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Phylogenetic tests of evolutionary scenarios in interdisciplinary studies: improving the protocol design

Frédéric Legendre

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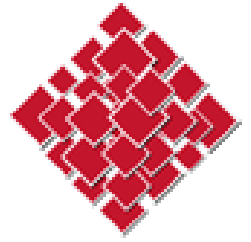
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**SORBONNE
UNIVERSITÉ**

CRÉATEURS DE FUTURS
DEPUIS 1257



EPHE

Habilitation à Diriger des Recherches de Sorbonne Université

FRÉDÉRIC LEGENDRE

Muséum national d'Histoire naturelle, Paris

Phylogenetic tests of evolutionary scenarios in interdisciplinary studies: improving the protocol design

Soutenue le 23 mars 2018, devant le jury d'examen :

Yves Desdèves	PR1 Sorbonne Université, BIOM UMR 7232, Banyuls-sur-Mer - Examineur
Marianne Elias	CR1 CNRS, ISYEB UMR7205, Paris - Examinatrice
Gonzalo Giribet	PR Harvard University, Cambridge, MA, USA - Rapporteur
Gaël Kergoat	DR2 INRA, CBGP UMR 1062, Montpellier - Rapporteur
Emmanuel Paradis	DR2 IRD, ISEM UMR 226/5554, Montpellier - Rapporteur

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A. Curriculum Vitae

LEGENDRE Frédéric
Associate Professor
Head of the EvoFonc team

ISYEB, UMR CNRS 7205, MNHN
Département Origines et Evolution CP 50
75231 Paris Cedex 05, France

A.1 Personal Information

Telephone: 01.40.79.81.26

Fax: 01.40.79.56.79

E-mail address: legendre@mnhn.fr

Webpages: <http://isyeb.mnhn.fr/annuaire-et-pages-personnelles/pages-personnelles/article/legendre-frederic>; https://www.researchgate.net/profile/Frederic_Legendre

Orcid ID: orcid.org/0000-0001-5900-8048

Publons ID: publons.com/a/1248854

A.2. Professional Experience

Head of the team Evolution Fonctionnelle et Systématique (EvoFonc)	2014 - present
Associate Professor , Institut de Systématique et Evolution (UMR 7205), MNHN Paris.	Dec. 2008 - present
Curator of Isoptera, Embioptera, Ephemeroptera, Plecoptera, Psocoptera, Trichoptera, Zoraptera	Dec. 2008 - present
Postdoctoral Fellow, Reginald B. Cocroft, University of Missouri-Columbia (USA).	2007 - 2008
Doctoral fellow, Philippe Grandcolas, UPMC (Paris VI, France)	2004 - 2007

A.3. Education

Ph.D. in Life Sciences, University Pierre et Marie Curie (Paris VI, France), Philippe Grandcolas, advisor. Dissertation title: *Phylogeny and Evolution of Social Behavior in Blattaria and Isoptera*. 2007.

Master's Degree in Biodiversity and Evolution, *Summa Cum Laude*, University Pierre et Marie Curie (Paris VI, France). 2004.

Bachelor's Degree in Biology of Populations and Ecosystems, *Summa Cum Laude*, University Rennes I (France). 2003.

A.4. Mentoring

Dominic Evangelista (2016-2018). Post-doctoral fellow, NSF grant: Phylogenomics and diversification in Blaberoidea. Co-advisor: Akito Kawahara (Florida Museum of Natural History, USA). Dominic's project involves a large part of exon capture procedures that he is currently developing. This project is a fundamental step for Dictyoptera phylogenetics. Publications: one manuscript is submitted.

Julien Troudet (2014-2017). PhD fellow, ED227 grant: Latitudinal diversity gradient and biodiversity databases. Co-advisor: Régine Vignes-Lebbe (HDR). Defense planned for the end of 2017. Julien's project aims at understanding global patterns of biodiversity, relying on the Global Biodiversity Information Facility (GBIF) database. Publications: Troudet *et al.* 2017; one manuscript is accepted providing major modifications.

Sandra Goutte (2010-2014). PhD fellow, ENS grant: Adaptations to noisy torrent environments in frogs: combining morphological, eco-ethological and phylogenetic approaches. Co-advisor: Alain Dubois (HDR). Très honorable avec félicitations du jury. Publications: Goutte *et al.* 2013, 2016, 2018.

Thomas Schubnel (2018). Master 2nd year SEP MNHN, ATM grant : Losses and re-acquisitions of wings in Insects. Co-advisor : André Nel. This project has just begun in February.

Julien Malem (2018). Master 2nd year SEP MNHN, New-Caledonia colonization from an 'ancient' group of cockroaches: phylogenetics and biogeography of Blattidae (Insecta: Blattaria). Co-advisor : Tony Robillard. This project has just begun in February.

France Thouzé (2016). Master 2nd year SEP MNHN, Labex BCDiv grant: Phylogenetic Signal and networks: a pilot study in Dictyoptera. Co-advisor: Philippe Lopez. Note : 15/20. In her project, France used phylogenetic networks and signal analyses to untangle robust results from potential tree reconstruction artefacts, and to target the most appropriate markers and taxa to address unresolved phylogenetic and evolutionary issues. Publications : Legendre *et al.* 2017; one manuscript is submitted.

Augustin Lafond (2014). Master 2nd year SEP MNHN : Evolution of stridulatory mechanisms in *Agnotecous* crickets (Grylloidea, Eneopterinae, Lebinthini). Co-advisor: Tony Robillard. Note : 15/20. Augustin's project relied on an integrative approach combining phylogenetics, comparative morphology and behaviour.

Charlène Verbeke (2018). Master 1st year Toulouse. Charlène's project is part of the RESCUE project aiming at quantify the benefits from Natural History Collections to biogeography scenarios. Charlène will start her project in May.

Thomas Schubnel (2017). Master 1st year SEP MNHN. Thomas' project was to investigate systematics and convergence in a group of Asian Mantids.

Lili Cardoni (2017). Master 1st year SEP MNHN. Lili's project was to build a Xper identification key for three Panesthiinae genera of Papua-New-Guinae. She was co-supervised by Régine Vignes-Lebbe.

Delia Dupre (2012). Master 1st year SEP MNHN. Delia's project aims at reconstructing the phylogeny of the Blaberidae cockroach family.

Laetitia Laborde (2011). Master 1st year SEP MNHN. Laetitia's project was tied to the PhD of Sandra Goutte. Laetitia characterized the communication system of two closely related frog species analyzing multiple audio and video recordings. She was co-supervised by Sandra Goutte.

Camille Colinet (2014-2015). Licence 2 Cergy-Pontoise. Co-advisor: Tony Robillard. Camille and Mylène (see below) were part of a project aiming at assessing the added value of an altitudinal gradient to quantify biodiversity in Papua New Guinea forests. Publication : Colinet, Exbrayat *et al.* 2016.

Mylène Exbrayat (2013-2014). Licence 3 Nancy. See Camille Colinet above.

Fabien Barno (2017-2018). BTS 1st and 2nd years Bioanalyses et contrôles.

Lauriane Pindrais (2016). BTS 2nd year Bioanalyses et contrôles.

François Guichard (2015). BTS 2nd year Bioanalyses et contrôles.

Quentin Lefèvre (2012-2013). BTS 2nd year Bioanalyses et contrôles.

François Moreau (2012-2013). BTS 2nd year Bioanalyses et contrôles.

Gabin Colombini (2011-2012) BTS 2nd year Bioanalyses et contrôles; co-advisor: Cyrille D'Haese.

A.5. Publications

32 publications in indexed journals, 1 book co-edited, 5 chapters, h-index = 14, >650 citations (Google profile: <https://scholar.google.fr/citations?user=K6IqTW0AAAAJ&hl=fr&oi=ao>)

1. Legendre F. & Condamine F. 2018. When Darwin's Special Difficulty Promotes Diversification in Insects. **Systematic Biology** (in press).
2. **Goutte S**, Dubois A, Howard SD, Márquez R, Rowley JJJ, Dehling JM, Grandcolas P, Xiong R & Legendre F. 2018. Testing the Acoustic Adaptation Hypothesis in torrent frogs. **Journal of Evolutionary Biology** 31: 148-158.
3. Legendre F & Grandcolas P. Order Dictyoptera: Blattodea. *In: Les Insectes du monde – classification – clés pour la reconnaissance des principales familles* (Aberlenc, H-P. and Delvare, G., Eds) (in press).
4. **Troudet J**, Grandcolas P, Blin A, Vignes-Lebbe R & Legendre F. 2017. Taxonomic bias in biodiversity data and societal preferences. **Scientific Reports** 7: 9132.
5. Nattier R, Pellens R, Robillard T, Jourdan H, Legendre F, Caesar M, Nel A, Grandcolas P. 2017. Updating the Phylogenetic Dating of New Caledonian Biodiversity with a Meta-analysis of the Available Evidence. **Scientific Reports** 7: 3705.
6. Legendre F, Grandcolas P & **Thouzé F**. 2017. Molecular phylogeny of Blaberidae (Dictyoptera, Blattodea) with implications for taxonomy and evolutionary scenarios. **European Journal of Taxonomy** 291: 1-13.
7. Vicente N, Kergoat GJ, Dong J, Yotoko K, Legendre F, Nattier R, Robillard T. 2017. In and out of the Neotropics: historical biogeography of Eneopterinae crickets. **Journal of Biogeography** 44: 2199–2210.
8. **Colinet C**, **Exbrayat M**, Robillard T & Legendre F. 2016. Species richness and composition in cockroaches (Dictyoptera: Blattodea) along an elevational gradient in

- Papua New Guinea. *In: Insects of Mount Wilhelm, Papua New Guinea* (Robillard T, Legendre F, Villemant C & Leponce M, Eds). Muséum national d'Histoire naturelle, Paris: 129-140 (Mémoires du Muséum national d'Histoire naturelle; 209). ISBN: 978-2-85653-784-8.
9. Leponce M, Novotny V, Pascal O, Robillard T, Legendre F, Villemant C *et al.* 2016. Land module of Our Planet Reviewed - Papua New Guinea: aims, methods and first taxonomical results. *In: Insects of Mount Wilhelm, Papua New Guinea* (Robillard T, Legendre F, Villemant C & Leponce M, Eds). Muséum national d'Histoire naturelle, Paris: 11-48 (Mémoires du Muséum national d'Histoire naturelle; 209). ISBN: 978-2-85653-784-8.
 10. Robillard T, Dong J, Legendre F & Agauvoa S. 2016. The brachypterous Lebinthini crickets from Papua New Guinea, with description of two genera and four new species (Orthoptera: Gryllidae: Eneopterinae). *In: Insects of Mount Wilhelm, Papua New Guinea* (Robillard T, Legendre F, Villemant C & Leponce M, Eds). Muséum national d'Histoire naturelle, Paris: 149-202 (Mémoires du Muséum national d'Histoire naturelle; 209). ISBN: 978-2-85653-784-8.
 11. Robillard T, Legendre F, Villemant C & Leponce M. 2016. *Insects of Mount Wilhelm, Papua New Guinea*. Muséum national d'Histoire naturelle, Paris; Mémoires du Muséum national d'Histoire naturelle, tome 209.
 12. **Goutte S**, Dubois A, Howard SD, Márquez R, Rowley JJJ, Dehling JM, Grandcolas P, Xiong R, Legendre F. 2016. Environmental constraints and call evolution in torrent dwelling frogs. **Evolution** 70: 811–826.
 13. **Chintauan-Marquier IC***, Legendre F*, Hugel S, Robillard T, Grandcolas P, Nel A, Zuccon D & Desutter-Grandcolas L. 2016. Laying the foundations of evolutionary and systematic studies in crickets (Insecta, Orthoptera): a multilocus phylogenetic analysis. **Cladistics** 32: 54-81. * = equal contributions.
 14. Legendre F, Nel A, Svenson GJ, Robillard T, Pellens R & Grandcolas P. 2015a. Phylogeny of Dictyoptera: Dating the Origin of Cockroaches, Praying Mantises and Termites with Molecular Data and Controlled Fossil Evidence. **PLoS ONE**, 10 (7): e0130127.
 15. Legendre F, Deleporte P, **Depraetere M**, **Gasc A**, Pellens R & Grandcolas P. 2015b. Dyadic behavioural interactions in cockroaches (Blaberidae): ecomorphological and evolutionary implications. **Behaviour** 152: 1229-1256.
 16. **Caesar M**, Roy R, Legendre F, Grandcolas P & Pellens R. 2015. Catalogue of Dictyoptera from Syria and neighbouring countries (Lebanon, Turkey, Iraq and Jordan). **Zootaxa** 3948: 71-92.
 17. Picart L, Forget P-M, D'Haese CA, Daugeron C, Beni S, Bounzel R, Kergresse E, Legendre F, Muriene J & Guilbert E. 2014. The cafotrop method: an improved rope-climbing method for access and movement in the canopy. **Ecotropica** 20: 45-52.
 18. Grandcolas P, Nattier R, Pellens R & Legendre F. 2014. Diversity and distribution of the genus *Rothisilpha* (Dictyoptera, Blattidae) in New Caledonia: Evidence from new microendemic species. *In: Zoologia Neocedonica 8. Biodiversity studies in New Caledonia* (Guilbert, E., Robillard, T., Jourdan, H and Grandcolas, P. (Eds), Muséum national d'Histoire naturelle, Paris: 299-308.

19. Nel A, Prokop J, Grandcolas P, Garrouste R, Lapeyrie J, Legendre F, Anisyutkin L & Kirejtshuk, AG. 2014. The beetle-like Palaeozoic and Mesozoic roachoids of the so-called “umenocoleoid” lineage (Dictyoptera: Ponopterixidae fam. nov.). **Comptes Rendus Palevol.** 13: 545-554.
20. Coty D, Aria C, Garrouste R, Wils P, Legendre F & Nel A. 2014. The first ant-termite syninclusion in amber with CT-scan analysis of taphonomy. **PLoS ONE** 9: e104410.
21. Legendre F, D’Haese CA, Deleporte P, Pellens R, Whiting MF, Schliep K & Grandcolas P. 2014. The evolution of social behaviour in Blaberid cockroaches with diverse habitats and social systems: phylogenetic analysis of behavioural sequences. **Biological Journal of the Linnean Society** 111: 58-77.
22. Goutte S, Dubois A & Legendre F. 2013. The importance of ambient sound level to characterise anuran habitat. **PLoS ONE** 8: e78020.
23. Legendre F, Whiting MF & Grandcolas P. 2013. Phylogenetic analyses of termite post-embryonic sequences illuminate caste and developmental pathway evolution. **Evolution & Development** 15: 146-157.
24. Legendre F, **Marting PR** & Cocroft RB. 2012. Competitive masking of vibrational signals during mate searching in a treehopper. **Animal Behaviour** 83: 361-368.
25. Grandcolas P, Nattier R, Legendre F & Pellens R. 2011. Mapping extrinsic traits such as extinction risks or modelled bioclimatic niches on phylogenies: does it make sense at all? **Cladistics** 27: 181-185.
26. Legendre F, Robillard T, Song H, Whiting MF & Desutter-Grandcolas L. 2010. One hundred years of instability in Ensiferan relationships. **Systematic Entomology** 35: 475-488.
27. Legendre F, Robillard T, Desutter-Grandcolas L, Whiting MF & Grandcolas P. 2008. Phylogenetic analysis of non-stereotyped behavioral sequences with a successive event-pairing method. **Biological Journal of the Linnean Society** 94: 853-867.
28. Legendre F. 2008. Cockroaches: Ecology, Behavior, and Natural History (by Bell, W. J., Roth, L. M. et Nalepa, C. A.) Book Review. **The Quarterly Review of Biology** 83: 222.
29. Legendre F, Whiting MF, Bordereau C, Canello EM, Evans T & Grandcolas P. 2008. The phylogeny of termites (Dictyoptera: Isoptera) based on mitochondrial and nuclear genes: implications for the evolution of the worker and pseudergate castes, and foraging behaviors. **Molecular Phylogenetics and Evolution** 48: 615-627.
30. Legendre F, Pellens R & Grandcolas P. 2008. A comparison of behavioral interactions in solitary and presocial Zetoborinae cockroaches (Blattaria, Blaberidae). **Journal of Insect Behavior** 21: 351-365.
31. Desutter-Grandcolas L, Legendre F, Grandcolas P, Robillard T & Muriene J. 2007. Distinguishing between convergence and parallelism is central to comparative biology: a reply to Williams and Ebach. **Cladistics** 23: 90-94.
32. Pellens R, D’Haese CA, Bellés X, Piulachs M-D, Legendre F, Wheeler W & Grandcolas P. 2007. The evolutionary transition from subsocial to eusocial behavior in Dictyoptera: phylogenetic evidence for modification of the “shift-in-dependent-care” hypothesis with a new subsocial cockroach. **Molecular Phylogenetics and Evolution** 43: 616-626.
33. Pellens R, Legendre F & Grandcolas P. 2007. Phylogenetic analysis of social behavior evolution in [Zetoborinae + Blaberinae + Gyninae + Diplopterinae] cockroaches:

- an update with the study of endemic radiations from the Atlantic forest. **Studies in Neotropical Fauna** 42: 25-31.
34. Robillard T, Legendre F, Desutter-Grandcolas L & Grandcolas P. 2006. Phylogenetic analysis and alignment of behavioral sequences by direct optimization. **Cladistics** 22: 602-633.
35. Desutter-Grandcolas, L., Legendre, F., Grandcolas, P., Robillard, T. and Murienne, J. (2005). Convergence and parallelism: is a new life ahead of old concepts? **Cladistics** 21:51-61.
36. Murienne J, Grandcolas P, Piulachs MD, Bellés X, D’Haese C, Legendre F, Pellens R & Guilbert E. 2005. Evolution on a shaky piece of Gondwana: is local endemism recent in New Caledonia? **Cladistics** 21: 2-7.
37. Grandcolas P, Legendre F, Park YC, Bellés X, Murienne J & Pellens R. 2005. The genus *Cryptocercus* in East Asia: distribution and new species (Insecta, Dictyoptera, Blattaria, Polyphagidae). **Zoosystema** 27: 725-732.
38. Grandcolas P, Guilbert E, Robillard T, D’Haese CA, Murienne J & Legendre F. 2004. Mapping characters on a tree with or without the outgroups. **Cladistics** 20: 579-582.

A.6. Scientific Meetings

- Troudet, J.*, Vignes-Lebbe, R., Legendre, F. 2016. Latitudinal diversity gradient and taxonomic bias. The International Biogeography Society Special Meeting – The Biogeography of Ecology. May 2016.
- Lafond, A., Legendre, F., Yotoko, K., Robillard, T.* 2015. Evolution of mechanisms of sound production in Agnotecous crickets: multiple strategies to produce high-frequencies. IBAC meeting. November 2015, Murnau, Germany.
- Goutte, S., Dubois, A., Legendre F*. Environmental constraints and call evolution in torrent-dwelling frogs. Modern phylogenetic comparative methods, Seville, Spain, Seville, 11-15 November 2014.
- Grandcolas, P.*, Pellens, R., Robillard, T., Jourdan, H., Legendre, F., Nel, A. and Nattier, R. Updating the dating : how old is New Caledonian biota ? Island Biology, Honolulu, Hawaii, 7-11 July 2014.
- Goutte S.*, Dubois A., Legendre F. Evolution of advertisement calls in torrent dwelling frogs. International Bioacoustic Council XXIV, Pirenopolis, Brazil, 8-13 September 2013.
- Legendre F.*, Nel A., Svenson G.J., Grandcolas P. Phylogeny and timing of diversification in Dictyoptera. XXXII Willi Hennig Society, Rostock, Germany, 3-7 August 2013.
- Legendre, F.*, Whiting, M. F. and Grandcolas, P. Phylogenetic analyses of termite post-embryonic sequences illuminate caste and developmental pathway evolution. Form2012, MNHN, Paris, November 2012.
- Goutte, S.*, Dubois, A. and Legendre, F. Evolution of advertisement calls in torrent Ranids: communicating despite noise. 5th Asian Herpetological Conference, Chengdu (China), June 2012.
- Goutte, S*., Dubois, A. and Legendre, F. Missing the sound ambient sound level is an important measure in animal ecology. *SERL Ecology and Behaviour 8th meeting*, Chizé (France), April 2012.

- Goutte, S.*, Dubois, A. and Legendre, F. Communicating despite noise: evolution of advertisement call in torrent *Raninae*. International Bioacoustic Council XXIII, La Rochelle, September 2011.
- Legendre, F.* and Grandcolas, P. Evolution of behavior and conflict among data sets in Blaberidae cockroaches. Hennig XXVIII, Singapore, June 2009.
- Legendre, F.*, Nel, A., Bordereau C., Whiting, M. F. and Grandcolas P. A phylogenetic study of the evolution of caste system and developmental pathways in termites. Hennig XXVI, meeting of the Willi Hennig Society, New-Orleans (USA), June-July 2007.
- Legendre, F., Robillard, T., Desutter-Grandcolas, L. and Grandcolas, P*. Revisiting Lorenz's earlier studies of behavior evolution: aligning behavioral sequences in Anatidae birds. Hennig XXVI, meeting of the Willi Hennig Society, New-Orleans (USA), June-July 2007.
- Legendre, F.*, Whiting, M. F., Bordereau, C., Canello, E. M., Evans, T. and Grandcolas, P. Termites phylogeny and caste evolution. Hennig XXV, meeting of the Willi Hennig Society, Oaxaca (Mexico), August 2006.
- Robillard, T., Legendre, F.*, Desutter-Grandcolas, L. and Grandcolas, P. Phylogenetic analysis and alignment of behavioral sequences by direct optimization. Hennig XXV, meeting of the Willi Hennig Society, Oaxaca (Mexico), August 2006.
- Legendre, F., Robillard, T., Desutter-Grandcolas, L. and Grandcolas, P*. Phylogenetic analysis of non-stereotyped behavioral sequences: from successive event-pairing method to direct optimization? Hennig XXV, meeting of the Willi Hennig Society, Oaxaca (Mexico), August 2006.
- Legendre, F.*, Packer, L., Agolin, M. and Grandcolas, P. The logical content of the classification of social behavior: a cladistic study. Hennig XXIV, meeting of the Willi Hennig Society, Fagernes (Norway), July 2005.
- Legendre, F.*, Grandcolas, P., Bellés, X., Piulachs, M. D., Park, Y. C. and Murienne, J. Phylogenetics and biogeography in *Cryptocercus*: the old cockroach out (Dictyoptera: Blattaria). Hennig XXIII, meeting of the Willi Hennig Society, Paris (France), July 2004.
- Desutter-Grandcolas, L.*, Grandcolas, P., Robillard, T., Murienne, J. and Legendre, F. Convergence and parallelism: is a new life ahead of old concepts? Hennig XXIII, meeting of the Willi Hennig Society, Paris (France), July 2004.
- Grandcolas, P.*, Desutter-Grandcolas, L., Robillard, T., Legendre, F. and Murienne, J. Transaptation, a new concept to describe historical continuity of function with change of the associated structure. Hennig XXIII, meeting of the Willi Hennig Society, Paris (France), July 2004.
- Murienne, J.*, Grandcolas, P., Piulachs, M. D., Bellés, X., D'Haese, C., Legendre, F., Pellens, R. and Guilbert, E. Evolution on a shaky piece of Gondwana: a phylogenetic analysis of the endemism in the cockroach genus *Angustonicus* in New Caledonia (Blattaria, Tryonicinae). Hennig XXIII, meeting of the Willi Hennig Society, Paris (France), July 2004.

A.7. Invited Lectures

- Legendre F.** 2016. Phylogeny and evolution of social behaviour in Dictyoptera. *Seminars of the Museu de Zoologia da USP, Sao Paulo, Brazil.*
- Legendre, F.** 2011. Trop de préjugés tuent le préjugé. *XVII^{ème} congrès du Bureau des Doctorants et Etudiants du Museum, MNHN, Paris (France).*
- Legendre, F.** 2008. Phylogeny and evolution of social behavior in cockroaches and termites. *Seminars of the Division of Biological Sciences, University of Missouri-Columbia (USA).*
- Legendre, F.** 2006. Phylogenetic analysis of non-stereotyped behavioral sequences. *Seminars of the Department Systematics and Evolution, Museum national d'Histoire naturelle, Paris (France).*
- Legendre, F.** 2005. Phylogenetics and biogeography in the genus *Cryptocercus* (Dictyoptera: Blattaria). *Journées du Département Systématique et Evolution, Museum national d'Histoire naturelle, Paris (France).*

A.8. Teaching

Doctoral School 227, MNHN. Class « La phylogénie : support à l'analyse de l'évolution » (Class Coordinator : E. Guilbert)

- *Phylogenetic analyses of behavioural sequences* 2009 – 2016
- *Non-traditional characters in phylogenetics, from behaviour to geographic distribution: how to analyze them and according to what principles* 2009

Master 2 Sciences de l'Univers, Environnement, Ecologie (SDUEE) with emphasis in Systématique, Evolution, Paléobiodiversité (SEP), Université Paris VI.

- *Probabilistic phylogenetic inferences (SEP22)* 2016

Master 1 Sciences de l'Univers, Environnement, Ecologie (SDUEE) with emphasis in Systématique, Evolution, Paléobiodiversité (SEP), Université Paris VI. Classes « Bases de la phylogénie » and « Bases de la systématique » (Classes coordinator : P. Tassy and R. Vignes-Lebbe)

- *Probabilistic phylogenetic inferences* 2011 – present
- *Information sources in systematics : behavioural data* 2009 – 2017
- *Phylogenetic tests of evolutionary hypotheses* 2008, 2010 - 2017

Formation of High School teachers. Direction de l'Enseignement, de la Pédagogie et des Formations (DEPF), MNHN Paris.

- *Phylogenetic reconstruction : why and how ?* 2009 – 2015
- *Teaching classification and evolution of life, scientific contribution to a website ressource (<http://plateforme-depf.mnhn.fr>)* 2009 – 2010
- *Classification of living beings.* Guest lecture in Paul Eluard Middle School, Montreuil (France) 2009

A.9. Grants & Distinctions:

2017. Synthesys grant to visit NHM (London) for two weeks.
 2016. Labex BCDiv – gratification for M2 France Thouzé.
 2011 – 2015. Six specific and generic calls at MNHN (23 k€).
 2007 – 2008. Lavoisier Grant (18 k€), Ministère des Affaires Etrangères, France.
 2006 – 2007. Two Grants from Paris Doctoral School ED 392 (2 k€).
 2006. Rosen Price (500 \$), 3rd best student oral presentation, Hennig XXV, Oaxaca (Mexico).
 2005 – 2007. Three Marie Stopes Student Travel Award (500 \$ each), Willi Hennig Society.
 2004 – 2007. PhD Grant from Ministère de l'Education Nationale, de la Recherche et des Technologies (France).
 2003 – 2004. DEA Grant from Ministère de l'Education Nationale, de la Recherche et des Technologies (France).

A.10. Professional Services

- Co-responsible** of the teaching major 'Systematics and Evolution' in Master SEP (2015-).
 Member of two **recruitment committees** at the Museum national d'Histoire naturelle (Paris, France).
 Member of the **ISYEB council** (2005-2007; 2013-present).
 Member of **grant decision panel** at MNHN (2013-present).
 Member of the **SFS** (Société Française de Systématique) **council** (2012-2015).
 Member of the **Willi Hennig Society** (WHS; 2008-present).
 Member of the **WHS travel award committee** (2013-present).
Reviewer (Granting Agencies): National Science Foundation (NSF, USA); Agence Nationale de la Recherche (ANR, France); Mission Europe et International pour la Recherche, l'Innovation et l'Enseignement Supérieur (MEIRIES, France).
Reviewer for > 15 journals: Annals of the Entomological Society of America, Behavioural Processes, Cladistics, Ethology, Insects, Journal of Biogeography, Molecular Biology and Evolution, Molecular Phylogenetics and Evolution, Plos One, The Science of Nature, Zoological Journal of the Linnean Society, Zootaxa...

A.11. Field work

- New Caledonia. 2017. Our Planet Reviewed. Study of cockroach communities and micro-endemism in Aoupiné and Inédète (Province Nord).
 New Caledonia. 2016. Our Planet Reviewed. Study of cockroach communities and micro-endemism in Bwabwi (Province Sud).
 French Guiana. 2015. Our Planet Reviewed. Collecting Orthopteroid Insects in Mitaraka.
 Philippines. 2014. Study of cockroach communities in Palawan and around Manila.
 United States. 2013. Collecting *Cryptocercus punctulatus* in Virginia (Jefferson National Forest).
 Papua New Guinea. 2012. Our Planet Reviewed, IBISCA Niugini. Collecting Orthopteroid Insects along an altitudinal transect on Mount Wilhelm.

- New Caledonia. 2010. Rapid Assessment Program (Conservation International) on Mount Panié. In charge of Orthopteroïd Insects.
- Indonesia. 2010. Study of cockroach communities with emphasis on *Perisphaerus* sp. (Blaberidae: Perisphaeriinae).
- Singapore. 2009. Collect of cockroaches with a special emphasis on the subsocial species *Perisphaerus flexicollis* (Blaberidae: Perisphaeriinae).
- United States. 2008. Field observations and collect of *Tylopelta* sp. (Hemiptera: Membracidae) in Missouri.
- French Guyana. 2006. Study of cockroach communities on Kaw Mountain with emphasis on Blaberinae and Zetoborinae (Blaberidae).

A.12. Scientific Diffusion & Popularisation

Scientific contribution on biodiversity, systematics, cockroaches and termites for french **TV shows** (E=M6, 2013 and 2015), **popularization magazine** (Wapiti, 2011) and **ARTE documentary**.

Lecturer for *Empreintes* association (2012, 2013) and lay public (MNHN, 2013).

INTRODUCTION

My research interests revolve around phylogenetics and are deeply anchored in a tree-thinking biology approach. I try to craft phylogenetic tests as carefully as possible, paying special attention to evolutionary questions and the protocol to test them. Because I study evolutionary questions linked to diverse fields, I am also at the interface between diverse disciplines. I thus tend towards interdisciplinarity, with all the difficulties and richness it brings. So far, I mainly focused on three decisive aspects of phylogenetic tests that have significant consequences on the outcomes: i) taxonomic sampling, ii) character coding/delimitation, and iii) methodological developments. I provide here a brief introduction to contextualize my research before developing my research themes in three dedicated chapters and presenting my future projects in a fourth one.

Phylogenetics in evolutionary biology

Evolution lies at the heart of biology, as famously stated by Dobzhansky (1973) when he wrote: “Nothing in Biology makes sense except in the light of Evolution”. Dobzhansky emphasized how evolution explains altogether the unity and diversity of life, and we measure now how visionary this sentence was (Losos *et al.* 2013). With evolutionary concepts and methods, we have the ability to address an almost endless list of problems, including those assessed as the most challenging for humanity, such as environmental and health issues (NRC 2009).

The academic discipline “evolutionary biology” encompasses numerous subfields, sometimes seen as opposed to each other according to their scale of studies or their ultimate aims. Macro-scale studies apprehending global patterns of evolution, for instance, have been distinguished from micro-scale studies investigating evolutionary mechanisms or processes (Eldredge & Cracraft 1980; Futuyama 1998). Yet, beyond these divisions, evolutionary biology is a vivid discipline whose subfields complement and feed on one another (Sandvick 2008; Losos 2011b; Weber & Agrawal 2012). At the macro-evolutionary scale, phylogenetics has become a prevalent discipline nurturing numerous others.

Phylogenetic systematics was in its infancy fifty years ago (Hennig 1966) but, now, its importance is universally recognized. We are firmly placed in what is called a tree-thinking biology era that originated in the 80s (Coddington 1988; Grandcolas *et al.* 1994; O’Hara 1997; Baum *et al.* 2005; Omland *et al.* 2008; Baum & Smith 2013; Losos *et al.* 2013). Phylogenetics, the study of evolutionary relationships among organisms, has travelled a long way since Hennig, and it was suggested twelve years ago that phylogeneticists were already producing no less than 15 evolutionary trees per day (Rokas 2006; see also Pagel 1999 and Parr *et al.* 2012 to visualize the exponential growth of publications on phylogenetics). Phylogenetic trees serve to study a multitude of evolutionary questions and help investigating forensic, or medical issues among other applications (Gregory 2008; Arnold & Nunn 2010). They bring a historical frame, wherein evolutionary questions are addressed (Huelsenbeck & Rannala 1997; O’Hara 1997; Baum *et*

al. 2005). This growing importance will undoubtedly carry on as ‘better’ trees should be reconstructed while genomic methods and computer sciences improve (*e.g.*, Segata *et al.* 2013; Jarvis *et al.* 2014; Faurby & Svenning 2015). Consequently, some people rephrased Dobzhansky’s famous statement: nothing in evolution makes sense except in the light of phylogeny (on “SSB support for teaching evolution” webpage – consulted on 7th march 2014; “Tree-thinking group, 2015” webpage – consulted on 2015-08-20).

Given the importance of tree-thinking in biology (McTavish *et al.* 2017), turnkey solutions to use phylogenies have been proposed in several domains (*e.g.*, Pearse & Purvis 2013; Thomas *et al.* 2013). This commendable initiative helps people grasping the main concepts and tools of phylogenetics. Here, I do not provide turnkey solutions but rather underline the importance of referring to keystone phylogenetic concepts each time one engages in a phylogenetic test of evolutionary scenario. I also show that, sometimes, new tools must be proposed or refined to respect these fundamental principles, especially in interdisciplinary studies.

Phylogenetics and experimental design

A common element of most scientific methods is the process of testing. Since undergraduate school, young scientists are taught the importance and power of testing in sciences and are explained that it requires an adequate, well-formulated protocol or experimental design. Some disciplines, such as medicine or ethology, often rely on typical experimental designs, where a treatment helps assessing the causal relationship between two variables (called explanatory and response variables). Like so, during my post-doctoral project, my colleagues and I developed an experimental design when investigating the signal, supposedly competitive, emitted by males of *Tylopelta gibbera* (Hemiptera: Membracidae) during mate localisation (Legendre *et al.* 2012). Like all experimental designs, it implied delimiting an adequate sample, choosing the methods to use, and defining the measures to perform. This experimental design step was critical; as Martin & Bateson (2007) underlined, “careful attention to the design of experiments will save many a headache at a later stage in a study”.

Martin & Bateson’s advice also stands for phylogenetic tests of evolutionary scenarios, *i.e.* studies whose aim is to answer evolutionary questions beyond phylogenetic relationships (even though getting a robust phylogenetic pattern remains a necessary first step). Clear hypotheses must be formulated and a sound protocol with proper data gathering must be designed. These stages represent mandatory steps entitling scientists to obtain promising results. Yet, meticulous designing has been somehow overlooked in the tree-thinking paradigm because phylogenetics was not initially developed in a so prosperous context. In phylogenetics, data gathering involves taxon and character sampling, as well as character delimitation, two points that I develop in chapters 1 and 2.

Phylogenetics in interdisciplinary studies

The success of phylogenetics in evolutionary biology explains why phylogenetics is such a vibrant field of research. But it comes at a price: Along with increased relevance comes responsibility. People using phylogenetic trees, *i.e.* tree users, extend well beyond phylogeneticists *sensu stricto*. Tree users comprise scientists from different fields and with various backgrounds. As such, they might fail to fully grasp each and every concepts or methods of phylogenetics (Omland *et al.* 2008). Ecologists, ethologists or physiologists, for instance, have to master phylogenetics to adequately tackle some of their specific issues (Rezende & Diniz-Filho 2012; Pozzi *et al.* 2014; Roquet *et al.* 2013). They must either own multiple skills or collaborate with phylogeneticists. In both cases, they have to engage in interdisciplinary studies. Reciprocally, a phylogeneticist's interest might spread over very different fields, also resulting in interdisciplinary studies.

Interdisciplinary studies are desirable: They allow tackling a scientific issue from different perspectives, different background, and with various tools. Interdisciplinary studies are also highly rewarding (Masel & Promislow 2016) but, as for any merging process, they can also be challenging. Data gathered in a given discipline cannot always be used readily in another one, and spurious outcomes might be produced if one fails to identify these limitations. To overcome this impediment, new methodological developments are often needed in interdisciplinary studies. Some authors even argue that it is a pre-requisite of a 'real', *i.e.* highly integrated, interdisciplinarity, contrary to multidisciplinary approaches with a lower degree of integration and a loose cooperation between disciplines (*e.g.*, Tress *et al.* 2005). In the 2nd and 3rd chapters, I illustrate how I tackle these two predicaments of interdisciplinary studies (character delimitation issues and the need of new methods) using phylogenetics to investigate social behaviour evolution.

I. SAMPLING
STRATEGIES TO ADDRESS
EVOLUTIONARY
HYPOTHESES IN
PHYLOGENETICS

Hypothesis testing has always been central in biology (Mahner & Bunge 1997). It relates to the hypothetico-deductive scientific method that we all learned early in science classes: We formulate a hypothesis, design a protocol, gather some data accordingly, analyse the results and conclude about the hypothesis. This routine is commonly applied in several disciplines such as ecology, ethology or medicine, among many other fields of science.

For example, my colleagues and I followed this scientific approach in a recent behavioural study about sexual communication in treehoppers: we stated a problematic (*is there a specialized signal produced by male treehoppers, *Tylopelta gibbera*, that disrupts competitors' duets?*), designed a protocol (*characterizing search path of single males duetting with a female; characterizing the behaviour of two males duetting with the same female; measuring female response and time to localize the female, with and without competitor in natural conditions and with playbacks*), gathered some data following this protocol, compared them (*the overlapping signal strongly decreased female response; males took longer to localize the female in the presence of a competitor*) and concluded about the hypothesis (*yes, the signal functions as to disrupt communication*; Legendre *et al.* 2012 – [Figure 1](#)).

Protocol design is a central task in the research agenda and is carried out in advance. Species choice belongs to the sampling step of the protocol design and should thus be anticipated, like the number of replicates for instance. Choosing species to study is, however, rarely considered as an equivalent issue to the number of replicates (Westoby 2002). Our study on signal competition (Legendre *et al.* 2012) illustrates this topic: We did not ask whether *Tylopelta gibbera* was, or not, the best model species to show a male-male competition in vibrational communication, but we did wonder how many replicates would be necessary to test our hypothesis. Yet, this species choice is significant, as it impacts the rest of the experimental design and the outcomes. Sampling is hypothesis-dependent, whether performed in a phylogenetic context or not, and must be conducted with special care. In phylogenetics, although the perfect taxonomic sampling (*i.e.* an exhaustive sampling of past and extant taxa) is out of reach – numerous extant and extinct taxa are unknown or hard to acquire – some samplings are better than others to test a given hypothesis, like some protocols in ethology are better than others to answer a particular question.

In phylogenetics, species sampling has long been recognized as of utmost importance. Several authors have emphasized the role and impact of taxon sampling on phylogenetic relationships *per se* or on clades support and robustness (*e.g.*, Lecointre *et al.* 1993; Philippe & Douzery 1994; Hillis 1998; Zwickl & Hillis 2002; Grandcolas *et al.* 2004; Heath *et al.* 2008). In a hypothesis-testing context, this role takes on another dimension: Species sampling impacts both the phylogenetic pattern and the answer to the evolutionary question. This supplemental attribute has given birth to what has been called either 'phylogenetic experimental design' or 'phylogenetic-targeting', with connected methods proposed and illustrative examples produced

(Goldman 1998; San Mauro *et al.* 2009, 2012; Arnold & Nunn 2010; Plazzi *et al.* 2010). These methods still have to be sharpened but, until it happens, a sampling strategy must be stated explicitly (Westoby 2002). I illustrate below, using two published examples, how I design taxonomic samplings strategically to ensure phylogenetic tests of evolutionary hypotheses as powerful as possible.

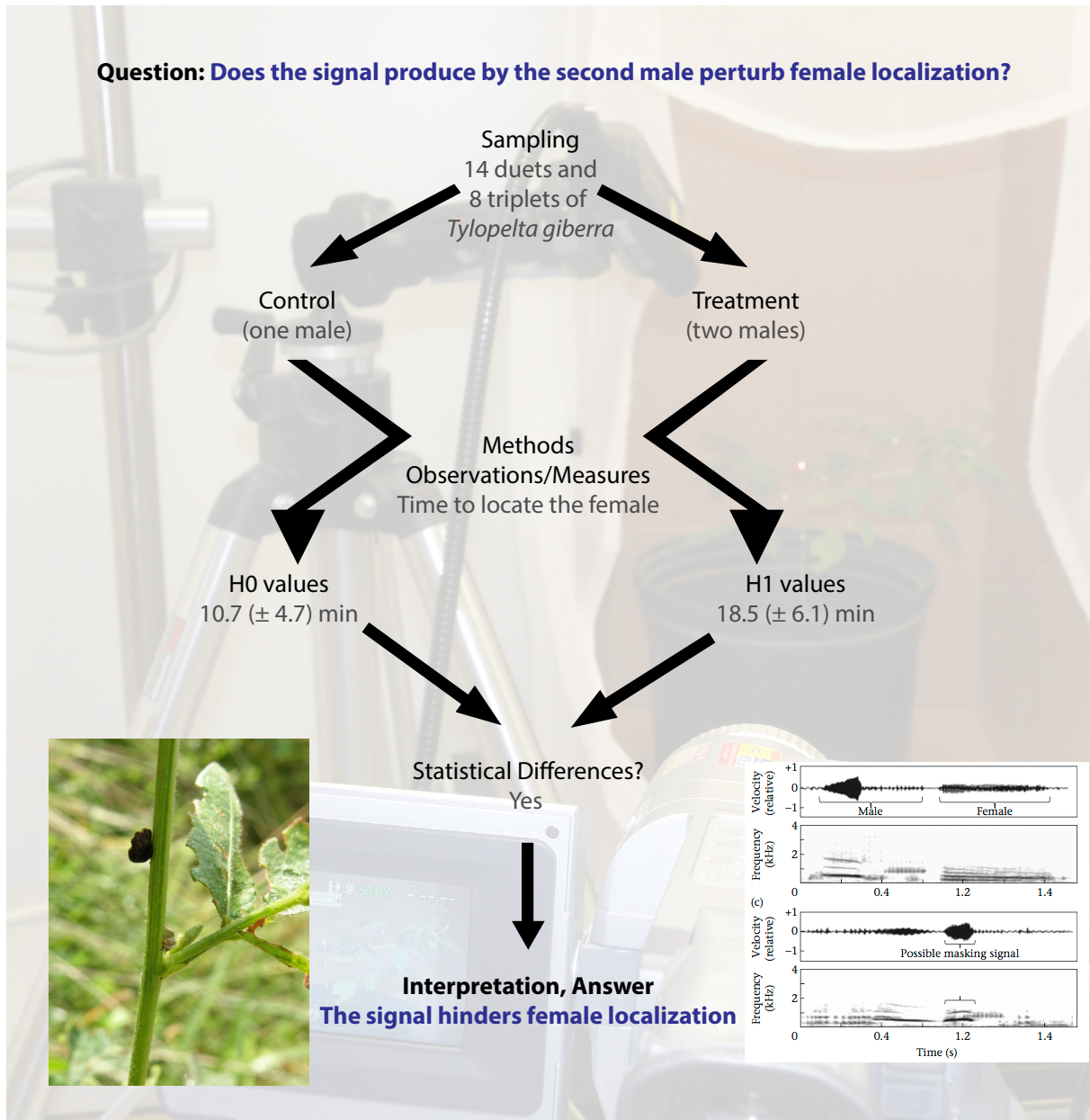


Figure 1. Brief overview of the experimental design followed when investigating mate localisation in *Tylopelta giberra* (Insecta: Hemiptera). Left: an adult and a nymph of *Tylopelta giberra* photographed in Missouri; Right: Oscillograms and spectrograms - note the possible masking signal; Background: part of the experimental design (laser vibrometry).

I. 1. Sampling the actual biodiversity to address classification issues in Insects: phylogenetic test of the Orthoptera Species File classification (*Chintauan-Marquier**, *Legendre** et al. 2016 – *Cladistics* – *equal contributions)

I. 1. 1. *Classifications and phylogenies*

Taxonomic classifications are “information system(s) from which to comprehend evolution” (de Carvalho *et al.* 2014). Because of this definition, classifications are powerful tools widely used in evolutionary biology. Nevertheless, some classification systems can be unreliable or used blindly, a problem that might recur with the current taxonomy crisis because less and less experts exist to evaluate the classifications at hand (Godfray 2002; Agnarsson & Kuntner 2007; Bacher 2012; de Carvalho *et al.* 2014). If taxonomic classifications are flawed or unwisely used, biased evolutionary conclusions will be drawn. Classifications being now

consistently derived from phylogenetic trees, thorough phylogenetic analyses are clearly needed to limit these issues.



- superorder [Orthopterida](#)
- order [Orthoptera](#)
- suborder [Ensifera](#)

infraorder **Grylloidea**

LSID urn:lsid:Orthoptera.speciesfile.org:TaxonName:24743

Distribution:



Ecology:

- Terrestrial.

Citations (7):

- Vickery. 1977. Lyman Entomological Museum and Research La
- Kevan, D.K.M. 1982. In Parker [Ed.]. Synopsis and Classificatio
- Desutter-Grandcolas. 1987. Ann. Soc. ent. Fr. Nouvelle série 2
- Gorochov. 1995. Proceedings of the Zoological Institute of the
- Desutter-Grandcolas. 2003. Zool. Scripta 32(6):525-561 >> N
- Storozhenko. 2004. Long-horned orthopterans (Orthoptera: Ei
- Chintauan-Marquier, Legendre, Hugel, Robillard, Grandcolas, /

- superfamily [Grylloidea](#) Laicharting, 1781
 - synonym [Grylloidea](#) Laicharting, 1781
 - synonym [Grylloides](#) Laicharting, 1781
 - family †[Baisso gryllidae](#) Gorochov, 1985
 - family [Gryllidae](#) Laicharting, 1781
 - family [Mogoplistidae](#) Brunner von Wattenwyl, 1873
 - family [Phalangopsidae](#) Blanchard, 1845
 - family [Protogryllidae](#) Zeuner, 1937
 - family [Trigonidiidae](#) Saussure, 1874
 - subfamily [Pteroplistinae](#) Chopard, 1936
 - genus †[Bellosichnus](#) Genise & Sánchez, 2017
- superfamily [Gryllotalpoidea](#) Leach, 1815
 - family [Gryllotalpidae](#) Leach, 1815
 - family [Myrmecophilidae](#) Saussure, 1874

In Ensiferan research (tettigonids and crickets *sensu lato*), biologists largely relate to the online database called the Orthoptera Species File (hereafter OSF – **Figure 2**). Given both the prevalence of the OSF and the use of crickets as model species in various fields (*e.g.*, neurobiology or acoustics – Huber *et al.* 1989; Bailey 1991; Field 2001), the classification system derived from this database must be reliable to enable robust results. Yet, in 2015, no well-supported phylogenetic study of Ensifera was published, especially for true crickets and their allies. Mugleston *et al.* (2013) studied the phylogeny of Tettigonioidea, but crickets, a large group of Orthoptera (*ca.* 5000 species), were missing for a global achievement of Ensifera phylogeny. The latest molecular study (Jost & Shaw 2006) comprised 51 taxa, i.e. less than 0.5 % of ensiferan specific diversity, and it was poorly supported. We showed (Legen-

Figure 2. The Orthopterist File Online (consulted on the 02-16-2018).

dre *et al.* 2010) that the dataset used was insufficient to derive a robust phylogenetic hypothesis, let alone a robust classification. Still, it was mainly used to refine the classification implemented in OSF. In addition, numerous subfamilies were not sampled and kept in diverse positions in the OSF classification according to previous, non phylogenetic, hypotheses (Chopard 1967,1968; Otte 1994). Therefore, as usual in phylogenetics, more data were needed and we developed a sampling strategy to test the OSF classification. We focused on Grylloidea and tested as many subfamilies and upper taxonomic levels as possible (Chintauan-Marquier *et al.* 2016).

I. 1. 2. Taxonomic sampling strategy to test the cricket OSF classification system

In 2014, the OSF classification included 25 cricket subfamilies. To test the validity of these groups, at least two representatives of each group had to be sampled. A dataset complying with this criterion would approach the ‘ideal’ minimum taxonomic sampling to test the OSF classification. Unfortunately, and as too often in phylogenetics, what is judged as the ‘ideal’ sampling to answer a given question was unreachable (Westoby 2002). We then built a taxonomic sample matching this objective as closely as possible.

We included species belonging to as many supra generic groups as possible among those listed in the OSF on the 1st September 2014. We also sampled genera not currently classified in a supra generic category in the OSF, to improve the phylogenetic diversity of the ingroup, and to limit sampling biases. In addition, we took into account the genera classified in tribal or subfamilial groups that are no more in use in the OSF. In total, we included 205 species (152 genera) representing 22 of the 25 subfamilies (i.e. 88 %) and 37 of the 52 tribes (i.e. 71 %) listed in the OSF. This sampling covered all the families (four) and “subfamily groups” (three) listed in the OSF. We increased the taxonomic sample for a cricket molecular phylogenetic study and were able to test most of the cricket supra-generic groups.

I. 1. 3. Laying the foundation of a phylogenetic classification for crickets and of evolutionary hypotheses on this group

We sequenced seven molecular markers and obtained a ~3600 bp alignment. We then performed maximum parsimony, maximum likelihood and Bayesian inference analyses. We showed that some traditional groups are supported while others are not (Chintauan-Marquier *et al.* 2016 ; **Figure 3**). Three out of the four families were monophyletic but only one of the “sub-family group” was monophyletic. As for subfamilies, only 6 out of 22 were monophyletic. Different situations must be distinguished though for the non-monophyletic subfamilies. Some of them could be recovered monophyletic providing minor changes in cricket classification (most often, this means to move a few genera from one clade to another), while others were polyphyletic or nested within larger clades. These different situations imply different solutions to obtain a phylogeny-based classification system. Furthermore, our results suggested nomenclatural amendments (*e.g.*, new names, new ranks) and questioned the possibility to consider an entirely phylogenetically-derived classification, with all names reflecting tree topology. Overall, our

results showed that the OSF classification system must be updated according to the most recent phylogenetic results, considering phylogenetic uncertainty when relevant. Only then shall it be used for the numerous evolutionary questions addressed in this Insect group, especially on communication for which crickets comprises important models (Gerhardt & Huber 2002).

In short, we tested the OSF classification system and brought the foundations for a future classification system that should become the new benchmark for crickets and for evolutionary studies on this group. A similar approach with equivalent outcomes has been recently undertaken for Blaberidae cockroaches (Legendre *et al.* 2017). It helped differentiating results supported on not, controversial or not with previous works, a report useful to prioritize future samplings and future phylogenetic tests, from the simplest (*e.g.*, classification) to much more complex evolutionary scenarios.

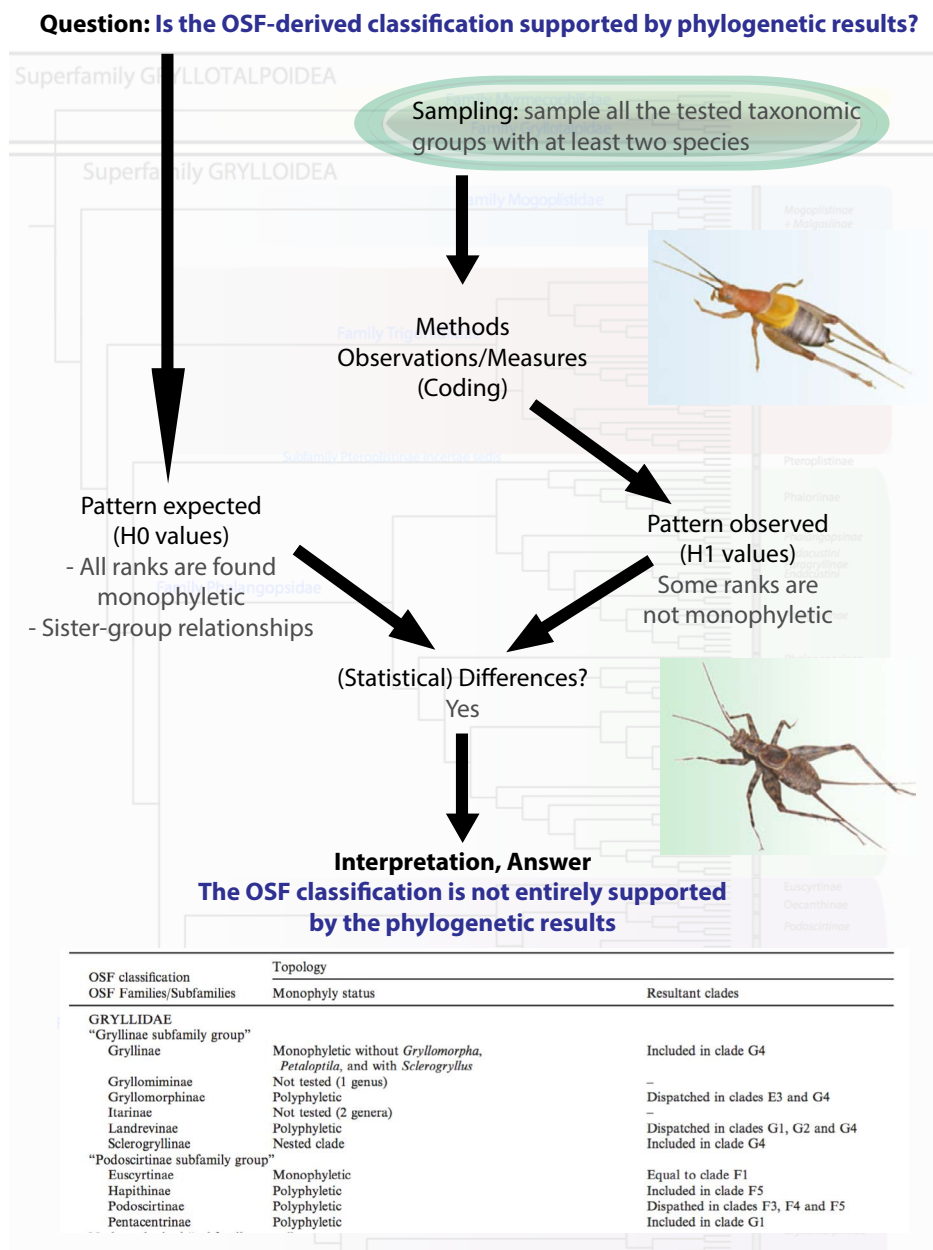


Figure 3. Phylogenetic design underlining the sampling step to test the OSF-derived classification system. Figures, table and background from Chintauan-Marquier *et al.* (2016).

I. 2. Analytical sampling of fossil evidence: phylogenetic test of the timing of diversification in Dictyoptera (*Legendre et al. 2015b – PLoS*)

I. 2. 1. Tempo of evolution, fossils and datings

Tempo of evolution has long fascinated evolutionary biologists (Simpson 1944). What is the rate of evolution of a taxonomic group? Why and how does it accelerate or decelerate in some groups? When do two sister-groups diversified? Concomitantly or not? All these questions, and numerous others, are gathered under the word “*tempo*”. Nowadays, questions about tempo of evolution are commonly tackled in a phylogenetic framework, thanks to numerous advances in diversification and dating analyses (Drummond *et al.* 2006; Morlon 2014). For these analyses, designing the taxonomic sampling is again a crucial step, and it is also true for Dictyoptera, the insect super-order that illustrates this section. But studies on tempo of evolution comprise another component sensitive to sampling issues: fossils. We only know 2 to 30 % of the actual species diversity (May 1990a), which itself represents less than 1 % of the past diversity (Benton 1995). These figures underline why sampling carefully extinct taxa is of prime importance.

Fossils bring original character combinations and are associated with an age, more or less accurate. They help deciphering the evolution of forms and behaviours and allow delimiting an absolute temporal frame (Donoghue *et al.* 1989). In phylogenetics, fossils can be part of the taxa whose relationships are reconstructed and/or be used as calibration points in dating estimates, analyses adding a temporal dimension to phylogenetic relationships. In the latter, more restrictive case, fossils enable us to transform a phylogram into a chronogram. Chronograms are pivotal to investigate evolutionary questions about tempo so that the role of fossils in dating analyses cannot be underestimated and their choice (*i.e.* their sampling) is of uppermost importance (Quental & Marshall 2010; Parham *et al.* 2012). Like a biased or superficial taxonomic sampling can be detrimental to tree reconstruction, inadequate fossil calibrations can constrain or orientate dating analyses towards misleading estimates. In both cases, evolutionary interpretations will be erroneous. Hence, a careful sampling of both terminals and calibration points is required.

The problem of incomplete or controversial fossil record occurs in countless taxonomic groups, and, when investigating tempo-related problems, it adds up to the issue of molecular phylogenies with limited samples. Dictyoptera – an insect super-order including cockroaches, praying mantises and termites, the latter being now most often considered as a suborder of Blattodea (Inward *et al.* 2007a; Beccaloni & Eggleton 2013) – illustrate these issues. First, the oldest ‘Dictyoptera-like’ fossils would be useful to date the oldest nodes, but these fossils are controversial (see below). They cannot be used as long as they have not been re-examined. Second, even if well-established molecular phylogenies have been proposed for praying mantises and termites (Inward *et al.* 2007b; Legendre *et al.* 2008b; Svenson & Whiting 2009), studies

where the three groups were considered together had much smaller taxonomic and molecular samples or did not incorporate attempts of molecular dating estimates (Inward *et al.* 2007a; Djernaes *et al.* 2015). These limitations impede our understanding of dictyopteran evolution. Yet, the study of this charismatic group of insects, which is deeply rooted in a long chronological timescale (Davis *et al.* 2009; Laurentiaux 1960), could shed light on the evolution of a variety of important traits from social or predatory behaviours, to digestive or intracellular symbioses (Grandcolas 1996; Grandcolas & Deleporte 1996; Inward *et al.* 2007b; Legendre *et al.* 2008b; Svenson & Whiting 2004).

Therefore, I conducted a collaborative project testing the controversial tempo of diversification of praying mantises, cockroaches and termites. We designed a sampling strategy to overcome the aforementioned limitations. We sampled ca. 800 species, while previous dictyopteran phylogenies included less than 80 taxa, and chose fossils critically in Parham *et al.*'s (2012) spirit to produce dating estimates.

I. 2. 2. Critical fossil sampling and conservative test

Since the nineteenth century, cockroaches are thought to be very ancient because of the existence of numerous cockroach-like Palaeozoic and Mesozoic fossils (also called “roachoids”), and are traditionally conceived as ancestral to termites and praying mantises (Cornwell 1968; Imms 1937; Rau 1941; Roth 1970, 1989; Tillyard 1936). These “roachoids” are, however, controversial. The best-preserved female “roachoid” fossils show external ovipositors (long or short depending on the taxa), a morphological character that is never found in extant cockroaches (Figure 4). Moreover, other characters such as wing venation or mouthparts are often incomplete or difficult to interpret. Hence, the systematic relationships of “roachoid” fossils remain disputed. The question, still unresolved, is whether these “roachoids” are indeed true cockroaches or rather a stem-group of Dictyoptera (Grandcolas 1996; Hennig 1981; Figure 5), even if the Dictyoptera (including these “roachoids”) seems to be monophyletic, with the Palaeozoic Paoliida as its sister group (Prokop *et al.* 2014).



Figure 4. A “roachoid” fossil with an external ovipositor (Grimaldi & Engel 2005).

Mantises are understood as much more recent than these “roachoids”, according to the fossil record (*i.e.* Early Jurassic; Grimaldi 2003; Svenson & Whiting 2004; Vršanský 2002). The most recent phylogenetic hypotheses postulate, however, that praying mantises are sister-group to the modern cockroaches or to all other modern Dictyoptera (Trautwein *et al.* 2012). The relatively young age of crown-mantises seems to contradict the hypothesis that all Palaeozoic and Early Mesozoic “roachoids” could belong to the crown Blattodea. Recently, some Palae-

ozoic fossils were thought to be stem-mantis lineages, sharing synapomorphic characters with modern praying mantises within the wings and maybe raptorial forelegs (Béthoux & Wieland 2009; Béthoux *et al.* 2010). This hypothesis (Figure 5) would reconcile the latest molecular phylogenies with the fossil record but it has also been disputed (Aristov *et al.* 2013; Gorochov 2013; Kukalova-Peck & Beutel 2012, Guan *et al.* 2016).

Finally, termites were always considered as a recent group according to a rich fossil record (*i.e.* oldest record at the Jurassic/Cretaceous transition; Krishna *et al.* 2013; Nel & Paicheler 1993; Vršanský & Aristov 2014). Nevertheless, a few controversial fossil nesting traces would indicate that they are at least 50 Myr older (*i.e.* Jurassic or even Late Triassic; Bordy *et al.* 2004, 2009; Bumby & Bordy 2006; Hasiotis & Dubiel 1995; Tanner *et al.* 2006; Figure 5). Here again, these hypotheses have been criticized (Genise *et al.* 2005) and would need proper testing.

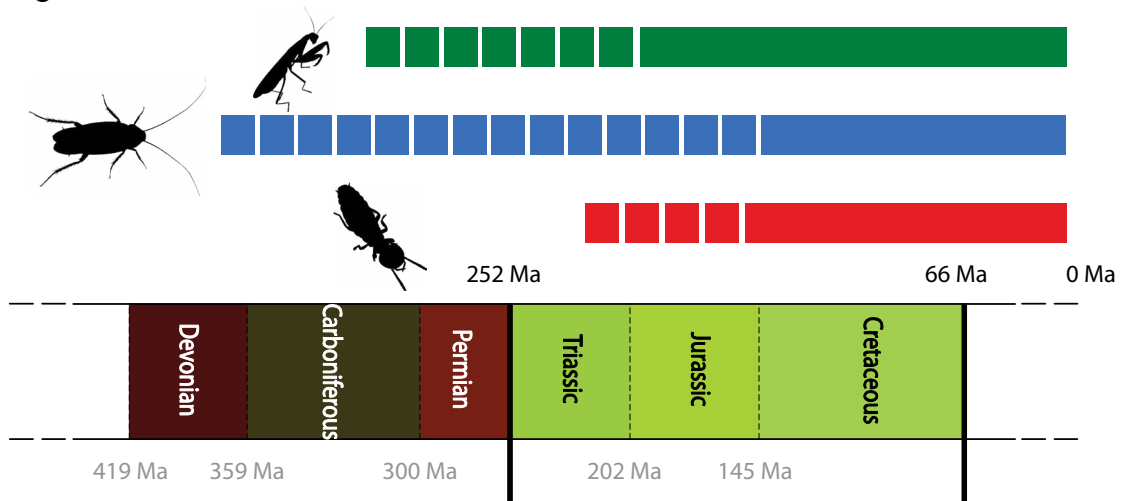


Figure 5. Timeline for Dictyoptera. Dashed lines refer to controversial fossils (Phylopic.org; credit: Melissa Broussard).

We did not use these controversial fossils but tested them with a conservative approach (Figure 6), wherein the possibility to infer old age estimates was kept as follows. Because we were testing the likelihood of old age estimates, our settings in datings needed to allow their potential recovery. We nested our analysis in a deeper group, well-represented in the fossil record, and selected outgroups accordingly (Graham *et al.* 2002; Grandcolas *et al.* 2004; Hedman 2010). In addition, we placed a maximal age constraint at the root, corresponding to the differentiation between Palaeoptera and Neoptera, of 470 Ma. This value corresponds to the maximum of the 95 % confidence interval inferred in Rehm *et al.* (2011) and is a very old limit given that the Palaeoptera/Neoptera diversification is commonly thought to have occurred around 400 Ma (Grimaldi & Engel 2005).

I. 2. 3. *Origins of cockroaches, praying mantises and termites: “roachoids”, ecological succession and sociality evolution*

We found relatively old age estimates for crown-Dictyoptera (293-315 Mya), and thus for stem-mantises and stem-cockroaches due to the topology recovered, estimates compatible with several controversial fossils. Some “roachoid” fossils and the oldest putative stem-mantises fossils cannot be ruled out. On the opposite, our results invalidate both the hypothesis suggesting that winged “blattoids” would date back to the Devonian (Zhang *et al.* 2013) and the putative Triassic nest evidence.

These age estimates raise new questions and new hypotheses of evolution can be postulated. First, given that termites would date back, at most, to the Early Jurassic and that they are crucial decomposers nowadays, one can wonder how warm ecosystems functioned in the Triassic or before (*e.g.*, Raymond *et al.* 2000). Myriapoda, Blattodea and some Orthoptera could have acted as decomposers, but further evidence is needed. It remains an open question, like for scavenger and coprophagous guilds, as these guilds are mainly composed of two recent lineages: Diptera and Coleoptera since the Cenozoic. Second, we found a large temporal gap of ca. 100 Myr between stem- and crown-mantises. This pattern of old origin and much more recent diversification is puzzling but it could be related to their major life history trait, carnivory. Before the Jurassic, several carnivorous lineages existed, including several polyneopterans: Titanoptera only known from the Triassic is now extinct; Mantophasmatodea was present (and may have flourished) before the diversification of the crown-mantises (Huang *et al.* 2008); some Palaeozoic and Early Mesozoic “roachoids” (Raphidiomimoidea) were likely carnivorous. Crown-mantises would have post-dated all these polyneopteran carnivores according to our results, a scenario of ‘ecological succession’ already hypothesized by Gorochov (2006). Given the controversial nature of anthracoptilids around both their taxonomic affinity and their possession of raptorial forelegs (Aristov *et al.* 2013), we cannot infer whether raptorial legs were a crown-mantis apomorphy that would have been a key acquisition for their diversification, after competitors had disappeared. This ‘ecological succession’ scenario would thus deserve to be further investigated.

This study clarified the debate around the origin of each crown-dictyopteran group but the debate is far from over. We reduced the temporal frame typically associated to Dictyoptera and suggested that modern Dictyoptera did not diversify before Hymenoptera, Diptera or Coleoptera. We also brought new hypotheses about dictyopteran evolution, like the possibility for eusociality (*i.e.* highly integrated social systems) to act as a key innovation promoting diversification, a hypothesis subsequently tested and validated (Legendre & Condamine, *in press*). In addition, the inferred age estimates allow targeting critical periods to look for dictyopteran fossils, where their presence is still disputable: praying mantises in the Permian and Triassic periods; cockroaches in the Permian; and termites in the Jurassic.

Question: Do controversial fossils and ichnofossils belong to Dictyoptera?

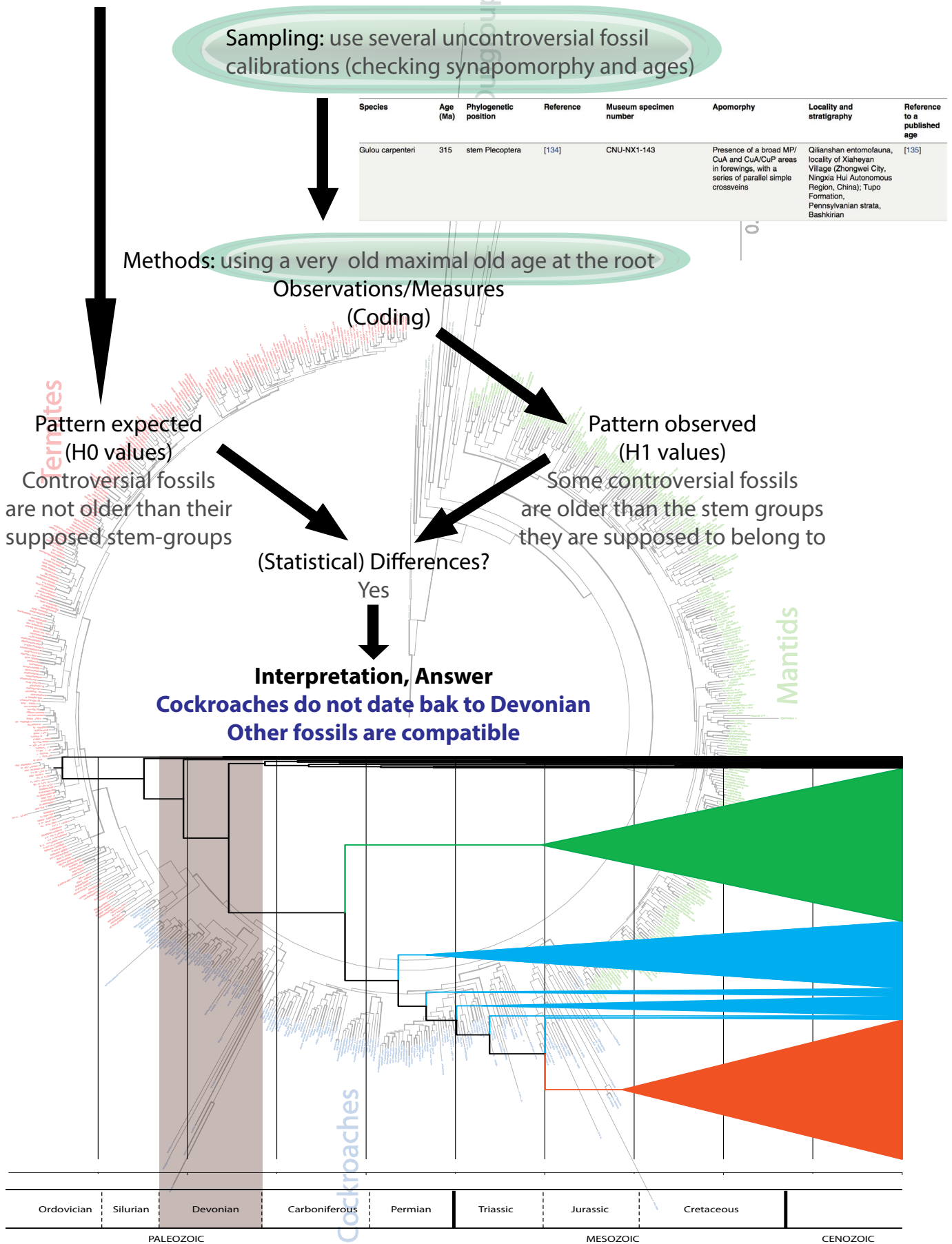


Figure 6. Phylogenetic design pinpointing the fossil sampling step and calibration options while testing for the tempo of evolution in Dictyoptera. Background: circular Dictyopteran tree including ca. 800 taxa.

I. 3. More on sampling: from fieldwork to “big data”

I have underlined the importance of a targeted sampling with regard to an evolutionary question, emphasizing taxonomic sampling. Extant and extinct taxa must be sampled critically to maximize the power of the phylogenetic test because ‘phylogenetic targeting’ (*sensu* Arnold & Nunn 2010) is hypothesis-dependent. In return, the answer to the tests suggests new sampling priorities and new research directions or projects. For these projects, increasing the phylogenetic sampling is a trivial but unavoidable perspective that concerns taxonomic and character sampling.

Both taxonomic and character samplings depend on the state of knowledge in taxonomy, an important aspect of my research. Taxonomy, and its related activities from fieldwork to curation and highlighting of natural history collections, is essential because it allows collecting and describing new taxa – it thus contributes to the ever going quest of a better taxonomic sampling – and providing traits (through direct or indirect observations) useful for diverse evolutionary investigations. These studies will be all the more interesting and complex that we know various features about the organisms.

I underline below the role of fieldwork in my research, especially with regard to sampling, before developing ongoing projects related to taxonomic and character sampling.

I. 3. 1. Taxonomy at the heart of phylogenetic tests of evolutionary scenarios

Taxonomy, an academic field dealing with organismal biology, encompasses the description and identification of organisms. The definition of taxonomy varies and I mean it here in a broad sense, including fieldwork and curation of natural history collections. By definition, taxonomy directly contributes to sampled taxa but, by extension, taxonomy underlies countless disciplines, such as evolution or ecology. To paraphrase Robert M. May (1990b), taxonomy helps us to better apprehend the bricks of “the house of biological science” and thus occupies a fundamental position in biology.

The role of taxonomy in evolutionary biology is exacerbated by three points related to the current situations in phylogenetics and in the study of biodiversity. First, we face a biodiversity crisis that threatens numerous species, most of which remain to be described or unearthed (Hortal *et al.* 2015). To collect specimens and describe species, two taxonomic activities, contributes fighting against this situation. Second, we are in the era of phylogenomics, wherein the number of molecular characters used to reconstruct a phylogenetic tree will not be a limitation anymore (Pyron 2015). Instead, the number of species sampled and for which we have information on traits to be studied, two pieces of information that taxonomy brings, will limit future studies. Third, we are in a tree-thinking paradigm, wherein numerous questions are addressed and various methods developed. Questions need characters to be as diversified as possible; methods need comprehensive sampling to provide results as robust as possible. Taxonomy is thus a rare

discipline – taxonomic skills keep disappearing despite several warnings (*e.g.*, Gaston & May 1995) – with a pivotal position.

My research comprises a taxonomic activity, including work in the field and on natural history collections. Fieldworks, especially for organisms not easily captured by traps like cockroaches (Colinet *et al.* 2016), bring natural history data: direct observation of behaviours, habitats, etc. The role of natural history data cannot be overemphasized (Losos *et al.* 2013), they contribute to our understanding of the tree of life and on its evolutionary dynamics. Fieldworks will constitute part of my future projects and will enrich Natural History Collections (NHC). Moreover, these collections comprise useful information beyond the specimens *per se* (*i.e.* information written on labels). Building on the wealth of information contained in NHC, I initiated the RESCUE project (funds: ATM and Synthesys). This pilot project aims at using NHC to investigate biogeographic scenarios. It uses the geographic data reported on specimen labels to overcome a well-known limitation, the Wallacean shortfall, which refers to the lack of knowledge about the geographical distribution of species (Lomolino 2004). This shortfall hampers accurate inferences in evolution and ecology (*e.g.*, biogeographic scenario, delimitation of priority conservation areas). This ongoing project is the foundation of a larger project developed in section IV.3.

I. 3. 2. Primary biodiversity data and taxonomic bias

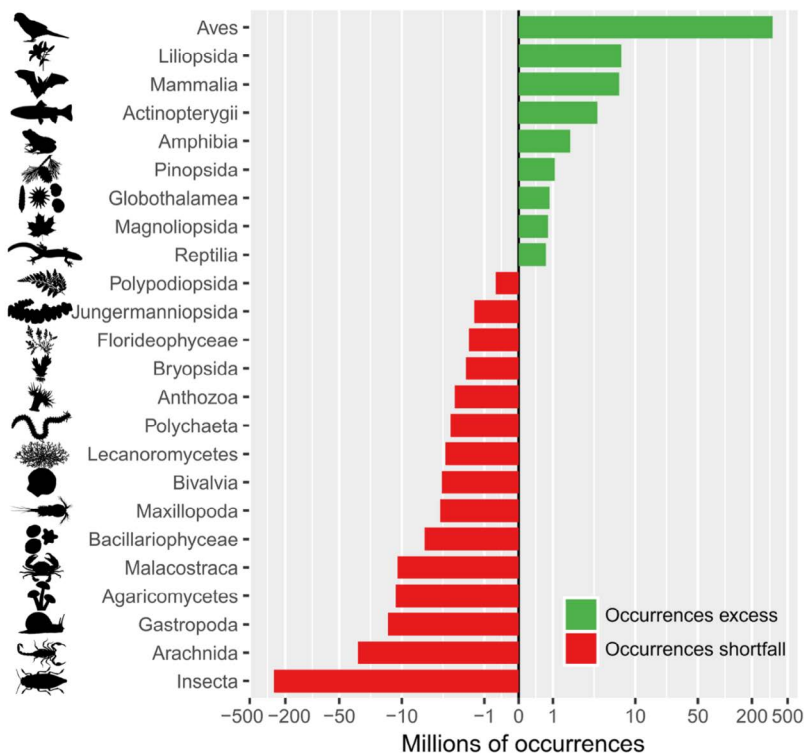


Figure 7. Taxonomic bias in biodiversity data. Green and red bars show the classes that are over- and under-represented in the GBIF mediated database compared to a 'ideal' sampling, as defined in Troudet *et al.* (2017).

The recently defended PhD thesis of Julien Troudet, about biodiversity data occurrences and biodiversity patterns, was an opportunity to engage in larger scale thoughts about taxonomic sampling in the study of biodiversity, a major concern in the current crisis of biodiversity. Using >600 million GBIF mediated data, we investigated taxonomic bias in primary biodiversity data. Taxonomic bias, although known for a long time as well as its negative consequences, is still conspicuous in biodiversity data (Figure 7). We also showed that it appears to be linked to societal preferences

rather than to research activity. We therefore call scientists to advertise more on non-charismatic species to help inverting this trend (Troudet *et al.* 2017).

In addition, we have reported that the practice of biodiversity data collating has changed recently (Troudet *et al.* submitted). More and more observations of biodiversity are performed, instead of specimens or samples collecting. One advantage of mere observations is that it is faster than capturing specimens, a quality in the current period of biodiversity crisis. But there are also disadvantages, such as the impossibility to *a posteriori* validate the taxonomic identity of an observation occurrence. Specimens are needed for obvious reasons such as validation of identification or species description, but also to maximize the research agenda of current and future studies dealing with biodiversity and phylogenetics. For instance, with a specimen, morpho-anatomic characters can be observed, which is essential for including fossils in phylogenetic analyses following, arguably, the most promising approach of age estimates, tip-datings (Pyron 2011; Ronquist *et al.* 2012).

In this light, the importance of taxonomy, fieldwork and NHC is even more striking. Taxonomists must keep advertising this role, as well as the importance of studying each and every organism and not only the most charismatic ones.

I. 3. 3. Networks and Next Generation Sequencing (NGS) – D. Evangelista current project

Character sampling is equally important to taxonomic sampling to get meaningful and robust phylogenetic hypotheses that, in turn, are used in phylogenetic test of evolutionary questions. In dictyopteran phylogenetics, only six short molecular markers are repeatedly used. We have investigated the phylogenetic signal of these markers, relying on modern phylogenetic signal measures and network analyses (Thouzé 2016; Evangelista *et al.* submitted; **Figure 8**). We have performed these analyses at two different taxonomic and temporal scales: the Blaberidae family (ca. 200 Mya) and the Dictyoptera super-order (ca. 380 Mya – Legendre *et al.* 2015b). We have compared the results and identified the phylogenetic profile of future markers that would best contribute to resolve difficult issues in tree reconstruction for these groups.

Subsequently, for the post-doctoral project of Dominic Evangelista on Blaberoidea phylogenetics (i.e. Blaberidae + Ectobiidae), we have targeted molecular markers with a supposedly adequate phylogenetic profile at this scale. We are currently working on these markers, relying on Next Generation Sequencing and more specifically on exon capture, a method that proved efficient for other taxonomic groups (*e.g.*, Bragg *et al.* 2016; Heyduk *et al.* 2016; Sass *et al.* 2016). We have targeted ca. 250 loci and the assembly stage on 93 taxa is in progress. Hopefully, this wealth of data will allow resolving unsupported or controversial nodes (Legendre *et al.* 2017).

In this chapter, I emphasized that sampling, of taxa and characters, is part of the protocol design in phylogenetics, and that it must be anticipated according to the question tested. Even though the perfect sampling is out of reach, some are better than others to answer as powerfully as possible to a specific question. In this quest of the best possible sampling, taxonomy, fieldwork and natural history collections play a pivotal role, which should be promulgated. With taxa and characters strategically targeted, one can engage in the following stage of the phylogenetic test of evolutionary scenarios: the coding step (including character delimitation).

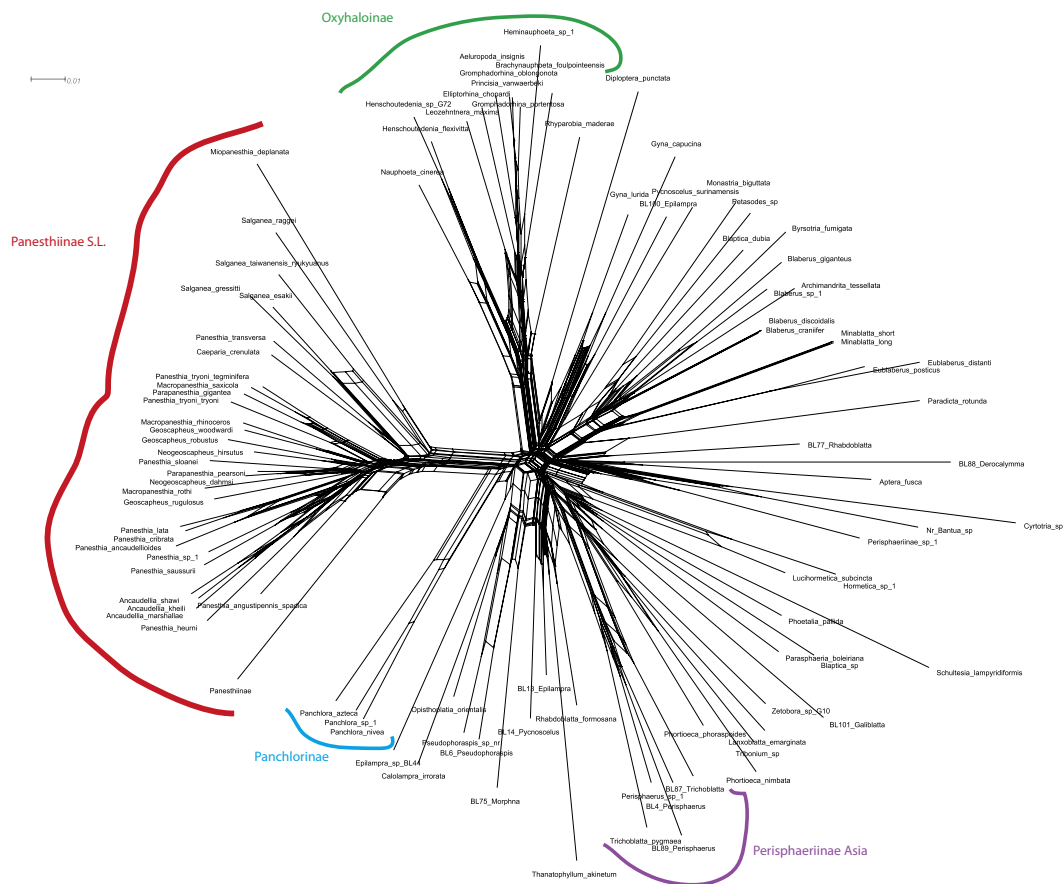


Figure 8. Split network of the 12S marker used in Blaberidae phylogenetics (Thouzé 2016). This figure illustrates conflicts existing in a phylogenetic marker.

II. CHARACTER CODING
AND PHYLOGENETIC
TEST OF ADAPTATION
IN INTEGRATIVE
APPROACHES

In phylogenetics, data gathering implies data coding, the way we try to accurately represent observations. As soon as this coding step is shaky, any subsequent step is flawed, and the whole scientific process is doomed to failure. Coding must therefore be performed with special care. To code characters for their matrix, phylogeneticists rely on homology criteria. These criteria help sorting out comparable things (putative homologous characters) from things that are not (non homologous characters), and they proved indispensable and helpful in numerous occasions. For instance, my colleagues and I explained, using homology criteria, why the stridulum (*i.e.* the song organ in Ensifera) of true crickets and tettigonids is not homologous to the stridulum of mole crickets (Desutter-Grandcolas *et al.* 2005, 2017).

Data coding has long been recognized as of fundamental importance for phylogenetic tree reconstructions and has been profusely discussed (*e.g.*, Stevens 1991; Lipscomb 1992; Wiens 1995; Simmons & Ochoterena 2000). These discussions related mainly, however, to characters included in the phylogenetic matrix, and much less often to the characters of interest: the characters involved, strictly speaking, in the evolutionary hypotheses tested (but see Deleporte 1993; de Queiroz 1996 and references cited; Grandcolas *et al.* 2011). Yet, in a tree-thinking biology paradigm where phylogenetics encompasses more and more disciplines, characters of interest are multiform. They are not always straightforwardly *integrated* in a phylogenetic test of evolutionary scenario, a process to perform ably.

Integrative approaches, studies overlapping different fields, are increasingly developed and promoted in research. In systematics, integrative taxonomy (Dayrat 2005) is trendy, even though it refers simply to the use of different sorts of characters (*e.g.*, molecules and morphology) to identify and describe species, so that the term ‘integrative’ seems usurped. But the use of phylogenies in various disciplines, from ethology to linguistics or ecology, does imply an interdisciplinarity, an integrative approach that is much more than the simple juxtaposition of two fields.

Interdisciplinarity is exciting, it can achieve more than the sum of the individual parts could do alone (Knapp *et al.* 2015), but it does not unfold without hurdles. Data from one field might not be suitable for the other field, and reciprocally (Michener & Jones 2012). As recalled above, the data used in a phylogenetic matrix or *a posteriori* reconstructed on a tree must satisfy homology criteria. Do all linguistic, behavioural or ecological data comply with this requirement? Probably not (Grandcolas *et al.* 2011). This problem is patent when one confounds categories with phylogenetic characters. Although classifying complex biological phenomenon into a limited number of discrete categories (*i.e.* the categorization process) is necessary to understand underlying biological processes, it remains a simplification of a complex reality. Categories are most often either too broad or too constraining to accurately reflect what we observe in nature (Wcislo 1997a,b; Doody *et al.* 2013; Legendre *et al.* 2015a). In other words, categories do not comply with homology criteria. This issue has been largely discussed with

regard to social categories, but is clearly not restricted to social behaviours (*e.g.*, Robillard *et al.* 2006a; Grandcolas *et al.* 2011). I illustrate below how it also applies to the phylogenetic test of putatively adaptive behaviours in frogs (Goutte *et al.* 2013, 2016).

II.1. Convergence, adaptation and character coding

II.1.1. Adaptive convergence

Phenotypic convergence occurs when similar traits evolved independently due to similar selective pressures (Wake *et al.* 2011). The notion of convergence is so tightly linked to the concept of adaptation that they have often been confused (Stayton 2015). But all authors agree that under strong environmental constraints, organisms may share similarly optimized solutions: adaptive convergence. Studying adaptive convergence enables us to understand how species adapted to their environment, at what pace they did so, and to identify ‘key’ adaptive characters (Agrawal 2017).

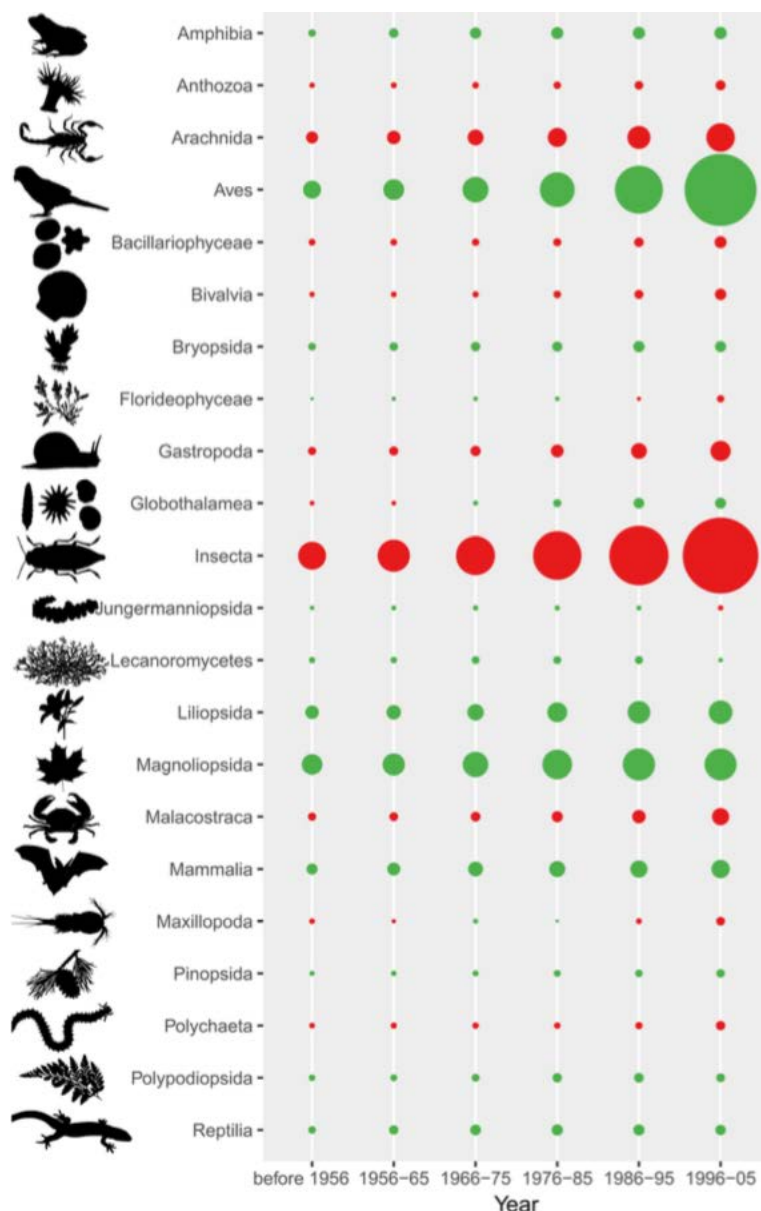


Figure 9. Evolution over time of taxonomic bias. The larger the circle, the higher the deviation from the ideal sampling as defined in Troudet *et al.* (2017). Although known for a long time, taxonomic bias is still pervasive in biodiversity studies, including about convergence evolution.

Convergent evolution is recognized as an important phenomenon in evolutionary biology but, despite decades of research, our knowledge on this phenomenon still suffers from major limitations (Stayton 2015): 1) we ignore how common convergent evolution is (Stayton 2008); 2) we do not know how convergent evolution happens, especially on the macroevolutionary adaptive landscape. Some authors have even argued that convergences cannot occur at large temporal and geographical scales (Moen *et al.* 2016); 3) Most studies were performed only on vertebrates, exemplifying a well-known taxonomic bias in ecology and evolution (Gaston & May 1992; Clark & May 2002; Troudet *et al.* 2017; **Figures 7,9**). Yet, from fundamental to applied research dealing with conservation issues, taxonomic bias is harmful because it hampers any generalization (Hortal *et al.* 2015); 4) Despite recent and fruitful developments in

evo-devo to better grasp the molecular mechanisms underlying convergent phenomena (Martin & Orgogozo 2013), the study of convergence is hindered by a lack of natural history data and of taxonomic reliability (Hortal *et al.* 2015). Without natural history data, evolutionary scenarios remain poor; without taxonomic expertise, scenarios might be spurious.

II.1.2. Coding of character and selective pressure to investigate adaptive convergence

The study of convergent characters is tightly linked to the character coding process, and thus to homology criteria. Despite several inconsistent definitions, convergence always implies two notions: similarity and independent evolution (Desutter-Grandcolas *et al.* 2005; Stayton 2015). If two similar characters – like stridulatory veins of true crickets and mole crickets – do not comply with homology criteria, then they are readily identified as convergent. If they do comply with the homology criteria, the phylogenetic congruence test (*sensu* Patterson 1982) will discriminate convergence from inherited similarity (Desutter-Grandcolas *et al.* 2005; Stayton 2015).

Convergence is a key concept in evolutionary biology because it helps, in particular, investigating adaptations to environmental constraints *s.l.* (including habitat, climate, other species, etc. – Schluter 2000). As Darwin put it: “We can clearly understand why analogical or adaptive character, although of the utmost importance to the welfare of the being, are almost valueless to the systematist. For animals, belonging to two most distinct lines of descent, may readily become *adapted to similar conditions*, and thus assume a *close external resemblance*” (Darwin 1859: 427; emphasises mine). In other words, under strong environmental constraints, organisms may share similarly optimized solutions: adaptations (Losos 2011a). Hence, convergence and adaptations are often perceived as “proofs” of the role of environmental constraints. This relation is widespread, for instance, in the literature on social systems, morphology or communication (*e.g.*, Morton 1975; Hansen 1979; Slobodchikoff 1984; Hatchwell 2009).

An adaptation can be defined as a novel character that has been shaped by natural selection for its current use (Gould & Vrba 1982; Grandcolas 2015 and references herein). Despite a long-standing focal issue, deciphering adaptation and its underlying mechanisms remain complex (Wake *et al.* 2011). On one hand, adaptations could be identified only from a combination of comparative, populational, and optimality perspectives (Olson & Arroyo-Santos 2015). But a character might have an optimized performance and be symplesiomorphic. On the other hand, convergent patterns can occur because of other reasons than adaptation to a similar environment (Wake 1991; Losos 2011a). Thus, convergence does not equate to adaptation, and reciprocally. Besides, the word ‘similar’ is too imprecise to characterize environments. Consequently, when done in a comparative angle, studying adaptation requires a proper coding of both the characters (*i.e.* the putative convergence) and the environmental constraints (*i.e.* the selective pressure).

Because my research is anchored in phylogenetic tests of evolutionary hypotheses linked to diverse fields, the characters of interest and their codings are heterogeneous. Regrettably,

Phylogenetic tests and protocol design

and maybe because they are less and less often integrated in the phylogenetic matrix – especially with the increased ease to gather molecular data, the coding of the characters of interest is sometimes overlooked. Here, I illustrate how and why the coding step must be achieved with special care, using the study of potential acoustic adaptations in a constraining environment. This problematic was tackled on Ranidae frogs living in torrents during the PhD thesis of Sandra Goutte.

II.2. Coding eco-ethological preferences beyond coarse categories: phylogenetic test of the Acoustic Adaptation Hypothesis (AAH)

Environmental pressure acts as one of the major selective forces on acoustic signals evolution. Environment affects both sound transmission and its content integrity, favouring some properties of calls in a given environment. Because a call that does not reach its intended receiver – or is too distorted to be efficiently recognizable or localizable – often reduces the fitness of the sender, the acoustic properties of a calling site are expected to constrain call evolution and might even lead to convergent calls in similar environments. This idea is referred to as the Acoustic Adaptation Hypothesis or AAH (Morton 1975; Marten & Marler 1977; Wiley & Richards 1978; Endler 1992; Ey & Fischer 2009; Weir *et al.* 2012).

The AAH has been investigated several times but studies proved inconclusive (Morton 1975; Dubois & Martens 1984; Nemeth & Brumm 2009; Peters & Peters 2010). Two main explanations have been proposed. First, it could result from shortcomings in the characterization of environmental constraints (Bosch & de la Riva 2004; Wells 2007; Ey & Fisher 2009). Calling sites are often simplified into coarse habitat categories such as “open” or “closed” habitats. This simplification does not account for the variability within those categories (Morton 1975; Zimmerman 1983; Kime *et al.* 2000; Bosh & de la Riva 2004; Vargas-Salinas & Amézquita 2014), leading to misinterpretations or biased results as shown in other broad typologies (*e.g.*, Doody *et al.* 2013; Legendre *et al.* 2014). Second, studies testing the adaptation of acoustic signals to the environment do not properly consider the role of phylogenetic history, a factor that might blur the relation between acoustic adaptation and environment (*e.g.*, Penna & Solis 1998; Kime *et al.* 2000; Bevier *et al.* 2008). I highlight these two aspects in the following sections, paying special attention on how characters are defined and coded before being integrated in the phylogenetic test of AAH.

II.2.1. Characterizing environmental constraints: what is a ‘torrent’? (Goutte *et al.* 2013 - PLoS; Goutte *et al.* 2016 - Evolution)

Context – Torrents are commonly perceived as constraining environments for acoustic communication; they are, however, inconsistently defined among ecologists. The ‘torrent’ habitat is usually characterized by variables such as slope, width and depth of a stream. But this set of variables is incomplete because both a steep, swift, narrow stream and a large tumultuous river on a flatter terrain can be understood as ‘torrents’. Moreover, the slope of a stream, a key component of torrents description, is inconsistently measured among studies and scales (Dubois & Martens 1984; Urbina-Cardona *et al.* 2006; Keller *et al.* 2009; Ernst *et al.* 2012). A torrent might then refer to different environmental constraints.

Correlatively, herpetologists inconsistently identified ‘torrent frogs’. They use ‘torrent frogs’ as a common phrasing to define an ecological unit – or guild (Simberloff & Dayan 1991) – comprising a group of anuran genera without necessarily direct phylogenetic relationships

(Lingnau & Bastos 2007; Feng & Narins 2008; Biju *et al.* 2010). The phrasing ‘torrent frogs’ designates animals that show morphological or behavioural traits thought to be adaptive to life (permanently or temporary) in fast flowing water (named torrents or not by ecologists). However, this ecological designation does not always relate to the genuine ecology of the species, as new species referred to ‘torrent frog’ genera are credited with a torrent dwelling ecology although their life history is largely unknown. The reverse can also be true, when an actual torrent dwelling frog species does not belong to one of the genera considered as torrent genera.

Then, which species shall we code as ‘torrent-dwelling’ if we want to study potential adaptations of frogs living in torrents? The coding step aims at not only conveying as accurately as possible observations but also helping to answer powerfully scientific questions. The ultimate goal here is to investigate whether frogs show acoustic adaptations to their habitats. We do not want to know what is a torrent *per se* but rather where do the species call and do they produce analogous vocalizations in similarly constraining environments (Morton 1975; Ey & Fischer 2009).

Methods – Instead of coding habitats as coarse and ill-defined categories (*e.g.*, a torrent or a forest), we recorded six ecological parameters at the exact calling sites of male frogs: depth, width, and average slope of the closest water body; air temperature; canopy coverage; ambient sound pressure level (SPL). We then contrasted two approaches using these parameters: one using directly the fine-grained characteristics; the other using categories derived from these fine-grained characteristics. These categories were inferred using a hierarchical clustering analysis that allows grouping points (here the environmental conditions of a calling frog) according to their proximity in a Multiple Factorial Analysis space.

Results and discussion – We identified three frog guilds, including one that could be called a ‘torrent’ guild, and showed that the ecological parameter ‘ambient noise’ contributes largely to the characterization of these guilds (Goutte *et al.* 2013). We also showed that some species (including *Odorrana schmackeri* – the common name for *Odorrana* being ‘torrent frogs’) had individuals belonging to different guilds. This might either illustrate a variability of choice in calling post for these species or reflect marginal behaviours, or more simply suggest that the coarse categorization process does not reflect accurately the microhabitat of calling males.

In a second step, we tested whether the level of details in habitat characterization influenced how we interpret environmental constraints. We contrasted two coding options for calling sites (‘fine scale’ vs ‘coarse type’ codings) and compared the reconstructed history of calling site preferences. We showed differences suggesting that fine scale approaches are required. First, we showed that torrents fit neither with the “open” nor with the “closed” habitat categories, but present some constraints similar to both habitats. Second, even though both coding options are based on precise measurements (the “coarse types” were defined using precise measurements), they suggest different scenarios for the frog lineage *Amolops*. This implies diverging apprais-

als on environmental constraints, and consequently on convergence and adaptation (Patterson 1988; Wake 1991). Our results illustrate that detailed habitat characterizations should always be preferred to categories to investigate the AAH (and probably much more other issues).

With a detailed coding, more than emphasizing the role of ambient noise in habitat description and identifying species that could be qualified of ‘torrent-dwelling’, we associated fine scale environmental variables to each singing frog individuals. We also showed that a fine-scale characterization of the environmental constraints is needed because it might induce different conclusions than with the less accurate categorization approach. We thus escaped from the first impediment of AAH studies: shortcomings in environmental constraints characterization. The second limitation concerns the way the phylogenetic history of species is considered, an issue addressed in the following section.

II.2.2. Acoustic Adaptation Hypothesis and ‘modern’ phylogenetic methods (Goutte et al. 2016 - Evolution; Goutte et al. 2018 – Journal of Evolutionary Biology)

Context – An adaptation to a given environment implies two important attributes: the adaptive character must be an evolutionary *novelty* and it must be somehow *associated* to the environment. The ‘novelty’ attribute can be assessed through Ancestral State Reconstructions (ASR; Grandcolas & D’Haese 2003; Glor 2010), analyses inferring when a character state evolved and whether an evolutionary novelty co-occurred with a change in the environmental context. The ‘association’ attribute can be evaluated through correlation test and GLS models. For this, because species share a phylogenetic history and are thus dependent, methods accounting for phylogenetic non-independence of species must be used; this topic was introduced ca. 30 years ago and flourished lately with numerous modern methods proposed (*e.g.*, Felsenstein 1985; Grafen 1989; Hansen 2014). ASR and modern phylogenetic comparative approaches complement one another to address adaptation hypotheses.

In the AAH context, confounding factors need to be considered such as the body mass of the calling males and the temperature because several call properties are dependent of these variables (*e.g.*, Ryan & Brenowitz 1985). To characterize potential adaptations to a torrent-dwelling life, we looked for acoustic evolutionary novelties of torrent species, while controlling for phylogenetic and physiological/morphological factors.

Methods – The Brownian motion model (Felsenstein 1985b), commonly used for analyses of trait evolution, assumes that continuous characters could diverge indefinitely towards any value, which is generally not realistic for biological characters. The Ornstein-Uhlenbeck (OU) model corresponds to a Brownian motion process model with a stabilizing selection toward an optimum, denoted θ (Hansen & Martins 1996).

For each acoustic trait of frog vocalizations, we tested a series of models of evolution: a Brownian motion process model (BM) assuming no trend or constraint (null model), an OU

model assuming a single optimum θ , and five OU models assuming two to three optima in the phylogeny. Models with multiple optima were defined according to biological hypotheses derived from the ancestral values estimation of calling site characteristics and previous hypotheses linking call features and environmental conditions (Morton 1975; Ryan & Kime 2003; Ey & Fischer 2009; Boonman & Kurniati 2011). They assume that extant taxa and ancestors belonging to the same “regime” are under the same evolutionary constraints.

We tested whether torrent-dwelling groups had optimal trait values different from those of non-torrent species, and if they all shared the same optimal trait values, or whether they exhibited different “strategies” evolving towards different optimal values. These analyses were performed while taking into account phylogenetic uncertainty and variance in parameter estimations.

Results and discussion – We reported that call spectral properties are correlated with habitat categories and ambient noise level, whereas temporal properties were not significantly correlated with habitat, noise level or canopy coverage. In other words, call spectral properties follow the predictions inferred from the AAH, but not the temporal properties (**Figure 10**). While considering body size and phylogenetic non-independence, call dominant frequency was strongly correlated with noise level, torrent-breeding species calling at higher frequencies than species calling in other habitats. Rapid species advertising in the noisy environment of fast flowing streams would thus escape noise masking with their higher pitched calls. Given that dominant frequency and noise level increased at the same evolutionary time (Goutte *et al.* 2016), this correlation is congruent with an adaptation hypothesis.

As expected from previous studies (*e.g.*, Hoskin *et al.* 2009; Gillooly & Ophir 2010), we have shown that body size and air temperature are significantly correlated with some of the vocalization characteristics investigated. We have also reported the existence of a phylogenetic signal in the residuals of half of the models tested. The presence of a phylogenetic signal within frog calls has been debated in previous studies focusing on different clades (*e.g.*, Cannatella *et al.* 1998; Tobias *et al.* 2011 *contra* Cocroft & Ryan 1995; Wollenberg *et al.* 2007; Gingras *et al.* 2013). It was also demonstrated how choices in acoustic character delimitation may alter the outcome of analyses of the phylogenetic signal (Robillard *et al.* 2006a; Goicoechea *et al.* 2010). The detection of a phylogenetic signal in frog vocalization thus appears to be group or method dependent and needs to be tested before being included in comparative analyses. Here, including phylogenetic relationships, body size and air temperature was statistically necessary in some, but not all, of the PGLS models. These results underline the importance of considering these confounding factors when studying potential adaptations in anuran vocalizations, and likely in other characters and taxa.

These mixed results demonstrate the need to consider multiple factors altogether when testing the Acoustic Adaptation Hypothesis. The task is not so much to continue testing the

AAH, but rather to assess more comprehensively the extent to which the environment has shaped signal evolution. Signals evolve as an integrated element of a communication system in a complex environment and in a historical context. Environmental constraints exist but they are not necessarily the primary factor of signal evolution. A limited hearing range, for instance, or a marked preference for a given call feature in females may overrule environmental constraints on call evolution. In addition to the factors considered here, other factors should be integrated in the future such as the roles of (inter- or intra-) sexual selection, sensory and physiological limitations, and predation or heterospecific acoustic competition.

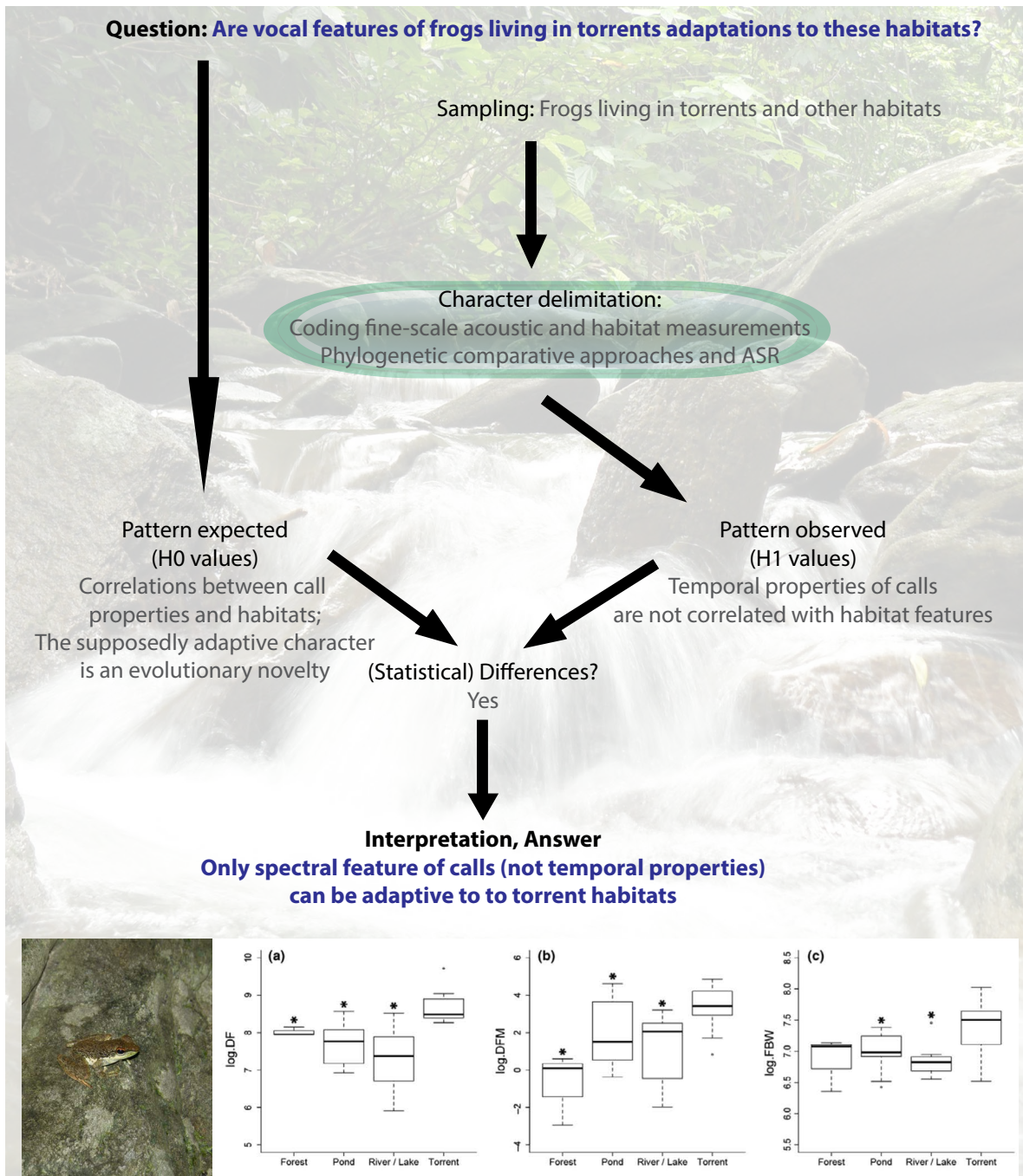


Figure 10. Phylogenetic design illustrating the importance of character delimitation when testing for the Acoustic Adaptation Hypothesis in torrent frogs (details in Goutte *et al.* 2016, 2018). Background: a fast-flowing stream in Philippines.

II. 3. More on coding: anticipating future studies

I have underlined the importance of the coding step in phylogenetic tests of evolutionary scenarios, a step that must be in mind at the very beginning of a given study and that must be conducted with care and details. This may sound obvious but it is not always carried out this way, especially at large taxonomic scale because obtaining detailed data for numerous taxa is very costly. Better coding becomes sometimes possible only due to technical advances so that a fine-scale coding was impossible earlier, but it is not always the case. The real challenge, then, is to be able to do it properly in the earliest stage of any investigation, which would allow future studies to build on it instead of replicating it but in a better way. To allow studies to build on each other and speed up researches, data sharing must also be encouraged, a direction in progress but still facing hurdles (Reichman *et al.* 2011; Duke & Porter 2013).

I have developed a project on ecomorphology and convergence evolution in Blaberidae cockroaches (more details in section IV.2.) that comes within this scope. This project builds on previous works allowing advances in our understanding of Blaberidae phylogenetics and behaviour (Legendre *et al.* 2015a, 2017) but still requiring significant advances in the morphology part. Previous works in taxonomy might help, but they are not sufficient because they did not necessarily emphasize on characters pertinent for this project.

In this project, I aimed at i) acquiring morphological data as precisely as possible and ii) making them available for future studies. For the first aim, I will rely on recent advances in ontology. Despite a large quantity of data available about morphology in the literature, most of it is useless in their actual form. Morphological data easily interpreted and compared across organisms is a current bottleneck that ontology aims at suppressing. Ontology helps reducing language discrepancies and favour future works. It can then be used as soon as the descriptive task in taxonomy (Yoder *et al.* 2010; Deans *et al.* 2012, 2015). For the second aim, making data available, many progresses have been done lately with data portal such as Dryad for instance and I will rely on them. In the same line of reasoning, I have launched side-projects where data sharing is of prime importance, from Xper identification databases (with a M1 student and on my own) to institutional databases (as part of curation task – Jacim MNHN) or catalogues (Caesar *et al.* 2015; Depraetere *et al.* in prep; **Figure 11**).

The screenshot displays the e-ReColNat project interface for the digitization of type specimens in Dictyoptera. The main content area shows a digital image of a specimen, identified as *Corydidarum magnifica* (Shelford, 1907). Below the image, there is a section titled 'HISTORIQUE DE DÉTERMINATION' which lists the specimen's history, including its identification by Shelford R. in 1907. The interface also includes a 'TAXONOMIE' section with a hierarchical classification: Embranchement: Arthropoda, Classe: Insecta, Ordre: Blattodea, Famille: Blaberidae, Genre: *Corydidarum*, Espèce: *Corydidarum magnifica*, and Nom: *Corydidarum magnifica* (Shelford, 1907). Additionally, there is an 'ORIGINE' section providing details about the specimen's origin, including the country (Vietnam), region (Tonkin), locality (Tuyen-Quan), collector (Weiss A.), and collection date (1901-06-01/1901-10-01).

Figure 11. Digitization of type specimens in Dictyoptera through the e-ReColNat project (<https://science.mnhn.fr>).

III. NEW METHODS
FOR INTERDISCIPLINARY
STUDIES IN A TREE-
THINKING PARADIGM

Integrative approaches, which are in vogue (Wake 2008), have been named differently according to the authors, their criteria and their definition. They can be qualified of multi-, inter- or trans-disciplinary. This categorization actually hides a whole continuum wherein the degree of integration is one important parameter to differentiate them and increases from multi- to trans-disciplinarity. These integrative approaches must be clearly differentiated to avoid mixing different approaches, at the risk of losing their interests and becoming a ‘trendy catchall’ word (Tress *et al.* 2005).

Regardless of the definition, integrative approaches are more than the mere juxtaposition of disciplines. They have a synergetic effect. Because of this quality, transdisciplinary fields of research were given birth: socioecology, ecomorphology, evo-devo; and now with all the progresses made in genomics, new fields of study emerge such as environmental genomics, phylogenomics and metagenomics to name a few (Losos *et al.* 2013; Wake 2008). These fields do not simply sum the knowledge of their constituting fields but integrate this knowledge in a new direction, giving birth to new methods, new theories and concepts.

New issues, both conceptual and practical, emerge in integrative approaches (Michener & Jones 2012; Losos *et al.* 2013) and they are even more challenging and rewarding than the degree of integration is high. This is also true in a tree-thinking paradigm, when phylogenetics merge with other disciplines. Real integrative approaches do not simply use a phylogenetic tree from the literature. This practice is fraught with danger, especially when tree users are not familiar enough with the tenant of phylogenetics. Incidentally, some authors have proposed, to limit this pitfall, guides to perform comparative analyses in ethology, ecology or physiology for instance (Rezende & Diniz-Filho 2012; Roquet *et al.* 2013; Pozzi *et al.* 2014). Instead, these approaches *integrate* the phylogenetic step *sensu lato* (i.e. from sampling to coding as well as both tree and post-tree reconstruction methods) within the complete experimental design. Then, new methods are often required because they are not always readily available to fit with the principles of the merged disciplines (Wickson *et al.* 2006).

I illustrate below the integrative nature of my research, using two case studies on the evolution of social behaviour in Dictyoptera. They merge either ethological or developmental data with phylogenetics, and both required methodological developments.

III.1. Phylogeny and ethology

III.1.1 A hectic history

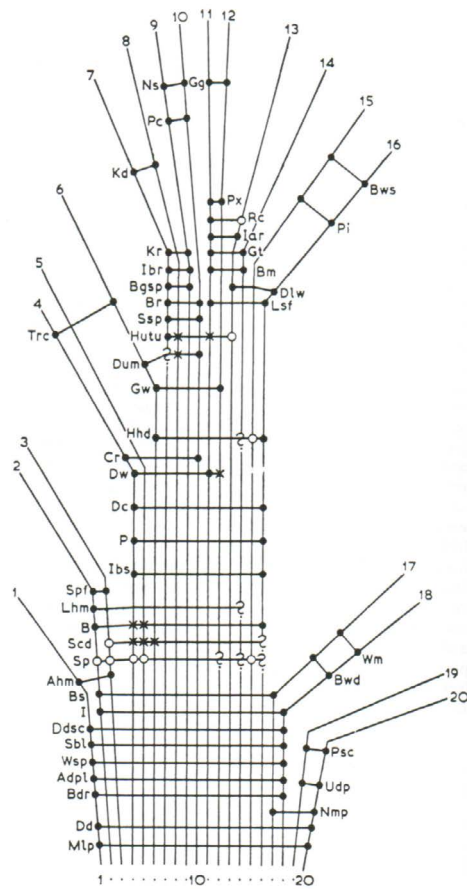


Figure 12. Comparative studies of motor patterns in Anatidae (Lorenz 1951). Species are represented by numbers while characters (*i.e.* motor patterns) are represented by abbreviations. Horizontal lines represent characters common to different species.

McLennan *et al.* 1988; Greene 1994; Proctor 1996; Ryan 1996; Stuart *et al.* 2002; Robillard *et al.* 2006b; Ord & Martins 2004; Rendall & Di Fiore 2007; Legendre *et al.* 2008a; Cap 2009; Pickett 2010; Deleporte & Grandcolas 2010; Nattier *et al.* 2011).

The challenge at hand now is not to answer whether behavioural data can be used in a phylogenetic context (yes, they can) or how homoplastic behavioural characters are (like other characters, it depends on the taxonomic scale, on the taxa, on the behaviours, etc.), but rather how behavioural data must be delimited to fit adequately within a phylogenetic study. Despite multiple warnings against characters too broadly defined (Mickey & Weller 1990; Proctor 1996; Luckow & Bruneau 1997; Weislo 1997a,b; Grandcolas *et al.* 2001; Grandcolas & D’Haese 2002, 2004; Noll 2002; Desutter-Grandcolas & Robillard 2003; Pellens *et al.* 2007;

The study of the evolution of behaviour has been traditionally linked to Systematics (*e.g.*, Ducke 1914; Petrunkevitch 1926; Baerends 1958; Hinde & Tinbergen 1958; Mayr 1958). Lorenz (1951) performed a comparative ethological study of Anatidae birds and produced a famous figure (**Figure 12**) perceived as an early cladistic study, twenty years before Hennig (1966). Well before Lorenz, as early as the beginning of the 20th century, references to what would now be called behavioural homology were also published (Heinroth 1910; Whitman 1898). The context for the study of evolution of behaviour was thus favourable.

At the beginning of the second part of the 20th century, however, the situation reversed. The paper of Atz (1970) illustrated this change, Atz concluding “the application of the idea of homology to behaviour is operationally unsound and fraught with danger”. This period was qualified as an eclipse of history in ethology (Brooks & McLennan 1991) because all previous works were disregarded. Fortunately, this eclipse stopped, notably with the work of Wenzel (1992) that re-stated that behaviour, like any other phenotypic character, can be studied in a phylogenetic framework, as soon as homology criteria are critically considered. This view seems now well-admitted (de Queiroz & Wimberger 1993;

Cap *et al.* 2008; Goicoechea *et al.* 2010), very few studies addressed this problem and broad classes remained used.

Today, studies in ethology are numerous but those inserting behavioural observations in a phylogenetic context remain too rare. Price *et al.* (2011) urge behavioural journals and authors to use more phylogenies. Several reasons might be invoked to explain this lack (from topics to impact factor and ‘traditions’) but one reason might also be the lack of ‘transversality’ between disciplines (here ethology and phylogeny) because of a lack of methods.

III.1.2. Phylogenetic test of the evolution of sociality in cockroaches (*Blaberidae*) using behavioural sequences (Legendre *et al.* 2014 – *Biological Journal of the Linnean Society*)

Context – The evolution of behaviour is a long-standing theme of research. It is known as the 4th question of Tinbergen (1963) but it has been of interest much before. Comparative and phylogenetic studies are needed to investigate this large problematic and to answer general questions such as why are some species solitary while close relatives are social, or how did eusociality evolve?

Answering these long-standing questions requires analysing behavioural data in a phylogenetic context. At first, isolated and stereotyped acts were *a posteriori* reconstructed on phylogenies, but this method has limitations. Two main problems exist and might induce non-optimal or, worse, misleading interpretations on behaviour evolution. First, most behavioural acts are not stereotyped. How can we expect better apprehending the evolution of behaviour in its wholeness if we ignore most behavioural interactions? Second, behavioural acts are not expressed in isolation but are context-dependent. Context-dependence is a common issue for ethologists (*cf.* character displacement) but it is neglected or only implicitly dealt with when it comes to phylogenetics.

With these limitations in mind, advances should be proposed and must satisfy premises of both disciplines (*i.e.* ethology and phylogeny) to allow relevant analyses of behaviour evolution using phylogenies. Applied to cockroaches, this process enabled us investigating behavioural changes associated to changes in social systems. For instance, the shifts from gregariousness to solitariness or subsociality imply the loss or gain of key features (‘tolerance to conspecifics’ and ‘parental care’, respectively) and related behaviours (Wilson 1971). In this context, we would expect either numerous behavioural changes concomitant to these shifts in social systems or at least a few but highly significant behavioural changes in species interactions. Moreover, given that it is often claimed that environmental conditions strongly influence the evolution of social systems (Jarman 1974; Slobodchikoff 1984; Gautier *et al.* 1988; Slobodchikoff & Shields 1988; Velicer *et al.* 1998; Foley & Gamble 2009; Hatchwell 2009; Kaplan *et al.* 2009), we also tracked behavioural changes with regard to habitats. In this ‘habitat’ hypothesis, major behavioural changes would be expected when a shift in habitat occurs.

Methods – Instead of working on isolated stereotyped acts, we proposed a method working on successive acts in a social interaction context (*i.e.* not stereotyped). We named it the successive event-pairing method (Legendre *et al.* 2008a), with reference to the event-pairing method developed for ontogenetic data (Smith 1997; Velhagen 1997 – see section III.2.1). The successive event-pairing method considers successive behavioural acts and so is context-dependent, satisfying a condition of studies in ethology. In addition, it allows to better following homology criteria, satisfying a condition of studies in phylogenetics. After defining the method and using it on an illustrative taxonomic sample, we used it on a larger sample to investigate the evolution of social behaviour in blaberid cockroaches.

Results and discussion – Even applied to a larger taxonomic sample, the methods remain operational and efficient. Non-stereotyped behavioural data coded with this method bring a substantial phylogenetic support to tree reconstruction and this type of data is not found more homoplastic than traditional characters (*i.e.* morphology and molecules).

More interestingly, we brought new insights into the evolution of social behaviour in these insects.

First, the solitary species (*Thanatophyllum akinetum* Grandcolas, 1991) does not have a very peculiar behavioural repertoire. It does not exhibit more aggressive behaviours and does not have more behavioural autapomorphies than expected by chance (**Figure 13**). Therefore, *T. akinetum* has not evolved solitary habits by deeply changing its behaviour. A closer look at the behavioural sequences of this species revealed that individuals do not refuse interactions, but they do not look for them either. Thus, solitariness would be explained by a simple lack of intraspecific attraction, except for reproduction purposes. In the field, individuals disperse away immediately after hatching so that conspecific interactions are rare, as already suggested by a 2-month field study (Grandcolas 1993). Given such dispersal habits, behavioural acts favouring social interactions are probably not expressed in the field and hence would not be submitted to strong selection. In other words, they cannot be counter-selected, if we consider that the cost of their cognitive maintenance is insignificant. Such evolution of solitariness would fit the notion of phylogenetic inertia because solitariness did not come with numerous or outstanding behavioural changes.

Second, the subsocial species *Parasphaeria boleiriana* Grandcolas & Pellens, 2002 is behaviourally the most autapomorphic of all species studied. The occurrence of such a high number of autapomorphies fits a model of evolution where a change in social system comes with numerous changes in social interactions. These behavioural changes could also result from using a very peculiar habitat (galleries in dead wood) because it is the only wood-eating and wood-living species behaviourally studied so far in this group.

A careful integration of behavioural data in phylogenetics allowed us investigating the

evolution of social systems with regard to phylogenetic history and habitats. These two factors remind two of the three main categories of factors emphasized by Gould in its aptive triangle derived from Seilacher's work (Seilacher 1970; Gould 2002): history and ecology. The third apex of the aptive triangle refers to structures. Indeed morphology is also an important component that must be analysed in depth, has suggested earlier (Legendre *et al.* 2015a; see section IV.2. for future directions).

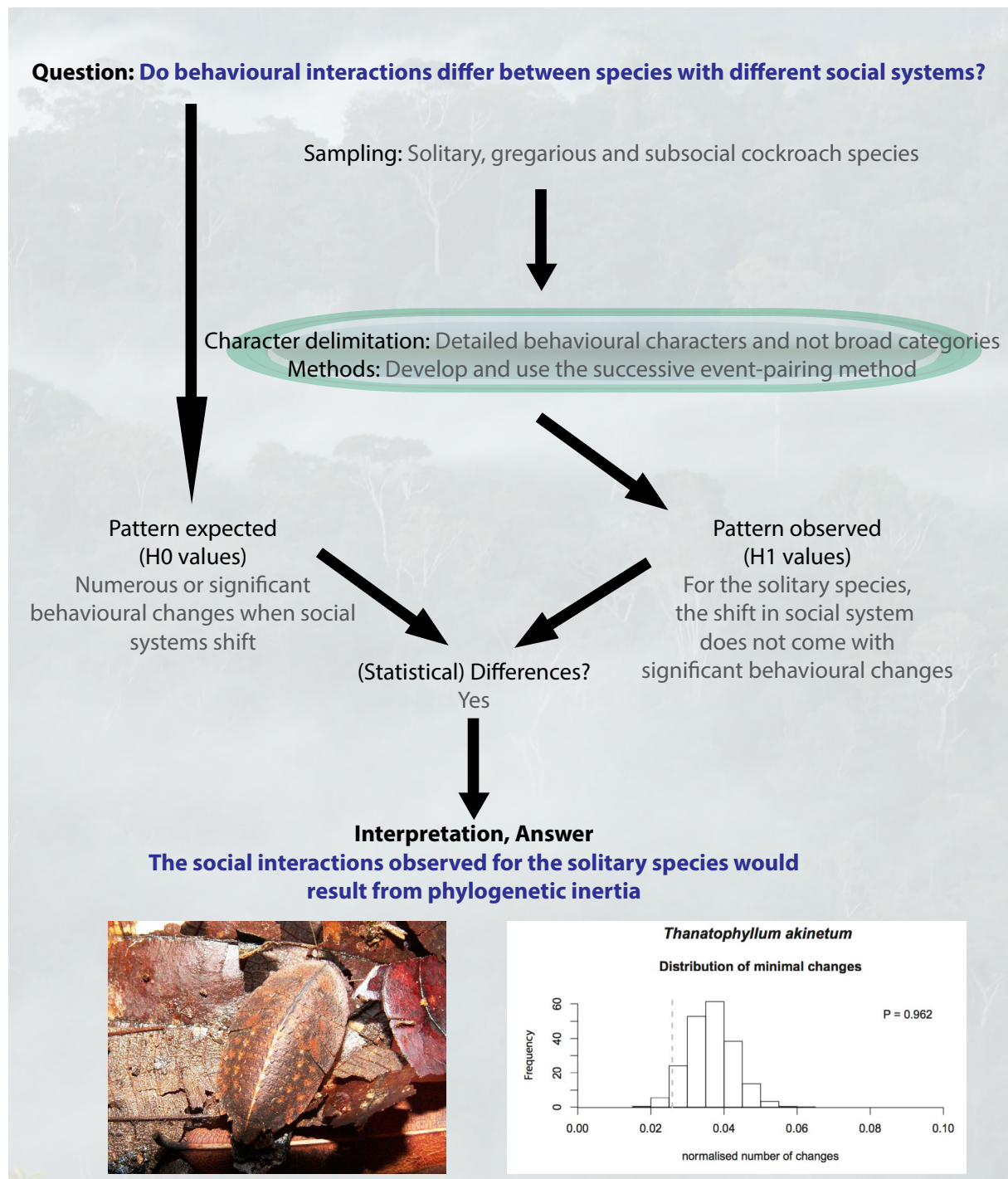


Figure 13. Phylogenetic design highlighting the development of a new method and the care in character delimitation to investigate behaviour evolution in Blaberidae cockroaches. The picture shows a female of *Thanatophyllum akinetum* collected in a French Guianan forest (background).

III.2. Phylogeny and development

III.2.1. History and methods

Well before “Ontogeny and phylogeny”, a hallmark work of S.J. Gould (1977), developmental observations were linked to evolution or later revised in the light of the evolutionary theory as the famous Haeckel’s biogenetic law (1866 in Gould 2002). Later, works on allometry or heterochrony (*e.g.*, D’Arcy Thompson 1917; De Beer 1930) were provided and have stimulated numerous research programs. Today, the field of evo-devo is vivid and illustrates the strong link between development and phylogeny.

One of the challenges in using developmental sequences in a phylogenetic framework has been the lack of computational tools to adequately deal with the data. Recent advances have resulted in more powerful phylogenetic tools, developed largely for the analysis of DNA sequence data (Thompson *et al.* 1994; Wheeler 1996; Edgar 2004) and developmental or behavioural sequences (Smith 1997; Velhagen 1997; Abbott & Tsay 2000; Bininda-Emonds *et al.* 2002; Jeffery *et al.* 2002, 2005; Hay *et al.* 2004; Schulmeister & Wheeler 2004; Robillard *et al.* 2006b; Legendre *et al.* 2008a). Smith (1997) and Velhagen (1997) concomitantly proposed an “event-pairing” method to compare developmental sequences. But this method, which partitions developmental sequences in paired events, suffers from strong methodological inconsistencies and can lead to erroneous results when it comes to phylogenetic tree reconstruction or optimization of hypothetical ancestors (Schulmeister & Wheeler 2004). Schulmeister & Wheeler (2004) showed that entire developmental sequences could be used instead of paired events and proposed to analyse them as a single character (*i.e.* one developmental sequence is treated as a single multistate character in a search-based optimization procedure – Wheeler 2003). This method necessitates, however, a pool of predetermined developmental sequences to reconstruct hypothetical ancestral sequences, and thus requires untestable assumptions. Hence, no adequate tool was available, which is why we proposed a new method, inspired from the use of nucleotide sequences in phylogenetics (Legendre *et al.* 2013).

III.2.2. Phylogenetic test of the evolution of sterile castes in termites using post-embryonic sequences (Legendre *et al.* 2013 – *Evolution and Development*)

Context – The evolution of complex and integrated social systems, Darwin’s “special difficulty” (Darwin 1859), triggered many concepts from inclusive fitness to altruism or group-level selection (*e.g.*, Hamilton 1964; Wilson 1971; Okasha 2006; Jablonski 2008), but it still challenges modern evolutionary biologists (*e.g.*, Nowak *et al.* 2010; Nonacs 2011; Rousset & Lion 2011; Johnstone *et al.* 2012). How could sterile individuals, which are incapable of reproducing, have possibly evolved? How could they evolve independently in different lineages (Duffy & Macdonald 2010)? How does one explain the evolution of sociality in diploid organisms (Costa 2006), given that the relatedness component of Hamilton’s hypothesis does not play as strong a role as in haplodiploid organisms? Even though several studies have conceptually addressed the

evolutionary origin of sterile caste in insects (*e.g.*, Bartz 1979; Roisin 1994; Boomsma 2009; see Howard & Thorne 2011 for a recent review), the origin of these castes is not yet clear.

The evolution of eusociality, studied in a phylogenetic framework, could bring substantial insights, but progresses have been hampered by one main reason linked to character delimitation: Like for behaviour, broad social categories, instead of fine-grained characters, were used (see section II.2). In other words, coarsely defined castes were used instead of developmental trajectories. Yet, considering that “true” workers in Mastotermitidae – which do not develop before the seventh instar – may not be homologous to “true” workers in Termitidae – which can develop as soon as the third instar – seems relevant (see also Bourguignon *et al.* 2012 about worker caste definition in *Psammotermes hybostoma* Desneux, 1902). Similarly, the caste ‘pseudergates’ raises questions. As advocated recently (Korb & Hartfelder 2008; Roisin & Korb 2011), the original definition of pseudergate is impractical and does not accurately characterize the instars of *Prorethra*, *Termitogeton* or *Glossotermes* species, so these authors proposed a broader definition, pseudergates *sensu lato*, which includes both larval and nymphal instars. However, combining larvae and nymphs into a single category may also result in non-homologous states.

In termites, while the developmental pathways leading to sterile castes are well known in many species, these pathways have yet to be thoroughly analysed from a phylogenetic standpoint (see Korb & Hartfelder 2008; Nalepa 2010 for attempts in this direction). One major hurdle was the inadequate methods available. We thus proposed a new method (Legendre *et al.* 2013) emphasizing the analogy between developmental sequences and molecular sequences.

Methods – Our method rests on the analogy between developmental sequences and molecular sequences and thus satisfies the prerequisites for using developmental data in a phylogenetic context. Just as DNA sequences are successions of nucleotides whose positional homology relative to another sequence is uncertain, post-embryonic developmental sequences are successions of instars or stages whose homology to stages in other species is uncertain. Using static and dynamic alignment tools classically used for nucleotide sequences was, however, not possible straightforwardly. It was especially true in a dynamic homology context so that we engaged in collaboration with developers of the software POY, implementing dynamic homology for more than four state characters. Indeed, we identified up to eight stages (and so eight character states) in termites developmental sequences: egg, larva, nymph, pre-soldier, soldier, alate, pseudergates and “true” workers.

In addition, to better understand sterile caste evolution – and so of altruism evolution – this method allows investigating the evolution of developmental sequences and of polymorphism, not only of developmental stages. We used existing reconciliation methods, used for host/parasite, gene/organism or organism/area associations, but developed the conceptual framework needed to interpret organism/ontogeny association.

To get a phylogenetic reference, we used the sample from one of our previous work (Legendre *et al.* 2008), whose taxonomic representativeness has been assessed independently (Plazzi *et al.* 2010). However, for the question at hand, it was important to add a key taxon in terms of caste and developmental pathway evolution, *viz.* *Glossotermes oculatus* Emerson, 1950.

Results and discussion – By analysing entire developmental sequences instead of mapping binary characters, we developed a more detailed pattern of caste evolution than in previous studies. Whereas it was impossible with binary characters to reconstruct an unambiguous scenario for the evolution of the “true” worker caste (Thompson *et al.* 2000, 2004; Grandcolas & D’Haese 2002, 2004; Inward *et al.* 2007b), we showed with this new approach that “true” workers, *i.e.* individuals belonging to a very specialized caste involving altruism, evolved multiple times in termites (from two to four independent origins). For pseudergates, results are less straightforward as both a single origin and multiple origins are still postulated according to the analyses. The latter hypothesis with convergent origins is congruent with Parmentier & Roisin’s work (2003), which emphasized the developmental differences between *Termitogeton planus* (Haviland, 1898) on one hand, and Kalotermitidae and Termopsidae on the other hand. These differences would be explained by different evolutionary origins and through different developmental processes, a conclusion that would have been impossible to reach if binary characters had been used.

Additionally, reconciliation analyses suggest that the developmental data set has a strong phylogenetic signal and that developmental plasticity is not an ancestral feature to termites but evolved convergently in different lineages (*e.g.*, Kalotermitidae, *Prorhinotermes*). Thus, our results mostly confirm Noirot’s hypothesis (1985a,b – multiple origins of the “true” worker caste, ancestral high flexibility and linear-like pathway), with multiple origins of a “true” worker caste in termites, which would have evolved from an ancestor with a weakly flexible and linear developmental pathway. Our results about ancestral flexibility are, however, more congruent with Watson & Sewell’s hypothesis (1985 – a single origin, ancestral medium flexibility and bifurcated pathway; **Figure 14**). High flexibility would have been acquired convergently mostly in Kalotermitidae, Termopsidae, and (*Termitogeton* + *Serritermitidae* + *Prorhinotermes*), three lineages in which species do not build “true” nests but live within their relatively ephemeral food source, the dead wood. Once their food is almost consumed, some individuals (alates) need to disperse to ensure colony survival, selecting therefore for a high flexibility and a late timing of differentiation.

While we are still puzzled by the underlying processes responsible for sterile caste evolution in diploid organisms under natural selection, the phylogenetic analysis of developmental sequences reveals that such a Darwinian paradox occurred repeatedly in termites. These results will help identify new model termite species for evo-devo studies, which is pivotal for any major advances in the field (Jenner & Wills 2007). For instance, *Hodotermes mossambicus* (Ha-

gen, 1853), with its convergent “true” workers origin and timing of differentiation, appears as an adequate taxon to compare with Termitidae species. Similarly, *Prorhinotermes canalifrons* (Sjöstedt, 1904) should be a valuable model species to start with on pseudergate evolution and to compare to Kalotermitidae species. In addition, we show here that obligatory sterile castes do not appear necessarily as an evolutionary dead-end, with transitions from “true” worker to pseudergate, contradicting Cope’s rule of specialization (1896). These results reveal that caste and developmental pathway evolution in termites is versatile.

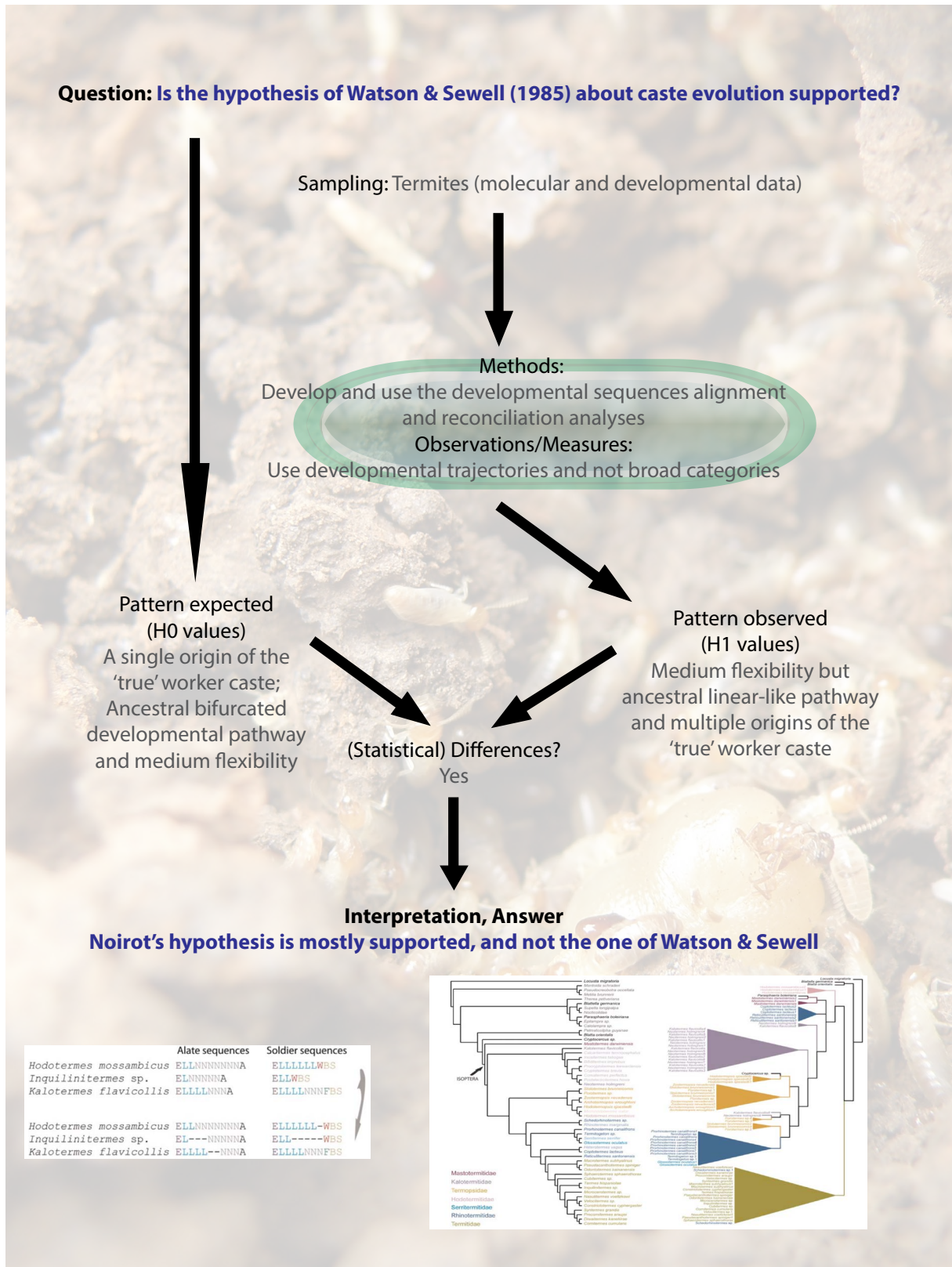


Figure 14. Phylogenetic design highlighting the development of a new method and the use of developmental sequences to investigate caste evolution in termites (details in Legendre *et al.* 2013). Background: a colony unearthed in New-Caledonia.

III. 3. More on methods in a multi-disciplinary context: the strength of collaborations

I underlined the need for methodological improvements and underlined that it is especially significant in multi-disciplinary studies. Since the beginning of my research activity, I have been engaged in integrative approaches and started to propose methodological novelties. My carrier as associate professor in ‘integrative studies in systematics’ and mentor of PhD students on different organisms and themes, has led me to increase this integrative approach of research.

By definition, integrative or multi-disciplinary approaches imply knowledge and skills from different fields. All these skills can hardly been mastered by a single person, or at least not so rapidly and so efficiently than when shared between different persons. This is why collaborative work is so essential and so rewarding. I realized it at the beginning of my career, when, during my PhD project, I interacted with a bioinformatician about dynamic optimization of characters with more than four states. I am grateful for this opportunity that contributed to make me aware of the importance of cross-field discussions early in my career.

I have benefited from collaborators, being either close or international colleagues or students in different research areas from ethology or ecology to bioinformatics and modern comparative and phylogenetic methods. The latter are particularly powerful and constitute an important research and teaching direction. I have learned on these methods mainly from mentoring students (PhD and M2 students) and I want to increase this knowledge for my own sake and for colleagues and students. In this regard, two directions are considered: an informal transversal axis within the UMR 7205 ISYEB and a course in M2 EBE mention SEP. I think that both tree-thinking and modern phylogenetic and comparative methods should be taught as early as possible in university courses in systematics and evolution.

IV. PERSPECTIVES

My research highlighted that special care is needed when a phylogenetic test of evolutionary scenario is conducted and that it must be considered from the very beginning of a project. One can be satisfied with ‘merely’ producing phylogenetic trees or using trees produced elsewhere but, most of the time, it does not allow conducting phylogenetic tests as powerfully as desired. It is even more striking in multi-disciplinary approaches, when prerequisites of the different disciplines do not perfectly match.

In the next few years, I plan to pursue improving the experimental design of phylogenetic tests of evolutionary scenarios, while extending the research questions addressed to embrace an integrative view of the evolution of organisms. But, because modern phylogenetic comparative methods (MPCM) multiply rapidly, and because I value confronting ideas, parts of my projects will require strengthening and developing collaborations, as well as increasing students mentoring.

I will develop two research directions, one with a strong ecomorphological dimension, the other included in a geographic context. I will tackle two broad evolutionary questions: 1) how species adapt to their environment; 2) what is the tempo of diversification of New Caledonian biota? These projects rely on some perspectives mentioned earlier, related to morphology coding and collaboration, or natural history collections for instance, respectively. In addition, because an evolutionary test relying on phylogenetic trees is worth the quality of the phylogenetic pattern, the first task will be to strengthen the phylogenetic hypotheses in each case.

IV.1. Sampling, taxonomy and natural history collections

I will rely on two main directions to improve the reconstructed phylogenetic trees. First, I will continue developing new-targeted molecular markers, a task recently initiated through the works of one Master 2 student and one post-doctoral fellow (NSF grant). With signal analyses and Next Generation Sequencing technologies, especially exon capture, we will increase spectacularly the number of informative characters used to reconstruct trees and produce more reliable phylogenetic hypotheses. Second, I will develop collaborations around fossil taxa. In addition to new morphological characters to be analysed in a phylogenetic context, fossils are the best option to calibrate trees and obtain chronograms. For this, I will put tip-dating strategies in practice, instead of node-dating. Morphological characters will be critically needed in the future (*e.g.*, Jenner 2004; Wiens 2004; Smith & Turner 2005; Yassin 2013; Pyron 2015; Wanninger 2015; Wipfler *et al.* 2016) and it is now time for me to engage in this process and benefit from the experience of my teammates.

In complement, to improve taxonomic coverage and limit taxonomic bias, two recurrent problems in the study of biodiversity, I will reinforce the link between natural history collections and research issues. We sit on an exceptional amount of data that remains underexploited despite the great advances it can produce. I expect two major outcomes, the first one being the possibility to use MPCM more robustly as they have been proved sensitive to taxonomic sampling. The second one is an increase in taxonomic activity, which is not as high as I would like but I am in the right team to be galvanized about it. This taxonomic activity will continue to be nurtured by fieldwork, which is also an endless opportunity to learn more about organisms, observe new behaviours, discover habitats and so on. As Losos *et al.* (2013) put it, “the importance of natural history data cannot be overemphasized”.

Thus, taxonomy, fieldwork and natural history collections are activities transversal to my research and will keep nurturing ongoing and future projects. In these projects, data sharing occupies a growing place and I hope it will feed other projects I am involved with or not.

IV.2. How species adapt to their environment?

While global changes are affecting biodiversity heavily, we still suffer from a lack of knowledge about how species adapt to their environment and diversify. A better understanding of the mechanisms behind species adaptation and diversification is therefore pivotal. Important insights can be gained from the study of phenotypic convergence, when similar traits evolved independently due to similar selective pressures.

The notion of convergence is so tightly linked to the concept of adaptation that they have often been confused. But all authors agree that under strong environmental constraints, organisms may share similarly optimized solutions: adaptive convergence. Studying adaptive con-

vergence enables us to understand how species adapt to their environment, at what pace they do so, and to identify ‘key’ adaptive characters.

Combining phylogenetic models of adaptive evolution, diversification models and morphology, I aim at testing whether i) similar microhabitats have driven the evolution of similar phenotypes and ii) specialized ‘key’ phenotypic innovations were related to changes in speciation/extinction rates. For the latter, I will capitalize on a recent collaboration in which we investigated the role of eusociality as a key character supporting species diversification in Dictyoptera (Legendre & Condamine in press; [Figure 15](#)). This project, which involves new collaborators, has been submitted to the Agence Nationale de la Recherche.

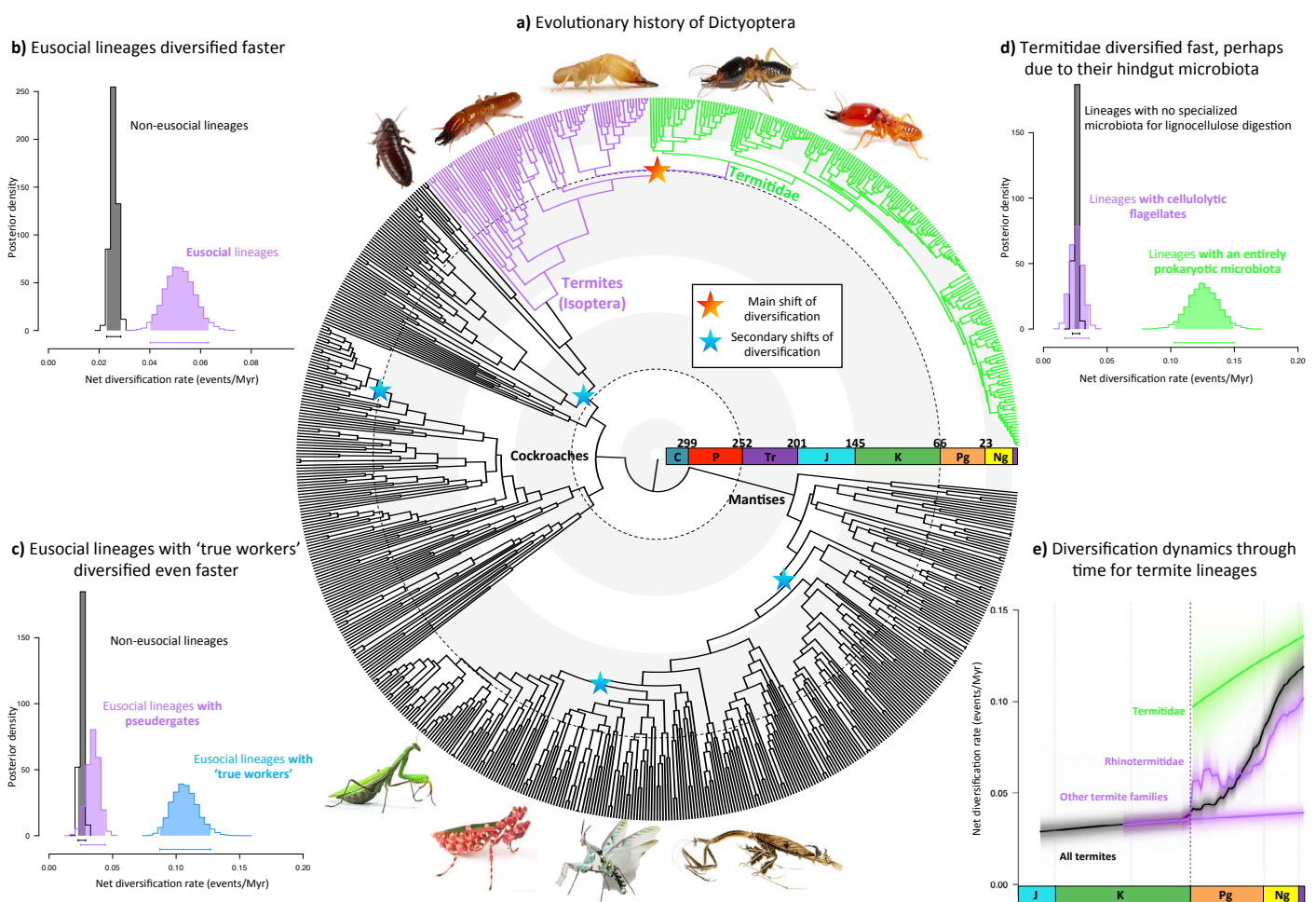


Figure 15. Diversification and eusociality in termites. A set of analyses suggests that eusociality acted as a key innovation that triggered termite diversification. Details in Legendre & Condamine (in press).

IV.3. Origin and diversification of organisms in a biodiversity hotspot: New Caledonia

Biodiversity hotspots have been defined as areas with exceptional concentrations of endemic and threatened species (Myers 2000; Bellard *et al.* 2014). In these regions, the study of biodiversity is particularly urgent if one wants to understand its composition, its origin and the services it provides to humans.

New Caledonia is a tropical hotspot of biodiversity with high rates of regional and local endemism (Caesar *et al.* 2017; **Figure 16**). The origin of this endemism has been traditionally attributed to the Gondwanan origin of the territory. A vicariant origin of the New Caledonian biota is however in contradiction with the general submersion of the territory 37 Myr ago, after the breakup of Gondwana.



Figure 16. Specimens of *Angustonicus* Grandcolas, 1997 (left) and *Pellucidonicus* Grandcolas, 1997 (right), two genera endemic of New Caledonia.

Lately, most studies found that, for diverse groups, New Caledonian biota originated after the general submersion of the island, thus favouring dispersal events (Nattier *et al.* 2017). However, studies too often focused on relatively recent clades, whereas concentrating on old clades would be more profitable. I therefore plan to use the cockroach family Blattidae, a >150 Myr old clade, to investigate the origin of New Caledonian biodiversity and its tempo of diversification.

Besides, because we lack knowledge on geographical distribution for most species (what has been called the Wallacean shortfall; Lomolino 2004), biogeographic scenarios are often incomplete or misleading. Natural History Collections (NHC) can help reducing the Wallacean shortfall though, and I plan using them on Blattidae to refine species distributions that will then be used in biogeographic studies. Indeed, NHC comprise useful information beyond the specimens *per se* (*i.e.* information written on labels). Building on the wealth of information contained in NHC, I initiated the RESCUE project (funds: Action Transversale du Museum and Synthesis). The RESCUE project aims at using NHC to investigate biogeographic scenarios. It uses

Phylogenetic tests and protocol design

the geographic data reported on specimen labels to overcome the current lack of knowledge about the geographical distribution of species. This shortfall prevents from performing accurate inferences in evolution and ecology (*e.g.*, biogeographic scenario, delimitation of priority conservation areas). Ultimately, this project needs a phylogenetic hypothesis to reconstruct the most likely biogeographic scenario for species whose distributions have been better estimated thanks to NHC and niche-modeling procedures.

C. References

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Abstract

In evolutionary biology, phylogenetic trees serve to study a multitude of evolutionary questions, a practice commonly referred to “phylogenetic tests of evolutionary scenarios”. These tests, to be as convincing as possible, must rely on clear hypotheses, robust phylogenetic trees and sound protocols (*i.e. the phylogenetic design*). Although known and obvious, these conditions are not always satisfied because phylogenetics was not initially developed in the rich context it thrives in now. My research agenda aims at meeting these conditions when testing evolutionary questions, from classification issues or social behaviour evolution to the tempo of diversification of organisms and their adaptations. I try to craft phylogenetic tests as carefully as possible, paying special attention to taxonomic sampling and character delimitation. I also engage in interdisciplinary studies, challenging and rewarding enterprises, that may require methodological developments to satisfy the foundations of each discipline involved.

Résumé

En biologie de l'évolution, les arbres phylogénétiques sont utilisés pour répondre à d'innombrables questionnements; on parle alors de tests phylogénétiques de scénario d'évolution. Ces tests sont d'autant plus convaincants qu'ils reposent sur des hypothèses clairement formulées, des phylogénies robustes et de solides protocoles expérimentaux (*i.e. phylogenetic design*). Bien qu'évidentes et connues, ces conditions ne sont pas toujours respectées, la discipline phylogénétique n'ayant pas été initialement développée dans un contexte aussi riche et varié que celui dans lequel elle est utilisée aujourd'hui. Mon programme de recherche vise à respecter chacune de ces conditions lors de tests de scénario d'évolution, portant aussi bien sur la classification des êtres vivants, l'évolution du comportement social, ou bien la dynamique de diversification des organismes et leurs adaptations. J'essaie d'élaborer des tests phylogénétiques aussi soigneusement que possible, en insistant sur les étapes d'échantillonnage et de délimitation des caractères. Je développe également des études inter-disciplinaires, défis stimulants et enrichissants, qui nécessitent parfois de développer de nouvelles méthodes respectant les fondements de chacune des disciplines impliquées.