia	Col des Roussettes	MNHN-EO-ENSIF2765	x	x	JX897362	1	JX897386	1	JX897322	1
Agnotecous robustus (Chopard, 1915)	GRYLLOIDEA Gryllidae	/	ENEO/ Leb	New Caledonia	Aoupinié	MNHN-EO-ENSIF2752	x	x	JX897359	1	JX897375	1	JX897333	1
Agnotecous sarramea Desutter-Grancolas, 1997	GRYLLOIDEA Gryllidae	/	ENEO/ Leb	New Caledonia	Mé Aréto	MNHN-EO-ENSIF2764	x	x	JX897372	1	JX897380	1	JX897342	1
Agnotecous yahoue Otte, 1987 Ko	GRYLLOIDEA Gryllidae	/	ENEO/ Leb	New Caledonia	Monts Koghis	MNHN-EO-ENSIF2766	x	x	JX897366	1	JX897387	1	JX897334	1
Agnotecous yahoue Otte, 1987 Mo	GRYLLOIDEA Gryllidae	/	ENEO/ Leb	New Caledonia	Mont Mou	MNHN-EO-ENSIF2773	x		JX897367	1	JX897388	1	JX897337	1

Anaxipha sp. affinis *nitida* (Chopard, 1925)	GRYLLOIDEA Trigonidiidae	/		French Guiana	Arataye	MNHN-EO-ENSIF3260		x	KR903735	[8]	KR903906	[8]	KR903396	[8]
Bullita sp.	GRYLLOIDEA Trigonidiidae	/		New Caledonia	Yahoue	MNHN-EO-ENSIF3393		x	KR903810	[8]	KR904001	[8]	KR903473	[8]
Cardiodactylus enkraussi Otte, 2007	GRYLLOIDEA Gryllidae	/	ENEO/ Leb	Vanuatu	Espiritu Santo, Vathé	MNHN-EO-ENSIF2366	x	x	JF972518 / JF972486	[4]	JF972502	[4]	N/A	
Cardiodactylus guttulus (Matsumura, 1913)	GRYLLOIDEA Gryllidae	/	ENEO/ Leb	Japan		MNHN-EO-ENSIF1193	x	x	JF972519	[4]	JF972503	[4]	JF972487	[4]
Cardiodactylus novaeguineae (Haan, 1842)	GRYLLOIDEA Gryllidae	/	ENEO/ Leb	Vanuatu	Espiritu Santo, Peavot	MNHN-EO-ENSIF2030	x	x	JF972521	[4]	JF972506	[4]	JF972490	[4]
Cardiodactylus novaeguineae (Haan, 1842) NC	GRYLLOIDEA Gryllidae	/	ENEO/ Leb	New Caledonia	Lifou	MNHN-EO-ENSIF1921	x	x	AY905299	[5]	AY905270	[5]	AY905353	[5]
Cardiodactylus tankara Robillard, 2009	GRYLLOIDEA Gryllidae	/	ENEO/ Leb	Vanuatu	Espiritu Santo, Butmas	MNHN-EO-ENSIF2410	x	x	JF972522	[4]	JF972508	[4]	JF972491	[4]
Cearacesa sp.	GRYLLOIDEA Gryllidae	/		Brazil	Pernambuco	MNHN-EO-ENSIF3270		x	KR903798	[8]	KR903985	[8]	KR903459	[8]
Diatrypa sp.	GRYLLOIDEA Gryllidae	/		French Guiana	Arataye	MNHN-EO-ENSIF3261		x	KR903728	[8]	KR903899	[8]	KR903389	[8]
Ectecous sp.	GRYLLOIDEA Phalangopsidae	/		French Guiana	Arataye	MNHN-EO-ENSIF3384		x	KR903726	[8]	KR903897	[8]	KR903387	[8]
Eneoptera guyanensis Chopard, 1931	GRYLLOIDEA Gryllidae	/	ENEO / Ene	French Guiana	Montagne de Kaw	MNHN-EO-ENSIF2741[1] / MNHN-EO-ENSIF3687[2]	x	x	AY905301	[5]	AY905272	[5]	AY905355	[5]
Eurepini sp.	GRYLLOIDEA Gryllidae	/	ENEO / Eur	Australia	Northern Territory, Litchfield National Park	MNHN-EO-ENSIF3155	x	x	XXXXXXXX	*	XXXXXXXX	*	XXXXXXXX	*
Fryerius sp.	GRYLLOIDEA Gryllidae	/		Comoros	Moheli	MNHN-EO-ENSIF3378		x	KR903730	[8]	KR903901	[8]	KR903391	[8]
Gryllotalpa sp.	GRYLLOTALPOIDEA / Gryllotalpidae			Mozambique	Cabo Delgado	MNHN-EO-ENSIF3315		x	KR903783	[8]	KR903961	[8]	KR903443	[8]

Gryllus bimaculatus De Geer, 1773	GRYLLOIDEA Gryllidae	/	GRYL / Gry	France	Laboratory strain	MNHN-EO-ENSIF3524/3404	x	x	AF248685 [2]		AY905292 [5]		AF248659 [2]	
Homeogryllus orientalis Desutter, 1985	GRYLLOIDEA Phalangopsidae	/		Mozambique	Cabo Delgado	MNHN-EO-ENSIF3603		x	KR903752 [8]		KR903925 [8]		KR903413 [8]	
Lebinthus lifouensis Desutter-Grandcolas, 1997	GRYLLOIDEA Gryllidae	/	ENEO/ Leb	New Caledonia	Lifou	MNHN-EO-ENSIF1346	x	x	AY905309 [5]		AY905279 [5]		AY905364 [5]	
Lebinthus luae Robillard & Tan, 2013	GRYLLOIDEA Gryllidae	/	ENEO/ Leb	Singapore	Labrador park	MNHN-EO-ENSIF2740	x	x	JF972524 [4]		XXXXXXXX	*	JF972493 [4]	
Lebinthus nattawa Robillard, 2009	GRYLLOIDEA Gryllidae	/	ENEO/ Leb	Vanuatu	Nattawa, Santo	MNHN-EO-ENSIF2564	x	x	JF972525 [4]		JF972510 [4]		JF972494 [4]	
Lebinthus santoensis Robillard, 2009 P	GRYLLOIDEA Gryllidae	/	ENEO/ Leb	Vanuatu	Espiritu Santo, Peavot	MNHN-EO-ENSIF2484		x	XXXXXXXX	*	XXXXXXXX	*	XXXXXXXX	*
Lebinthus santoensis Robillard, 2009 V	GRYLLOIDEA Gryllidae	/	ENEO/ Leb	Vanuatu	Espiritu Santo, Vathé	MNHN-EO-ENSIF2437	x	x	JF972527 [4]		JF972511 [4]		JF972495 [4]	
Lebinthus sp. PNG	GRYLLOIDEA Gryllidae	/	ENEO/ Leb	Papua New Guineae	New Ireland	MNHN-EO-ENSIF117[1] / MNHN-EO-ENSIF157[2]	x	x	JF972528 [4]		JF972513 [4]		XXXXXXXX	*
Lebinthus villemantae Robillard, 2010	GRYLLOIDEA Gryllidae	/	ENEO/ Leb	Indonesia	Sulawesi, Bulu Saraun	MNHN-EO-ENSIF2739	x	x	JF972526 [4]		JF972512 [4]		JF972496 [4]	
Luzaridella obscura Desutter-Grandcolas, 1992	GRYLLOIDEA Phalangopsidae	/		French Guiana	Arataye	MNHN-EO-ENSIF3253		x	KR903708 [8]		KR903871 [8]		KR903365 [8]	
Microlandreva sp. Chopard, 1958	GRYLLOIDEA Gryllidae	/		Mayotte		MNHN-EO-ENSIF3307		x	KR903782 [8]		KR903960 [8]		KR903442 [8]	
Nisitrus vittatus (Haan, 1842) Se	GRYLLOIDEA Gryllidae	/	ENEO / Nis	Malaysia	Selangor, Mount Kira	MNHN-EO-ENSIF3134	x		AY905314 [5]		AY905284		AY905369 [5]	
Nisitrus vittatus (Haan, 1842) Si	GRYLLOIDEA Gryllidae	/	ENEO / Nis	Singapore	Bukit Timah Natural Reserve	MNHN-EO-ENSIF2742	x	x	AY905314 [5]		AY905284		AY905369 [5]	

Ornebius xanthopterus Guérin-Méneville, 1844	GRYLLOIDEA Mogoplistidae	/		Mauritius	Le morne	Collection SH-2011-016		x	KR903769	[8]	KR903944	[8]	KR903430	[8]
Paranisitra longipes Chopard, 1925	GRYLLOIDEA Gryllidae	/	ENEO / Nis	Philippines	Luzon, Mount Makiling	MNHN-EO-ENSIF3157	x	x	XXXXXXXX	*	XXXXXXXX	*	N/A	
Pixibinthus sonicus Anso & Robillard, sp. nov. FN1	GRYLLOIDEA Gryllidae	/	ENEO/ Leb	New Caledonia	Forêt Nord	MNHN-EO-ENSIF99	x		XXXXXXXX	*	XXXXXXXX	*	XXXXXXXX	*
Pixibinthus sonicus Anso & Robillard, sp. nov. FN2	GRYLLOIDEA Gryllidae	/	ENEO/ Leb	New Caledonia	Forêt Nord	MNHN-EO-ENSIF83	x		XXXXXXXX	*	XXXXXXXX	*	XXXXXXXX	*
Pixibinthus sonicus Anso & Robillard, sp. nov. GK1	GRYLLOIDEA Gryllidae	/	ENEO/ Leb	New Caledonia	Grand Kaori	MNHN-EO-ENSIF150	x	x	XXXXXXXX	*	XXXXXXXX	*	XXXXXXXX	*
Pixibinthus sonicus Anso & Robillard, sp. nov. GK2	GRYLLOIDEA Gryllidae	/	ENEO/ Leb	New Caledonia	Grand Kaori	MNHN-EO-ENSIF125	x		XXXXXXXX	*	XXXXXXXX	*	XXXXXXXX	*
Pixibinthus sonicus Anso & Robillard, sp. nov. RB1	GRYLLOIDEA Gryllidae	/	ENEO/ Leb	New Caledonia	Rivière Bleue (Rivière Blanche)	MNHN-EO-ENSIF99	x		XXXXXXXX	*	XXXXXXXX	*	XXXXXXXX	*
Pixibinthus sonicus Anso & Robillard, sp. nov. RB2	GRYLLOIDEA Gryllidae	/	ENEO/ Leb	New Caledonia	Rivière Bleue (Rivière Blanche)	MNHN-EO-ENSIF133	x		XXXXXXXX	*	XXXXXXXX	*	XXXXXXXX	*
Pteroplistes masinagudi Jaiswara, 2014	GRYLLOIDEA *incertae sedis*			India	Tamil Nadu	Collection BNHS		x	KR903693	[8]	KR903854	[8]	KR903349	[8]
Swezwilderia sp.	GRYLLOIDEA Gryllidae	/	ENEO / ?	Fiji	Viti Levu	MNHN-EO-ENSIF2737	x	x	JF972529	[4]	JF972514	[4]	JF972498	[4]
Xenogryllus marmoratus Bolívar, 1890	GRYLLOIDEA Gryllidae	/	ENEO / Xen	Japan	Honshu, Nara City	MNHN-EO-ENSIF3161	x	x	XXXXXXXX	*	XXXXXXXX	*	XXXXXXXX	*

(continued)

Species	CO1	CO2	28SA	EF1a	H3	18S
Acheta domesticus (Linnaeus, 1758)	JX897403 [1]	JX897439 [1]	JX897465 [1]	GQ886692 [3]	XXXXXXXX *	XXXXXXXX *
Afrophaloria amani Desutter-Grandcolas, 2015	N/A	N/A	KR903524 [8]	N/A	KR903173 [8]	KR904049 [8]
Agnotecous albifrons Desutter-Grandcolas, 1997 CT	JX897418 [1]	JX897446 [1]	JX897490 [1]	JX897527 [1]	JX897572 [1]	JX897583 [1]
Agnotecous albifrons Desutter-Grandcolas, 1997 Ge	JX897416 [1]	JX897445 [1]	N/A	JX897529 [1]	JX897574 [1]	JX897585 [1]
Agnotecous azurensis Desutter-Grancolas, 2006 GK	JX897426 [1]	N/A	JX897472 [1]	JX897505 [1]	JX897565 [1]	JX897593 [1]
Agnotecous azurensis Desutter-Grancolas, 2006 RB	JX897423 [1]	JX897453 [1]	JX897475 [1]	JX897502 [1]	JX897566 [1]	JX897595 [1]
Agnotecous clarus Desutter-Grandcolas, 2006	JX897407 [1]	JX897451 [1]	JX897492 [1]	JX897523 [1]	JX897554 [1]	JX897590 [1]
Agnotecous meridionalis Desutter-Grandcolas, 2006 IDP	JX897420 [1]	N/A	JX897488 [1]	JX897519 [1]	JX897553 [1]	JX897579 [1]
Agnotecous meridionalis Desutter-Grandcolas, 2006 PB	JX897410 [1]	JX897442 [1]	JX897489 [1]	JX897520 [1]	JX897550 [1]	JX897597 [1]

Agnotecous obscurus (Chopard, 1970) Ao	JX897415	[1]	JX897449	[1]	N/A		JX897510	[1]	N/A		JX897591	[1]
Agnotecous obscurus (Chopard, 1970) Ma	JX897412	[1]	JX897450	[1]	JX897487	[1]	JX897525	[1]	JX897576	[1]	JX897587	[1]
Agnotecous occidentalis Desutter-Grandcolas, 2006	JX897434	[1]	JX897461	[1]	N/A		JX897512	[1]	JX897570	[1]	JX897589	[1]
Agnotecous robustus (Chopard, 1915)	JX897406	[1]	JX897443	[1]	N/A		JX897498	[1]	JX897555	[1]	JX897588	[1]
Agnotecous sarramea Desutter-Grancolas, 1997	JX897430	[1]	JX897456	[1]	JX897471	[1]	JX897511	[1]	JX897561	[1]	JX897598	[1]
Agnotecous yahoue Otte, 1987 Ko	JX897438	[1]	JX897463	[1]	JX897478	[1]	JX897500	[1]	JX897549	[1]	JX897602	[1]
Agnotecous yahoue Otte, 1987 Mo	JX897437	[1]	JX897462	[1]	JX897479	[1]	JX897501	[1]	N/A		N/A	
Anaxipha sp. affinis *nitida* (Chopard, 1925)	N/A		N/A		KR903570	[8]	N/A		KR903220	[8]	KR904094	[8]
Bullita sp.	N/A		N/A		KR903649	[8]	N/A		KR903307	[8]	KR904183	[8]
Cardiodactylus enkraussi Otte, 2007	XXXXXXXX	*	XXXXXXXX	*	N/A		XXXXXXXX	*	XXXXXXXX	*	JF972533	[4]
Cardiodactylus guttulus (Matsumura, 1913)	XXXXXXXX	*	N/A		XXXXXXXX	*	XXXXXXXX	*	XXXXXXXX	*	JF972534	[4]
Cardiodactylus novaeguineae (Haan, 1842)	XXXXXXXX	*	XXXXXXXX	*	XXXXXXXX	*	XXXXXXXX	*	XXXXXXXX	*	JF972537	[4]
Cardiodactylus novaeguineae (Haan, 1842) NC	XXXXXXXX	*	XXXXXXXX	*	XXXXXXXX	*	XXXXXXXX	*	XXXXXXXX	*	AY905329	[5]

Cardiodactylus tankara Robillard, 2009	XXXXXXXX	*	XXXXXXXX	*	XXXXXXXX	*	N/A		XXXXXXXX	*	JF972538	[4]
Cearacesa sp.	N/A		N/A		KR903638	[8]	N/A		KR903294	[8]	KR904170	[8]
Diatrypa sp.	N/A		N/A		KR903564	[8]	N/A		KR903214	[8]	KR904087	[8]
Ectecous sp.	N/A		N/A		KR903562	[8]	N/A		KR903212	[8]	KR904085	[8]
Eneoptera guyanensis Chopard, 1931	JX897404	[1]	XXXXXXXX	*	XXXXXXXX	*	JX897495	[1]	JX897547	[1]	AY905331	[5]
Eurepini sp.	XXXXXXXX	*	XXXXXXXX	*	XXXXXXXX	*	N/A		XXXXXXXX	*	XXXXXXXX	*
Fryerius sp.	N/A		N/A		KR903566	[8]	N/A		KR903216	[8]	KR904089	[8]
Gryllotalpa sp.	N/A		N/A		KR903621	[8]	N/A		KR903269	[8]	KR904147	[8]
Gryllus bimaculatus De Geer, 1773	N/A		XXXXXXXX	*	XXXXXXXX	*	N/A		XXXXXXXX	*	AF514509	[6]
Homeogryllus orientalis Desutter, 1985	N/A		N/A		KR903586	[8]	N/A		KR903235	[8]	KR904112	[8]
Lebinthus lifouensis Desutter-Grandcolas, 1997	XXXXXXXX	*	XXXXXXXX	*	XXXXXXXX	*	N/A		XXXXXXXX	*	AY905336	[5]
Lebinthus luae Robillard & Tan, 2013	XXXXXXXX	*	XXXXXXXX	*	XXXXXXXX	*	XXXXXXXX	*	XXXXXXXX	*	XXXXXXXX	*
Lebinthus nattawa Robillard, 2009	XXXXXXXX	*	XXXXXXXX	*	XXXXXXXX	*	N/A		XXXXXXXX	*	JF972541	[4]
Lebinthus santoensis Robillard, 2009 P	XXXXXXXX	*	XXXXXXXX	*	XXXXXXXX	*	N/A		XXXXXXXX	*	XXXXXXXX	*
Lebinthus santoensis Robillard, 2009 V	JX897405	[1]	JX897441	[1]	JX897467	[1]	N/A		JX897548	[1]	JF972542	[4]
Lebinthus sp. PNG	XXXXXXXX	*	XXXXXXXX	*	XXXXXXXX	*	XXXXXXXX	*	XXXXXXXX	*	JF972544	[4]
Lebinthus villemantae Robillard, 2010	XXXXXXXX	*	XXXXXXXX	*	XXXXXXXX	*	N/A		XXXXXXXX	*	JF972543	[4]

Luzaridella obscura Desutter-Grandcolas, 1992	N/A		N/A	KR903536	[8]	N/A		KR903186	[8]	KR904061	[8]
Microlandreva sp. Chopard, 1958	N/A		N/A	KR903620	[8]	N/A		KR903268	[8]	KR904146	[8]
Nisitrus vittatus (Haan, 1842) Se	XXXXXXXX	*	N/A	XXXXXXXX	*	N/A		XXXXXXXX	*	AY905340	[5]
Nisitrus vittatus (Haan, 1842) Si	XXXXXXXX	*	N/A	XXXXXXXX	*	JN887883	[7]	JX897546	[1]	AY905340	[5]
Ornebius xanthopterus Guérin-Méneville, 1844	N/A		N/A	KR903605	[8]	N/A		KR903254	[8]	KR904131	[8]
Paranisitra longipes Chopard, 1925	XXXXXXXX	*	N/A	XXXXXXXX	*	N/A		XXXXXXXX	*	XXXXXXXX	*
Pixibinthus sonicus Anso & Robillard, sp. nov. FN1	XXXXXXXX	*	N/A	XXXXXXXX	*	N/A		XXXXXXXX	*	XXXXXXXX	*
Pixibinthus sonicus Anso & Robillard, sp. nov. FN2	XXXXXXXX	*	N/A	XXXXXXXX	*	N/A		XXXXXXXX	*	XXXXXXXX	*
Pixibinthus sonicus Anso & Robillard, sp. nov. GK1	XXXXXXXX	*	N/A	XXXXXXXX	*	N/A		XXXXXXXX	*	XXXXXXXX	*
Pixibinthus sonicus Anso & Robillard, sp. nov. GK2	XXXXXXXX	*	N/A	XXXXXXXX	*	N/A		XXXXXXXX	*	XXXXXXXX	*
Pixibinthus sonicus Anso & Robillard, sp. nov. RB1	XXXXXXXX	*	N/A	XXXXXXXX	*	N/A		XXXXXXXX	*	XXXXXXXX	*
Pixibinthus sonicus Anso & Robillard, sp. nov. RB2	XXXXXXXX	*	N/A	XXXXXXXX	*	N/A		XXXXXXXX	*	XXXXXXXX	*
Pteroplistes masinagudi Jaiswara, 2014	N/A		N/A	KR903521	[8]	N/A		KR903170	[8]	KR904045	[8]
Swezwilderia sp.	XXXXXXXX	*	N/A	N/A		N/A		XXXXXXXX	*	JF972545	[4]

Xenogryllus marmoratus Bolívar, 1890	XXXXXXXX	*	XXXXXXXX	*	N/A		XXXXXXXX	*	XXXXXXXX	*	XXXXXXXX	*

The molecular sampling of dataset 2 was composed of a sub-sampling of dataset 1 to reduce each ingroup species to a single individual, except *Cardiodactylusnovaeguineae* that occurs in New Caledonia and other Pacific islands (Table 4.1). We also increased the species sampling of the Grylloidea superfamily in order both to better estimate divergence times and to use an appropriate calibration point (see below). We consequently added representatives of the major Gryllidea lineages delimited in Chintauan-Marquier et al. (Chintauan-Marquier *et al.*, 2016):Trigonidiidae (two species), Pteroplistinae (one species), Phalangopsidae (four species), and Gryllidae (six species). We finally used as most external outgroups, one species belonging to Mogoplistidae (Grylloidea) and one species of Gryllotalpidae (Gryllotalpoidea; Table 4.1).

4.4.4 Selection of DNA regions

We selected nine DNA loci, five mitochondrial and four nuclear, proved to have been useful in previous phylogenetic studies on Grylloidea (Robillard & Desutter-Grandcolas, 2006; Nattier *et al.*, 2011; Nattier *et al.*, 2012; Nattier *et al.*, 2013; Chintauan-Marquier *et al.*, 2016). These are fragments of the small (12S rRNA, ~ 400 bp) and large (16S rRNA, ~ 500 bp) mitochondrial ribosomal subunits, the mitochondrial gene coding for cytochrome b protein (cytb, ~ 400 bp), fragments of the mitochondrial cytochrome oxidase subunits 1 (CO1, ~ 750 bp) and 2 (CO2, ~ 400 bp) genes, a fragment of the small nuclear ribosomal subunit (18S rRNA, ~ 650 bp), a fragment of the large nuclear ribosomal subunit (28S rRNA, ~ 400 bp), and fragments of the genes coding for H3 protein (H3, ~ 330 bp) and elongation factor 1-α (EF1α, ~ 950 bp). We used these nine DNA loci for analyses of dataset 1, to refine and improve the internal phylogenetic resolution. However we observeda high level of missing sequences for the CO1 and CO2 regions, especially for outgroup species of dataset 2.We therefore used only the seven following loci for phylogenetic analyses of this dataset: 12S, 16S, 18S, 28SA, cytb, EF1a, and H3.

4.4.5 Laboratory procedures and Preparation of datasets

Molecular work was performed at the Service de Systématique Moléculaire of the MNHN. All sequences were generated by using the DNA extraction, amplification and sequencing protocols of the nine DNA loci, described in Nattier at al. (Nattier *et al.*, 2012). Some DNA extractions were made from median legs of crickets using the Epmotion 5075 robot (Eppendorf). In total we generated 106 new DNA sequences (33% of the total

samplings) for this study (Table 4.1), while other sequences were generated in previous studies and downloaded from Genbank(Flook *et al.*, 1999; Huang *et al.*, 2000; Jost & Shaw, 2006; Robillard & Desutter-Grandcolas, 2006; Regier *et al.*, 2010; Nattier *et al.*, 2011; Jaiswara *et al.*, 2012; Nattier *et al.*, 2012; Chintauan-Marquier *et al.*, 2016). Primers and annealing temperatures for each DNA locus are given in S3 Table A. Newly generated sequences were edited in Sequencher v.4.9 (Gene Codes Co.) and BioEdit v.7.0.5.3 (Hall, 1999), blasted with NCBI blast tools, and submitted to GenBank (Table 4.1).

Multiple alignments were generated for each DNA locus using the software Muscle v.3.7 (Edgar, 2004) with default parameter settings, by using the online portal Phylogeny.fr (Dereeper *et al.*, 2008). Subsequently we adjusted them manually. We concatenated the different DNA locus partitions with SequenceMatrix v.1.7.7 (Vaidya *et al.*, 2011). The datasets 1 and 2 resulted in a combined alignment of ~4750 bp and 3789 bp, respectively (Tables B and C in S3 table). Several ambiguous and large indel regions in the alignments of loci 12S, 16S, 18S, and EF1α were found within the dataset 2, and attributed to the inclusion of several distantly related Grylloidea taxa. This induced problematic homology hypotheses, and we consequently removed them from the DNA alignments (Table C in S3 table).

4.4.6 Phylogenetic analyses

Preliminary single-locus and combined phylogenetic inferences were carried out using maximum likelihood (ML) and Bayesian Markov Chain Monte Carlo (MCMC) analyses for both datasets 1 and 2. Best-fit model for each DNA locus was identified using jModelTest v.2.1.3 (Posada, 2008) based on the Akaike Information criterion (Tables B and C in S3). The combined datasets were partitioned to allow each locus to have its specific model parameters (Ronquist & Huelsenbeck, 2003; Nylander *et al.*, 2004).

The ML analyses were performed in RAxML v.7.4.2. (Stamatakis, 2006; Silvestro & Michalak, 2012) by running 500 likelihood searches. To evaluate node support, a supplementary bootstrap analysis (BS; (Felsenstein, 1985)) was performed using 500 replicates. A clade with a BS value > 95% was considered as well supported.

The Bayesian MCMC analyses were performed using MrBayes v.3.2.6 (Ronquist & Huelsenbeck, 2003). The single-locus and combined analyses were set as follows: four Metropolis-coupled Markov chains with an incremental heating temperature of 0.2 were run for 50 and 100 million generations with a tree sampled every 10000th generation for dataset 1

and dataset 2, respectively. The analysis was repeated four times for both datasets, all starting with random trees. Bayesian MCMC analyses were carried out using the CIPRES Science Gateway v.3.3 (Miller *et al.*, 2010). The MCMC sampling was considered sufficientwhen the effective sampling size (ESS) was higher than 200, as verified in Tracer v.1.6 (Rambaut & Drummond, 2009), or when the potential scale reduction factor was reasonably close to 1.0 for each parameter (PSRF; (Ronquist *et al.*, 2012)). After a burn-in period of $5\times 10^6$and $10 \times 10^6$for dataset 1 and dataset 2, respectively, the remaining trees were used to construct a majority rule consensus tree and its associated Bayesian posterior probabilities (PP). A clade with a PP value higher than 0.95 was considered as well supported. Trees were finally visualized with FigTree v.1.4.0. (http://tree.bio.ed.ac.uk/software/figtree/).

4.4.7 Bayesian divergence times estimates

The temporal evolution of *Pixibinthus* and its close relatives was estimated using the Bayesian MCMC approach implemented in BEAST v.1.8.0 for dataset 2 (Drummond & Rambaut, 2007). DNA loci were combined and partitions were set as in the preliminary Bayesian MCMC analyses (see above). We unlinked all DNA site models to analyze each locus under separate substitution models. An uncorrelated relaxed molecular clock model was selected to allow estimates of independent rate variation across branches following a lognormal distribution. The Birth-Death speciation process was implemented for the tree prior, assuming constant speciation and extinction rates per lineage. The mean of the branch rates (UCLD.mean) was set to follow a lognormal distribution with a log (mean) set to -4 and a log (standard deviation) set to 1. We started our analysis with a random tree. The MCMC was run for 100 million generations and sampled every 10000th generations. The analysis for each dataset was conducted three times, and was carried out using the CIPRES Science Gateway v.3.3 (Miller *et al.*, 2010). Convergence of runs and adequate MCMC sampling were checked using Tracer v.1.6(Rambaut & Drummond, 2009). The first 10×10^6generations of each run were manually discarded as burn-in. The remaining trees were summarized using a Maximum Clade Credibility target tree in TreeAnnotator v.1.8.0 (Drummond & Rambaut, 2007), as well as Bayesian posterior probability (PP), median height (=age estimate) and the 95% highest posterior density heights interval (95% HPD) of each node.

4.4.8 Calibration point

Divergence dates were previously estimated to test biogeographical hypotheses in Eneopterinae crickets by Nattier et al. (Nattier *et al.*, 2011). Age estimates were mainly obtained with several geological calibration points, considering that few fossils or dated trees were available at that time. Since that study, Song et al. (Song *et al.*, 2015) produced a large dated tree for Orthoptera which provided a secondary calibration for the present study in order to avoid the generally less accurate geological calibrations. We choose to use the secondary calibration point which corresponds to the divergence time between the Grylloidea and Gryllotalpoidea superfamilies. This calibration was assigned to the root node of our majority rule consensus tree generated in the preliminary Bayesian MCMC analyses of dataset 2. It corresponds to the divergence time between our most external outgroup species, *Gryllotalpa* sp. and all the other Grylloidea species of our dataset 2 sampling. This calibration was set to follow a uniform distribution, and by using a lower bound of 220 Myr and an upper bound of 250 Myr, which correspond to the 95% HPD of this divergence time, with a median value of 233.99 Myr (Song *et al.*, 2015).

4.4.9 Species richness and relative diversification rates

We tested the difference in species richness between *Pixibinthus* and its sister-clade (see below) using Equation (3) of Slowinski & Guyer (Slowinski & Guyer, 1993). To allow calculating this estimate and to ensure that the first basal split of this sister-clade in dating tree was assessed, we preliminary estimated its species richness, according to Desutter-Grandcolas & Robillard (Desutter-Grandcolas & Robillard, 2006), Robillard et al. (Robillard *et al.*, 2010), and our own knowledge.

4.4.10 Ensemble species distribution modelling

Ensemble Species Distribution Model (ESDM) analyses were carried out using combined R packages, and based on nine algorithms (GLM, GAM, MARS, GBM, CTA, RF, MAXENT, ANN and SVM) in order to test if the contemporary geographical range of *Pixibinthus* could have been more expanded, and would have been constrained by environmental changes. Dataset was composed of the coordinates of field sampling sites where *Pixibinthussonicus*has been recorded. Nine GIS ecological layers were used for the modelling analyses. Uncorrelated variables were selected among the 19 bioclimatic variables

available in New Caledonia from worldclim database(Hijmans *et al.*, 2005)leading to the selection of seven bioclimatic variables (BIO1, 2, 3, 4, 7, 12 and 15) at 30arc-second (Hijmans *et al.*, 2005).We also included altitude from Digital Elevation Model at 10m resolution, and main vegetation units distribution map available at 300m resolution. All layers were rescaled with a 300 m resolution. We used 30% randomly selected occurrence data as a testing dataset. The consensus model was built by summing algorithms suitability maps weighted with their area under the receiving operating characteristic (ROC) curve (AUC), only for model with an AUC > 0.75 (Marmion *et al.*, 2009). To evaluate the relative contribution of each variable to the model Pearson's correlation coefficient between the full model and one without each variable is measured (Thuiller *et al.*, 2009).

4.5 Results

4.5.1 Systematics and taxon description

The new genus and the new species are described here. Habitat, life history traits and calling song are also precisely defined.

Order: Orthoptera

Family: Gryllidae

Subfamily: Eneopterinae

Tribe: Lebinthini

Genus:*Pixibinthus* Robillard and Anso, gen. nov.

urn:lsid:zoobank.org:act:94405C62-C382-407F-BAC0-4B631EC5A0D3

Type species: *Pixibinthussonicus*Anso & Robillard, sp. nov.

Etymology: Genus named after ‘Pixie’, the diminutive mythical creatures of folklore, hidden by nature, close but unseen, as these crickets which were never encountered by previous authors despite past extensive studies on crickets in New Caledonia.

Diagnosis: Among Eneopterinae and Lebinthini genera, *Pixibinthus* is characterized by a diminutive size, smaller than all previously described species of *Lebinthus* from the Loyalties and Vanuatu (*L. lifouensis* Desutter-Grandcolas, 1997 and *L. santoensis* Robillard, 2009 respectively). For numerous aspects, the new genus appears as an intermediate form between *Lebinthus* and *Agnotecous*. It resembles these genera by microptery in both sexes (FW short and hind wings absent), but differs by the following characters: head shape more rounded with smaller eyes and wider fastigium; in dorsal view, combined width represents 35% of head width, against 50% in *L. santoensis* and 46% in *L. bitaeniatus*; head rounded in facial view, contrary to the triangular shape in *Lebinthus*; ocelli very small compared to *Lebinthus*; male FWs with dorsal field and lateral field of similar length, unlike in *Agnotecous*, but as in *Lebinthus*; female FWs as long as in males, unlike in most *Lebinthus* species, slightly overlapping.

Description: Genus characterized by its small size. Head shape uncommon, fastigium wider than long, three times as wide as scape. Eyes small, little prominent; Ocelli very small. Pronotum dorsal disk almost rectangular, wider than long, its posterior margin straight. Legs rather short. Fore tibiae with two tympana; inner tympanum covered by a sclerotized expansion (Fig. 4.1A), its membrane visible along a small longitudinal slit only; outer tympanum ellipsoidal, transversally plicate. Fore tibiae with two inner and one outer apical spurs. Tibiae II with two inner and two outer spurs. Hind femora very wide and muscular. Hind tibiae serrulated on their whole length, not furrowed longitudinally, with four pairs of subapical spurs and three pairs of apical spurs; inner spurs long and curved, outer spurs short and straight. Tarsomeres III-1 with two dorso-apical spines and a row of spines on outer dorsal edge; one lateral outer spine.FWs short, not reaching abdomen mid-length; hindwings absent.

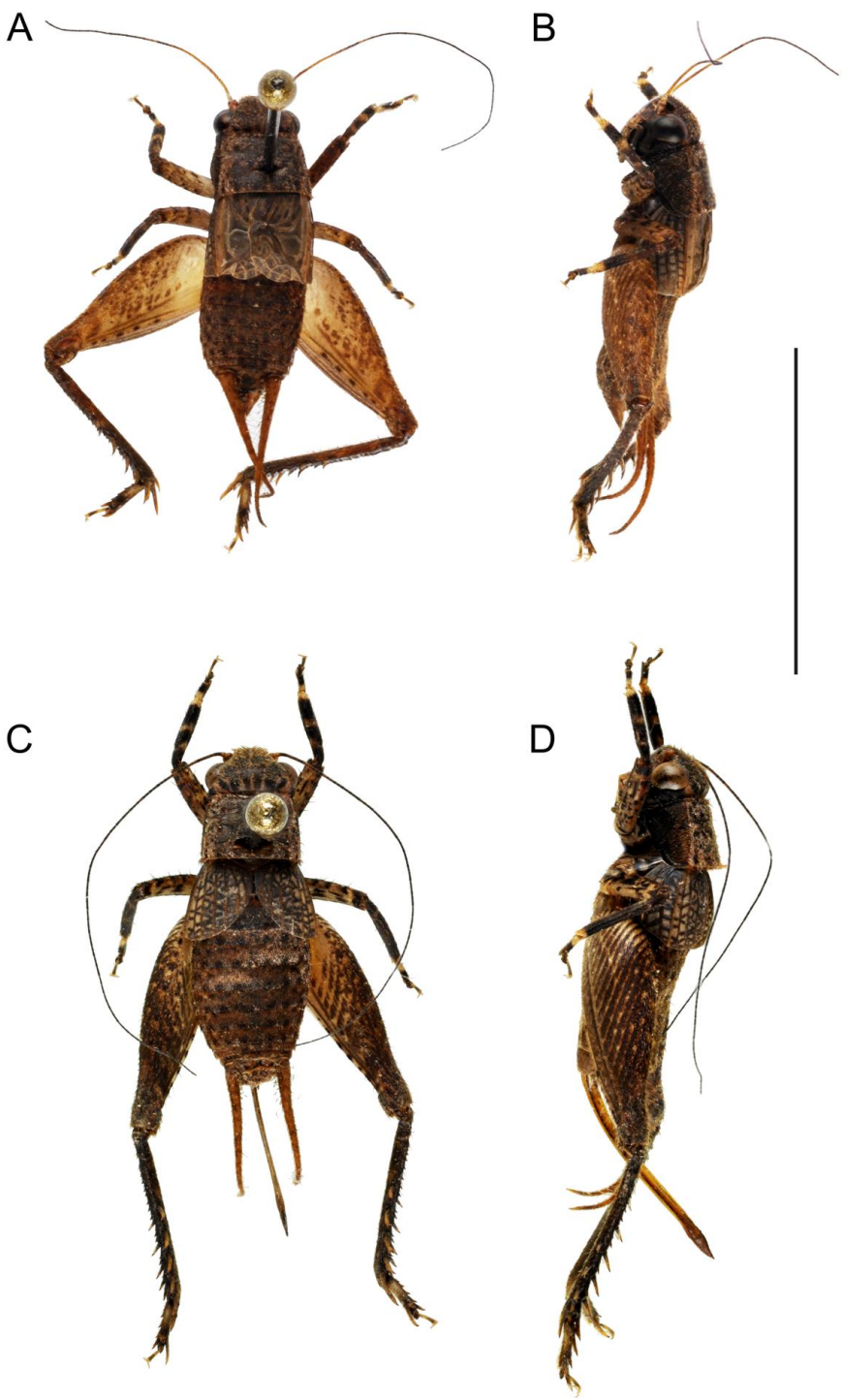

Figure 4.1. *Dorsal and lateral views of Pixibinthus sonicus. (A) & (B) Male. (C) & (D) Female. Scale bar = 5 mm.*

Male*:* Metanotal glands absent. Lateral and dorsal fields of FWs of similar lengths (Fig. 4.2, 3). 1A vein (file) with a marked angle (only curved in *Lebinthus*). Harp with one bisinuated oblique vein. Mirror and d2 cell not differentiated from other cells of D alignment. Stridulatory file with teeth both on transverse and longitudinal parts of 1A. Diagonal vein well visible. CuP absent but claval fold visible. CuA faint, slightly curved inward. Median fold small, located on dorsum as in *Lebinthus* and *Agnotecous*. Chord cells differentiated. Apical field including only few cells posterior to mirror (alignment E). Subgenital plate clog-shaped, twice as long as sternites; inner side of subgenital plate with lateral swellings.

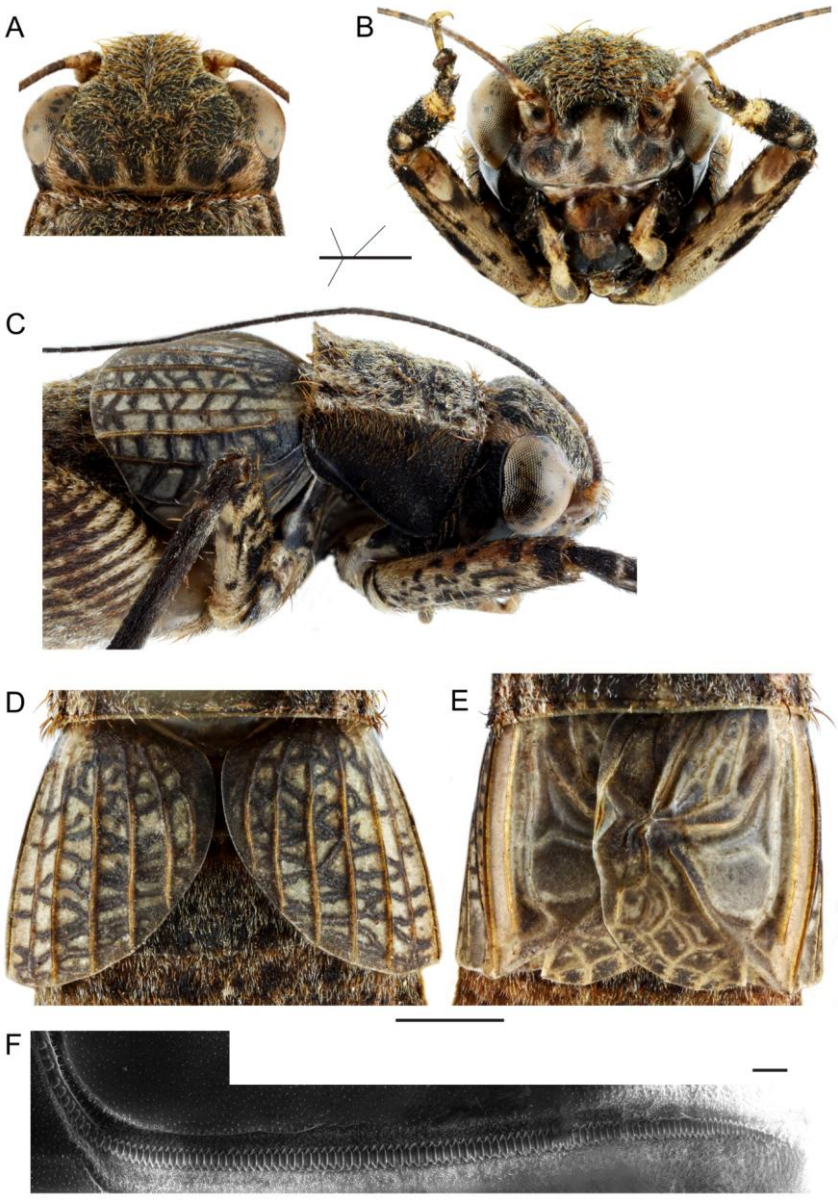

Figure 4.2. Detailed morphology of Pixibinthus sonicus. (A) Dorsal view of the female face. (B) Facial of the female face. (C) Lateral view of the anterior body part of female. (D) Dorsal view of detailed FWs for female. (E) Dorsal view of detailed FWs for male (E). (F) The stridulatory file with SEM. Scale bars: 1 mm for (A), (B), (C), (D), (E); 50 µm for (F)

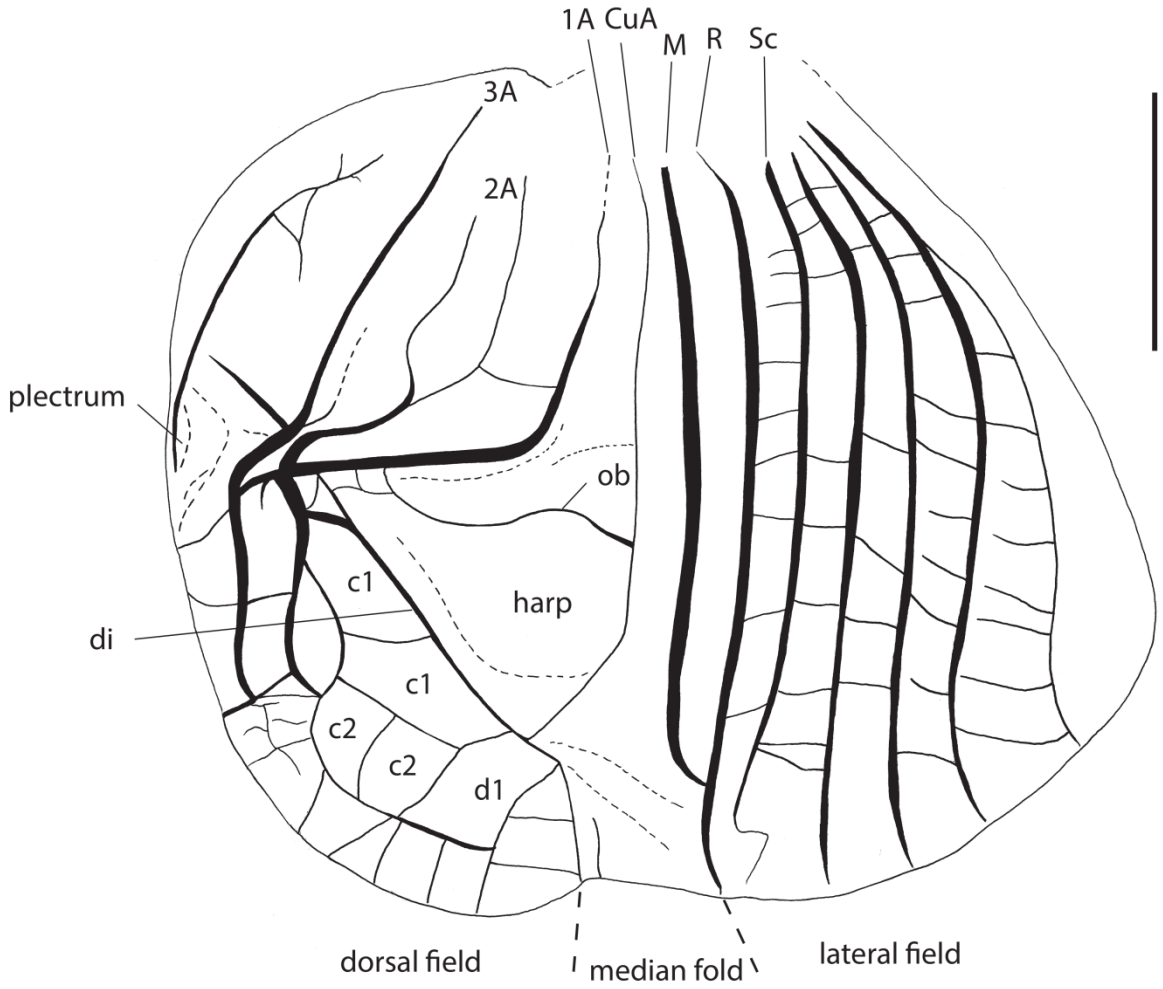

Figure 4.3. *Male forewing venation of Pixibinthus sonicus. For abbreviations and symbols, see Material and methods. Scale bar = 1 mm.*

Male genitalia: Pseudepiphallus triangular, basal margin straight, posterior apex elongate, without paired lophi and forming a wide gutter (Fig. 4.4). Rami straight, parallel and short. Ventral pseudepiphallic plate wide. Pseudepiphallic parameres sclerotized, convergent, their basis strong, with two posterior lobes, one oriented dorsally and one forming a rounded ventral plate, and a basal membranous lobe. Ectophallic apodemes parallel and long, their apex lamellate. Ectophallic arc well sclerotized, wide and slightly curved posteriorly, with a small medio-posterior expansion. Ectophallic fold long, with elongate lateral sclerites forming a “)(“ pattern; its apex triangular and membranous. Endophallic sclerite large, comprising posteriorly a short median expansion and lateral arms; sclerite very long anteriorly, exceeding pseudepiphallic sclerite. Endophallic apodeme with well-developed lateral lamellas and a narrow dorsal crest.

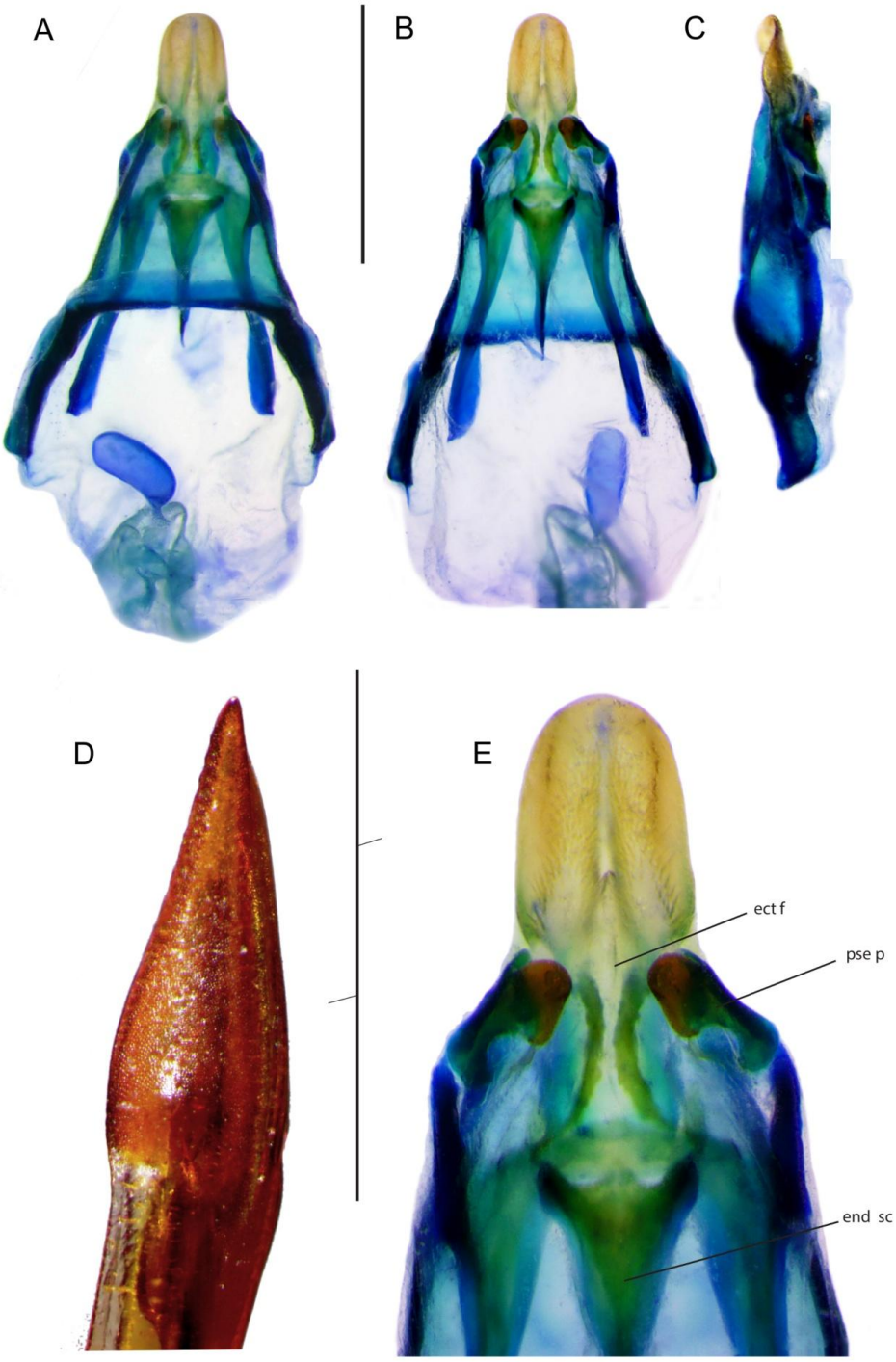

Figure 4.4. *Genitalia of Pixibinthus sonicus. (A) Dorsal, (B) ventral, and (C) lateral views of male genitalia. (D) Lateral view of apex of female ovipositor. (E) Ventral view of male genitalia. For abbreviations and symbols, see Material and methods. Scale bars = 1 mm.*

Female:FWs as long as in males (Fig. 4.2), slightly overlapping, dark brown with whitish veins; dorsal field with 7 strong longitudinal veins; lateral field with 4 longitudinal veins; Sc without bifurcations. Ovipositor rather short, as long as hind femur, laterally flattened, apex lanceolate and slightly denticulate dorsally (Fig. 4.4D).

Female genitalia: Copulatory papilla little sclerotized, with a basal sclerite forming a wide ring; apex little differentiated, slightly indented andfolded ventrally.

***Pixibinthus sonicus* Anso and Robillard, sp. nov.**

urn:lsid:zoobank.org:act:CA5D7BDC-7504-435C-8B67-5BDCF11987BB

Type material: Holotype male: New Caledonia, Grande Terre, Forêt Nord, milieu paraforestier, 22.191554 S 166.5608 E, 100 m, 1.XII.2013-12.II.2014, PAFN1-24, jour, litière, J. Anso (MNHN-EO-ENSIF244). **Allotype female:** Same locality, date and collector as HT, PAFN2-4, jour, litière (MNHN-EO-ENSIF71). **Paratypes:** New Caledonia, Grande Terre, Pic du Grand Kaori, 22.16471 S 166.53399 E, 260 m, 11.II.2014, 1♂, AGN1, jour, litière, J. Anso (MNHN-EO-ENSIF98); XI.2013, 1♀, Lfem1, J. Anso (MNHN-EO-ENSIF124). Forêt Nord, milieu paraforestier, 22.191554 S 166.5608 E, 100 m, 1.XII.2013-12.II.2014, J. Anso: 1♂, PAFN1-46, jour, litière (MNHN-EO-ENSIF70); 1♀, PAFN2-23, (MNHN-EO-ENSIF90); 1♀, PAFN2-2, jour, litière (IAC); 1♀, PAFN2-3, jour, litière (MNHN-EO-ENSIF144); 1♂, PAFN2-12, nuit, litière (IAC); 1♂, PAFN2-24, jour, litière (Nouméa); 1♀, PAFN2-33, nuit, litière (MNHN-EO-ENSIF361); 1♀, PAFN1-37, nuit, litière (MNHN-EO-ENSIF142); 1♂, PAFN1-38, nuit, litière (MNHN-EO-ENSIF81); 1♀, PAFN2-52, nuit, litière (MNHN-EO-ENSIF123); 1♀, PAFN1-1, jour, litière (MNHN-EO-ENSIF77); 1♂, PAFN1-13, jour, litière, molecular sample L66LeNCFN2 (MNHN-EO-ENSIF83); 1♀, PAFN1-15, jour, litière (Nouméa); 1♂, PAFN1-23, jour, litière, molecular sample L60LeNCFN1 (MNHN-EO-ENSIF99); 1♀, PAFN1-22, jour, litière (MNHN-EO-ENSIF127); 1♀, PAFN1-40, jour, litière(MNHN-EO-ENSIF362); 1♀, PAFN1-42, jour, litière (MNHN-EO-ENSIF118); 1♂, PAFN1-51, nuit, litière (MNHN-EO-ENSIF128). Nouvelle-Calédonie, Grande Terre, Pic du Grand Kaori, 22.16471 S 166.53399 E, 260 m, maquis, VI.2013, adultes en élevage, J. Anso: 3 males (MNHN-EO-ENSIF149, 150, 153); 4 males, enregistrement appel F0-males1-4 (MNHN-EO-ENSIF158, 154, 152, 125), 4 females, (MNHN-EO-ENSIF129, 132, 139, 140).

Additional material examined: Parc de la Rivière Bleue, maquis, 22.08375 S 166.424776 E, 200 m, 11-19.III.2014: 1 male, MARIV1-1, nuit, litière, molecular sample L59LeNCRBa1 (MNHN-EO-ENSIF105); 1 juvenile, MARIV1-15, jour, litière, molecular sample L67LeNCRBa2 (MNHN-EO-ENSIF133); 7 juveniles, MARIV1-3, 6, 7, 12, 13, 14, 19, litière (MNHN); 5 juveniles, MARIV2-2, 3, 7, 8, 9, litière (MNHN). Forêt Nord, milieu paraforestier, 22.191554 S 166.5608 E, 100 m, 1.XII.2013-26.II.2014: 12 juveniles, PAFN2-9,14,25,48,51,53,56, PAFN1-47,52,58,59,60, nuit, litière; 3 juveniles, PAFN2-49, PAFN1-16,45, jour, litière; 1♀, PAFN1-14, jour, litière; 1♀, PAFN1-7, nuit, litière (MNHN). Chute de la Madeleine, maquis, 22.23568 S 166.85268 E, 255m, 10-26.II.2014, J. Anso: 1 juvenile, MAMAD1-24, molecular sample L116PixMad1 (MNHN-EO-ENSIF65); 4 juveniles, MAMAD1-11, 24, 26, litière (MNHN); 3 juveniles, MAMAD2-7, 9, 22, litière (MNHN).

Type locality: New Caledonia, Grande Terre, Forêt Nord.

Etymology: Named after the very high dominant frequency of the species' calling song.

Distribution: New Caledonia, Grande Terre, Province Sud: Rivière Blanche, Chute de la Madeleine, Pic du Grand Kaori, Forêt Nord (Fig. 4.5).

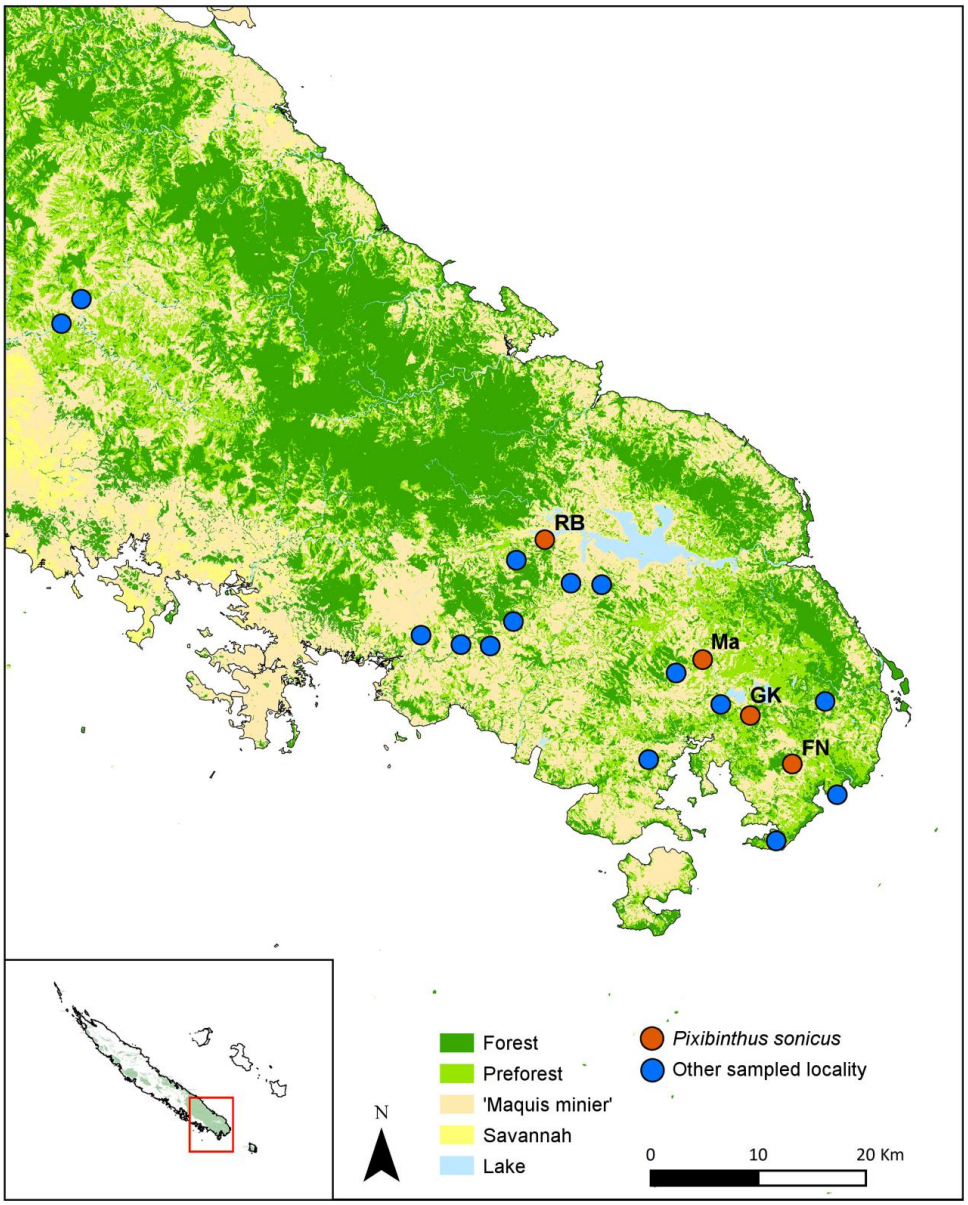

Figure 4.5. *Map of sampled localities in the southern part of New Caledonian Grande Terre. Blue dots indicate localities where populations of Pixibinthus sonicus were not found. Orange dots indicate localities where P. sonicus was found.*

Diagnosis. *Pixibinthus sonicus* is recognized by its small size, face light brown with seven black spots, male genitalia, and high dominant frequency of calling song.

Description: In addition to the characters of the genus: Size very small, stocky shape. Coloration: No contrasted sexual dimorphism (Figs. 4.1A & 1C). Body mostly brown to dark brown, slightly contrasted with lighter parts on legs. Head dorsum with six wide dark brown bands visible basally and fused between the eyes; fastigium dark brown; area posterior to eyes yellow; cheeks entirely shiny black;face light brown, with seven characteristic black spots:

four forming a square on the front head, one above epistomal suture, and two bellow antennal pits; spots variable in size and connectivity, sometimes more or less fused together in a complex pattern. Maxillary palpi: article 1-3 black, articles 4-5 lighter with apical darker ring on article 5. Pronotum brown to dark brown, with lighter lateral margins with small black dots; lateral lobes of pronotum homogeneously black. Pronotum dorsal disk and lateral lobes separated by a short concave yellow line. Legs: Tibiae I black with three small lighter flecks; tibiae II entirely black with a whitish apical ring; tibiae III dark brown; femora III yellowish with dark brown diagonal stripes strongly contrasted on external face; femora I and II yellowish with small brown flecks; first and third tarsomeres I-III dark yellowish basally, their apex dark brown. Abdomen brown, darker in apical part, with one yellowish small dot for each segment. Cerci yellowish, with small scattered darker flecks.

Male. FW mostly gray to dark brown with a pale area including bases of CuA, M and R veins. Area between M and R whitish, veins orange brown. FW venation: 1A with 110 stridulatory teeth, 12 on the basal angle and 98 on the transverse part of the file (n = 1; Fig. 4.2F). Cell c1 with a faint median transverse vein; c2 rectangular. M yellow brown, curved posteriorly, fused to R near FW apex, very thin near fusion; R straight, strong along its whole length. FW lateral field including Sc and 3-4 strong longitudinal veins. Hind tibia inner serrulation (n=3): no spine between the apical and the first subapical spur; one spine between subapical spurs 1 and 2; two spines (1-2) between spurs 2 and 3; two spines between subapical spurs 3 and 4; seven spines (4-10) above subapical spur 4; outer serrulation: no spine between apical and subapical spurs; one spine between subapical spurs 1 and 2; two spines (1-3) between subapical spurs 2 and 3; two spines (2-3) between subapical spurs 3 and 4; seven spines (6-8) above subapical spur 4. Tarsomeres III-1: four outer (3-4) and no inner spines, in addition to apical spines.

Female. Hind tibia inner serrulation (n=3): no spine between the apical and the first subapical spur; one spine between subapical spurs 1 and 2; two spines (1-2) between spurs 2 and 3; one spine (1-2) between subapical spurs 3 and 4; four (4-5) spines (4-10) above subapical spur 4; outer serrulation: no spine between apical and subapical spurs; one spine between subapical spurs 1 and 2; two spines between subapical spurs 2 and 3; two spines between subapical spurs 3 and 4; eight spines above subapical spur 4. Tarsomeres III-1: three outer and no inner spines, in addition to apical spines.

Measurements. See Table 4.2.

***Table 4.2**. Measurements of Pixibinthus sonicus sp. nov. (in mm).*

	PronL	PronW	FWL	FWW	FIIIL	FIIIW	TIIIL	TIII spines				TaIIIs	OL
								Ias	Ibs	Oas	Obs		
Male holotype	2	2.3	3.3	2.6	6.8	2.4	5.3	5	6	8	5		
Males paratype (n=5)	1.8-2.1	2.4-2.7	2.8-3.5	1.8-2.0	6.1-7.1	2.1-2.5	4.5-5.5	4-6	3-6	8-11	5-6	3-6	
(Male mean)	(2.0)	(2.5)	(3.1)	(2.0)	(6.7)	(2.3)	(5.2)	(5)	(4)	(9)	(5)	(3)	
Allotype female	1.7	2.5	2.1	-	6.5	2.4	5.3	4-6	3-5	7-9	4-6	3-4	5.5
Females paratype (n=5)	1.7-2.1	2.1-2.8	2.0-2.4	-	6.5-8.1	2.2-2.7	5.1-5.6	4-6	3-5	7-9	4-6	3-4	5.5-7.0
(Female mean)	(1.9)	(2.5)	(2.2)	-	(7.0)	(2.4)	(5.4)	(5)	(4)	(8)	(5)	(4)	(6.4)

Juvenile. Body color light brown mottled with dark brown to black spots. Head, including face, pronotum and legs with similar color patterns as in adults.

Habitat and life history traits: *Pixibinthus sonicus* was clearly identified as a new monotypic genus and new species after intensive sampling on various habitats, in the southern part of New Caledonia, representing an area of about 2150 km². Among 19 sampled localities, including shrubby vegetation, preforest and rainforest, *P. sonicus* was only found in low to tall sclerophyllous shrubland and was clearly absent from forested areas (Fig. 4.6). Four populations of *P. sonicus* were identified in our study sites. Three populations were found in low sclerophyllous 'maquis minier', with dominant strata lower than 5-6 meters.. One population was found in tall sclerophyllous 'maquis miniers' at Forêt Nord (22.32259 S 166.93134 E), 6 km away from the population of Pic du Grand Kaori, separated by high ridges. Adults and juveniles were both collected during day and night, in the leaf litter. In these three localities, abundances were relatively small with a dozen of specimens collected in each site.

Figure 4.6. Habitat of Pixibinthus sonicus. (A) Low sclerophyllous 'maquis minier' around the Madeleine Fall's. (B) Detailed view of habitat in leaf litter. (C) Juvenile of P. sonicus (size: approximately 1cm).

Behavior: Males of *Pixibinthus sonicus* emit their calling song starting from 16:30 PM until next morning at 03:00 AM, as attested by 72 hours ambient recording with SM2 Bat; this activity would characterize *P. sonicus* as a nocturnal species.

4.5.2 Acoustic description

Four males were recorded under laboratory controlled condition. Each call of *Pixibinthus sonicus* is a short trill lasting 38.2 ± 7.4 s (Fig. 4.7A) and made of 918 ± 130 syllables, with a period of 152.8 ± 72.2 s (as recorded at 25°C). Each syllable lasts about 18.4 ± 2.5 ms, with a period of 41.7 ± 16 ms, and with a duty cycle of 44.7 %. The sound amplitude gradually increases during the 300 to 400 first syllables (Fig. 4.7B), and remains twice higher and constant until the end of the trill. The dominant frequency is 27.9 ± 2.8 kHz, and corresponds to the second harmonic of the spectrum (Fig. 4.7C, E), the fundamental frequency f1 being almost silent.

4.5.3 Phylogenetic relationships of *Pixibinthus.*

The ML and Bayesian MCMC single-locus phylogenetic topologies yield no supported incongruence for both datasets 1 and 2 (with a PP > 0.95 or BS > 85%; data not shown) and are less resolved than the combined phylogenetic analyses. The ML (data not shown), Bayesian MCMC and BEAST combined analyses provide no supported incongruence between topologies (Fig. 4.8; S1 Figure; S2 Figure). Since the Bayesian MCMC combined analysis allows us together to take into account uncertainty only the results of this analysis are discussed hereafter (Fig. 4.8).

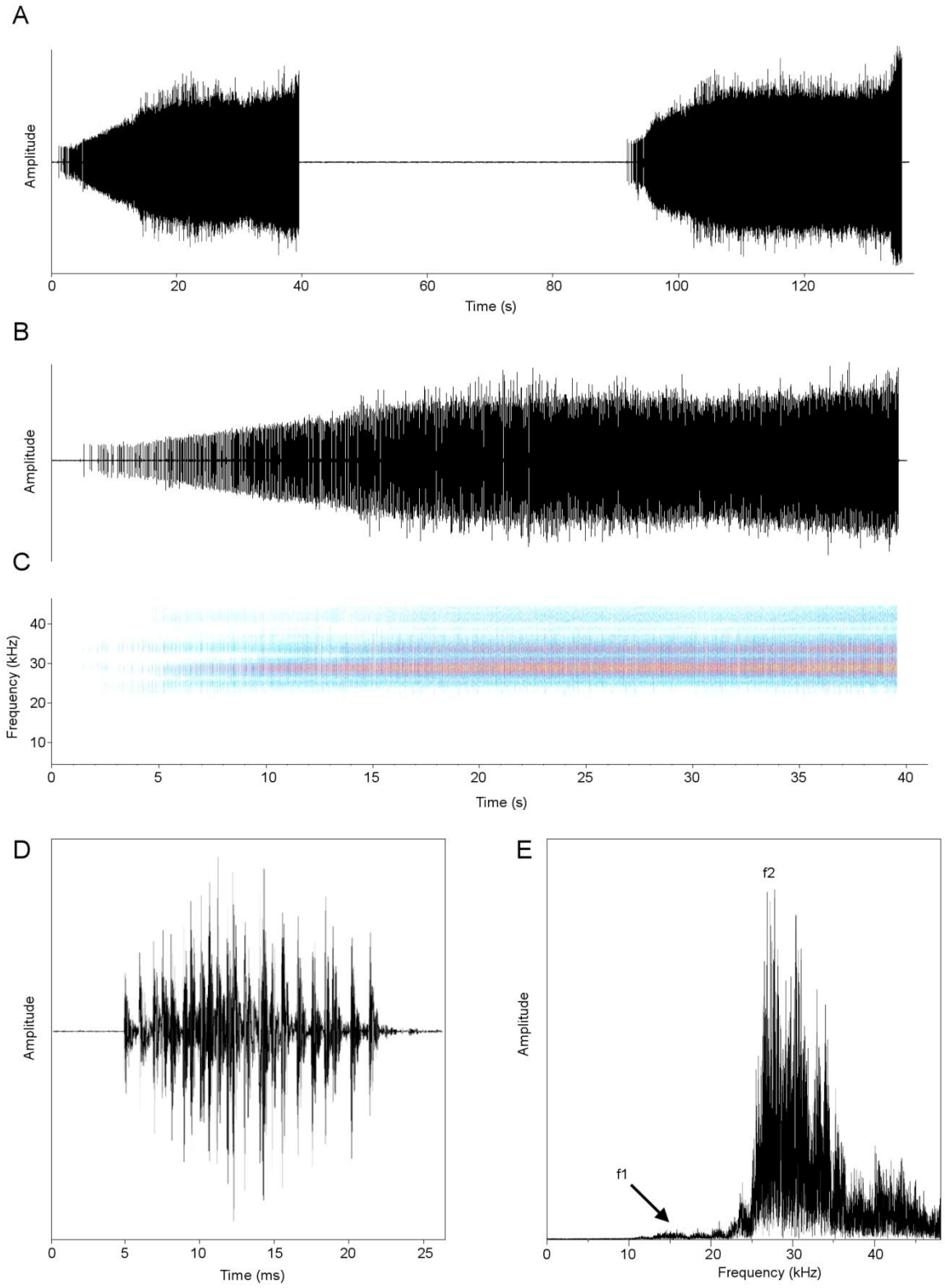

Figure 4.7. *Calling song of Pixibinthus sonicus. (A) Oscillogram showing two successive trills; (B) detailed oscillogram and (C) sonogram of one trill; (D) oscillogram of one syllable; (E) and linear spectrogram of one echeme. Symbols: f1, fundamental frequency; f2, second harmonic (dominant frequency).*

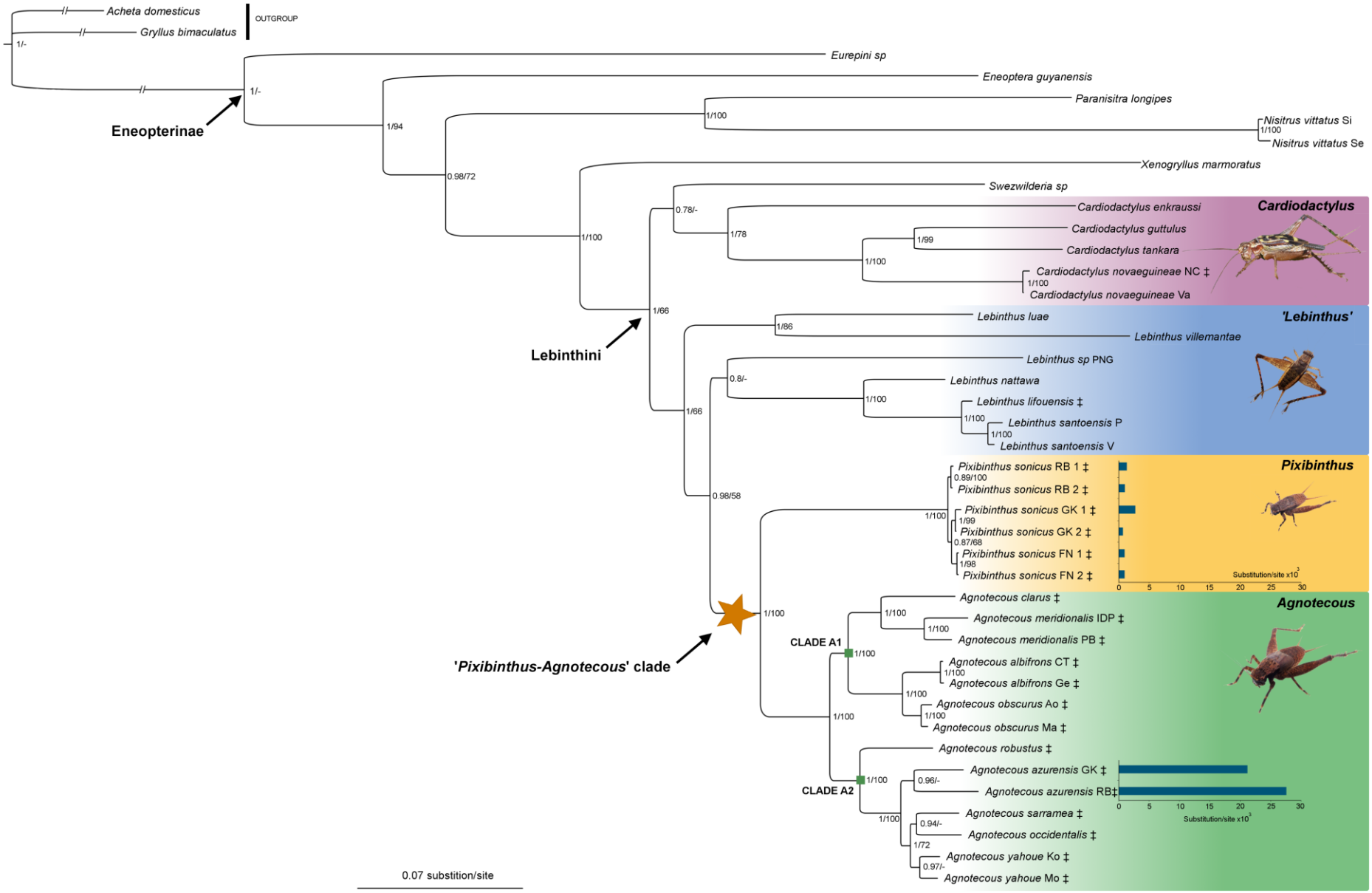
Acheta domesticus
Gryllus bimaculatus
OUTGROUP
Eurepini sp
Eneoptera guyanensis
Paranisitra longipes
Nisitrus vittatus Si
Nisitrus vittatus Se
Xenogryllus marmoratus
Swezwilderia sp
Cardiodactylus enkraussi
Cardiodactylus guttulus
Cardiodactylus tankara
Cardiodactylus novaeguineae NC ‡
Cardiodactylus novaeguineae Va
Cardiodactylus
Lebinthus luae
Lebinthus villemantae
Lebinthus sp PNG
Lebinthus nattawa
Lebinthus lifouensis ‡
Lebinthus santoensis P
Lebinthus santoensis V
'Lebinthus'
Pixibinthus sonicus RB 1 ‡
Pixibinthus sonicus RB 2 ‡
Pixibinthus sonicus GK 1 ‡
Pixibinthus sonicus GK 2 ‡
Pixibinthus sonicus FN 1 ‡
Pixibinthus sonicus FN 2 ‡
Pixibinthus
Substitution/site x10-3
Agnotecous clarus ‡
Agnotecous meridionalis IDP ‡
Agnotecous meridionalis PB ‡
Agnotecous albifrons CT ‡
Agnotecous albifrons Ge ‡
Agnotecous obscurus Ao ‡
Agnotecous obscurus Ma ‡
Agnotecous robustus ‡
Agnotecous azurensis GK ‡
Agnotecous azurensis RB‡
Agnotecous sarramea ‡
Agnotecous occidentalis ‡
Agnotecous yahoue Ko ‡
Agnotecous yahoue Mo ‡
Agnotecous
CLADE A1
CLADE A2
Eneopterinae
Lebinthini
'Pixibinthus-Agnotecous' clade
0.07 substition/site

Figure 4.8. *Bayesian half-compatible consensus tree of Eneopterine crickets based on dataset 1, including 28 species and nine DNA markers. Bayesian posterior probability (PP) / bootstrap (BS) support values are indicated for each node on the right. A clade with a BS < 50% or not recovered in the ML analyses is indicated with an asterisk. Major clades are shaded with a color scale.*

These analyses confirm that the genus *Pixibinthus* belongs to the Lebinthini tribe (PP=1; Fig. 4.8). The species *P. sonicus* is monophyletic, since all of the individuals sampled in this study group together with very short branch lengths (PP=1, see below). Moreover *P. sonicus* is placed as sister to the monophyletic genus *Agnotecous* (PP=1; Fig. 4.8), and both form the newly-defined '*Pixibinthus-Agnotecous'* clade, with a high support (PP=1). This latter lineage is nested with high support within the genus *Lebinthus* (PP=0.98), a paraphyletic group under revision (Robillard et al. in prep). Within *Agnotecous* two main clades are recovered as sister groups. The *Agnotecous* clade A1 includes the *A. clarus*, *A. meridionalis*, *A. albifrons* and *A. obscurus* samples (PP=0.99). The *Agnotecous* clade A2 comprises the *A. robustus*, *A. azurensis*, *A. sarramea*, *A. occidentalis*, and *A. yahoue* individuals (PP=1).

The phylogenetic branch lengths (BL) estimated in this study are short in all *Pixibinthus* individuals (between 0.69 and 2.8 × 10^3 substitutions/site; Fig. 4.8), and larger in *Agnotecous* samples (mostly between 3.23 and 27.51 × 10^3 substitutions/site, except *A. albifrons* with BL comprised between 1.38 and 1.69 × 10^3 substitutions/site). Moreover the BL of *Pixibinthus* samples from the localities Grand Kaori and Rivière Bleue are 12 and 23 times shorter, respectively, than the BL of *A.azurensis* from the same places (compare *P. sonicus* RB and *P. sonicus* GK with *A. azurensis* RB and *A. azurensis* GK; Fig. 4.8).

4.5.4 Divergence time estimates

The BEAST analyses showed that the most recent common ancestor of the '*Pixibinthus-Agnotecous'* clade appeared around the Eocene-Oligocene boundary (with a median divergence time estimate of 33.3 Myr, with a 95% HPD of 24.4-43.1 Myr; Fig. 4.9; Table 4.3). The crown ages of the genus *Agnotecous*, clade A1, and clade A2 were estimated around 20.2 Myr, 16.3 Myr, and 13.9 Myr, respectively (with 95% HPD of 14.9-25.82, 11.6-21.6, and 9.9-18.5 Myr, respectively; S2 Fig.).

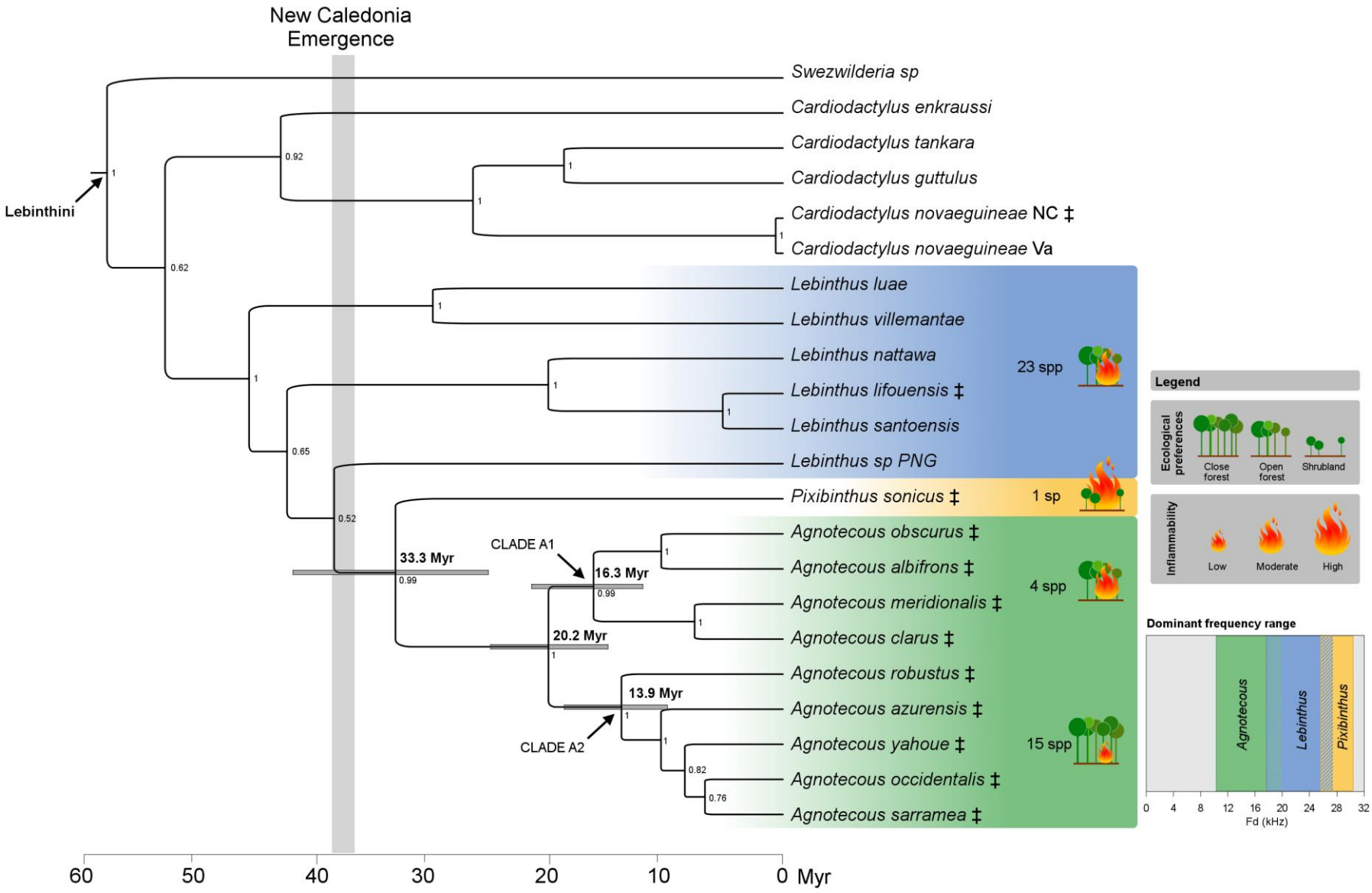
New Caledonia
Emergence
Lebinthini
Swezwilderia sp
Cardiodactylus enkraussi
Cardiodactylus tankara
Cardiodactylus guttulus
Cardiodactylus novaeguineae NC ‡
Cardiodactylus novaeguineae Va
Lebinthus luae
Lebinthus villemantae
Lebinthus nattawa
Lebinthus lifouensis ‡
Lebinthus santoensis
Lebinthus sp PNG
23 spp
Pixibinthus sonicus ‡
1 sp
Agnotecous obscurus ‡
Agnotecous albifrons ‡
Agnotecous meridionalis ‡
Agnotecous clarus ‡
Agnotecous robustus ‡
Agnotecous azurensis ‡
Agnotecous yahoue ‡
Agnotecous occidentalis ‡
Agnotecous sarramea ‡
4 spp
15 spp
CLADE A1
CLADE A2
33.3 Myr
16.3 Myr
20.2 Myr
13.9 Myr
0.92
0.62
0.65
0.52
0.99
0.82
0.76
60 50 40 30 20 10 0 Myr
Legend
Ecological preferences
Close forest
Open forest
Shrubland
Inflammability
Low
Moderate
High
Dominant frequency range
Agnotecous
Lebinthus
Pixibinthus
0 4 8 12 16 20 24 28 32
Fd (kHz)

***Figure 4.9**. BEAST maximum credibility clade chronogram of the main lineages of Lebinthini crickets, based on dataset 2, including 41 species and seven DNA markers (only the 21 species of Lebinthini tribe are shown). Divergence times, ecological preferences and species richness (inferred from (Desutter-Grandcolas & Robillard, 2006; Robillard et al., 2010) and from our personal observations in the field), and relative habitat inflammability (inferred from (McCoy et al., 1999))are indicated for the three main lineages: '*Lebinthus'*,*Pixibinthus, and* Agnotecous. *Bayesian posterior probabilities (PP) are indicated for each node on the right. Gray node bars correspond to the 95% highest posterior density of median age estimates and are only provided for clades that are discussed. Dominant frequency range for the three mains lineages are indicated, with stripped area for overlapping frequency ranges. Species occurring in New Caledonia are represented with the ‡ symbol.*

Table 4.3. *Ecological, biological, morphological and dating characteristics for the three Lebinthini groups. Acoustic recording impaired by inadequate recording material are indicate with an asterisk. Body sizes of species were inferred from the FIIIL femur length measurements. Abbreviation: N/A corresponds to non available data.*

	Pixibinthus	*Agnotecous* clade A1	*Agnotecous* clade A2	*Agnotecous*	*'Lebinthus'*
Characteristics					
Number of species	1	4	15	19	23
Habitat	Shrubland, low to tall = 'maquis minier'	Secondary and open forest, savannah	Forest	Forest, secondary forest and savannah	Coastal and secondary forest, open forest
Habitat openess	Open	Open	Closed	Mainly closed to open	open
Habitat inflammability	High	Moderate	Low	Mainly low to moderate	Moderate
Diets	Detritivorous	Detritivorous	Detritivorous	Detritivorous	Detritivorous
Dominant frequency range (kHz)	25.5-30.5	15-18	11-19.2	11-19.2	(12*) 16.7-27.5
Body size (mm)	6.1-6.8	10.9-15.2	9.5-16.4	9.5-16.4	7-15.7
Substrate	Ultramafic	Ultramafic and Non-ultramafic	Ultramafic and Non-ultramafic	Ultramafic and Non-ultramafic	Non-ultramafic
Age estimates					
Stem age (Myr)	34.7	22	22	34.7	N/A
95% HPD stem age (Myr)	[26.2-44.1]	[16.7-27.4]	[16.7-27.4]	[26.2-44.1]	N/A
Crown age (Myr)	N/A	18.7	17.4	22	N/A
95% HPD crown age (Myr)	N/A	[14-24.2]	[12.9-22.4]	[16.7-27.4]	N/A

4.5.5 Species richness estimates and relative diversification rates

The application of Equation (3) of Slowinsky and Guyer (1993) showed that *Pixibinthus* had significantly less species than its *Agnotecous* sister-clade (p = 0.0526*; one species *vs.* 19; Fig. 4.8).

4.5.6 Species distribution modelling

ESDM analyses revealed that the suitable habitat of *Pixibinthussonicus*was not restricted to the four occurrence sites (AUC = 0.986), but also covered a large area of the southern of Grande Terre, exclusively on metalliferous soils (Fig. 4.10).

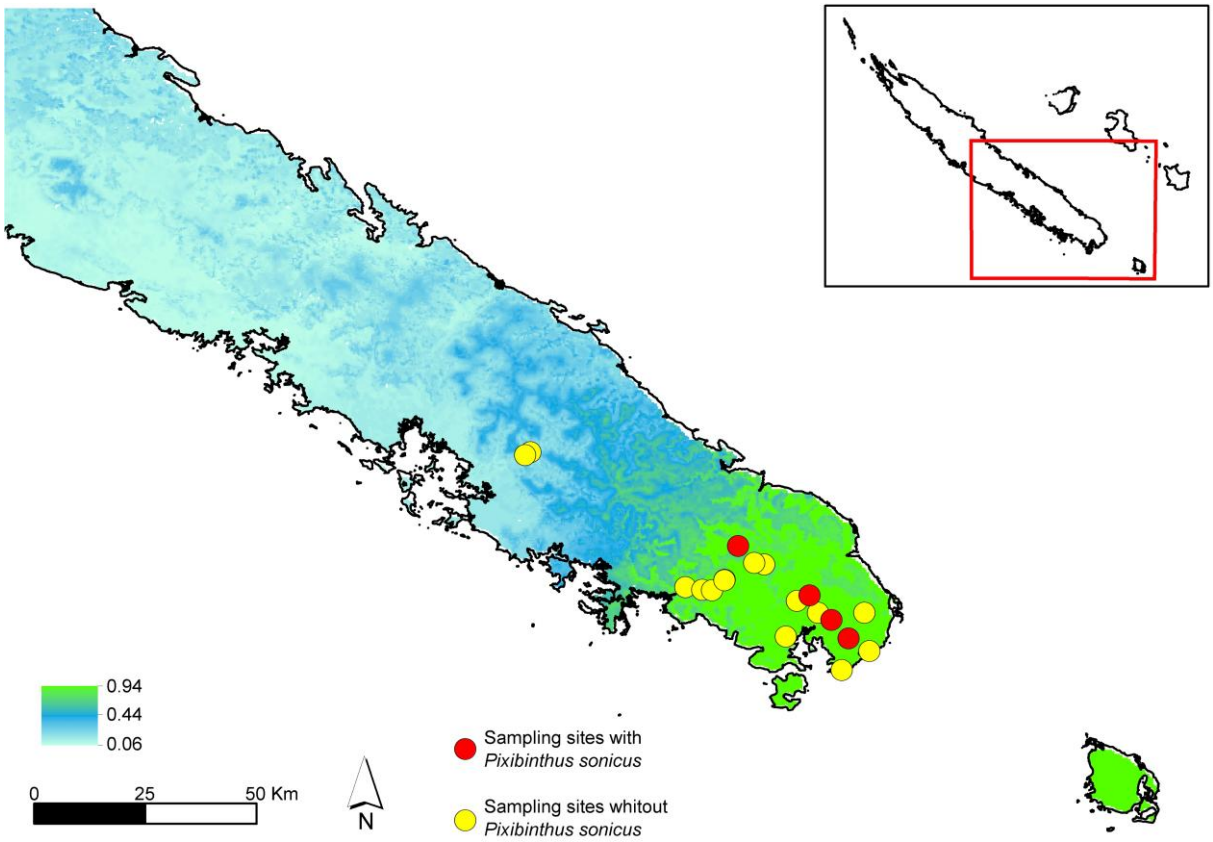

Figure 4.10. *Predicted ecological distribution of* Pixibinthus sonicus*using ESDM. Warmer colors indicate areas with higher habitat suitability for P. sonicus. Reddots show sampling sites where Pixibinthus* sonicus *was recorded; yellowdots show sampling sites where* P. sonicus*was not observed.*

4.6 Discussion

4.6.1 The discovery of a new original cricket genus in 'maquis minier'

In this study we described a new monotypic cricket genus, *Pixibinthus*, endemic to New Caledonia. Its single species *P. sonicus*, has only been observed in the southern part of New Caledonian main island, living in specific open shrubby vegetation on ultramafic rocks (i.e. 'maquis minier'; Table 4.3). Unexpectedly, *P. sonicus* exhibits the highest calling frequency ever recorded for any Grylloidea species, a record previously heldby *Lebinthus santoensis* at 26.5 kHz in Vanuatu (Robillard, 2009). Our phylogenetic study placed *Pixibinthus* as sister to the genus *Agnotecous*, also endemic to Grande Terre (Fig. 4.8). This study confirms that the genus *Lebinthus* is paraphyletic as suggested by recent taxonomic (Vicente *et al.*, 2015) and phylogenetic studies (Nattier *et al.*, 2011; Nattier *et al.*, 2012).

4.6.2 Origin of the '*Pixibinthus-Agnotecous*' clade in New Caledonia

The origin of the '*Pixibinthus-Agnotecous'* clade in New Caledonia was estimated in our study to ca. 33.3 Myr (with a 95% HPD of 24.4-43.1 Myr; Fig. 4.9; Table 4.3). Before the discovery of the close relationship between these two genera, the early colonization of New Caledonia by *Agnotecous* was previously estimated between 10.6 and 15.3 Myr (with a 95% HPD of 5.3-21.9 Myr; (Nattier *et al.*, 2011)). The inclusion of *Pixibinthus* in our DNA sampling also helped refining the age estimate of *Agnotecous* in New Caledonia. Our dating results pushed back the crown age of the *'Pixibinthus-Agnotecous* clade' up to ca. 23 Myr. (Nattier *et al.*, 2011) also tentatively incorporated an extreme fossil calibration using a very old but dubious fossil of Grylloidea in order to test some specific biogeographical hypotheses. Their second analysis dated *Agnotecous* at approximately 24 Myr, which already permitted to reject the assumption of a clade older than the island. However this result was not retained as a robust estimate within that study, given the uncertainty on the fossil used for calibration. Strikingly our results however gave very similar estimates, despite the differences in dating methods, calibrations, and taxonomic and gene samplings.

According to our results, the '*Pixibinthus-Agnotecous* clade'is an old New Caledonian lineage that arrived not long after the postulated re-emergence of New Caledonia, estimated by geologists around 37 ± 2 Myr (Pelletier, 2006; Schellart *et al.*, 2006), similarly to some other groups of terrestrial arthropods such as fig wasps (Cruaud *et al.*, 2012) or caddisflies

(Espeland & Johanson, 2010a). Although *Pixibinthus* presently appears as a relict, actually a unique taxon on a long phylogenetic branch (Grandcolas *et al.*, 2014), its origin does not seem to predate the emergence of the island as for some harvestmen (Sharma & Giribet, 2012) tentatively assumed to have jumped over now-drowned islands earlier than 37 My ago (Nattier *et al.*, 2011). This provisional relict status depends on further sampling that could reveal other extant species belonging to the same genus, though several and extensive previous studies focusing on forest habitats did not find any species (Desutter-Grandcolas, 1997c; Desutter-Grandcolas & Robillard, 2006; Nattier *et al.*, 2012).

According to classical accounts on New Caledonia, old clades should primarily occupy habitats on metalliferous soils which were dominant at the time of emergence of the island (Morat *et al.*, 1986; Espeland & Johanson, 2010b; Pillon *et al.*, 2010; Pillon, 2012). The relationship between *Pixibinthus* and 'maquis minier' is consistent with this assumption, though its sister-group *Agnotecous* is not restricted to metalliferous soils (Nattier *et al.*, 2012).

The common ancestor of this cricket clade probably settled in early New Caledonian open habitats, a preference which can be inferred as ancestral for this lineage, also considering the preference for open forests of close relatives such as Indo-Pacific *Lebinthus* species (Robillard, 2009, 2010; Robillard *et al.*, 2013) (Fig. 4.9). A similar pattern has already been observed in *Cardiodactylus novaeguineae*, whose ongoing colonization is documented in open backshore habitats of New Guinean and Melanesian archipelagoes, including New Caledonia (Robillard & Ichikawa, 2009). New Caledonia would then have been successively colonized three times by crickets of the subfamily Eneopterinae: the '*Pixibinthus-Agnotecous* clade', *C. novaeguineae*, which has a wide distribution in the Western Pacific, and *L. lifouensis*, restricted to the Loyalty Islands ((Desutter-Grandcolas & Robillard, 2006; Nattier *et al.*, 2011); Fig. 4.8).

4.6.3 Two different ecological specializations within the '*Pixibinthus-Agnotecous*' clade

Interestingly, the *Pixibinthus* lineage would have persisted in the seemingly ancestral choice of open habitats since its origin in New Caledonia. This species appears to have specialized upon the emblematic and peculiar sclerophyllous shrubby'maquis minier' growing on ultramafic rocks ((Jaffré, 1980; Proctor, 2003); Table 4.3). The exact timing of this specialization could not be inferred in this study, but only estimated between around 33 Myr to present, as this species is the only representative of the genus.

The sister-group *Agnotecous* differs, as 16 out of its 19 species are rainforest-dwellers (*Agnotecous* clade A2 plus *A. meridionalis*), while only three other species (clade A1) are known from more open forests ((Desutter-Grandcolas & Robillard, 2006; Robillard *et al.*, 2010; Nattier *et al.*, 2012); Table 4.3; S4 Table). According to the topology, occurring in closed habitatsis however a secondary specialization within *Agnotecous* (clade A2: 13.9 Myr; Fig. 4.9). We can confidently hypothesize that the postulated radiation of *Agnotecous* in forest habitats started around 20 Myr (crown age of the genus *Agnotecous*; Table 4.3).

4.6.4 Ecological specializations suggest mutual evolution of body size and airborne signal

To the best of our knowledge, the clear-cut ecological specializations in two vegetation types of two sister-clades (*Agnotecous* mostly in closed forest and *Pixibinthus* in open 'maquis minier'; Table 4.3) is undocumented within the New Caledonian insect fauna. In this unusual case, the study of acoustic behavior could be a relevant feature to understand such different ecological preferences.

Before the discovery of *Pixibinthus*, (Robillard & Desutter-Grandcolas, 2004a)described the few Lebinthini as 'living paradoxes', since they were producing high-frequency calls in forested habitats (S4 Table), which are characterized by greater attenuation and absorption on those frequencies (Wiley & Richards, 1978; Richards & Wiley, 1980). But now, the significantly lower frequency calls observed in *Agnotecous* species (compared to *Pixibinthus*) might be explained by new acoustic and ecological constraints inherent to forest habitats (Fig. 4.9, dominant frequency range diagram). The colonization of forested areas would have allowed more favorable living conditions for the ancestor of *Agnotecous*, with a release of ecological pressures. Resources, including food and shelter from predators, were presumably greater than in open habitats (Langellotto & Denno, 2004; Fartmann *et al.*, 2012), which is usually associated with an increase of body size((Atkinson, 1994; Gardner *et al.*, 2011); Table 4.3). Consequently, the *Agnotecous* lineage would have undergone a relative reduction of their call frequencies as a consequence to a larger body size (Bennet-Clark, 1998), whereas *Pixibinthus* would have conserved a smaller body size and a high-frequency song (S4 Table). A formal test of this hypothesis will necessitate further studies taking into account precise acoustic analyses at the scale of whole clade analyzed with phylogenetic comparative methods, especially to identify the role of body size and habitat characteristics on the evolution of call frequencies (e.g. (Garamszegi, 2014)).

In crickets, calling songs are crucial to attract females, and are strongly influenced by environmental conditions (Forrest, 1994). *Pixibinthus sonicus* exhibits a high-frequency call compared to *Agnotecous*, and this species lives in open habitats, where sound transmission is strikingly different than in forest areas: amplitude fluctuations are higher and reverberation is lower, which tends to facilitate high-frequency communication (Wiley & Richards, 1978; Ryan & Brenowitz, 1985; McCracken & Sheldon, 1997). In addition, the open 'maquis minier' where *P. sonicus* lives is usually composed of patchy 'leaf litter islands', where conspecific potential receivers are likely to be concentrated in the close vicinity of male signalers (as according to our field observations). These circumstances may have concurred to maintain, or favor, high-frequency communication in *Pixibinthus*.

4.6.4.1 *Pixibinthus*: failing to diversify?

Despite a large temporal window, we observed imbalanced species richness between *Pixibinthus* and *Agnotecous* (as shown by a significant p-value of the Slowinsky and Gruyer test). We noticed also important dissimilarities in species richness with a single species for *Pixibinthus* vs. 19 for *Agnotecous* (Table 4.3). Both genera are detritivorous, as most crickets, meaning that diet might not explain this difference. Furthermore, although the knowledge on their predation pressure and biotic interactions is scarce, similar categories of potential predators seem present in both environments (mainly spiders and lizards). Based on that statement, we propose a working hypothesis to explain these uneven diversifications considering past and recent abiotic events, relative to climatic oscillations and fire regimes.

4.6.4.2 Impact of past climatic fluctuations?

Climatic fluctuations are greatly suspected to have been an important factor responsible for the natural expansion and contraction of New Caledonian rainforests over time (Pintaud *et al.*, 2001; Poncet *et al.*, 2013; Pouteau *et al.*, 2015). As an example, allopatric speciation has been documented as one of the main diversification driver for the rainforest-dwelling *Agnotecous* (Nattier *et al.*, 2012). Past expansion-contractions of this vegetation have been shown in southern main land through palynological records (Hope & Pask, 1998; McCoy *et al.*, 1999; Stevenson, 2004). If such weather shifts had been critical in open shrubby habitats, leading to the isolation of 'maquis minier' patches, we should observe as many allopatric speciations in *Pixibinthus* as in *Agnotecous* a situation that is not supported

by our data. On the contrary, the southern plain 'maquier miniers' could have been permanently connected (Hope & Pask, 1998; Stevenson, 2004; Stevenson & Hope, 2005). *Pixibinthus* may then have failed to diversify because of relatively high habitat connectivity, regardless to its dispersal ability. The gene flux between distant populations could have been maintained over time, limiting allopatric speciation, as suggested by short internal phylogenetic branches within *P. sonicus.* The contrast with some *Agnotecous* species, whose isolated forested populations begin to be genetically isolated (such as illustrated by long branches of *A. azurensis*; Fig. 4.8), could then be particularly significant.

4.6.5 Impact of fire regimes?

Fire regime may have equally played a key role in the apparent lack of diversification of *Pixibinthus*. Before human arrival (ca. 3000 year ago), New Caledonian landscapes were shaped by low natural fire regime (Hope & Pask, 1998; Jaffré *et al.*, 1998b). As the exclusive ecological preference of *Pixibinthus* matches the most flammable habitat of New Caledonia (McCoy *et al.*, 1999), which are now exposed to repeated fires (Curt *et al.*, 2015), could have led to occasional and localized extinctions, enhancing isolation of its populations in a first phase. However, these newly burnt areas would in time have constituted a favorable matrix for recolonization, ultimately leading to population reconnections. By contrast, fire damages are expected to be buffered by dense forested areas (Jaffré, 1995; Jaffré *et al.*, 1998b). The specialization of *Agnotecous* in forest habitats would have preserved its populations, allowing the emergence of many species according to the hypothesis proposed by Nattier et al. (Nattier *et al.*, 2012). In this likely scenario, we might assume that *Pixibinthus* would be more sensitive to fire damages than *Agnotecous*.

4.6.6 *Pixibinthus*: on the way to extinction?

More recently, fire regime was dramatically increased by human's arrival in New Caledonia, as documented in the southern region by palynological and charcoal records from Quaternary sediments (Hope & Pask, 1998; McCoy *et al.*, 1999; Stevenson, 2004). According to McCoy et al. (McCoy *et al.*, 1999), fire frequency has increased from one fire to five every century since human settlement. This recent (less than 3000 years) and abnormally high fire regime would have increased the effect of natural fire on native vegetation, and especially in shrubby 'maquis minier'. Though, repeated occurrence of dramatic fire events would have led to the loss of 10.000 ha of vegetation per year in New Caledonia, of which 10% in the

southern part (civilian security of New Caledonia, pers. comm.). These recent human-made fires are mostly sudden and destroy very large areas in short time. For example, 4300 and 800 ha were burnt in 2005 and 2013, respectively (civilian security of New Caledonia, pers. comm.). This increasing change in fire regime created a large vegetation mosaic of maquis-forest, dominated by flammable maquis, especially in the southern part of New Caledonia. This mosaic influence fire regime with more maquis prone to burn rather than forest remnants (Curt *et al.*, 2015; Gomez *et al.*, 2015). Before man arrival, the low regime of fire was related to a maquis-forest mosaic dominated by forest, which we hypothesize offer more opportunity of stable open shrubby maquis areas available for *Pixibinthus* population with a low turn over (a mosaic of maquis minier of differents ages in a matrix of forest). According to the actual fire regime, Curt et al. (Curt *et al.*, 2015) estimate that more than 10 000 ha of maquis have burnt over the period 1999-2010. These authors also estimate that with a such fire regime it would take 34 years to burn an area equivalent to the whole area of maquis in New Caledonia. The known distribution of *Pixibinthus* being ca. 1.200 ha (Fig. 4.5), means that its geographical range could have been virtually entirely burnt within one year. Furthermore, since the potential sustainable habitat of *Pixibinthus* is larger than its actual distribution, as inferred by both niche modelling analyses (Fig. 4.10), the geographical expansion of this cricket lineage could have been held back by environmental perturbations, like drastic fire regimes, rather than by limited living conditions. As a consequence, the probability of extinction of *Pixibinthus* populations may have been greatly enhanced by human arrival, preventing recolonization processes and reconnection between isolated populations, even if the favorable habitat of this *Pixibinthus* is considerably enlarged.

4.7 Conclusion

Our study highlights an original discovery for the cricket fauna in emblematic south-eastern ‘maquis miniers’ from New Caledonia. The new endemic monotypic genus *Pixibinthus* appears to have originated from an old lineage contemporary to the 37 Myr-re-emergence of the main island. Its single species would have conserved ancestral traits for open habitats with high-frequency calls (up to 30 kHz). This lineage could be the result of a tumultuous history involving two mutually non-exclusive evolutionary patterns: (1) an apparent non-speciation linked to the past dynamics of its particular habitat, and (2) extinctions caused by a recent high human-made fire regime. Nevertheless, the long-branch

phylogenetic signature of the new genus is difficult to interpret, which could be elucidated by a relevant genetic population study on the entire distribution range of this species. So far, the scarceness and the observed distribution of the species, restricted to the south raises issues about its presence in the other parts of New Caledonia. Additional sampling efforts should be done in other localities, well distant from the current known distribution, as for example in 'maquis minier' located at high-elevations or those located in north-western isolated mountains, on which allopatric speciation events have occurred in plants (Schmid, 1982; Pillon, 2008), geckos (Bauer *et al.*, 2006; Skipwith *et al.*, 2014), skinks (Sadlier *et al.*, 2009; Sadlier *et al.*, 2014) and grasshoppers (Nattier *et al.*, 2013). In New Caledonia clear-cut specializations between two sister lineages have been frequently highlighted for different geological substrates in insects (e.g. in caddisflies(Espeland *et al.*, 2008), or in grasshopper (Murienne *et al.*, 2005; Nattier *et al.*, 2013)), in squamata (Sadlier *et al.*, 2009; Sadlier *et al.*, 2014; Skipwith *et al.*, 2014) or in plants (e.g. in *Codia sp.* (Pillon *et al.*, 2009), or *Diospyros sp.* (Paun *et al.*, 2015)). However ecological specialization in contrasted vegetation types, such as shown in our study, was undocumented for New Caledonia, even if it is strongly suspected in some insect groups (e.g. in some Chrysomelid beetles or weevil beetles, in some Mogoplistidae lineages, or in the *Bullita-Koghiella* clade) or plant groups (e.g. in the *Morierina–Thiolliera* clade or within the large *Psychotria*). Our findings stressed the importance to study animal or plant diversifications by considering all stages of ecological succession, such as disturbed habitat (e.g. shrubby vegetation), which could provide valuable information to understand the origins of New Caledonian biodiversity, massively threatened by anthropogenic pressures.

4.8 Acknowledgments

We would like to thank Frédéric Rigault & Edouard Bourget (IMBE/IRD Noumea), Léa Colmas, and Alexia Omont who provided help for field work, habitat characterization and for mapping our sampled localities. We also thank Céline Gomez (IMBE/IRD Noumea) and Sylvain Schmitt (AMAP/IAC) who performed Ensemble Species Distribution Modelling. We are also grateful to Eric Vidal (IMBE/IRD Noumea) for interesting discussion and logistic support. We thank the New Caledonian Direction de l'Environnement de la Province Sud, for collecting permits. We thank the Grand Observatoire du Pacifique Sud (GOPS) for its contribution to funding through the project entitled 'Bioacoustique des grillons de Nouvelle-

Calédonie' in the context of their call for proposal 2013. We also thank the Labex BCDIV (Diversités biologiques et culturelles) for funding a part of this study, under the project entitled "A diachronic study of biodiversity and a test of biogeographic scenarios in New Caledonia as based on field inventories of fossil and present-day insects".

4.9 Supporting information

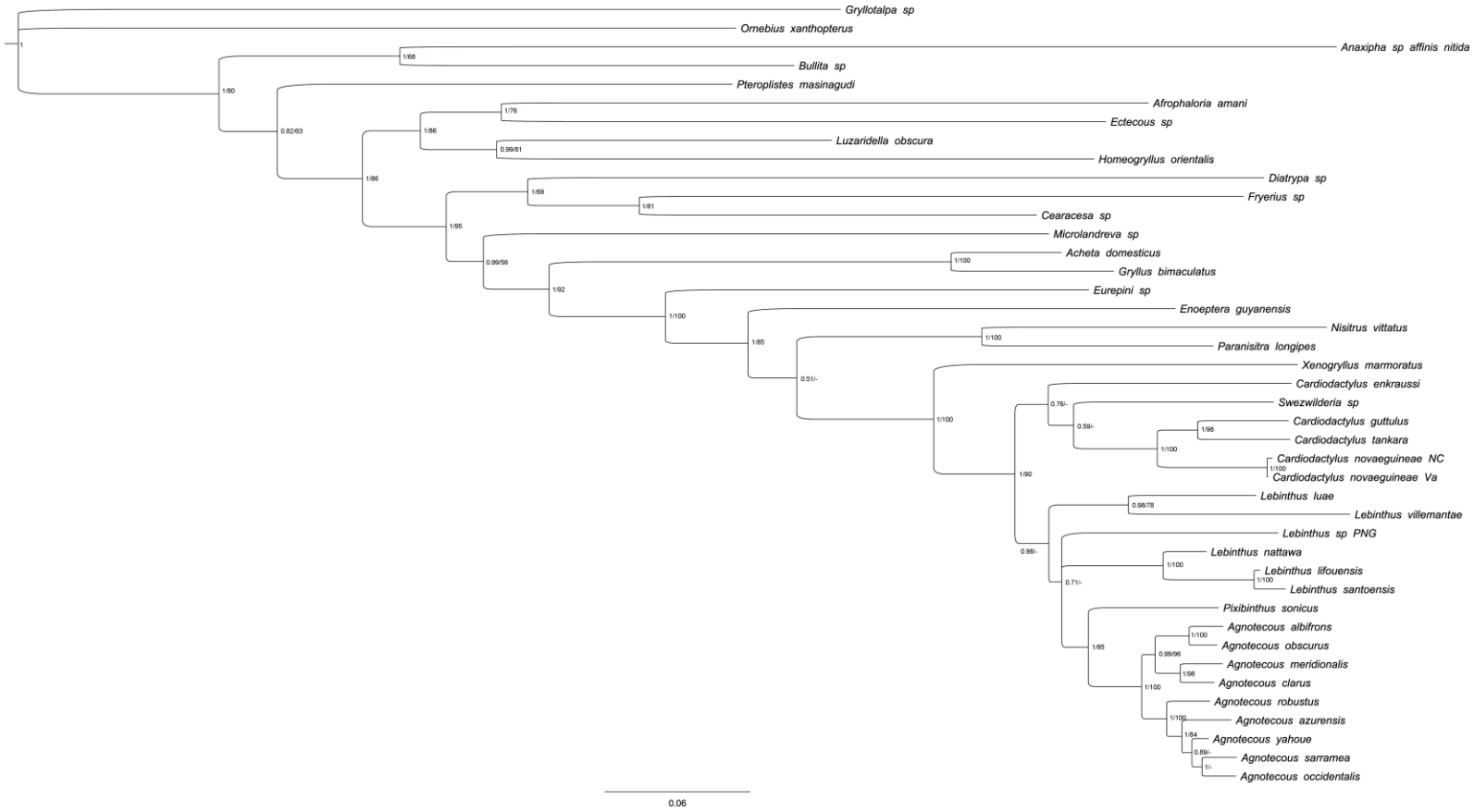

Figure 4.11. *Bayesian half-compatible consensus tree of Grylloidea crickets based on dataset 2, including 41 species and nine DNA markers. Bayesian posterior probability (PP) / bootstrap (BS) support values are indicated for each node on the right. A clade with a BS < 50% or not recovered in the ML analyses is indicated with an asterisk.*

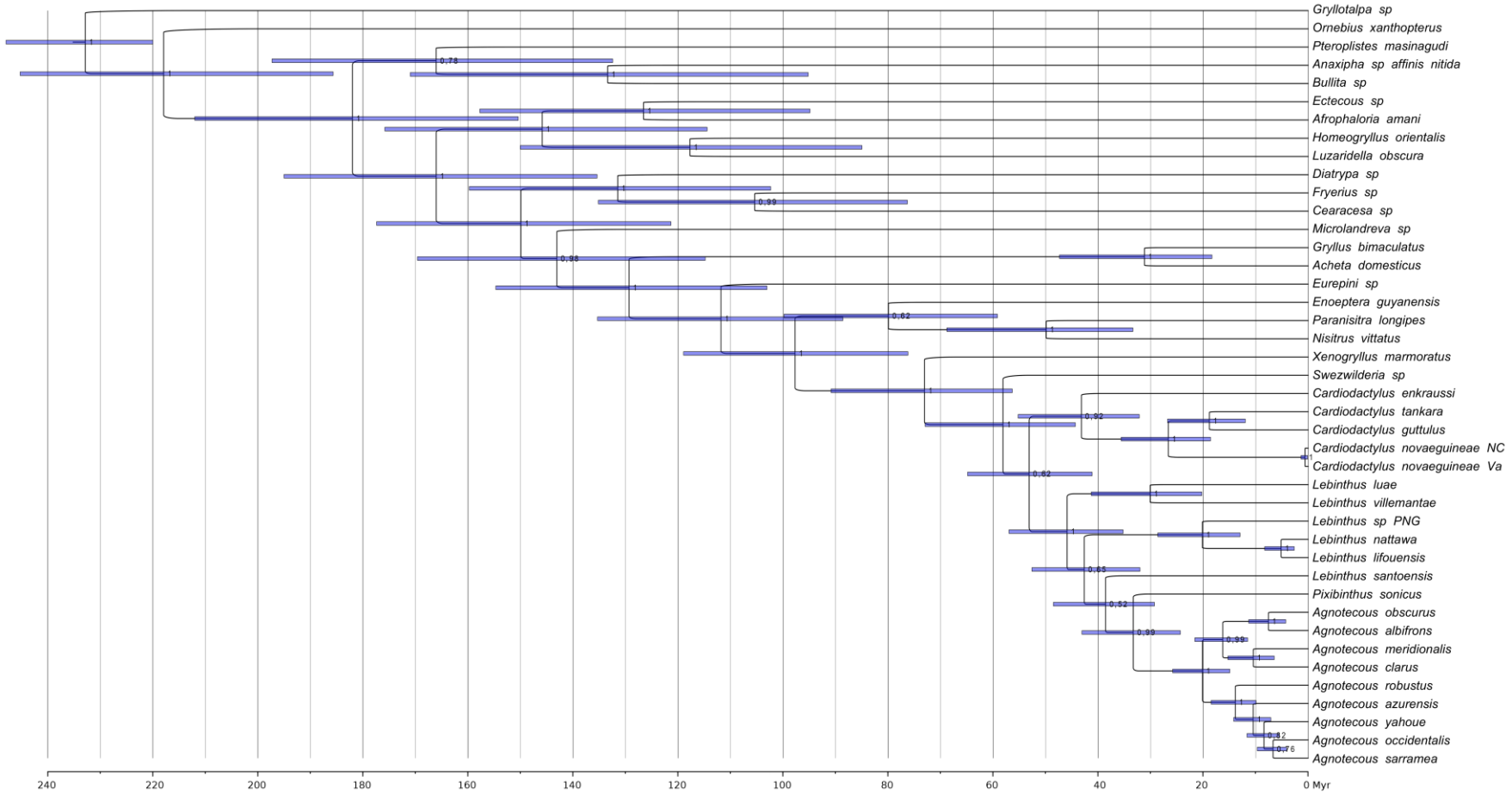

Figure 4.12. *BEAST maximum credibility clade chronogram of Grylloidea crickets based on dataset 2, including 41 species and nine DNA markers. Bayesian posterior probability (PP) / bootstrap (BS) support values are indicated for each node on the right. A clade with a BS < 50% or not recovered in the ML analyses is indicated with an asterisk. Grey node bars correspond to the 95% highest posterior density of median age estimates*

Table 4.4. *Characteristics of the nine DNA loci used in this study and in the phylogenetic analyses of Pixibinthus and closely related genera. A) Characteristics of primers (names, sequences, annealing temperatures, references where they were firstly designed). Characteristics of the DNA partitions, used in the phylogenetic analyses: B) 'dataset 1': for phylogenetic relationships; C) 'dataset 2': for dating estimates.*

A)

	Gene	Primer name	Sequencing primers (5' - 3')	Reference	Annealing temperature
mitochondrial	CO1	L2	GCAACGATGATTATTTTCCACT	Nattier et al. (2012), modified from Folmer et al. (1994)	48-50°C
		H2	CCTGGTAAAATTAGAATGTAAACTTCTG		
	CO2	co2a	GGTCAAACAATTGAGTCTATTTGAAC	Shapiro et al. (2006)	55°C
		co2e	CCACAAATTTCTGAACATTGACCA		
		RNa	TACWMAYCGWTTYCTTYTTGAAGGWC	Nattier et al. (2012), modified from Contreras & Chapco (2006)	47°C
		Rne	CGACCTGGAGTTGCATCAG		
	Cytb	427F	YTWGTWCAATGARTMTGAGG	Robillard & Desutter-Grandcolas (2006)	48°C
		800R	CCYARTTTATTAGGAATTGATCG		
	12S	F	TACTATGTTACGACTTAT	Kambhampati (1995)	48°C
		R	AAACTAGGATTAGATACCC		
	16S	AG	CGCCTGTTTATCAAAAACATGT	Robillard & Desutter-Grandcolas (2006)	55°C
		BG	AGATCACGTAAGAATTTAATGGTC		
nuclear	EF1a	M1F	GCWGCGGGTACTGGTGAR	Nattier et al. (2012), modified from Marshall et al. (2008)	54°C
		M1R	ACACCWGTTTCAACWCGRCC		
		M51F	CTTCAGGATGTRTACAAAATTGGTG	Nattier et al. (2012), modified from Cho et al. (1995)	54°C
		M53R	GCAATATGAGCWGTGTGGCA		
	H3	HexAF	ATGGCTCGTACCAAGCAGACGGC	Maroja et al. (2009)	58°C
		HexAR	ATATCCTTGGGCATGATGGTGAC		
	28SA	C1'	ACCCGCTGAATTTAAGCAT	Jamieson et al. (2002)	55°C
		D2b	GTTAGACTCCTTGGTCCGT		
	18S	A2	ATGGTTGCAAAGCTGAAAC	Giribet et al. (1999)	52°C
		9R	GATCCTTCCGCAGGTTCACCTA	Giribet et al. (1996)	

References

Cho, S., Mitchell, A., Regier, J.C., Mitter, C., Poole, R.W., Friedlander, T.P. & Zhao, S. (1995) A highly conserved nuclear gene for low-level phylogenetics: elongation factor-1 alpha recovers morphology-based tree for heliothine moths. Molecular Biology and Evolution, 12, 650-656.

Contreras, D. & Chapco, W. (2006) Molecular phylogenetic evidence for multiple dispersal events in gomphocerine grasshoppers. Journal of Orthoptera Research, 15, 91-98.

Folmer, O., Black, M., Hoeh, W., Lutz, R. & Vrijenhoek, R. (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Molecular Marine Biology and Biotechnology, 3, 294-299.

Giribet, G., Carranza, S., Baguna, J., Riutort, M. & Ribera, C. (1996) First molecular evidence for the existence of a Tardigrada plus arthropoda clade. Molecular Biology and Evolution, 13, 76-84.

Giribet, G., Carranza, S., Riutort, M., Baguna, J. & Ribera, C. (1999) Internal phylogeny of the Chilopoda (Myriapoda, Arthropoda) using complete 18S rDNA and partial 28S rDNA sequences. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences, 354, 215-222.

Jamieson, B.G.M., Tillier, S., Tillier, A., Justine, J.-L., Ling, E., James, S., McDonald, K. & Hugall, A.F. (2002) Phylogeny of the Megascolecidae and Crassiclitellata (Annelida, Oligochaeta): combined versus partitioned analysis using nuclear (28S) and mitochondrial (12S, 16S) rDNA. Zoosystema, 24, 707-734.

Kambhampati, S. (1995) A Phylogeny of Cockroaches and Related Insects Based on DNA-Sequence of Mitochondrial Ribosomal-Rna Genes. Proceedings of the National Academy of Sciences of the United States of America, 92, 2017-2020.

Maroja, L.S., Andrés, J.A. & Harrison, R.G. (2009) Genealogical Discordance and Patterns of Introgression and Selection Across a Cricket Hybrid Zone. Evolution, 63, 2999-3015.

Marshall, D.C., Slon, K., Cooley, J.R., Hill, K.B.R. & Simon, C. (2008) Steady Plio-Pleistocene diversification and a 2-million-year sympatry threshold in a New Zealand cicada radiation. Molecular Phylogenetics and Evolution, 48, 1054-1066.

Nattier, R., Grandcolas L., Jourdan H., Couloux A., Robillard T. (2012) Secondary sympatry caused by range expansion informs on the dynamics of microendemism in a biodiversity hotspot.

Robillard, T. & Desutter-Grandcolas, L. (2006) Phylogeny of the cricket subfamily Eneopterinae (Orthoptera, Grylloidea, Eneopteridae) based on four molecular loci and morphology. Molecular Phylogenetics and Evolution, 40, 643-661.

Shapiro, L.H., Strazanac, J.S. & Roderick, G.K. (2006) Molecular phylogeny of Banza (Orthoptera: Tettigoniidae), the endemic katydids of the Hawaiian Archipelago. Molecular Phylogenetics and Evolution, 41, 53-63.

B) Dataset 1

	CO1	**CO2**	**cytb**	**12S**	**16S**	**EF1a**	**H3**	**28SA**	**18S**	**Total**
Number of samples	40	27	39	41	41	24	39	34	39	41
Number of aligned characters	710	335	346	433	526	1045	328	382	654	4759
Number of included characters	710	335	346	433	526	1045	328	382	654	4759
Evolution models	GTR+I+G	GTR+I+G	GTR+I+G	GTR+I+G	GTR+I+G	GTR+I+G	GTR+I+G	GTR+I+G	GTR+I+G	

C) Dataset 2

	CO1	**CO2**	**cytb**	**12S**	**16S**	**EF1a**	**H3**	**28SA**	**18S**	**Total**
Number of samples	28	24	40	42	42	19	42	37	42	42
Number of aligned characters	710	335	346	472	545	1045	328	387	666	4834
Number of included characters	710	335	346	306	395	921	328	348	633	4322
Evolution models	GTR+G	GTR+I+G	GTR+I+G	HKY+I+G	GTR+G	GTR+G	GTR+I+G	GTR+I+G	SYM+I+G	

Table 4.5. *Preferential habitat and dominant frequency range of Lebinthus (only species including in the molecular study), Agnotecous and Pixibinthus species. Acoustic recording impaired by inadequate recording material are indicated with an asterisk. Unpublished data are indicated with two asterisk. Species only known from the type specimen are indicated with three asterisk. Abbreviation: N/A corresponds to non available data.*

Genus	Genus/species	Clades recovered in this study	Habitat	Habitat openness	Dominant frequency (kHz)	References
Pixibinthus	*Pixibinthus sonicus*	-	Shrubland / 'maquis minier'	Open	25.5-30.5	This study
Lebinthus	*Lebinthus bitaeniatus*	-	Open forest / Secondary forest	Open	19.9	Robillard and Tan, 2013
Lebinthus	*Lebinthus villemantae*	-	Open forest	Open	20	Robillard, 2010
Lebinthus	*Lebinthus santoensis*	-	Open forest / Coastal area	Open	25.7-27.5	Robillard, 2009
Lebinthus	*Lebinthus sanchezi*	-	Open forest / Secondary forest	Open	24.4	Robillard, Yap et .al, 2013
Lebinthus	*Lebinthus nattawa*	-	Open forest	Open	N/A	Robillard, 2009
Lebinthus	*Lebinthus lifouensis*	-	Open forest / Coastal area	Open	12 *	Desutter-Grandcolas, 1997
Lebinthus	*Lebinthus puyos*	-	Open forest / Secondary forest	Open	20 **	Robillard, Yap et .al, 2013
Lebinthus	*Lebinthus truncatipennis*	-	Open forest	Open	18.9**	**
Lebinthus	*Lebinthus luae*	-	Open forest / Secondary forest	Open	16.7	Robillard and Tan, 2013
Lebinthus	*Lebinthus sp PNG*	-	N/A	N/A	N/A	
Agnotecous	*Agnotecous obscurus*	A1	Open forest / Savannah	Open	15 **	Chopard 1970
Agnotecous	*Agnotecous albifrons*	A1	Open forest	Open	16 **	Desutter-Grandcolas and Robillard, 2006
Agnotecous	*Agnotecous meridionalis*	A1	Forest	Closed	16 **	Desutter-Grandcolas and Robillard, 2006
Agnotecous	*Agnotecous clarus*	A1	Open forest	Open	18 **	Desutter-Grandcolas and Robillard, 2006
Agnotecous	*Agnotecous sarramea*	A2	Forest	Closed	14.2	Desutter-Grandcolas and Robillard, 2006
Agnotecous	*Agnotecous yahoue*	A2	Forest	Closed	15.2	Desutter-Grandcolas and Robillard, 2006
Agnotecous	*Agnotecous pinsula*	A2	Forest	Closed	17	Robillard et .al, 2010
Agnotecous	*Agnotecous brachypterus pocquensis*	A2	Secondary forest	Closed	19.2	Desutter-Grandcolas and Robillard, 2006
Agnotecous	*Agnotecous azurensis*	A2	Forest	Closed	16 **	Desutter-Grandcolas and Robillard, 2006
Agnotecous	*Agnotecous robustus*	A2	Forest	Closed	11 **	Desutter-Grandcolas and Robillard, 2006

Agnotecous	*Agnotecous chopardi*	A2	Forest	Closed	N/A	Desutter-Grandcolas and Robillard, 2006
Agnotecous	*Agnotecous doensis*	A2	Forest	Closed	14 **	Desutter-Grandcolas and Robillard, 2006
Agnotecous	*Agnotecous minoris*	A2	Forest	Closed	13 **	Robillard et .al, 2010
Agnotecous	*Agnotecous novaecaledoniae*	A2	Forest	Closed	N/A	Desutter-Grandcolas and Robillard, 2006
Agnotecous	*Agnotecous petchekara*	A2	Forest	Closed	N/A	Robillard et .al, 2010
Agnotecous	*Agnotecous tapinopus*	A2	Forest	Closed	11 **	Desutter-Grandcolas and Robillard, 2006
Agnotecous	*Agnotecous occidentalis*	A2	Forest **	Closed	15 **	Desutter-Grandcolas and Robillard, 2006
Agnotecous	*Agnotecous humboldti* ***	A2	N/A	N/A	N/A	Robillard et .al, 2010
Agnotecous	*Agnotecous nekando* ***	A2	N/A	N/A	N/A	Robillard et .al, 2010

.

Table 4.6. *List of localites for the cricket sampling with geographical coordinates.*

Locality	**Coordinates in decimal degrees**
Mouiranges	166.68086E/22.20416S
Pic du Pin	166.82715E/22.24680S
Pépinière	166.96355E/22.27103S
Cap N Dua	166.91742E/22.38645S
Port boisé	166.97343E/22.34820S
Prony	166.80473E/22.31902S
Kaori extérieur	166.86960E/22.27110S
Bois du sud	166.76093E/22.17321S
257	166.60168E/22.21933S
259	166.63571E/22.22461S
260	166.65508E/22.22543S
261	166.68022E/22.20525S
262	166.74043E/22.16994S
888	166.288243E/21.94673S
889	166.277802E/21.95276S
Grand Kaori	166.89674E/22.28535S
Forêt nord	166.93134E/22.32259S
Rivière blanche	166.70796E/22.13625S
Madeleine	166.85268E/22.23568S

5 Les communautés de grillons en tant que potential indicateurs écologiques d'une succession forestière dans un hotspot de biodiversité

Cette section fait l'objet d'un article de recherche en préparation pour *Austral Ecology*, sous la forme suivante :

Anso, J., Desutter-Grandcolas, L., Vidal, E., Bourguet, E., Jourdan, H. Crickets as potential ecological indicators for succession in an insular biodiversity hotspot. In preparation for *Austral Ecology*.

5.1 Résumé

Les Orthoptères sont largement reconnus et utilisés en tant qu'indicateurs écologiques des programmes de restauration ou de la destruction des habitats. Parmi les Orthoptères, les grillons (Ensifère, Grylloidea) sont généralement exlus des études écologiques. Pourtant, la faune de grillons doit être aussi sensible aux conditions environnementales et à la gestion des habitats que les Orthoptères. Au cours de ce travail de recherche, nous avons étudiés la réponse des espèces de grillons au niveau des communautés dans un gradient environnemental (des maquis arbustifs aux forêts denses humides), dans le but de déterminer leur rôle en tant qu'indicateur écologique. Pour cela, les spécimens ont été collectés de jour et de nuit à vu, dans trois habitats : i) les forêts denses humides, ii) les maquis paraforestiers et iii) les maquis arbustifs appelés « maquis minier ». Plusieurs variables environnementales ont été mesurées simultanément dans chaque site échantillonné. Les commaunautés de grillons ont montré une réponse marquée à la succession forestière suivant le gradient environnemental avec la richesse spécifique la plus élevée dans les forêts denses humides, et la plus faible dans les maquis arbustifs. Les communautés de grillons évoluent selon un *turnover* au sein des habitats, avec les densités de population les plus élevées dans les milieux forestiers (i.e. les forêts denses humides et les maquis paraforestiers) traduisant le meilleur compromis entre les conditions bioclimatiques, les ressources alimentaires et les abris contre les prédateurs. Les trois habitats considérés dans cette succession forestière possèdent tous des enjeux importants de conservation puisqu'ils présentent tous des espèces uniques et endémiques de l'archipel. Toutefois, cette étude met en avant l'importance significative des milieux forestiers (i.e. les deux derniers stades de la succession) en termes de biodiversité et densité de population. Nos travaux démontrent la sensibilité des grillons en tant qu'indicateur écologique, notamment dans les écosystèmes insulaires et les hotspot de biodiversité.

Mots clés: Orthoptère, communauté, forêt dense humide, maquis arbustif, Nouvelle-Calédonie, insect.

5.2 Abstract

Orthoptera are widely recognized and used as ecological indicators to assess habitat quality or restoration processes. Among them, crickets (Ensifera, Grylloidea) remained the poor relatives as they have been mostly excluded from ecological studies. However, cricket species are probably as sensitive as others Orthoptera to environmental conditions and landscape use. In this study, we have investigated the response of cricket species at the community level along an environmental gradient (shrubland to forest), in order to assess their use as ecological indicator. Cricket species were collected day and night by sight, in each stage of succession: i) forest, ii) preforest and iii) open shrubland also called "maquis minier". Environmental variables were simultaneously collected in each sampling sites. Crickets showed a clear response to succession. Each habitat demonstrated a turnover in species composition, with the highest densities in forested environment mirroring the best trade-off between environmental and climatic conditions, access to food and shelters toward predators. Several unique species were found in each habitat, highlighting that all successional stages are important for conservation. However, preforest and forest tended to be the most important vegetation type in terms of species diversity and density. Our findings highlighted the potential use cricket fauna in island ecosystems and biodiversity hotspot as ecological indicators.

Keywords: Orthoptera, community, forest, shrubland, New Caledonia, habitat monitoring, ecological succession.

5.3 Introduction

Global biodiversity is experiencing an unprecedented crisis (Barnosky *et al.*, 2011; Ceballos *et al.*, 2015), where habitat loss is considered as a main driver in reduction and extinction of species (Brooks *et al.*, 2002; Hoekstra *et al.*, 2005; Brook *et al.*, 2008). In this context, regions with striking biodiversity, habitats and landscapes which are increasingly threatened deserved special attention for conservation and restoration programs (Myers *et al.*, 2000; Mittermeier *et al.*, 2011; Dawson *et al.*, 2014). Biological conservation programs usually involved biodiversity monitoring, commonly based on diversity indices (Barlow *et al.*, 2007). Species richness and steadiness of their relative abundance are the two most used indices in ecological studies (Ricotta, 2005). Diversity indices relied widely on species inventories, which are time-consuming, expensive, and require highly skilled specialists who are often already involved in other project (Levrel *et al.*, 2010). As an alternative to time demanding and invasive samplings, the United Nations has strongly encouraged scientific community to enhance knowledge on biodiversity assessment and to develop efficient monitoring project with biodiversity indicators (http://www.cbd.int/2011-2020/).

Indicators or proxies are generally used to assess environmental change, to monitor a specific disturbances or to estimate the taxonomic diversity (McGeoch *et al.*, 2011; Gerlach *et al.*, 2013). More precisely, bioindicators could be classified in three categories depending on their responses to stress or disturbance according to Gerlach *et al*. (2013): (i) detectors (which decrease with the added stress), (ii) exploiters (which increase with the added stress), and (iii) accumulators (which can store chemicals that can be quantify). Such bioindicators could efficiently substitute expensive species inventories of numerous taxa in order to assess the condition of the environment (Niemi & McDonald, 2004), to follow ecosystem restoration programs (Alignan *et al.*, 2014), or to prioritize management of habitats (Fartmann *et al.*, 2012). Nonetheless, taxa used as bioindicators in complex habitats such as tropical forests require sufficient knowledge about distributions, natural fluctuations with a fairly resolved taxonomic identification, which is frequently missing in tropical environments (Moritz *et al.*, 2001).

Among invertebrates, Orthoptera which account for more than 27.000 valid species are widely used to assess ecological or environmental changes (Gerlach *et al.*, 2013; Alignan *et al.*, 2014). They are a key-resource for upper food web species, such as lizards, spiders or birds (Shea *et al.*, 2009; Taylor *et al.*, 2012; Borges *et al.*, 2013; Pretelli *et al.*, 2014), with

important role in recycling organic matter (Prather *et al.*, 2013). Among them, cricket species (Orthoptera, Grylloidea) are a large group, composed by ~ 5000 species (Orthoptera Species Files, OSF) and supported by recent and robust phylogenetic framework (Chintauan-Marquier *et al.*, 2016). Most studies involving crickets focused rather on acoustic communication (Desutter-Grandcolas, 1997a; Bennet-Clark & Bailey, 2002; Desutter-Grandcolas, 2003; Jain & Balakrishnan, 2011), speciation patterns (Nattier *et al.*, 2011; Nattier *et al.*, 2012) or escape behavior (Dangles *et al.*, 2006; Dangles *et al.*, 2007; Lagos *et al.*, 2014) than ecological responses toward disturbances.

Related to ecological changes, Orthoptera species richness and composition have been negatively associated with mowing and grazing (Rambo & Faeth, 1999; Rada *et al.*, 2014), and they are regularly used to assess success of restoration programs (Szinwelski *et al.*, 2012; Rácz *et al.*, 2013; Alignan *et al.*, 2014). In ecological studies based on Orthoptera assemblages to assess ecological restoration or habitat management, grasshoppers, katydids and cricket species are entangled. Unfortunately, grasshoppers and katydids received more attention by scientific community, leading to unbalanced data with crickets. This bias in favor to grasshoppers and katydids was experienced and highlighted by Hoffmann *et al.* (2002), while documenting the negative effect of pollution on cricket assemblages in relation to changes in ground vegetation. They were in a challenging position to compare their results with a poor scientific literature on cricket community. Obviously, ecological studies which focused on grasshoppers and bush crickets are restricted to habitats where living conditions are more suitable (i.e., open habitats) (Schirmel *et al.*, 2011; Fartmann *et al.*, 2012). As a consequences, habitat selection by Caelifera and Tettigoniidae is decently known compared to crickets (Ensifera, Gryllidea), and mainly driven by vegetation structure and microclimate (Willott & Hassall, 1998; Gardiner & Dover, 2008; Poniatowski & Fartmann, 2008). Marini *et al.* (2009) provided some evidences in this line, with a strong loss of Caelifera and Tettigoniidae species in forest habitat, whereas Barlow *et al.* (2007) have found mitigated results with no clear difference in Orthoptera richness between primary forest, secondary forest and plantations, considering grasshoppers only.

The aim of our study was to assess the effect of habitat type, bioclimatic and vegetation attributes along a forest to shrubland gradient on cricket assemblages. Samplings were performed in New Caledonia, a so-called hotspot of biodiversity (Myers *et al.*, 2000), with outstanding endemism rate (Grandcolas *et al.*, 2008), uniqueness of the biota and threatened by multiple disturbances (Jaffré *et al.*, 1998a; Jaffré *et al.*, 1998b; Pellens &

Grandcolas, 2009). Ultimately, this study is a preliminary attempt to assess if crickets, at the species or community level, might be qualified as relevant bioindicator in vulnerable ecosystems. We addressed the following issues in this paper: (i) How habitat types affect the diversity and composition of cricket assemblages? (ii) How the cricket communities shift along the gradient from low sclerophyllous shrubland to old forest? (iii) Does habitat types demonstrate specific assemblages of cricket species?

5.4 Material and methods

5.4.1 Sampling sites

Cricket communities were studied in the southern part of the main island of New Caledonia called Grande Terre, located in the South-West Pacific Ocean (Fig. 5.1). Study sites were on ultramafic rocks at low-altitude (231 ± 66 m). Each locality was at least separated by 2 km. In order to study forest succession on cricket fauna, three successional stages were considered (Fig. 5.2):

(i) Forest (n = 8). These habitats were characterized by a depth leaf litter, an entirely closed canopy and a maximum vegetation height at 30m. Forests were denser than shrublands, with larger stems (but very comparable to preforest, except for vegetation height and plant species). Leaf litter covered entirely the ground, without bare ground, as in preforest succession. Tree layer is composed by diverse dominant families such as Araucariacea (Agathis and Araucaria), Sapotacea (Iteiluma, Planchonella and Pichonia), Myrtacae (Syzigium and Eugania) and Proteacea (Kermadecia and Macadamia). Palm trees, pandanus and ferns dominated the shrub layer.

(ii) Preforest (n = 8). This successional stage was similar to forest regarding canopy openness, number and size of stems, vegetation layers and bare ground covering. Preforest patches were characterized by an assemblage of plant species both present in forest and shrubland, and with an intermediate vegetation height. *Styphellia cymbulae*, *Hibbertia lucens*, *Alphitonia neaocaledonica*, and *Gymnostoma deplancheanum* dominated preforest successions with an herbaceous layer dominated by *Lepidosperma perteres*.

(iii) Shrublands (n = 8). Habitats were characterized by high bare ground cover, the absence of tree layer and canopy with a low number of stems. Shrublands were composed by

patches of vegetations with thin leaf litter and spaced by bare ground. Maximum vegetation height was at 3m with an important herbaceous and shrub layers. *Sannantha sp.*, *Eugenia sp.*, *Alphitonia neocaledonica*, *Hibbertia lucens* and *H. pancheri* dominated shrubland succession.

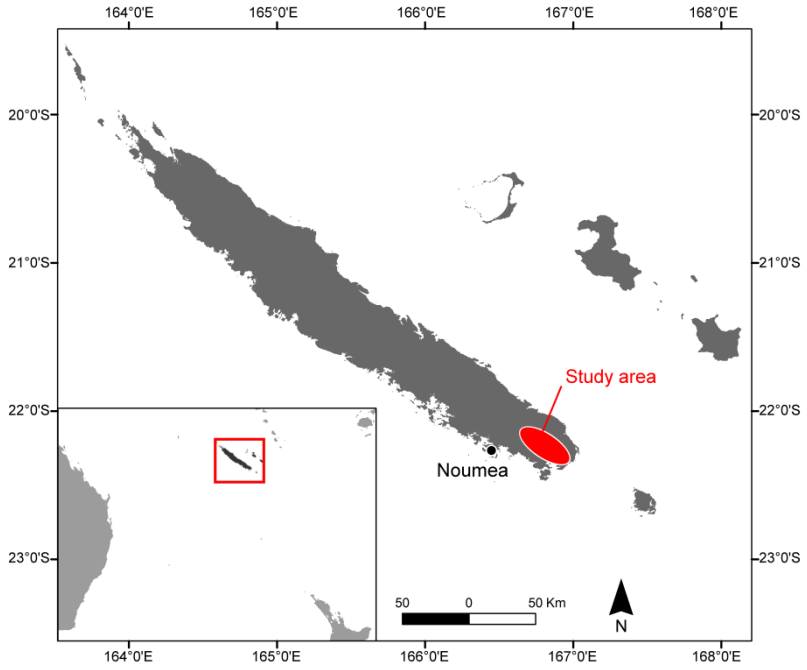

Figure 5.1. *Study area of cricket sampling in the southern part of New Caledonian under ultramafic soil.*

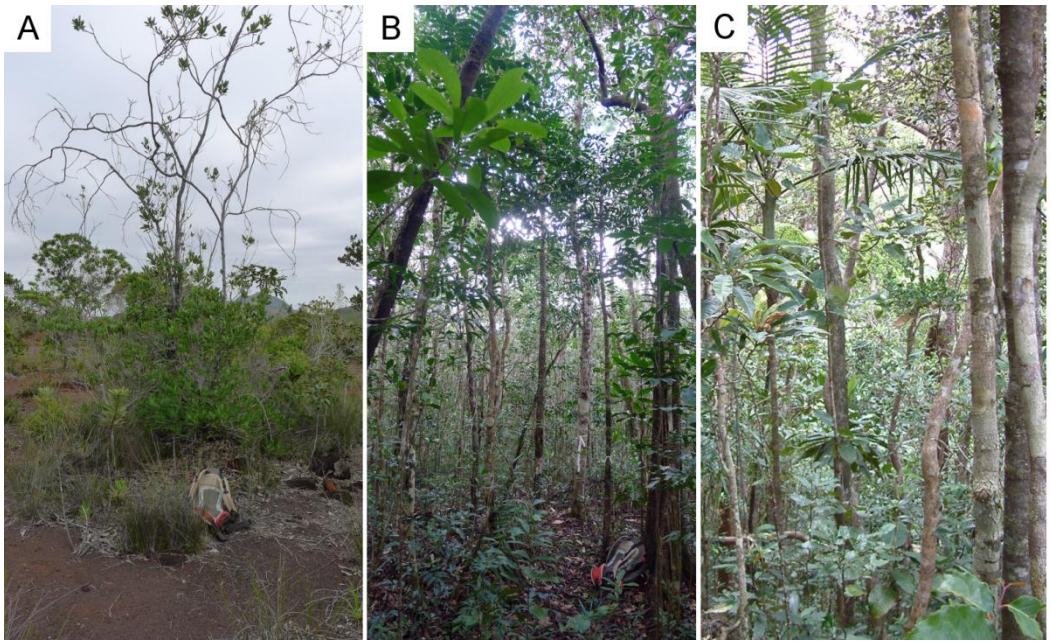

Figure 5.2. *Ecological succession in the southern part of New Caledonia, with three habitats type: (A) open shrubland, (B) preforest and (C) forest.*

5.4.2 Crickets sampling

Crickets were collected in the field between November 2013 and April 2014. In each selected site, we defined 2 randomized plots of 10x10 m. 24 plots have been investigated. under sunny meteorological conditions, by day between 09:00 to 17:00 , and by night 19:00 to 00:00. We applied a standard collecting effort for each plot with ten sessions (five times by day and night) of 30 min each. Specimens were located using both sight and song cues in the field. For each individual, time of day, activity (e.g. singing and resting) and microhabitat (e.g. trunk, leaf litter, vegetation, and rocks) were noted. Specimens were collected and killed with arsenic, then prepared in the lab for further identification to species level. Identification of species have been done in the context of following the most used classification of the Orthoptera species files (OSF) and the latest phylogenetic work on crickets (Chintauan-Marquier *et al.*, 2016).

5.4.3 Environmental variables

In every plot, several environmental attributes were collected. The percentage of bare ground, vegetation layer (herbaceous, shrub and tree layers), number and diameter (dbh) of stems, plant species richness, canopy openness and height were collected in the field. Canopy openness was assessed with hemispherical canopy photography with a 180° hemispherical (fisheye) lens in each plot's corners and in the middle. Canopy openness was then measured with the Gap Light Analyzer software (2.0, Simon Fraser University, Cary Institute of Ecosystem Studies) by counting the percentage of light in the forest overstory (Frazer *et al.*, 1999). Daily temperature (°C) and relative humidity (%) were recorded in each sampling site using waterproof thermo-hygrometer sensors (HOBO U23 Pro v2). These two climatic parameters were recorded every 30 minutes at 50 cm height on trunks or large branches, according to vegetation attributes. Data were finally extracted at the laboratory using HOBOware software.

Table 5.1. *Mean values (± SD) of vegetation attributes and climatic parameters in three successional stages.*

	Abb.	Shrubland (n=8)	Preforest (n = 8)	Forest (n = 8)	*P*
Herbaceous layer (%)	HER	55.4 ± 26.4 a	23.8 ± 20.3 a	12.5 ± 12.5b	*
Shrub layer (%)	SHR	53.8 ± 14.1 a	31.3 ± 12.2 b	32.8 ± 11.8 b	*
Tree layer (%)	TRE	2.5 ± 2.7 a	37.2 ± 17.3 b	35.3 ± 8.7 b	***
Bare ground (%)	BAR	27.5 ± 11 a	0.6 ± 1.8 b	0 ± 0 b	***
Vegetation height (m)	VH	2.3 ± 1 a	14.9 ± 3.6 b	23.8 ± 4.4 b	***
Number of stems (n°.)	DN	0.5 ± 1.1 a	19 ± 12.8 b	15.9 ± 7.1 b	***
DBH of stems (n°.)	DM	12.6 ± 23.6 a	56 ± 14.8 b	57.5 ± 16.1 b	*
Canopy openess (%)	CO	90.6 ± 6.8 a	9.8 ± 3.1 b	7.2 ± 2.2 b	***
Mean temperature (°C)	MT	21.5 ± 0.7 a	19.5 ± 0.5 b	18.6 ± 0.4 b	***
Highest temperature (°C)	HT	28.8 ± 1.8 a	23.9 ± 0.6 b	21.2 ± 0.6 c	***
Daily temperature variation (°C)‡	DT	12.6 ± 2.4 a	7.5 ± 1.2 b	4.6 ± 0.5 c	***
Mean humidity (%)	MH	78.5 ± 4.4 a	82.6 ± 1.4 b	88.1 ± 1.5 c	***
Lowest humidity (%)	LH	47.4 ± 8.3 a	59.1 ± 1.4 b	68.8 ± 2.4 c	***
Daily humidity variation (%)‡	DH	48.8 ± 6 a	37.9 ± 1.2 b	27.6 ± 1.3 c	***

Different letter indicate significant differences after a Dunn test ($p < 0.01$) performed after a Kruskall-Wallis test (abbreviation: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$). ‡ Daily humidity and temperature variations correspond to the difference between the highest and lowest recordings for each day, respectively

5.4.4 Analysis

Nonmetric Multidimensional Scaling (NMDS) was performed on abundance data of cricket species across sampling sites, using Bray-Curtis distances ((Minchin, 1987; Legendre & Legendre, 2012). We first run one NMDS analysis set at 1000 re-iteration, with two dimensions, and then run a second NMDS on the basis of the previous best solution with the same configuration in order to obtain the most stable stress. NMDS was used with the function *metaMDS* from the *vegan* R package (Oksanen *et al.*, 2007; Oksanen *et al.*, 2013). Environmental and climatic variables were fitted into ordination and their significance was assessed with permutation test (set here at 999), using the function *envfit* from the *vegan* R package. The effect of habitat type and the patch size of vegetation on cricket assemblages were assessed with a permutations test of the raw data, using the *Adonis* function. The effect of patch size on cricket community in forest and preforest formation was also assessed with permutations test of the raw data, using the *Adonis* function. Another NMDS was performed only on abundance of crickets with a stridulatory apparatus, with the same protocol described

above, as a preliminary test for bioacoustics research and monitoring using this peculiar group of insect.

The beta diversity of assemblages of cricket, with the turnover (β_{SIM}) and nestedness (β_{NES}) components, were assessed using the function *beta.multi* from the *betapart* R package (Baselga & Orme, 2012; Baselga *et al.*, 2012). Hierarchical cluster were performed to analyzed dissimilarity composition of cricket communities as a function of habitat type, using *hclust* function. We then used an analysis of similarities to test for significant differences in community structure in relation to habitat type, using also permutation test with the *anosim* function. Species richness and relative abundances were compared between habitats using generalized linear mixed-effects models (GLMMs) (function *lmer*), with sites as a random factor. The level of significance was set to 0.05. Kruskal-Wallis test followed by the post hoc Dunn test for multiple comparisons (Dunn, 1964), with the Bonferroni correction for non-normal distribution. All analyses were conducted with R 3.2.2 (R Development Core Team 2012).

Similarity percentage analysis (SIMPER, *vegan* R package) was performed on crickets community matrix to evaluate the most relevant species between paired habitats (shrubland, preforest and forest). We used C-score of Stone & Roberts (1990) to quantify the normalized mean number of checkerboard combinations in our community matrix. Co-occurrence patterns were assessed using the *bipartite* R package, giving results between 0 and 1. A C-score close to zero indicates high randomness in the distribution of species across studied modalities. After, we compared observed C-scores with those generated from 5000 randomly constructed assemblages, using the function *cooc_null_model* from the *EcoSimR* R package (Gotelli *et al.*, 2015). As suggested by Sanders et al. (2007) and Gotelli (2000), we used the "SIM9" algorithm in our null model analysis which is appropriated for analyzing co-occurrence patterns of species in island archipelago, such as in New Caledonia (with low Type I errors).

Standardized effect sized (SES) which measure the number of standard deviations that each of the observed indices is above or below the mean index of the simulated null assemblages was also calculated (Gurevitch *et al.*, 1992). It is calculated as $(I_{obs} - I_{sim})/S_{sim}$, where I_{obs} corresponds to the index for the observed assemblage, I_{sim} corresponds to the index for the null assemblages, and S_{sim} is the standard deviation of the null assemblages. 95% of the SES values should be comprised between -2.0 and 2.0 according to a normal distribution

of deviations. Values larger than c. 2.0 indicate non-random species segregation, and values lower than -2.0 indicate non-random species aggregation.

5.5 Results

5.5.1 Cricket species in the succession

In total, 1035 specimens belonging to four families and six subfamilies, and 29 species and 16 genera have been collected (Table 5.2). Cumulated species richness increased gradually along the environmental gradient, with the highest and the lowest values for forest with 20 species, shrubland with seven species, and 15 species in preforest. The most abundant species were *Bullita fusca* and *Agnotecous azurensis* in forest (43% and 34%) and in preforest (52% and 22%), while *Koghiella flammea* was the most abundant species in shrublands (83%).. No unique assemblages were found in habitat types, however each habitat harbor exclusive species. Forest demonstrated the highest ratio of unique species (twelve species, 60%) followed by shrublands (three species, 43%) and preforest (two species, 14%). Forest and preforest shared eight species, while preforest and shrublands shared four species. Forest and shrubland shared no species. Species richness and abundances increased between shrublands and preforests, but no differences were found between forests and preforests (Dunn test comparison, $p > 0.05$) (Fig. 5.3). Forests show the lowest percentage of acoustic species compared to total species richness (65%), followed by shrublands (71.4%) and preforest (78.6%).

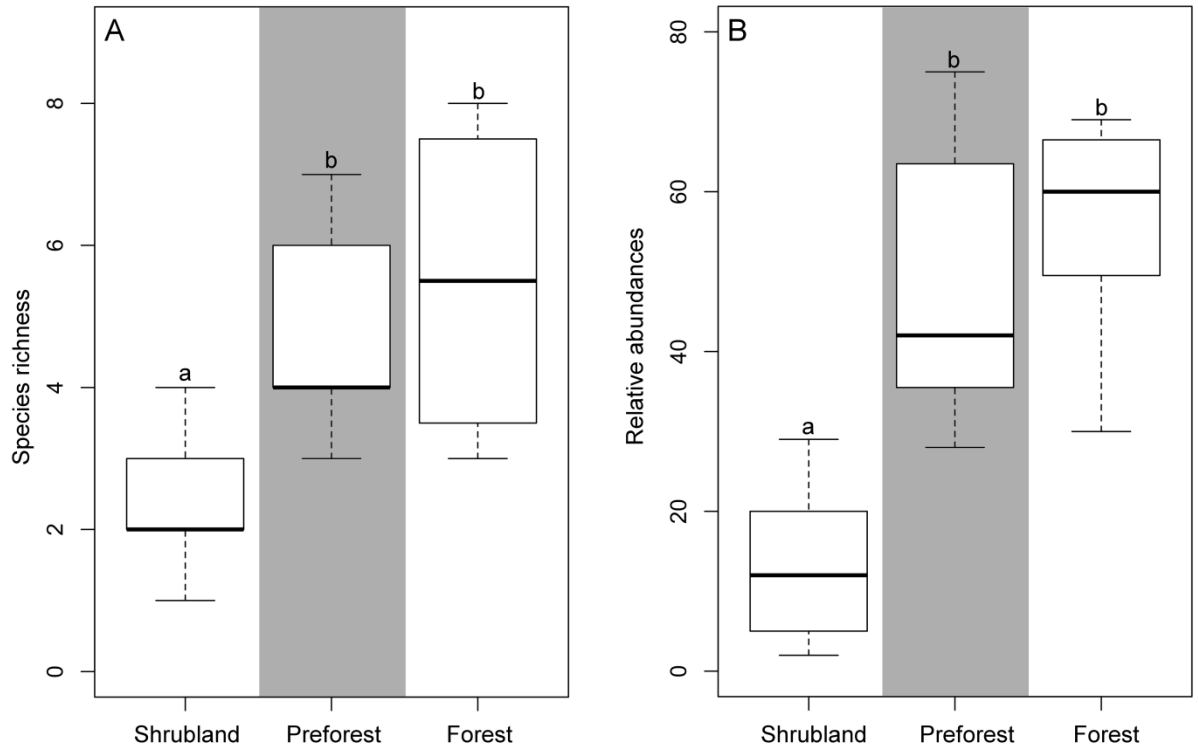

Figure 5.3. *Mean (± SE) of (A) species richness and (B) relative abundance of cricket communities in each successional stage. Differences between habitats were tested for species richness and abundance using a Poisson GLMM with sites as a random factor. Statistics of GLMM: species richness : df = 20, P =0.001; abundance: df = 20, P = 0.001. Different letter indicate significant differences between habitats (Dunn test; p < 0.05).*

5.5.2 Beta diversity of cricket assemblages

Considering NMDS ordination based on abundance (stress = 0.0929, two dimensions), each habitat showed clear separated crickets assemblages, with eight environmental variables which significantly contributed to the ordination model (Fig. 5.4, Table 5.1). Shrubland assemblage is the most distinctive between forest and preforest, characterized by an open canopy, a high coverage of bare soil, herbaceous and shrub layer. Species assemblages in forest and preforest are closer but also well separated, and characterized by a higher canopy height, number and circumference of stems with a denser tree layer. Cricket assemblages with the habitat type as factor explained 45.3% of the total variation in cricket composition (ADONIS $R^2 = 0.45$, $p < 0.001$). We found a positive effect of the forest patch size on the cricket communities in forest and preforest (ADONIS $R^2 = 0.2$, $p = 0.009$).

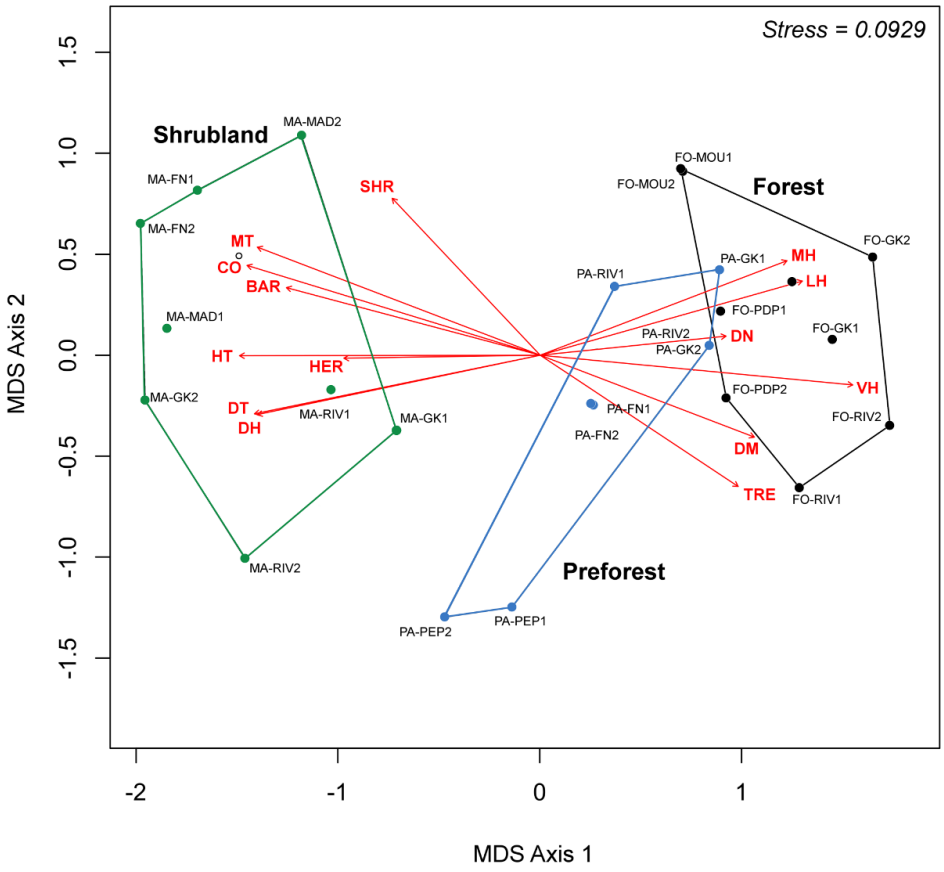

Figure 5.4. *NMDS (stress = 0.093, two dimensions) based on cricket abundances and environmental parameters. 14 significant environmental variables are shown (envfit, $p < 0.05$ with 999 permutations). Polygons were drawn according to habitat type. Abbreviations: see Table 1.5*

NMDS based on cricket abundances with stridulatory apparatus demonstrate a clear succession of cricket communities along the forest succession abundance (stress = 0.072, two dimensions; ANOSIM = 0.63, P < 0.001) (S1 Fig 1.5).

The dendrogram built using hierarchical cluster analysis based on crickets abundances showed two clear clusters based on habitat type: 1) open shrubland habitats, including the eight shrublands plots, and 2) closed habitats, including the eight forest and preforest plots (ANOSIM R = 0.64, p < 0.001) (Fig. 5.5). The latter group could be divided into three subgroups: 2a) Preforest formation located in Pépinière (PA-PEP1 and 2); 2b) Forest habitats, including most forest formations (six out of eight) with one preforest formation (PA-RIV1 and 2); 2c) Preforest habitats, including four preforest formation (PA-FN1, 2 and PA-GK1, 2), with two forests formations (FO-MOU1 and 2). When analyzing the spatial turnover and the

nestedness variables of cricket assemblages, results indicated that spatial turnover have almost exclusively contributed to the beta diversity observed (β_{SIM} = 0.89, β_{NES} = 0.04).

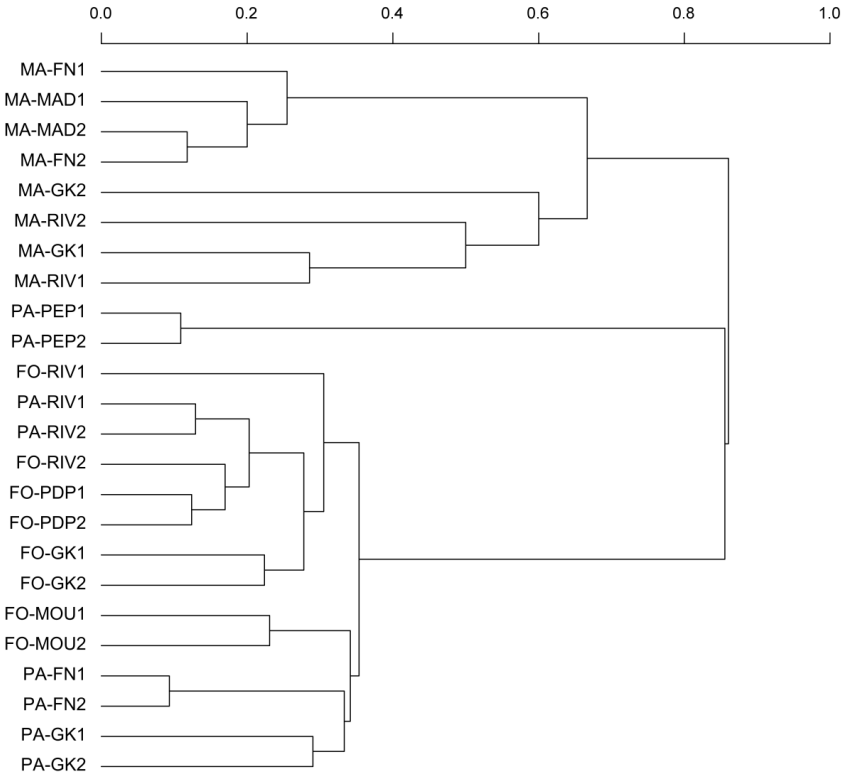

Figure 5.5. *Dendrogram of the study sites based on dissimilarity matrix of cricket abundances obtained with Bray-Curtis distance (values indicated in the top of the dendrogram), and constructed using hierarchical clustering with the single linkage method.*

SIMPER analysis showed that specific cricket species were relevant to distinguish species composition of cricket communities in the succession (Table 5.2). Between shrubland and preforest, *Koghiella flammea*, *Agnotecous azurensis*, *Bullita fusca* and *A. clarus* were the most important species, with close contribution revealed SIMPER analysis. These four species live in leaf litter, with the ability to produce species-specific calling song. *K. flammea* is active all day, both *Agnotecous* species are active by night whereas *B. fusca* is active by day. Between shrubland and forest, the four most important species were *A. azurensis*, *K. flammea*, *Calthatra meunieri* and *B. fusca*. *C. meunieri* is a nocturnal Phalangopsidae living on large trunks or roots, without stridulatory apparatus (i.e. "silent species"). In the last pair of habitat between forest and preforest, the four most important species in grouping were *C. meunieri*, described above, and *A. clarus*, *K. nigris* and *Pseudotrigonidium ana*. *K. nigris* is a small nocturnal Nemobiinae living strictly in forested habitat, in peculiar microhabitat (i.e. bareground) and emitting calling song. *P. ana* is a medium-sized Phalangospsidae, living preferentially by night on trunks or leaf litter.

Table 5.2. *Most important species for each pair of habitats and their contribution to species composition groups forming in SIMPER analysis. Taxa contribution alone in bold (A) and cumulative contribution in brackets (B, in %).*

Habitat type	**Forest**	A	B	**Shrubland**	A	B
Preforest	*Calthatra meunieri*	**6,95**	(10,90)	*Koghiella flammea*	**11,88**	(13,25)
	Agnotecous clarus	**6,01**	(20,33)	*Agnotecous azurensis*	**11,23**	(25,78)
	Koghiella nigris	**5,02**	(28,20)	*Bullita fusca*	**11,23**	(38,30)
	Pseudotrigonidium ana	**4,24**	(34,85)	*Agnotecous clarus*	**9,00**	(48,35)
Shrubland	*Agnotecous azurensis*	**13,65**	(13,65)			
	Koghiella flammea	**13,65**	(27,31)			
	Calthatra meunieri	**11,66**	(38,96)			
	Bullita fusca	**8,88**	(47,85)			

5.5.3 Species co-occurrence

Co-occurrence patterns of cricket communities would be a result of segregation across habitat type, as suggested by C-score analysis close to one (0.76), and SES obtained from null model analysis (3.41) larger than 2.0 (i.e. randomness threshold).

5.5.4 Environmental conditions

All vegetation parameters differed between shrubland and preforest and shrubland and forest, excepted for the herbaceous layer (identical between shrubland and preforest) (Table 5.1). By contrast, all vegetation parameters were identical between preforest and forest, excepted for herbaceous layer lower in forest and higher in open shrubland. Significant climatic parameters (temperature and relative humidity) differed in the succession. Highest temperature with daily temperature variation follows the ecological gradient, with highest and lowest values for shrubland and forests respectively. Mean and lowest relative humidity differed significantly across habitats, with lowest and highest values for shrublands and forests, respectively. Daily humidity variation was highest in shrublands, followed by preforest and then by forests with lowest value. Species richness of plant species, lowest temperature and highest relative humidity were not significant in our analysis.

Table 5.3. *List of crickets species in our community matrix*

Family	Sufamily	Species	Habitat	Micro-habitat	Stridulatory apparatus
Gryllidae	Podocirtinae	*Adenopterus crouensis* †	Shrubland	Understory	no
Gryllidae	Podocirtinae	*Adenopterus meridionalis**	Forest	Understory	no
Gryllidae	Eneopterinae	*Agnotecous azurensis*	Forest/preforest	Leaf litter	yes
Gryllidae	Eneopterinae	*Agnotecous clarus*	Forest/preforest	Leaf litter	yes
Gryllidae	Eneopterinae	*Agnotecous meridionalis**	Forest	Leaf litter	yes
Trigonidiidae	Nemobiinae	*Bullita fusca*	Forest/preforest	Leaf litter	yes
Trigonidiidae	Nemobiinae	*Bullita mouirangensis**	Forest	Leaf litter	yes
Trigonidiidae	Nemobiinae	*Bullita obscura* ‡	Preforest	Leaf litter	yes
Gryllidae	Podocirtinae	*Calscirtus amoa**	Forest	Understory	unknown
Gryllidae	Podocirtinae	*Calscirtus magnus**	Forest	Canopy	yes
Phalangopsidae	Paragryllinae	*Caltathra balmessae*	Forest/preforest	Trunks/roots	no
Phalangopsidae	Paragryllinae	*Caltathra meunieri*	Forest/preforest	Trunks/roots	no
Trigonidiidae	Nemobiinae	*Kanakinemobius sp**	Forest	Understory	no
Trigonidiidae	Nemobiinae	*Koghiella flammea*	Preforest/Shrubland	Leaf litter	yes
Trigonidiidae	Nemobiinae	*Koghiella nigris*	Forest/preforest	Bare soil	yes
Gryllidae	Podocirtinae	*Matuanus sp. affinis mirabilis**	Forest	Understory	yes
Mogoplistidae	N/A	*Mogoplistidae sp1*	Preforest/Shrubland	Understory	yes
Mogoplistidae	N/A	*Mogoplistidae sp2*	Preforest/Shrubland	Understory	yes
Mogoplistidae	N/A	*Mogoplistidae sp3* †	Shrubland	Leaf litter	yes
Mogoplistidae	N/A	*Mogoplistidae sp7**	Forest	Understory	yes
Gryllidae	Gryllinae	*Notosciobia minoris*	Forest/Preforest	Leaf litter/burrows	yes
Gryllidae	Gryllinae	*Notosciobia sp1**	Forest	Leaf litter/burrows	yes
Gryllidae	Gryllinae	*Notosciobia sp. affinis paranola* ‡	Preforest	Leaf litter/burrows	yes
Trigonidiidae	Nemobiinae	*Paniella bipuntatus**	Forest	Trunks	no

Gryllidae	Eneopterinae	*Pixibinthus sonicus*	Preforest/Shrubland	Leaf litter	yes
Gryllidae	Podocirtinae	*Pixipterus punctulatus* †	Shrubland	Understory	no
Phalangopsidae	Phaloriinae	*Protathra nana**	Forest	Trunks/roots	yes
Phalangopsidae	Phaloriinae	*Pseudotrigonidium ana*	Forest/preforest	Trunks/leaf litter/understorey	no
Phalangopsidae	Phaloriinae	*Pseudotrigonidium caledonia**	Forest	Understory	yes

** Species unique to forest; ‡ Species unique to preforest; † Species unique to maquis; N/A indicate not available data.*

5.6 Discussion

Cricket assemblages along our environmental gradient showed clear-cut responses to succession. It is mainly explained by species turnover, environmental and climatic attributes. Each habitat is composed by numerous unique species, with the highest value for forest. Species richness and abundance were highest in forested habitats (i.e. forest and preforest succession) and lowest in open habitat (i.e. shrubland), while species accumulation followed the succession with the most and least occurring in forest and shrubland, respectively.

Overall cricket abundances were higher in forested habitats (i.e., forest and preforest) suggesting that forest and preforest provide the best trade-off between food resources, presumably linked with a higher canopy cover (Barberena-Arias & Aide, 2003; Williams *et al.*, 2008), shelter from predators (Brouwers & Newton, 2009), and favorable moisture conditions which may favor higher densities . Oviposition sites may also be more important in forested habitats than in more open ones, especially for litter-dwelling species explaining higher densities in closed habitats (Huber, 1989). These results are opposed with most *Caelifera* and *Tettigoniidae* species which demonstrate higher densities in open habitats (Fartmann *et al.*, 2012) according to warm ambient temperatures (Gardiner & Dover, 2008). By contrast, lower cricket densities in shrublands might be explained by warmer mean and maximum temperature, with lower relative humidity and limited food resources (Shik & Kaspari, 2010). Moreover, cricket density in drier habitats, such as in shrublands, might be constraint by higher predator biomass (McCluney & Sabo, 2014), higher subsequent effect of predation on crickets (McCluney & Sabo, 2009) or by limited shelters from predators.

Species richness followed the same pattern to succession as for abundance, with the highest mean diversity in forested habitats, presumably reflecting greater habitat complexity and microhabitat availability (Shik & Kaspari, 2010). Forest and preforest exhibit denser and larger trees, also a denser tree layer with a canopy almost entirely closed than in shrublands. As an example, phalangopsid species such as *Caltathra balmessae*, *C. meunieri* and *Paniella bipuntatus* were only found in large trunks and roots in forested environments. Several leaf litter-dwelling genera (e.g. *Agnotecous* and *Bullita*) are already described living almost exclusively in forested habitat (Desutter-Grandcolas, 1997d; Robillard *et al.*, 2010), with climatic conditions and habitat heterogeneity opposed to shrublands, which is corroborated by our findings.

Despite the facts that preforest and forest were similar in terms of species richness and abundance, the latter habitat is however characterized by higher total species diversity (i.e. species accumulation) and higher percentage of unique species. This pattern is somewhat expected for rich forest ecosystem (Rahman *et al.*, 2012), and comparable with fruit-feeding butterflies, birds, leaf litter amphibians and crickets documented in Brazilian forests (Barlow *et al.*, 2007; Szinwelski *et al.*, 2012). Habitat complexity and heterogeneity might explain higher species richness in forest or older habitats (Shik & Kaspari, 2010). Nevertheless, preforests and forests were surprisingly close in terms of vegetation attributes but clearly different in terms of climatic conditions (i.e. temperature and relative humidity) (see Table 5.1). These observations highlight probably that unconsidered fine vegetation attributes or microhabitats (e.g. dead trunks or woody debris), with higher buffered climatic condition (i.e. higher moisture condition, lower variation of temperature and humidity) might explain community differences between these two advanced stages in the southern part of New Caledonia. Interestingly, among the ten species exclusively found in forest, eight were found on vegetation strata suggesting a close relationship with vegetation attributes (i.e., plant species), and probably interrelated with the older age of forest habitat.

Few studies have been performed about the response of cricket communities to succession, with mostly contrasted or inconclusive results, since little taxonomic expertise is available for this group and crickets respond usually insufficiently to classical insect traps. For example, Araújo *et al.* (2015) found no relationship between habitat degradation (from highly degraded to natural forested habitats) and crickets abundance. They explained this pattern with the omnivorous scavengers diet of crickets which made them presumably less sensitive to habitat change. However, the passive trapping system (i.e. pitfalls trap) used in this study was not adequate enough to estimate efficiently diversity and abundance of cricket communities (Gardiner *et al.*, 2005), leading to potential bias for this group. Numerous cricket species lives on vegetation, rocks or trunk with restricted displacements on leaf-litter (Desutter-Grandcolas, 1992, 2002; Jain & Balakrishnan, 2011), making ground traps presumably inefficient without trampling (Sperber *et al.*, 2007). As a consequence, Araújo *et al.* (2015) have only estimated cricket response to succession with low abundances (3-5 individuals per habitat), without consideration for species richness and community composition or structure.

Several studies were inconclusive for crickets because of the low species richness recorded (Marini *et al.*, 2009; Fartmann *et al.*, 2012). Nevertheless, with only two cricket

species out of 49 orthopteran collected in different successional stages, Marini *et al.* (2009) suggested an effect of succession on crickets. Specifically, *Nemobius sylvestris* (Bosc) was mainly a forest-dwelling species whereas *Gryllus campestris* (Linnaeus) was found in more open habitats (e.g. mown meadows and young fallows). Desutter-Grandcolas (1997d) has described cricket community in New Caledonia solely in forested habitat, under different soil constraints (volcano-sedimentary rocks). In this study, the response of cricket to succession was not investigated, but Desutter-Grandcolas (1997d) described a surprisingly close community structure with our forest community (in terms of species richness and dominant species) with 23 species found. Finally, the most comprehensive study was performed in Brazilian semi-deciduous and mixed forest where cricket communities were studied along a large forest regeneration gradient (i.e. in a 300 year time period) (Szinwelski *et al.*, 2012). As a main result, they found positive correlations between species richness and forest age, canopy cover and with litter depth. More importantly, Szinwelski *et al.* (2012) provide a persuasive evidence of cricket species succession and specificity along a large habitat chronosequence, including very open to closed habitats, with a comparable turnover in species composition than we found in New Caledonia.

5.7 Implications for conservation

Our findings provide solid evidences that cricket species and communities are sensitive indicators to succession in the island biodiversity hotspot of New Caledonia, with interesting application in conservation as well as other Orthoptera (Gerlach *et al.*, 2013). According to bioindicator evaluation provided by Gerlach *et al.* (2013), New Caledonian crickets appear highly suitable as bioindicators for terrestrial monitoring since they demonstrate high densities throughout the year; they are easily sampled by trampling by sight; they benefit of a fairly taxonomic knowledge with various range of bioclimatic preferences.

In our study, all habitats considered in the succession are important in the light of conservation as they harbor a unique assemblage of cricket species, giving valuable insight for managers and decision-makers. Older and preserved habitats such as forest and preforest in our study might be depicted as the most important formations as we found the highest densities and species diversity in these habitats. These findings are corroborated by favorable bioclimatic conditions (i.e. temperature, humidity, resources, microhabitat availability) which confirm the outstanding biodiversity of New Caledonian forests with numerous endemic

genera and species. More importantly, our study stresses the importance to act decisively to manage and protect these forested habitats (e.g. by increasing protected areas surface), as their destruction would lead to irreversible loss of unique biodiversity in New Caledonia. .

However, open shrublands which are usually defined as highly degraded by human activities, and less studied for its fauna (Chazeau, 1993) also demonstrate importance for conservation. As for older habitats, open shrubland harbored several unique species and genera with special interest to understand the impact of peculiar disturbances (i.e. fires, climatic oscillations). In this context, the discovery of the new monotypic genus *Pixibinthus* Robillard & Anso, 2015, found exclusively in open shrubland, provided useful information about fire regimes and climatic fluctuations and their influences on diversification processes in the history of New Caledonia. The evolutionary history of this small leaf-litter dwelling cricket was recently investigated by Anso *et al.* (2015c, *Plos ONE*), assuming that the ecological specialization for shrublands have led to higher sensitivity to fires (especially after the increasing fire regimes after human's settlement) and climatic fluctuations.

As a unique opportunity for bioindication, New Caledonian cricket fauna is mainly composed by acoustically active species. Interestingly, community analysis performed on stridulating crickets only revealed a clear-cut specialization to succession. Crickets emit pure-tone calls by rubbing their forewings together mainly to attract a mate (Bennet-Clark, 1998, 1999). Calling songs are composed by stereotyped repetition of syllables (Ragge & Reynolds, 1998), with a narrow carrier frequency allowing highly reliable species identifications (Riede, 1997; Diwakar & Balakrishnan, 2007a; Jain *et al.*, 2014). As crickets and others Orthoptera are also sensitive to ecological stresses and habitat quality, acoustic inventorying and monitoring of Orthoptera can be an efficient and innovative alternative for conservation (Fischer *et al.*, 1997; Riede, 1998). By contrast with other method, such as fogging of traditional taxonomic inventories, acoustic samplings are a non-invasive method, easy to implement with a relatively low cost for materials (Farina *et al.*, 2014). This acoustic approach of biodiversity monitoring is also meaningful in species-rich ecosystems, such as tropical rainforests, where taxonomic impediments might be overcome by recognizable taxonomic unit of songs (Riede, 1998). Our findings highlight the importance to study the peculiar group of crickets, widely found around the world, especially in endangered biodiversity hotspot where local communities can be exploited for conservation programs.

5.8 Acknowledgments

We would like to thank Frédéric Rigault & Edouard Bourget (IMBE IRD Noumea), Léa Colmas, and Alexia Omont (Master students) who provided help for field work, habitat characterization and for mapping our sampled localities. We are also grateful to Eric Vidal (IMBE IRD Noumea) for logistic and funding supports and Alexandre Millon (IMBE AMU) for helpful comment for our statistical analysis. We also thank Thomas Ibanez who provides helpful information about community analysis. We thank the New Caledonian Direction de l'Environnement de la Province Sud, for collecting permits. This study was partly funded by a PhD grant, 'Bourse d'encouragement à la recherche universitaire, attributed to JA by the Government of New Caledonia. The bioacoustic study was supported by a grant from the Grand Observatoire du Pacifique Sud: AAP GOPS 2013 / 'Bioacoustique des grillons de Nouvelle-Calédonie'. The laboratory procedures were realized through the two research programs: Action Transversale du Muséum (ATM) 'Biodiversité actuelle et fossile. Crises, stress, restaurations et panchronisme: le message systématique', and ATM 'Barcode'.

5.9 Supporting information

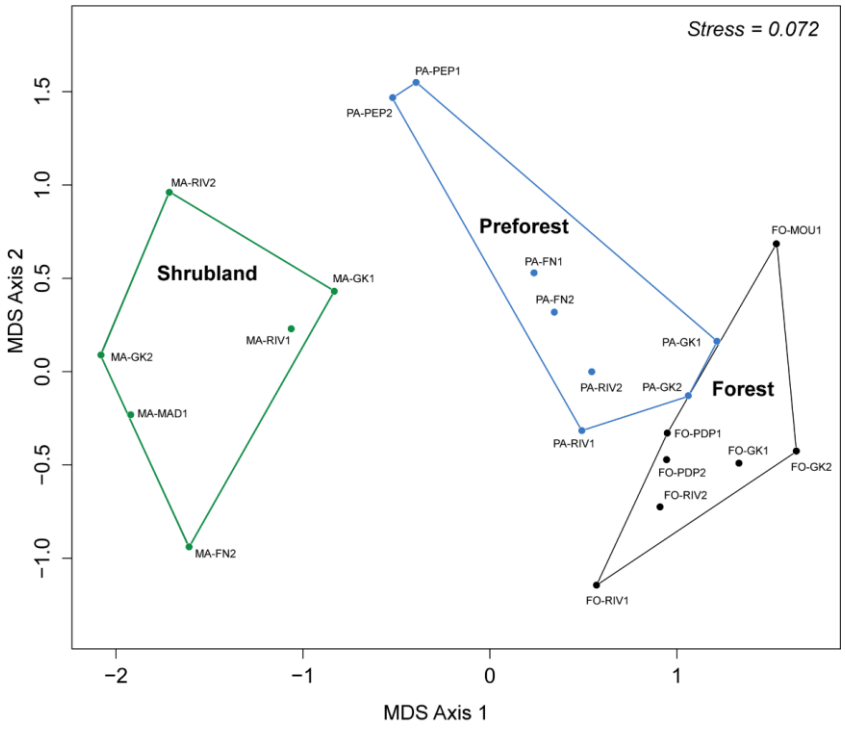

Figure 5.6. *NMDS (stress = 0.072, two dimensions) based on abundances of cricket with a functional stridulatory apparatus Polygons were drawn according to habitat type.*

6 Mesure de l'impact de deux fourmis invasives (*Wasmannia auropunctata* Roger, *Anoplolepis gracilipes* Smith) sur les communautés de grillons: implication pour la conservation dans un hotspot de biodiversité

Cette section fait l'objet d'un article de recherche en préparation pour *Biological Invasion*, sous la forme suivante :

Anso, J., Desutter-Grandcolas, Vidal, E., Bourguet, E., Jourdan, H. Contrasted impact of invasive ants (*Wasmannia auropunctata* Roger, *Anoplolepis gracilipes* Smith) on cricket communities: implication for conservation in a biodiversity hotspot. In preparation for *Biological Invasion*.

6.1 Résumé

A notre connaissance, peu d'études ont permis d'estimer l'impact de *Wasmannia auropunctata* et d'*Anoplolepis gracilipes*, deux espèces invasives majeures, sur la faune de grillons (Ensifère, Grylloidea). Les travaux précédent ayant mesurés l'impact des fourmis envahissantes sur cette faune de macro-arthropodes terrestres trouvent des résultats très contrastés ou bien délicat à exploiter. Dans cette étude, nous avons testés la vulnérabilité des communautés de grillon facent à *W. auropunctata*, au sein d'une succession forestière, et facent à *A. gracilipes* uniquement dans des maquis arbustifs. Les grillons ont été échantillonnés à vue dans la partie méridionale de la Nouvelle-Calédonie, de jour et nuit. Les communautés d'insectes ont été comparées entre les milieux envahies ou non par les deux fourmis envahissantes selon un effort d'échantillonnage standard. Les résultats majeurs de ce travail indiquent que les espèces de grillons ont presque intégralement disparu dans les milieux envahis par *W. auropunctata*, avec des densités très faibles, dans tous les stades de la succession. 29 espèces et plus de 1000 spécimens ont été collectés dans les milieux non envahis comparé à seulement deux espèces et trois individus dans les sites envahis par *W. auropunctata*. Nos résultats suggèrent que *W. auropunctata* impactent dramatiquement les grillons terrestres de Nouvelle-Calédonie. Nous discutons dans cette étude des mécanismes d'exclusions les plus probables entre les fourmis et les grillons, et du rôle de ces derniers en tant que détecteur d'une invasion biologique majeure. Ainsi, nous suspectons (i) un déplacement des populations de grillons à faible risque de prédation en dehors des zones envahis, et (ii) des phénomènes de prédations directes sur les stades de grillons les plus sensibles, comme les œufs, les nymphes et les individus vulnérables (e.g. de petite taille). En revanche, les communautés de grillons semblent ne pas être impactées par la présence de *A. gracilipes*, puisque qu'aucune différence de richesse spécifique et d'abondance n'a été observée. Nos résultats suggèrent que la faune de grillons est fortement sensible à l'invasion par *W. auropunctata*, ouvrant des perspectives en tant que détecteur de cette perturbation, tandis qu' semble être dans une phase dite de latence, sans impact négatif significatif sur la faune terreste. D'autres études sont nécessaires pour connaître les mécanismes sous-jacents des exclusions entre grillons et fourmis.

Mots clés: insects, espèces exotiques, petite fourmi de feu, fourmi folle jaune, compétition, predation, Orthoptère.

6.2 Abstract

Few studies have been able to appreciate the impact of *Wasmannia auropunctata* and *Anoplolepis gracilipes*, two major invasive ants, on the peculiar cricket fauna (Ensifera, Orthoptera). Previous works, which have studied the relation between invasive ants and crickets, found contrasted or inconclusive results. Here, we assessed the vulnerability of cricket communities toward the biological invasion of two major invasive ants (*Wasmannia auropunctata*, along a forest to shrubland gradient, and *Anoplolepis gracilipes* only in shrubland). Crickets were sampled, according to a standard sampling effort, day and night, by sight, in the southern part of New Caledonia. Cricket communities were compared between invaded and non-invaded plots,. We illustrated a different environmental filtering of both invasions: *W. auropunctata* showing a strong negative impact on crickets (from 31 species with more than 1000 individuals to only 2 species and 3 individuals) when *A. gracilipes* co-exist with a more conserved assemblage in shrubland (with at least 4 species still present). We discuss in this paper the most likely exclusions mechanisms involved between ants and crickets, and the role of cricket communities as detector of biological invasion. We hypothesize (i) a strong displacement of crickets with low risk of predation outside invaded areas, and (ii) direct predation on various sensitive stages of crickets, such as eggs, nymphs or vulnerable individuals (e.g. small sized). By contrast, cricket communities in shrubland were presumably unaffected by *A. gracilipes*, with no change in species richness and density. Our findings suggest that cricket fauna in insular systems are highly sensitive to biological invasion by ants, but that the impact appears highly context and species dependant. Ant size may be involved especially in the context of cricket ability to detect threats and may be responsive of a latency phase, before obvious negative impacts with A. gracilipes. Further experiments are needed to better assess and measure exact mechanisms involved in these interactions.

Keywords: insect, exotic species, little fire ant, yellow crazy ant, competition, predation, orthoptera

6.3 Introduction

Biological invasions imply the displacement and the establishment of alien species outside their native range, generally followed by detrimental impacts on ecosystem properties and functions (Mack *et al.*, 2000; Walsh *et al.*, 2012; Simberloff *et al.*, 2013). Nowadays, the adverse effects of biological invasions are magnified by globalization (e.g., travels, tourism), as the number and the frequency of displaced exotic species have dramatically increased with trade and communication routes (Ricciardi, 2007; Hulme, 2009). Henceforth, in the context of the current biodiversity crisis, exotic species represents the second and the first cause of biodiversity decline in continental and insular ecosystems, respectively (Vitousek *et al.*, 1997; Mooney & Cleland, 2001; Tershy *et al.*, 2015). In addition to serious damages to native ecosystems, invasive species are also associated with huge economical impacts (spread of pests for agriculture, forestry, or livestock (Pimentel *et al.*, 2001; Pimentel *et al.*, 2005)), but also with disruption of ecosystem services and function (e.g. pollination, soil stabilization, water availability, fire regime) with negative effects on human well-being (Pejchar & Mooney, 2009; Simberloff, 2011; Strayer, 2012).

Among alien species, ants are well-known to be highly destructive for both continental and island biodiversity (Holway *et al.*, 2002; Lach & Hooper-Bui, 2010; Wittman, 2014). Five ants species are described as the most widespread, abundant and damaging ant species (*Anoplolepis gracilipes*, *Linepithema humile*, *Pheidole megacephala*, *Solenopsis invicta*, and *Wasmannia auropunctata*), with 5 of them being among the most noxious species for biodiversity (Lowe *et al.*, 2000). Typically, invasive ants are omnivorous, with unicolonial social system without competition between conspecifics, and also with polygyne nests (Holway *et al.*, 2002). These invasive ants have higher abilities compared to native species, especially for resource competition, including efficient foraging with rapid mass recruitment (Holway, 1999). As a main consequence of an invasion, native ant species and other local arthropods are strongly and negatively affected by invasive ant (Lach & Thomas, 2008; Vonshak *et al.*, 2010). In addition, introduced ant could indirectly leads to a shift in composition of plant community by disrupting seed-dispersal mutualism between native-ant species and plants, and then, driving to an unbalanced regeneration of plant communities (Christian, 2001).

Among these threats, the little fire ant (*Wasmannia auropunctata*) held all the characteristics of other major invasive ants (Jourdan, 1997), with a great aggressiveness and a

venomous sting. The range of *W. auropunctata* extends from moist to semi-arid habitats, including anthropogenic habitats (Holway *et al.*, 2002). Originally, this ant is from the Central and South America, and has been introduced through the tropical belt, like North America, Middle east, central Africa, Australia, Caribbean, and various Pacific islands (Foucaud *et al.*, 2010). After *W. auropunctata* become established in a new area, the recipient community will likely to be negatively affected by spreading of foraging workers and colonies, as reported for various arthropods (i.e. scorpions, pseudo-scorpions, spiders, native ants….) (Lubin, 1984; Jourdan, 1997; Le Breton *et al.*, 2003; Le Breton *et al.*, 2005; Walker, 2006); lizards (Jourdan *et al.*, 2001) or mammals (Jourdan, 1997; Walsh *et al.*, 2004). By contrast, spreading of colonies is generally positively correlated with the abundance of sap sucking hemipteran (Jourdan, 1997; Souza *et al.*, 1998). These Coccids can cause also damages to wild plants and crop plants by sucking nutrients and by increasing the occurrence of certain diseases (Souza *et al.*, 2008).

However, our knowledge remains scarce about the response of Orthoptera, which involved up to 27.000 terrestrial species, in the light of biological invasions by exotic ants. Orthoptera richness and abundance are widely used to assess habitat quality in various context (Hoffmann *et al.*, 2002; Jana *et al.*, 2006; Fartmann *et al.*, 2012; Szinwelski *et al.*, 2012), where orthoptera species are usually recognised as a key-resource for upper food web species, such as spiders (Dangles *et al.*, 2005), lizards (Shea *et al.*, 2009; Borges *et al.*, 2013), or birds (Gámez-Virués *et al.*, 2007). To our knowledge, the vulnerability of Orthoptera by invasive ants have been poorly investigated. Two studies have shown negative impacts from major invasive ants (*S. invicta* and *P. megacephala*) on crickets fauna (Orthoptera, Grylloidea), with strong decrease of abundance and even a complete extirpation (Nichols, 1989; LaPolla *et al.*, 2000). By contrast, Orthoptera populations were significantly seven fold more abundant in infested area with the exotic ant *S. invicta* compared to non-infested area (Porter & Savignano, 1990). Two additional studies have investigated the vulnerability of several arthropod species by *L. humile* and *P. megacephala* with inconclusive results for crickets(too low level of abundance of crickets in both case) (Human & Gordon, 1997; Krushelnycky & Gillespie, 2010). Finally, Haines & Haines (1978b) have reported detrimental impact of *A. gracilipes* on various arthropods species.

In this context, our study aim to evaluate the response of the cricket fauna at the community level (Orthoptera, Grylloidea) in New Caledonia facing two different biological invaders: (i) *Wasmannia auropunctata* and (ii) *Anoplolepis gracilipes*. These two invasive

ants are widespread in the New Caledonia archipelago with detrimental impact on biodiversity and human activities (Jourdan & Mille, 2006). We selected the cricket fauna because of the correct taxonomic knowledge of this group, the relatively high diversity (more than 180 species already described) and abundance all year round (Chopard, 1915; Otte *et al.*, 1987; Desutter-Grandcolas, 1997e, 2002; Robillard *et al.*, 2010). Our study is a preliminary assessment of the role of the cricket fauna as an efficient bioindicator for major disturbances affecting natural and altered ecosystems by invasive ants.

6.4 Material and methods

6.4.1 Sampling sites

Our study area is located in the southern part of the main island of New Caledonia (Fig. 6.1); an area mainly dominated by an ultramafic soil, very rich in certain elements like iron, nickel, chrome, cobalt, and poor in others, aluminum, calcium or potassium. This region is characterized by an oceanic tropical climate with high rainfall (1500-3500 mm per year) and average minimum and maximum temperature of 15 and 29°C. The geography of this area include coastal plains, mountain pass of moderate altitude; the vegetation varying from bare soil to low vegetation maquis (shrub) with higher stages of vegetation (preforest formation) and forests to rainforests formations. This southern region is characterized by many human impacts including, reduction of native forest cover and promoting habitat fragmentation by mining activity and wild bush fires , spread of invasive species and pollutions.

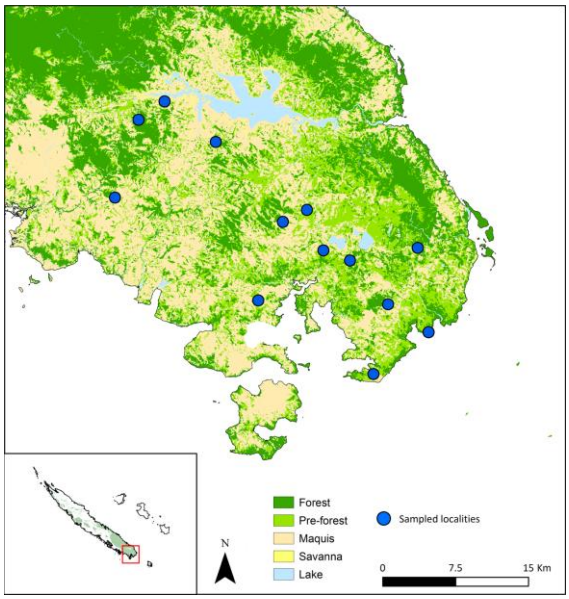

Figure 6.1. *Sampling sites of cricket communities with and without invasive ants (Wasmannia auropunctata and Anoplolepis gracilipes) in the southern part of New Caledonia.*

In the context of an ecological succession to forest on ultramafic soils (3 stages: forest, pre-forest and maquis shrubland), we have chosen 13 different localities spaced by at least 2 kilometers in southern New Caledonia (Fig. 6.1). In each locality, at least 2 plots of 10x10 meters where randomly placed in homogeneous habitat. 24 plots were selected (with eight plots per habitat modality), in non-invaded context (without any major invasive ants present in New Caledonia (*Wasmannia. auropunctata*; *Pheidole megacephala*; *Anoplolepis gracilipes* and *Solenopsis geminata*.24 additional plots were selected with the presence of the little fire ant (*W. auropunctata),* with the same configuration than previously (eight plots per habitat). Regarding *Anoplolepis gracilipes*, our investigation are more preliminary and have been limited to maquis shrublands (4 plots). To define ant invasion status, we used a food baiting protocol (five baits made of tuna and honey placed in the fourth corner and one at the center of each designed plot). We considered that when all baits were colonized by ants, we were in invaded plots. Non-invaded plots were selected when no invasive ants have been baited in the plots

Each habitat selected (forest, pre-forest, and maquis shrubland) were similar about climate, soil (ultramafic) and vegetation, with the same similar low-altitude of 189 ± 83 m (n = 24).

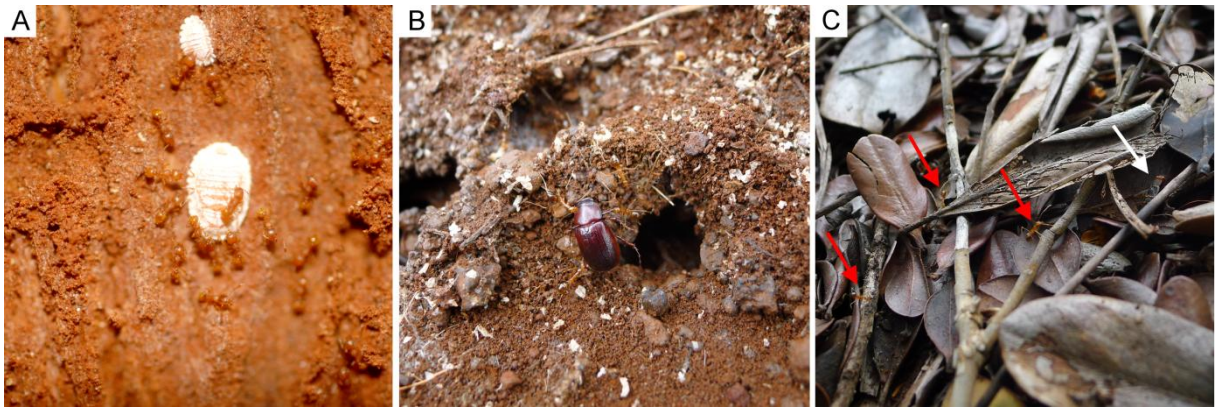

Figure 6.2. *Colony of Wasmannia auropunctata found under tree bark with coccids at Forêt Nord (A); nest entrance of Anoplolepis gracilipes with dead predated Scarabid in invaded maquis shrubland (B); Koghiella flammea adult still active in leaf litter but surrounded by several foraging workers of A. gracilipes (C).*

6.4.2 Sampling method

Cricket communities have been sampled by sight during the wet season between November 2013 and April 2014. Specimens were collected in each selected plots (10x10 m.) under sunny meteorological conditions, by day (between 09:00 to 17:00) and by night (between 19:00 to 00:00). Invaded and non invaded plots were sampled at the same time,. Each plot was sampled ten times (five times during day-time and five times during night-time) during 30 min. Insects were collected in the field with small plastic tubs and then placed into bigger plastic box in order to be killed by vapour pressure of cyanhydric acid. For each insect, time of day, activity (e.g. singing and resting) and microhabitat (e.g. trunk, leaf litter, vegetation, rocks) were noted. After one day, crickets were sorted by morphospecies characters and phenology (adults and nymphs) on polyester plates, in order to dry during two or three days. Then crickets were pin up in the definitive collection boxes with a specific labeling, including the locality, the name of the plot, the time of collect, the preliminary identification, with one unique code

6.4.3 Species identification

All specimens were identified at the species level according to morphological and anatomical characteristics (coloration, shape, male genitalia), including morphometric measures of pronotom length and width, head length, third femora and tibia lenght based on digital photo images using ImageJ 1.4 (Rasband 1997-2011). Occasionally, early stage of nymphs were reared in the lab in order to allow identification of newly emerged imago and to record the calling song if the adult were a male. We used collection specimens in MNHN and all available literature descriptions to validate the identification.

6.4.4 Analysis

Species richness and relative abundances were compared between habitats using the Kruskal-Wallis test followed by the post hoc Dunn test for multiple comparisons (Dunn, 1964), with the Bonferroni correction. All analyses were conducted with R 3.2.2 (R Development Core Team 2012).

6.5 Results

6.5.1 Non-invaded cricket communities

We collected 1035 specimens belonging to 32 species from non-invaded plots (Table 6.2). In forests, 458 specimens belonging to 20 species were collected, with a mean abundance of 56 ± 13 specimens per plot and a species richness of 5.6 ± 2.3 species per plot respectively. In preforests, 414 specimens belonging to 14 species have been collected, with mean abundance of 48 ± 18 specimens per plot and 4.8 ± 1.4 species per plot, respectively. In maquis shrublands, 104 specimens belonging to 7 species have been collected, with mean abundance and species richness per plot of 13 ± 10 and 2.4 ± 1, respectively (Fig. 6.3).

The two most abundant species are *Bullita fusca* and *Agnotecous azurensis* in both forest and pre-forest plots,. In maquis shrubland plots, *Koghiella flammea*, is the most abundant species. This species is absent in forest, but present in preforest with very low contribution to community (very few specimens).

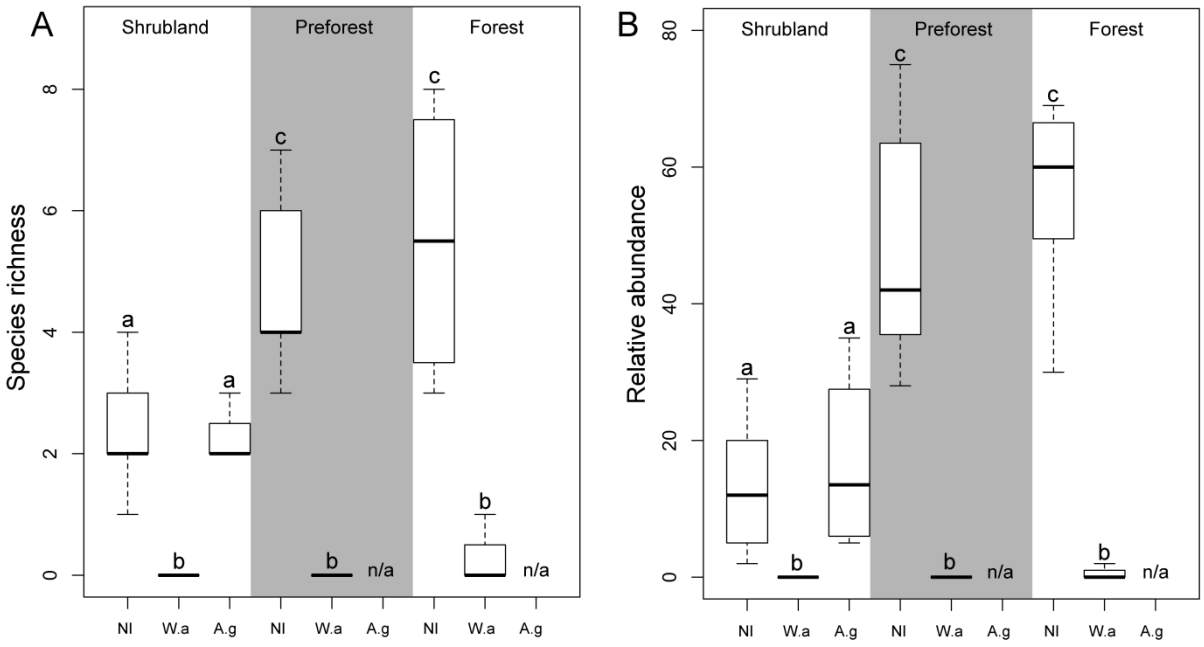

Figure 6.3. *Mean (± SE) species richness (A) and relative abundance (B) of cricket communities in three different habitat type (shrubland, preforest and forest). Abbreviation: NI = non invaded or free from invasive ants; W.a = Wasmannia auropunctata; A.g = Anoplolepis gracilipes; n/a = data not available. Different letter indicate significant differences after a Dunn test ($p < 0.01$) performed after a Kruskall-Wallis test (species richness: $\chi^2 = 41.68$, $p < 0.001$; relative abundance: $\chi^2 = 41.70$, $p < 0.001$).*

6.5.2 Singers versus mute species

Overall species collected in habitat modalities had functional stridulatory apparatus, allowing to produce sound (Table 6.1). Eight species had not stridulatory apparatus, while two species were only known by female which are mandatory wingless. Twelve species in forest, 11 species in preforest and five species in shrubland had stridulatory apparatus (Table 6.1).

6.5.3 Invaded plots by Wasmannia auropunctata and Anoplolepis gracilipes

In invaded plots by *Wasmannia auropunctata*, only three specimens belonging to two species were collected in forested invaded plots (Table 6.1). No crickets were found in preforest and shrubland habitats (Table 6.1). Species richness and abundance in forests were both statistically lower compared to non-invaded plots (Fig. 6.3).

The presence of *Anoplolepis gracilipes*, four species and 67 specimens were collected, with a relative abundance and species richness per plot of 17 ± 14 specimens and 2 ± 1 species, respectively. *Koghiella flammea* was still the most abundant species (75% of total abundance) and was found in all investigated plots (Table 6.1).

Table 6.1. *Abundance of cricket species in non infested and infested habitats by Wasmannia auropunctata and Anoplolepis gracilipes.*

	Non infested			Infested by *W. auropunctata*			Infested by *A. gracilipes*
Species/Morphospecies	Forest (N=8)	Preforest (N=8)	Maquis shrubland (N=8)	Forest (N=8)	Preforest (N=8)	Maquis shrubland (N=8)	Maquis shrubland (N=4)
Adenopterus crouensis			1				
Adenopterus meridionalis	1						
Agnotecous azurensis	142	123		2			
Agnotecous clarus	1	37					
Agnotecous meridionalis	16						
Bullita fusca	186	113					
Bullita mouirangensis	18						
Bullita obscura		70					
Calscirtus amoa	1						
Calscirtus magnus	1						
Caltathra balmessae	2	2					
Caltathra meunieri	17	2					
Kanakynemobius sp	3						
Koghiella flammea		6	89				50
Koghiella nigris	46	3					
Matuanus sp. affinis mirabilis	1			1			
Mogoplistidae sp1		2	1				6
Mogoplistidae sp 2		4	2				
Mogoplistidae sp 3			5				10
Mogoplistidae sp 7	8						
Notosciobia minoris	1	1					
Notosciobia sp1		1					
Notosciobia sp. affinis paranola	1						
Paniella bipuntatus	1						
Pixibinthus sonicus		17	5				

Pixipterus punctulatus			1				1
Protathra nana	1						
Pseudotrigonidium ana	3	4					
Pseudotrigonidium caledonia	1						
Total abundance				3	0	0	67
Total species richness	20	14	7	2	0	0	4

Table 6.2. *List of species identified in non-invaded and invaded plots by ants, with ecological and morphological characteristics.*

Species/Morphospecies	Habitat	Micro-habitat	Stridulatory apparatus
Adenopterus crouensis	Shrubland	Understory	No
Adenopterus meridionalis	Forest	Understory	No
Agnotecous azurensis	Forest/preforest	Leaf litter	Yes
Agnotecous clarus	Forest/preforest	Leaf litter	Yes
Agnotecous meridionalis	Forest	Leaf litter	Yes
Bullita fusca	Forest/preforest	Leaf litter	Yes
Bullita mouirangensis	Forest	Leaf litter	Yes
Bullita obscura	Preforest	Leaf litter	Yes
Calscirtus amoa	Forest	Understory	Unknown
Calscirtus magnus	Forest	Canopy	Yes
Caltathra balmessae	Forest/preforest	Trunks/roots	No
Caltathra meunieri	Forest/preforest	Trunks/roots	No
Kanakynemobius sp	Forest	Leaf litter	No
Koghiella flammea	Preforest/Shrubland	Leaf litter	Yes
Koghiella nigris	Forest/preforest	Bare soil	Yes
Matuanus sp. affinis mirabilis	Forest	Understory	Yes
Mogoplistidae sp1	Preforest/Shrubland	Understory	Yes
Mogoplistidae sp2	Preforest/Shrubland	Understory	Yes
Mogoplistidae sp3	Shrubland	Leaf litter	Yes
Mogoplistidae sp7	Forest	Understory	Yes
Notosciobia minoris	Forest/Preforest	Leaf litter/burrows	Yes
Notosciobia sp1	Forest	Leaf litter/burrows	Yes
Notosciobia sp. affinis paranola	Preforest	Leaf litter/burrows	Yes
Paniella bipuntatus	Forest	Trunks	No
Pixibinthus sonicus	Preforest/Shrubland	Leaf litter	Yes

Pixipterus punctulatus	Shrubland	Understory	No
Protathra nana	Forest	Trunks/roots	Yes
Pseudotrigonidium ana	Forest/preforest	Trunks/leaf litter/understorey	No
Pseudotrigonidium caledonia	Forest	Understory	Yes

6.6 Discussion

6.6.1 Contrasted responses of cricket communities toward ant invasions

New Caledonian cricket fauna is mainly composed by ground-dwelling species and assumed to be sensitive from spreading of terrestrial invasion by exotic ant species (Jourdan 1997; Jourdan 1999) . Cricket communities have responded in drastically different ways according, *Wasmannia auropunctata* and *Anoplolepis gracilipes*,.

In plots invaded by *Wasmannia auropunctata*, five crickets and three species were collected contrary to 1035 crickets and 30 species in non invaded plots. Our results suggest that the presence of this small invasive myrmicine is negatively associated with New Caledonian cricket fauna without ambiguity, and are in agreement with scientific literature which confirms the great detrimental impact on numerous terrestrial invertebrates by *Wasmannia auropunctata* (Lubin, 1984; Le Breton *et al.*, 2003; Walker, 2006), even more for insular species generally considered as naïve toward new predators (Carthey & Banks, 2012). To the best of our knowledge, our study provides the first assessment of a clear detrimental impact of the little fire ant on the cricket fauna (LaPolla *et al.*, 2000; Holway *et al.*, 2002). This pattern was consistent along our three habitat type selected. Forest and preforest held the most suitable bioclimatic and ecological conditions in terms of temperature, humidity, nesting sites and prey availability (Lubin, 1984). In these habitats, ongoing invasions were easily remarkable as numerous leaves and trunks were actively foraged by ants, generally associated with coccids populations (pers. obs.). Numerous colonies with brood were found directly under the litter in forest and preforest. By contrast, ongoing invasions were not as easy as in forest habitat to detect. Shrublands are not as suitable as forest, with higher temperatures, lower humidity, limited nesting sites and resources. Nevertheless, these open habitats which are composed of bare soil and patchy islands of vegetation with leaf litter, were also deprived of cricket species as they are suspected to share the same micro-habitat than invasive ants.

For the case of invasion by *Anoplolepis gracilipes*, only shrublands were considered in this study with relatively high population levels; *A. gracilipes* was virtually absent in forested and preforest habitats. Nonetheless, the impact of *A. gracilipes* on shrublands cricket communities was strikingly different from *Wasmannia auropunctata*, with virtually no impact on crickets. Even these results are preliminary, they indicate a strong contrast between

damaging invasive species, and even more with other regions where *A. gracilipes* hardly impacts the terrestrial fauna (O'Dowd *et al.*, 2003; Lester & Tavite, 2004; Abbott, 2006; Thomas *et al.*, 2010; Misso & West, 2014). As a result, it is possible that *A. gracilipes* is still in a latency phase with impacts yet to be assessed on this peculiar fauna as suggested by Jourdan and Mille (2006). Recently, Berman *et al.* (2013a) have corroborated our findings, suggesting that *A. gracilipes* has no impact on native ants. Though, *A gracilipes* might be also responsible for biodiversity decline, as reported by Bernman *et al.* (2013b) which characterized this invasive ant as a 'back-seat driver' and 'front-seat driver' of biodiversity decline in native ant, in disturbed (burnt) and undisturbed areas (unburnt).

6.6.2 Predation and competition hypothesis between ants and crickets

Wasmannia auropunctata and *Anoplolepis gracilipes* are both defined as the most destructive invasive species for natural ecosystems with, however, very different characteristics which may explain our different responses of New Caledonian crickets. Contrary to *A. gracilipes*, *W. auropunctata* is greatly smaller with higher aggressiveness level, and has the ability to use venomous stings. They both forage on leaf-litter and vegetation, but *W. auropunctata* could establish denser colonies with mass recruitment.

In terms of predation, both invasive ant species may directly impact cricket fauna through predation on eggs laid on various substrates (bare soil, leaf litter, rotten wood). Eggs may constitute a substantial and interesting nutrient intake for ants (Lee *et al.*, 1994; Duhrkopf *et al.*, 2011), and are likely to be preyed with an ongoing invasion (LaPolla *et al.*, 2000), as suggested by Ross (2006) with an egg mortality increased 2.5 fold with ant infestation. Conversely, juveniles and adults crickets are assumed to be a challenging prey for the slow-moving *Wasmannia auropunctata* and the erratic-moving *Anoplolepis gracilipes*. Younger and older crickets demonstrate remarkable escape performance with hundreds of mechanoreceptive cuticular hairs especially tuned to detect wind currents (Magal *et al.*, 2006), with a striking sensitivity (Shimozawa & Kanou, 1984) in their cerci. As a consequence, this particularly efficient air-sensing system, coupled with high evasion ability using hypertrophied hind femora may prevent excessive predation event (Dangles *et al.*, 2006; Dupuy *et al.*, 2011), and rather drive predation toward on slow-moving, dying or smaller arthropods (Human & Gordon, 1997; Holway *et al.*, 2002).

In terms of competition, crickets rely on many and diversified food resources such as flowers, organic matters, eggs, leaves, dead animals which are virtually unlimited in forested habitats. In this way, exploitative competition between ants and crickets is expected to be low and rather oriented on interference competition. The presence of invasive ants might be seen as an increased predation risk which is linked with a decrease of food intake and higher probability of mortality in Orthoptera (Beckerman *et al.*, 1997; Rothley *et al.*, 1997; Schmitz, 1997). Specifically, feeding activity and foraging effort would decrease while evasion behavior increase with the exposure to predators (Danner & Joern, 2003b; Verdolin, 2006), leading to potential negative impact on population dynamics of cricket (Danner & Joern, 2003a; Danner & Joern, 2004). Applied to biological invasion, dense colonies (i.e., *Wasmannia auropunctata*) whose forage on various micro-habitats inhabited by crickets (leaf litter, trunks, rocks, leaves) may act as a persistent stressing agent. Nocturnal and diurnal cricket species are likely to be affected by this ecological pressure as the exotic ants remain active during the circadian cycle (Haines & Haines, 1978a; Clark *et al.*, 1982). As a consequence, we might expect that crickets would increase evasion behavior and undergo more stress and energy consuming allowing less resource in crucial activities, such as foraging, feeding, singing to attract a mate, or copulating. Ultimately, such invasion would tend to decrease population dynamics of crickets in invaded areas, and to push cricket communities out of the expansion range.

6.6.3 Implications in conservation

Across a large cricket monitoring in the southern part of New Caledonia, our findings highlight the dramatic sensitivity of these peculiar fauna to biological invasions, particularly by *Wasmannia auropunctata*. Our study confirms the dramatic impact of this invasive ant in undisturbed and varied habitat type as a ‘front-seat driver’ of biodiversity decline (Jourdan, 1999; Jourdan & Mille, 2006; Berman *et al.*, 2013b). More interestingly, cricket species could be viewed as a promising invertebrate group to assess major ecological stress, such as biological invasion, especially with specific responses according to the species considered. In this way, our findings suggest that densities of *Anoplolepis gracilipes* do not impact cricket fauna at the very moment, confirming a kind of latency phase in New Caledonia (Jourdan & Mille, 2006; Berman *et al.*, 2013a).

In the context of New Caledonian fauna, two-thirds of cricket species are able to produce pure-tone calls, easily identifiable by ears or with acoustic software (Diwakar *et al.*,

2007). This feature, largely shared by most tropical or temperate regions (Riede, 1997, 1998; Diwakar & Balakrishnan, 2007a), open up interesting bioacoustics monitoring which could limit taxonomic impediment for this rich insect group. To conclude, further studies are urgently needed in the light of growing threat by biological invasions, and cricket species should be more studied as a proxy for 'ecosystem health' (Gerlach *et al.*, 2013; Gerlach *et al.*, 2014), providing valuable information for decision makers.

6.7 Acknowledgment

We would like to thank Frédéric Rigault, Léa Colmas, and Alexia Omont who provided help for field work, habitat characterization and for mapping our sampled localities. We are also grateful to Eric Vidal for logistic and funding supports. We thank the Direction de l'Environnement de la Province Sud (DENV), for collecting permits and field sites acess authorisations. This study was partly funded by a phD grant, 'Bourse d'encouragement à la recherche universitaire, attributed to JA by the Government of New Caledonia. Also, we thank the Grand Observatoire du Pacifique Sud (GOPS) for its contribution to funding through the project entitled 'Bioacoustique des grillons de Nouvelle-Calédonie' in the context of their call for proposal 2013.

Chapitre III

Présentation du chapitre sur l'utilisation de l'acoustique passive pour la caractérisation de la biodiversité

Pour communiquer entre eux, de nombreux animaux utilisent des productions sonores (notamment pour la reproduction ou le rassemblement en groupes sociaux) ou la défense de leur territoire. Les animaux peuvent aussi utiliser des sons pour localiser leur proie ou se déplacer dans le milieu par l'écholocation. Par ailleurs, les signaux émis par les animaux sont organisés en unités sonores et émises selon un rythme particulier, qui permettent une identification propre. Aussi, les communautés naturelles rencontrées peuvent être caractérisée par leur signature acoustique, qui résulte de l'activité sonore de toutes les espèces présentes. On parle aussi de bio-acoustique. Ainsi, l'acoustique passive permet d'explorer différentes échelles d'études écologiques : depuis *l'individu*, les *populations*, l'espèce, *Communauté* (souvent dans le contexte de Rapid Biodiversity Assessment (RBA)) ou encore du *Paysage*. Le concept du paysage sonore (soundscape) couple les caractéristiques de l'échelle du paysage (landscapes) et de l'acoustique (Pijanowski *et al.*, 2011a, 2011b, Farina & Pieretti, 2012).

Le paysage sonore est composé de sons issus de l'activité acoustique des organismes ou « biophonie », de sons issus de l'activité anthropique ou « antrophonie » et de l'activité non-biologique ou « geophonie » (Pijanowski *et al*., 2011b).

Par ailleurs, le changement des caractéristiques des habitats peuvent alors agir sur la capacité de ces espèces à interagir ou à se reproduire. Les signaux acoustiques peuvent avoir une propagation altérée (altération de leur structure temporelle et spectrale) et une dégradation de l'information originale portée (identité spécifique, localisation et qualité de l'émetteur) (Wiley & Richards, 1982). Le fond sonore propre à chaque milieu naturel peut également changer, masquant les signaux, et interférant sur la compétition interspécifique au sein de la communauté acoustique (Wollerman, 1999), et/ou en modifiant la visibilité vis-à-vis des autres espèces, notamment les prédateurs (Ryan & Wilczynski, 1991). Si l'altération des milieux est reconnue comme une source majeure d'interférences pour les signaux acoustiques utilisés dans les communautés (Kaiser *et al.*, 2011), l'effet à long terme de ces modifications pour la survie des espèces et la résilience des communautés demeure incertain.

Dans ce contexte, l'enregistrement passif de l'activité sonore permet un accès direct et non invasif aux communautés d'espèces et devient une méthode d'évaluation rapide de la

biodiversité locale, dans la perspective de mettre en place des mesures conservatoires ou répondre à des nécessités sociétales (Sueur *et al.*, 2008, 2012, Depraetere *et al.*, 2012).

Pour tester le potentiel de ces méthodes pour le suivi à long terme et la détection de facteurs responsables de la dégradation des communautés, nous avons travaillé avec les communautés d'orthoptères Grylloidea (grillons) en Nouvelle-Calédonie. Ces derniers constituent l'un des groupes d'insectes dominants dans les écosystèmes forestiers tropicaux, tant par leur diversité que par leur abondance que leur activité sonore principale dans la plupart des milieux naturels en Nouvelle-Calédonie (Robillard *et al.* 2007).

L'espace acoustique néo-calédonien

En Nouvelle-Calédonie, la biophonie qui inclue toutes les productions acoustiques des espèces animales (Pijanowski *et al.*, 2011a), n'a jamais été étudiée d'une manière quantitative. Elle comprend principalement des insectes et des oiseaux, mais également des mammifères introduits (cerf, chat par exemple) qui ne participent que très ponctuellement et minoritairement à la biophonie générale, avec une seule espèce introduite d'amphibien, *Litoria aurea* Lesson, 1827, connue à ce jour (Bauer & Sadlier, 2000; Pyke & White, 2001).

D'une manière générale, la biophonie de la Nouvelle-Calédonie possèdent donc les mêmes caractéristiques que d'autres régions tropicales, avec les insectes et les oiseaux représentant la principale source de signaux acoustiques (Riede, 1997; Nischk & Riede, 2001; Diwakar & Balakrishnan, 2007a; Jain *et al.*, 2014), mais avec cependant l'absence de communauté d'amphibiens, qui participent activement à la biophonie d'autres régions tropicales (Hsu *et al.*, 2006; Bardier *et al.*, 2014; Heard *et al.*, 2015).

Caractéristique de la biophonie néo-calédonienne

Parmi les espèces émettrices de signaux acoustiques, les oiseaux représentent plus de 109 espèces sur l'archipel (Beauvais *et al.*, 2006) ; ils émettent leurs productions sonores principalement de jour, et les concentrent à l'aube et au crépuscule. Les oiseaux sont actifs toute l'année et ne présentent pas de saisonnalité marquée sur le territoire.

La biophonie néo-calédonienne est également marquée par la diversité et l'abondance des insectes (Fig. 6.4). Ainsi, plusieurs groupes d'invertébrés sont responsables à des degrés divers de la biophonie selon des cycles temporels différents et particuliers, comme les orthoptères (grillons, les sauterelles, les criquets) ou encore les cigales. Les cigales

représentent un groupe majeur et emblématique du territoire calédonien et de sa biophonie, avec plus de 45 espèces décrites (Boulard, 1988; Boulard, 1991, 1992, 1993, 1997; Delorme *et al.*, 2015) produisant des signaux acoustiques variés avec des fréquences comprises entre 2 et 10 kHz (Bennet-Clark & Young, 1994; Sueur, 2002), de jour principalement, crépusculaire ou même nocturne. Ce groupe présente une forte saisonnalité avec des espèces majoritairement actives en saison chaude et humide (de novembre a mars-avril selon les années) lors de l'émergence des adultes (i.e., de décembre à février). Les grillons représentent un groupe majeur dans la composition de la biophonie de l'archipel. Avec plus de 150 espèces décrites, une part importante de ces espèces produisent des signaux sonores par stridulation élytrale toute l'année et durant toutes les heures de la journée (Alexander et al. 1987 ; Desutter 1997 ; Desutter *et al*. 2002 ; Robillard *et al.* 2006, 2010). Bien qu'aucune étude précise sur le rôle de ce groupe dans la biophonie n'a été réalisé, les nombreuses observations sur le terrain et les premières données sur les ambiances sonores du territoire suggèrent une forte domination de ce groupe, principalement de nuit. La faune acoustique de grillons de Nouvelle-Calédonie produit des chants très variés tant au niveau de la structure temporelle que spectrale, avec des fréquences d'émissions comprises entre 3 et 35 kHz.

Les sauterelles participent également aux ambiances sonores néo-calédoniennes, mais à moindre mesure et sans saisonnalité prononcée, possédant une diversité d'espèces chanteuses moins importante que les groupes précédemment considérés. Les sauterelles sont principalement actives de nuit, avec des émissions acoustiques éparse de jour.

D'une manière générale, la biophonie néo-calédonienne est marquée par le cycle journalier : les oiseaux seraient le groupe dominant durant la journée, tandis que les insectes domineraient la biophonie de nuit.

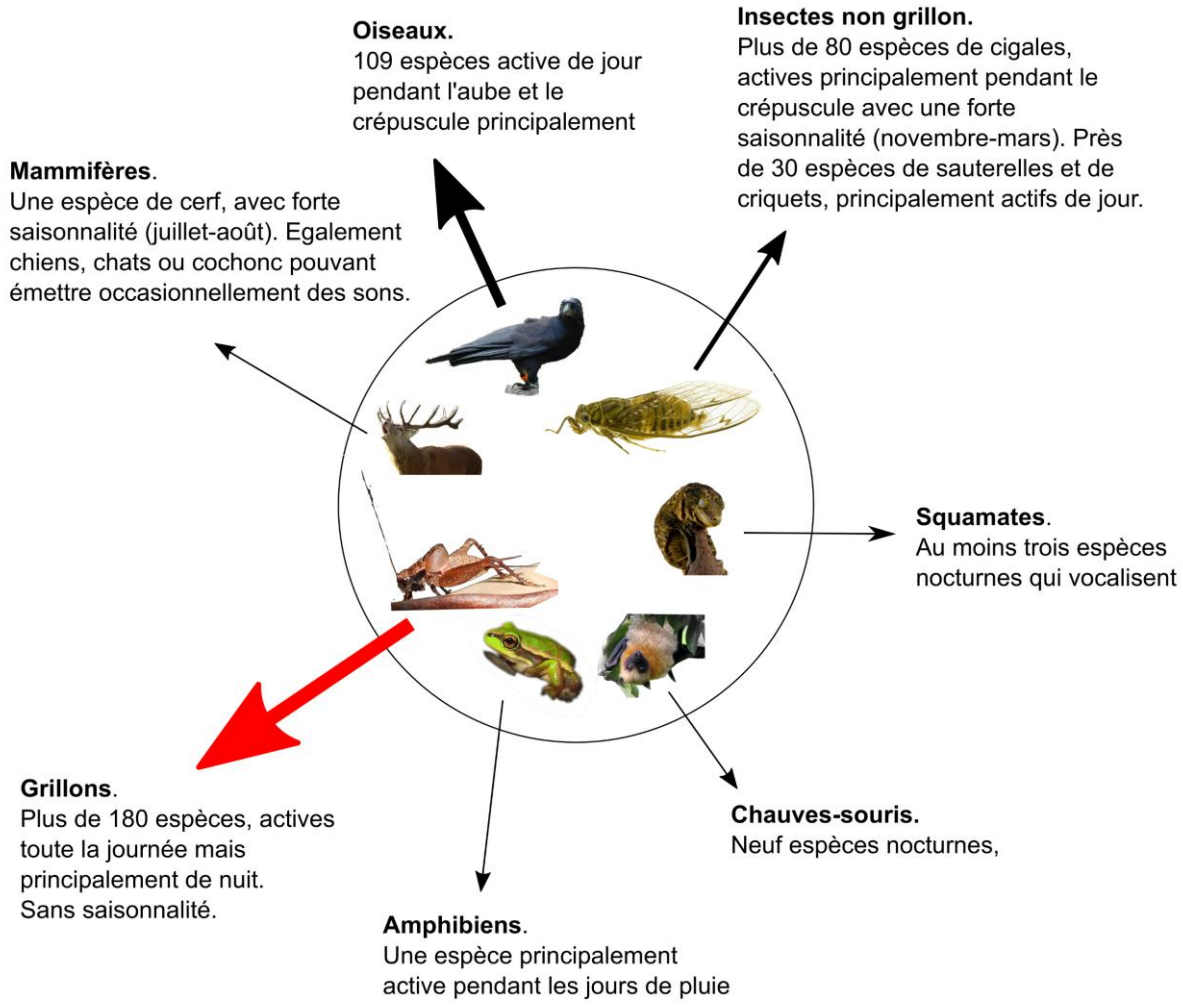

***Figure 6.4**. Biophonie de la Nouvelle-Calédonie avec les principaux groupes qui émettent des productions sonores.*

Méthodologie : acquisition des données acoustiques

Les communautés acoustiques des grillons du sud de la Nouvelle-Calédonie ont été enregistrées dans les différentes modalités étudiées : (1) dans un gradient de perturbation de l'habitat et (2) en fonction de la présence de fourmis exotiques envahissantes, à l'aide d'enregistreurs automatiques (Song Meter) commercialisés par Wildlife Bioacoustics. Un enregistreur est placé dans chaque modalité, sur un tronc à 1.50 m de hauteur, avec 200 m d'espacement entre eux au minimum. Le boîtier est fixé par des câbles en fer en veillant à bien conserver l'étanchéité du système (qui supporte des pluies tropicales fortes). 2 microphones sont installés pour chaque boîtier, l'un directement sur l'enregistreur à 1.50 m et

le second au niveau de la litière pour favoriser l'échantillonnage acoustique des espèces de litière qui émettent des chants de faible intensité. Nous avons à notre disposition deux versions des enregistreurs de Wildlife Bioacoustic : des SM2 et SM2+, ces derniers étant la dernière version commercialisée. Afin d'éviter un biais d'échantillonnage entre les deux versions, nous avons placés 2 appareils de chaque version pour chaque modalité. Les boîtiers offrent de bonne performance d'échantillonnage et une bonne autonomie (4 piles LR 20), jusqu'à 20 jours d'enregistrement. Les boîtiers automatiques ont été configurés pour enregistrer 2 minutes d'ambiance sonore toutes les 28 minutes, avec une fréquence d'échantillonnage de 48 kHz (audible). Pour chaque enregistreur, les coordonnées satellites ont été renseignées avec l'acronyme d'identification de la localité (par exemple GK pour « Grand Kaori ») et ont été testé en laboratoire pour vérifier l'état de bon fonctionnement. Les fichiers sonores ont été générés en « WAC » afin d'augmenter le volume disponible (au lieu du « WAV » plus classique) pour être ensuite transformés en « WAV » à l'aide du logiciel Kaléidoscope fournit par Wildlife bioacoustic. Nous avons choisi le format « WAC » car celui-ci de détériore pas la qualité du signal (par compression notamment).

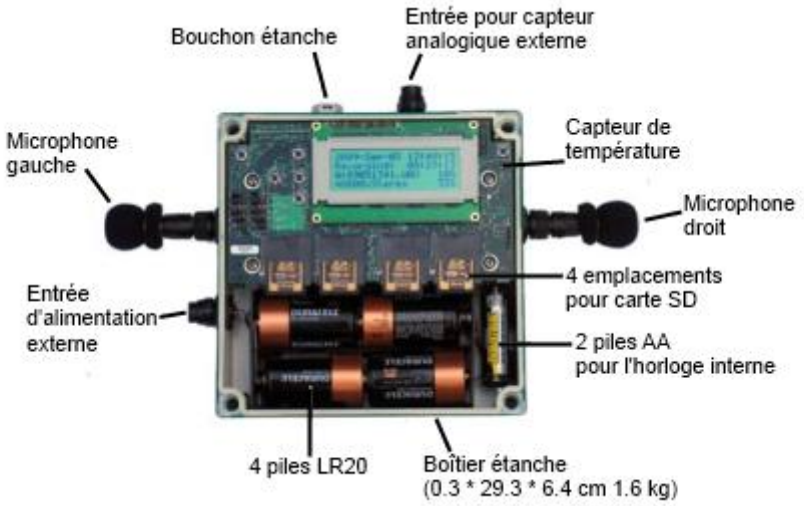

Figure 6.5. *Illustration d'un boîtier enregistreur automatique (SM2) utilisé pour l'acquisition des données acoustiques dans le sud de la Grande Terre (adapté de Le Gaillard, J-L., Guarini, J-M. and Gaill, F. (2012) Sensors for ecology. CNRS, Paris. Chapter 1: Global estimation of animal diversity using automatic acoustic sensors. Jérôme Sueur, Amandine Gasc, Philippe Grandcolas, Sandrine Pavoine)*

Tous les enregistreurs ont été accompagnés d'une sonde thermo-hygrométrique qui réalisait un relevé de la température et de l'humidité toutes les 5 minutes. Une fois l'enregistreur installé puis configuré, et la sonde installé, les cartes mémoires (16 Go pour les SM2 et SM2 + et 32 Go pour les SM2+) ont été vidées 4 à 6 jours plus tard pour contrôler d'une part le bon fonctionnement de l'appareil (le niveau des piles, la qualité de l'enregistrement, le fonctionnement des deux microphones, l'espace disponible des cartes mémoires SD) et vider les cartes sur un ordinateur de terrain. La date et l'heure de la visite ont été notées pour exclure dans les analyses ultérieures le fichier parasité par les voix et les manipulations des membres de l'équipe.

7 Suivi de la biodiversité par l'analyse globale des ambiances sonores: détection d'une invasion terrestre silencieuse par la fourmi *Wasmannia auropunctata*

Cette section fait l'objet d'un article de recherche en préparation pour *Journal of Applied Ecology*, sous la forme suivante :

†Gasc, A., †**Anso, J**., Desutter-Grandcolas, L., Sueur, J., Jourdan, H. Monitoring ecosystems facing invasive species spread using innovative acoustic tools: When soundscape turn to silence facing invasive ant spread. En preparation pour *Journal of Applied Ecology*.

† Premiers auteurs de cette publication.

Communications Internationales

Anso, J., Gasc, A., Desutter-Grandcolas L., Vidal, E., Jourdan, H., Sueur, J. Meta-acoustic approach of cricket communities to detect biological invasion by exotic ants. – oral presentation First Ecology and Acoustics meeting, Paris, France, 16-18 June 2014.

Gasc A., Pijanowski, B., **Anso J.**, Jourdan H., Sueur J., and Desutter-Grandcolas L. Soundscape measurements to evaluate impacts of habitat degradation on acoustic animal communities. – Oral presentation First Ecology and Acoustics meeting, Paris, France, 16-18 June 2014.

Gasc A., Pijanowski, B., **Anso J.**, Jourdan H., Sueur J., Jung J. and Desutter-Grandcolas L. Soundscape measurements to evaluate disturbance impacts on natural ecosystems. – oral presentation International Association for the Landscape Ecology meeting, Anchorage, Alaska, 18-22 May 2014.

7.1 Résumé

1. Dans le contexte de la crise actuelle de la biodiversité sous la pression des changement globaux anthropiques, prioriser les milieux naturels les plus à risques est un enjeu de conservation majeur pour les scientifiques et les décideurs/gestionnaires de l'environnement. L'approche d'acoustique globale est souvent décrite comme intéressante pour le suivi écologique à long terme sur d'importantes superficies. C'est une méthode rapide, non-invasive et automatique, basée sur l'utilisation d'enregistreurs acoustiques passifs et du calcul automatique d'indices,. Nous avons testé la capacité de cette méthode dans une problématique concrète de conservation dans un hotspot de biodiversité : détecter la présence d'une fourmi envahissante majeure, *Wasmannia auropunctata* (Roger 1963), en Nouvelle-Calédonie.

2. Les ambiances sonores ont été enregistrées pendant 2 minutes toutes les heures pendant 15 jours (n=24 sites) dans trois stades différents au sein d'une succession écologique forestière sur sols miniers– des maquis arbustifs, des maquis paraforestiers et des forêts denses humides – avec et sans la présence de la fourmi invasive. Plusieurs indices de diversité acoustique (dont le nombre de pics fréquentiels, NP) ont été mesurés et confrontés à des inventaires taxonomiques classiques.

3. Nos résultats indiquent une signature spécifique pour chacun des trois stades de la succession et une baisse significative de la diversité acoustique des ambiances sonores, en particulier nocturnes dans les sites envahis par *Wasmannia auropunctata*. La présence de *W. auropunctata* altère le paysage sonore avec une baisse de la diversité d'espèces chanteuses et du nombre global de chants émis dans tous les stades écologiques.

4. Synthèse et applications. Notre étude démontre l'efficacité de l'enregistrement et de l'analyse des paysages sonores à l'aide d'indice de diversité pour détecter une invasion biologique en cours. Cette approche globale d'acoustique permet de réaliser une surveillance en temps réel, d'une manière passive et non-invasive des écosystèmes d'intérêts, apportant des informations stratégiques pour la gestion des écosystèmes naturels. Ce type de méthode apparaît prometteur pour le développement d'outils de suivi simples pour détecter des perturbations écologiques majeures telles que les invasions biologiques, notamment pour les services en charge de la gestion de l'environnement.

Mots clés : Indice de diversité acoustique, écologie acoustique, biologie de la conservation, invasion biologique, communauté acoustique, paysage sonore.

7.2 Abstract

1. Increasingly strong biotic pressures from global change urge scientists and decision-makers to prioritize areas of interest for conservation. The global acoustic approach, a rapid, non-invasive and automatic method based on acoustic recorder units and automatic indices calculation, is claimed to be an attractive method for long-term ecological monitoring on large spatial areas. We tested the ability of this method to help in the detection of natural area disturbance in a concrete conservation issue: the major invasive ant species *Wasmannia auropunctata* (Roger 1963) in the hotspot and pacific Island of New Caledonia.

2. Acoustic ambiances were recorded every hour during 15 days on sites (n=24) at three successional stages – shrubland, preforest and forest – with and without the presence of invasive ant. Acoustic diversity indices (i.e. number of frequency peaks or *NP*) were measured and confronted to classical taxonomic inventories.

3. Our results show a specific acoustic ambient for each successional stages and a significant reduction in acoustic diversity, especially in night-time ambient sound recorded on sites invaded by *Wasmannia auropunctata.* Night-time ambient sounds are heavily reduced as the impact of *W. auropunctata* leads to a decrease of both singing species and calls in all ecological stages.

4. *Synthesis and applications*. Our study provides the first experimental approach which demonstrates that ambient sound produced by living species can be recorded and processed through acoustic indices to reveal ongoing biological invasion. This global acoustic approach ensures a non-invasive and passive biodiversity surveillance in real time, bringing valuable information for immediate decisions to preserve natural ecosystems.

Keywords: acoustic diversity index, acoustic ecology, conservation biology, biological invasion, acoustic community, soundscape.

7.3 Introduction

Invasive species are one of the most distressing threats for native ecosystems, including terrestrials and marines ecosystems (Mack *et al.*, 2000; Molnar *et al.*, 2008; Simberloff *et al.*, 2013). Insular ecosystems appear to be more vulnerable from introduced species than continental ones (Vitousek *et al.*, 1997), with even more dramatic impact as these areas contain a large number of endemic species (Walsh *et al.*, 2012). Pacific islands such as New Caledonia are described as biodiversity hotspot with the highest level of endemism for a terrestrial region, two components which can emphasize negative impact of introduced species (Myers *et al.*, 2000; Kier *et al.*, 2009). To date, New Caledonia is infested by numerous invasive species, especially by three exotics ants which are ranked by the IUCN as ones of the most harmful species in the world (Lowe *et al.*, 2000). Negative impacts of *Pheidole megacephala (Wetterer, 2007)*, *Anoplolepis gracilipes* (Bos *et al.*, 2008) and *Wasmannia auropunctata* have been previously documented on native fauna and flora, with specific attention for the last one, considered as the greatest threat for New Caledonian biodiversity (Jourdan, 1997; Jourdan *et al.*, 2000; Jourdan *et al.*, 2001) and one of the most harmful for terrestrial biodiversity (Lowe *et al.*, 2000).

Three strategies against invasive species are classically defined: (i) prevention, with quarantine or legislation measures to prevent introduction of exotic species; (ii) early detection, with interception, early removal or monitoring and surveillance; and (iii) management, with eradication or control when introduced species are well established. In this way, early detection of invasive species is considered as a cost-effective tradeoff for the management of this serious threats (Harris & Timmins, 2009; Simberloff *et al.*, 2013). Current detection methods of invasive often involved intensive and expensive field works, complicated to accomplish in dense-forested areas and mountainous relief, just as found in New Caledonia. Regularly, introductions of exotic species are passively detected by non-experts (Wilson *et al.*, 2004). Also, new innovative methods are deployed in this major field of interest, with, for example, aerial surveying for fire ants (*Solenopsis invicta*) with infrared and thermal camera system, helped by odor detection dogs on the ground (Eradication program in Australia, Department of Agriculture and Fisheries; https://www.daf.qld.gov.au/plants/weeds-pest-animals-ants/invasive-ants/fire-ants/national-red-imported-eradication-program/fire-ant-eradication.)

In response to the growing need of complementary methods to detect invasive species, passive acoustic recordings become increasingly attractive and efficient to study biodiversity, as they are non-invasive, allow automatic surveys on large temporal and spatial scale, and can simultaneously record several taxa (Acevedo & Villanueva-Rivera, 2006; Furnas & Callas, 2014). Such acoustic recordings allow experts and non-experts to identify species directly by ear (Raghuram *et al.*, 2014), helped by the growing acoustic database available and considerably speed up by spectral visualization of sound (Truskinger *et al.*, 2013). Recent advances in automatic analysis of songs allow scientist to process large samples, with high recognition rates (Wimmer *et al.*, 2013; Potamitis, 2014), as well as for invasive species (Kottege *et al.*, 2015). Automatic recognition is efficient for well-defined songs, in relatively simple to moderate acoustic environment or soundscape, with low overlapping signals between different emitters (Obrist *et al.*, 2010). As a result, passive acoustic analysis could be perform at higher level than individual or species, relying on rapid acoustic survey to estimate local diversity or specific stress (Sueur *et al.*, 2008).

Biological sound emitted in a specific time and space could be entirely processed through soundscape (i.e. sonic environment) analysis, without any species identification, by quantifying the global complexity of the acoustic community output. Body of convincing evidences has linked acoustic complexity of a soundscape recording with local biodiversity (Sueur *et al.*, 2012), changes in animal communities (Lellouch *et al.*, 2014), also with the number of singing species (Depraetere *et al.*, 2012) or with the number of vocalizations or song types (Pieretti *et al.*, 2011). Recent application of this global acoustic method has indicated the ability to distinguish sites with the same high level of biodiversity with different structure and composition (Gasc *et al.*, 2013). These preliminary results suggest that global acoustic method could be seen as an innovative alternative to traditional inventories and cost-effective for speed-up environmental and biodiversity monitoring. Such a tool could reveal changes in animal species composition induced by external disturbance and help in the conservation of large protected area.

The aim of the present study is to test the ability of the global acoustic method to detect the presence of one major invasive ants species *Wasmannia auropunctata* (Hymenoptera: Formicidae) under natural conditions, in the actual conservation context of the insular biodiversity hotspot of New Caledonia. To carry out this research, sites representing a typical vegetation succession – low sclerophyllous shrubland corresponding to an early successional stage called ‘maquis minier’, edge forest corresponding to an advanced stage

called ‘preforest’, and a final stage called ‘forest’ – and, sites invaded or un-invaded by *W. auropunctata* were monitored using passive acoustic recorders. On each recording, deeper human-based analyses to identify and describe the main acoustic groups of singing species and, global acoustic analysis through the measure of acoustic diversity index (i.e. Number of frequency Peaks or *NP* index) were processed and compared. The interpretation of such findings provided new highlights for the use of global acoustic method in concrete conservation issues, regarding biological invasion.

7.4 Material and methods

7.4.1 Study sites

Twenty-four sites were selected in the southern part of the New Caledonian main island, located in the South-West Pacific Ocean. Using manual inventories on site, twelve sites were classified as “invaded” by *W. auropunctata* and twelve others were classified as “un-invaded” by any invasive ants present in New Caledonia – *Wasmannia auropunctata*; *Pheidole megacephala*; *Solenopsis geminata* and *Anoplolepis gracilipes* – (for protocol details, see Anso *et al*. (section suivante). Among each category, “invaded” and “un-invaded”, three different types of habitats representing a classical forest succession were selected: four sites in forests; four in preforests; and four in maquis were selected following a rapid field survey of botanical conditions to ensure the assignation to a successional stage for each selected plot. All Sites (n = 24) shared comparable conditions in term of climate and soil (ultramafic-rocks), at low-altitude (189 ± 83 m). The geographic coordinates of the sites are available in the Table S1.

7.4.2 Acoustic sampling by automated sensors

One automatic recorder (weather resistant SongMeter SM2 and SM2+ (Wildlife Acoustics, concord, NY, U.S.A.)) was placed on each selected site. To avoid bias between recent and older versions of acoustic sensors, we have placed the same number of SM2 and SM2+ for each modality (see Table S1). Each acoustic sensor (both SM2 and SM2+) were equipped with two omnidirectional microphones (frequency response: −35±4 dB between 20 Hz and 20 kHz) oriented horizontally, one at a height of 1.5 m, and the second at a height of 30 cm (Figure 7.1). Acoustic recordings were realized for 2 minutes every 28 minutes and

digitized at a sampling frequency of 48 kHz. Files were stored in the lossless compression format *.wac* and transformed into *.wav* with the software Kaleidoscope version 1.1.20 (Wildlife Acoustics, concord, NY, U.S.A.). Acoustic sensors were configured to record two minutes every half-hour leading to a total of 25,512 files. Thermo-hygrometric sensors (Hobo) were attached on tree (0.7 m) near acoustic sensors. Temperature and humidity were collected every five minutes.

In case of closed sites, a minimum of 200 meters was respected between two recorders to avoid detection overlap. Recordings were collected from 17 October 2013 to 16 December 2013.All files were checked examined to discard files with rain, anthropogenic and wind noises, in order to avoid bias for further analysis. Final database resulted in a selection of 14,455 files.

Figure 7.1. *Acoustic sampling in the field using automated recorded. White arrows indicate microphones, one directly plugged on the sensor at 1.5 meters and the other remaining at 30 centimeters above ground on vegetation. Red arrow indicate thermo-hygrometric sensor attached on vegetation above the ground*

7.4.3 Acoustic measurements on field recordings

In order to measure the global acoustic complexity of the recordings, ten acoustic diversity indices the acoustic diversity (see Table1 for the references associated to each of them) were calculated for each of the 14,455 recording collected. Given the results of a first analyses the index called *NP* for "Number of frequency Peaks" was selected for the rest of the analyses. This index, developed by Gasc *et al.* (2013) in New Caledonia, count the number of major frequency peaks obtained with the analysis of the mean spectrum of our recordings. It has been related to a level of acoustic activity defined in Gasc et al. (2013) as a number of different song types. The *NP* index was calculated using the function 'fpeaks' of the package *Seewave* (Sueur et al. 2008b) under the software R (R Core Team 2013). The parameters used for the peak detection on the mean spectrum are amplitude setting equal to 1/90 and frequency setting equal to 200hz.

7.4.4 Analyses

To confirm the ability of the indices to reveal cricket community acoustic activity, we compared the results obtained with the ten acoustic diversity indices with the results found with other methodology. On the recording level, we compared the results obtained with the acoustic diversity indices and the aural identification by calculating a Pearson coefficient correlation between the two types of measurement on the same subsample of recordings, based on the one used for the aural identification. On a site level, a comparison of the three methodologies: global acoustic indices, diversity values from the species identification and the taxonomic inventory was processed by calculated pair-wise Pearson correlation coefficient between the methodologies results.

The temporal variation of the acoustic activity in New-Caledonian animal community has been highlighted in previous papers (Gasc *et al.*, 2013, Anso *et al.* section suivante). To confirm this pattern in the different conditions studied here, we looked at the daily variation of the acoustic diversity index *NP*. This analysis confirmed the necessary separation of the day and night time for comparison tests between conditions.

In order to test if the acoustic diversity is significantly different in the presence of the invasive species under different environmental conditions (night/day; invaded/non-invaded; forest/pre-forest/maquis) we run a non-parametric Mann-Whitney test on the *NP* values measured on the recordings collected for the different modalities.

7.5 Results

7.5.1 Daily pattern differences in acoustic diversity

The overall acoustic diversity in un-invaded sites showed a clear daily pattern for each habitat (Fig. 7.2, plain lines). The daily pattern in forest and preforest were closely similar, with the highest and lowest acoustic activity during night-time and day-time respectively. In maquis, the reverse pattern was observed with the highest acoustic diversity measured during day-time, close to dawn and dusks chorus. The lowest acoustic activity was observed during the night-time in maquis sites.

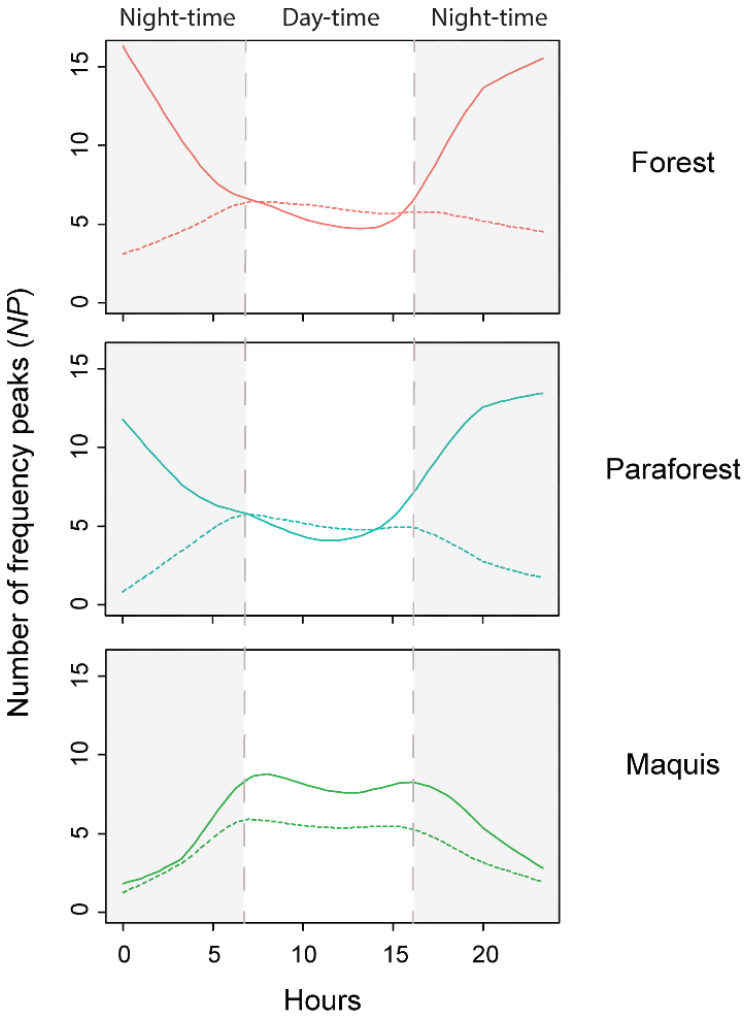

Figure 7.2. *Daily variation of the acoustic diversity index called Number of frequency Peaks (NP). The lines represents the results of a locally-weighted polynomial regression (LOWESS,*

smoother span = 1/3) of the NP index calculated from recorded collected in un-invaded sites (plain line) and in invaded sites (dashed line).

7.5.2 Comparison of acoustic activity between invaded and un-invaded sites.

The comparison of the curve obtained for un-invaded sites (Fig. 7.2, plain lines) and invaded sites (Fig. 7.2, dashed lines) suggested that daily pattern of acoustic diversity were strongly different for invaded sites by the little fire ant *Wasmannia auropunctata*. In all invaded sites, this daily pattern was also closely similar throughout habitats and almost represented by flat responses (dashed lines, Fig. 7.2). Differences in *NP* values were highest in forest and preforest during night-time, whereas the difference in maquis was less obvious. The daily pattern of acoustic activity in invaded maquis was close than in un-invaded ones, but with a lower magnitude of the *NP* index. These observations confirmed by the statistical test comparing the overall differences between invaded and un-invaded acoustic diversity at night-time (Fig. 7.3). The Mann-Whitney statistical test results are significant for the three habitats (*p-value* > 0.001). Moreover the values distributions of *NP* illustrated by the boxplots show a higher difference for the forest and preforest habitat than for the maquis habitat.

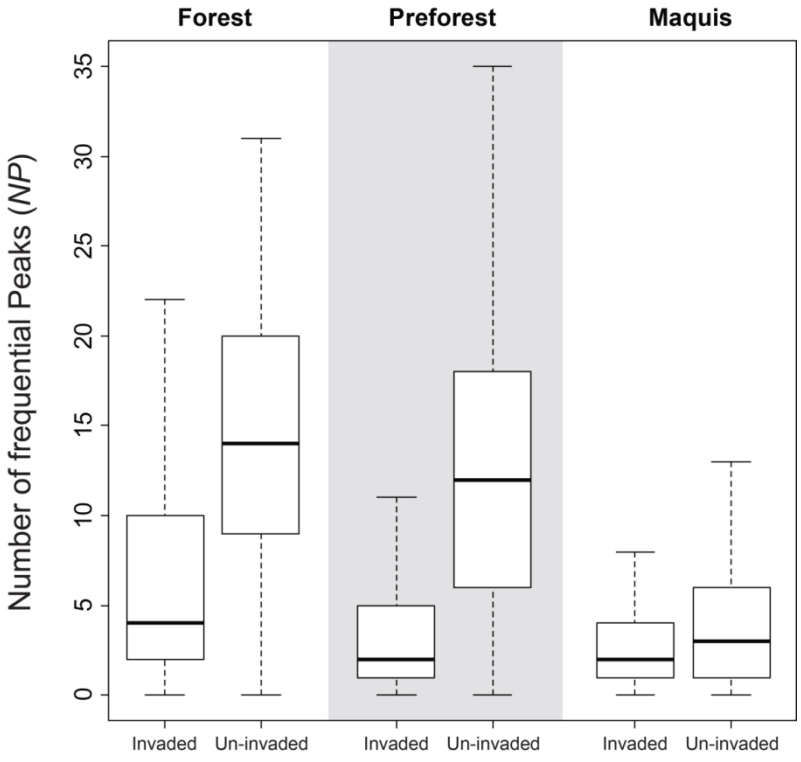

Figure 7.3. *Number of frequency peaks for invaded and un-invaded sites. The comparison of the NP values has been done independently for the three types of habitats: forest, preforest and maquis. The NP values presented in this figure has been measured on night-time recordings only.*

7.5.3 Correlations between acoustic diversity index and calling cricket community.

Among all correlations between acoustic diversity indices and descriptors of cricket community, *NP* index showed the higher correlation coefficients (Table 7.1). Overall correlations between the acoustic diversity index *NP* and the calling cricket parameters (i.e. calling species richness, number of calls and Shannon index) were positively and statistically correlated for each habitat ($p < 0.001$, Pearson's coefficient correlation) (Fig. 7.4). The correlation coefficient calculated between the index *NP* and the number of species identified by listening are equal to 0.53 in the forest habitat, 0.36 in the preforest habitat and 0.52 in the maquis habitat, knowing that the number of species identified in the recording in maquis do not go up to 5 whereas the maximal number of species identified in one recording is 7 in forest and 8 in preforest. The correlation coefficient calculated between the index *NP* and the number of vocalization per recording counted by listening is overall lower with values of 0.17, 0.27 and 0.33 for respective the habitat forest, preforest and maquis. The correlation coefficient calculated between the index *NP* and the Shannon index per recording are 0.49, 0.34 and 0.55 for respectively forest, preforest and maquis habitats. It is interesting to notice that the Shannon values equal to zero correspond to animal community composed of 0 or 1 species and that for this value, the *NP* index values are mostly low but show an interesting variation. This would be discussed in terms of other taxon activity such as grasshoppers that in absence of cricket become the dominated taxon of the acoustic space.

Looking at both the correlation coefficient value and the shape of the relationship, the relationship between number of species and number of frequency peak seems to be the stronger relationship.

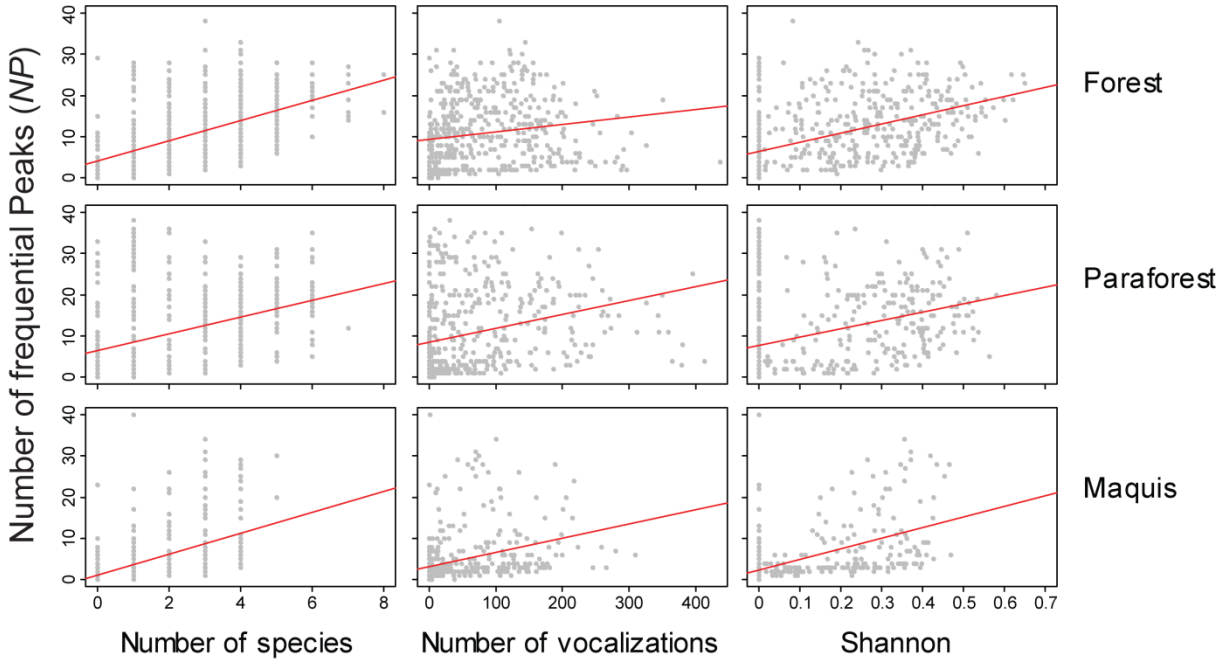

Figure 7.4. *Relationship between the acoustic diversity index called Number of frequency Peaks (NP) and the three descriptors of the nocturnal cricket community: the number of species identified, the number of vocalization per species and the Shannon index measured from the two first descriptors. The plain line represent the linear model explaining fitting the index values by descriptor values. This relationship has been independently investigate for the three type of habitat studied: the forest, the preforest and the maquis. The values presented in this figure has been measured on night-time recordings only.*

7.6 Discussion

7.6.1 When soundscapes become silent

Soundscapes are highly variable from one ecosystem to another (Bormpoudakis *et al.*, 2013). Some soundscapes can be naturally silent in isolated places with low biological activity and low exposure to weather events. However, silence or reduction in soundscape complexity in usually acoustically-rich areas, such as in tropical forests, might be regarded as a warning of local change in ecosystem (Lomolino *et al.*, 2015). The findings of this research demonstrated that the nocturnal soundscape characteristics can be used as a strong indicator of the presence of *Wasmannia auropunctata* in the New Caledonian forest and preforest habitat,

one major invasive ant. In these two habitats, the soundscape complexity is significantly reduced in the presence of the invasive ant based on the Number of frequency Peaks index (*NP*) (Gasc *et al.*, 2013). Moreover, the major finding of this paper is that the rapid acoustic survey – defined as the application of acoustic diversity indices on massive recording data collection – is efficient in revealing these differences. The results presented in the present paper are interpreted with respect to two previous surveys conducted on the exact same sites: 1) the strong negative impact of *W. auropunctata* on cricket community composition as described in detail by Anso *et al.* (unpublished data) and 2) the subsequent negative impact of *W. auropunctata* on the calling cricket community described by manual acoustic identification of calls (Anso *et al.* unpublished data).

The daily pattern of the soundscape complexity is found to be higher at night-time for forest and preforest habitat as supported by previous studies in New Caledonia (Gasc *et al.*, 2013) and in other tropical forest areas (Pieretti *et al.*, 2015). Moreover, based on previous results, the natural soundscapes of New Caledonia are dominated by birds in the day-time and crickets in the night-time in the three habitats studied – up nearly 90% of night-time vocalizations have been counted as cricket calls (Anso *et al.*, section suivante). The significant difference in the value of the *NP* acoustic diversity index between invaded sites and un-invaded sites is likely explained by the negative effect of *Wasmannia auropunctata* on the whole fauna. The presence of *W. auropunctata* appears associated with a great decrease in number of vocalizations of singing species and a disappearance of several song types, as a consequence of the disappearance of peculiar leaf litter-dwelling singing species, strikingly more vulnerable than perched species (Anso *et al.*, Chap. II), especially among crickets.

7.6.2 The strength of the global acoustic method

A fine monitoring of cricket community can be used as an indicator of the presence of *Wasmannia auropunctata* with subsequent potential negative impacts on insect communities, using either taxonomic or acoustic inventories (Anso *et al.*, Chap II). Unfortunately, the former methodology requires taxonomic expertise and extensive, time-consuming field work. Based on the classic taxonomic inventories conducted in Anso *et al.* (Chap II), we estimate that this methodology required a minimum of 15 days in the field and 30 days in the lab considering the 24 sites studied. Similarly, we estimate the time necessary to describe the cricket community based on the identification of acoustic signals in field recordings to be at least six days for the recording steps (given a schedule of two minutes of recording every half

an hour) plus another six days for the identification process. This former methodology requires also a specific knowledge on species-specific calls, with however lower impediments than taxonomic inventories. Alternatively, the global acoustic method required six days of automatic recordings in the field and three days of automatic computation (system configuration: 8 Go RAM) that require relatively less human effort and time. Moreover, the computational tools are implemented in packages developed for the free and open source R software, unlocking these analyses for limited budget programs. Additionally, new technologies offer the possibility to record soundscapes using cheap but efficient acoustic recorders (Farina *et al.*, 2014). Considering limited time and financial resources available to natural area managers, the global acoustic method might be advantageous. To manage small and highly mobile invasive species, managers need a methodology that can: 1) be applicable for both small and large protected areas across large spatial scales and 2) be repeated regularly in order to monitor changes. In the case of New Caledonia and the invasion of *W. auropunctata*, the global acoustic method presented here represents an early warning of the arrival of the ant in a protected site. However, the global acoustic approach must be validated by one of the other methods during a preliminary short-term study before being applied for a long-term study.

7.6.3 Concrete application in the field: Needs and limitations

As demonstrated in the present paper, the global acoustic method might be viewed as an efficient tool to detect the presence of the small, silent and cryptic invasive ant *Wasmannia auropunctata*, which is recognized world-wide as a major terrestrial plague for ecosystem functioning (Lowe *et al.*, 2000; Lach & Hooper-Bui, 2010).

This indirect approach to detect one biological invasion was successfully applied in all habitats considered. These findings provide important insight for two habitats of interest, forest and preforest with high conservation value. Imperatively, preliminary survey based on soundscape recordings and analyses should be performed under undisturbed environment, as a calibration and baseline for all future comparisons between different localities. This soundscape composition could be described by identifying the species singing, but also the different song types knowing that some species can have an acoustic repertory of vocalizations. This preliminary survey should be used to explore: 1) the best location for the automatic recorder to be set up (an automatic recorder is to date the most efficient tool to capture the entire variability of the soundscape of a location), 2) the time schedule of the

recordings along the day and the period of the collection – months or years, and 3) the number of recorders for the preliminary survey should represent the variability within the conditions considered. For example, in this paper, 4 recorders have been deployed under each particular modality, for example 'forest with the presence of *W. auropunctata'*.

The choice of the acoustic index is also an important step, as previous works have demonstrated the different efficiency of several indices to reflect bird species diversity under different field conditions (Gasc *et al.*, 2015). The results of such work support the idea of preliminary investigations to compare the responses and their sensitivity for acoustic diversity indices in relation to controlled soundscapes characteristics. As indices are based on specific mathematical formula, they will be more or less sensitive and correlated to classical diversity indices (i.e. species richness) or to other components of the local biodiversity (i.e. functional and phylogenetic diversities). Correlations between acoustic diversity indices and calling species which compose the soundscape are expected to vary depending of the specificity of the emitting species. In the case of soundscapes dominated by cricket calls, we showed that the *NP* index was the most sensitive with the highest correlation significance with the calling species richness.

Table 7.1. *Pearson correlation coefficients between acoustic diversity indices and the three descriptors of the nocturnal cricket community: the number of species identified, the number of vocalization per species and the Shannon index measured from the two first descriptors. The values presented in this figure has been measured on night-time recordings only.*

Index	Reference	Number of species	Number of vocalizations	Shannon
NP	Gasc *et al.* 2013	0.49	0.28	0.46
ACI	Pieretti *et al*. 2011	0.38	0.26	0.36
ADI	Villanueva-Rivera *et al.* 2011	0.25	0.21	0.20
Bioacoustic	Boelman *et al.* 2008	0.24	0.33	0.14
Ht	Sueur *et al.* 2008a	-0.04	-0.05	-0.03
M	Depraetere *et al.* 2012	-0.04	-0.06	-0.01
H	Sueur *et al.* 2008a	-0.14	-0.05	-0.14
AR	Depraetere *et al.* 2012	-0.12	-0.14	-0.07
Hf	Sueur *et al.* 2008a	-0.18	-0.02	-0.19
AEI	Villanueva-Rivera *et al.* 2011	-0.21	-0.21	-0.21

These results can be explained by a strong acoustic competition between calling crickets in rich acoustic community. In this particularly competitive environment, spectral segregation of calling song is likely observed as an evolutionary response to avoid acoustic interferences (Schmidt *et al.*, 2013; Jain *et al.*, 2014). As a consequence, in such soundscapes dominated by a rich cricket community, the *NP* index based on frequential peaks appears the most relevant to use. Indices could have been chosen differently depending on the type of acoustic community. For example, the high frequency modulation of bird songs is usually measured with the Acoustic complexity index (ACI, Pieretti *et al.* 2011). Indices can also be more or less sensitive to other components of the soundscapes, such as wind noise (Gasc *et al.* 2015).

7.6.4 What is next?

Our findings presented here highlight how an alternative and non-invasive method, relatively fast and inexpensive, could be deployed over large natural areas for biodiversity and biosecurity surveillance, using automated acoustic sensors coupled with acoustic diversity

indices. In the case of New Caledonia, this work represents a preliminary and necessary step for a long-term surveillance project application. Without changing the global acoustic method framework, it would be interesting to test the sensitivity and robustness of this approach under different disturbances (e.g. different invasive species, pollution, deforestation) or ecological conditions (e.g. in mainland or marine environment). Interestingly, this global acoustic method also provides promising results to distinguish post-fire succession vegetation, with presumably strong implications for restoration applied in hotspot of biodiversity, increasingly threatened by multiple factors (Myers *et al.*, 2000; Brooks *et al.*, 2002). This study opens up a major field for bioacoustics researches applied in conservation biology, especially in the light of the increasing threats from invasive species, which urge scientists and managers to develop non-invasive and efficient early warnings systems.

7.7 Acknowledgment

This work was supported by NSF and an ATM form grants (Action Transversale du Muséum (ATM) 'Biodiversité actuelle et fossile. Crises, stress, restaurations et panchronisme: le message systématique'). The bioacoustic study was supported by a grant from the Grand Observatoire du Pacifique Sud: AAP GOPS 2013 / 'Bioacoustique des grillons de Nouvelle-Calédonie'. We thank the New Caledonian Direction de l'Environnement de la Province Sud, for collecting permits. This study was partly funded by a PhD grant, 'Bourse d'encouragement à la recherche universitaire, attributed to JA by the Government of New Caledonia. We would like to thank Garett Pignotti for greatly improving the language of the manuscript. We would like to thank Jérôme Sueur (MNHN Paris) for providing us nine acoustic recorders (SM2) to perform this study. We also thank Frédéric Rigault and Jean-François Julien who provided help for field work. We are grateful for the work of several Master students, Julien Lansiaux and Morgane Aubert.

7.8 Supporting information

Table 7.2. *Localities sampled with two models (SM2 and SM2+) of acoustic sensors, with the invaded status by Wasmannia auropunctata.*

Localities		Abbreviations	Acoustic recorders	Coordinates
1	Mouirange	FO-MOU	SM2+	166.68086E/22.20416S
2	Pic du Pin	FO-PDP	SM2	166.82715E/22.24680S
3	Grand Kaori	FO-GK	SM2	166.89674E/22.28535S
4	Rivière Blanche	FO-RIV	SM2+	166.68643E/22.15142S
5	Pépinière	PA-PEP	SM2+	166.96355E/22.27103S
6	Grand Kaori	PA-GK	SM2	166.89383E/22.28000S
7	Forêt Nord	PA-FN	SM2+	166.93134E/22.32259S
8	Rivière Blanche	PA-RIV	SM2	166.68033E/22.15280S
9	Grand Kaori	MA-GK	SM2	166.89436E/22.28460S
10	Rivière Blanche	MA-RIV	SM2	166.70796E/22.13625S
11	Madelaine	MA-MAD	SM2+	166.85268E/22.23568S
12	Forêt Nord	MA-FN	SM2+	166.93501E/22.32277S
13	Grand Kaori	FO-GK-W	SM2	166.89601E/22.28226S
14	Forêt Nord	FO-FN-W	SM2+	166.92987E/22.32372S
15	Cap N'Dua	FO-KA-W	SM2+	166.91742E/22.38645S
16	Port Boisé	FO-BOI-W	SM2	166.97343E/22.34820S
17	Grand Kaori	PA-GK-W	SM2	166.89510E/22.28345S
18	Forêt Nord	PA-FN-W	SM2+	166.93361E/22.32385S
19	Cap N'Dua	PA-KA-W	SM2+	166.91881E/22.38629S
20	Prony	PA-PRO-W	SM2	166.80473E/22.31902S
21	Rivière Blanche	MA-RIV-W	SM2	166.70937E/22.13480S
22	Rte Grand Kaori	MA-GKE-W	SM2+	166.86960E/22.27110S
23	Cap N'Dua	MA-KA-W	SM2	166.93486E/22.32278S
24	Bois du Sud	MA-BDS-W	SM2+	166.76093E/22.17321S

Abbreviation "W" identify localities invaed by *Wasmannia auropunctata; MA: low shrubland; PA: preforest formation; FO; forest; SM2: SongMeters.*

Chapitre IV

8 Etude des communautés acoustiques de grillons en tant que bio-indicateur d'une succession forestière et d'une invasion biologique terrestre

Cette section fait l'objet d'un article de recherche en préparation pour *Ecological indicators*, sous la forme suivante :

†**Anso, J**., †Gasc, A., Desutter-Grandcolas, L., Sueur, J., Jourdan, H. Listen to the crickets: Calling cricket community as a new bioindicator for forest succession and biological invasion. En preparation pour *Ecological indicators*.

† Premiers auteurs de cette publication.

Communication Internationale

Anso, J., Gasc, A., Desutter-Grandcolas L., Vidal, E., Jourdan, H. Cricket community acoustics: a new tool to detect invasive ants. – Oral presentation XVIIth International Union for the Study of Social Insects meeting, Cairns, Australia, 14-18 July 2014.

8.1 Résumé

Les bio-indicateurs sont des proxys majeurs et essentiels pour suivre les changements de la biodiversité et l'état de santé des milieux naturels d'intérêts. Parmi les bio-indicateurs disponibles, les grillons représentent un groupe prometteur car ils sont sensibles aux changements écologiques, ils sont également facile à échantillonner et peuvent être identifiés à l'oreille puisqu'ils reposent largement sur l'emission de signaux sonores. Dans cette étude, nous évaluons l'utilisation des communautés acoustiques de grillon en tant bio-indicateur d'une succession et d'une perturbation écologique en Nouvelle-Calédonie. Nous avons utilisé une méthode d'acoustique passive pour i) évaluer l'importance des grillons dans les communités acoustiques, ii) décrire les communautés acoustiques de grillons au sein d'une succession forestière et iii) caractériser ces mêmes communautés sous la pression d'une espèce envahissante majeure, la fourmi *Wasmannia auropunctata*. Pour mener à bien ces travaux, les ambiances sonores au sein de la succession ont été enregistrées à l'aide d'enregistreurs autonomes et automatiques. Pour chaque fichier sonore, les groupes chanteurs principaux ont été identifiés, et leur vocalisations comptées. Une attention particulière a été faite sur les grillons, avec une identification de toutes les espèces chanteuses et le décompte des vocalisations. Nos premiers résultats décrivent les grillons comme le groupe acoustique dominant sur 24h. Chaque stade de la succession héberge une communauté acoustique unique de grillons, avec des espèces uniques pour chaque stade. Plusieurs caractéristiques de la végétation ont été significativement correlées avec la structure et la composition des communautés. Finalement, la présence de *W. auropunctata* a été correctement détectée à travers une activité acoustique et une richesse spécifique plus faible dans les milieux envahis. L'utilisation des productions acoustiques des grillons représentent une alternative non-invasive, peu coûteuse et pertinente dans l'évaluation de la qualité des écosystèmes naturels menacés et des programmes de gestion mis en place.

Mots clés: *Wasmannia auropunctata*, espèces envahissantes, grillons, bioacoustiques, communautés, hotspot de biodiversité, Nouvelle-Calédonie

8.2 Abstract

Bioindicators are urgently needed as a proxy for biodiversity monitoring and to evaluate the health of valuable natural area. Among these bioindicators, crickets appear promising as they are sensitive to ecological changes, easy to collect and acoustically detectable as they largely rely on airborne signals. In this paper, we propose to evaluate the use of cricket acoustic community as a bioindicator of ecological succession and disturbance impacts in New Caledonia. We used a passive acoustic method to i) evaluate the dominance of the cricket group in the acoustic community, ii) describe the cricket animal community structure and diversity along a low shrubland to forest gradient and iii) characterize the cricket animal community structure and diversity in the light of ongoing invasion by one major invasive ant named *Wasmannia auropunctata*. To carry out this research, we collected soundscape recordings using automatic sensors. Using human-listening and spectral visualization, each recording was described by counting the number of vocalizations per main acoustic taxonomic groups - cricket, bird, grasshopper - as well as by identifying the cricket species and measuring the number of vocalization per crickets species. Our results define cricket communities as the dominant acoustic group in 24-hour analysis. Cricket communities were significantly different along our shrubland to rainforest gradient, mainly due to numerous exclusive species in each habitat type. Several vegetation attributes were significant factors in these communities specificity. The presence of *W. auropunctata* was efficiently detected through a lower acoustic activity and species richness of crickets. In such island tropical ecosystems, the use of cricket sound could be a non-invasive, cheap and reliable alternative method to assess the quality and the management of natural and endangered ecosystems.

Key-words: *Wasmannia auropunctata*, invasive species, crickets, bioacoustics, community, biodiversity hotspot, New Caledonia

8.3 Introduction

Recent advances in bioacoustics contributed to the idea of using animal sounds as a bioindicator of environmental or ecological conditions (Sueur *et al.*, 2012; Lellouch *et al.*, 2014). In terrestrial and aquatic environments, a large number of animals rely on acoustic signals to interact with conspecifics or/and different species, in order to perform numerous decisive behaviors. These calling species in a given space can be considered as an acoustic animal community and contribute to the ambient noise of the area, a remarkable feature of the landscape (Pijanowski *et al.*, 2011a). Several studies have linked sounds from acoustic animal community with habitat characteristics (e.g., vegetation, patch sizes and connectivity) (Bormpoudakis *et al.*, 2013; Tucker *et al.*, 2014), or related to human disturbances (Slabbekoorn & Ripmeester, 2008; Hu & Cardoso, 2010). Recordings of animal communities have also revealed important features of bird population structure and dynamic, such as densities and breeding sites (Frommolt & Tauchert, 2014; Lellouch *et al.*, 2014). However, the influence of biological invasion on acoustic animal community in natural environment has not been investigated.

Biological invasion, described as a main component of environmental changes, and a devastating cause of biodiversity decline (Suarez & Tsutsui, 2008; Simberloff *et al.*, 2013; Tershy *et al.*, 2015), might potentially impact acoustic animal communities. At the present-day, no study has been performed in natural conditions to assess the impact of invaders on acoustically active native fauna. Though, Farina *et al.* (2011) have suggested that the arrival of new invasive species relying on acoustic communication (e.g., birds, frogs) may directly disrupt acoustic community of native species. This assumption is usually accepted and was partially confirmed by Both and Grant (2012) with simulated acoustic invasion by American bullfrog (*Lithobates catesbeianus*) on tree frogs (*Hypsiboas albomarginatus*). They showed that tree frogs shifted calls to higher frequencies in response to American bullfrog calls, with potentially negative effect on reproductive success of tree frogs. An interesting body of evidences has focused their effort to improved direct detection of sounds produced by invasive species (Mankin *et al.*, 2011; Kottege *et al.*, 2015), aiming automatic monitoring using bioacoustics in natural environment (Kottege *et al.*, 2015). Nonetheless, several inaudible and damaging invasive species, such as ants (Hoffmann *et al.*, 1999; Holway *et al.*, 2002), may be indirectly detected through acoustic recordings of acoustic animal communities impacted.

Among communicating species, the community of crickets (Ensifera, Grylloidea) may be a good candidate as bioacoustics indicators. First of all, they are widely distributed around the world with decent abundance, and associated with a fairly good taxonomic knowledge. Secondly, they mostly rely on acoustic signals to attract a mate, with easily identifiable species-specific calls (Riede et al. 2006, Diwakar et al. 2007), mainly because of a great partitioning in the acoustic niche for efficient communication (Schmidt et al. 2013, Schmidt and Balakrishnan 2015). Thirdly, their acoustic production mechanism, called stridulation, is one of the best known among insects (Bennet-Clark & Bailey, 2002; Montealegre-Z et al., 2009). Finally, convincing evidences placed them as sensitive to environmental changes (McGeoch et al. 2011, Gerlach et al. 2013), including ecological succession (Schirmel *et al.*, 2011; Fartmann *et al.*, 2012), pollution (Hoffmann *et al.*, 1999) and biological invasion (Nichols, 1989; LaPolla *et al.*, 2000). In this context, cricket acoustic community survey could represent a fast and efficient approach for ecosystem monitoring and thus could be critical for decision-maker and manager in hotspot of biodiversity.

To test this hypothesis, we studied the diverse and well-studied acoustic assemblages of cricket species in the southern New Caledonia, a hotspot of biodiversity (Myers et al. 2000) threatened by cryptic invasive species (Jourdan, 1997; Jourdan *et al.*, 2001) and human activities (Jaffré *et al.*, 1998b), according to two critical ecological conditions: habitat type and the presence of an invasive species. We collected and analyzed passive acoustic recordings to i) evaluate the dominance of the cricket group in the acoustic community, ii) describe the cricket animal community structure and diversity along a low shrubland to forest gradient and iii) characterize the cricket animal community structure and diversity in the light of ongoing invasion by one major invasive ant *Wasmannia auropunctata*. We pointed out limits in animal model as proxy for ecological and environmental assessment.

8.4 Material and methods

8.4.1 Study sites

Sites were selected in the southern part of New Caledonia, an area on metalliferous soils (Fig. 8.1). Three habitat types following a vegetation gradient were selected: rainforest, preforest and shrubland. In addition, in order to estimate the impact of one major invasive species (*W. auropunctata*), invaded (see below for detailed method in selection of habitats

invaded) and non-invaded sites were selected leading to total of 6 modalities (3 habitat types*2 invasion types). Each modality was replicated 4 times for a total of 24 sites. All sites were located at a similar low-altitude of 189 ± 83 m (n = 24) and with a minimum separation of 200 m. We deployed one recorder per site.

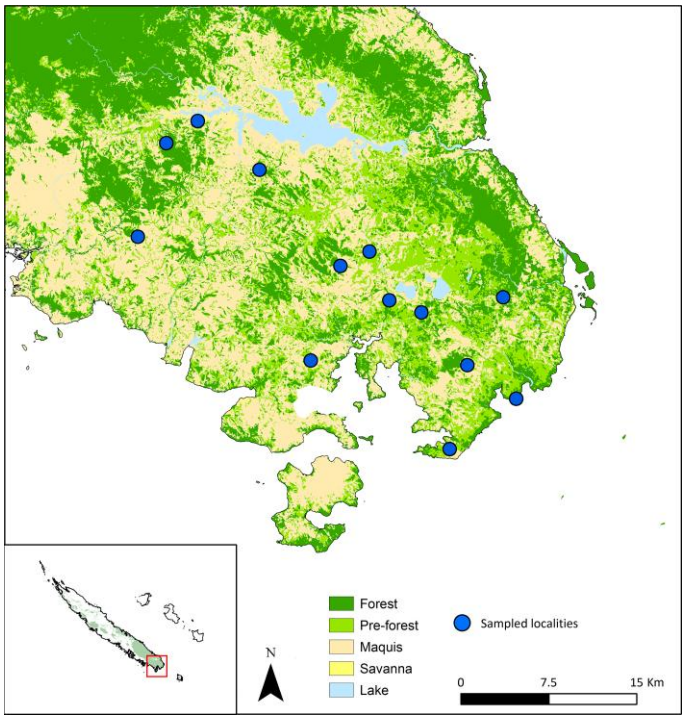

Figure 8.1. *Localities acoustically sampled with automated sensors in the southern part of New Caledonia.*

8.4.2 Selection of sites invaded by W. auropunctata

The ‘invaded sites’ were pre-selected based on previsous records of *Wasmannia auropunctata* in the field. In order to confirm the current state of invasion by *W. auropunctata* on each site, two perpendiculars transects of 200 meters along the line North-Sud, East-West were plotted and centered on the acoustic sensor. The presence/absence of the exotic ant was investigated during 5 min at the sensor location and at 50 m and 100 m from the recorder along the transect. A total of 108 check-points per modality confirmed their invasion states: for the ‘non-invaded’ sites, 12 out of 108 check-points were invaded by the invasive ant whereas for the ‘invaded’ sites, 95 out of 108 check-points were invaded by *W. auropunctata*.

8.4.3 Soundscape recording procedure

Automatic recordings were collected from October, 17th to December, 26th 2013 with SongMeter SM2 and SM2+ (Wildlife Acoustics, concord, NY, U.S.A.), weatherproof and vented acoustic sensors. To avoid bias between recent and older versions of acoustic sensors, we placed the same number of SM2 and SM2+ for each modality. These acoustic sensors were equipped with two omnidirectional microphones (frequency response: −35 ± 4 dB between 20 Hz and 20 kHz) oriented horizontally, one at a height of 1.5 m. Acoustic recordings were digitized at a sampling frequency of 48 kHz (16 bit). Files were stored in the lossless compression format *.wac* and transformed into *.wav* with the software Kaleidoscope version 1.1.20. Acoustic sensors were configured to record 2 min every 58 min. Thermo-hygrometric sensors were attached on tree (0.7 m) near acoustic sensors. Temperature and humidity were collected every 5 min. All files were examined by A.G. and J.A. to discard files with rain, anthropogenic noise (e.g. human voices) or wind, in order to avoid bias for further analysis, especially during listening identification.

8.4.4 Species-specific calls recordings database

In order to discriminate and describe as accurately as possible calling species in our field recordings, we previously created a database of species-specific call recordings. Crickets calls were described following Ragge and Reynolds(1998): one song unit is called a syllable and corresponds to one opening–closing cycle of the male forewings; a group of syllables forming a cricket call is named an echeme. To do this, several males from different species were recorded in the field and laboratory conditions. In the field, calling songs were recorded with a microphone (Seinnheiser K6/ME62, frequency range: 20 - 20 kHz ± 2.5 dB), placed at 40 cm from the calling male, connected to a Field memory recorder Fostex FR-2LE (48 kHz sampling frequency, stereo). At the lab, males were placed in round boxes covered by a mosquito net, and then, recorded as the same in the field with the same audio materials. Time of day, temperature and singing site (on leaft litter, trunks, or vegetation) were measured for every calling male.

8.4.5 Identification of calling groups and counting of vocalizations

We analyzed one soundscape recording per hour – at the beginning of the hour— between 07:00 hrs to 16:00 hrs and 19:00 hrs to 04:00 hrs, during 6 days. Dusk and dawn

choruses, between 05:00 to 06:00 hrs and 17:00 to 18:00 hrs, were deliberately avoided because of the greater complexity of calling species community (mainly bird species) and overlapping acoustic signals during these particular periods (Riede, 1997). A total of 120 one-minute recordings were analyzed for each site by human-listening with the visualization of spectrogram using the acoustic software GoldWave (v5.25), allowing a more accurate discrimination of overlapping songs and the counting process (Truskinger *et al.*, 2013) (Fig. 8.2). First, songs were classified in 4 main acoustic groups as follow: birds, crickets, grasshoppers and others (cicadas, anurans, cats and bats). Songs, defined here as one distinct acoustic production from one individual, were counted from each acoustic group. According to already described songs (Otte *et al.*, 1987; Robillard *et al.*, 2010) and those available in our database, identification at a species level and counting of the number of songs per species were performed for the cricket group.

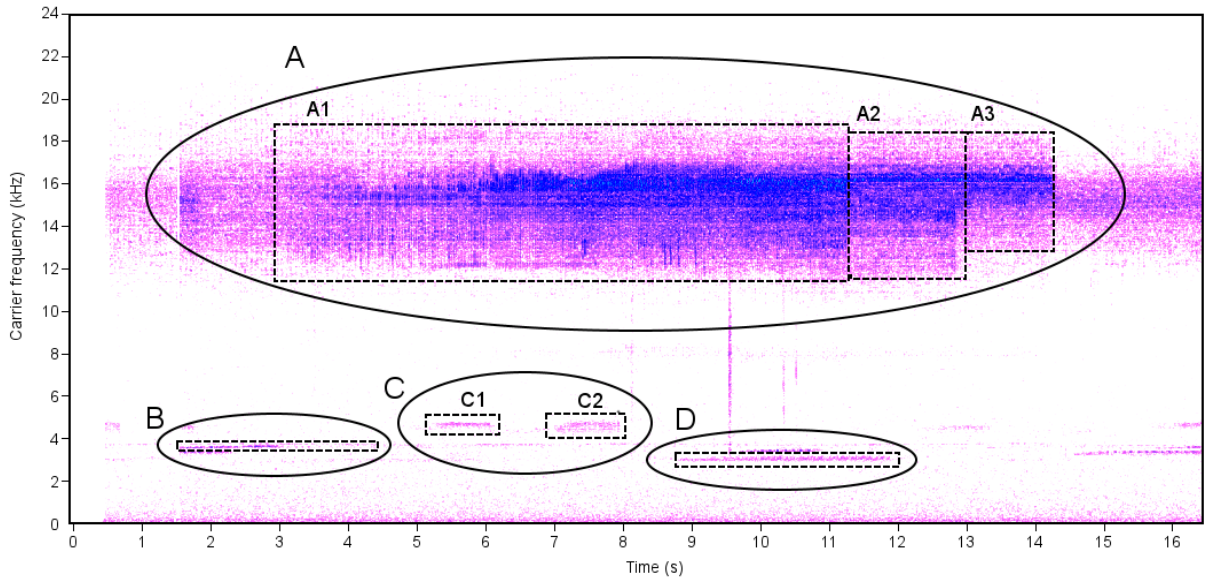

Figure 8.2. *Spectrogram of one recording of forest succession at Pic du Pin by night. Four species are calling in this example; A = Agnotecous azurensis with three individuals (A1, A2 and A3); B = Archenopterus bouensis; C = Koghiella nigris with two individuals (C1 and C2); and D = Pseudotrigonidium caledonica.*

8.4.6 Analysis

Analyses performed on the entire day will be referred as 24-hour analyses. Some analyses focusing on a particular time period of the day, from 05:00 hrs to 16:00 hrs or from 19 hrs to 04:00 hrs, were respectively referred as day-time and night-time analyses. To evaluate the dominance of the acoustic groups in the New Caledonian soundscape, we calculated the percentage of occurrence– defined here as the total number of song counted through the entire set of recordings – for each group and in the three selected habitat. We computed this calculation separately on 24-hours, day-time and night-time periods.

The species richness accumulation curves were calculated for a certain number of recordings following Ugland *et al.* (2003), Colwell *et al.* (2004) and Kindt *et al.* (2006)'s methods and the conditional standard deviation was estimated following Oksanen (not published, sd=0 for all samples). These curves were obtained with the function 'specaccum' available in the R package *vegan* version 2.2-1 (Oksanen et al. 2013). One curve was obtained

for each habitat and for each time-period – day-time and night-time – in order to assess the efficiency of the recording effort for the cricket community description depending in these different conditions. We also computed the same accumulation curves but considering the average value of species richness by habitat type, thus with species richness values averaged among the four replication sites of the same habitat type.

Nonmetric Multidimensional Scaling (NMDS) was performed with Bray-Curtis distances. The distance was calculated on presence/absence data of cricket species across sampling sites (Minchin, 1987). The NMDS find the more stable solution using random iteration set at 1000, with 2 dimensions. Then, sampling sites were plotted together according to habitat type. Environmental variables were fitted into ordination, and significant variables were assessed with permutation test (set at 999, $p < 0.05$). The stress value obtained with the NMDS was set to 0.1 as acceptable for interpreting the results (Baselga, 2008). We then performed an analysis of similarities (ANOSIM) to test for significant differences in community structure with habitat type as explaining factor, using also permutation test. NMDS was performed using the function 'metaMDS' from the R package *vegan* (Oksanen *et al.*, 2013). Environmental variables were fitted into ordination using the 'envfit' function.

To evaluate the effect of the presence of *Wasmannia Auropunctata* on the acoustic crickets community, we calculated for each recording the species richness (number of species identified), the total abundance of songs considering the entire cricket's community, and the acoustic diversity of the cricket community but computing the Shannon index. The value of abundance per species in the Shannon index was defined by the number of song per species. We compared these three measures – acoustic species richness, number of songs and Shannon index – between invaded and non-invaded conditions considering separately the type of habitat and the time-period of the day. We also evaluated the differences of the overall number of bird songs per recordings between invaded and non-invaded conditions. In order to evaluate the significance of the differences observed, we performed non-parametric pairwise comparisons using Mann-Whitney test with a Bonferroni adjustment. All analyses were conducted using the open-access software R (2.15.2, R Core Team 2012).

8.5 Results

8.5.1 Occurrence of calling species

Overall occurrence of calling species detected through 24-hour analysis and among the three habitats, placed cricket as the dominant acoustic group with a value of 59.5%. Birds are the second acoustic group present in our recordings through 24-hour analysis (31%), followed by Grasshoppers (7.9%). We observed different patterns of dominance between the day-time and night-time period (Fig. 3). During the day, birds are the main acoustic group with 58.8% of occurrence in our three habitats, followed by crickets (34.1%) and grasshoppers (5.6%). However, nocturnal cricket species are largely dominating in our three habitats occurring in 85% of recordings, followed by grasshoppers (10.1%) and birds (3.3%). Considering the three different habitat types, occurrence of cricket calls during the night-time period account for 85.2% in forest, 73.4% in preforest and for 96.4% in maquis. (Fig. 8.3).

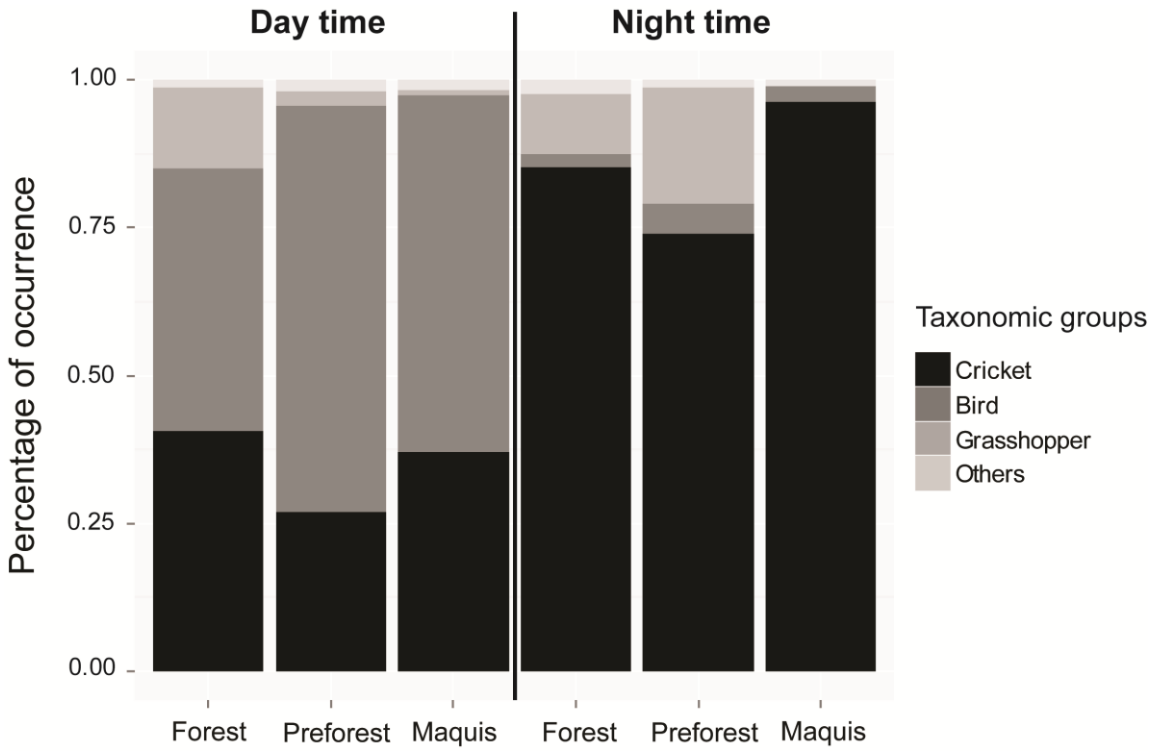

Figure 8.3. *Percentage of occurrence of calls in audio recordings for each acoustic group.*

8.5.2 Calling cricket community

In total, 19 cricket species were identified in our recordings, belonging to two family (Gryllidae, 15 species and Mogoplistidae, 4 species) and to six subfamilies, namely Eneopterinae (3 species), Podocirtinae (2 species), Nemobiinae (5 species), Trigonidiinae (1 species), Gryllinae (3 species) and Phalangopsidae (1 species). Among these 19 species, 11 were identified on day-time, and 16 during night-time recordings (Table 8.1).

In forest habitat, five of the 12 species identified were identified only in the forest habitat (41.7%): *Mogoplistidae sp7*, living in *Cyperacea* or Palm trees and calling at night; *Agnotecous meridionalis*, living in leaf litter and calling at night; *Koghiella nigris*, living in bare soil and calling day and night; *Pseudotrigonidium caledonica*, living in low vegetation and calling on understory at night; and *Bullita mouirangensis*, living in leaf litter and calling at day. Six species identified are found in both rainforest and preforest habitat: *Agnotecous azurensis*, *Agnotecous clarus*, *Archenopterus bouensis*, *Calcirtus magnus*, *Bullita fusca*, *Notosciobia SP1*, *Notosciobia SP2*. In preforest habitat, three of the 13 species identified are unique to this habitat (23.1%): *Notosciobia SP3*, living in borrows in leaf litter and calling at night; *Metioche SP1*, living in upper vegetation and calling at day; and *Bullita obscura*, living in leaf litter and calling day and night. Ten species are shared by both forest (7 species) and shrubland (3 species) habitats. In maquis habitat, 5 species were identified, with one species unique to this habitat (20%): *Mogoplistidae sp3*, living in leaf litter and calling at night. The four last species are shared with preforest and rainforest habitat (80%).

Table 8.1. *List of calling species or morphospecies recorded and identified in successional vegetation. For each species/morphospecies, corresponding family, subfamily, habitat, calling diel preference and calling sites are noted. N/A indicate when data are not available.*

Family	Sufamily	Species/Morphospecies	Habitat	Diel calling	Calling sites
Gryllidae	Eneopterinae	*Agnotecous meridionalis* *‡	Rainforest	Night	Leaf litter
Gryllidae	Eneopterinae	*Agnotecous azurensis*	Rainforest/preforest	Night	Leaf litter
Gryllidae	Eneopterinae	*Agnotecous clarus* ‡	Rainforest/preforest	Night	Leaf litter
Gryllidae	Podocirtinae	*Archenopterus bouensis*	Rainforest/preforest	Night	Canopy
Gryllidae	Podocirtinae	*Calscirtus magnus*	Rainforest/preforest	Night	Canopy
Gryllidae	Nemobiinae	*Bullita fusca* ‡	Rainforest/preforest	Day	Leaf litter
Gryllidae	Nemobiinae	*Bullita mouirangensis* * ‡	Rainforest	Day	Leaf litter
Gryllidae	Nemobiinae	*Koghiella nigris* *	Rainforest	Day/Night	Bare soil
Gryllidae	Nemobiinae	*Bullita obscura* §‡	Preforest	Day	Leaf litter
Gryllidae	Nemobiinae	*Koghiella flammea*	Preforest/Shrubland	Day/Night	Leaf litter
Gryllidae	Trigonidiinae	*Metioche sp1* §	Preforest	Day	Understorey
Mogoplistidae	N/A	*Mogoplistidae sp 1*	Preforest/Shrubland	Night	Low vegetation
Mogoplistidae	N/A	*Mogoplistidae sp 2*	Preforest/Shrubland	Night	Low vegetation
Mogoplistidae	N/A	*Mogoplistidae sp 3* • ‡	Shrubland	Night	Leaf litter
Mogoplistidae	N/A	*Mogoplistidae sp 7* *	Rainforest	Night	Low vegetation
Gryllidae	Gryllinae	*Notosciobia sp 1*	Rainforest/preforest	Night	Burrow/leaf litter
Gryllidae	Gryllinae	*Notosciobia sp 2* †	Rainforest/preforest	Night	Burrow/leaf litter
Gryllidae	Gryllinae	*Notosciobia sp 3* §‡	Preforest	Night	Burrow/leaf litter
Gryllidae	Phalangopsinae	*Pseudotrigonidium caledonica* * ‡	Rainforest	Night	Understorey

** Species unique to rainforest ; § Species unique to preforest; • Species unique to maquis; ‡ Species absent in invaded area; † Species only present in invaded area*

8.5.3 Species accumulation curves

Species accumulation curves reached an asymptote over the period analyzed (3 days and nights), suggesting than acoustic communities has been almost completely sampled in our habitat gradient (Fig. 8.4). Considering the night-time period, preforest held the highest species richness with 10 species, followed by forest with nine species, and by shrubland habitats with five species (Fig. 4). Considering the day-time period, the species accumulations followed the same pattern as during night-time period: preforest held the highest species accumulation of acoustic species with six species, followed by forest with five species and by shrubland with three species recorded.

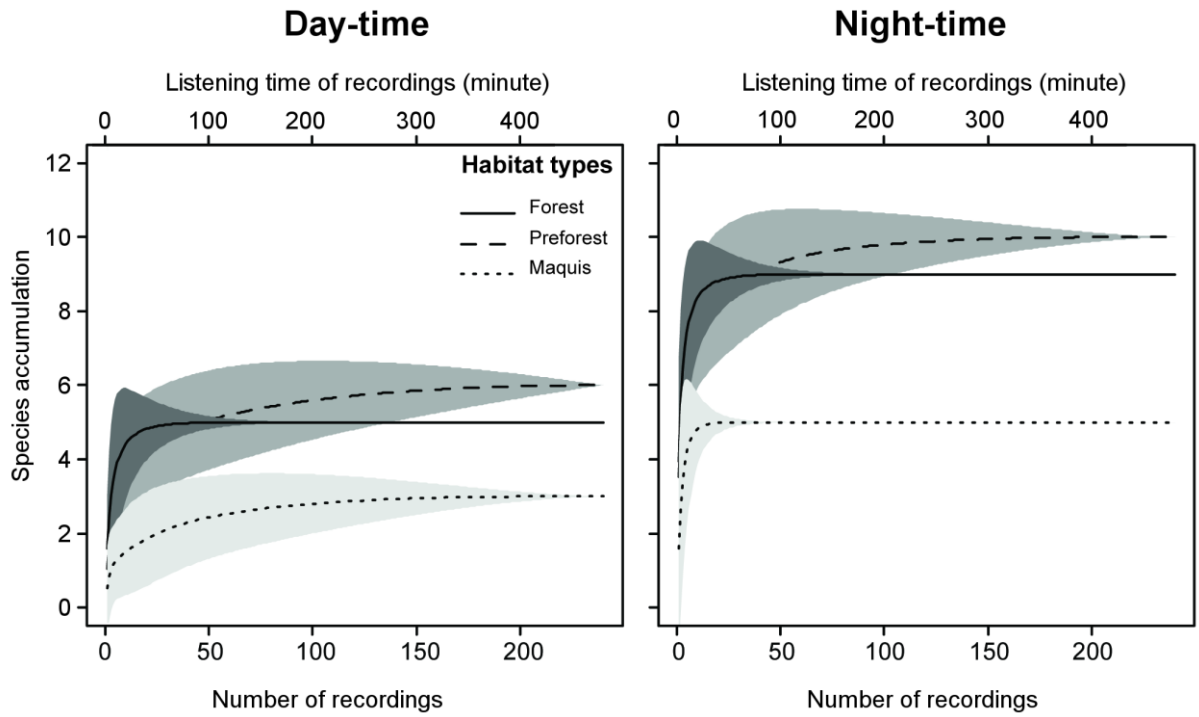

Figure 8.4. *Species richness cumulated curves for cricket species in forest, preforest and shrubland. Gray clouds around curves indicate the 95% standard error.*

8.5.4 NMDS and hierarchical clusters of cricket communities

NMDS ordination (stress = 0.0433) in two dimensions showed a clear effect of habitat type on acoustic communities, based on the presence/absence data of cricket species (Fig. 8.5). Each habitat was fully discriminated with no overlap and supported by robust analysis of

similarties (ANOSIM R^2 0.94, $p < 0.001$). The ordination was significantly explained by five environmental variables (permutation test). Hierarchical analysis based on the presence/absence data of cricket species mainly clustered species by habitat type (Fig. 8.7).

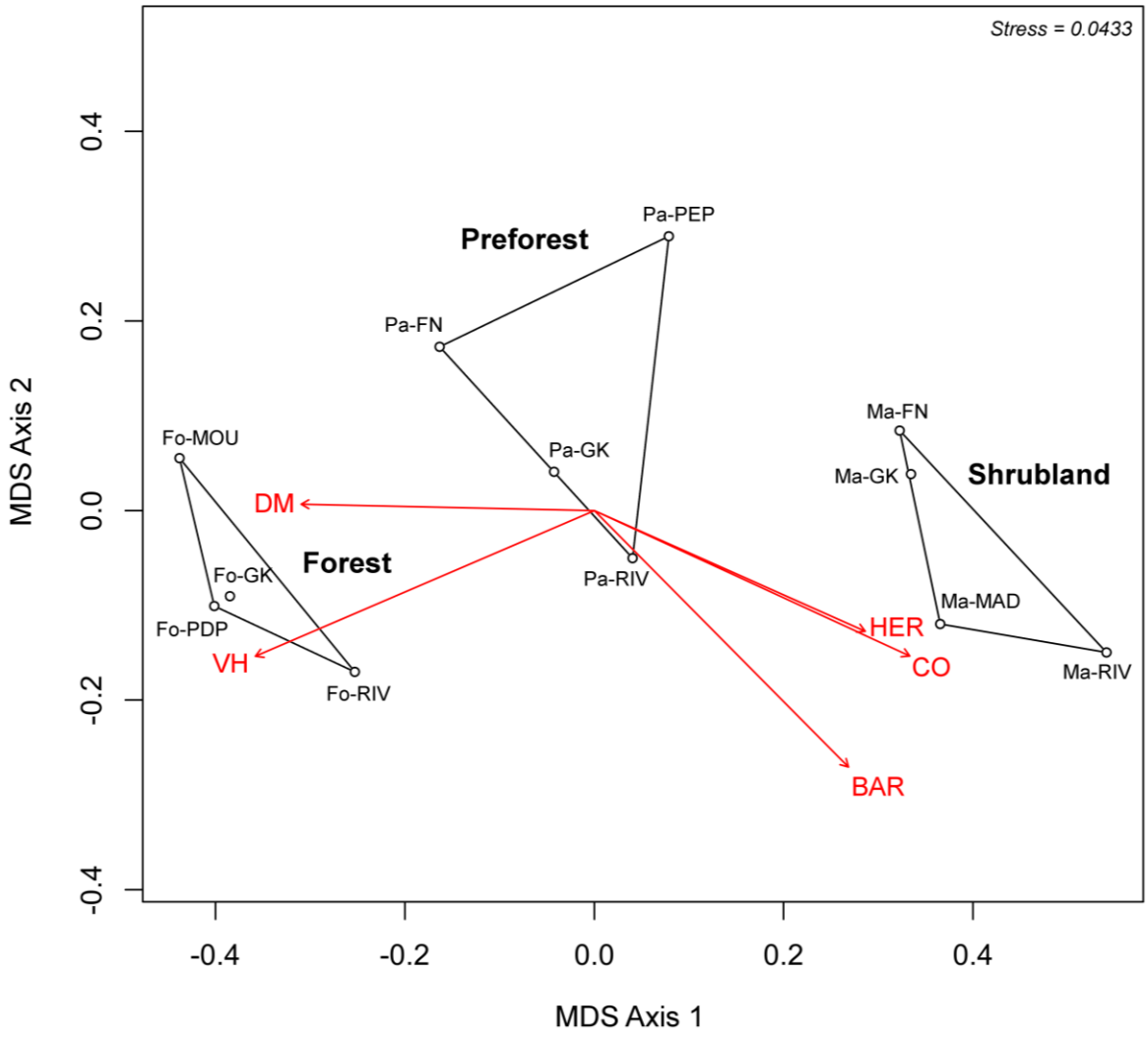

Figure 8.5. *NMDS (stress = 0.0433, two dimensions) based on cricket presence/absence data and environmental parameters. Five significant environmental variables are shown (ENVFIT, $p < 0.05$ with 999 permutations). Polygons were drawn according to habitat type: dark grey for rainforest; medium grey for preforest and light grey for shrubland. Abbreviations: HER, herba; BAR, bare ground; CO, canopy openness; VH, vegetation height; DM, mean diameter of large trees.*

8.5.5 Species richness and acoustic activity of crickets with Wasmannia auropunctata

The number of cricket species, calls and the Shannon index were significantly lower in invaded than in non-invaded area in all types of vegetations studied (Fig. 8.6). Considering diurnal period, mean species richness, number of songs and Shannon index values were all significantly lower in invaded area, except for the Shannon index in preforest and maquis which is equal to zero in non-invaded and invaded habitats. By contrast for nocturnal period, mean species richness, number of songs and Shannon index values were all significantly lower in invaded area in our three habitat types: rainforest, preforest and shrubland (Fig. 8.6). Eight acoustics species recorded in non invaded habitats were absent in invaded areas by *W. auropunctata* (*Pseudotrigonidium caledonica*, *Agnotecous meridionalis*, *Agnotecous clarus*, *Bullita mouirangensis*, *Bullita obscura*, *Mogoplistidae SP3* and *Notosciobia SP3*). By contrast, one species, *Notosciobia SP2*, was only recorded in invaded habitats. 8 species were both recorded in invaded and non invaded habitats, with significant lower vocalizations in presence of *W. auropunctata* (83.4 ± 21.3% of reduced vocalizations). One species, *Mogoplistidae SP7*, did not demonstrate changes in counted vocalizations in invaded conditions.

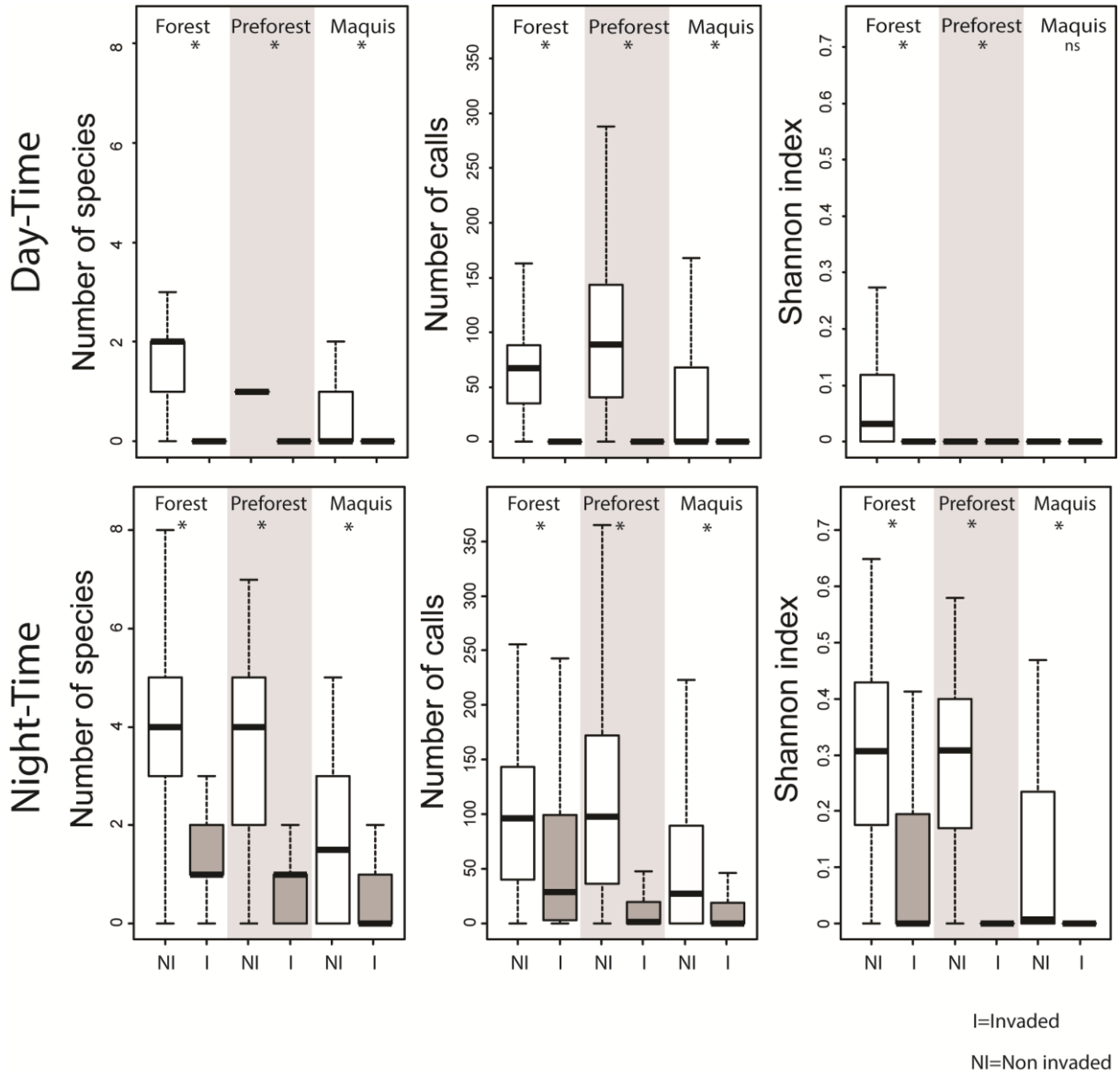

Figure 8.6. *Number of species, calls and Shannon index of cricket communities in habitat and invaded modalities. Rainforest, preforest and shrubland free from invasive species are in blank plots, while invaded habitats by Wasmannia are in gray plots, for (A) day-time and (B) night-time periods. Abbreviations: I, invaded habitats; NI, non-invaded habitats.*

8.6 Discussion

Our knowledge on ecological indicators based on acoustic signals is fairly documented for bird species (Laiolo, 2010), with poor attention for communicating insects. In a review devoted to terrestrial invertebrates as bioindicators, bioacoustics were only mentioned by

Gerlach *et al.* (2013) to pointed out that inaccessible species in canopy could be identified through acoustic recordings. As far as we know, no study has been carried out to investigate the effect of forest succession or biological invasion on acoustic insect community. However, Penone *et al.* (2012; 2013) used with success *Tettiigoniidae* communities to measure the impact of urbanization in sound road-tracking.

In this study, we have focused our attention on calling cricket species, representing one major terrestrial insect group and the main feature of the New Caledonian biophony. Biophony is likely to reflect habitat selection and suitability by calling species, which might be as heterogeneous and specific as landscapes. Here we demonstrated how habitat types were fully discriminated by acoustically active cricket communities. Additionally, one specific biological invasion by a small invasive ant (*W. auropunctata*) was efficiently detected by species richness, Shannon index and vocalizations of these cricket communities

8.6.1 Acoustic signatures by habitat type

As a main result of this research, our forest succession represented by three habitat type was successfully discriminated by the acoustic signature of cricket communities. NMDS and hierarchical cluster analysis showed the high accuracy of our results, demonstrating that calling cricket species are likely to be habitat specific, and thus confirm their sensitivity to different environmental conditions (Fartmann *et al.*, 2012; Gerlach *et al.*, 2013) with the habitat-acoustic signature specificity (Bormpoudakis *et al.*, 2013). These results are supported by peculiar cricket species only recorded in each habitat type, as documented for others Orthoptera (Schirmel *et al.*, 2011; Fartmann *et al.*, 2012), suggesting that peculiar microclimatic conditions (Gardiner & Dover, 2008), environmental constraints for communication (Romer & Lewald, 1992; Romer, 1993), and micro-habitat availability (Sueur & Aubin, 2003; Jain & Balakrishnan, 2011) allow the establishment of these species.

The significant differences observed between shrubland and forested environments (preforest and rainforest) are easily interpretable because of the opposed environmental conditions. Canopy cover is almost absent in shrublands, with very localized and dense low vegetation surrounded by bare ground. These characteristics are known to affect species diversity (MacArthur & MacArthur, 1961; Ishii *et al.*, 2004; Müller & Brandl, 2009) and acoustic diversity (Pekin *et al.*, 2012). Additionally, shrublands held one of the most remarkable and very different plant diversity compared to forest/preforest habitats (Jaffré,

1980, 1996), emphasizing the contrast between these formations. Habitat suitability in these shrubland habitat is strikingly different from preforest/forest habitats, especially in ecological terms (food, shelter from predators and calling sites) and also for acoustic transmissions (Wiley & Richards, 1978; Richards & Wiley, 1980).

Interestingly, rainforest and preforest habitats were clearly discriminated by calling cricket communities despite environmental variables almost identical. These similar vegetation attributes are likely to affect propagation of sounds in the same way (Wiley & Richards, 1978; Romer, 1993), without filtering species distribution as suggested by species found in both habitats (e.g., *Agnotecous azurensis*, *A. clarus* and *Bullita fusca*). This observation may highlight that fine ecological parameter played major role in species distribution (Sueur & Aubin, 2003). In fact, rainforest and preforest sites were separated on the basis of plant species assemblages. Preforests are composed by advanced pioneer species from shrublands with few and young forest plant species. By contrast, no pioneer species remained in rainforest with only forest plant species. Though, unconsidered environmental parameters such as fine micro-habitat (e.g., dead trunk, woody debris or humidity) or large habitat characteristics (e.g., patch size, connectivity) may have acted here as important factors in habitat selection and then cricket assemblage.

Previous studies have succeed to identify different habitat types using soundscape recordings (Radford *et al.*, 2010). Without species identification, Bormpoudakis et al. (2013) have acoustically identified six different habitats according to several acoustic parameters, reinforcing the novel approach of "soundtope" developed by Farina et al. (2011). They linked these different acoustic signatures to vegetation attributes and communicating animal communities, mainly birds and insects. By contrast, Tucker al. (2014) have recently linked the relative soundscape power of different habitats with landscape characteristics, such as patch size and connectivity, whereas vegetation attributes did not responded significantly. More interestingly, they also demonstrated that bird communities were nicely clustered in relation to aforementioned landscape attributes.

Among cricket related studies, communities are commonly recorded and analyzed in forest habitats, without targeting the effect of vegetation or landscape attributes on assemblages (Riede, 1993, 1997; Nischk & Riede, 2001; Diwakar & Balakrishnan, 2007a). Therefore, the strength of this research rely both on soundscape and bioacoustics approaches

with the complete deciphering of calling groups species, especially for the cricket species defined as the main acoustic group .

8.6.2 Cricket calls as a detector of *W. auropunctata*

Overall species abundance, richness, vocalizations and the Shannon index of cricket communities were all significantly lower in habitats invaded by the small introduced myrmicine, *W. auropunctata*. Spreading of *W. auropunctata* is usually negatively associated with terrestrial invertebrates (Lubin, 1984; Jourdan *et al.*, 2001; Walker, 2006), as it has been recently documented for crickets group in New Caledonia (Anso *et al*., 2015, in prep.). In this study, two complementary mechanisms have been put forward, mainly involving (i) non-lethal interactions by indirect competition for calling sites, shelters or food resources, and in a lesser extent with (ii) lethal interactions by direct predation on eggs, nymphs or small individuals. The significant decrease of vocalizations recorded might be a consequence of *W. auropunctata* on cricket species. Interestingly, among the acoustic species absent from invaded area (see Table 8.1), seven species were leaf litter-dwellers demonstrating higher sensitivity than perched crickets on vegetation to foraging workers. This trend is somewhat confirmed by the *Mogoplistidae* family with four species recorded in non-invaded habitats. Only one species, *Mogoplistidae SP3*, living in leaf litter was absent in invaded area, whereas others species living in vegetation remained present. By contrast, *Pseudotrigonidium caledonica* is one discreet *Phalangopsinae* which remain perched on vegetation for calling, but was not recorded in invaded areas. This pattern probably highlights a peculiar vulnerability of *P. caledonica* to foraging ants, perhaps during other activities, such as feeding, resting or copulating. According to our findings, the lack of several species could be defined as a relevant detector of the presence of the little fire ant: *B. mouirangensis, P. caledonica* and *A. meridionalis* could be defined as a flag species in forests. Three other species (*B. fusca*, *B. obsucra* and *A. clarus*) might be also good candidate for the detection of *W. auropunctata*, both in forest and preforest habitats. In shrubland, *Mogoplistidae SP3* seems to be the unique reliable species to assess the presence of the little fire ant. *Notosciobia SP3* was only recorded in 3 files in one non invaded habitat (Forêt Nord), and thus might not be a consequence of the invasive ant.

As aforementioned, species calling in less exposed micro-habitats such as in vegetation (*Mogoplistidae SP1*, *SP2*, *SP7*, *Metioche SP1*) or in canopy (i.e., *Calscirtus magnus* and *Archenopterus bouensis*) were both recorded in invaded and non-invaded

habitats. More surprisingly, numerous species (*Koghiella* and *Agnotecous*) living in micro-habitat exposed to foraging ants (leaf litter, bare soil) were also recorded in invaded areas. These observations could be in part explained by our protocol. Invaded areas were only characterized by 9 check-points in a radius of 50 meters (representing more than 31.000 m²). In this configuration, habitats classified as 'invaded' by our protocol could have still hosted of few non-invaded patches. These non-invaded patches are difficult to estimate and may have acted as a 'refugium' for several species. Nevertheless, the comparison of the number of vocalization per species between non-invaded and invaded might indicate the importance of these 'refugium'. For 6 species (*A. azurensis*, *K. nigris*, *K. flammea*, *Mogoplistidae SP1*, *Mogoplistidae SP2* and *Notosciobia SP1*), the number of vocalizations have been strongly reduced up to 89 ± 6% in invaded areas, that can be interpreted by a major decrease in individuals in the population densities. Additionally, long-range calls of canopy species might have biased the count of vocalizations in closed-by modalities (e.g., one canopy species (*C. magnus*) living in rainforest and preforest was recorded in five shrublands, due to the long-distance call of this species).

Our findings provide the first successful attempt to detect the occurrence of one major invasive ant species (*W. auropunctata*) using airborne signals of cricket communities in natural environment. So far as we know, acoustic detection and monitoring of invasive are mostly used for localized root-infesting species with economical impact (e.g. trees in cities, crops field), such as Coleoptera, Isoptera, Diptera or Hymenoptera (reviewed in (Mankin *et al.*, 2011). Mankin & Benshemesh (2006) provide one possible application for invasive ant with the successful detection of *Solenopsis invicta*, one major invasive ant with *W. auropunctata* (Lowe *et al.*, 2000), using geophones in field experiments. Slight stridulations and ticks were directly recorded near the entrance of ant colony as a consequence of ant activity. Unfortunately, this method seems hardly generalized in monitoring applied to invasive ants, as invaded area are large and would requisite a massive amount of work and time. Traditional detection methods lie mainly on intense field work involving several personals, which are time and cost-consuming. Innovative methods are now deployed in specific regions (e.g., Australia), such as infrared camera on helicopter and odor detector dogs to detect invasive ant. Before this tool box becomes more affordable by less equipped managers, bioacoustics surveillance using airborne signals of sensitive species could be a promising way in conservation programs.

8.7 Conclusion and perspectives

Bioacoustics related studies are becoming increasingly interesting as they provide a reliable monitoring method for study biodiversity. In this study performed in New Caledonia, a hotspot of biodiversity, we provided the first evidence that calling cricket community could be used as a relevant proxy to monitor ecological processes, at the habitat level. Cricket species held the double advantages to be sensitive to environmental changes, and to produce simple, stereotyped and highly reliable airborne signals. This paired features open up perspective in conservation biology, mostly in rich tropical ecosystem with great taxonomic impediments, and emphasizing the importance to study cricket fauna. Further studies should be perfomed to create a comprehensive acoustic data base, associated with specific ecological conditions (e.g. a biological invasion). This field of research might be strikingly interesting for managers, moreover if cricket calls could be analyzed and classified with automatic recognition. Cricket calls, with peculiar temporal structure and specific spectral parameters, are particularly adapted for automatic identifications.

8.8 Acknowledgments

We would like to thank Jérôme Sueur (MNHN Paris) for providing us nine acoustic recorders (SM2) to perform this study. We also thank Frédéric Rigault and Jean-François Julien who provided help for field work. We are grateful for the work of several Master students, Julien Lansiaux and Morgane Aubert. We are also grateful to Eric Vidal (IRD Noumea) for logistic and funding supports. We thank the New Caledonian Direction de l'Environnement de la Province Sud, for collecting permits. This study was partly funded by a PhD grant, 'Bourse d'encouragement à la recherche universitaire, attributed to JA by the Government of New Caledonia. The bioacoustic study was supported by a grant from the Grand Observatoire du Pacifique Sud: AAP GOPS 2013 / 'Bioacoustique des grillons de Nouvelle-Calédonie'. The laboratory procedures were realized through the two research programs: Action Transversale du Muséum (ATM) 'Biodiversité actuelle et fossile. Crises, stress, restaurations et panchronisme: le message systématique', and ATM 'Barcode'

8.9 Supporting information

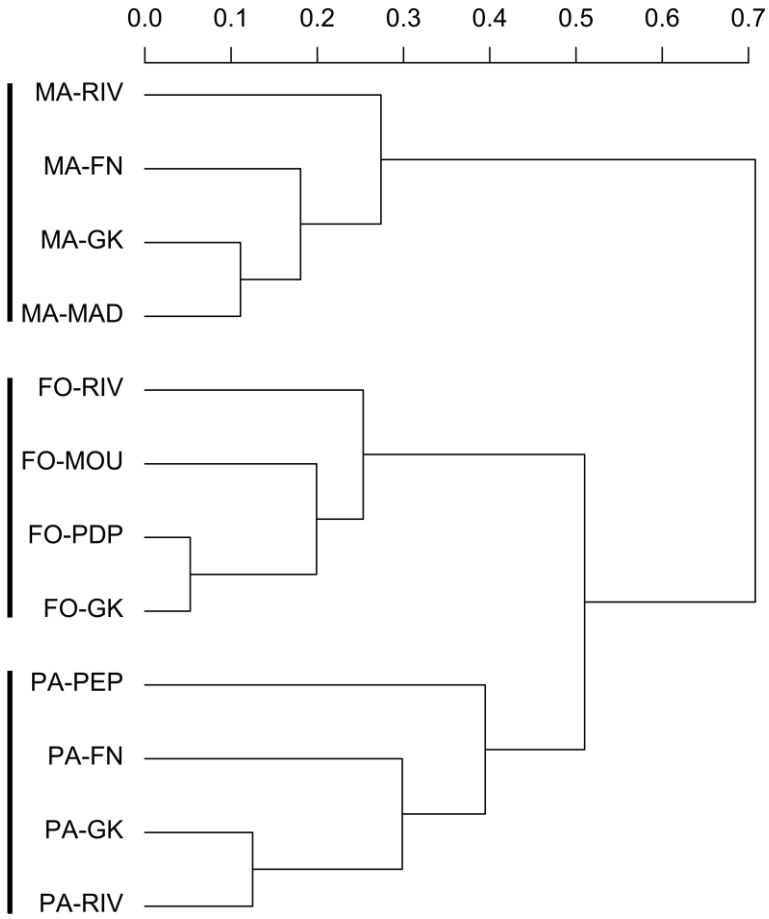

Figure 8.7. *Dendrogram of the study sites based on dissimilarity matrix of cricket presence/absence obtained with Bray-Curtis distance (values indicated in the top of the dendrogram), and constructed using hierarchical clustering with average method*

9 Discussion générale, applications et perspectives

9.1 Enrichissement de la biodiversité calédonienne

La Nouvelle-Calédonie possède une faune de grillons unique, riche et très diversifiée (Chopard, 1915; Gorochov, 1986; Otte *et al.*, 1987; Desutter-Grandcolas, 1997d, e; Robillard & Desutter-Grandcolas, 2006; Robillard, 2010). Au cours de notre travail de recherche, nous avons pu contribuer à enrichir les connaissances fondamentales sur la biodiversité de ce groupe de macro-arthropodes, avec trois nouveaux genres et 22 nouvelles espèces décrites portant ainsi ce groupe à plus de 40 genres et 180 espèces avec un endémisme supérieur à 95% (Chapitre I, section 3 & Chapitre II, section 4).

L'intégralité de nos collectes *in situ* a été réalisée dans le sud de la Grande Terre, au niveau du bouclier ultramafique qui recouvre pratiquement un tiers de l'île (Cluzel *et al.*, 2012). Cette intense campagne d'échantillonnage, menée dans une région localisée, laisse supposer qu'une partie encore importante de la biodiversité de l'archipel demeure inconnue pour la science. Cette partie encore inexplorée de la biodiversité calédonienne est renforcée par le patron de répartition généralement restreint des espèces de grillons, ainsi que d'autres groupes terrestres, présentent sur le territoire (i.e. microendémisme) (Grandcolas *et al.*, 2008; Nattier *et al.*, 2011; Nattier *et al.*, 2012). Ainsi, nous imaginons que des collectes complémentaires dans la partie septentrionale de l'île et aux Iles Loyautés voisines, sur d'autres types de sols (i.e. volcano-sédimentaire, calcaire) et de formations végétales différentes (i.e. forêts sèches, forêts denses sur substrats non ultramafiques), pourraient permettre de découvrir de nouveaux assemblages faunistiques, avec des communautés locales de grillons présentant des nouvelles espèces, notamment chez les clades abondants tels que les Nemobiinae (Anso *et al.* 2016. *Zootaxa*). Ces nouveaux assemblages et ces nouvelles espèces devraient augmenter probablement le taux d'endémisme, déjà très élevé pour ce groupe d'insectes.

Par ailleurs, l'un des résultats forts de notre travail de thèse concerne la mise en évidence de l'importance des habitats dégradés (i.e. maquis miniers arbustifs) en termes de biodiversité et d'enjeu de conservation, ainsi que les stades plus avancés (i.e. maquis paraforestiers) qui

abritent également des assemblages uniques et représentatifs d'une réelle succession écologique (Chapitre II).

Les nouvelles données taxonomiques obtenues ont également permis de valoriser des années de travail et de connaissances indispensables pour l'identification des représentants de ce groupe d'insectes, avec la finalisation d'une clé d'identification des genres de Nouvelle-Calédonie (Desutter-Grandcolas, Anso & Jourdan, 2016, *soumis*.) (Chapitre I, section 3). Ce travail de synthèse des données taxonomiques les plus récentes, valorisé sous la forme d'une clé d'identification des genres présents en Nouvelle-Calédonie, est fondamental pour tous les futurs projets de recherche ou de conservation sur le territoire néo-calédonien. Faciliter ainsi les identifications de ce groupe d'insectes est une condition importante pour généraliser son utilisation à des fins de conservation par la communauté scientifique et les gestionnaires (McGeoch *et al.*, 2011; Gerlach *et al.*, 2013).

Parmi ces découvertes taxonomiques inédites de Nouvelle-Calédonie, nous soulignons la découverte d'une nouvelle espèce d'Eneopterinae, appartenant à un nouveau genre (*Pixibinthus sonicus*, Anso & Robillard 2015, Chapitre II). Ce taxon possède une histoire évolutive inédite, et contribue à lever un voile sur les dynamiques paysagères passées en Nouvelle-Calédonie, et notamment sur l'influence du régime des oscillations climatiques et des feux sur les formations végétales et espèces animales associées (Chapitre II, section 5). Cette espèce qui est l'unique représentante de ce nouveau genre a été décrite en tant que groupe frère des *Agnotecous*, des grillons forestiers de grande taille endémiques de la Grande Terre, et caractérisé par une fréquence dominante pour le chant d'appel comprise entre 11 et 18 kHz (Robillard *et al.*, 2010; Nattier *et al.*, 2012). *P. sonicus*, quant à lui, n'est connu que de zones d'habitat ouvert (maquis arbustifs et paraforestiers) ; il est plus petit et la fréquence dominante de son chant d'appel est située entre 30 et 40 kHz, faisant de ce grillon l'espèce émettant dans les fréquences ultrasonores parmi les plus élevées (Robillard, 2009). Cette découverte illustre l'effet d'une spécialisation contrastée pour les milieux ouverts d'une part, avec *P. sonicus*, et pour les milieux fermés d'autre part, avec le genre *Agnotecous*. Cette spécialisation écologique pour les milieux ouverts aurait ainsi exposé davantage *Pixibinthus* aux phénomènes climatiques et aux feux, expliquant l'absence d'une diversification de ce groupe (comparé aux 19 espèces chez *Agnotecous*) ou bien l'existence d'extinction localisée sous pression du climat et de l'augmentation du régime d'incendies sous contraintes anthropiques (Hope & Pask, 1998; Stevenson, 2004; Curt *et al.*, 2015; Gomez *et al.*, 2015).

9.2 Les grillons sont-ils des bio-indicateurs pertinents ?

9.2.1 L'étude des peuplements de grillons par inventaire taxonomique

L'une des parties centrales de notre travail de recherche a porté sur l'étude de la structure et de la composition des communautés de grillons en fonction (i) des formations végétales dans une succession écologique sur sols issus de roches ultramafiques et (ii) de la présence de fourmis envahissantes (Chapitre II, sections 5 et 6). Dans un premier temps, la richesse spécifique, l'abondance et la structure des communautés de grillons ont été comparées au sein de trois formations végétales caractéristiques du sud de la Nouvelle-Calédonie : les maquis arbustifs bas, les maquis paraforestiers et les forêts denses mixtes sur substrat ultramafique. Dans un second temps, ces communautés de grillons dans nos trois habitats ont été comparées selon les mêmes conditions d'habitat, mais eux-mêmes soumis à l'invasion de deux fourmis envahissantes majeures, la petite fourmi de feu (*Wasmannia auropunctata*) et la fourmi folle jaune (*Anoplolepis gracilipes*).

L'objectif de notre travail de thèse était donc double :

(1) Déterminer l'effet d'une succession forestière sur la composition et la structure des communautés de grillons associées.

(2) Identifier l'impact d'invasions biologiques sur les communautés de grillons de ce gradient forestier.

9.2.1.1 Dans le cadre d'une succession forestière

A l'inverse des communautés de Caelifera et de Tettigoniidea (i.e., respectivement les criquets et les sauterelles) dont les abondances et les richesses spécifiques augmentent dans les milieux ouverts et se raréfient dans les milieux fermés (Marini *et al.*, 2009; Fartmann *et al.*, 2012), nous attendions chez les grillons une augmentation progressive de la richesse spécifique et de l'abondance dans la succession forestière vers les stades les plus avancés et les plus fermés (i.e., maquis paraforestiers puis forêts denses mixtes), avec une spécialisation des espèces pour chaque habitat.

Nos résultats permettent de distinguer les habitats selon l'organisation des communautés de grillons (voir Chapitre II, section 5). Au sein de la succession forestière, la richesse

spécifique cumulée (i.e. le nombre total d'espèces tous sites confondus) suit le gradient sélectionné avec les richesses les plus élevées observées pour les forêts denses mixtes (20 espèces), puis pour les maquis paraforestiers (14 espèces) et les maquis arbustifs bas (7 espèces). Ces résultats préliminaires obtenus en Nouvelle-Calédonie rejoignent ceux de Szinwelski *et al.* (2012) menés au Brésil sur les communautés de grillons exclusivement. Ces auteurs indiquent une augmentation progressive de la richesse spécifique au sein de la succession forestière étudiée (de 0 à 150 ans), et jusqu'à l'obtention d'un « plateau » (de 150 à 300 ans environ), ainsi qu'une spécialisation des espèces en fonction du stade sélectionné (sept stades sélectionnés : 0, 6, 15, 35, 70, 130, 300 ans) (Szinwelski *et al.*, 2012).

Toutefois, la richesse stationnelle (i.e. la richesse moyenne des espèces par habitat) et l'abondance augmentent au sein de la succession entre les deux premiers stades de la succession (maquis arbustifs et maquis paraforestiers) mais se stabilisent entre les deux derniers stades de la succession (maquis paraforestiers et forêts mixtes). Au final, il n'y pas de recouvrement faunistique entre les termes de la succession, principalement expliqué par la présence de cortèges uniques d'espèces (i.e. *turnover* des espèces) : la communauté des maquis arbustifs est complètement distincte dans sa composition de celle des forêts denses humides. Par contre, les maquis paraforestiers possèdent le pourcentage le plus faible d'espèces uniques de ces habitats (deux sur 14), mais hébergent une partie des espèces de maquis arbustifs et de forêts denses humides. Il existe des espèces spécifiques de la forêt et des espèces spécifiques du maquis. Il y a bien une succession de communautés de grillons dans le contexte de la succession écologique végétale rencontrée sur roches ultramafiques, avec un *turnover* complet de la composition des espèces entre les premiers stades de la succession (i.e. les maquis arbustifs), et les derniers stades (i.e. les forêts denses humides), en réponse à des conditions de milieux très contrastées (milieu ouvert très fluctuant du point de vue des conditions climatiques versus milieu fermé tamponné).

Nos résultats soulignent que les milieux fermés et forestiers offrent des conditions bioclimatiques favorables au développement d'importantes populations de grillons ainsi qu'à une diversité spécifique plus élevée, phénomène sans doute amplifié par la stratification de ces milieux plus complexes (opportunité de niches). En effet, dans notre succession écologique forestière, les maquis paraforestiers et les forêts denses humides possèdent une canopée presque entièrement recouvrante et plusieurs strates de végétation, un facteur augmentant la complexité de la structure des habitats, et permettant ainsi d'augmenter les niches écologiques disponibles pour les différentes espèces de grillons (Shik & Kaspari,

2010). La fermeture de la canopée pourrait également être associée à l'augmentation de ressources alimentaires disponibles (e.g., fruits, accumulation de litière) (Barberena-Arias & Aide, 2003; Williams *et al.*, 2008), des abris contre les prédateurs (Brouwers & Newton, 2009), et des conditions d'humidité plus favorables pour les communautés de grillons (McCluney & Date, 2008). De plus, la litière qui recouvre le sol de la quasi-totalité des maquis paraforestiers et des forêts denses humides offre des opportunités accrues de sites de ponte lesquels sont importants pour toutes les espèces qui pondent leurs œufs directement dans la litière ou dans le sol (Huber, 1989).

A l'opposé, les maquis miniers bas (arbustif/ligno-herbacés) qui représentent les premiers stades de notre succession n'apportent pas des conditions aussi favorables que les stades plus avancés de la succession écologique. Ces maquis bas sont caractérisés par l'absence de canopée, une faible stratification et l'absence de litière recouvrante. Ces habitats sont caractérisés par une litière peu épaisse et localisée seulement sous forme d'îlots de végétation, isolés les uns des autres par des espaces de sol nu. L'ensemble de ces conditions semble limiter à la fois les ressources alimentaires disponibles, les abris contre les prédateurs, les conditions thermo-hygrométriques favorables ainsi que la diversité des niches pour l'installation des différentes espèces.

Nos travaux préliminaires sur cette faune spécifique de l'archipel néo-calédonien nous permettent de confirmer une sensibilité et spécificité aux différentes conditions (bioclimatiques) des habitats dans lesquels ils évoluent. La faune de grillons pourrait tenir en Nouvelle-Calédonie un rôle majeur en tant que bio-indicateur de la restauration ou de la régénération des habitats, à travers l'analyse des communautés et l'identification d'espèces spécifiques, et particulièrement sensibles aux conditions des milieux.

9.2.1.2 Dans le cadre d'invasions biologiques

Deux invasions biologiques par des fourmis exotiques ont été considérées au cours de ce travail de thèse afin de mesurer leur impact sur la structure et la composition des communautés de grillons.

Premièrement, l'impact de la petite fourmi de feu (*Wasmannia auropunctata*) a été mesuré sur les communautés de grillons en forêts denses humides, en maquis paraforestiers et en maquis arbustifs bas. Dans les trois habitats considérés, les communautés de grillons sont

virtuellement absentes. Aucune espèce n'a été collectée dans les maquis arbustifs et les maquis paraforestiers, tandis que trois espèces représentées par cinq individus ont été collectées en forêts denses humides envahies par la fourmi, contre 20 espèces et plus de 400 individus dans les forêts denses humides non envahies (Chapitre II, section 6). Ces résultats préliminaires en Nouvelle-Calédonie confirment l'impact extrêmement négatif de *W. auropunctata* sur les communautés animales terrestres dans les milieux nouvellement envahis (Lubin, 1984; Jourdan, 1997; Jourdan *et al.*, 2001; Wetterer & Porter, 2003; Walker, 2006).

Ainsi, nos résultats apportent la première évidence de la sensibilité très prononcée de cette faune de macro-arthropodes face à une fourmi envahissante introduite dans de nombreuses régions à travers le monde. En effet, la littérature disponible sur ce sujet demeure rare en dehors de l'impact sur les communautés de fourmis (Jourdan, 1999; Le Breton *et al.*, 2003). Les travaux sur ce sujet ont principalement porté sur *Solenopsis invicta* (Nichols, 1989; Porter & Savignano, 1990), *Pheidole megacephala* (LaPolla *et al.*, 2000; Krushelnycky & Gillespie, 2010) et *Linepithema humile* (Human & Gordon, 1997) avec des effets contrastés.

Bien que les mécanismes d'exclusion de la faune de grillons par *Wasmannia auropunctata* n'aient pas été explorés au cours de ce travail de recherche, plusieurs hypothèses, incluant de la compétition par interférence, de la prédation directe ou de la gène passive, entrainant le déplacement des populations de grillons (à tous les stades de développement, ou seulement pour les plus jeunes stades larvaires) pourraient être à l'origine du dépeuplement massif observé en zones envahies (voir Chapitre II, section 6).

Deuxièmement, l'impact de la fourmi folle jaune (*Anoplolepis gracilipes*) a été mesuré sur les communautés de grillons, mais dans une seule modalité d'habitat (maquis arbustifs bas). Bien que préliminaire, faute de répétition dans d'autres conditions d'habitats (*A. gracilipes* se rencontre également en conditions de maquis paraforestiers et très rarement en forêt), nos résultats contrastent fortement avec ceux de *Wasmannia auropunctata*. Ainsi, nous n'avons observé aucune différence sur la richesse spécifique et l'abondance des communautés de grillons entre les maquis arbustifs envahis et non envahis pour *A. gracilipes*. Malgré des abondances très élevées d'*A. gracilipes*, avec plusieurs nids relevés aux abords des îlots de végétation, les grillons de litière tels que *Koghiella flammea* et *Mogoplistidae sp1* ont été abondamment retrouvés sur les sites envahis. Aucun acte de prédation n'a par ailleurs été observé durant les périodes d'échantillonnages à l'encontre des grillons dans les maquis

envahis par la fourmi folle jaune, ni aucune observation de transport de proie par ces fourmis vers leurs nids ou de présence de ces proies à l'intérieur des nids (J. Anso, obs. pers.).

Le défaut d'impact suspecté d'*A. gracilipes* en Nouvelle-Calédonie doit être cependant mis en perspective avec d'une part, son statut de nuisance environnementale observé dans de nombreuses autres régions du monde, entraînant l'effondrement de plusieurs communautés d'invertébrés (Holway *et al.*, 2002; Lester & Tavite, 2004; Bos *et al.*, 2008; Hoffmann & Saul, 2010), et d'autre part, avec une possible phase de latence durant laquelle les populations restent relativement faibles sans impact significatif. *A. gracilipes* serait ainsi selon plusieurs auteurs en phase de latence sur l'archipel (Jourdan & Mille, 2006; Berman *et al.*, 2013a; Berman *et al.*, 2013b), malgré une présence estimée en Nouvelle-Calédonie antérieure à 1881 (Emery, 1883).

Dans les sites de maquis arbustifs étudiés, la faune de grillons ne semble donc pas affectée par l'invasion et ne pourrait donc pas être utilisée pour détecter la présence de cette fourmi envahissante en Nouvelle-Calédonie. Ce résultat nous rappelle le caractère variable et contexte-dépendant de la bio-indication mais également de la nature de l'impact mesuré.

9.2.2 Recommandations appliquées en conservation

Nos résultats obtenus par des échantillonnages taxonomiques sur le terrain sont encourageants quant à l'utilisation des grillons en Nouvelle-Calédonie en tant que bio-indicateur de l'intégrité et de la régénération des habitats forestiers sur substrats issus des roches ultramafiques. La réponse la plus forte de la communauté des grillons a été observée en présence de *Wasmannia auropunctata*. D'après nos seuls échantillonnages, la présence de *W. auropunctata* est associée avec une perte très marqué des communautés de grillons, et cela dans tous les habitats considérés au cours de notre travail de thèse. La faune de grillon pourrait être à ce titre un "détecteur" pertinent (i.e. un élément diagnostique) de ce stress écologique majeur. Sous réserve d'études complémentaires pour affiner le diagnostique environnemental associé, ces bio-indicateurs pourraient être intégrés à des programmes de suivi de la biodiversité en tant qu'alarme d'un dysfonctionnement écosystémique. Ainsi, les programmes de suivi des milieux naturels et de leur régénération pourraient s'appuyer sur le suivi de cette faune particulière d'insectes, sensibles aux modifications de l'environnement.

A propos des successions écologiques, plusieurs espèces de grillons ont été observées uniquement dans un seul type d'habitat, indiquant un potentiel rôle de bio-indicateur de la

régénération de la forêt. Ainsi, parmi les Phalangopsidae, *Pseudotrigonidium caledonica*, *Protathra nana*, ou encore au sein des Gryllidae *Adenopterus meridionalis* pourraient marquer des stades avancés de régénération forestière pour lesquels les conditions bioclimatiques (e.g., humidité, température) et écologiques (e.g., disponibilité de l'habitat) sont compatibles avec leur maintien à long terme (Fig. 9.1). Ainsi, la faune de grillons de Nouvelle-Calédonie, mais également celles présentes dans les autres régions du globe, apparaît comme un groupe candidat pour servir de bio-indicateur pertinent à l'occasion de campagnes d'échantillonnages menées dans les milieux fermés, dans le cadre de suivis environnementaux.

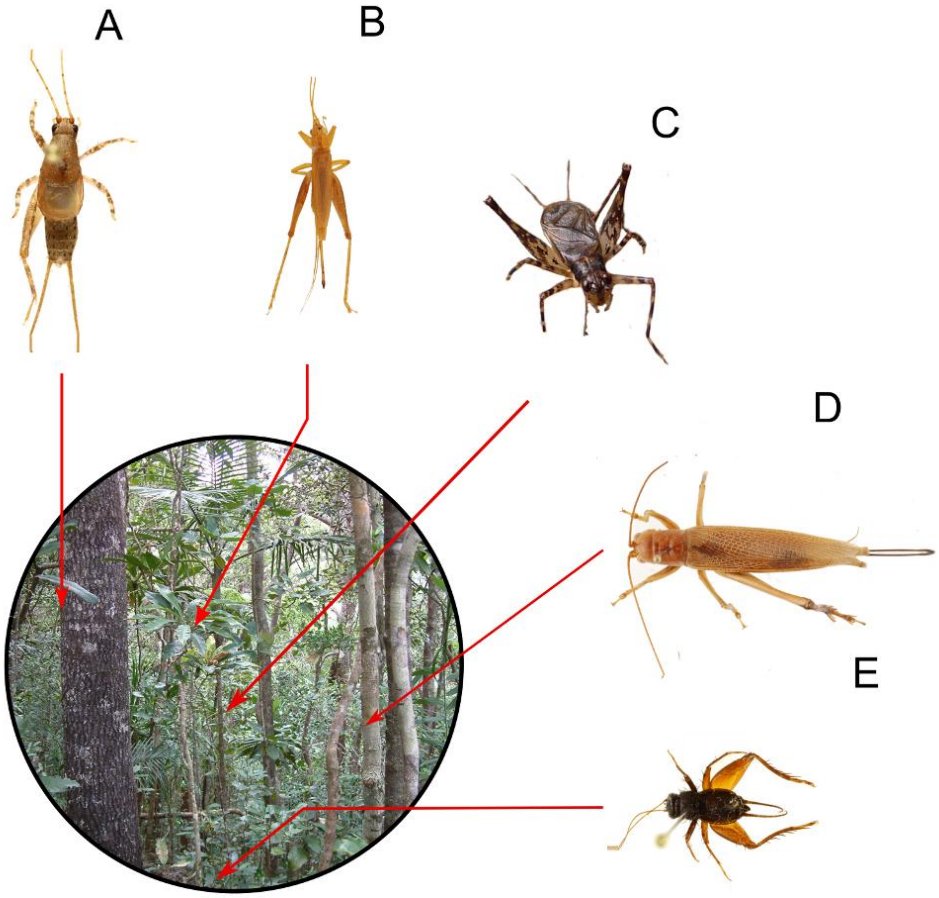

Figure 9.1. *Stratification des postes de chants de cinq espèces indicatrices des forêts denses humides sur substrat ultramafique, avec (A) Mogoplistidae sp7, (B) Adenopterus meridionalis, (C) Pseudotrigonidium caledonica, (D) Calscirtus magnus et (E) Bullita mouirangensisi. Ces cinq espèces sont des bio-indicateurs potentiels des stades avancés d'une succession forestière.*

Toutefois, l'utilisation des grillons nécessite des connaissances taxonomiques spécifiques associées à un important effort de terrain pour échantillonner les spécimens. Il y a un investissement également important au laboratoire après les échantillonnages sur le terrain pour les préparer, les conditionner, les conserver dans de bonnes conditions puis les identifier formellement avec les outils de la systématique classique (morphologie, morphométrie). Devant l'importante diversité de la faune de grillons présente en milieux tropicaux, qui nécessite un travail taxonomique conséquent dans l'identification des espèces connues et inconnues, le développement d'outil complémentaire de mesure de la biodiversité est un enjeu majeur. A ce titre, les signaux acoustiques produits par les mâles pour attirer les femelles, et qui sont hautement spécifiques de l'espèce émettrice, peuvent être utilisés et valorisés dans l'estimation globale de la diversité de cette faune principalement chanteuse.

9.3 Utilisation des signaux acoustiques pour l'évaluation de l'ambiance acoustique globale et de la communauté de grillons

Deux volets de ce travail de recherche ont été consacrés à l'analyse des signaux sonores enregistrés par boîtiers automatiques sur les deux gradients de perturbation étudiés (i.e., la succession forestière et la présence d'une fourmi invasive majeure) en suivant deux méthodologies différentes (Chapitre III et IV). Dans un premier temps, tous les fichiers sonores enregistrés sur le terrain ont été analysés d'une manière globale, sans identification préalable des espèces émettrices, à l'aide d'indice de diversité acoustique (i.e., notamment l'indice des pics fréquentiels, NP, développé initialement par Gasc *et al.* (2013) en Nouvelle-Calédonie). Dans un second temps, un sous-échantillonnage des fichiers sonores a été analysé par l'oreille humaine afin d'identifier tous les groupes chanteurs (i.e., oiseaux, grillons, sauterelles, autres), pour ensuite réaliser une identification complète de toutes les espèces de grillons émettrices dans les enregistrements en comptabilisant les vocalisations.

9.3.1 Analyse globale des ambiances sonores

A travers l'enregistrement des ambiances sonores ou des 'paysages sonores' avec des boîtiers enregistreurs étanches et autonomes (SongMeter, Wildlife Acoustics, concord, NY, U.S.A), nous avons analysé globalement et sans identification toutes les émissions acoustiques des espèces animales au sein de notre succession forestière (maquis arbustifs, maquis paraforestiers et forêts denses humides), avec ou sans la fourmi invasive *Wasmannia*

auropunctata. Seuls les éléments constitutifs de la biophonie des habitats étudiés (ensemble des productions sonores d'origine animale (e.g., oiseaux, insectes en particulier orthoptères dont les grillons, grenouilles, geckos, mammifères…) ont été pris en considération (Pijanowski *et al.*, 2011a; Pijanowski *et al.*, 2011b) ; les fichiers sonores contenant des sons d'origine humaine (anthrophonie) ou géophysique (e.g., pluie, vent fort, bruissement de feuilles) n'ont pas été pris en compte (voir Chapitre III, section 7).

Sur la base de 15 jours d'enregistrements en continue (2 min toutes les 28 min), les premiers résultats nous ont permis de distinguer les habitats envahis par *W. auropunctata,* des habitats non envahis. Ainsi, les comparaisons des indices NP (i.e. le nombre de pics fréquentiels des espèces animales) suivent le même patron avec une réduction significative de la valeur de l'indice avec la présence de la fourmi invasive, dans les trois stades de la succession forestière (Gasc, Anso *et al.*, 2015, *in prep.*). L'indice NP mesure la complexité du spectre fréquentiel dans les bandes sonores, et estime donc la diversité acoustique sur la base des différentes signatures fréquentielles. Ces résultats semblent donc indiquer une simplification de la diversité acoustique en présence de *W. auropunctata*. Cette baisse significative de la diversité acoustique pourrait être la conséquence d'une érosion des communautés acoustiques, notamment des communautés de grillons. En effet, nos résultats précédents indiquent que cette faune s'est révélée très sensible à l'invasion de *W. auropunctata* (Chapitre II, section 6), avec une exclusion quasi-intégrale des individus (Anso et al. 2016, *in prep*). De plus, l'indice NP semble particulièrement adapté aux ambiances sonores composées de grillons puisque plusieurs travaux indiquent que les grillons chanteurs d'une communauté se partitionnent selon le spectre fréquentiel (Schmidt *et al.*, 2013; Jain *et al.*, 2014; Schmidt & Balakrishnan, 2015).

A notre connaissance, les méthodes d'analyses globales des signaux sonores basées sur des indices de diversité n'ont jamais été appliquées à la détection d'une espèce envahissante *in situ*. En la matière, nos résultats préliminaires constituent donc une première dans la détection d'une espèce envahissante silencieuse et cryptique telle que la petite fourmi de feu, dans différents habitats caractéristiques d'une succession forestière. L'idée de réaliser le suivi d'une espèce envahissante à travers son impact sur le paysage sonore a déjà été suggérée par Farina *et al.* (2011) avec l'exemple du passereau Léiothrix jaune (*Leiothrix lutea*). Cet oiseau invasif pourrait directement modifier et interférer par les vocalisations qu'il produit avec les ambiances sonores naturelles, mais également indirectement en menaçant l'établissement d'espèces d'oiseaux natives qui participent au paysage sonore (Farina *et al.*,

2011). La détection de cette espèce pourrait donc se réaliser directement par l'analyse des ambiances sonores, et la détection automatique des vocalisations qu'il émet. Dans cette logique, Kottege *et al.* (2015) ont fourni des résultats préliminaires permettant la détection automatique d'un poisson d'eau douce invasif (*Tilapia mariae*) en condition de laboratoire. Ce type de résultats montre un taux élevé de détection en condition contrôlée et suggèrent que des suivis de l'ambiance sonore pourraient être mis en place en condition naturelle, dans des cours d'eau afin de réaliser des suivis en temps réel de la propagation de cette espèce envahissante (Kottege *et al.*, 2015).

9.3.2 Analyse fine des ambiances sonores à travers les peuplements de grillons

Le second volet de notre travail de recherche (Chapitre IV) axé sur le suivi de la biodiversité en utilisant les signaux sonores des espèces animales se base sur l'identification des différents groupes chanteurs (e.g. oiseaux, insectes dont orthoptères type sauterelles, mammifères, ou autres) et de toutes les espèces de grillons avec le comptage des vocalisations associées. Ces analyses acoustiques fines s'avèrent nécessaires pour caractériser la composition des paysages sonores et permettre ainsi de mieux comprendre les résultats obtenus avec les méthodes globales et les mécanismes associés.

En Nouvelle-Calédonie, la biophonie est donc caractérisée par une disharmonie prononcée, comparée aux autres milieux tropicaux du globe (Aide *et al.*, 2013; Rodriguez *et al.*, 2014). Par exemple, les singes, qui peuvent émettre des vocalisations territoriales sur de très longue distance (Sekulic, 1982) sont absents du territoire. Les amphibiens qui sont fortement représentés ailleurs dans le monde n'occupent qu'une place très réduite en Nouvelle-Calédonie, avec une seule espèce introduite (*Litoria aurea*) (Nicolas *et al.*, 2015) dont l'activité acoustique est limitée aux jours de pluie. En revanche, la biophonie de l'archipel néo-calédonien semble être majoritairement composée de deux groupes (au moins à la saison à laquelle nous avons conduit nos expérimentations): les oiseaux et les grillons. Nos premières analyses d'identification et de quantification des groupes chanteurs confirment cette hypothèse, et indiquent que les grillons sont les principaux acteurs de la biophonie durant la nuit (jusqu'à près de 95% de l'activité sonore produite), tandis qu'ils occupent la seconde place derrière les oiseaux durant la journée. Contrairement aux oiseaux qui concentrent la majorité de leurs productions sonores à l'aube et au crépuscule (on parle de chœurs d'oiseaux), les espèces de grillons chanteurs émettent des signaux sonores d'une manière plus diffuse sur la journée ou la nuit avec une intensification au cours de la nuit, ce

qui est supporté par les pics d'activité acoustique de notre indice NP. Ces premiers résultats sont généralement mis en avant dans les études portant sur les communautés acoustiques (Diwakar & Balakrishnan, 2007a) ou sur les paysages sonores (Bormpoudakis *et al.*, 2013), mais notre étude est à notre connaissance la première qui quantifie précisément la place des groupes acoustiques dans la biophonie d'une région (voir Chapitre IV, section 8).

Par la suite, nous avons réalisé l'analyse écologique des communautés acoustiques de grillons au sein de la succession forestière. Les résultats basés sur la matrice de présence/absence des espèces de grillons nous permettent de distinguer avec fiabilité les trois stades de la succession forestière. Ces résultats indiquent et corroborent les analyses taxonomiques sur la spécificité de cette faune en fonction de l'environnement (Chapitre III), avec notamment pour chaque habitat une ou plusieurs espèces uniques. Les analyses complémentaires basées sur des variables environnementales confirment que la structure de l'habitat est un facteur significatif dans l'organisation de la structure des communautés acoustiques, avec notamment la hauteur et la fermeture de la canopée, le pourcentage de sol nu, le pourcentage de la strate herbacée et le diamètre des troncs.

Toutefois, la richesse spécifique des communautés acoustiques identifiées de jour et de nuit ne suit pas le gradient écologique forestier. Ainsi, la richesse spécifique de jour et de nuit est la plus élevée dans les maquis paraforestiers (6 et 10 respectivement), suivi des forêts denses humides (5 et 9 respectivement) puis des maquis arbustifs bas (2 et 5 respectivement). Cela est cohérent avec le fait que de nombreuses espèces strictement forestières sont aptères, comme les *Caltathra* et plusieurs genres de Nemobiinae.

Finalement, l'effet de la présence de la fourmi envahissante *Wasmannia auropunctata* a pu être estimé selon différentes mesures réalisées sur les communautés acoustiques de grillons. De jour comme de nuit, et dans les trois stades de la succession forestière, toutes les variables mesurées (i.e. la diversité spécifique de grillons chanteurs, l'indice de Shannon et le nombre de stridulations) sont significativement inférieures en présence de *W. auropunctata*, excepté dans les maquis arbustifs en journée. Nos résultats indiquent une disparition très marquée des espèces de litière, telles que *Mogoplistidae sp3*, *Agnotecous clarus*, et *Bullita mouirangensis*, qui sont les plus exposées lors d'une invasion qui s'étend principalement dans la litière. Les espèces de canopée (i.e. *Archenopterus bouensis* et *Calscirtus magnus*) sont toujours présentes dans les habitats envahis par *W. auropunctata* mais accusent une forte

réduction du nombre de stridulations, pouvant révéler l'avancée de l'invasion vers les strates élevées de la végétation (Anso *et al.*, 2015g, *in prep*.).

9.3.3 Recommandations appliquées en conservation

Nos résultats préliminaires obtenus en acoustique, avec l'utilisation d'une méthode globale sans identification et un travail d'identification fine des grillons chanteurs apportent des éléments pertinents dans le suivi et potentiellement pour les méthodes de gestion environnementale associées à la régénération forestière ou de surveillance d'une invasion biologique (i.e. la petite fourmi de feu). En effet, les analyses réalisées à partir de l'indice de diversité acoustique NP, basé sur le nombre de pics fréquentiels, et à partir de l'identification des espèces de grillons permettent sur une durée de 6 à 15 jours de distinguer les stades de la succession forestière et de détecter la présence d'une fourmi envahissante majeure.

En Nouvelle-Calédonie, les services gestionnaires de l'environnement, tels que les parcs naturels du sud de la Grande Terre, pourraient prendre en considération ces suivis acoustiques de la biodiversité des grillons, notamment à travers la recherche des espèces sensibles, identifiées au cours de ce travail de thèse, qui possèdent des conditions bioclimatiques et environnementales d'établissements particulières mais également une sensibilité aux perturbations écologiques, comme l'introduction d'une espèce envahissante. Ainsi, le Phalangopsidae *Pseudotrigonidium caledonica* est une espèce uniquement retrouvée en forêt dense humide, et qui disparait sous la pression de la petite fourmi de feu *Wasmannia auropunctata*. Ce grillon émet un chant d'appel de nuit uniquement, qui est facilement identifiable dans le paysage sonore. Ce chant possède une fréquence dominante de 2.8 kHz, faisant de lui l'un des chants aux plus basses fréquences de Nouvelle-Calédonie, avec une structure temporelle bien spécifique : un trille d'une centaine de syllabes. La présence de ce chant d'appel dans les habitats cibles indique à la fois une régénération forestière avancée, avec des conditions climatiques favorables pour l'installation de l'espèce, ainsi que l'absence d'une invasion biologique comme *W. auropunctata.* De la même manière, *Agnotecous meridionalis* et *Bullita mouirangensis* sont tous les deux uniquement présents dans les forêts denses humides et disparaissent sous l'invasion de la petite fourmi de feu. Ils possèdent des chants d'appels ayant des structures temporelles et spectrales uniques et pourraient être intégrés dans des programmes de suivis acoustiques de la biodiversité.

Deux espèces de grillons, *Bullita obscura* et *Notosciobia sp3*, pourraient remplir les mêmes fonctions d'indicateur de la régénération forestière et de la présence de *Wasmannia auropunctata* puisque ces deux espèces sont uniquement présentes en maquis paraforestiers et disparaissent lors de l'invasion de *W. auropunctata.* En maquis arbustif, une seule espèce (i.e. *Mogoplistidae sp3)* possède un chant d'appel aisément reconnaissable. Cette espèce pourrait donc indiquer les premiers stades d'une succession forestière.

9.4 Perspectives de recherche

9.4.1 Reconnaissance automatique des signaux sonores

Les méthodes de suivi de la biodiversité par les enregistrements acoustiques automatiques permettent de récolter des quantités importantes de données, d'une manière non invasive et sur de grandes surfaces. Comme nous l'avons vu, ces données peuvent être soit directement exploitées sans identification spécifique à l'aide d'indices de biodiversité (Sueur *et al.*, 2008; Farina *et al.*, 2011; Gasc *et al.*, 2013; Sueur *et al.*, 2014), soit finement analysées afin d'identifier toutes les espèces présentes (Aide *et al.*, 2013) (Chapitre III, section 7). Cette dernière procédure peut s'avérer très longue puisque les fichiers sonores doivent être analysés à vitesse réelle. La vitesse de cette méthode d'analyse peut toutefois être augmentée avec la visualisation simultanée des sonagrammes au cours de l'écoute effective des fichiers sonores (Truskinger *et al.*, 2013) (voir Fig. 9.2).

A la frontière entre l'identification manuelle des espèces et l'utilisation d'indices acoustiques globaux, la reconnaissance automatique des signaux représente l'alternative la plus prometteuse pour permettre le traitement rapide d'importantes quantités de données, en évitant le long travail d'identification manuelle, avec des taux d'identifications positifs de plus en plus élevés (Acevedo & Villanueva-Rivera, 2006; Acevedo *et al.*, 2009; Potamitis *et al.*, 2009; Potamitis, 2014). Les programmes de reconnaissance automatique se basent sur l'analyse de la fréquence dominante des harmoniques, de la périodicité du signal ou bien des caractéristiques temporelles (e.g. répétitions de syllabes) (Potamitis, 2014). Chez plusieurs espèces de chauve-souris, la performance des réseaux de neurones artificiels pour identifier les écholocations a été comparée avec des identifications réalisées par des humains expérimentés (Jennings *et al.*, 2008). Les auteurs de l'étude indiquent que les réseaux de neurones artificiels ont été plus performants que les humains, avec un rendement supérieur à

75% (Jennings *et al.*, 2008). Les méthodes d'apprentissages automatiques utilisant des transformations du signal permettent de distinguer très efficacement plusieurs espèces émettrices simultanément, avec par exemple plus de 96% d'identifications positives chez 13 espèces d'oiseaux (Briggs *et al.*, 2012). Potamitis *et al.* (2009) ont également utilisé des protocoles d'apprentissages automatiques pour détecter la présence de deux charançons qui ravagent les plantations de palmiers, *Rhynchophorus ferrugineus* Olivier 1780, et le riz dans les silos de stockage, *Sitophilus oryzae* Linnaeus 1763. Lors d'essais en conditions naturelles, les auteurs indiquent des taux de détection positifs très élevés, de 99,1% pour *R. ferrugineus* et de 100% pour *S. oryzae (*Potamitis *et al.*, 2009*).* La reconnaissance automatique des signaux sonores a été appliquée sur les chants des Orthoptères, qui émettent des signaux sonores généralement stéréotypés et simples, tant sur la structure temporelle que spectrale. Ainsi, plusieurs travaux utilisant des méthodes d'apprentissages automatiques ou des réseaux de neurones artificiels ont permis d'obtenir des taux d'identifications positifs très élevés pour de nombreuses espèces. Chesmore (2001) a obtenu 100% d'identification automatique positive en utilisant des réseaux de neurones artificiels chez 13 espèces de grillons et de criquets dans des conditions peu bruyantes. En conditions naturelles, Chesmore & Ohya (2004) atteignent des taux d'identifications réussis entre 70 et 100% pour quatre espèces de criquets. Les auteurs indiquent que le système de reconnaissance automatique a également permis de discriminer des sons émis par des oiseaux et par les humains ('anthrophonie') (Chesmore & Ohya, 2004). Uniquement chez les grillons, plusieurs travaux utilisant les propriétés temporelles et spectrales des signaux acoustiques obtiennent des taux d'identifications positifs très élevés, de l'ordre de 93,5% chez 28 espèces (Dietrich *et al.*, 2004), et de 93,4% chez 35 espèces (Schwenker *et al.*, 2003).

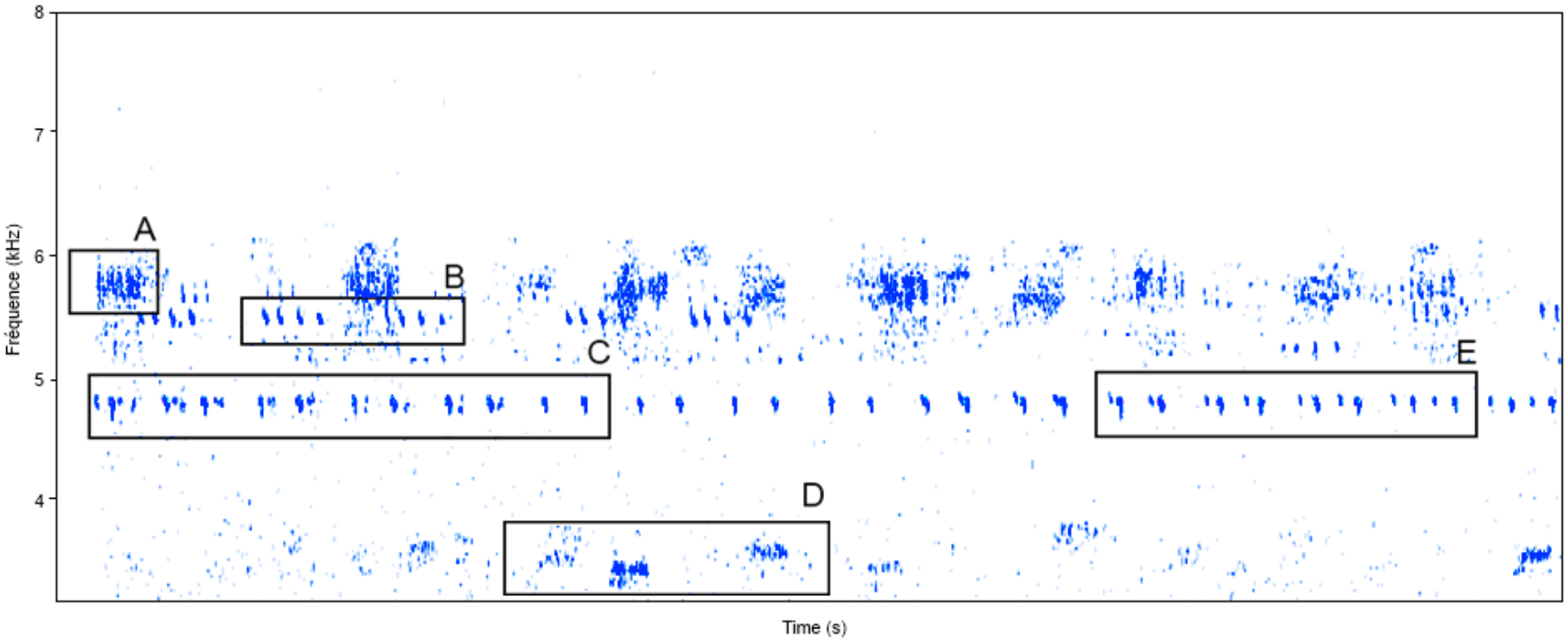

Figure 9.2. *Exemple d'un sonagramme de l'ambiance sonore d'un maquis arbustif non envahi au Pic du Grand Kaori, le 2 octobre 2013 à 19h, visualisé à l'aide du logiciel d'analyse GoldWave (v 5.25). Le sonagramme nous indique que quatre espèces sont en train d'émettre des signaux acoustiques (A, B, C et D). Dans cet exemple, le sonagramme de l'espèce A est difficile à interpréter mais l'écoute à l'oreille permet d'identifier* Koghiella flammea*. L'espèce B et C sont aisément identifiables à l'aide de la structure du chant d'appel (des motifs quadrisyllabiques pour l'espèce B et disyllabiques pour l'espèce C) et avec l'écoute du chant. L'espèce B correspond à* Mogoplistidae sp2 *et* Mogoplistidae sp1 *pour l'espèce C. Dans l'encadré E, on peut différencier deux individus* Mogoplistidae sp1 *qui émettent simultanément. L'espèce D enregistrée ici correspond à* Calscirtus magnus, *un grillon de canopée de la forêt à proximité qui émettent des chants puissants mais non pris en compte dans l'analyse du maquis arbustif.*

La reconnaissance automatique des signaux acoustiques émis par les grillons ou d'autres groupes nécessite une base de données acoustiques conséquente et de bonne qualité sur l'ensemble d'une région (Lehmann *et al.*, 2014). Des enregistrements uniques pour chaque espèce doivent être à disposition afin de calibrer les logiciels d'apprentissages automatiques et d'extraire les informations caractéristiques des signaux sonores. Pour les grillons, il faut en plus des enregistrements à différentes températures. En Nouvelle-Calédonie, la faune de grillons bénéficie d'une importante base de données acoustiques (sonothèque Muséum National d'Histoire Naturelle, base de données IMBE /cf Chapitre I -Anso *et al.* 2015), qui pourrait être valorisée par des recherches sur la reconnaissance automatique, afin de généraliser et d'automatiser le suivi de la biodiversité à travers l'écoute des chants des grillons. De plus, les paysages sonores (« *soundscapes* ») de Nouvelle-Calédonie sont principalement dominés par les grillons de nuit, avec des interférences minimes d'autres espèces émettrices (e.g. quelques sturnidés, mammifères ou des cigales). La particularité des paysages sonores calédoniens offre donc une opportunité unique de créer un premier réseau de surveillance acoustique basée sur l'identification automatique des productions sonores des grillons, dont une partie importante a été identifiée durant ce travail de thèse, et de le coupler avec des installations autonomes (i.e. cellules photovoltaïques) qui permettent un suivi en temps réel sur du long terme (Aide *et al.*, 2013).

Cette perspective de recherche apparaît toutefois contrainte par la richesse des îles tropicales telles qu'en Nouvelle-Calédonie, avec les nombreuses nouvelles espèces qui restent à décrire. Cette partie inconnue de la biodiversité pourrait générer des ambigüités et des incertitudes dans l'identification des productions sonores, notamment dans le cas de chants très proches, tant sur la structure temporelle (i.e. *Mogoplistidae sp1* et *M. sp7*) ou spectrale du signal (i.e. *Koghiella flammea* et *Bullita fusca*).

9.4.2 Perspectives de bio-indication des grillons face à d'autres espèces envahissantes

Au cours de ce travail de thèse le rôle d'indicateur écologique des communautés de grillons a été étudié en détail face à la menace de la petite fourmi de feu, *Wasmannia auropunctata*, selon la réponse taxonomique et acoustique des communautés. Dans une moindre mesure, la réponse taxonomique des communautés de grillons a été étudiée face à la menace de la fourmi folle jaune, *Anoplolepis gracilipes*. Toutefois, en conservant les grillons en tant que bio-indicateur potentiel, l'impact d'autres espèces envahissantes terrestres pourrait être évalué à travers la réponse taxonomique et écologique de cette faune sensible. La fourmi

à grosse tête, *Pheidole megacephala*, est présente sur le territoire calédonien avec des impacts négatifs encore non documentés sur le territoire. Une étude réalisée à Hawaï sur le genre *Laupala* Otte 1994 indique que les grillons pourraient être des indicateurs écologiques pertinents pour détecter la présence de cette fourmi invasive, (LaPolla *et al.*, 2000) (LaPolla *et al.*, 2000) (LaPolla *et al.*, 2000) (LaPolla *et al.*, 2000) (LaPolla *et al.*, 2000) (LaPolla *et al.*, 2000) (LaPolla *et al.*, 2000) (LaPolla *et al.*, 2000) (LaPolla *et al.*, 2000) (LaPolla *et al.*, 2000) (LaPolla *et al.*, 2000) les habitats envahis par *P. megacephala* étant virtuellement dépeuplés de grillons (LaPolla *et al.*, 2000).

La fourmi de feu, *Solenopsis geminata* Fabricius 1804, également présente en Nouvelle-Calédonie avec des impacts potentiellement dramatiques sur la faune terrestre (Wauters *et al.*, 2014) pourrait être suivie selon la richesse et l'abondance des communautés de grillons. Selon le même principe développé durant ce travail de recherche, *S. geminata* pourrait entraîner la disparition de nombreuses espèces présentes dans la litière et sur la végétation. Si cette fourmi envahissante impacte elle aussi cette faune sensible, un réseau de surveillance acoustique peut être envisagé dans les habitats à fort enjeu de conservation (i.e. les forêts denses humides, sèches, les maquis climaciques), comme dans les parcs et réserves naturelles, afin d'avertir le plus rapidement possible les autorités compétentes pour l'organisation d'une lutte ciblée.

9.4.3 Vers la détection automatique d'une invasion biologique majeure

Les invasions biologiques menacent directement et indirectement le fonctionnement des écosystèmes, pouvant entraîner des extinctions locales de la biodiversité (Sax & Gaines, 2008), ainsi que des perturbations dans les services rendus par les écosystèmes pour les sociétés humaines (e.g. pollinisation, production de nourriture) (Ricciardi, 2007; Vilà *et al.*, 2009; Vilà *et al.*, 2011; Veer & Nentwig, 2014). Devant l'ampleur de la menace, la gestion des espèces envahissantes est un point majeur des programmes de protection de la biodiversité. Selon Simberloff *et al.* (2013), la gestion la plus efficace des espèces introduites envahissantes créant le moins d'impact négatif et de coût de gestion se base sur la prévention des introductions par un système de contrôle aux frontières, de mise en quarantaine et d'information générale (Figure 1). A l'inverse, la gestion la moins efficace s'observe avec des espèces envahissantes introduites de longue date qui impactent négativement et durablement les écosystèmes, avec des coûts de gestion très important (Pimentel *et al.*, 2005; Kettunen *et al.*, 2009; Kelly *et al.*, 2013). Dans cette problématique, la détection précoce des espèces

envahissantes constitue une alternative efficace après leur introduction dans un nouveau territoire (Simberloff *et al.*, 2013). Ainsi, le suivi et la surveillance des habitats avec l'interception des espèces introduites, et l'extirpation potentielle des individus représentent des moyens de lutte contre les espèces envahissantes.

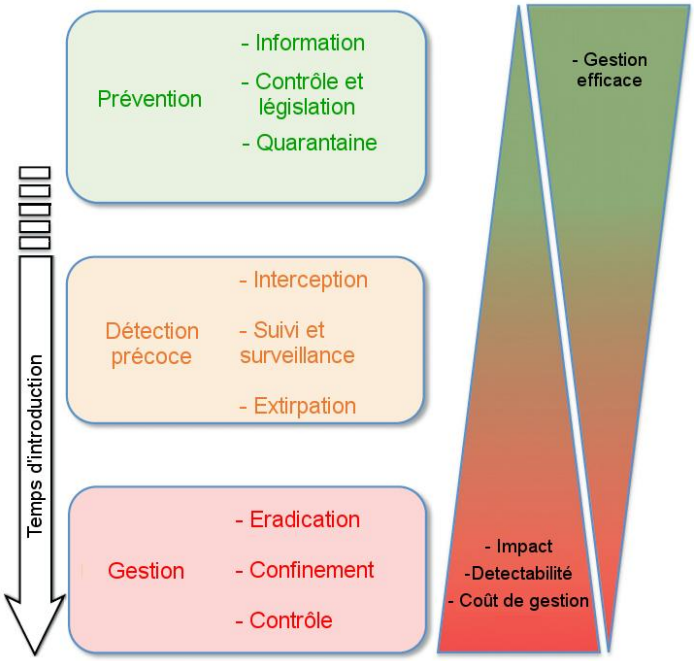

Figure 9.3. *Les stratégies de gestion des espèces envahissantes. La meilleure stratégie évolue en fonction du temps d'introduction : plus le temps d'introduction sera long lors de la détection, plus les coûts associés (éradication / contrôle des espèces envahissantes) seront élevés et les résultats seront plus aléatoires (moindre efficacité pour un règlement définitif de l'invasion). D'après Simberloff et al. (2013).*

Dans ce contexte, le développement de méthode pour améliorer la détection, le suivi et la surveillance des écosystèmes face à la pression des espèces invasives déjà introduites, représente un enjeu important pour limiter les impacts négatifs sur la biodiversité et les services éco-systémiques, mais également pour limiter les coûts de contrôle. Ce travail de recherche propose une méthode préliminaire pour la détection d'une fourmi envahissante, *Wasmannia auropunctata*, d'une manière indirecte en analysant les signaux sonores des communautés terrestres animales impactées par cette invasion biologique. Ainsi, à travers l'analyse automatique des ambiances sonores à l'aide des indices de diversité acoustique, et

notamment l'indice NP, il pourrait être envisagé de détecter automatiquement une perte de diversité acoustique avec la chute de l'indice NP (Fig. 9.4B)

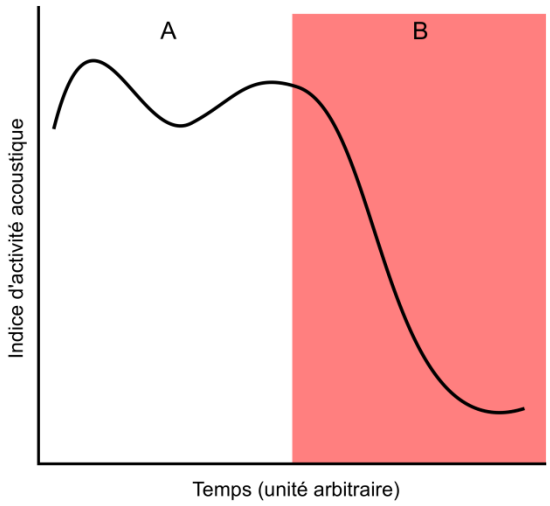

Figure 9.4. *Projection théorique d'un calcul automatisé de l'indice NP, (A) avec la situation sans invasion biologique et (B) la progression de l'invasion avec la chute de l'indice.*

9.5 Conclusions

Dans le contexte de la crise de la biodiversité, nos travaux de recherche apportent des éléments stratégiques dans la perspective de la sélection d'un nouvel indicateur de l'état des écosystèmes dans un point chaud mondial de la biodiversité, en explorant le groupe candidat des grillons.

Cette faune de macro-arthropodes abondante et très diversifiée n'avait jamais fait l'objet d'un travail de recherche pour mesurer leur spécificité et leur sensibilité à différents stades d'une succession forestière et à la présence d'une espèce invasive majeure, *Wasmannia auropunctata*. La sensibilité de cette faune déjà avérée pour certains type de pollution, est dans ce travail étendue jusqu'à la propagation d'une espèce introduite de fourmi envahissante. La spécificité de cette faune aux successions écologiques végétales ouvre des champs de recherche appliqués à la restauration des habitats, notamment dans le cadre d'un suivi de programme de restauration écologique.

La sélection de tels bio-indicateurs représente un outil important pour la mise en œuvre de suivis à long terme de l'état des écosystèmes, mais également pour la détection et l'évaluation de perturbations majeures (i.e. fragmentation, invasion …) qui pourraient affecter les écosystèmes sensibles dans le contexte du changement global. Compte tenu de l'urgence

des pressions et du niveau de l'effort restant à accomplir pour une connaissance plus exhaustive des composantes de la biodiversité, nos travaux fournissent des premiers résultats et ouvrent des perspectives pour la recherche de proxys efficaces pour l'évaluation de l'état de l'environnement au travers de l'étude de la faune des grillons présente en Nouvelle-Calédonie.

Ces résultats restent préliminaires mais sont prometteurs et permettent, d'ores et déjà, de vérifier la pertinence de ce modèle pour un diagnostique environnemental. Ainsi, les grillons sont des macro-arthropodes relativement faciles à collecter sur le terrain. Les adultes, qui sont nécessaires pour les identifications à l'espèce, et se retrouvent principalement dans la litière et sont généralement de taille moyenne pour les *Agnotecous*, et de plus petite taille pour les *Koghiella* ou les *Bullita*. Par ailleurs, au cours des nombreuses sessions d'échantillonnages réalisées sur les grillons dans le milieu naturel, des abondances relativement élevées ont été enregistrées tout au long de l'année, avec toutefois une baisse lors de la « saison sèche » entre mi-octobre à mi-janvier.

La faune néo-calédonienne de grillons présente une importante diversité d'espèces avec des préférences écologiques et de micro-habitats spécifiques (e.g. litière, troncs, rochers, en milieu ouvert ou fermé) et des capacités de dispersion différentes (i.e. colonisation rapide versus lente) potentiellement pertinentes pour estimer des processus de régénération/restauration à différentes échelles de temps, comme le mentionne Gerlach *et al.* (2013) dans sa synthèse sur les invertébrés bio-indicateurs. Ainsi, les premiers stades de restauration d'un habitat pourraient être estimés par la présence d'espèces mobiles, et se déplaçant préférentiellement dans la litière, telles que les *Agnotecous* ou les *Bullita*. D'autres groupes, comme la famille des *Mogoplistidae*, qui s'établissent sur des micro-habitats particuliers et fins (végétation basse, Cypéracées) présentent des capacités de dispersion à priori réduite du fait de leur petite taille. Les espèces de ce groupe pourraient ainsi indiquer la récupération à long terme d'un écosystème. Cependant, pour être opérationnel, l'utilisation d'un tel groupe d'insectes doit pouvoir s'appuyer sur un niveau d'expertise taxonomique disponible suffisant (description taxonomique bien avancée pour le groupe, pour permettre l'identification individuelle des taxons présents). Ce groupe d'insectes bénéficie en Nouvelle-Calédonie d'une expertise taxonomique avancée, en particulier au travers de la connaissance taxonomique accumulée depuis les premières collectes scientifiques (Chopard, 1915; Gorochov, 1986; Otte *et al.*, 1987; Desutter-Grandcolas, 1997b, c, d, e, 2002; Desutter-Grandcolas & Robillard, 2006; Robillard & Desutter-Grandcolas, 2008; Robillard *et al.*, 2010). Ces connaissances pourraient servir de base pour les études écologiques et les

programmes de restauration basés sur la réponse des communautés de grillons. Par ailleurs, notre travail de thèse a permis de compléter l'inventaire, avec notamment la description de trois nouveaux genres et de 21 nouvelles espèces et ainsi que la publication d'une clé d'identification générique des grillons de Nouvelle-Calédonie.

Finalement, les données préliminaires obtenues avec nos analyses de méta-acoustique apportent des perspectives innovantes pour de futurs projets de recherche. La validation et le perfectionnement des analyses acoustiques automatiques pourraient permettre le suivi en temps réel des écosystèmes et de la biodiversité, et motiver l'installation de systèmes de vigies performants permettant de déclencher des plans de gestion ou de sauvegarde dans les milieux considérés (Aide *et al.*, 2013).

10 Références

Abbott, K. L. (2006). Spatial dynamics of supercolonies of the invasive yellow crazy ant, Anoplolepis gracilipes, on Christmas Island, Indian Ocean. *Diversity and Distributions* **12**:101-110.

Acevedo, M. A., Corrada-Bravo, C. J., Corrada-Bravo, H., Villanueva-Rivera, L. J., and Aide, T. M. (2009). Automated classification of bird and amphibian calls using machine learning: A comparison of methods. *Ecological Informatics* **4**:206-214.

Acevedo, M. A. and Villanueva-Rivera, L. J. (2006). Using automated digital recording systems as effective tools for the monitoring of birds and amphibians. *Wildlife Society Bulletin* **34**:211-214.

Aerts, R. and Honnay, O. (2011). Forest restoration, biodiversity and ecosystem functioning. *BMC ecology* **11**:29.

Aide, T. M., Corrada-Bravo, C., Campos-Cerqueira, M., Milan, C., Vega, G., and Alvarez, R. (2013). Real-time bioacoustics monitoring and automated species identification. *PeerJ* **1**:e103.

Albert, V. A., Barbazuk, W. B., Der, J. P., Leebens-Mack, J., Ma, H., Palmer, J. D., Rounsley, S., Sankoff, D., Schuster, S. C., and Soltis, D. E. (2013). The Amborella genome and the evolution of flowering plants. *Science* **342**:1241089.

Alexander, R. D. (1961). Aggressiveness, territoriality, and sexual behavior in field crickets (Orthoptera: Gryllidae). *Behaviour*:130-223.

Alexander, R. D. (1962). Evolutionary change in cricket acoustical communication. *Evolution*:443-467.

Alexander, R. D. and Bigelow, R. S. (1960). Allochronic speciation in field crickets, and a new species, Acheta veletis. *Evolution*:334-346.

Alignan, J.-F., Debras, J.-F., and Dutoit, T. (2014). Effects of ecological restoration on Orthoptera assemblages in a Mediterranean steppe rangeland. *Journal of Insect Conservation* **18**:1073-1085.

Amedegnato, C. (1997). Diversity of an Amazonian canopy grasshopper community in relation to resource partitioning and phylogeny. *Canopy Arthropods. Chapman & Hall, London* **512**.

Amédégnato, C. and Descamps, M. (1980a). Étude comparative de quelques peuplements acridiens de La forêt nèotropicale. *Acrida (9)*:171-216.

Amédégnato, C. and Descamps, M. (1980b). Évolution des populations d'orthoptères d'amazonie du nord-ouest dans les cultures traditionnelles et les formations secondaires d'origine anthropique. *Acrida*.

Amézquita, A., Hödl, W., Lima, A. P., Castellanos, L., Erdtmann, L., and Araújo, M. C. (2006). Masking interference and the evolution of the acoustic communication system in the Amazonian dendrobatid frog Allobates femoralis. *Evolution* **60**:1874-1887.

Anderson, L. G., Rocliffe, S., Haddaway, N. R., and Dunn, A. M. (2015). The Role of Tourism and Recreation in the Spread of Non-Native Species: A Systematic Review and Meta-Analysis. *PLoS ONE* **10**:e0140833.

Angulo, A. and Reichle, S. (2008). Acoustic signals, species diagnosis, and species concepts: the case of a new cryptic species of Leptodactylus (Amphibia, Anura, Leptodactylidae) from the Chapare region, Bolivia. *Zoological Journal of the Linnean Society* **152**:59-77.

Araújo, A. S. F., Eisenhauer, N., Nunes, L. A. P. L., Leite, L. F. C., and Cesarz, S. (2015). Soil Surface-Active Fauna in Degraded and Restored Lands of Northeast Brazil. *Land Degradation & Development* **26**:1-8.

Atkinson, D. (1994). Temperature and organism size: a biological law for ectotherms? *Advances in ecological research* **25**:1-1.

Badiou-Bénéteau, A., Benneveau, A., Géret, F., Delatte, H., Becker, N., Brunet, J.-L., Reynaud, B., and Belzunces, L. (2013). Honeybee biomarkers as promising tools to monitor environmental quality. *Environment international* **60**:31-41.

Banks, P. B. and Dickman, C. R. (2007). Alien predation and the effects of multiple levels of prey naiveté. *Trends in Ecology & Evolution* **22**:229-230.

Barberena-Arias, M. and Aide, T. (2003). Species diversity and trophic composition of litter insects during plant secondary succession. *Caribbean Journal of Science* **39**:161-169.

Bardier, C., Canavero, A., and Maneyro, R. (2014). Temporal and Spatial Activity Patterns of Three Species in the Leptodactylus fuscus Group (Amphibia, Leptodactylidae). *The American Biology Teacher* **9**:106-113.

Barlow, J., Gardner, T. A., Araujo, I. S., Ávila-Pires, T. C., Bonaldo, A. B., Costa, J. E., Esposito, M. C., Ferreira, L. V., Hawes, J., and Hernandez, M. I. (2007). Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. *Proceedings of the National Academy of Sciences* **104**:18555-18560.

Barnosky, A. D., Matzke, N., Tomiya, S., Wogan, G. O. U., Swartz, B., Quental, T. B., Marshall, C., McGuire, J. L., Lindsey, E. L., Maguire, K. C., Mersey, B., and Ferrer, E. A. (2011). Has the Earth/'s sixth mass extinction already arrived? *Nature* **471**:51-57.

Barrabé, L., Maggia, L., Pillon, Y., Rigault, F., Mouly, A., Davis, A. P., and Buerki, S. (2014). New Caledonian lineages of Psychotria (Rubiaceae) reveal different evolutionary histories and the largest documented plant radiation for the archipelago. *Molecular Phylogenetics and Evolution* **71**:15-35.

Barré, N., Chazeau, J., and Jourdan, H. 2010. La faune des milieux sur roches ultramatiques.*in* L'Huillier L., Jaffré Tanguy, Wulff A., editor. Mines et environnement en Nouvelle Calédonie : les milieux sur substrats ultramafiques et leur restauration.

Baselga, A. (2008). Determinants of species richness, endemism and turnover in European longhorn beetles. *Ecography* **31**:263-271.

Baselga, A. and Orme, C. D. L. (2012). betapart: an R package for the study of beta diversity. *Methods in Ecology and Evolution* **3**:808-812.

Baselga, A., Orme, D., and Villeger, S. (2012). Partitioning beta diversity into turnover and nestedness components. *Package 'betapart', Version* **1**.

Bauer, A. M. and Jackman, T. 2006. Phylogeny and microendemism of the New Caledonian lizard fauna. Page 13 *in* Proceedings of the 13th Congress of the Societas Europaea Herpetologica.

Bauer, A. M., Jackman, T., Sadlier, R. A., and Whitaker, A. H. (2006). A revision of the Bavayia validiclavis group (Squamata: Gekkota: Diplodactylidae), a clade of New Caledonian geckos exhibiting microendemism. *Proceedings - California Academy of Sciences* **57**:503.

Bauer, A. M. and Sadlier, R. A. 2000. The Herpetofauna of New Caledonia. Society for the Study of Amphibians and Reptiles.

Bax, N., Williamson, A., Aguero, M., Gonzalez, E., and Geeves, W. (2003). Marine invasive alien species: a threat to global biodiversity. *Marine policy* **27**:313-323.

Beauvais, M., Coléno, A., and Jourdan, H., editors. 2006. Les espèces envahissantes dans l'archipel néo-calédonien. IRD edition.

Beckerman, A. P., Uriarte, M., and Schmitz, O. J. (1997). Experimental evidence for a behavior-mediated trophic cascade in a terrestrial food chain. *Proceedings of the National Academy of Sciences* **94**:10735-10738.

Bel, S., Salas, M., Chardonnet, P., and Bianchi, M. (1997). Rusa deer (Cervus timorensis russa) farming in New Caledonia: impact of different feed levels on herd breeding rate and performance of newborn fawns. *Australian veterinary journal* **75**:199-203.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., and Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. *Ecology Letters*:no-no.

Bellard, C., Cassey, P., and Blackburn, T. M. (2016). Alien species as a driver of recent extinctions. *Biology Letters* **12**:20150623.

Bellard, C., Thuiller, W., Leroy, B., Genovesi, P., Bakkenes, M., and Courchamp, F. (2013). Will climate change promote future invasions? *Global change biology* **19**:3740-3748.

Belovsky, G. and Slade, J. (2000). Insect herbivory accelerates nutrient cycling and increases plant production. *Proceedings of the National Academy of Sciences* **97**:14412-14417.

Bennet-Clark, H. (2003). Wing resonances in the Australian field cricket Teleogryllus oceanicus. *Journal of Experimental Biology* **206**:1479-1496.

Bennet-Clark, H. and Young, D. (1994). The scaling of song frequency in cicadas. *Journal of Experimental Biology* **191**:291-294.

Bennet-Clark, H. C. (1998). Size and scale effects as constraints in insect sound communication. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **353**:407-419.

Bennet-Clark, H. C. (1999). Resonators in insect sound production: how insects produce loud pure-tone songs. *Journal of Experimental Biology* **202**:3347-3357.

Bennet-Clark, H. C. and Bailey, W. J. (2002). Ticking of the clockwork cricket: the role of the escapement mechanism. *Journal of Experimental Biology* **205**:613-625.

Berman, M., Andersen, A. N., Hély, C., and Gaucherel, C. (2013a). Overview of the distribution, habitat association and impact of exotic ants on native ant communities in New Caledonia. *PLoS ONE* **8**:e67245.

Berman, M., Andersen, A. N., and Ibanez, T. (2013b). Invasive ants as back-seat drivers of native ant diversity decline in New Caledonia. *Biological Invasions* **15**:2311-2331.

Bertram, S. M., Harrison, S. J., Thomson, I. R., and Fitzsimmons, L. P. (2013). Adaptive plasticity in wild field cricket's acoustic signaling. *PLoS ONE* **8**:e69247.

Bianchi, F., Mendonça, M., and Campos, L. (2014). Comparing Vegetation Types and Anthropic Disturbance Levels in the Atlantic Forest: How Do Pentatomoidea (Hemiptera: Heteroptera) Assemblages Respond? *Environmental Entomology* **43**:1507-1513.

Blumstein, D. T. and Daniel, J. C. (2005). The loss of anti-predator behaviour following isolation on islands. *Proceedings of the Royal Society of London B: Biological Sciences* **272**:1663-1668.

Bocquet, A., Chambrey, C., Derroire, G., and Tassin, J. (2007). Modalities of colonization of woody savannah by dry forest plants in New Caledonia. *Revue D Ecologie-La Terre Et La Vie* **62**:87-91.

Bonnaud, E., Berger, G., Bourgeois, K., Legrand, J., and Vidal, E. (2012). Predation by cats could lead to the extinction of the Mediterranean endemic Yelkouan Shearwater Puffinus yelkouan at a major breeding site. *Ibis* **154**:566-577.

Borges, V. S., Pires, R. C., Linares, A. M., and Eterovick, P. C. (2013). Diet of Enyalius bilineatus (Leiosauridae: Squamata) at a site in southeastern Brazil: effects of phylogeny and prey availability. *Journal of Natural History* **47**:2785-2794.

Bormpoudakis, D., Sueur, J., and Pantis, J. D. (2013). Spatial heterogeneity of ambient sound at the habitat type level: ecological implications and applications. *Landscape Ecology* **28**:495-506.

Bos, M., Tylianakis, J., Steffan-Dewenter, I., and Tscharntke, T. (2008). The invasive Yellow Crazy Ant and the decline of forest ant diversity in Indonesian cacao agroforests. *Biological Invasions* **10**:1399-1409.

Boulard, M. (1988). Homoptères Cicadoidea de Nouvelle-Calédonie. 1. Description d'un genre nouveau et de deux espèces nouvelles de Tibicinidae. *Zoologia Neocaledonica* **1**:61-66.

Boulard, M. (1991). Description de trois nouvelles espèces de Cigales néo-calédoniennes (Hom. Cicadoidea, Tibicinidae). *L'Entomologiste* **47**:1991.

Boulard, M. (1992). Descriptions de six espèces nouvelles de Cigales néocalédoniennes premières notes éthologiques (Homoptera, Cicadoidea). *Bulletin de la Société entomologique de France* **97**:119-133.

Boulard, M. (1993). Sur quatre nouvelles Cigales néo-calédoniennes et leurs cymbalisations particulières (Homoptera, Cicadoidea, Tibicinidae). *École Pratique des Hautes Études, Travaux du Laboratoire Biologie et évolution des Insectes* **6**:111-125.

Boulard, M. (1997). Nouvelles cigales remarquables originaires de la Nouvelle-Calédonie (Homoptera, Cicadoidea, Tibicinidae). *Mémoires du Muséum national d'histoire naturelle* **171**:179-196.

Bouyer, J., Sana, Y., Samandoulgou, Y., Cesar, J., Guerrini, L., Kabore-Zoungrana, C., and Dulieu, D. (2007). Identification of ecological indicators for monitoring ecosystem health in the trans-boundary W Regional park: a pilot study. *Biological Conservation* **138**:73-88.

Bowen, L. and Vuren, D. V. (1997). Insular endemic plants lack defenses against herbivores. *Conservation Biology* **11**:1249-1254.

Briggs, F., Lakshminarayanan, B., Neal, L., Fern, X. Z., Raich, R., Hadley, S. J., Hadley, A. S., and Betts, M. G. (2012). Acoustic classification of multiple simultaneous bird species: A multi-instance multi-label approach. *The Journal of the Acoustical Society of America* **131**:4640-4650.

Brook, B. W., Sodhi, N. S., and Bradshaw, C. J. (2008). Synergies among extinction drivers under global change. *Trends in Ecology & Evolution* **23**:453-460.

Brooks, T. M., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A., Rylands, A. B., Konstant, W. R., Flick, P., Pilgrim, J., Oldfield, S., and Magin, G. (2002). Habitat loss and extinction in the hotspots of biodiversity. *Conservation Biology* **16**:909-923.

Brothers, R. and Lillie, A. 1988. Regional geology of New Caledonia. Pages 325-374 *in* Nairn, Alan, Stehli, Francis, and Uyeda, Seiyda, editors. The ocean basins and margins. Plenum Press, New-York.

Brouwers, N. C. and Newton, A. C. (2009). Habitat requirements for the conservation of wood cricket (Nemobius sylvestris)(Orthoptera: Gryllidae) on the Isle of Wight, UK. *Journal of Insect Conservation* **13**:529-541.

Brown, B. J., Mitchell, R. J., and Graham, S. A. (2002). Competition for pollination between an invasive species (purple loosestrife) and a native congener. *Ecology* **83**:2328-2336.

Burgess, L. and Hinks, C. (1987). Predation on adults of the crucifer flea beetle, Phyllotreta cruciferae (Goeze), by the northern fall field cricket, Gryllus pennsylvanicus Burmeister (Orthoptera: Gryllidae). *The Canadian Entomologist* **119**:495-496.

Byrne, M., Steane, D. A., Joseph, L., Yeates, D. K., Jordan, G. J., Crayn, D., Aplin, K., Cantrill, D. J., Cook, L. G., and Crisp, M. D. (2011). Decline of a biome: evolution, contraction, fragmentation, extinction and invasion of the Australian mesic zone biota. *Journal of Biogeography* **38**:1635-1656.

Cade, W. (1975). Acoustically orienting parasitoids: fly phonotaxis to cricket song. *Science* **190**:1312-1313.

Cade, W. H. (1984). Effects of fly parasitoids on nightly calling duration in field crickets. *Canadian Journal of Zoology* **62**:226-228.

Cade, W. H., Ciceran, M., and Murray, A.-M. (1996). Temporal patterns of parasitoid fly (Ormia ochracea) attraction to field cricket song (Gryllus integer). *Canadian Journal of Zoology* **74**:393-395.

Capinera, J. 2011. Insects and wildlife: arthropods and their relationships with wild vertebrate animals. John Wiley & Sons.

Capinha, C., Essl, F., Seebens, H., Moser, D., and Pereira, H. M. (2015). The dispersal of alien species redefines biogeography in the Anthropocene. *Science* **348**:1248-1251.

Cappellari, L. H., Lema, T. d., Prates Jr, P., and Rocha, C. F. D. d. (2007). Diet of Teius oculatus (Sauria, Teiidae) in southern Brazil (Dom Feliciano, Rio Grande do Sul). *Iheringia. Série Zoologia* **97**:31-35.

Carlquist, S. J. (1965). Island life; a natural history of the islands of the world.

Carthey, A. J. and Banks, P. B. (2012). When does an alien become a native species? A vulnerable native mammal recognizes and responds to its long-term alien predator. *PLoS ONE* **7**:e31804.

Carthey, A. J. and Banks, P. B. (2014). Naïveté in novel ecological interactions: lessons from theory and experimental evidence. *Biological Reviews* **89**:932-949.

Ceballos, G., Ehrlich, P. R., Barnosky, A. D., García, A., Pringle, R. M., and Palmer, T. M. (2015). Accelerated modern human–induced species losses: Entering the sixth mass extinction. *Science Advances* **1**:e1400253.

Chazeau, J. (1993). Research on New Caledonian terrestrial fauna: achievements and prospects. *Biodiversity letters*:123-129.

Chazeau, J., Jourdan, H., and Le Breton, J. (2002). Etude de l'invasion de la Nouvelle-Calédonie par la fourmi pionnière Wasmannia auropunctata (Roger) : modalités, impact sur la diversité et le fonctionnement des écosystèmes, moyens d'une maîtrise de la nuisance.

Chek, A. A., Bogart, J. P., and Lougheed, S. C. (2003). Mating signal partitioning in multi-species assemblages: a null model test using frogs. *Ecology Letters* **6**:235-247.

Chesmore, E. and Ohya, E. (2004). Automated identification of field-recorded songs of four British grasshoppers using bioacoustic signal recognition. *Bulletin of entomological Research* **94**:319-330.

Chesmore, E. D. (2001). Application of time domain signal coding and artificial neural networks to passive acoustical identification of animals. *Applied Acoustics* **62**:1359-1374.

Chevillotte, V., Chardon, D., Beauvais, A., Maurizot, P., and Colin, F. (2006). Long-term tropical morphogenesis of New Caledonia (Southwest Pacific): Importance of positive epeirogeny and climate change. *Geomorphology* **81**:361-375.

Chintauan-Marquier, I. C., Legendre, F., Hugel, S., Robillard, T., Grandcolas, P., Nel, A., Zuccon, D., and Desutter-Grandcolas, L. (2016). Laying the foundations of evolutionary and systematic studies in crickets (Insecta, Orthoptera): a multilocus phylogenetic analysis. *Cladistics*.

Chopard, L. 1915. Gryllidae de la Nouvelle-Calédonie et des Îles Loyautés. Pages 131–167 *in* (Eds)., Sarasin F. & Roux J., editor. Nova Caledonia, Recherches scientifiques en NouvelleCalédonie et aux Îles Loyalty. C.W. Kreideis, Wiesbaden.

Christian, C. E. (2001). Consequences of a biological invasion reveal the importance of mutualism for plant communities. *Nature* **413**:635-639.

Clark, D. B., Concepcion, G., Pazmino, O., Donoso, C., and Villacis, Y. P. d. (1982). The Tramp Ant Wasmannia auropunctata: Autecology and Effects on Ant Diversity and Distribution on Santa Cruz Island, Galapagos. *Biotropica* **14**:196-207.

Clavero, M., Brotons, L., Pons, P., and Sol, D. (2009). Prominent role of invasive species in avian biodiversity loss. *Biological Conservation* **142**:2043-2049.

Clavero, M. and Garcia-Berthou, E. (2005). Invasive species are a leading cause of animal extinctions. *TRENDS in Ecology and Evolution* **20**:110-110.

Cluzel, D., Maurizot, P., Collot, J., and Sevin, B. (2012). An outline of the geology of New Caledonia; from Permian-Mesozoic Southeast Gondwanaland active margin to Cenozoic obduction and supergene evolution. *Episodes* **35**:72-86.

Cochrane, M. A. (2003). Fire science for rainforests. *Nature* **421**:913-919.

Collins, N., Berghe, E. v. d., and Carson, L. (2014). Two new species of Neoxabea, three new species of Oecanthus, and documentation of two other species in Nicaragua (Orthoptera: Gryllidae: Oecanthinae). *Transactions of the American Entomological Society* **140**:163-184.

Cox, J. G. and Lima, S. L. (2006). Naiveté and an aquatic–terrestrial dichotomy in the effects of introduced predators. *Trends in Ecology & Evolution* **21**:674-680.

Crespin, L., Duplantier, J.-M., and Granjon, L. (2012). Demographic aspects of the island syndrome in two Afrotropical Mastomys rodent species. *Acta Oecologica* **39**:72-79.

Cruaud, A., Jabbour-Zahab, R., Genson, G., Ungricht, S., and Rasplus, J.-Y. (2012). Testing the Emergence of New Caledonia: Fig Wasp Mutualism as a Case Study and a Review of Evidence. *PLoS ONE* **7**:e30941.

Crutzen, P. J. (2002). Geology of mankind. *Nature* **415**:23-23.

Crutzen, P. J. and Stoermer, E. F. (2000). Global change newsletter. *The Anthropocene* **41**:17-18.

Cummins, K. W. (1974). Structure and function of stream ecosystems. *BioScience* **24**:631-641.

Curt, T., Borgniet, L., Ibanez, T., Moron, V., and Hély, C. (2015). Understanding fire patterns and fire drivers for setting a sustainable management policy of the New-Caledonian biodiversity hotspot. *Forest Ecology and Management* **337**:48-60.

Dale, V. H. and Beyeler, S. C. (2001). Challenges in the development and use of ecological indicators. *Ecological Indicators* **1**:3-10.

Dangles, O., Magal, C., Pierre, D., Olivier, A., and Casas, J. (2005). Variation in morphology and performance of predator-sensing system in wild cricket populations. *The Journal of Experimental Biology* **208**:461-468.

Dangles, O., Ory, N., Steinmann, T., Christides, J. P., and Casas, J. (2006). Spider's attack versus cricket's escape: velocity modes determine success. *Animal Behaviour* **72**:603-610.

Dangles, O., Pierre, D., Christides, J. P., and Casas, J. (2007). Escape performance decreases during ontogeny in wild crickets. *Journal of Experimental Biology* **210**:3165-3170.

Danner, B. and Joern, A. (2003a). Resource-mediated impact of spider predation risk on performance in the grasshopper Ageneotettix deorum (Orthoptera: Acrididae). *Oecologia* **137**:352-359.

Danner, B. J. and Joern, A. (2003b). Stage-specific behavioral responses of Ageneotettix deorum (Orthoptera: Acrididae) in the presence of lycosid spider predators. *Journal of Insect Behavior* **16**:453-464.

Danner, B. J. and Joern, A. (2004). Development, growth, and egg production of Ageneotettix deorum (Orthoptera: Acrididae) in response to spider predation risk and elevated resource quality. *Ecological Entomology* **29**:1-11.

David, J. A. d. O., Zefa, E., and Fontanetti, C. S. (2003). Cryptic species of Gryllus in the light of bioacoustic (Orthoptera: Gryllidae). *Neotropical Entomology* **32**:75-80.

Dawson, J., Oppel, S., Cuthbert, R. J., Holmes, N., Bird, J. P., Butchart, S. H., Spatz, D. R., and Tershy, B. (2014). Prioritizing islands for the eradication of invasive vertebrates in the United Kingdom Overseas Territories. *Conservation Biology*.

Dayrat, B. (2005). Towards integrative taxonomy. *Biological Journal of the Linnean Society* **85**:407-415.

De Carvalho, T. R. and Giaretta, A. A. (2013). Taxonomic circumscription of Adenomera martinezi (Bokermann, 1956)(Anura: Leptodactylidae: Leptodactylinae) with the recognition of a new cryptic taxon through a bioacoustic approach. *Zootaxa* **3701**:207-237.

de Garine-Wichatitsky, M., Soubeyran, Y., Maillard, D., and Duncan, P. (2005). The diets of introduced rusa deer (Cervus timorensis russa) in a native sclerophyll forest and a native rainforest of New Caledonia. *New Zealand Journal of Zoology* **32**:117-126.

Delcourt, P. A. and Delcourt, H. R. (1983). Late-Quaternary vegetational dynamics and community stability reconsidered. *Quaternary Research* **19**:265-271.

Delorme, Q., Jourdan, H., and Mille, C. (2015). Description of two new cicada species of the genus Poviliana Boulard (Insecta: Hemiptera, Cicadoidea, Cicadidae) from New Caledonia. *Zootaxa* **3957**:489-500.

Depraetere, M., Pavoine, S., Jiguet, F., Gasc, A., Duvail, S., and Sueur, J. (2012). Monitoring animal diversity using acoustic indices: implementation in a temperate woodland. *Ecological Indicators* **13**:46-54.

Dereeper, A., Guignon, V., Blanc, G., Audic, S., Buffet, S., Chevenet, F., Dufayard, J.-F., Guindon, S., Lefort, V., and Lescot, M. (2008). Phylogeny. fr: robust phylogenetic analysis for the non-specialist. *Nucleic acids research* **36**:W465-W469.

Desutter-Grandcolas, L. (1992). Les Phalangopsidae de Guyane française (Orthoptères, Grylloidea) : systématique, éléments de phyologénie et de biologie. *Bulletin du Musem national d'Histoire Naturelle* **14**:93-177.

Desutter-Grandcolas, L. (1997a). Acoustics Communication in Crickets (Orthoptera: Grylloidae): A Model of Regressive Evolution Revisited Using Phylogeny. *Mémoire du Muséum national d'Histoire naturelle* **173**:182-202.

Desutter-Grandcolas, L. (1997b). First Record of Ant-loving Crickets (Orthoptera: Myrmecophilidae: Myrmecophilinae) in New Caledonia. *Australian Journal of Entomology* **36**:159-163.

Desutter-Grandcolas, L. (1997c). Le peuplement de grillons (Orthoptères, Grylloidae) : espèces et données nouvelles. *Mémoire du Muséum national d'Histoire naturelle* **171**:165-177.

Desutter-Grandcolas, L. (1997d). Le peuplement de grillons (Orthoptères, Grylloidae) des sous-bois forestiers du Col d'Amieu (Nouvelle-Calédonie). I. Etude du peuplement. *Mémoire du Muséum national d'Histoire naturelle* **171**:125-135.

Desutter-Grandcolas, L. (1997e). Le peuplement de grillons (Orthoptères, Grylloidae) des sous-bois forestiers du Col d'Amieu (Nouvelle-Calédonie). II. Analyse systématique. *Mémoire du Muséum national d'Histoire naturelle* **171**:137-163.

Desutter-Grandcolas, L. (2002). The Phalangopsidae (Orthoptera Grylloidea) of New Caledonia, with descriptions of four new species. *Mémoire du Muséum national d'Histoire naturelle* **187**:103-115.

Desutter-Grandcolas, L. (2003). Phylogeny and the evolution of acoustic communication in extant Ensifera (Insecta, Orthoptera). *Zoologica Scripta* **32**:525-561.

Desutter-Grandcolas, L. (2014). New taxa and data for Neotropical Phalangopsidae (Orthoptera, Grylloidea). *Zootaxa* **3866**:398-420.

Desutter-Grandcolas, L. (2015). Phalangopsidae crickets from Tropical Africa (Orthoptera, Grylloidea), with descriptions of new taxa and an identification key for African genera. *Zootaxa* **3948**:451-496.

Desutter-Grandcolas, L. and Robillard, T. (2003). Phylogeny and the evolution of calling songs in Gryllus (Insecta, Orthoptera, Gryllidae). *Zoologica Scripta* **32**:173-183.

Desutter-Grandcolas, L. and Robillard, T. (2004). Acoustic evolution in crickets: need for phylogenetic study and a reappraisal of signal effectiveness. *Anais da Academia Brasileira de Ciências* **76**:301-315.

Desutter-Grandcolas, L. and Robillard, T. (2006). Phylogenetic systematics and evolution of Agnotecous in New Caledonia (Orthoptera: Grylloidea, Eneopteridae). *Systematic Entomology* **31**:65-92.

Desutter-Grandcolas, L., Robillard, T., and Anso, J. 2014. Redefinition of the cricket genus Protathra Desutter-Grandcolas, 1997 (Orthoptera, Grylloidea, Phalangopsidae), with description of the calling song of Protathra centralis Desutter-Grandcolas, n. sp.*in* Guilbert, E., Robillard, T., Jourdan, H. & Grandcolas, P., editor.

Desutter-Grandcolas, L. (1993). New nemobiine crickets from Guianese and Peruvian Amazonia (Orthoptera, Grylloidea, Trigonidiidae). *Studies on Neotropical fauna and environment* **28**:1-37.

Desutter, L. (1987). Structure et évolution du complexe phallique des Gryllidea (orthoptères) et classification des genres néotropicaux de Grylloidea. I. *Bulletin de la Société entomologique de France* **23**:213-239.

Desutter, L. 1990. Etude phylogénétique biogéographique et écologique des Grylloidea néotropicaux (Insectes Orthoptères). Paris 11.

Diaz, R., Knutson, A., and Bernal, J. S. (2004). Effect of the Red Imported Fire Ant on Cotton Aphid Population Density and Predation of Bollworm and Beet Armyworm Eggs. *Journal of Economic Entomology* **97**:222-229.

Dietrich, C., Palm, G., Riede, K., and Schwenker, F. (2004). Classification of bioacoustic time series based on the combination of global and local decisions. *Pattern Recognition* **37**:2293-2305.

Dirzo, R. and Raven, P. H. (2003). Global state of biodiversity and loss. *Annual Review of Environment and Resources* **28**:137-167.

Dirzo, R., Young, H. S., Galetti, M., Ceballos, G., Isaac, N. J., and Collen, B. (2014). Defaunation in the Anthropocene. *Science* **345**:401-406.

Diwakar, S. and Balakrishnan, R. (2007a). The Assemblage of Acoustically Communicating Crickets of a Tropical Evergreen Forest in Southern India: Call Diversity and Diel Calling Patterns. *The International Journal of Animal Sound and its Recording* **16**:113-135.

Diwakar, S. and Balakrishnan, R. (2007b). Vertical stratification in an acoustically communicating ensiferan assemblage of a tropical evergreen forest in southern India. *Journal of Tropical Ecology* **23**:479-486.

Diwakar, S., Jain, M., and Rohini Balakrishnan, R. B. (2007). Psychoacoustic sampling as a reliable, non-invasive method to monitor orthopteran species diversity in tropical forests. *Biodiversity and Conservation* **16**:4081-4093.

Donlan, C. J. and Wilcox, C. (2008). Diversity, invasive species and extinctions in insular ecosystems. *Journal of Applied Ecology* **45**:1114-1123.

Drescher, J. (2011). The ecology and population structure of the invasive yellow crazy ant Anoplolepis gracilipes. *Doktorgrade (Doctor of Philosophy) dissertation. Julius-Maximillians-Universität, Würzburg, Germany*.

Drummond, A. J. and Rambaut, A. (2007). BEAST: Bayesian evolutionary analysis by sampling trees. *BMC evolutionary biology* **7**:214.

Duellman, W. E. and Pyles, R. A. (1983). Acoustic resource partitioning in anuran communities. *Copeia*:639-649.

Duhrkopf, R., Baldridge, R., Crino, O., and Dillen, J. (2011). Predation by Solenopsis invicta Buren (Hymenoptera: Formicidae) on Eggs, Larvae, and Pupae of Aedes albopictus Skuse (Diptera: Culicidae). *Southwestern Entomologist* **36**:119-124.

Duncan, R. P., Boyer, A. G., and Blackburn, T. M. (2013). Magnitude and variation of prehistoric bird extinctions in the Pacific. *Proceedings of the National Academy of Sciences* **110**:6436-6441.

Dunn, A. M. and Hatcher, M. J. (2015). Parasites and biological invasions: parallels, interactions, and control. *Trends in parasitology* **31**:189-199.

Dunn, O. J. (1964). Multiple comparisons using rank sums. *Technometrics* **6**:241-252.

Dupuy, F., Casas, J., Body, M., and Lazzari, C. R. (2011). Danger detection and escape behaviour in wood crickets. *Journal of Insect Physiology* **57**:865-871.

Edgar, R. C. (2004). MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic acids research* **32**:1792-1797.

Ekstrom, J., Jones, J. P., Willis, J., Tobias, J., Dutson, G., and Barre, N. (2002). New information on the distribution, status and conservation of terrestrial bird species in Grande Terre, New Caledonia. *Emu* **102**:197-207.

Elliott, C. and Koch, U. (1985). The clockwork cricket. *Naturwissenschaften* **72**:150-153.

Emery, C. (1883). Alcune formiche della nuova caledonia. *Bollettino della Societa Entomologica Italiana* **15**:145-151.

Endler, J. A. (1992). Signals, signal conditions, and the direction of evolution. *American Naturalist*:S125-S153.

Epifanio, C. E. (2013). Invasion biology of the Asian shore crab Hemigrapsus sanguineus: a review. *Journal of Experimental Marine Biology and Ecology* **441**:33-49.

Espeland, M. and Johanson, K. A. (2010a). The diversity and radiation of the largest monophyletic animal group on New Caledonia (Trichoptera: Ecnomidae: Agmina). *Journal of evolutionary biology* **23**:2112-2122.

Espeland, M. and Johanson, K. A. (2010b). The effect of environmental diversification on species diversification in New Caledonian caddisflies (Insecta: Trichoptera: Hydropsychidae). *Journal of Biogeography* **37**:879-890.

Espeland, M., Johanson, K. A., and Hovmöller, R. (2008). Early Xanthochorema (Trichoptera, Insecta) radiations in New Caledonia originated on ultrabasic rocks. *Molecular Phylogenetics and Evolution* **48**:904-917.

Fagúndez, J. (2012). Heathlands confronting global change: drivers of biodiversity loss from past to future scenarios. *Annals of botany*:mcs257.

Fahmy, S. R., Abdel-Ghaffar, F., Bakry, F. A., and Sayed, D. A. (2014). Ecotoxicological effect of sublethal exposure to zinc oxide nanoparticles on freshwater snail biomphalaria alexandrina. *Archives of environmental contamination and toxicology* **67**:192-202.

FAO. 2010. Global Forest Ressources Assessment 2010. FAO Forestry paper. Food and Agricultural Organisation of the United Nations, Rome, Italy.

Farina, A., James, P., Bobryk, C., Pieretti, N., Lattanzi, E., and McWilliam, J. (2014). Low cost (audio) recording (LCR) for advancing soundscape ecology towards the conservation of sonic complexity and biodiversity in natural and urban landscapes. *Urban Ecosystems* **17**:923-944.

Farina, A., Lattanzi, E., Malavasi, R., Pieretti, N., and Piccioli, L. (2011). Avian soundscapes and cognitive landscapes: theory, application and ecological perspectives. *Landscape Ecology* **26**:1257-1267.

Fartmann, T., Krämer, B., Stelzner, F., and Poniatowski, D. (2012). Orthoptera as ecological indicators for succession in steppe grassland. *Ecological Indicators* **20**:337-344.

Felsenstein, J. (1985). Confidence limits on phylogenies: an approach using the bootstrap. *Evolution*:783-791.

Fischer, F. P., Schulz, U., Schubert, H., Knapp, P., and Schmöger, M. (1997). Quantitative assessment of grassland quality: acoustic determination of population sizes of orthopteran indicator species. *Ecological Applications* **7**:909-920.

Flook, P., Klee, S., and Rowell, C. (1999). Combined molecular phylogenetic analysis of the Orthoptera (Arthropoda, Insecta) and implications for their higher systematics. *Systematic biology* **48**:233-253.

Foley, J. A., DeFries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., Chapin, F. S., Coe, M. T., Daily, G. C., and Gibbs, H. K. (2005). Global consequences of land use. *Science* **309**:570-574.

Forrest, T. (1994). From sender to receiver: propagation and environmental effects on acoustic signals. *American Zoologist* **34**:644-654.

Forys, E., Allen, C., and Wojcik, D. (2001). The likely cause of extinction of the tree snail Orthalicus reses reses (Say). *Journal of Molluscan Studies* **67**:369-376.

Foucaud, J., Orivel, J., Loiseau, A., Delabie, J. H. C., Jourdan, H., Konghouleux, D., Vonshak, M., Tindo, M., Mercier, J.-L., Fresneau, D., Mikissa, J.-B., McGlynn, T., Mikheyev, A. S., Oettler, J., and Estoup, A. (2010). Worldwide invasion by the little fire ant: routes of introduction and eco-evolutionary pathways. *Evolutionary Applications* **3**:363-374.

Frankham, R. (1997). Do island populations have less genetic variation than mainland populations? *Heredity* **78**:311-327.

Frazer, G. W., Canham, C., and Lertzman, K. (1999). Gap Light Analyzer (GLA), Version 2.0: Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, users manual and program documentation. *Simon Fraser University, Burnaby, British Columbia, and the Institute of Ecosystem Studies, Millbrook, New York* **36**.

Frommolt, K.-H. and Tauchert, K.-H. (2014). Applying bioacoustic methods for long-term monitoring of a nocturnal wetland bird. *Ecological Informatics* **21**:4-12.

Furnas, B. J. and Callas, R. L. (2014). Using automated recorders and occupancy models to monitor common forest birds across a large geographic region. *The Journal of Wildlife Management*.

Gámez-Virués, S., Bonifacio, R. S., Gurr, G. M., Kinross, C., Raman, A., and Nicol, H. I. (2007). Arthropod prey of shelterbelt-associated birds: linking faecal samples with biological control of agricultural pests. *Australian Journal of Entomology* **46**:325-331.

Gangwere, S. K. (1961). A monograph on food selection in Orthoptera. *Transactions of the American Entomological Society*:67-230.

Garamszegi, L. Z. 2014. Modern phylogenetic comparative methods and their application in evolutionary biology. Springer.

Garda, A. A., Costa, G. C., França, F. G., Giugliano, L. G., Leite, G. S., Mesquita, D. O., Nogueira, C., Tavares-Bastos, L., Vasconcellos, M. M., and Vieira, G. H. (2012). Reproduction, body size, and diet of Polychrus acutirostris (Squamata: Polychrotidae) in two contrasting environments in Brazil. *Journal of Herpetology* **46**:2-8.

Gardiner, T. and Dover, J. (2008). Is microclimate important for Orthoptera in open landscapes? *Journal of Insect Conservation* **12**:705-709.

Gardiner, T., Hill, J., and Chesmore, D. (2005). Review of the Methods Frequently Used to Estimate the Abundance of Orthoptera in Grassland Ecosystems. *Journal of Insect Conservation* **9**:151-173.

Gardner, J. L., Peters, A., Kearney, M. R., Joseph, L., and Heinsohn, R. (2011). Declining body size: a third universal response to warming? *Trends in Ecology & Evolution* **26**:285-291.

Gasc, A., Pavoine, S., Lellouch, L., Grandcolas, P., and Sueur, J. (2015). Acoustic indices for biodiversity assessments: analyses of bias based on simulated bird assemblages and recommendations for field surveys. *Biological Conservation* **191**:306-312.

Gasc, A., Sueur, J., Pavoine, S., Pellens, R., and Grandcolas, P. (2013). Biodiversity Sampling Using a Global Acoustic Approach: Contrasting Sites with Microendemics in New Caledonia. *PLoS ONE* **8**:e65311.

Gavlas, V., Bednár, J., and Krištín, A. (2007). A comparative study on orthopteroid assemblages along a moisture gradient in the Western Carpathians. *Biologia* **62**:95-102.

Gérard, A. 2015. Naïveté, nouveauté et indigénisation: vers une meilleure compréhension de l'impact des espèces animales invasives sur les faunes natives. Aix Marseille, Marseille.

Gerhardt, H. C. and Huber, F. 2002. Acoustic communication in insects and anurans: common problems and diverse solutions. University of Chicago Press.

Gerlach, J., Samways, M., and Pryke, J. (2013). Terrestrial invertebrates as bioindicators: an overview of available taxonomic groups. *Journal of Insect Conservation* **17**:831-850.

Gerlach, J., Samways, M. J., Hochkirch, A., Seddon, M., Cardoso, P., Clausnitzer, V., Cumberlidge, N., Daniel, B., Black, S. H., and Ott, J. (2014). Prioritizing non-marine invertebrate taxa for Red Listing. *Journal of Insect Conservation* **18**:573-586.

Gioria, M. and Osborne, B. A. (2014). Resource competition in plant invasions: emerging patterns and research needs. *Frontiers in plant science* **5**.

Glaw, F., Köhler, J., De la Riva, I., Vieites, D. R., and Vences, M. (2010). Integrative taxonomy of Malagasy treefrogs: combination of molecular genetics, bioacoustics and comparative morphology reveals twelve additional species of Boophis. *Zootaxa* **2383**:82.

Gnatzy, W. and Heusslein, R. (1986). Digger wasp against crickets. *Naturwissenschaften* **73**:212-215.

Gnatzy, W. and Kämper, G. (1990). Digger wasp against crickets. II. An airborne signal produced by a running predator. *Journal of Comparative Physiology A* **167**:551-556.

Gnatzy, W. and Otto, D. (1996). Digger wasp vs. cricket: application of the paralytic venom by the predator and changes in behavioural reactions of the prey after being stung. *Naturwissenschaften* **83**:467-470.

Gogala, M. and Riede, K. (1995). Time sharing of song activity by cicadas in Temengor Forest Reserve, Hulu Perak, and in Sabah, Malaysia. *Malayan Nature Journal* **48**:297-305.

Gomez, C., Mangeas, M., Curt, T., Ibanez, T., Munzinger, J., Dumas, P., Jérémy, A., Despinoy, M., and Hély, C. (2015). Wildfire risk for main vegetation units in a biodiversity hotspot: modeling approach in New Caledonia, South Pacific. *Ecology and Evolution* **5**:377-390.

Gorbi, S., Lamberti, C. V., Notti, A., Benedetti, M., Fattorini, D., Moltedo, G., and Regoli, F. (2008). An ecotoxicological protocol with caged mussels, Mytilus galloprovincialis, for monitoring the impact of an offshore platform in the Adriatic sea. *Marine Environmental Research* **65**:34-49.

Gorochov, A. (1996). New and little known crickets from the collection of the Humboldt University and some other collections (Orthoptera: Grylloidea). Part 2. *Zoosystematica Rossica* **5**:29-90.

Gorochov, A. (2003). Taxonomy of Podoscirtinae (orthoptera: gryllidae). Part 2: indo-Malayan and Australo-oceanian Podoscirtini. *Zoosystematica Rossica* **11**:267-303.

Gorochov, A. (2010). New cricket taxa of the subfamilies Phaloriinae and Pteroplistinae (Orthoptera: Gryllidae) from South-East Asia. *Proceedings of the Zoological Institute RAS* **314**:184-190.

Gorochov, A. V. (1986). New and little known crickets (Orthoptera, Gryllidae) from Australia and Oceania. *Revue d'Entomologie de l'URSS* **65**.

Gotelli, N. J. (2000). Null model analysis of species co-occurrence patterns. *Ecology* **81**:2606-2621.

Gotelli, N. J., Hart, E. M., and Aaron, M. E. (2015). EcoSimR: Null model analysis for ecological data. R package version 0.1.0.

Gotzek, D., Axen, H. J., Suarez, A. V., Helms Cahan, S., and Shoemaker, D. (2015). Global invasion history of the tropical fire ant: a stowaway on the first global trade routes. *Molecular Ecology* **24**:374-388.

Grandcolas, P., Murienne, J., Robillard, T., Desutter-Grandcolas, L., Jourdan, H., Guilbert, E., and Deharveng, L. (2008). New Caledonia: a very old Darwinian island? *Philosophical Transactions of the Royal Society B: Biological Sciences* **363**:3309-3317.

Grandcolas, P., Nattier, R., and Trewick, S. (2014). Relict species: a relict concept? *Trends in Ecology & Evolution* **29**:655-663.

Gurevitch, J., Morrow, L. L., Wallace, A., and Walsh, J. S. (1992). A meta-analysis of competition in field experiments. *American Naturalist*:539-572.

Gurevitch, J. and Padilla, D. K. (2004a). Are invasive species a major cause of extinctions? *Trends in Ecology & Evolution* **19**:470-474.

Gurevitch, J. and Padilla, D. K. (2004b). Response to Ricciardi. Assessing species invasions as a cause of extinction. *TRENDS in Ecology and Evolution* **19**:620-620.

Haines, I. and Haines, J. (1978a). Colony structure, seasonality and food requirements of the crazy ant, Anoplolepis longipes (Jerd.), in the Seychelles. *Ecological Entomology* **3**:109-118.

Haines, I. and Haines, J. (1978b). Pest status of the crazy ant, Anoplolepis longipes (Jerdon)(Hymenoptera: Formicidae), in the Seychelles. *Bulletin of entomological Research* **68**:627-638.

Hairston, N. G., Smith, F. E., and Slobodkin, L. B. (1960). Community structure, population control, and competition. *American Naturalist*:421-425.

Hall, T. A. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Pages 95-98 *in* Nucleic acids symposium series.

Harrington, R., Anton, C., Dawson, T. P., de Bello, F., Feld, C. K., Haslett, J. R., Kluvankova-Oravska, T., Kontogianni, A., Lavorel, S., and Luck, G. W. (2010). Ecosystem services and

biodiversity conservation: concepts and a glossary. *Biodiversity and Conservation* **19**:2773-2790.

Harris, S. and Timmins, S. M. (2009). Estimating the benefit of early control of all newly naturalised plants. *Science for conservation*.

Hawkins, C. P. and MacMahon, J. A. (1989). Guilds: the multiple meanings of a concept. *Annual review of entomology* **34**:423-451.

Heads, M. (2010). Evolution and biogeography of primates: a new model based on molecular phylogenetics, vicariance and plate tectonics. *Zoologica Scripta* **39**:107-127.

Heads, M. (2011). Old taxa on young islands: a critique of the use of island age to date island-endemic clades and calibrate phylogenies. *Systematic biology*:syq075.

Heard, G. W., Canessa, S., and Parris, K. M. (2015). Interspecific variation in the phenology of advertisement calling in a temperate Australian frog community. *Ecology and Evolution* **5**:3927-3938.

Hedrick, A. V. (2000). Crickets with extravagant mating songs compensate for predation risk with extra caution. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **267**:671-675.

Hedwig, B. 2014. Towards an understanding of the neural basis of acoustic communication in crickets.*in* B, In Hedwig, editor. Insect hearing and acoustic communication. Animal signals

and communication. Springer, Berlin.

Heink, U. and Kowarik, I. (2010). What are indicators? On the definition of indicators in ecology and environmental planning. *Ecological Indicators* **10**:584-593.

Henderson, G. and Akre, R. D. (1986). Biology of the myrmecophilous cricket, Myrmecophila manni (Orthoptera: Gryllidae). *Journal of the Kansas Entomological Society*:454-467.

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., and Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International journal of climatology* **25**:1965-1978.

Hirtenlehner, S. and Römer, H. (2014). Selective phonotaxis of female crickets under natural outdoor conditions. *Journal of Comparative Physiology A* **200**:239-250.

Hoekstra, J. M., Boucher, T. M., Ricketts, T. H., and Roberts, C. (2005). Confronting a biome crisis: global disparities of habitat loss and protection. *Ecology Letters* **8**:23-29.

Hoffmann, B. D., Andersen, A. N., and Hill, G. J. E. (1999). Impact of an introduced ant on native rain forest invertebrates: *Pheidole megacephala* in monsoonal Australia. *Oecologia* **120**:595-604.

Hoffmann, B. D., Lowe, L. M., and Griffiths, A. D. (2002). Reduction in cricket (Orthoptera: Ensifera) populations along a gradient of sulphur dioxide from mining emissions in northern Australia. *Australian Journal of Entomology* **41**:182-186.

Hoffmann, B. D. and Parr, C. L. (2007). An invasion revisited: the African big-headed ant (Pheidole megacephala) in northern Australia. *Biological Invasions* **10**:1171-1181.

Hoffmann, B. D. and Saul, W.-C. (2010). Yellow crazy ant (Anoplolepis gracilipes) invasions within undisturbed mainland Australian habitats: no support for biotic resistance hypothesis. *Biological Invasions* **12**:3093-3108.

Holway, D. A. (1998). Loss of Intraspecific Aggression in the Success of a Widespread Invasive Social Insect. *Science* **282**:949-952.

Holway, D. A. (1999). Competitive mechanisms underlying the displacement of native ants by the invasive argentine ant. *Ecology* **80**:238-251.

Holway, D. A., Lach, L., Suarez, A. V., Tsutsui, N. D., and Case, T. J. (2002). The Causes and Consequences of Ant Invasions. *Annual Review of Ecology and Systematics* **33**:181-233.

Hope, G. and Pask, J. (1998). Tropical vegetational change in the late Pleistocene of New Caledonia. *Palaeogeography, Palaeoclimatology, Palaeoecology* **142**:1-21.

Hsu, M. Y., Kam, Y. C., and Fellers, G. M. (2006). Temporal organization of an anuran acoustic community in a Taiwanese subtropical forest. *Journal of Zoology* **269**:331-339.

Hu, Y. and Cardoso, G. C. (2010). Which birds adjust the frequency of vocalizations in urban noise? *Animal Behaviour* **79**:863-867.

Huang, Y., Ortí, G., Sutherlin, M., Duhachek, A., and Zera, A. (2000). Phylogenetic relationships of North American field crickets inferred from mitochondrial DNA data. *Molecular Phylogenetics and Evolution* **17**:48-57.

Huber, F. 1989. Cricket behavior and neurobiology. Cornell University Press.

Hugel, S. (2012). Impact of native forest restoration on endemic crickets and katydids density in Rodrigues island. *Journal of Insect Conservation* **16**:473-477.

Hulme, P. E. (2009). Trade, transport and trouble: managing invasive species pathways in an era of globalization. *Journal of Applied Ecology* **46**:10-18.

Human, K. G. and Gordon, D. M. (1997). Effects of Argentine ants on invertebrate biodiversity in northern California. *Conservation Biology* **11**:1242-1248.

Hunt, G. R., Hay, R., and Veltman, C. J. (1996). Multiple Kagu Rhynochetos jubatus deaths caused by dog attacks at a high-altitude study site on Pic Ningua, New Caledonia. *Bird Conservation International* **6**:295-306.

Ibanez, T. 2012. Dynamiques des forêts denses humides et des savanes en réponse aux incendies en Nouvelle-Calédonie. Université Paul Cezanne Aix-Marseille III, Marseille.

Ibanez, T., Curt, T., and Hely, C. (2013). Low tolerance of New Caledonian secondary forest species to savanna fires. *Journal of Vegetation Science* **24**:177-188.

Iorgu, I. Ş. (2012). Acoustic analysis reveals a new cryptic bush–cricket in the Carpathian Mountains (Orthoptera, Phaneropteridae). *ZooKeys*:1.

Ishii, H. T., Tanabe, S.-i., and Hiura, T. (2004). Exploring the relationships among canopy structure, stand productivity, and biodiversity of temperate forest ecosystems. *Forest Science* **50**:342-355.

IUCN. (2000). Invasive species specialist group (SSC), IUCN guidelines for the prevention of biodiversity loss caused by alien invasive species. *51st Meeting of the IUCN Council, Gland Switzerland.*:15.

Jaffré, T. 1980. Étude écologique du peuplement végétal des sols dérivés de roches ultrabasiques en Nouvelle Calédonie.

Jaffré, T. (1993). The relationship between ecological diversity and floristic diversity in New Caledonia. *Biodiversity letters*:82-87.

Jaffré, T. (1995). Distribution and ecology of the conifers of New Caledonia.

Jaffré, T. 1996. Etude comparative des formations végétales et des flores des roches ultramafiques de Nouvelle-Calédonie et d'autres régions tropicales du monde.

Jaffré, T., Bouchet, P., and Veillon, J.-M. (1998a). Threatened plants of New Caledonia: Is the system of protected areas adequate? *Biodiversity & Conservation* **7**:109-135.

Jaffré, T., Morat, P., Veillon, J., Dagostini, G., and Rigault, F. (2001). Composition and characterisation of the native flora of New Caledonia. Doc. *Sci., et Tech. II* **4**.

Jaffré, T., Munzinger, J., and Lowry II, P. P. (2010). Threats to the conifer species found on New Caledonia's ultramafic massifs and proposals for urgently needed measures to improve their protection. *Biodiversity and Conservation* **19**:1485-1502.

Jaffré, T., Rigault, F., and Dagostini, G. (1998b). Impact des feux de brousse sur les maquis ligno-herbacés des roches ultramafiques de Nouvelle-Calédonie. *Adansonia* **20**:173-189.

Jaffré, T., Rigault, F., Dagostini, G., Tinel-Fambart, J., Wulff, A., and Munzinger, J. (2009). Input of the different vegetation units to the richness and endemicity of the New Caledonian flora. *Flora* **162**:54.59.

Jain, M. and Balakrishnan, R. (2011). Microhabitat selection in an assemblage of crickets (Orthoptera: Ensifera) of a tropical evergreen forest in Southern India. *Insect Conservation and Diversity* **4**:152-158.

Jain, M. and Balakrishnan, R. (2012). Does acoustic adaptation drive vertical stratification? A test in a tropical cricket assemblage. *Behavioral Ecology* **23**:343-354.

Jain, M., Diwakar, S., Bahuleyan, J., Deb, R., and Balakrishnan, R. (2014). A rain forest dusk chorus: cacophony or sounds of silence? *Evolutionary Ecology* **28**:1-22.

Jaiswara, R., Balakrishnan, R., Robillard, T., Rao, K., Cruaud, C., and Desutter-Grandcolas, L. (2012). Testing concordance in species boundaries using acoustic, morphological, and molecular data in the field cricket genus Itaropsis (Orthoptera: Grylloidea, Gryllidae: Gryllinae). *Zoological Journal of the Linnean Society* **164**:285-303.

Jana, G., Misra, K., and Bhattacharya, T. (2006). Diversity of some insect fauna in industrial and non-industrial areas of West Bengal, India. *Journal of Insect Conservation* **10**:249-260.

Jansen, R. K., Cai, Z., Raubeson, L. A., Daniell, H., Leebens-Mack, J., Müller, K. F., Guisinger-Bellian, M., Haberle, R. C., Hansen, A. K., and Chumley, T. W. (2007). Analysis of 81 genes from 64 plastid genomes resolves relationships in angiosperms and identifies genome-scale evolutionary patterns. *Proceedings of the National Academy of Sciences* **104**:19369-19374.

Jennings, N., Parsons, S., and Pocock, M. (2008). Human vs. machine: identification of bat species from their echolocation calls by humans and by artificial neural networks. *Canadian Journal of Zoology* **86**:371-377.

Jones, H. P., Tershy, B. R., Zavaleta, E. S., Croll, D. A., Keitt, B. S., Finkelstein, M. E., and Howald, G. R. (2008). Severity of the effects of invasive rats on seabirds: a global review. *Conservation Biology* **22**:16-26.

Jost, M. and Shaw, K. (2006). Phylogeny of Ensifera (Hexapoda: Orthoptera) using three ribosomal loci, with implications for the evolution of acoustic communication. *Molecular Phylogenetics and Evolution* **38**:510-530.

Jourdan, H. (1997). Threats on Pacific Islands: The Spread of the Tramp Ant'Wasmannia auropunctata'(Hymenoptera: Formicidae). *Pacific Conservation Biology* **3**:61.

Jourdan, H. 1999. Dynamique de la biodiversité de quelques écosystèmes terrestres néo-calédoniens sous l'effet de l'invasion de la fourmi peste Wasmannia auropunctata(Roger) 1863(Hymenoptera: Formicidae).

Jourdan, H. and Mille, C. (2006). Les invertébrés introduits dans l'archipel néo-calédonien: espèces envahissantes et potentiellement envahissantes. Première évaluation et recommandations pour leur gestion. *M.-L. Beauvais et al.: Les espèces envahissantes dans l'archipel néo-calédonien, Paris, IRD Éditions*:163-214.

Jourdan, H., Sadlier, R., and Bauer, A. (2000). Premières observations sur les conséquences de l'invasion de Wasmannia auropunctata 1863 (Roger) sur les prédateurs supérieurs dans les écosystèmes néo-calédoniens. *Insectes Sociaux* **12**:121-126.

Jourdan, H., Sadlier, R. A., and Bauer, A. M. (2001). Little fire ant invasion (Wasmannia auropunctata) as a threat to New Caledonian lizards: evidence from a sclerophyll forest (Hymenoptera: Formicidae). *Sociobiology* **38**:283-299.

Katsanevakis, S., Wallentinus, I., Zenetos, A., Leppäkoski, E., Çinar, M. E., Oztürk, B., Grabowski, M., Golani, D., and Cardoso, A. C. (2014). Impacts of invasive alien marine species on ecosystem services and biodiversity: a pan-European review. *Aquatic Invasions* **9**:391-423.

Kelly, J., Tosh, D., Dale, K., and Jackson, A. (2013). The economic cost of invasive and non-native species in Ireland and Northern Ireland. *A report prepared for the Northern Ireland Environment Agency and National Parks and Wildlife Service as part of Invasive Species Ireland* **86**.

Kettunen, M., Genovesi, P., Gollasch, S., Pagad, S., Starfinger, U., ten Brink, P., and Shine, C. (2009). Technical support to EU strategy on invasive alien species (IAS) - Assessment of the impacts of IAS in Europe and the EU. Final report for the European Commission. *Institut for European Environnemental Policy (IEEP)*:44.

Kier, G., Kreft, H., Lee, T. M., Jetz, W., Ibisch, P. L., Nowicki, C., Mutke, J., and Barthlott, W. (2009). A global assessment of endemism and species richness across island and mainland regions. *Proceedings of the National Academy of Sciences* **106**:9322-9327.

Koch, U. T., Elliott, C. J., Schäffner, K.-H., and Kleindienst, H.-U. (1988). The mechanics of stridulation of the cricket Gryllus campestris. *Journal of Comparative Physiology A* **162**:213-223.

Koivula, M. J. (2011). Useful model organisms, indicators, or both? Ground beetles (Coleoptera, Carabidae) reflecting environmental conditions. *ZooKeys*:287.

Kopf, R. K., Finlayson, C. M., Humphries, P., Sims, N. C., and Hladyz, S. (2015). Anthropocene Baselines: Assessing Change and Managing Biodiversity in Human-Dominated Aquatic Ecosystems. *BioScience* **65**:798-811.

Kottege, N., Jurdak, R., Kroon, F., and Jones, D. (2015). Automated detection of broadband clicks of freshwater fish using spectro-temporal featuresa). *The Journal of the Acoustical Society of America* **137**:2502-2511.

Krushelnycky, P. and Gillespie, R. (2010). Correlates of vulnerability among arthropod species threatened by invasive ants. *Biodiversity and Conservation* **19**:1971-1988.

Kumar, D. and Yashkamal, K. (2011). Study of prey spectrum of social spider Stegodyphus sarasinorum (Karsch)(Araeneae: Eresidae) and its potential as biological control agent. *Pro. Nat Acad Sci IndiaSect*:171-179.

Kumschick, S., Gaertner, M., Vilà, M., Essl, F., Jeschke, J. M., Pyšek, P., Ricciardi, A., Bacher, S., Blackburn, T. M., and Dick, J. T. (2015). Ecological impacts of alien species: quantification, scope, caveats, and recommendations. *BioScience* **65**:55-63.

Lach, L. and Hooper-Bui, L. M. 2010. Consequences of ant invasions. Pages 261-286 *in* Lach, Lori, Parr, Catherine L., and Abbott, K., editors. Ant Ecology. Oxford University Press, New York.

Lach, L., Parr, C. L., and Abott, K. L. 2010. Ant ecology. Oxford University Press.

Lach, L. and Thomas, M. L. (2008). Invasive ants in Australia: documented and potential ecological consequences. *Australian Journal of Entomology* **47**:275-288.

Lagabrielle, Y., Maurizot, P., Lafoy, Y., Cabioch, G., Pelletier, B., Régnier, M., Wabete, I., and Calmant, S. (2005). Post-Eocene extensional tectonics in Southern New Caledonia (SW Pacific): Insights from onshore fault analysis and offshore seismic data. *Tectonophysics* **403**:1-28.

Lagos, P. A., Ebensperger, L. A., and Herberstein, M. E. (2014). A quantitative test of the 'economic'and 'optimal'models of escape behaviour. *Animal Behaviour* **97**:221-227.

Laiolo, P. (2010). The emerging significance of bioacoustics in animal species conservation. *Biological Conservation* **143**:1635-1645.

Langellotto, G. A. and Denno, R. F. (2004). Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. *Oecologia* **139**:1-10.

Langemann, U., Gauger, B., and Klump, G. M. (1998). Auditory sensitivity in the great tit: perception of signals in the presence and absence of noise. *Animal Behaviour* **56**:763-769.

LaPolla, J. S., Otte, D., and Spearman, L. A. (2000). Assessment of the effects of ants on Hawaiian crickets. *Journal of Orthoptera Research*:139-148.

Lawton, J. H., Bignell, D., Bolton, B., Bloemers, G., Eggleton, P., Hammond, P., Hodda, M., Holt, R., Larsen, T., and Mawdsley, N. (1998). Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. *Nature* **391**:72-76.

Le Breton, J., Chazeau, J., and Jourdan, H. (2003). Immediate impacts of invasion by Wasmannia auropunctata (Hymenoptera: Formicidae) on native litter ant fauna in a New Caledonian rainforest. *Austral Ecology* **28**:204-209.

Le Breton, J., Delabie, J., Chazeau, J., Dejean, A., and Jourdan, H. (2004). Experimental Evidence of Large-Scale Unicoloniality in the Tramp Ant Wasmannia auropunctata (Roger). *Journal of Insect Behavior* **17**:263-271.

Le Breton, J., Jourdan, H., Chazeau, J., Orivel, J., and Dejean, A. (2005). Niche opportunity and ant invasion: the case of Wasmannia auropunctata in a New Caledonian rain forest. *Journal of Tropical Ecology* **21**:93-98.

Le Breton, J., Orivel, J., Chazeau, J., and Dejean, A. (2007). Unadapted behaviour of native, dominant ant species during the colonization of an aggressive, invasive ant. *Ecological Research* **22**:107-114.

Lee, D., Bhatkar, A., Vinson, S., and Olson, J. (1994). Impact of foraging red imported fire ants (Solenopsis invicta)(Hymenoptera: Formicidae) on Psorophora columbiae eggs. *Journal of the American Mosquito Control Association* **10**:163-173.

Legendre, P. and Legendre, L. F. 2012. Numerical ecology. Elsevier.

Lehmann, G. U., Frommolt, K.-H., Lehmann, A. W., and Riede, K. (2014). Baseline data for automated acoustic monitoring of Orthoptera in a Mediterranean landscape, the Hymettos, Greece. *Journal of Insect Conservation* **18**:909-925.

Leidenberger, S., Obst, M., Kulawik, R., Stelzer, K., Heyer, K., Hardisty, A., and Bourlat, S. J. (2015). Evaluating the potential of ecological niche modelling as a component in marine non-indigenous species risk assessments. *Marine pollution bulletin* **97**:470-487.

Lellouch, L., Pavoine, S., Jiguet, F., Glotin, H., and Sueur, J. (2014). Monitoring temporal change of bird communities with dissimilarity acoustic indices. *Methods in Ecology and Evolution* **5**:495-505.

Lenda, M., Skórka, P., Knops, J. M., Moroń, D., Sutherland, W. J., Kuszewska, K., and Woyciechowski, M. (2014). Effect of the internet commerce on dispersal modes of invasive alien species. *PLoS ONE*.

Lester, P. J. and Tavite, A. (2004). Long-legged ants, Anoplolepis gracilipes (Hymenoptera: Formicidae), have invaded Tokelau, changing composition and dynamics of ant and invertebrate communities. *Pacific Science* **58**:391-401.

Letocart, Y. and Salas, M. (1997). Spatial organisation and breeding of kagu Rhynochetos jubatus in Rivière Bleue Park, New Caledonia. *Emu* **97**:97-107.

Levrel, H., Fontaine, B., Henry, P.-Y., Jiguet, F., Julliard, R., Kerbiriou, C., and Couvet, D. (2010). Balancing state and volunteer investment in biodiversity monitoring for the implementation of CBD indicators: A French example. *Ecological Economics* **69**:1580-1586.

Lewis, S. L., Edwards, D. P., and Galbraith, D. (2015). Increasing human dominance of tropical forests. *Science* **349**:827-832.

Lomolino, M. V., Pijanowski, B. C., and Gasc, A. (2015). The silence of biogeography. *Journal of Biogeography*.

López, H., Hernández-Teixidor, D., Macías-Hernández, N., Juan, C., and Oromí, P. (2013). A taxonomic revision and species delimitation of the genus Purpuraria Enderlein, 1929 (Orthoptera: Pamphagidae) using an integrative approach. *Journal of Zoological Systematics and Evolutionary Research* **51**:173-186.

Lowe, S., Browne, M., Boudjelas, S., and De Poorter, M. (2000). 100 of the World's Worst Invasive Alien Species A selection from the Global Invasive Species Database. *Aliens*:1-11.

Lowry, P. 1998. Diversity, endemism, and extinction in the flora of New Caledonia: a review. Pages 181-206 *in* Proc Int Symp on Rare, Threatened, and Endangered Floras of Asia and the Pacific. Monograph ed. Taipei, Taiwan: Institute of Botany, Academica Sinica.

Lubin, Y. D. (1984). Changes in the native fauna of the Galápagos Islands following invasion by the little red fire ant, Wasmannia auropunctata. *Biological Journal of the Linnean Society* **21**:229-242.

Luther, D. A. (2008). Signaller: receiver coordination and the timing of communication in Amazonian birds. *Biology Letters* **4**:651-654.

MacArthur, R. H. and MacArthur, J. W. (1961). On bird species diversity. *Ecology* **42**:594-598.

MacArthur, R. H. and Wilson, E. O. 1967. The theory of island biogeography. Princeton University Press.

Mack, R. N., Simberloff, D., Mark Lonsdale, W., Evans, H., Clout, M., and Bazzaz, F. A. (2000). Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* **10**:689-710.

MacNally, R. and Fleishman, E. (2002). Using "indicator" species to model species richness: model development and predictions. *Ecological Applications* **12**:79-92.

MacNally, R. and Fleishman, E. (2004). A successful predictive model of species richness based on indicator species. *Conservation Biology* **18**:646-654.

Magal, C., Dangles, O., Caparroy, P., and Casas, J. (2006). Hair canopy of cricket sensory system tuned to predator signals. *Journal of Theoretical Biology* **241**:459-466.

Maia, T., Almeida-Gomes, M., Siqueira, C. C., Vrcibradic, D., Kiefer, M. C., and Rocha, C. F. D. (2011). Diet of the lizard Ecpleopus gaudichaudii (Gymnophthalmidae) in Atlantic Rainforest, state of Rio de Janeiro, Brazil. *Zoologia (Curitiba)* **28**:587-592.

Mankin, R. and Benshemesh, J. (2006). Geophone detection of subterranean termite and ant activity. *Journal of Economic Entomology* **99**:244-250.

Mankin, R., Hagstrum, D., Smith, M., Roda, A., and Kairo, M. (2011). Perspective and promise: a century of insect acoustic detection and monitoring. *American entomologist* **57**:30-44.

Marcó, M. V. P., Larriera, A., and Piña, C. I. (2015). Red Fire Ant (Solenopsis invicta) Effects on Broad-Snouted Caiman (Caiman latirostris) Nest Success. *Journal of Herpetology* **49**:70-74.

Marini, L., Fontana, P., Battisti, A., and Gaston, K. J. (2009). Response of orthopteran diversity to abandonment of semi-natural meadows. *Agriculture, ecosystems & environment* **132**:232-236.

Marmion, M., Parviainen, M., Luoto, M., Heikkinen, R. K., and Thuiller, W. (2009). Evaluation of consensus methods in predictive species distribution modelling. *Diversity and Distributions* **15**:59-69.

Marten, K. and Marler, P. (1977). Sound transmission and its significance for animal vocalization. *Behavioral Ecology and Sociobiology* **2**:271-290.

Marten, K., Quine, D., and Marler, P. (1977). Sound Transmission and Its Significance for Animal Vocalization: II. Tropical Forest Habitats. *Behavioral Ecology and Sociobiology* **2**:291-302.

Martin, G. D. and Coetzee, J. A. (2011). Pet stores, aquarists and the internet trade as modes of introduction and spread of invasive macrophytes in South Africa. *Water SA* **37**.

Mazzoni, R., da Silva, R. C., and Pinto, M. P. (2015). Invasion and Colonisation of a Tropical Stream by an Exotic Loricariid Fish: Indices of Gradual Displacement of the Native Common Pleco (Hypostomus punctatus) by the Red Fin Dwarf Pleco (Parotocinclus maculicauda) over Fifteen Years. *PLoS ONE* **10**:e0139968.

McBride, A. C., Dale, V. H., Baskaran, L. M., Downing, M. E., Eaton, L. M., Efroymson, R. A., Garten, C. T., Kline, K. L., Jager, H. I., and Mulholland, P. J. (2011). Indicators to support environmental sustainability of bioenergy systems. *Ecological Indicators* **11**:1277-1289.

McCallum, M. L. (2015). Vertebrate biodiversity losses point to a sixth mass extinction. *Biodiversity and Conservation*:1-23.

McCluney, K. E. and Date, R. C. (2008). The effects of hydration on growth of the house cricket, Acheta domesticus. *Journal of Insect Science* **8**:32.

McCluney, K. E. and Sabo, J. L. (2009). Water availability directly determines per capita consumption at two trophic levels. *Ecology* **90**:1463-1469.

McCluney, K. E. and Sabo, J. L. (2014). Sensitivity and tolerance of riparian arthropod communities to altered water resources along a drying river. *PLoS ONE* **9**:e109276.

McConkey, K. R., Drake, D. R., Meehan, H. J., and Parsons, N. (2003). Husking stations provide evidence of seed predation by introduced rodents in Tongan rain forests. *Biological Conservation* **109**:221-225.

McCoy, S., Jaffré, T., Rigault, F., and Ash, J. (1999). Fire and succession in the ultramafic maquis of New Caledonia. *Journal of Biogeography* **26**:579-594.

McCracken, K. G. and Sheldon, F. H. (1997). Avian vocalizations and phylogenetic signal. *Proceedings of the National Academy of Sciences* **94**:3833-3836.

McGeoch, M. A. (1998). The selection, testing and application of terrestrial insects as bioindicators. *Biological Reviews of the Cambridge Philosophical Society* **73**:181-201.

McGeoch, M. A., Sithole, H., Samways, M. J., Simaika, J. P., Pryke, J. S., Picker, M., Uys, C., Armstrong, A. J., Dippenaar-Schoeman, A. S., and Engelbrecht, I. A. (2011). Conservation and monitoring of invertebrates in terrestrial protected areas. *koedoe* **53**:131-143.

McNatty, A., Abbott, K., and Lester, P. (2009). Invasive ants compete with and modify the trophic ecology of hermit crabs on tropical islands. *Oecologia* **160**:187-194.

Medina, F. M., Bonnaud, E., Vidal, E., Tershy, B. R., Zavaleta, E. S., Josh Donlan, C., Keitt, B. S., Corre, M., Horwath, S. V., and Nogales, M. (2011). A global review of the impacts of invasive cats on island endangered vertebrates. *Global change biology* **17**:3503-3510.

Meybeck, M. (2003). Global analysis of river systems: from Earth system controls to Anthropocene syndromes. *Philosophical Transactions of the Royal Society B: Biological Sciences* **358**:1935-1955.

Meyer, J.-Y. and Butaud, J.-F. (2009). The impacts of rats on the endangered native flora of French Polynesia (Pacific Islands): drivers of plant extinction or coup de grâce species? *Biological Invasions* **11**:1569-1585.

Millennium Ecosystem Assessment. 2005. Ecosystems and human well-being. Island Press Washington, DC.

Miller, M., Pfeiffer, W., and Schwartz, T. (2010). Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *In: Proceedings of the Gateway Computing Environments Workshop (GCE), New Orleans, LA*:1-8.

Minchin, P. R. 1987. An evaluation of the relative robustness of techniques for ecological ordination. Pages 89-107 Theory and models in vegetation science. Springer.

Miranda, A., Altamirano, A., Cayuela, L., Pincheira, F., and Lara, A. (2015). Different times, same story: Native forest loss and landscape homogenization in three physiographical areas of south-central of Chile. *Applied Geography* **60**:20-28.

Misso, M. and West, J. (2014). Conservation management of the terrestrial biodiversity of Christmas Island: challenges and perspectives. *Raffles Bulletin of Zoology*:17-23.

Mittermeier, R. A., Turner, W. R., Larsen, F. W., Brooks, T. M., and Gascon, C. 2011. Global biodiversity conservation: the critical role of hotspots. Pages 3-22 Biodiversity hotspots. Springer.

Molnar, J. L., Gamboa, R. L., Revenga, C., and Spalding, M. D. (2008). Assessing the global threat of invasive species to marine biodiversity. *Frontiers in Ecology and the Environment* **6**:485-492.

Montealegre-Z, F., Jonsson, T., and Robert, D. (2011). Sound radiation and wing mechanics in stridulating field crickets (Orthoptera: Gryllidae). *The Journal of Experimental Biology* **214**:2105-2117.

Montealegre-Z, F., Windmill, J. F., Morris, G. K., and Robert, D. (2009). Mechanical phase shifters for coherent acoustic radiation in the stridulating wings of crickets: the plectrum mechanism. *Journal of Experimental Biology* **212**:257-269.

Monteith, L. (1971). Crickets as predators of the apple maggot, Rhagoletis pomonella (Diptera: Tephritidae). *The Canadian Entomologist* **103**:52-58.

Mooney, H. A. and Cleland, E. E. (2001). The evolutionary impact of invasive species. *Proceedings of the National Academy of Sciences* **98**:5446-5451.

Morales-Hidalgo, D., Oswalt, S. N., and Somanathan, E. (2015). Status and trends in global primary forest, protected areas, and areas designated for conservation of biodiversity from the Global Forest Resources Assessment 2015. *Forest Ecology and Management* **352**:68-77.

Morat, P. (1993). Our knowledge of the flora of New Caledonia: endemism and diversity in relation to vegetation types and substrates. *Biodiversity letters*:72-81.

Morat, P., Jaffré, T., Tronchet, F., Munzinger, J., Pillon, Y., Veillon, J.-M., Chalopin, M., Birnbaum, P., Rigault, F., and Dagostini, G. (2012). Le référentiel taxonomique Florical et les caractéristiques de la flore vasculaire indigène de la Nouvelle-Calédonie. *Adansonia* **34**:179-221.

Morat, P., Jaffré, T., Veillon, J.-M., and MacKee, H. (1986). Affinités floristiques et considérations sur l'origine des maquis miniers de la Nouvelle-Calédonie. *Adansonia* **2**:133-182.

Moritz, C., Richardson, K. S., Ferrier, S., Monteith, G. B., Stanisic, J., Williams, S. E., and Whiffin, T. (2001). Biogeographical concordance and efficiency of taxon indicators for establishing conservation priority in a tropical rainforest biota. *Proceedings of the Royal Society of London B: Biological Sciences* **268**:1875-1881.

Müller, J. and Brandl, R. (2009). Assessing biodiversity by remote sensing in mountainous terrain: the potential of LiDAR to predict forest beetle assemblages. *Journal of Applied Ecology* **46**:897-905.

Murienne, J., Pellens, R., Budinoff, R., Wheeler, W., and Grandcolas, P. (2008). Phylogenetic analysis of the endemic New Caledonian cockroach Lauraesilpha. Testing competing hypotheses of diversification. *Cladistics* **24**:802-812.

Murienne, J. m., Grandcolas, P., Piulachs, M. D., Bellés, X., D'Haese, C., Legendre, F., Pellens, R., and Guilbert, E. (2005). Evolution on a shaky piece of Gondwana: is local endemism recent in New Caledonia? *Cladistics* **21**:2-7.

Myers, N. (1988). Threatened biotas:" hot spots" in tropical forests. *Environmentalist* **8**:187-208.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., and Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature* **403**:853-858.

Naguib, M. (2003). Reverberation of rapid and slow trills: implications for signal adaptations to long-range communication. *The Journal of the Acoustical Society of America* **113**:1749-1756.

Nattier, R., Grandcolas, P., Elias, M., Desutter-Grandcolas, L., Jourdan, H., Couloux, A., and Robillard, T. (2012). Secondary sympatry caused by range expansion informs on the dynamics of microendemism in a biodiversity hotspot.

Nattier, R., Grandcolas, P., Pellens, R., Jourdan, H., Couloux, A., Poulain, S., and Robillard, T. (2013). Climate and Soil Type Together Explain the Distribution of Microendemic Species in a Biodiversity Hotspot.

Nattier, R., Robillard, T., Desutter-Grandcolas, L., Couloux, A., and Grandcolas, P. (2011). Older than New Caledonia emergence? A molecular phylogenetic study of the eneopterine crickets (Orthoptera: Grylloidea). *Journal of Biogeography* **38**:2195-2209.

Neall, V. E. and Trewick, S. A. (2008). The age and origin of the Pacific islands: a geological overview. *Philosophical Transactions of the Royal Society B: Biological Sciences* **363**:3293-3308.

Nichols, B., Sites, RW. (1989). A comparison of arthropods species within and outside the range of *Solenopsis invicta* Buren in central Texas. *Southwestern Entomologist* **14**:345-350.

Nicolas, V., Grandcolas, P., Braux, F., Jourdan, H., Malau, A., Couloux, A., and Ohler, A. (2015). Recent species in old Islands: the origin of introduced populations of Litoria aurea (Anura: Hylidae) in New Caledonia and Wallis. *Amphibia-Reptilia* **36**:65-81.

Niemi, G. J. and McDonald, M. E. (2004). Application of ecological indicators. *Annual Review of Ecology, Evolution, and Systematics*:89-111.

Nischk, F. and Otte, D. (2000). Bioacoustics, Ecology and Systematics of Ecuadorian Rainforest Crickets (Orthoptera: Gryllidae: Phalangopsinae), with a Description of Four New Genera and Ten New Species. *Journal of Orthoptera Research* **9**:229-254.

Nischk, F. and Riede, K. (2001). Bioacoustics of two cloud forest ecosystems in Ecuador compared to a lowland rainforest with special emphasis on singing cricket species. *Epiphytes and canopy fauna of the Otongan rainforest (Ecuador)* **2**:217-242.

Nityananda, V. and Bee, M. A. (2011). Finding your mate at a cocktail party: frequency separation promotes auditory stream segregation of concurrent voices in multi-species frog choruses. *PLoS ONE* **6**:e21191.

Novosolov, M., Raia, P., and Meiri, S. (2013). The island syndrome in lizards. *Global Ecology and Biogeography* **22**:184-191.

Nylander, J. A., Ronquist, F., Huelsenbeck, J. P., and Nieves-Aldrey, J. (2004). Bayesian phylogenetic analysis of combined data. *Systematic biology* **53**:47-67.

O'Dowd, D. J., Green, P. T., and Lake, P. S. (2003). Invasional 'meltdown'on an oceanic island. *Ecology Letters* **6**:812-817.

O'Neill, K. M., Olson, B. E., Rolston, M. G., Wallander, R., Larson, D. P., and Seibert, C. E. (2003). Effects of livestock grazing on rangeland grasshopper (Orthoptera: Acrididae) abundance. *Agriculture, ecosystems & environment* **97**:51-64.

Obrist, M. K., Pavan, G., Sueur, J., Riede, K., Llusia, D., and Márquez, R. (2010). Bioacoustics approaches in biodiversity inventories. *Abc Taxa* **8**:68-99.

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R., Simpson, G. L., Solymos, P., Stevens, M., and Wagner, H. (2013). Package 'vegan'. *R Packag ver* **254**:20-28.

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Stevens, M. H. H., Oksanen, M. J., and Suggests, M. (2007). The vegan package. *Community ecology package*:631-637.

Orci, K. M., Szoevenyi, G., and Nagy, B. (2010). Isophya sicula sp. n.(Orthoptera: Tettigonioidea), a new, morphologically cryptic bush-cricket species from the Eastern Carpathians (Romania) recognized from its peculiar male calling song. *Zootaxa* **2627**:57-68.

Orivel, J., Grangier, J., Foucaud, J., Le Breton, J., Andrès, F.-X., Jourdan, H., Delabie, J. H. C., Fournier, D., Cerdan, P., Facon, B., Estoup, A., and Dejean, A. (2009). Ecologically heterogeneous populations of the invasive ant *Wasmannia auropunctata* within its native and introduced ranges. *Ecological Entomology* **34**:504-512.

Orwin, K. A., Stevenson, B. A., Smaill, S. J., Kirschbaum, M. U., Dickie, I., Clothier, B. E., Garrett, L. G., Van Der Weerden, T. J., Beare, M. H., and Curtin, D. (2015). Effects of climate change on the delivery of soil-mediated ecosystem services within the primary sector in temperate ecosystems: a review and New Zealand case study. *Global change biology*.

Ostrand, S. L. and Bollinger, E. K. (2012). Nestling Diet of Eastern Meadowlarks in East-central Illinois. *The Wilson Journal of Ornithology* **124**:399-402.

Otte, D. (1992). Evolution of cricket songs. *Journal of Orthoptera Research*:25-49.

Otte, D. (1994). The Crickets of Hawaii: Origin, Systematics and Evolution. *The Orthopterists» Society: Academy of Natural Sciences of Philadelphia*.

Otte, D. and Alexander, R. (1983). The Australian Crickets (Orthoptera: Gryllidae)(Acad Nat Sci Philadelphia Monograph 22). *Allen, Lawrence*.

Otte, D., Alexander, R. D., and Cade, W. (1987). The Crickets of New Caledonia (Gryllidae). *Proceedings of the Academy of Natural Sciences of Philadelphia* **139**:375-457.

Otte, D. and Pérez-Gelabert, D. E. 2009. Caribbean crickets. Orthopterists' Society.

Pascal, M., Barré, N., de Garine-Wichatitsky, M., Lorvelec, O., Frétey, T., Brescia, F., and Jourdan, H. (2006). Les peuplements néo-calédoniens de vertébrés: invasions, disparitions. *ML Beauvais, A. Coléno & A. Jourdan (coords): Les espèces envahissantes dans l'archipel néo-calédonien. IRD Éditions (collection Expertise Collégiale), Paris*:111-162.

Pascal, M., Deforges, B., Leguyader, H., and Simberloff, D. (2008). Mining and other threats to the New Caledonia biodiversity hotspot. *Conservation Biology* **22**:498-499.

Paun, O., Turner, B., Trucchi, E., Munzinger, J., Chase, M. W., and Samuel, R. (2015). Processes Driving the Adaptive Radiation of a Tropical Tree (Diospyros, Ebenaceae) in New Caledonia, a Biodiversity Hotspot. *Systematic biology*:syv076.

Pearce, J. and Venier, L. (2005). Small mammals as bioindicators of sustainable boreal forest management. *Forest Ecology and Management* **208**:153-175.

Pearce, J. and Venier, L. (2006). The use of ground beetles (Coleoptera: Carabidae) and spiders (Araneae) as bioindicators of sustainable forest management: a review. *Ecological Indicators* **6**:780-793.

Pejchar, L. and Mooney, H. A. (2009). Invasive species, ecosystem services and human well-being. *Trends in Ecology & Evolution* **24**:497-504.

Pekin, B. K., Jung, J., Villanueva-Rivera, L. J., Pijanowski, B. C., and Ahumada, J. A. (2012). Modeling acoustic diversity using soundscape recordings and LIDAR-derived metrics of vertical forest structure in a neotropical rainforest. *Landscape Ecology* **27**:1513-1522.

Pellens, R. and Grandcolas, P. (2009). Conservation and management of the biodiversity in a hotspot characterized by short range endemism and rarity: the challenge of New Caledonia. *Environmental Research Journal* **5**.

Pelletier, B. (2006). Geology of the New Caledonia region and its implications for the study of the New Caledonian biodiversity. *Compendium of marine species from New Caledonia*:17-30.

Penone, C., Kerbiriou, C., Julien, J.-F., Julliard, R., Machon, N., and Viol, I. (2012). Urbanisation effect on Orthoptera: which scale matters? *Insect Conservation and Diversity* **6**:319-327.

Penone, C., Le Viol, I., Pellissier, V., Julien, J.-F., Bas, Y., and Kerbiriou, C. (2013). Use of Large-Scale Acoustic Monitoring to Assess Anthropogenic Pressures on Orthoptera Communities. *Conservation Biology* **27**:979-987.

Pereira, H. M., Leadley, P. W., Proença, V., Alkemade, R., Scharlemann, J. P., Fernandez-Manjarrés, J. F., Araújo, M. B., Balvanera, P., Biggs, R., and Cheung, W. W. (2010). Scenarios for global biodiversity in the 21st century. *Science* **330**:1496-1501.

Pereira, M. J. R., Rebelo, H., Rainho, A., and Palmeirim, J. M. (2002). Prey selection by Myotis myotis (Vespertilionidae) in a Mediterranean region. *Acta Chiropterologica* **4**:183-193.

Perry, G. L. and Enright, N. J. (2002). Humans, fire and landscape pattern: understanding a maquis-forest complex, Mont Do, New Caledonia, using a spatial 'state-and-transition'model. *Journal of Biogeography* **29**:1143-1158.

Peters, W. L. 2001. The Ephemeroptera of New Zealand and New Caledonia. Pages 43-45 Trends in Research in Ephemeroptera and Plecoptera. Springer.

Pieretti, N., Duarte, M., Sous-Lima, R., Rodrigues, M., Young, R., and Farina, A. (2015). Determining temporal sampling schemes for passive acoustic studies in different tropical ecosystems. *Tropical Conservation Science* **8**:215-234.

Pieretti, N., Farina, A., and Morri, D. (2011). A new methodology to infer the singing activity of an avian community: the Acoustic Complexity Index (ACI). *Ecological Indicators* **11**:868-873.

Pijanowski, B. C., Farina, A., Gage, S. H., Dumyahn, S. L., and Krause, B. L. (2011a). What is soundscape ecology? An introduction and overview of an emerging new science. *Landscape Ecology* **26**:1213-1232.

Pijanowski, B. C., Villanueva-Rivera, L. J., Dumyahn, S. L., Farina, A., Krause, B. L., Napoletano, B. M., Gage, S. H., and Pieretti, N. (2011b). Soundscape ecology: the science of sound in the landscape. *BioScience* **61**:203-216.

Pillon, Y. 2008. Biodiversité, origine et évolution des Cunoniaceae: implications pour la conservation de la flore de Nouvelle-Calédonie. Citeseer.

Pillon, Y. (2012). Time and tempo of diversification in the flora of New Caledonia. *Botanical Journal of the Linnean Society* **170**:288-298.

Pillon, Y., Munzinger, J., Amir, H., Hopkins, H. C., and Chase, M. W. (2009). Reticulate evolution on a mosaic of soils: diversification of the New Caledonian endemic genus Codia (Cunoniaceae). *Molecular Ecology* **18**:2263-2275.

Pillon, Y., Munzinger, J., Amir, H., and Lebrun, M. (2010). Ultramafic soils and species sorting in the flora of New Caledonia. *Journal of Ecology* **98**:1108-1116.

Pimentel, D., McNair, S., Janecka, J., Wightman, J., Simmonds, C., O'Connell, C., Wong, E., Russel, L., Zern, J., Aquino, T., and Tsomondo, T. (2001). Economic and environmental threats of alien plant, animal, and microbe invasions. *Agriculture, Ecosystems & Environment* **84**:1-20.

Pimentel, D., Zuniga, R., and Morrison, D. (2005). Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics* **52**:273-288.

Pimm, S., Jenkins, C., Abell, R., Brooks, T., Gittleman, J., Joppa, L., Raven, P., Roberts, C., and Sexton, J. (2014). The biodiversity of species and their rates of extinction, distribution, and protection. *Science* **344**:1246752.

Pintaud, J.-C., Jaffré, T., and Puig, H. (2001). Chorology of New Caledonian palms and possible evidence of Pleistocene rain forest refugia. *Comptes Rendus de l'Académie des Sciences-Series III-Sciences de la Vie* **324**:453-463.

Plentovich, S., Hebshi, A., and Conant, S. (2009). Detrimental effects of two widespread invasive ant species on weight and survival of colonial nesting seabirds in the Hawaiian Islands. *Biological Invasions* **11**:289-298.

Polis, G. A. and Strong, D. R. (1996). Food web complexity and community dynamics. *American Naturalist*:813-846.

Pollack, G. (2000). Who, what, where? Recognition and localization of acoustic signals by insects. *Current opinion in neurobiology* **10**:763-767.

Poncet, V., Munoz, F., Munzinger, J., Pillon, Y., Gomez, C., Couderc, M., Tranchant-Dubreuil, C., Hamon, S., and Kochko, A. (2013). Phylogeography and niche modelling of the relict plant Amborella trichopoda (Amborellaceae) reveal multiple Pleistocene refugia in New Caledonia. *Molecular Ecology* **22**:6163-6178.

Poniatowski, D. and Fartmann, T. (2008). The classification of insect communities: lessons from orthopteran assemblages of semi-dry calcareous grasslands in central Germany. *Eur. J. Entomol* **105**:659-671.

Porter, S. D. and Savignano, D. A. (1990). Invasion of polygyne fire ants decimates native ants and disrupts arthropod community. *Ecology* **71**:2095-2106.

Posada, D. (2008). jModelTest: phylogenetic model averaging. *Molecular biology and evolution* **25**:1253-1256.

Potamitis, I. (2014). Automatic classification of a taxon-rich community recorded in the wild. *PLoS ONE* **9**:e96936.

Potamitis, I., Ganchev, T., and Kontodimas, D. (2009). On automatic bioacoustic detection of pests: the cases of Rhynchophorus ferrugineus and Sitophilus oryzae. *Journal of Economic Entomology* **102**:1681-1690.

Pouteau, R., Trueba, S., Feild, T. S., and Isnard, S. (2015). New Caledonia: a Pleistocene refugium for rain forest lineages of relict angiosperms. *Journal of Biogeography*.

Prather, C. M., Pelini, S. L., Laws, A., Rivest, E., Woltz, M., Bloch, C. P., Del Toro, I., Ho, C. K., Kominoski, J., and Newbold, T. (2013). Invertebrates, ecosystem services and climate change. *Biological Reviews* **88**:327-348.

Prentice, I. C. (1986). Vegetation responses to past climatic variation. *Vegetatio* **67**:131-141.

Pretelli, M. G., Cardoni, D. A., and Isacch, J. P. (2014). Diet of Nestling Spectacled Tyrants (Hymenops perspicillatus) in the Southeast Pampas Region, Argentina. *The Wilson Journal of Ornithology* **126**:754-759.

Proctor, J. (2003). Vegetation and soil and plant chemistry on ultramafic rocks in the tropical Far East. *Perspectives in plant ecology, evolution and systematics* **6**:105-124.

Pyke, G. H. and White, A. W. (2001). A review of the biology of the green and golden bell frog Litoria aurea. *Australian Zoologist* **31**:563-598.

Rácz, I. A., Déri, E., Kisfali, M., Batiz, Z., Varga, K., Szabó, G., and Lengyel, S. (2013). Early changes of Orthopteran assemblages after grassland restoration: a comparison of space-for-

time substitution versus repeated measures monitoring. *Biodiversity and Conservation* **22**:2321-2335.
Rada, S., Mazalová, M., Šipoš, J., and Kuras, T. (2014). Impacts of Mowing, Grazing and Edge Effect on Orthoptera of Submontane Grasslands: Perspectives for Biodiversity Protection. *Polish Journal of Ecology* **62**:123-138.
Radford, C., Stanley, J., Tindle, C., Montgomery, J., and Jeffs, A. (2010). Localised coastal habitats have distinct underwater sound signatures. *Mar Ecol Prog Ser* **401**:21-29.
Ragge, D. R. (1955). The wing venation of the Orthoptera Saltatoria. *British Museum (Natural History), London*:159
Ragge, D. R. and Reynolds, W. J., editors. 1998. The songs of the grasshoppers and crickets from Western Europe.
Raghuram, H., Jain, M., and Balakrishnan, R. (2014). Species and acoustic diversity of bats in a paleotropical wet evergreen forest in southern India. *Curr. Sci.* **107**:631-641.
Rahman, P. M., Varma, R., and Sileshi, G. (2012). Abundance and diversity of soil invertebrates in annual crops, agroforestry and forest ecosystems in the Nilgiri biosphere reserve of Western Ghats, India. *Agroforestry systems* **85**:165-177.
Rambaut, A. and Drummond, A. J. (2009). Tracer v.1.5. In: http://beast.bio.ed.ac.uk/tracer/.
Rambo, J. L. and Faeth, S. H. (1999). Effect of Vertebrate Grazing on Plant and Insect Community Structure Efecto del Pastoreo de Vertebrados en la Estructura Comunitaria de Plantas e Insectos. *Conservation Biology* **13**:1047-1054.
Raup, D. M. (1986). Biological extinction in earth history. *Science* **231**:1528-1533.
Regier, J. C., Shultz, J. W., Zwick, A., Hussey, A., Ball, B., Wetzer, R., Martin, J. W., and Cunningham, C. W. (2010). Arthropod relationships revealed by phylogenomic analysis of nuclear protein-coding sequences. *Nature* **463**:1079-1083.
Régnier, C., Achaz, G., Lambert, A., Cowie, R. H., Bouchet, P., and Fontaine, B. (2015). Mass extinction in poorly known taxa. *Proceedings of the National Academy of Sciences* **112**:7761-7766.
Rhymer, J. M. and Simberloff, D. (1996). Extinction by hybridization and introgression. *Annual Review of Ecology and Systematics*:83-109.
Ricciardi, A. (2004). Assessing species invasions as a cause of extinction. *TRENDS in Ecology and Evolution* **19**:619-619.
Ricciardi, A. (2007). Are modern biological invasions an unprecedented form of global change? *Conservation Biology* **21**:329-336.
Richards, D. G. and Wiley, R. H. (1980). Reverberations and Amplitude Fluctuations in the Propagation of Sound in a Forest: Implications for Animal Communication. *The American Naturalist* **115**:381-399.
Richardson, D. M., Pyšek, P., Rejmánek, M., Barbour, M. G., Panetta, F. D., and West, C. J. (2000). Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions* **6**:93-107.
Ricklefs, R. E. and Bermingham, E. (2002). The concept of the taxon cycle in biogeography. *Global Ecology and Biogeography* **11**:353-361.
Ricotta, C. (2005). Through the jungle of biological diversity. *Acta biotheoretica* **53**:29-38.
Riede, K. (1993). Monitoring biodiversity: analysis of Amazonian rainforest sounds. *Ambio*:546-548.
Riede, K. 1997. Bioacoustic diversity and resource partitioning in tropical calling communities. Pages 275-280 *in* Tropical biodiversity and systematics. Proceedings of the International Symposium on Biodiversity and Systematics in Tropical Ecosystems, Bonn.
Riede, K. (1998). Acoustic monitoring of Orthoptera and its potential for conservation. *Journal of Insect Conservation* **2**:217-223.
Robillard, T. (2009). Eneopterinae crickets (Insecta, Orthoptera, Grylloidea) from Vanuatu. *Zoosystema* **31**:577-618.
Robillard, T. (2010). New species of the genus Lebinthus (Orthoptera, Grylloidea, Eneopterinae, Lebinthini) from Indonesia and the Solomon islands. *Zootaxa* **2386**:25-48.
Robillard, T. and Desutter-Grandcolas, L. (2004a). High-frequency calling in Eneopterinae crickets (Orthoptera, Grylloidea, Eneopteridae): adaptive radiation revealed by phylogenetic analysis. *Biological Journal of the Linnean Society* **83**:577-584.

Robillard, T. and Desutter-Grandcolas, L. (2004b). Phylogeny and the modalities of acoustic diversification in extant Eneopterinae (Insecta, Orthoptera, Grylloidea, Eneopteridae). *Cladistics* **20**:271-293.

Robillard, T. and Desutter-Grandcolas, L. (2006). Phylogeny of the cricket subfamily Eneopterinae (Orthoptera, Grylloidea, Eneopteridae) based on four molecular loci and morphology. *Molecular Phylogenetics and Evolution* **40**:643-661.

Robillard, T. and Desutter-Grandcolas, L. (2008). Clarification of the taxonomy of extant crickets of the subfamily Eneopterinae (Orthoptera: Grylloidea; Gryllidae). *Zootaxa* **1789**:66-68.

Robillard, T. and Desutter-Grandcolas, L. (2011). Evolution of calling songs as multicomponent signals in crickets (Orthoptera: Grylloidea: Eneopterinae). *Behaviour* **148**:627-672.

Robillard, T., Gorochov, A. V. e., Poulain, S., and Suhardjono, Y. R. (2014). Revision of the cricket genus Cardiodactylus (Orthoptera, Eneopterinae, Lebinthini): the species from both sides of the Wallace line, with description of 25 new species. *Zootaxa* **3854**:1-104.

Robillard, T., Grandcolas, P., and Desutter-Grandcolas, L. (2007). A shift toward harmonics for high-frequency calling shown with phylogenetic study of frequency spectra in Eneopterinae crickets (Orthoptera, Grylloidea, Eneopteridae). *Canadian Journal of Zoology* **85**:1264-1275.

Robillard, T. and Ichikawa, A. (2009). Redescription of two Cardiodactylus species (Orthoptera, Grylloidea, Eneopterinae): the supposedly well-known C. novaeguineae (Haan, 1842), and the semi-forgotten C. guttulus (Matsumura, 1913) from Japan. *Zoological science* **26**:878-891.

Robillard, T., Nattier, R., and Desutter-Grandcolas, L. (2010). New species of the New Caledonian endemic genus *Agnotecous* (Orthoptera, Grylloidea, Eneopterinae, Lebinthini). *Zootaxa* **2559**:17-35.

Robillard, T., Yap, S., and Yngente, M. V. (2013). Systematics of cryptic species of Lebinthus crickets in Mount Makiling (Grylloidea, Eneopterinae). *Zootaxa* **3693**:049-063.

Robinet, O., Craig, J., and Chardonnet, L. (1998). Impact of rat species in Ouvea and Lifou (Loyalty Islands) and their consequences for conserving the endangered Ouvea Parakeet. *Biological Conservation* **86**:223-232.

Rocha, J. C., Peterson, G. D., and Biggs, R. O. (2015). Regime Shifts in the Anthropocene: drivers, risk, and resilience.

Rodriguez, A., Gasc, A., Pavoine, S., Grandcolas, P., Gaucher, P., and Sueur, J. (2014). Temporal and spatial variability of animal sound within a neotropical forest. *Ecological Informatics* **21**:133-143.

Romeo, C., Ferrari, N., Lanfranchi, P., Saino, N., Santicchia, F., Martinoli, A., and Wauters, L. A. (2015). Biodiversity threats from outside to inside: effects of alien grey squirrel (Sciurus carolinensis) on helminth community of native red squirrel (Sciurus vulgaris). *Parasitology research*:1-8.

Romer, H. (1993). Environmental and Biological Constraints for the Evolution of Long-Range Signalling and Hearing in Acoustic Insects. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **340**:179-185.

Römer, H. 2013. Masking by noise in acoustic insects: problems and solutions. Pages 33-63 Animal communication and noise. Springer.

Römer, H. and Bailey, W. (1998). Strategies for hearing in noise: peripheral control over auditory sensitivity in the bushcricket Sciarasaga quadrata (Austrosaginae: Tettigoniidae). *Journal of Experimental Biology* **201**:1023-1033.

Römer, H. and Krusch, M. (2000). A gain-control mechanism for processing of chorus sounds in the afferent auditory pathway of the bushcricket *Tettigonia viridissima* (Orthoptera; Tettigoniidae). *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology* **186**:181-191.

Romer, H. and Lewald, J. (1992). High-frequency sound transmission in natural habitats: implications for the evolution of insect acoustic communication. *Behavioral Ecology and Sociobiology* **29**:437-444.

Ronquist, F. and Huelsenbeck, J. P. (2003). MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* **19**:1572-1574.

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D. L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M. A., and Huelsenbeck, J. P. (2012). MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic biology* **61**:539-542.

Root, R. B. (1967). The niche exploitation pattern of the blue-gray gnatcatcher. *Ecological monographs* **37**:317-350.

Ross, C. L. (2006). Ant predation as a selective agent on overwintering eggs in a field cricket mosaic hybrid zone. *Journal of Orthoptera Research* **15**:13-21.

Rothley, K., Schmitz, O. J., and Cohon, J. L. (1997). Foraging to balance conflicting demands: novel insights from grasshoppers under predation risk. *Behavioral Ecology* **8**:551-559.

Roughgarden, J. (1976). Resource partitioning among competing species—a coevolutionary approach. *Theoretical population biology* **9**:388-424.

Rowles, A. and O'Dowd, D. (2007). Interference competition by Argentine ants displaces native ants: implications for biotic resistance to invasion. *Biological Invasions* **9**:73-85.

Ruiz, G. M., Carlton, J. T., Grosholz, E. D., and Hines, A. H. (1997). Global invasions of marine and estuarine habitats by non-indigenous species: mechanisms, extent, and consequences. *American Zoologist* **37**:621-632.

Ryan, M. J. and Brenowitz, E. A. (1985). The Role of Body Size, Phylogeny, and Ambient Noise in the Evolution of Bird Song. *The American Naturalist* **126**:87-100.

Sabrosky, C. W. (1953a). Taxonomy and host relations of the tribe Ormiini in the Western Hemisphere (Diptera, Larvaevoridae). *Proceedings of the Entomological Society of Washington.* **55**:167-183.

Sabrosky, C. W. (1953b). Taxonomy and host relations of the tribe Ormiini in the Western Hemisphere II (Diptera, Larvaevoridae). . *Proceedings of the Entomological Society of Washington.* **55**:289-305.

Sadlier, R. A., Bauer, A. M., Wood, P. L., Smith, S. A., Whitaker, A. H., and Jackman, T. R. (2014). Cryptic speciation in the New Caledonian lizard genus Nannoscincus (Reptilia: Scincidae) including the description of a new species and recognition of Nannoscincus fuscus Günther. *Mémoires du Muséum national d'histoire naturelle* **206**:45-68.

Sadlier, R. A., Smith, S. A., Bauer, A. M., and Whitaker, A. H. (2009). Three new species of skink in the genus Marmorosphax Sadlier (Squamata: Scincidae) from New Caledonia. *Mémoires du Muséum national d'histoire naturelle* **198**:373-390.

Sakaluk, S. K. and Belwood, J. J. (1984). Gecko phonotaxis to cricket calling song: a case of satellite predation. *Animal Behaviour* **32**:659-662.

Salomon, M. (2011). The natural diet of a polyphagous predator, Latrodectus hesperus (Araneae: Theridiidae), over one year. *Journal of Arachnology* **39**:154-160.

Samways, M. J., McGeoch, M. A., and New, T. R. 2010. Insect conservation: a handbook of approaches and methods. Oxford University Press Oxford.

Sanders, N. J., Gotelli, N. J., Wittman, S. E., Ratchford, J. S., Ellison, A. M., and Jules, E. S. (2007). Assembly rules of ground-foraging ant assemblages are contingent on disturbance, habitat and spatial scale. *Journal of Biogeography* **34**:1632-1641.

Sax, D. F. and Gaines, S. D. (2008). Species invasions and extinction: the future of native biodiversity on islands. *Proceedings of the National Academy of Sciences* **105**:11490-11497.

Sax, D. F., Stachowicz, J. J., Brown, J. H., Bruno, J. F., Dawson, M. N., Gaines, S. D., Grosberg, R. K., Hastings, A., Holt, R. D., and Mayfield, M. M. (2007). Ecological and evolutionary insights from species invasions. *Trends in Ecology & Evolution* **22**:465-471.

Schellart, W., Lister, G., and Toy, V. (2006). A Late Cretaceous and Cenozoic reconstruction of the Southwest Pacific region: tectonics controlled by subduction and slab rollback processes. *Earth-Science Reviews* **76**:191-233.

Schiller, A., Hunsaker, C. T., Kane, M. A., Wolfe, A. K., Dale, V. H., Suter, G. W., Russell, C. S., Pion, G., Jensen, M. H., and Konar, V. C. (2001). Communicating ecological indicators to decision makers and the public. *Conservation Ecology* **5**:19.

Schirmel, J., Mantilla-Contreras, J., Blindow, I., and Fartmann, T. (2011). Impacts of succession and grass encroachment on heathland Orthoptera. *Journal of Insect Conservation* **15**:633-642.

Schmid, M. (1982). Endémisme et spéciation en Nouvelle-Calédonie. *Compte Rendu des Séances de la Société de Biogéographie* **48**:52-60.

Schmidt, A. K. and Balakrishnan, R. (2015). Ecology of acoustic signalling and the problem of masking interference in insects. *Journal of Comparative Physiology A* **201**:133-142.

Schmidt, A. K., Riede, K., and Römer, H. (2011). High background noise shapes selective auditory filters in a tropical cricket. *The Journal of Experimental Biology* **214**:1754-1762.

Schmidt, A. K., Riede, K., and Römer, H. (2015). No phenotypic signature of acoustic competition in songs of a tropical cricket assemblage. *Behavioral Ecology*:arv141.

Schmidt, A. K. and Römer, H. (2011). Solutions to the cocktail party problem in insects: selective filters, spatial release from masking and gain control in tropical crickets. *PLoS ONE* **6**:e28593.

Schmidt, A. K., Römer, H., and Riede, K. (2013). Spectral niche segregation and community organization in a tropical cricket assemblage. *Behavioral Ecology* **24**:470-480.

Schmitz, O. J. (1997). Press perturbations and the predictability ofecological interactions in a food web. *Ecology* **78**:55-69.

Schoener, T. W. (1974). Resource partitioning in ecological communities. *Science* **185**:27-39.

Schoener, T. W. (1983). Field experiments on interspecific competition. *American Naturalist*:240-285.

Schwenker, F., Dietrich, C., Kestler, H. A., Riede, K., and Palm, G. (2003). Radial basis function neural networks and temporal fusion for the classification of bioacoustic time series. *Neurocomputing* **51**:265-275.

Sekulic, R. (1982). The function of howling in red howler monkeys (Alouatta seniculus). *Behaviour* **81**:38-54.

Sharma, P. P. and Giribet, G. (2012). Out of the Neotropics: Late Cretaceous colonization of Australasia by American arthropods. *Proceedings of the Royal Society of London B: Biological Sciences*:rspb20120675.

Shaw, K. L. (1996). Sequential radiations and patterns of speciation in the Hawaiian cricket genus Laupala inferred from DNA sequences. *Evolution*:237-255.

Shea, G., Jourdan, H., Sadlier, R., and Bauer, A. (2009). Natural history of the New Caledonian whiptailed skink Tropidoscincus variabilis (Bavay, 1869)(Squamata: Scincidae). *Amphibia-Reptilia* **30**:207-220.

Shieh, B.-S., Liang, S.-H., and Chiu, Y.-W. (2015). Acoustic and Temporal Partitioning of Cicada Assemblages in City and Mountain Environments. *PLoS ONE* **10**.

Shik, J. Z. and Kaspari, M. (2010). More food, less habitat: how necromass and leaf litter decomposition combine to regulate a litter ant community. *Ecological Entomology* **35**:158-165.

Shimozawa, T. and Kanou, M. (1984). Varieties of filiform hairs: range fractionation by sensory afferents and cereal interneurons of a cricket. *Journal of Comparative Physiology A* **155**:485-493.

Silvestro, D. and Michalak, I. (2012). raxmlGUI: a graphical front-end for RAxML. *Organisms Diversity & Evolution* **12**:335-337.

Simberloff, D. (1995). Why do introduced species appear to devastate islands more than mainland areas? *Pacific Science* **49**:87-97.

Simberloff, D. (2011). How common are invasion-induced ecosystem impacts? *Biological Invasions* **13**:1255-1268.

Simberloff, D. and Dayan, T. (1991). The guild concept and the structure of ecological communities. *Annual Review of Ecology and Systematics*:115-143.

Simberloff, D., Martin, J.-L., Genovesi, P., Maris, V., Wardle, D. A., Aronson, J., Courchamp, F., Galil, B., García-Berthou, E., and Pascal, M. (2013). Impacts of biological invasions: what's what and the way forward. *Trends in Ecology & Evolution* **28**:58-66.

Simberloff, D. S. (1974). Equilibrium theory of island biogeography and ecology. *Annual Review of Ecology and Systematics*:161-182.

Simmons, A. M. (2013). "To Ear is Human, to Frogive is Divine": Bob Capranica's legacy to auditory neuroethology. *Journal of Comparative Physiology A* **199**:169-182.

Simmons, L. and Ritchie, M. (1996). Symmetry in the songs of crickets. *Proceedings of the Royal Society of London B: Biological Sciences* **263**:1305-1311.

Skipwith, P., Jackman, T., Whitaker, A. H., Bauer, A. M., and Sadlier, R. A. (2014). New data on Dierogekko (Squamata: Gekkota: Diplodactylidae), with the description of a new species from

Île Baaba, Province Nord, New Caledonia. *Mémoires du Muséum national d'histoire naturelle* **206**:13-30.

Slabbekoorn, H. and Ripmeester, E. A. (2008). Birdsong and anthropogenic noise: implications and applications for conservation. *Molecular Ecology* **17**:72-83.

Slowinski, J. B. and Guyer, C. (1993). Testing whether certain traits have caused amplified diversification: an improved method based on a model of random speciation and extinction. *American Naturalist*:1019-1024.

Smith, D. (1959). Note on destruction of grasshopper eggs by the field cricket Acheta assimilis luctuosus (Serville)(Orthoptera: Gryllidae). *The Canadian Entomologist* **91**:127-127.

Song, H., Amédégnato, C., Cigliano, M. M., Desutter-Grandcolas, L., Heads, S. W., Huang, Y., Otte, D., and Whiting, M. F. (2015). 300 million years of diversification: elucidating the patterns of orthopteran evolution based on comprehensive taxon and gene sampling. *Cladistics*.

Souza, A. d., Delabie, J., and Fowler, H. (1998). Wasmannia spp.(Hym., Formicidae) and insect damages to cocoa in Brazilian farms. *Journal of Applied Entomology* **122**:339-341.

Souza, E., Follett, P. A., Price, D. K., and Stacy, E. A. (2008). Field suppression of the invasive ant Wasmannia auropunctata (Hymenoptera: Formicidae) in a tropical fruit orchard in Hawaii. *Journal of Economic Entomology* **101**:1068-1074.

Spaggiari, J. and de Garine-Wichatitsky, M. (2006). Home range and habitat use of introduced rusa deer (Cervus timorensis russa) in a mosaic of savannah and native sclerophyll forest of New Caledonia. *New Zealand Journal of Zoology* **33**:175-183.

Sperber, C. F., Soares, L. G., and Pereira, M. R. (2007). Litter disturbance and trap spatial positioning affects the number of captured individuals and genera of crickets (Orthoptera: Grylloidea). *Journal of Orthoptera Research* **16**:77-83.

Stamatakis, A. (2006). RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* **22**:2688-2690.

Steffen, W., Grinevald, J., Crutzen, P., and McNeill, J. (2011). The Anthropocene: conceptual and historical perspectives. *Philosophical Transactions of the Royal Society of London A: Mathematical, Physical and Engineering Sciences* **369**:842-867.

Steffen, W., Sanderson, R. A., Tyson, P. D., Jäger, J., Matson, P. A., Moore III, B., Oldfield, F., Richardson, K., Schellnhuber, H. J., and Turner, B. L. 2006. Global change and the earth system: a planet under pressure. Springer Science & Business Media.

Stevenson, J. (2004). A late-Holocene record of human impact from the southwest coast of New Caledonia. *The Holocene* **14**:888-898.

Stevenson, J. and Hope, G. (2005). A comparison of late Quaternary forest changes in New Caledonia and northeastern Australia. *Quaternary Research* **64**:372-383.

Stone, L. and Roberts, A. (1990). The checkerboard score and species distributions. *Oecologia* **85**:74-79.

Stork, N. E. (2010). Re-assessing current extinction rates. *Biodiversity and Conservation* **19**:357-371.

Strayer, D. L. (2012). Eight questions about invasions and ecosystem functioning. *Ecology Letters* **15**:1199-1210.

Suarez, A. V. and Tsutsui, N. D. (2008). The evolutionary consequences of biological invasions. *Molecular Ecology* **17**:351-360.

Sueur, J. (2002). Cicada acoustic communication: potential sound partitioning in a multispecies community from Mexico (Hemiptera: Cicadomorpha: Cicadidae). *Biological Journal of the Linnean Society* **75**:379-394.

Sueur, J. and Aubin, T. (2003). Is microhabitat segregation between two cicada species (*Tibicina haematodes* and *Cicada orni*) due to calling song propagation constraints? *Naturwissenschaften* **90**:322-326.

Sueur, J., Farina, A., Gasc, A., Pieretti, N., and Pavoine, S. (2014). Acoustic Indices for Biodiversity Assessment and Landscape Investigation. *Acta Acustica united with Acustica* **100**:772-781.

Sueur, J., Gasc, A., Grandcolas, P., and Pavoine, S. (2012). Global estimation of animal diversity using automatic acoustic sensors. *Sensors for ecology. Paris: CNRS*:99-117.

Sueur, J., Pavoine, S., Hamerlynck, O., and Duvail, S. (2008). Rapid Acoustic Survey for Biodiversity Appraisal. *PLoS ONE* **3**:e4065.

Swift, M. J., Heal, O. W., and Anderson, J. M. 1979. Decomposition in terrestrial ecosystems. Univ of California Press.

Szabo, J. K., Khwaja, N., Garnett, S. T., and Butchart, S. H. (2012). Global patterns and drivers of avian extinctions at the species and subspecies level.

Szinwelski, N., Rosa, C. S., Schoereder, J. H., Mews, C. M., and Sperber, C. F. (2012). Effects of forest regeneration on crickets: evaluating environmental drivers in a 300-year chronosequence. *International Journal of Zoology* **2012**.

Tahir, H. M., Butt, A., and Sherawat, S. M. (2009). Foraging strategies and diet composition of two orb web spiders in rice ecosystems. *Journal of Arachnology* **37**:357-362.

Taylor, D. J., Titus-Mcquillan, J., and Bauer, A. M. (2012). Diet of Chalcides ocellatus (Squamata: Scincidae) from Southern Egypt. *Bulletin of the Peabody Museum of Natural History* **53**:383-388.

Tershy, B. R., SHEN, K., Newton, K. M., Holmes, N. D., and Croll, D. A. (2015). The Importance of Islands for the Protection of Biological and Linguistic Diversity. *BioScience* **20**:1-6.

Thomas, M. L., Becker, K., Abbott, K., and Feldhaar, H. (2010). Supercolony mosaics: two different invasions by the yellow crazy ant, Anoplolepis gracilipes, on Christmas Island, Indian Ocean. *Biological Invasions* **12**:677-687.

Thuiller, W., Lafourcade, B., Engler, R., and Araújo, M. B. (2009). BIOMOD–a platform for ensemble forecasting of species distributions. *Ecography* **32**:369-373.

Truskinger, A., Cottman-Fields, M., Johnson, D., and Roe, P. 2013. Rapid scanning of spectrograms for efficient identification of bioacoustic events in big data. Pages 270-277 *in* eScience (eScience), 2013 IEEE 9th International Conference on. IEEE.

Tucker, D., Gage, S. H., Williamson, I., and Fuller, S. (2014). Linking ecological condition and the soundscape in fragmented Australian forests. *Landscape Ecology* **29**:745-758.

Vaidya, G., Lohman, D. J., and Meier, R. (2011). SequenceMatrix: concatenation software for the fast assembly of multi-gene datasets with character set and codon information. *Cladistics* **27**:171-180.

Valiente-Banuet, A., Aizen, M. A., Alcántara, J. M., Arroyo, J., Cocucci, A., Galetti, M., García, M. B., García, D., Gómez, J. M., and Jordano, P. (2015). Beyond species loss: the extinction of ecological interactions in a changing world. *Functional Ecology* **29**:299-307.

van Damme, R. and Castilla, A. M. (1996). Chemosensory predator recognition in the lizardPodarcis hispanica: Effects of predation pressure relaxation. *Journal of chemical ecology* **22**:13-22.

Vanderwoude, C., Lobry de Bruyn, L., and House, A. (2000). Response of an open-forest ant community to invasion by the introduced ant, Pheidole megacephala. *Austral Ecology* **25**:253-259.

Veer, G. and Nentwig, W. (2014). Environmental and economic impact assessment of alien and invasive fish species in Europe using the generic impact scoring system. *Ecology of Freshwater Fish*.

Verdolin, J. L. (2006). Meta-analysis of foraging and predation risk trade-offs in terrestrial systems. *Behavioral Ecology and Sociobiology* **60**:457-464.

Vicente, N. M., Olivero, P., Lafond, A., Dong, J., and Robillard, T. (2015). Gnominthus gen. nov., a new genus of crickets endemic to Papua New Guinea with novel acoustic and behavioral diversity (Insecta, Orthoptera, Gryllidae, Eneopterinae). *Zoologischer Anzeiger-A Journal of Comparative Zoology* **258**:82-91.

Vilà, M., Basnou, C., Pyšek, P., Josefsson, M., Genovesi, P., Gollasch, S., Nentwig, W., Olenin, S., Roques, A., and Roy, D. (2009). How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. *Frontiers in Ecology and the Environment* **8**:135-144.

Vilà, M., Espinar, J. L., Hejda, M., Hulme, P. E., Jarošík, V., Maron, J. L., Pergl, J., Schaffner, U., Sun, Y., and Pyšek, P. (2011). Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters* **14**:702-708.

Vitousek, P. M., D'Antonio, C. M., Loope, L. L., Rejmanek, M., and Westbrooks, R. (1997). Introduced species: a significant component of human-caused global change. *New Zealand Journal of Ecology* **21**:1-16.

Vitousek, P. M., D'Antonio, C. M., Loope, L. L., and Westbrooks, R. (1996). Biological invasions as global environmental change. *American Scientist* **84**:468-478.

Vonshak, M., Dayan, T., and Hefetz, A. (2011). Interspecific displacement mechanisms by the invasive little fire ant Wasmannia auropunctata. *Biological Invasions*.

Vonshak, M., Dayan, T., Ionescu-Hirsh, A., Freidberg, A., and Hefetz, A. (2010). The little fire ant *Wasmannia auropunctata*: a new invasive species in the Middle East and its impact on the local arthropod fauna. *Biological Invasions* **12**:1825-1837.

Vuillaume, B., Valette, V., Lepais, O., Grandjean, F., and Breuil, M. (2015). Genetic Evidence of Hybridization between the Endangered Native Species Iguana delicatissima and the Invasive Iguana iguana (Reptilia, Iguanidae) in the Lesser Antilles: Management Implications. *PLoS ONE* **10**.

Walker, K. L. (2006). Impact of the Little Fire Ant, Wasmannia auropunctata, on Native Forest Ants in Gabon1. *Biotropica* **38**:666-673.

Walker, T. J. (1964). Cryptic Species Among Sound-Producing Ensiferan Orthoptera (Gryllidae and Tettigoniidae). *The Quarterly Review of Biology* **39**:345-355.

Walker, T. J. (1986). Monitoring the flights of field crickets (Gryllus spp.) and a tachinid fly (Euphasiopteryx ochracea) in north Florida. *Florida Entomologist*:678-685.

Walsh, J. C., Venter, O., Watson, J. E., Fuller, R. A., Blackburn, T. M., and Possingham, H. P. (2012). Exotic species richness and native species endemism increase the impact of exotic species on islands. *Global Ecology and Biogeography* **21**:841-850.

Walsh, P. D., Henschel, P., Abernethy, K. A., Tutin, C. E. G., Telfer, P., and Lahm, S. A. (2004). Logging Speeds Little Red Fire Ant Invasion of Africa. *Biotropica* **36**:637-641.

Wauters, N., Dekoninck, W., Herrera, H. W., and Fournier, D. (2014). Distribution, behavioral dominance and potential impacts on endemic fauna of tropical fire ant Solenopsis geminata (Fabricius, 1804)(Hymenoptera: Formicidae: Myrmicinae) in the Galápagos archipelago. *The Pan-Pacific Entomologist* **90**:205-220.

Wellstein, C., Schröder, B., Reineking, B., and Zimmermann, N. E. (2011). Understanding species and community response to environmental change–A functional trait perspective. *Agriculture, ecosystems & environment* **145**:1-4.

Wetterer, J. K. (2007). Biology and Impacts of Pacific Island Invasive Species. 3. The African Big-Headed Ant, Pheidole megacephala (Hymenoptera: Formicidae). *Pacific Science* **61**:437-456.

Wetterer, J. K. and Porter, S. D. (2003). The Little Fire Ant, *Wasmannia auropunctata*: Distribution, Impact and Control. *Sociobiology* **41**:1-41.

Wheeler, W. M. (1900). The habits of Myrmecophila nebrascensis Bruner. *Psyche* **9**:111-115.

Whittaker, R. J. and Fernández-Palacios, J. M. 2007. Island biogeography: ecology, evolution, and conservation. Oxford University Press.

Wiley, H. R. and Richards, D. G. (1982). Adaptations for Acoustic Communication in Birds: Sound Transmission and Signal Detection. *In: Acoustic communication in birds, Vol. 1 (D.E. Kroodsma & E.H. Miller, eds). Academic Press, New York* **1**:131-170.

Wiley, R. H. (1994). Errors, exaggeration, and deception in animal communication. *Behavioral mechanisms in evolutionary ecology*:157-189.

Wiley, R. H. and Richards, D. G. (1978). Physical constraints on acoustic communication in the atmosphere: Implications for the evolution of animal vocalizations. *Behavioral Ecology and Sociobiology* **3**:69-94.

Williams, B. K., Rittenhouse, T. A., and Semlitsch, R. D. (2008). Leaf litter input mediates tadpole performance across forest canopy treatments. *Oecologia* **155**:377-384.

Willott, S. and Hassall, M. (1998). Life-history responses of British grasshoppers (Orthoptera: Acrididae) to temperature change. *Functional Ecology* **12**:232-241.

Wilson, J., Stephenson, B., Gill, G., Randall, J., and Vieglais, C. (2004). Principles of response to detections of new plant pest species and the effectiveness of surveillance. *New Zealand Plant Protection* **57**:156.

Wimmer, J., Towsey, M., Planitz, B., Williamson, I., and Roe, P. (2013). Analysing environmental acoustic data through collaboration and automation. *Future Generation Computer Systems* **29**:560-568.

Witte, K., Farris, H. E., Ryan, M. J., and Wilczynski, W. (2005). How cricket frog females deal with a noisy world: habitat-related differences in auditory tuning. *Behavioral Ecology* **16**:571-579.

Wittman, S. E. (2014). Impacts of invasive ants on native ant communities (Hymenoptera: Formicidae). *Myrmecol News* **19**:111-123.

Wojcik, D. P., Allen, C. R., Brenner, R. J., Forys, E. A., Jouvenaz, D. P., and Lutz, S. R. (2001). Red Imported Fire Ants: Impact on Biodiversity. *American entomologist* **47**:16-23.

Wulff, A. S., Hollingsworth, P. M., Ahrends, A., Jaffré, T., Veillon, J.-M., L'Huillier, L., and Fogliani, B. (2013). Conservation priorities in a biodiversity hotspot: analysis of narrow endemic plant species in New Caledonia. *PLoS ONE* **8**:e73371.

Zalasiewicz, J., Williams, M., Haywood, A., and Ellis, M. (2011). The Anthropocene: a new epoch of geological time? *Philosophical Transactions of the Royal Society of London A: Mathematical, Physical and Engineering Sciences* **369**:835-841.

Zarones, L., Sussman, A., Morton, J. M., Plentovich, S., Faegre, S., Aguon, C., Amar, A., and Ha, R. R. (2015). Population status and nest success of the Critically Endangered Mariana crow Corvus kubaryi on Rota, Northern Mariana Islands. *Bird Conservation International* **25**:220-233.

Zuk, M. and Kolluru, G. R. (1998). Exploitation of Sexual Signals by Predators and Parasitoids. *The Quarterly Review of Biology* **73**:415-438.

Zuk, M., Simmons, L. W., and Cupp, L. (1993). Calling characteristics of parasitized and unparasitized populations of the field cricket Teleogryllus oceanicus. *Behavioral Ecology and Sociobiology* **33**:339-343.

11 Annexes

11.1 Liste des publications

11.1.1 Articles publiés

(1) Desutter-Grandcolas, L., Robillard, T. & **Anso, J**. (2014) Redefinition of the cricket genus Protathra Desutter-Grandcolas, 1997 (Orthoptera, Grylloidea, Phalangopsidae), with description of the calling song of Protathra centralis Desutter-Grandcolas, n. sp., in Guilbert, E., Robillard, T., Jourdan, H. & Grandcolas, P. (eds), Zoologia Neocaledonica 8. Biodiversity studies in New Caledonia. Muséum national d'Histoire naturelle, Paris : 279-290

(2) Desutter-Grandcolas L, Cadena-Castañeda OJ, Jaiswara R, **Anso J**. (2014). Zebragryllus Desutter- Grandcolas & Cadena-Casteñada, n. gen. a new Gryllinae genus from Eastern and Western Amazonia, South America (Orthoptera, Grylloidea, Gryllidae). Zootaxa, 3768(1), 001-022.

(3) **Anso, J.**, Barrabé, L., Desutter-Grandcolas, L., Jourdan, H., Grandcolas, P., Dong, J., and Robillard, T. (in press). Old lineage on an old island: Pixibinthus, a new cricket genus endemic to New Caledonia shed light on Gryllid diversification in a hotspot of biodiversity. *PloS ONE*.

(4) **Anso, J.**, Jourdan, H., Desutter-Grandcolas, L. (in press). Crickets (Insecta, Orthoptera, Grylloidea) from Southern New Caledonia, with descriptions of new taxa. *Zootaxa*.

11.1.2 Articles soumis

(5) Desutter-Grandcolas, L., **Anso, J.,** & Jourdan, H. Crickets of New Caledonia (Insecta, Orthoptera, Grylloidea): a key to genera, with diagnoses of extant genera and descriptions of new taxa. (submitted). *Zoosystema*.

11.1.3 Article en préparation

(6) **Anso, J.,** Desutter-Grandcolas, Vidal, E., L., Jourdan, H. Crickets as potential ecological indicators for succession in an insular biodiversity hotspot. In prep for Austral Ecology

(7) **Anso, J.**, Desutter-Grandcolas, Vidal, E., L., Jourdan, H. Contrasted impact of invasive ants (*Wasmannia auropunctata* Roger and *Anoplolepis gracilipes* Smith) on cricket communities: implication for conservation in a biodiversity hotspot. In prep for *Biological invasion.*

(8) †Gasc, A., †**Anso, J**., Desutter-Grandcolas, L., Sueur, J., Jourdan, H. Monitoring protected fauna facing invasive species using rapid acoustic survey: when natural soundscapes dominated by cricket's songs become indicators of biological invasion. † Co-premiers auteurs. In prep for *Journal of Applied Ecology*.

(9) **Anso, J.,** Gasc, A., Desutter-Grandcolas, L., Sueur, J., Jourdan, H. Listen to the crickets: Calling cricket community as a new bioindicator for forest succession and biological invasion in a biodiversity hotspot. In prep for *Ecological indicators*

11.2 Congrès Internationaux

(1) **Anso, J.,** Gasc, A., Desutter-Grandcolas L., Vidal, E., Jourdan, H. Cricket Using Cricket Communities as an Innovative Bio Indicators for Conservation of Threatened Areas Using Meta-Acoustic Approach. IInd Society for Ecological Restoration Australasia meeting, Noumea, New Caledonia, 17-21 November 2014.

(2) **Anso, J.,** Gasc, A., Desutter-Grandcolas L., Vidal, E., Jourdan, H. Cricket community acoustics: a new tool to detect invasive ants. – oral presentation XVIIth International Union for the Study of Social Insects meeting, Cairns, Australia, 14-18 July 2014.

(3) **Anso, J.,** Gasc, A., Desutter-Grandcolas L., Vidal, E., Jourdan, H., Sueur, J. Meta-acoustic approach of cricket communities to detect biological invasion by exotic ants. – oral presentation First Ecology and Acoustics meeting, Paris, France, 16-18 June 2014.

(4) Gasc A., Pijanowski, B., **Anso J.**, Jourdan H., Sueur J., and Desutter-Grandcolas L. Soundscape measurements to evaluate impacts of habitat degradation on acoustic animal communities. – Oral presentation First Ecology and Acoustics meeting, Paris, France, 16-18 June 2014.

(5) Gasc A., Pijanowski, B., **Anso J.**, Jourdan H., Sueur J., Jung J. and Desutter-Grandcolas L. Soundscape measurements to evaluate disturbance impacts on natural ecosystems. – oral presentation International Association for the Landscape Ecology meeting, Anchorage, Alaska, 18-22 May 2014.

11.3 Liste des sites sélectionnés pour l'étude, Détection de *Wasmannia auropunctata*, matériel déposé sur place et période d'enregistrement.

Sans fourmi envahissante

Forêt	Site	Abréviations	Matériel	Date pose du matériel	date retrait du matériel	ETAT	N° Sonde	Présence/Absence fourmis	GPS
1	Mouirange	FO-MOU	SM2+ (N°1)	2/10 à 19H00	17/10 à 8H30	TERMINE	34	OK 9/9	166.68086E/22.20416S
2	Pic du Pin	FO-PDP	SM2 (N°8)	3/10 à 18H00	17/10 à 15H30	TERMINE	83	OK 9/9	166.82715E/22.24680S
3	Grand Kaori	FO-GK	SM2 (N°9)	2/10 à 16H00	30/10 à 16H00	TERMINE	29	OK 8/9	166.89674E/22.28535S
4	Rivière Blanche	FO-RIV	SM2+ (N°2)	4/10 à 15h00	17/10 à 10H00	TERMINE	28	OK 9/9	166.68643E/22.15142S
Parafo.									
1	Pépinière	PA-PEP	SM2+ (N°3)	2/10 à 12H30	17/10 à 16H00	TERMINE	25	OK 9/9	166.96355E/22.27103S
2	Grand Kaori	PA-GK	SM2 (N°11)	2/10 à 15H00	16/10 à 12H00	TERMINE	26	OK 9/9	166.89383E/22.28000S
3	Forêt Nord	PA-FN	SM2+ (N°5)	3/10 à 16H00	23/10 à 13H30	TERMINE	24	OK 5/9	166.93134E/22.32259S
4	Rivière Blanche	PA-RIV	SM2 (N°7)	4/10 à 15H00	17/10 à 09H30	TERMINE	33	OK 9/9	166.68033E/22.15280S
Maquis									
1	Grand Kaori	MA-GK	SM2 (N°4)	2/10 à 18H00	17/10 à 16H30	TERMINE	23	OK 7/9	166.89436E/22.28460S
2	Rivière Blanche	MA-RIV	SM2 (N°10)	4/10 à 17H00	17/10 à 11H30	TERMINE	84	OK 6/9	166.70796E/22.13625S
3	Madelaine	MA-MAD	SM2+ (N°2)	17/10 à 13H30	14/11 à 12H00	TERMINE	28	OK 9/9	166.85268E/22.23568S
4	Forêt Nord	MA-FN	SM2+ (N°6)	23/10 à 13H00	14/11 à 15H30	TERMINE	30	OK 7/9	166.93501E/22.32277S

Avec *Wasmannia auropunctata*

Forêt	Site	Abréviations	Matériel	Date pose du matériel	date retrait du matériel	ETAT	N° Sonde	Présence/Absence fourmis	GPS
1	Grand Kaori	FO-GK-W	SM2 (n°16)	2/10 à 17H00	30/10 à 14H30	TERMINE	36	OK 5/9	166.89601E/22.28226S
2	Forêt Nord	FO-FN-W	SM2+ (N°6)	3/10 à 15H00	23/10 à 14H30	TERMINE	27	OK 9/9	166.92987E/22.32372S
3	Cap N'Dua	FO-KA-W	SM2+ (N°1)	17/10 à 17H45	14/11 à 16H30	TERMINE	9	OK 9/9	166.91742E/22.38645S
4	Port Boisé	FO-BOI-W	SM2 (N°3)	23/10 à 14H30	14/11 à 14H30	TERMINE	27	OK 7/9	166.97343E/22.34820S
Parafo.									
1	Grand Kaori	PA-GK-W	SM2 (N°6)	2/10 à17H00	30/10 à 16H00	TERMINE	31	OK 7/9	166.89510E/22.28345S
2	Forêt Nord	PA-FN-W	SM2+ (N°4)	3/10 à 16H00	23/10 à 13H00	TERMINE	32	OK 9/9	166.93361E/22.32385S
3	Cap N'Dua	PA-KA-W	SM2+ (N°3)	17/10 à 17H15	14/11 à 16H00	TERMINE	33	OK 9/9	166.91881E/22.38629S
4	Prony	PA-PRO-W	SM2 (N°7)	23/10 à 11H00	15/11 à 12H00	TERMINE	85	OK 8/9	166.80473E/22.31902S
Maquis									
1	Rivière Blanche	MA-RIV-W	SM2 (N°10)	17/10 à 12H00	07/11 à10H30	TERMINE	34	OK 6/9	166.70937E/22.13480S
2	Rte Grand Kaori	MA-GKE-W	SM2+ (N°4)	23/10 à 16H00	14/11 à 12H30	TERMINE	26	OK 9/9	166.86960E/22.27110S
3	Cap N'Dua	MA-KA-W	SM2 (N°4)	17/10 à 17H00	14/11 à 17H15	TERMINE	25	OK 8/9	166.93486E/22.32278S
4	Bois du Sud	MA-BDS-W	SM2+ (N°4)	20/11 à 11H30	09/12 à 11h30	TERMINE	33	OK 9/9	166.76093E/22.17321S

Maintien à long terme des communautés d'insectes forestiers dans un contexte de changement global : Réponses écologiques des communautés d'Orthoptères dans une succession forestière et face à la progression d'espèces invasives

Résumé

Dans le contexte de la crise de la biodiversité que traverse actuellement la biosphère, en particulier les milieux insulaires tropicaux, il est important de pouvoir sélectionner des groupes d'organismes susceptibles d'apporter des éléments diagnostiques pour orienter les choix de gestion, de conservation et de restauration des écosystèmes. Ainsi, en Nouvelle-Calédonie, les grillons représentent des macro-arthropodes majeurs des écosystèmes terrestres, de part leur richesse, diversité et endémisme, et la gamme des conditions d'habitats colonisées. Outre leur abondance dans les écosystèmes, ils émettent des signaux acoustiques spécifiques à l'espèce et contribuent fortement à l'ambiance acoustique des écosystèmes. Aussi, dans le contexte de recherche d'éléments diagnostiques rapides de la biodiversité, nous avons mesurés la réponse des assemblages de grillons par inventaire classique et l'acoustique passive, dans une succession écologique forestière sur sols miniers et face à la progression de plusieurs fourmis envahissantes (*Wasmannia auropunctata* et *Anoplolepis gracilipes*). Les communautés de grillons, définies par des relevés taxonomiques et acoustiques, démontrent une spécificité pour chacun des stades de la succession, ainsi qu'une sensibilité marquée face aux invasives majeures. Par ailleurs, l'analyse globale des ambiances sonores (la méthode acoustique globale), largement dominées par les émissions des grillons, permet d'obtenir des résultats prometteurs sans avoir recours à de l'identification taxonomique et acoustique. Ces premiers résultats apportent des éléments d'intérêt pour la gestion des écosystèmes néo-calédoniens, avec la possibilité de réaliser des programmes de surveillance basés sur la présence d'espèces indicatrices clés. Nos résultats ouvrent des perspectives de recherches prometteuses pour généraliser des concepts innovants de bio-indication dans les régions tropicales qui abritent des assemblages de grillons diversifiés.

Mots clés: Nouvelle-Calédonie, grillons, indices de diversité acoustique, fourmis envahissantes, succession forestière.

Long-term maintenance of forest-dwelling insect communities in a global change context: Ecological responses of Orthoptera communities in forest succession and toward the spread of invasive species

Abstract

In the context of global biodiversity crisis at world scale, research of efficient environmental proxies are urgently required, especially in tropical island ecosystems, to better assess environment quality and select conservation priorities. In New Caledonia ecosystems, crickets have a dominant contribution to natural communities, according to their richness, diversity and range of colonized habitats. They are highly abundant in ecosystems and also have a high contribution to the soundscape with their ability to produce species-specific airborne signals. In this context of search of efficient environmental proxies, we measured the response of cricket communities in a ecological succession on utlramafic soils and facing the spread of 2 invasive ants (*Wasmannia auropunctata* and *Anoplolepis gracilipes*). Through both classical community census and bioacoustic approach through passive acoustic monitoring, we have been able to characterize specific cricket assemblage of species in each succession stage, with a striking sensitivity for biological invasions. Also, a global acoustic analysis of soundscape, greatly dominated by crickets, provides similar results without taxonomic or acoustic identification or knowledge. These preliminary results provide critical insights for the management of ecosystems, Our findings open up promising field of research in order to generalized innovative bio-indication concepts using cricket community in other cricket rich tropical regions.

Keywords New Caledonia, crickets, index of acoustic diversity, invasive ants, forest succession.