Université de Montpellier
Ecole doctorale GAIA

Dossier de candidature pour Habilitation à Diriger des Recherches (HDR)

Aires de répartitions, métacommunautés et biodiversité : du théorique à l'appliqué

Christine N. Meynard
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Contenu

Curriculum Vitae

CHRISTINE N MEYNARD
Née le 21 juillet 1976 à Santiago du Chili
Nationalité française
Mariée, deux enfants (nés en 2009 et 2015)

Coordonnées professionnelles
Position : Chercheur CRCN – INRA SPE
Adresse : UMR CBGP, 755, avenue du campus Agropolis, 34988 Montferrier sur Lez Cedex, France
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Web : https://sites.google.com/site/cnmeynard/home

CURSUS UNIVERSITAIRE

2001-2006	PhD en écologie, avec mention en conservation biologique, Université de Californie à Davis. Titre de la thèse : "Species distributions and local richness patterns: from simulations with artificial species to conservation planning for birds of the Chilean forests". Dirigée par James F. Quinn. Autres membres du comité de thèse: Alan Hastings, Arthur Shapiro, Steven Greco.
1999	Titre professionnel en Gestion de Ressources Naturelles, Pontificia Universidad Católica de Chile, Santiago du Chili.
1995-1998	Licence en Biologie, Pontificia Universidad Católica de Chile, Santiago du Chili.

CURSUS PROFESSIONNEL

2017 - Présent	CR1 INRA-SPE, puis CRCN au CBGP, Monferrier-sur-Lez, France (retour de disponibilité en Septembre 2017)
2014-2017	Research Assistant Professor, Virginia Institute of Marine Science, College of William & Mary, Virginia, USA
2010-2014	CR2 INRA-SPE au CBGP, Monferrier-sur-Lez, France (départ en disponibilité en juillet 2014)
2008-2010	Chercheur postdoctoral Diversité phylogénétique et fonctionnelle, et métacommunautés. Co-encadrée par Dr Nicolas Mouquet et Dr Wilfried Thuiller, ISEM, Montpellier, France
2007-2008	Chercheur postdoctoral Incorporation des informations phylogénétiques et fonctionnelles dans la compréhension des assemblages d'espèces aux échelles biogéographiques. Co-encadrée par Dr Nicolas Mouquet et Dr David Mouillot, ISEM, Montpellier, France
2006-2007	Chercheur postdoctoral Génération de cartes de services écosystémiques dans l'écorégion de forêts Valdiviennes et exploration du rôle de la forêt tempérée sur la régulation du cycle d'eau. Encadrée par Dr Antonio Lara, Universidad Austral de Chile, Valdivia, Chile

2001-2006	Assistant de recherche (travail à mi-temps en parallele à la thèse) Construction de la base de données du National Biological Information Infrastructure (NBII) et coordination avec le réseau interaméricain (IABIN) et autres bases de données spatialisées pour le partage de données biologiques entre pays des Amériques. Cartographie de la biodiversité dans divers contextes. Sous la supervision de Dr James F Quinn, Information Center for the Environment, Université de Californie à Davis, Californie.
2000-2001	Assistante de recherche Effets de la fragmentation des forêts relictes sur la dynamique des populations d'oiseaux au Chili. Sous la supervision de Dr Pablo Marquet, Pontificia Universidad Católica de Chile, Santiago du Chili.
1999	Assistante de recherche Ecologie du comportement : compromis de manutention du poids corporel entre le risque de déprédation et le risque de faim dans le petit mammifère *Octodon degus*. Sous la supervision de Dr Francisco Bozinovic et Dr Rodrigo Vasquez, Pontificia Universidad Católica de Chile, Santiago du Chili.
1998	Assistante de recherche Ecophysiologie de la digestion de l'oiseau herbivore *Phytotoma rara*. Sous la supervision du Dr Francisco Bozinovic

PRIX ET HONNEURS

Toutes les bourses ci-dessous ont été octroyées sous base compétitive

2007-2008	Bourse postdoctorale région de l'Hérault, Université de Montpellier 2
2005-2006	Dissertation year fellowship, University of California, Davis
2002-2005	Block grant, University of California, Davis
2002-2006	Non-resident tuition fee fellowship, University of California, Davis
2001-2003	Fulbright fellowship, département d'état des Etats-Unis
1999	Graduation avec honneurs: meilleure élève de la promotion, P. Universidad Católica de Chile, Chili
1998	State University of New York, Plattsburgh, bourse d'échange
1995 et 1997	Matrícula de honor, P. Universidad Católica de Chile, Chili

ACTIVITÉS ÉDITORIALES

En qualité d'éditeur:

2019-Présent	*Journal of Biogeography*, Deputy-Editor-in-Chief
2014-Présent	*Ecography*, subject editor
2016-2019	*Journal of Biogeography*, subject editor
2016-2018	*Functional Ecology*, subject editor
2014-2016	*Marine Conservation and Sustainability*, review editor

En qualité de réviseur:

Ecology Letters; Ecography; Journal of Biogeography; Plos One; The American Naturalist; Methods in Ecology and Evolution; Global Ecology and Biogeography; Global Change

Biology; Diversity and Distributions; Conservation Letters; Marine Ecology Progress Series; Oikos; Oecologia; Journal of Plant Ecology; Plant Ecology, Evolution and Systematics; Journal of Vegetation Science; Theoretical Ecology; Biological Conservation; Biodiversity and Conservation; Journal of Ecology; Animal Ecology; Austral Ecology; Forest Ecology and Management; Journal of Field Ornithology; Annales Zoologici Fennici; BMC Ecology; Mammalia; Annals of Botany; Mammalian Biology; Diversity; Web Ecology; El Hornero; Forests; Frontiers of Biogeography; Diversity; Journal of Sea Research; Environmental Modelling & Software.

PARTICIPATION A L'EVALUATION DE PROJETS

Evaluation de projets soumis à l'ANR, le « Vienna science and technology fund » (Austria), le « Israeli Ministry of Science, Technology and Space » (Israel), Biodiversa et BioDivScen, le « Fondo Nacional de Ciencia y Tecnologia » (Chili), et le « Swiss National Science Foundation » (Suisse).

ENCADREMENT DE LA RECHERCHE

1 étudiant de doctorat (en cours), 8 étudiants de M2, 1 étudiant de M1, 1 étudiant de « masters » (système américain), 2 étudiants de licence.

Encadrement d'étudiants

2019-Présent	Doctorant	Simon Roy (Ecole doctorale GAIA, Université de Montpellier) « Pratiques agricoles et processus écologiques déterminants les communautés des bords de champs : approches fonctionnelles et multi-échelles » . Thèse co-encadrée avec Guillaume Fried (LSV-ANSES, Montpellier).
2018	Master 2	Livia Rodrigues de Sa (M2, BEE, Université de Montpellier) « Le concept de conservatisme de niche et son intérêt dans l'anticipation des invasions biologiques ». Encadrante principale, étudiante co-encadrée avec Gael Kergoat (CBGP, Montpellier).
2015-2016	Master	Luke Bassett (Master of Science, Marine Science, Virginia Institute of Marine Science, College of William and Mary, USA) "Climate Change Impacts on Phylogenetic and Functional Diversity of Chesapeake Bay Teleosts". Encadrante unique.
2014	Master 2	Valentine Delattre (Master 2 BEE, Université de Montpellier). "Functional diversity loss among marine mammals under different scenarios of extinction." Co-encadrement en collaboration avec Fabien Leprieur, Camille Albouy, Bastien Mérigot. Voir publication (Albouy et al. 2017).
2013	Master 1	Valentine Delattre (Master 1, BEE, Université de Montpellier). "Defining functional groups within marine mammals of the world." Co-encadrement en collaboration avec Fabien Leprieur, Camille Albouy, Bastien Mérigot.
2013	Master 2	Paula Iturralde (Master 2 Biodiversité, Université de Tours). "Mammalian species distributions under climate change and conservation implications in Ecuador." Encadrante unique. Voir publication (Iturralde-Pólit et al. 2017).
2013	Master 2	Bastien Louboutin (Master 2 BEE, Université de Montpellier). "Defining typical species for Natura 2000 habitats: a case study in

		Languedoc-Roussillon using grasshoppers, butterflies and dragonflies.” Encadrante unique.
2012	Master 2	Andrea Murillo (Master 2 ERASMUS) “Intraspecific relationship between probability of occurrence and abundance patterns.” Encadrante unique.
2012	Master 2	Annabelle Sueur (Master 2 Bioinformatique, Université de la Loire). “Incorporating phylogenetic and functional diversity into systematic conservation planning: does it really change the results?” Encadrante principale, en collaboration avec David Mouillot.
2012	Master 2	Rémi Genevest (Master 2, Ecole Agronomique de Toulouse). “Mechanistic species distribution models for Tetranychidae: potential effects of climate change and evolution on species distributions.” Encadrante principale, en collaboration avec Maria Navajas (CBGP).
2010	Master 2	Manon Perrigault (Master 2, Programme gestion de biodiversité, Université de Montpellier) “ Description of the environmental niche of the African striped mouse at two spatial scales: within sub-Saharan Africa and within the Republic of South Africa.” Co-encadrante avec Guila Ganem (ISEM). Voir publications (Ganem et al. 2012, Meynard et al. 2012a)
2009	Licence 3	Gwénaelle Delaruelle (License 3, biologie, Université de Montpellier). “Using geographic information systems (GIS) in the study of Teleost distribution and conservation in the Mediterranean Sea.” Co-encadrement avec Nicolas Mouquet et David Mouillot.
2006-2007	Licence	Carlos Lara (Programme de licence, Universidad Austral de Chile, Valdivia, Chili) ; « Macrophyte vegetation cover in the Valdivia river estuary: a multi-temporal analysis using satellite images. » Encadrante unique.

Collaborations qui ont donné lieu au co-encadrement d’étudiants en thèse

2018-2019	Doctorant	Rémi Tournebize (Université de Montpellier). “Vulnerability of *Coffea canephora* to ongoing climate change”. Collaboration avec Stéphanie Manel (CEFE, Montpellier) et Valérie Poncet (IRD, Montpellier) et qui a donné lieu à un article en préparation.
2014-2017	Doctorante	Laura Henckel (Université de La Rochelle) “The structuring processes of farmland bird’s communities in european agro-ecosystems: Effect of landscape heterogeneity (crops composition and configuration) and agricultural intensification”. Collaboration avec Nicolas Mouquet, Vincent Devictor et Vincent Bretagnoles qui a donné lieu à une publication avec l’étudiante (Henckel et al. 2019)
2015-2016	PhD Marine Science, VIMS, USA	Mark Stratton (PhD VIMS, College of William and Mary). “Defining borders between Large Marine Ecosystems: Cape Hatteras as an example of a dynamic ecotone” Collaboration avec Robert Latour (VIMS, College of William and Mary) qui a donné lieu à un article en préparation.
2014-2017	Doctorante	Lilian Ouchi de Melo (Universidade Estadual Paulista, Sao Paulo, Brasil) “Integrating phylogenetic and functional biodiversity facets to guide conservation: a case study using anurans in a global biodiversity hotspot” Collaboration avec Thiago Gonçalves-Souza and Denis Feres qui a donné lieu à 1 publication (Ouchi-Melo et al. 2018)

2014-2016	Doctorante	Sophie Monsarrat (Université de Montpellier). Collaboration avec Ana Rodrigues (CEFE, Montpellier) qui a donné lieu à deux publications avec l'étudiante (Monsarrat et al. 2015, 2016)
2012-2015	Doctorante	Victoria Granger (Université de Montpellier). Collaboration avec Bastien Mérigot qui a donné lieu à 2 publications avec l'étudiante (Granger et al. 2015a, b)
2013	Doctorante UFZ, Allemagne	Natalia Carrasco (Doctorante au Centre de recherche pour l'environnement de Helmholzt, Allemagne). Stage de Natalia dans mon labo, en lien avec deux chapitres de sa thèse.
2013-2014	Doctorante	Claire Dufour (Université de Montpellier). Collaboration avec Guila Ganem (ISEM, Montpellier) qui a donné lieu à 1 publication avec l'étudiante (Dufour et al. 2015)
2013-2014	Doctorante	Anne-Christine Monnet (U. Pierre et Marie Currie). Collaboration avec Vincent Devictor et Frédéric Jiguet qui a donné lieu à une publication avec l'étudiante (Monnet et al. 2014).
2012-2013	Doctorante	Alice Latinne (Université de Liège, Belgique). Collaboration avec Johan Michaux (Université de Liège) qui a donné lieu à une publication avec l'étudiante (Latinne et al. 2015).

ACTIVITES D'ENSEIGNEMENT ET DE FORMATION

2014 et 2016	Approx. 96h / an	Systèmes d'information géographique (SIG) pour les étudiants de master et doctorat, Virginia Institute of Marine Science (VIMS), College of William and Mary, Etats-Unis.
2012	6h	Introduction aux modèles de répartition d'espèces pour les étudiants de doctorat, Rhodes University, Grahamstown, Afrique du Sud.
2007	24h	Introduction à R pour les étudiants de doctorat, Université Australe du Chili, Valdivia, Chili.
2005	Approx. 96h	Ateliers pratiques dans une classe de dynamique des populations, Université de Californie à Davis.
2003	4h	Evolution des traits d'histoire de vie des oiseaux pour des professeurs d'école, DQ Community College, Winters, Californie.
2002	40h	Ateliers pratiques dans un cours d'introduction aux méthodes de terrain et de laboratoire en écologie, Université de Californie, Davis.
2001	3h	Atelier d'éducation environnementale sur les oiseaux de la forêt tempérée chilienne, Festival de aves de Caulín, Chile.
2000	10h	Flore et faune de Los Molles (Chili), Universidad Diego Portales, Santiago, Chili.
1999	20h	Interactions entre l'homme et son environnement en Amérique Latine. Pontificia Universidad Católica de Chile, Santiago, Chili

PARTICIPATION A DES JURYS ET COMITES DE THESE

2013 et 2019	Participation au jury d'évaluation des master 2 à BEE, Université de Montpellier
2016-Présent	Comité de thèse de Jingwei Song, étudiant de PhD à VIMS, Etats-Unis. Thèse dirigée par Jan McDowell, "Understanding local adaptation of Spotted Seatrout (*Cynoscion nebulosus*) along the U.S. southeast coast".
2014-2018	Comité de thèse de Adela Roa-Varon, étudiante de PhD à VIMS, Etats-

	Unis. Thèse dirigée par Eric Hilton, “Multi-scale phylogenetics of Gadiformes with emphasis on hakes (Merluccius, Merlucciidae), a high-priority group for fisheries conservation”.
2014	Comité de thèse de Florian Holon, étudiant de doctorat à l’ISEM , thèse dirigée par Nicolas Mouquet, “Diversity of coral assemblages in the French coastal Mediterranean Sea: study of distributions, with applications in conservation and ecological monitoring”.
2012-2014	Comité de thèse de Victoria Sundov (maintenant Victoria Granger), étudiante de SIBAGHE à l’EME (marine exploited ecosystems, Sète-France), thèse co-dirigée par Bastien Mérigot et Jean-Marc Fromentin. “Spatio-temporal modeling of diversity in demersal exploited fish within the Mediterranean Sea”.
2012-2014	Claire Dufour, SIBAGHE PhD student at the ISEM (Institute of evolution of Montpellier) lab, directed by Guila Ganem. Ecological niche of sympatric and allopatric populations of the African Striped Mice (Rhabdomys): identifying relevant dimensions for the radiation of the clade.
2012-2013	Arame Ndiaye-Ndao, PhD student at the University of CA Diop-Dakar, Senegal (Healt-environment-life graduate program at Dakar), co-directed by Mbacké SEMBENE and Laurent Granjon. Phylogeny and phylogeography of rodents within the genre Gerbillus.
2011-2013	Jeanne Tonnabel, PhD student at the ISEM (institute of evolution of Montpellier) lab, thesis directed by Ophélie Ronce. Evolution of life-history traits in fire-prone systems: theoretical and empirical approaches using the South-African fynbos Leucadendron.

PARTICIPATION A DES JURYS DE RECRUTEMENT

2013	Rapporteur recrutement poste de maître de conférence « Écosystèmes Insulaires Océaniens », Université de Polynésie française
2014	Président du jury recrutement poste d’ingénieur de recherche « Modélisation des systèmes socio-écologiques en Bolivie » IRD

PROJETS DE RECHERCHE ET FINANCEMENT

2018-2019	Projet SPE NicoTools: Niche and trait conservatism as tools to assess new agricultural risks under climate change scenarios: a case study with stemborer moths (Noctuidae: Apameini: Sesamiina) in Africa
2016-2018	NOAA- FATE Incorporating climate into distribution and abundance indices for stock assessment: looking into the past and planning for the future. Leader du projet: Christine N Meynard and Tim Miller (NOAA).
2014-2017	GENOMITES- ERANET on climate smart agriculture. Using genomic, metabolomic and modelling methods to study potential effects of climate change on major agricultural crops. Leader français du projet: Maria Navajas.
2013-2015	CLIF- Métaprogramme ACCAFF (INRA) Climate change Impact on Fungal pathosystems: estimating disease variation using models and indicators, designing adaptation strategies and mitigating several key knowledge gaps. Leader du projet: Laurent Huber.
2013-2015	AAP-SPE ADA-COM Adaptation and evolution of plant-insect communities: the case of Bruchinidae and Fabaceae. Leader du projet: Gaël Kergoat.
2011-2014	ANR MORSE Management of Ocean Resources under Shifting Expectations:

	bringing the historical perspective into marine mammal conservation. Leader du projet: Ana Rodrigues.
2011-2012	INRA-SPE Modelling current and future potential distributions of Tetranychidae worldwide. Leader du projet: Christine Meynard.
2010-2013	ANR EvoRange How does evolution affect extinction and species range dynamics in the context of global change? Implications for ecological forecasting. Leader du projet: Ophélie Ronce.
2010-2012	FRB FACETS Spatial mismatch between biodiversity facets: a new challenge for conservation. Leader du projet: Vincent Devictor.
2009	PICS-CNRS (International Cooperation Projects) Identifier des marqueurs biologiques indicateurs des variations climatiques et des capacités des organismes à s'adapter à ces changements, au travers de l'étude d'un organisme modèle : la souris striée africaine. Leader du projet: Guila Ganem.
2008	Fonds IFR- Analyse spatiale. Leader du projet : Christine Meynard.
2008-2010	National Geographic Committee for Exploration and Research Grant (NGS): une prestigieuse bourse de recherche pour le projet intitulé "Bats of the Chilean temperate rainforest : elucidating patterns of landscape occurrence and use in a mosaic of land-use types within a South American biodiversity hotspot". Leader du projet : Christine Meynard
2003 – 2004	Rufford Small Grant et Jastro Shields Grant, deux bourses de recherche pour le déroulement de labeurs de terrain pendant les printemps australes 2003 et 2004 dans la forêt tempérée du Chili. Etude de communautés d'oiseaux dans la forêt tempérée chilienne.

ANIMATION DE LA RECHERCHE

2020	Animation groupe de travail sur les effets des pratiques agricoles sur la biodiversité de bordures de champs (oiseaux, coléoptères, plantes, verres de terre), à l'intérieur du réseau 500 ENI (réseau de surveillance des effets non-intentionnels de l'agriculture, fédéré par le ministère de l'agriculture et l'ANSES).
2010	Comité d'organisation de Phylocom, conférence sur l'intégration des phylogénies dans l'étude de l'écologie des communautés, Montpellier
2008	Comission de selection d'aires pour la conservation dans la region méditerranéenne au Chili (fédéré par The Nature Conservancy et la comission nationale pour l'environnement)
2006	Comité d'organisation de la première réunion de la société néotropicale sur les services écosystémiques, Valdivia, Chili
2001-2003	Groupe de travail sur les méthodes de partage d'informations liées à la biodiversité aux Amériques à l'intérieur du Inter American Biodiversity Infrastructure Network (IABIN)

LISTE DES TRAVAUX

Statistiques GoogleScholars (novembre 2019) : 2778 citations, h-index = 22.
Statistiques Web of Science (novembre 2019) : 1876 citations, h-index = 20.

Publications scientifiques dans des revues à comité de lecture (48 publications)

Les co-auteurs soulignés ci-dessous représentent des collaborations avec des étudiants au moment de la publication.

2019

Meynard, C. N., Leroy B. & D. M. Kaplan (2019) Testing methods in species distribution modelling using virtual species: what have we learnt and what are we missing? *Ecography* 42: 2021-2036. DOI: 10.1111/ecog.04385

Meynard, C. N., Kaplan, D. M. & B. Leroy (2019) Detecting outliers in species distribution data: some caveats and clarifications on a virtual species study. *Journal of Biogeography*. DOI: 10.1111/jbi.13626

Henckel, L., **Meynard, C. N.**, Devictor, V., Mouquet, N. & V. Bretagnolle (2019) On the relative importance of space and environment in farmland bird community assembly. *PlosOne* 14(3): e0213360, DOI:10.1371/journal.pone.0213360.

2018

Ouchi-Melo, L. S. , **Meynard, C.N.**, Gonçalves-Souza, T., & D. de Cerqueira Rossa-Feres (2018) Integrating phylogenetic and functional biodiversity facets to guide conservation: a case study using anurans in a global biodiversity hotspot. *Biodiversity & Conservation* 27: 3247-3266. DOI: 10.1007/s10531-018-1600-4

Leroy, B., Delsol, R., Hugueny, B., **Meynard, C. N.**, Barhoumi, C., Barbet-Massin, M., & C. Bellard. (2018) Without quality presence-absence data, discrimination metrics such as TSS can be misleading measures of model performance. *Journal of Biogeography* 45: 1994-2002. DOI: 10.1111/jbi.13402

2017

Meynard, C. N., Gay, P. E., Lecoq, M., Foucart, A., Piou, C. & M. P. Chapuis. (2017) Climate-driven geographic distribution of the desert locust during recession periods: subspecies' niche differentiation and relative risks under scenarios of climate change. *Global Change Biology* 23: 4739-4749, DOI: 10.1111/gcb.13739.

Iturralde-Pólit, P., Dangles, O., Burneo, S.F. & **C. N. Meynard**. (2017) The effects of climate change impact on a mega-diverse country: predicted shifts in mammalian species richness and turnover in continental Ecuador. *Biotropica* 49: 821-831, DOI: 10.1111/btp.12467.

Albouy, C., Delattre, V.L., Mérigot, B., **Meynard, C.N.**, Leprieur, F. (2017) Multifacetted biodiversity hotspots of marine mammals for conservation priorities. *Diversity & Distributions* 23: 615-626, DOI: 10.1111/ddi.12556

2016

Monsarrat, S., Pennino, M. G., Smith, T. D., Reeves, R. R., **Meynard, C. N.**, Kaplan, D. M. & A. S. L. Rodrigues. 2016. A spatially explicit estimate of the prewhaling abundance of the endangered North Atlantic right whale. *Conservation Biology* 30: 783-791, DOI: 10.1111/cobi.12664

Veran, S., Piry, S., Ternois, V., **Meynard, C.N.,** Facon, B. & A. Estoup (2016) Modeling spatial expansion of invasive alien species: relative contributions of environmental and anthropogenic factors to the spreading of the harlequin ladybird in France. *Ecography* 39: 665-675, DOI: 10.1111/ecog.01389/epdf

Leroy, B., **Meynard, C.N.**, Bellard, C. & F. Courchamp (2016) virtualspecies, an R package to generate virtual species distributions. *Ecography,* 39: 599-607*,* DOI:10.1111/ecog.01388

2015

Albouy, C., Lasram, F. B. R., Guilhaumon, F., Velez, L., **Meynard, C.N.**, Boyer, S., Benestan, L., Mouquet, N., Douzery, E., Aznard, R., Troussellier, M., Somot, S., Leprieur, F., Le Loc'h F. & D. Mouillot (2015) FishMed: traits, phylogeny, current and projected species distribution of Mediterranean fishes, and environmental data. *Ecology* 96:2312–2313. http://dx.doi.org.proxy.wm.edu/10.1890/14-2279.1

Latinne, A., **Meynard, C. N.**, Herbreteau, V., Morand, S., Waengsothorn, S. & J. R. Michaux. (2015) Influence of past and future climate changes on the distribution of three Southeast Asian murine rodents. *Journal of Biogeography,* 42: 1714-1726. doi: 10.1111/jbi.12528.

Monsarrat, S., Pennino, M.G., Smith, T.D., Reeves, R.R., **Meynard, C.N.**, Kaplan, D.M., & A.S.L. Rodrigues. (2015) Historical summer distribution of the endangered North Atlantic right whale (*Eubalaena glacialis*): a hypothesis based on environmental preferences of a congeneric species. *Diversity & Distributions* 21: 925-937. DOI: 10.1111/ddi.12314

Albouy, C., Leprieur, F., Le Loc'h, F., Mouquet, N., **Meynard, C.N.**, Douzery, E.J.P. & D. Mouillot (2015) Projected impacts of climate warming on the functional and phylogenetic components of coastal Mediterranean fish biodiversity. *Ecography,* 38: 681-689. DOI: 10.1111/ecog.01254

Granger, V., Bez, N., Fromentin, J.M., **Meynard, C.N.**, Jadaud, A. & B. Mérigot (2015) Mapping diversity indices: not a trivial issue. *Methods in Ecology and Evolution* 6: 688-696. doi: 10.1111/2041-210X.12357

Granger, V., Fromentin, J. M., Bez, N., Relini, G., **Meynard, C. N.**, Gaertner, J. C., Maiorano, P., Garcia Ruiz, C., Follesa, C., Gristina, M., Peristeraki, P., Brind'Amour, A., Carbonara, P., Charilaou,C., Esteban, A., Jadaud, A., Joksimovic, A., Kallianiotis, A., Kolitari, J., Manfredi, C., Massuti, E., Mifsud, R., Quetglas, T., Refes, W., Sbrana, M., Vrgoc, N., Spedicato, M. T. & B. Mérigot. (2015) Large-scale spatio-temporal monitoring highlights hotspots of demersal fish diversity in the Mediterranean. *Progress in Oceanography* 130: 65-74. DOI: 10.1016/j.pocean.2014.10.002

Guilhaumon, F., Albouy, C., Claudet, J., Velez, L., Ben Rais Lasram, F., Tomasini, J.A., Douzery, E.J.P., **Meynard, C.N.**, Mouquet, N., Araújo, M.B. & D. Mouillot (2015) Representing taxonomic, phylogenetic, and functional diversity : new challenges for Mediterranean marine protected areas. *Diversity & Distributions*, 21: 175-187. DOI: 10.1111/ddi.12280

Dufour, C. M. S., **Meynard, C. N.**, Watson, J., Rioux, C., Benhamou, S., Perez, J., du Plessis, J. J., Avenant, N., Pillay, N. & G. Ganem (2015) Space use variation in co-occurring sister species: response to environmental variation or competition? *PlosOne* 10: e0117750. doi:10.1371/journal.pone.0117750

2014

Meynard, C. N., Soto-Gamboa, M., Heady III, P. A., & W. F. Frick. (2014) Bats of the Chilean temperate rainforest: patterns of landscape use in a mosaic of native forests, eucalyptus plantations and grasslands within a South American biodiversity hotspot. *Biodiversity & Conservation* 23: 1949-1963. DOI: 10.1007/s10531-014-0697-3

Monnet, A. C., Jiguet F., **Meynard C. N.**, Mouillot D., Mouquet N., Thuiller W., Devictor V. (2014) Asynchrony of taxonomic, functional and phylogenetic diversity in birds. *Global Ecology and Biogeography* 23: 780-788. DOI: 10.1111/geb.12179

2013

Meynard, C.N., A. Migeon & M. Navajas. (2013) Uncertainties in predicting species distributions under climate change: a case study using *Tetranychus evansi* (Acari: Tetranychidae), a widespread agricultural pest. *PLoS ONE* 8: e66445. DOI:10.1371/journal.pone.0066445.

Meynard C. N., Lavergne S., Boulangeat I., Garraud L., Van Es J., Mouquet N., and Thuiller W. (2013). Disentangling the drivers of metacommunity structure across spatial scales. *Journal of Biogeography* 40: 1560-1571. DOI: 10.1111/jbi.12116

Moritz C., **Meynard C.N.**, Devictor V., Guizien K., Labrune C., Guarini J.-M., Mouquet N. (2013) Disentangling the role of connectivity, environmental filtering, and spatial structure on metacommunity dynamics. *Oikos* 122: 1401-1410. DOI: 10.1111/j.1600-0706.2013.00377.x

Meynard, C. N. & D. M. Kaplan (2013) Guest Editorial: Using virtual species to study species distributions and model performance. *Journal of Biogeography* 40: 1-8. DOI: 10.1111/jbi.12006

2012

Meynard, C.N., Mouillot D., Mouquet N., Douzery E.J.P. (2012) A Phylogenetic Perspective on the Evolution of Mediterranean Teleost Fishes. PLoS ONE 7: e36443. DOI: 10.1371/journal.pone.0036443

Meynard, C. N., Pillay, N., Perrigault, M., Caminade, P., Ganem, G. (2012) Assessment of environmental differentiation in the striped mouse (*Rhabdomys sp.*) over southern Africa: the influence of past climate change on current distributions. *Ecology & Evolution* 2: 1008-1023. DOI: 10.1002/ece3.219

Mouquet, N.*, Devictor, V.*, **Meynard, C. N.***, Munoz, F.*, Bersier, L. F., Chave, J., Couteron, P., Dalecky, A., Fontaine, C., Gravel, D., Hardy, O. J., Jabot, F., Lavergne, S., Leibold, M., Mouillot, D., Münkemüller, T., Pavoine, S., Prinzing, A., Rodrigues, A. S. L., Rohr, R. P., Thébault, E. & Thuiller, W. (2012) Ecophylogenetics: advances and perspectives. *Biological Reviews* 87: 769-785. *First four authors contributed equally to this manuscript. DOI: 10.1111/j.1469-185X.2012.00224.x

Ganem, G., **Meynard, C. N.**, Perrigault, M., Lancaster, J., Edwards, S., Caminade, P., Watson, J. & Pillay, N. (2012) Environmental correlates and co-occurrence of three mitochondrial lineages of striped mice (*Rhabdomys*) in the Free State Province (South Africa). *Acta Oecologica* 42: 30-40. DOI: 10.1016/j.actao.2012.01.003

Münkemüller, T., de Bello, F., **Meynard, C.N.**, Gravel, D., Lavergne, S., Mouillot, D., Mouquet, N. & Thuiller, W. (2012) From diversity indices to community assembly processes: a test with simulated data. *Ecography*, 35: 468-480. DOI: 10.1111/j.1600-0587.2011.07259.x

Meynard, C. N. & D. M. Kaplan (2012) The effect of a gradual response to the environment on species distribution modeling performance. *Ecography* 35: 499-509. DOI: 10.1111/j.1600-0587.2011.07157.x

2011

Mouillot D., Albouy C., Guilhaumon F., Ben Rais Lasram F., Coll M., Devictor V., Douzery E., **Meynard C. N.**, Pauly D., Troussellier M., Velez L., Watson R. & N. Mouquet (2011) Protected and threatened components of fish biodiversity in the Mediterranean Sea. *Current Biology* 21: 1044-1050.

Meynard, C. N., V. Devictor, D. Mouillot, W. Thuiller, F. Jiguet & N. Mouquet (2011) Beyond taxonomic diversity patterns: how do α, β and γ components of bird functional and phylogenetic diversity respond to environmental gradients across France? *Global Ecology and Biogeography* 20: 893-903.

2010

Devictor, V., D. Mouillot, **C. Meynard**, F. Jiguet, W. Thuiller & N. Mouquet (2010) Spatial mismatch between taxonomic, phylogenetic and functional biodiversity facets challenges conservation strategies. *Ecology Letters* 13: 1030-1040.

Venail, P. A., R. C. Maclean, M. E. Hochberg, **C. N. Meynard** & N. Mouquet (2010) Scaling up the diversity-productivity relationship in an experimental source-sink metacommunity. *Proceedings of the Royal Society of London B* 277: 2339-2345.

de Bello, F., S. Lavergne, **C. N. Meynard**, J. Leps& W. Thuiller (2010) The spatial partitioning of diversity: showing Theseus a way out of the labyrinth. *Journal of Vegetation Science* 21: 992-1000.

Zurell, D., U. Berger, J. S. Cabral, J. Calabrese, F. Jeltsch, **C. N. Meynard**, T. Münkemüller, N. Nehrbass, J. Pagel, B. Reineking, B. Schröder & V. Grimm (2010) The Virtual Ecologist approach: simulating data and observers. *Oikos* 119: 622-635.

2009

Meynard, C. N., C. Howell & J. F. Quinn (2009) Comparing alternative systematic conservation planning strategies against a politically driven conservation plan. *Biodiversity & Conservation* 18: 3061-3083.

Sepúlveda, M. A., J. L. Bartheld, **C. N. Meynard**, M. Benavides, C. Astorga, D. Parra & G. Medina-Vogel (2009) Landscape features and crustacean prey as predictors of the Southern river otter (*Lontra provocax*) distribution in Chile. *Animal Conservation* 12: 522-530.

2008 et antérieurs

Meynard, C. N. & J. F. Quinn (2008) Bird metacommunities in the temperate forests of South America: direct and indirect effects of vegetation structure, area and climate. *Ecology* 89: 981-990.

Meynard, C. N. & J. F. Quinn (2007) Predicting species distributions: a critical comparison of the most common statistical models. *Journal of Biogeography* 34: 1455-1469.

Meynard, C. N., A. Lara, M. Pino, D. Soto, L. Nahuelhual, D. Núñez, C. Echeverría, C. Jara, C. Oyarzún, M. Jiménez, & F. Morey. (2007) Integrando ciencia, economía y sociedad: servicios ecosistémicos en la ecoregión de bosques lluviosos valdivianos. *Gaceta Ecológica de México* **84-85**: 29-38.

Meynard, C. N., A. Lara, M. Pino, D. Soto, L. Nahuelhual, D. Núñez, C. Echeverría, C. Jara, C. Oyarzún, M. Jiménez, & F. Morey. (2007) Integrando ciencia, economía y sociedad: servicios ecosistémicos en la ecoregión de bosques lluviosos valdivianos. *Gaceta Ecológica de México* **84-85**: 29-38.

Meynard, C. & A. M. Venegas (2005) Avifauna en un bosque de Roble-Hualo en Chile Central. *Boletín de Ornitólogos de Chile* **11**: 18-21.

Meynard, C., Samaniego, H. & P. A. Marquet (2004) Biogeography of Chilean raptors. *Book chapter in* Aves Rapaces de Chile. Andrés Muñoz-Pedreros, Jaime Rau & José Yánez Editors, CEA Ediciones, Chile. pp. 129-143.

Reid, S., Cornelius, C., Barbosa, O., **Meynard, C.**, Silva, C., & P.A. Marquet. (2002) Conservation of temperate forest birds in Chile: implications from the study of an isolated forest relict. *Biodiversity & Conservation* 11: 1975-1990.

Meynard, C. & Hajek, E., (1999) Pobreza y Medio Ambiente en América Latina. *Persona y Sociedad*, Volúmen XIII (**1**): 185-199.

Meynard, C. N., Sabat, P., López-Calleja, M. V. & F. Bozinovic (1999) Digestive enzymes of a small avian herbivore, the rufous-tailed plantcutter. *The Condor* 101: 904-907.

Chapitres d'ouvrage et ouvrages

Meynard, C., Samaniego, H. & P. A. Marquet (2004) Biogeography of Chilean raptors. *Chapitre de livre dans* Aves Rapaces de Chile. Andrés Muñoz-Pedreros, Jaime Rau & José Yánez Editors, CEA Ediciones, Chile. pp. 129-143.

Bustos F., R. Rivera, P. Peña, **C. Meynard**, P. Donoso, F. Morey, E. Cuq (2008) Guía práctica laboratorios urbanos. Publié par Nucleo Científico Milenio FORECOS.

Rapports scientifiques

Meynard, C. N., M. Soto-Gamboa, W. F. Frick, P. A. Heady III (2010) Bats of the Chilean temperate rainforest: elucidating patterns of landscape occurrence and use in a mosaic of land-use types within a South American biodiversity hotspot. Final report for the National Geographic CRE grant 8538-08.

Meynard, C. N. (2007) Wildlife habitat modeling on Catalina Island. Report for the Catalina Island Conservancy, California, USA.

Meynard, C. N. (2007) Road ecology: a preliminary annotated bibliography and recommendations for wildlife passages. Report for the California Transportation Department (CalTrans), California, USA.

Meynard, C. N. (2006) Species distributions and local richness patterns: from simulations with artificial species to conservation planning for birds of the Chilean temperate forests. Ph.D. Thesis Dissertation, University of California, Davis, USA.

Meynard, C. N. (1999) Plasticity and trade-offs in behavioral ecology: information, time and energy use in changing environments using the model species of *Octodon degus*. Tésis para el título profesional de biología con mención en manejo de recursos naturales, Pontificia Universidad Católica de Chile.

Présentations orales en congrès

Meynard, C. N. (2018) "Bringing macroecology into agricultural science: promises and challenges". International Conference on Ecological Sciences, Réunion de la Société Française d'Ecologie et Evolution, Rennes, France, 22-25 octobre 2018.

Meynard, C. N., Gay, P. E., Lecoq, M., Foucart, A., Piou, C. & M. P. Chapuis (2019) Climate-driven geographic distribution of the desert locust during recession periods: subspecies' niche differentiation and relative risks under scenarios of climate change. Invitée au symposium "Effects of climate change and environmental change" dans le colloque "13th International congress of orthopterology", Agadir-Maroc, 24-28 mars 2019.

Meynard, C. N., B. Leroy & D. M. Kaplan (2019) "Testing methods in species distribution modelling using virtual species" The 9th Biennial Conference of the International Biogeography Society, Malaga, Spain, 8-12 janvier 2019.

Meynard, C.N. (2014) Indices of phylogenetic and functional diversity: understanding their applicability in ecology and conservation science. Ecological Society of America Annual Meeting, Baltimore-USA, August 2014.

Navajas, M., **Meynard, C.N.** & A. Migeon (2014) Molecules and models for tracking invasion processes: *Tetranychus evansi* as an emerging pest. Annual meeting of the entomological society of America, Portland, Oregon, USA, November 15-19th 2014.

Meynard, C.N., A. Migeon, M. Navajas (2013) Uncertainties in predicting species distributions under climate change: a case study using *Tetranychus evansi* (Acari: Tetranychidae), a widespread agricultural pest. 8e réunion annuelle du Réseau d'écologie des interactions durables (REID), Bordeaux, France, 4-6 February 2013.

Meynard, C.N., V. Devictor, E. Douzery, F. Jiguet, D. M. Kaplan, D. Mouillot, N. Mouquet (2010) Systematic conservation planning: influence of phylogenetic and functional information. Ecologie 2010, Montpellier, France, September 2010.

Meynard, C.N., V. Devictor, N. Mouquet, D. Mouillot & F. Jiguet (2008) Variation de la diversité des oiseaux par rapport à la structure spatiale et environnementale. Journées d'écologie fonctionelle, La Grande Motte, France, March 2008.

Meynard, C. N., Lara, A., Nahuelhual, L., Echeverría, C., Núñez, D., Soto, D., Pino, M., Jara, C., Mulsow, S. & M. Jiménez (2007) Integrating science, economics and people: forest ecosystem services in the Valdivian rainforest ecoregion. Meeting of the Association for Tropical Biology and Conservation, Morelia, Mexico, July 2007.

Meynard, C. N. (2007) The Latin American Network for Ecosystem Services (LANES). Meeting of the Association for Tropical Biology and Conservation, Morelia, Mexico, July 2007.

Meynard, C. N. (2006) Modelling species distributions: choosing conservation priorities. Invited speaker for a special session on "GIS and conservation" within the first international meeting on ecosystem services in the Neotropics., Valdivia, Chile, November 2006.

Meynard, C. N. & J. F. Quinn (2006) Using Bird Species Distribution Modeling to Assess Conservation Needs in the Temperate Forest of Central Chile. Annual Meeting of the Society for Conservation Biology, San José, Californie, June 2006.

Meynard, C. N. (2006) Modelación De Distribución De Especies E Identificación De Sitios Prioritarios Para La Conservación De Aves Del Bosque En El Centro-sur De Chile. Sociedad de Biología de Chile, November 2006, Pucón, Chile.

Meynard, C. N. & J. F. Quinn (2006) Using Bird Species Distribution Modeling to Assess Conservation Needs in the Temperate Forest of Central Chile. Bay Area Conservation Symposium, February 2006, SFSU San Francisco, California, USA.

Meynard, C. N. & J. F. Quinn (2005) Bird Diversity Patterns In The Chilean Temperate Forest. British Ecological Society Annual Meeting, Hatfield England.

Meynard, C. N. & J. F. Quinn (2005) Comparing species distribution models using artificial species in a real landscape. Ecological Society of America Annual Meeting, Montréal Canada, August 2005.

Meynard, C. N. & Quinn, James F. (2004) Forest bird conservation in Chile: Challenges for a developing country. Bay Area Conservation Symposium, Janvier 2004, Davis, California, USA.

Bozinovic, F., **Meynard, C.**, Iriarte-Díaz, J., & Vásquez, R. A. (2001) Rol de la masa corporal sobre la energética del forrajeo y la conducta de escape antidepredatoria en pequeños mamíferos. Reunión binacional de la Sociedad de Ecología de Chile y Argentina, Bariloche, Argentina.

M. V. López-Calleja, **Meynard, C.**, Resende, E., Sabat, P., & Bozinovic, F. (1999) Herbivory in birds: digestive and energetic strategies in a bird of small body size. VI Neotropical Ornithological Congress, Mexico.

Présentations sous invitation

Meynard, C. N. 2019. Species distribution models: from theory to practice, forecasting agricultural risk under climate change scenarios. Rhodes University, Grahamstown, South Africa & Nelson Mandela University, Port Elizabeth, South Africa.

Meynard, C.N. 2016. Of species distributions and diversity: challenges and perspectives for ecological studies at large scales. Universidad Austral de Chile, Valdivia, Chile.

Meynard, C.N. 2012. Metacomunidades: buscando reglas de ensamble a partir de patrones espaciales, filogenias e historias de vida. Pontificia Universidad Católica de Chile, Department of Ecology seminar series, Santiago, Chile.

Meynard, C.N. 2012. Species distribution modelling: promising applications, challenging future. Department of Botany and Zoology seminar series, Stellenbosch University, South Africa.

Meynard, C.N. 2012. Metacommunities: looking for assembly rules from spatial patterns, phylogenies and life histories. Department of Zoology and Entomology seminar series, Rhodes University, South Africa.

Meynard, C.N. 2012. Species distribution modeling. Numerical ecology course, Rhodes University, South Africa.

Meynard, C.N., Latine, A., Michaux, J.R. 2012. Distributions of three Murinae rodent species in Southeast Asia: biogeographic and conservation consequences of past and future climate changes. Réunion annuelle du groupe rongeurs, CBGP, France.

Meynard, C.N. 2011. Systematic conservation planning considering phylogenetic and functional diversity. Evolutionary community ecology discussion group organized by Nicolas Mouquet, Saint André de Buège, France.

Meynard, C. N. Phylogénies, traits fonctionels et écologie des communautés. 2010. Séries de séminaires ECOLAG-UM2, Montpellier, France.

Meynard, C. N., Perrigault, N Pillay, G Ganem. 2010. Habitat characterization for *Rhabdomys* (Muridae, Rodentia): a potential model for studies of adaptation under climate change. GDRI Biodiversity and Global Change in Southern Africa meeting, Stellenbosch, South Africa.

Meynard, C.N. 2009. Distribution of taxonomic, functional and phylogenetic diversity in the Mediterranean Sea. CRH (Centre de Recherche Halieutique) seminar series, Sète, France.

Meynard, C.N. 2009. Bird diversity in France: distribution of taxonomic, functional and phylogenetic diversity. Institut des sciences de l'evolution de Montpellier (ISEM) seminar series, Montpellier, France.

Meynard, C. N. 2008. Biodiversité: diverses mesures, diverses échelles, et perspectives pour la conservation. Institut des sciences de l'evolution de Montpellier (ISEM) seminar series, Montpellier, France.

Meynard, C.N. 2008. Phylogenetic and functional diversity, distance decay, and diversity indices. Workshop Diversitalp organized by Wilfried Thuiller, Lautaret, France.

POSTERS

Leroy, B., **Meynard, C.N.**, Bellard, C. & F. Courchamp. (2015) Testing species distribution modelling techniques and hypotheses with virtual species: the 'virtualspecies' R package. 7th Biennal conference of the International society of Biogeography, University of Bayreuth, Germany.

Meynard, C. N. & A. Venegas. (2007) Avifauna of Roble-Hualo forests in the Maule Valley, Central Chile. VIII Neotropical Ornithological Congress, May 2007, Venezuela.

Meynard, C. N. (2006) Combining different statistical tools to study local bird species diversity: an example in the temperate forest of South America. Annual meeting of the Ecological Society of America, Memphis, USA, August 2006.

Meynard, C. N. & J. F. Quinn (2004) Bird habitat preferences in the temperate forest of central Chile. Ecological Society of America Annual Meeting Abstracts 89: 349. USA.

Meynard C & P. A. Marquet (2002) Bird vulnerability in the relict forest of Fray Jorge. Sociedad de Biología de Chile, November 2002, Chile.

Barbosa, O., Cornelius, C., Reid, S., **Meynard, C**., & P.A. Marquet. (2000) Structure and dynamics of the bird assemblage of the Fray Jorge relict forest: The interaction between time and area. Sociedad de Biología de Chile, November 2000, Chile.

Meynard, C., Sabat, P., López-Calleja, M. V. & Bozinovic, F. (1999) Enzimas Digestivas en un ave herbívora pequeña, *Phytotoma rara*. Sociedad de Biología de Chile, November 1999, Chile.

LISTE DES ANNEXES

Les articles listés ci-dessous ont représente la diversité de systèmes étudiés dans le contexte de la repartition des espèces et l'étude de la biodiversité à grandes échelles. Tous ces papiers représentent des collaborations étroites avec des étudiants de doctorat et de master.

Moritz C., **Meynard C.N.**, Devictor V., Guizien K., Labrune C., Guarini J.-M., Mouquet N. (2013) Disentangling the role of connectivity, environmental filtering, and spatial structure on metacommunity dynamics. Oikos 122: 1401-1410.

Dufour, C. M. S., **Meynard, C. N.**, Watson, J., Rioux, C., Benhamou, S., Perez, J., du Plessis, J. J., Avenant, N., Pillay, N. & G. Ganem (2015) Space use variation in co-occurring sister species: response to environmental variation or competition? PlosOne 10: e0117750.

Latinne, A., **Meynard, C. N.**, Herbreteau, V., Morand, S., Waengsothorn, S. & J. R. Michaux. (2015) Influence of past and future climate changes on the distribution of three Southeast Asian murine rodents. Journal of Biogeography, 42: 1714-1726.

Iturralde-Pólit, P., Dangles, O., Burneo, S.F. & **C. N. Meynard**. (2017) The effects of climate change impact on a mega-diverse country: predicted shifts in mammalian species richness and turnover in continental Ecuador. Biotropica 49: 821-831

Ouchi-Melo, L. S., **Meynard, C.N.**, Gonçalves-Souza, T., & D. de Cerqueira Rossa-Feres (2018) Integrating phylogenetic and functional biodiversity facets to guide conservation: a case study using anurans in a global biodiversity hotspot. Biodiversity & Conservation 27: 3247-3266.

Henckel, L., **Meynard, C. N.**, Devictor, V., Mouquet, N. & V. Bretagnolle (2019) On the relative importance of space and environment in farmland bird community assembly. PlosOne 14(3): e0213360.

Mémoire scientifique

Avant-propos et remerciements

« Pour qu'un amour soit inoubliable, il faut que les hasards s'y rejoignent dès le premier instant comme les oiseaux sur les épaules de saint François d'Assise »

Milan Kundera, dans « L'insupportable légèreté de l'être »

Quand j'ai commencé ma licence en biologie en 1995 à Santiago du Chili, j'avais en tête une carrière en biologie cellulaire. J'étais, en effet, attirée par un concept simpliste de la démarche scientifique où l'on recherche le corps de littérature existante, on se pose une question, on fait des expériences qui permettent d'y répondre, et le cycle recommence. Hélas, mes expériences en laboratoire m'ont démontré que le concept était (depuis ma perspective- et sans vouloir offenser personne) bien plus intéressante que la pratique.

Je dois remercier mes copains naturalistes, notamment Jean Paul de la Harpe et Andrés Charrier, et mes premiers tuteurs en écologie, Francisco Bocinovic et Ernst Hayek, qui m'ont laissé la porte ouverte à leur laboratoire ainsi qu'à maintes discussions, et m'ont encouragé à chercher des alternatives ; Juan Armesto qui, toujours avec une gentillesse irréprochable, m'a donné de bons conseils et un positivisme dont j'avais grand besoin, et m'a ouvert les portes de la « Senda Darwin », une station de recherche en plein milieu de la forêt tempérée de la Patagonie où se concoctaient les discussions scientifiques les plus intéressantes auxquelles j'ai pu participer. Trouver ma place comme une femme en science dans un Chili post-dictature ne s'avérait pas facile, mais c'est des personnes comme Juan et le Dr Hayek qui ont fait de tout ça une possibilité.

N'empêche que mes premières lectures d'articles scientifiques en écologie s'avéraient difficiles : des expériences où l'on ne peut pas contrôler tous les facteurs importants, des corrélations qui sont censées montrer des liens avec des hypothèses un peu obscures, des suppositions implicites dans des analyses compliquées, rien n'entrait dans le cadre de ce que j'avais initialement entendu comme la démarche scientifique classique. C'est donc dans cette recherche de nouvelle vocation que j'ai fini par lire, alors que je passais du temps à la Senda Darwin, un livre qui aura changé ma vocation : « The diversity of life » par E. O. Wilson (il faut dire, l'ambiance était aussi importante que le contenu du livre !).

C'est à partir de là que tout a pris du sens pour moi, et l'étude des patrons de diversité et des causes qui peuvent unir petites et larges échelles sont devenus la raison d'être de ma recherche ; je dois ensuite remercier Pablo Marquet, qui m'a pointé vers la macroécologie et tous les classiques qui ont pu m'inspirer, Fabian Jaksic et Juan Carlos Castilla, pour avoir donné du sens à des questions qui semblaient disparates, Sergio Navarrete pour m'avoir introduit au bonheur des stats multivariées, et les filles avec qui j'ai passé ensuite d'innombrables heures sur le terrain à monitorer des communautés d'oiseaux et de végétation dans les forêts rélictes de la côte chilienne : Olga Barbosa, Sharon Reid, Cynthia Cornelius, vous avez été d'une grande inspiration !

J'ai eu la chance de connaitre mon mari, alors que j'étais encore au Chili mais je venais d'accepter une Fulbright pour commencer un PhD à l'université de Californie à Davis. Je dois remercier le destin pour cette rencontre, remercier David d'avoir voulu retourner aux Etats-Unis alors qu'il en avait pas envie, et surtout je dois le remercier d'avoir été toujours là pour m'encourager dans les moments difficiles. Je remercie pareillement mon tuteur de thèse, Jim Quinn, qui a toujours cru en moi, avec ou sans évidence, et les nombreuses personnes à Davis qui ont aidé à ma formation : Alan Hastings, pour tout ce qui est des modèles mathématiques en écologie, et sa vision très éclairée sur l'écologie des populations ; Peter Chesson et Sharon Lawler, pour me montrer les diverses théories de coexistance en écologie ; Art Shapiro, avec sa passion pour la biogéographie, son enthousiasme infini, et sa bizarrerie assumée ; Susan Harrison pour sa vision macroécologique ; et Marcel Holyoak, pour m'avoir montré la voie des métacommunautés, qui a marqué ma recherche a posteriori ; j'oublie sûrement nombre d'autres personnes qui ont partagé des moments de discussions et de convivialité, en mélangeant discussions scientifiques et divagations multiples. Une pensée très spéciale va à Erin Espeland, qui a fait de confidente et assistante de terrain, guide culturel et copine avisée. Je ne peux pas croire que tu ne sois plus parmi nous !

Après un retour furtif au Chili, je me suis retrouvée à Montpellier pour trois ans de postdoc à l'ISEM, puis un recrutement INRA au CBGP à partir de 2010. Je dois remercier très particulièrement Nicolas Mouquet, sans qui je n'aurais pas connu tout le réseau de recherche qui a tellement contribué à ma croissance scientifique : David Mouillot, Vincent Devictor, Wilfried Thuiller, entre autres. Dans ce contexte, un grand merci va aussi très particulièrement à Wilfried, qui a soutenu mon financement à travers ma première grossesse, et qui a toujours organisé des ateliers de travails très productifs et conviviaux.

Je remercie mes collaborateurs actuels à Montpellier et ailleurs, qui font de mon travail un grand plaisir : Guillaume Fried, Nicolas Sauvion, Marie Pierre Chapuis, Maria Navajas, Gael Kergoat, pour ne nommer que quelques-uns. Un grand merci aux équipes éditoriales à *Ecography* et au *Journal of Biogeography*, plus particulièrement Miguel Araújo, Peter Linder et Michael Dawson, avec qui j'ai souvent des discussions très intéressantes qui me font penser au-delà de mon petit cercle de recherche pour sortir de ma bulle.

Finalement, je remercie le destin de m'avoir donné tous les privilèges dont je profite jour à jour, et qui font que je sois là où je suis. Et c'est ainsi que tous les oiseaux se sont réuni sur les épaules de Saint François d'Assise…

Contexte général

"Our efforts to develop theories of the way ecosystems or communities are organized must revolve around attempts to discover patterns that can be quantified within systems, and compared across systems"

Simon Levin (1992) Ecology 73: 1943-1967

Comment les espèces se répartissent dans le temps et dans l'espace, et pourquoi est-ce que certaines régions ont plus d'espèces que d'autres ? Voilà des questions qui sont fondamentales en écologie et en biogéographie, et qui ont été explorées par les fondateurs de nos disciplines. En 1869, Ernest Haeckel définissait l'écologie comme la discipline qui s'occupait de l'étude des interactions entre les organismes et l'environnement (Begon et al. 1996). James H. Brown définira plus tard la macroécologie comme une discipline, à l'intérieur de l'écologie, qui cherche à étudier ces relations entre organismes et environnement à grandes échelles spatiales ou temporelles à l'aide d'outils statistiques plutôt que de l'expérimentation, et qui cherche à introduire une approche écologique à des questions qui avaient été étudiées plus traditionnellement dans les domaines de l'écologie à petites[1] échelles, ou de la biogéographie à grandes échelles (Brown 1995). L'accent est mis sur l'intégration d'échelles spatiales (il faut trouver des patterns qui sont commun à plusieurs communautés), les outils statistiques, et des règles qui vont au-delà du local. La biogéographie est une discipline un peu antérieure, mais qui a surgit plus clairement comme une discipline cohésive à partir des années 60 et 70, notamment avec l'apparition en 1967 de la théorie d'équilibre de biogéographie des îles (MacArthur and Wilson 2016), la meilleure compréhension des effets du mouvement tectonique sur la géographie des répartitions des espèces, et les méthodes de reconstruction phylogénétique. La discipline sera ensuite consolidée par la publication d'un journal dédié (le *Journal of Biogeography* à partir de 1973) et l'apparition d'un grand classique de la biogéographie (première édition de Brown & Lomolino apparu en 1983). Il s'agit donc ici d'étudier à très large échelle les patterns de distribution et biodiversité, en intégrant biologie avec géographie, et en essayant souvent de comprendre le rôle du passé sur les patterns observés au présent (Brown and Lomolino 1998). Le but commun : comprendre les origines et diversification de la biote (Brown and Lomolino 1998).

Aujourd'hui, l'existence d'une technologie bien plus avancée et toujours en évolution pour caractériser les organismes (cf biologie moléculaire), leur environnement (cf télédétection), pour analyser leur interactions (cf puissance de calcul et de stockage), et pour stocker et partager de grands volumes d'information (cf internet et réseaux de médias sociaux) donne une nouvelle dimension à ces questions (Chave 2013). En effet, ces développements technologiques nous permettent de faire des analyses qui vont de petite à grande échelle avec une efficacité sans précédent, ainsi que de surveiller des systèmes naturels, cumuler et partager des données à niveau global, et diffuser des informations au large.

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[1] Je parle de petites ou grandes échelles dans le sens écologique (qui est l'inverse du sens géographique) : petite échelle = échelle locale ; grande échelle = échelle régionale.

De plus, les effets des interventions humaines sur la biodiversité actuelle et les services écosystémiques qui en découlent imposent qu'on puisse se poser des questions à niveau régional, souvent même à niveau global. En 1989, en acceptant le prix MacArthur, Simon Levin identifiait comme l'un des principaux défis pour pouvoir résoudre des problèmes appliqués en écologie (et en particulier par rapport aux changements globaux) le besoin d'intégrer différentes échelles de temps, d'espace et de niveau organisationnel (Levin 1992). Vingt ans plus tard, Jérôme Chave identifiait quatre disciplines qui avaient été avancées par rapport à ce défi (Chave 2013) : l'accouplement d'échelles écologiques et évolutives ; l'intégration entre échelles sur les changements globaux ; l'étude de la modularité dans les réseaux d'interaction ; et l'étude des patterns spatiaux de la biodiversité. En paraphrasant Chave, nous devons chercher des patterns pour caractériser les communautés au-delà des patterns de distribution d'abondances, si nous voulons affronter les défis imposés par les changements globaux.

Ma recherche se trouve quelque part à l'intersection de l'écologie, la macroécologie, et la biogéographie. Dans les chapitres qui suivent, j'espère montrer comment ma propre recherche s'insère dans ce contexte, et contribue avec un petit grain de sable à des problématiques qui vont du théorique à l'appliqué. Mon projet de recherche se décline en deux axes principaux, tous les deux liés à la compréhension des mécanismes qui maintiennent la diversité biologique à grandes échelles. Les deux axes qui seront détaillées ci-dessous sont : modélisation de la répartition des espèces (Chapitre 1) et relations biodiversité - environnement (Chapitre 2) ; dans une troisième partie je parlerai plutôt des applications dans le domaine de l'agriculture (Perspectives).

A l'intérieur de chacun de ces axes, ma stratégie de travail consiste à poser des questions qui permettent d'améliorer les méthodes d'analyse, souvent en utilisant soit des simulations (écologie virtuelle, voir Figure 1), soit des bases de données qui sont exceptionnellement bien renseignées. Dans un deuxième temps, j'applique ces méthodes sur des systèmes réels, souvent pour connaître les risques liés à certains ravageurs de cultures, et aux changements climatiques.

Pour chacune de ces deux axes j'aurai donc une section théorique et une section plus appliquée. Je finirai sur un chapitre de perspectives et conclusions.

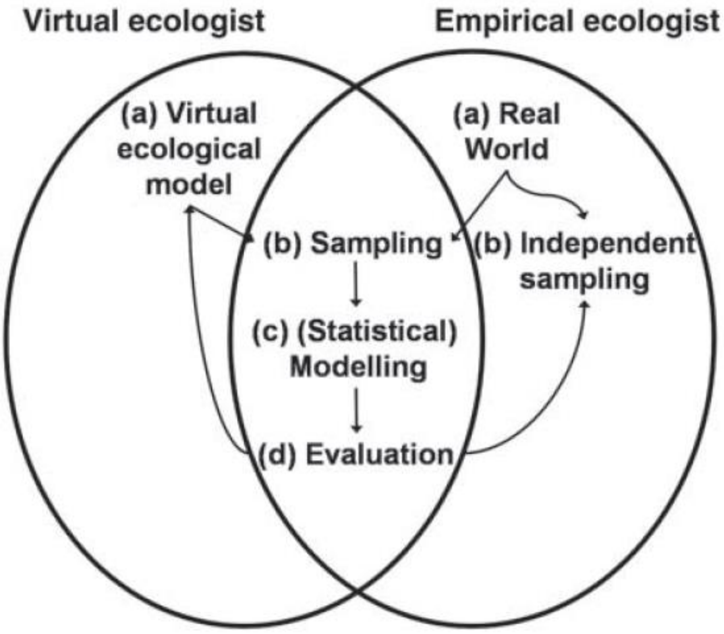

Figure 1 : Ecologie virtuelle : la génération de données artificielles permet de tester des méthodes statistiques en simulant des données, des stratégies d'échantillonnage, des processus écologiques ou / et des outils d'analyse. En effet, cette stratégie se révèle très utile à des échelles temporelles et spatiales macroécologiques où l'expérimentation n'est pas possible. Développer ou raffiner des méthodes avec des stratégies d'écologie virtuelle permet ensuite des applications dans le monde réel ou, à l'inverse, de générer des méthodes d'analyse qui sont mieux adaptées aux problèmes souvent trouvés avec des données imparfaites. Figure reprise de Zurrel et al (2010).

I- Répartition des espèces

La connaissance d'où se trouvent les espèces et qu'est-ce qui limite leur répartition est fondamentale depuis plusieurs points de vues (Brown and Lomolino 1998, Guisan and Thuiller 2005, Bellard et al. 2012). Dans le contexte de la conservation, nous avons intérêt à savoir où se trouvent les espèces en danger pour pouvoir choisir des réseaux de conservation appropriés au niveau régional, national, ou même global (Pressey 2004). Du point de vue de prévisions de risques, si nous voulons évaluer le potentiel d'une nouvelle espèce pour envahir une région où elle pourrait être introduite ou dans laquelle elle se trouve en expansion, souvent cette évaluation commence par poser la question « est-ce que le climat est propice à son établissement dans cette région » ? Il s'agit donc, dans ce contexte, de savoir quelle serait sa répartition potentielle étant donné ses tolérances climatiques (Gallien et al. 2010). Du point de vue de prévisions face aux changements globaux (y-inclus réchauffement climatique, changements d'utilisations des sols, fragmentation du paysage, etc.), nous voulons connaître les changements potentiels d'aires de répartition d'espèces d'intérêt pour la conservation, d'espèces invasives, d'espèces d'intérêt agricole, par exemple, sous différents scénarios de changements environnementaux (Araújo et al. 2004, Araújo and Rahbek 2006). Dans tous ces contextes, l'étude de la répartition de ces espèces individuellement suppose une connaissance géographique des occurrences actuelles de l'espèce d'intérêt, et une relation entre ces occurrences et les conditions environnementales (souvent limitées au climat quand il s'agit de grandes échelles, mais parfois des données d'utilisation des sols sont inclues).

Mes études de la répartition des espèces à grande échelle ont commencé avec des modèles conceptuels assez simples basés sur des descriptions générales trouvées dans la littérature (par exemple, on sait qu'une telle espèce se trouve à moins de 1000 mètres d'altitude, dans des zones semi-désertiques, entre les latitudes 28°S et 31°S). En combinant ces descriptions avec des cartes d'altitude, végétation et autres, et en consultant des experts de chaque taxon, ces descriptions peuvent être traduites en cartes de répartition à l'aide d'un système d'information géographique (SIG) (Meynard et al. 2004). Cependant, faute d'une analyse statistique complémentaire, cette stratégie ne nous permet pas d'établir une relation entre distribution et environnement, et donc d'envisager des changements de répartition sous différents scénarios environnementaux.

Pour aller plus loin, il faut donc modéliser la répartition des espèces par rapport aux gradients environnementaux d'intérêt. Il s'agit ici de mettre en relation des données d'occurrences d'espèces d'intérêt avec des gradients environnementaux à travers des modèles statistiques souvent appelés « Species Distribution Models » (SDM[2]). Cette stratégie est aujourd'hui considérée comme la stratégie de prévision la plus importante en écologie (Dawson et al. 2011, Bellard et al. 2012). En effet, en caractérisant la relation actuelle entre occurrences et environnement, cette information peut ensuite être utilisée pour prévoir des changements potentiels dans la distribution d'une espèce sous des scenarios de changement climatique, pour prévoir des aires géographiques qui seraient vulnérables à l'invasion d'espèces

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[2] Ce genre de modèle de répartition corrélatif est aussi connu comme modèle de niche (ENM) ou modèle d'enveloppe climatique. Dans le reste du rapport je n'utiliserai que « SDM » puisque je mets l'accent sur la traduction du modèle sur une carte de répartition plutôt que sur le concept de niche. Voir par exemple (Soberón 2010) pour une discussion de la nomenclature.

introduites à partir d'autres régions, ou même pour comprendre le potentiel invasif relatif de deux taxons similaires (Figure 2).

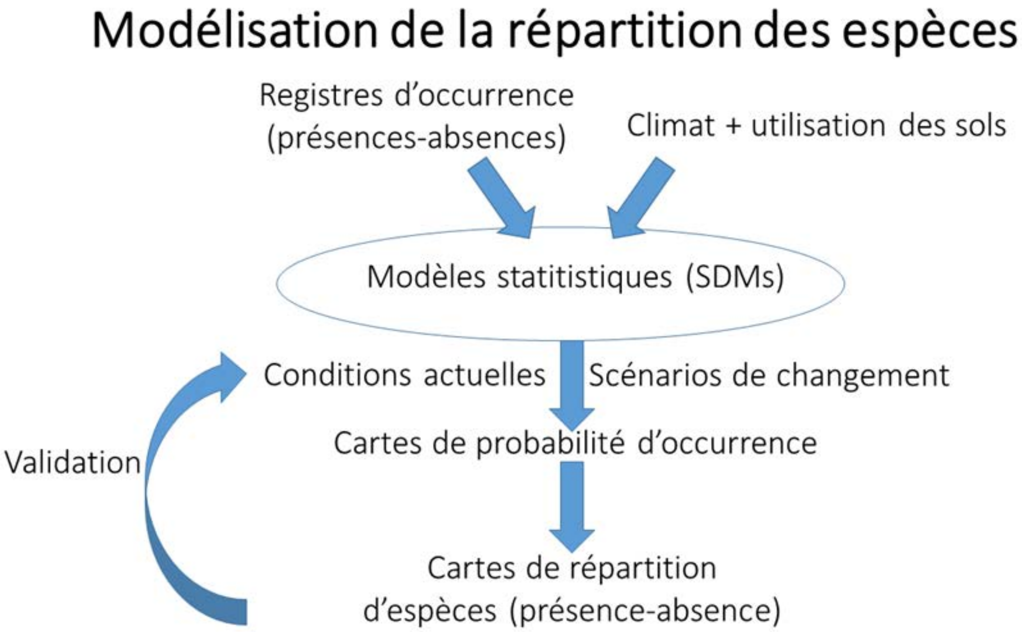


Figure 2: Schéma général de la modélisation de la distribution des espèces par des modèles corrélatifs (connus par leur sigle en anglais comme SDM)

Même si ce genre de modèle a été critiqué à maintes reprises à cause de leurs simplifications extrêmes (par exemple, on suppose que la distribution des espèces est en équilibre avec leur environnement, que les occurrences utilisées représentent la variabilité dans la réponse occurrence-environnement à l'intérieur de l'espèce ou du groupe taxonomique modélisé, et que cette réponse est conservée aux échelles de temps concernés par la modélisation, entre autres), ils présentent le gros avantage d'avoir besoin d'informations qui sont aujourd'hui largement disponibles en ligne. Les données environnementales, notamment les données climatiques, sont aujourd'hui facilement téléchargeables à échelle globale avec des résolutions de 1km (Hijmans et al. 2005, Kriticos et al. 2012), et les données d'occurrence peuvent être téléchargées de sources telles que le Global Biodiversity Information Facility (GBIF) ou peuvent être compilées à partir de la littérature, des données de muséum, ou de campagnes de terrain.

C'est donc dans le contexte de la modélisation à l'aide de SDMs que je présenterai mes travaux sur cet axe, tout d'abord d'un point de vue théorique, puis sur les aspects les plus appliqués.

Volet théorique : espèces virtuelles et test de méthodes

De multiples choix méthodologiques sont nécessaires au cours du processus de modélisation, dont certains peuvent avoir un impact important sur les résultats de prévision. Or, les échelles d'application des SDM, souvent au niveau régional, voire global, empêche l'utilisation de l'expérimentation pour le test et développement de méthodes. Dans ce contexte, les espèces virtuelles, c'est-à-dire l'utilisation de simulations impliquant une espèce fictive pour laquelle nous avons une connaissance parfaite de ses relations occurrence-environnement et d'autres caractéristiques pertinentes, sont devenues de plus en plus populaires pour tester les SDMs. Cette approche fournit un cadre écologique virtuel simple dans lequel tester les propriétés du modèle, ainsi que les effets des différents choix méthodologiques, et permet de maîtriser les effets de facteurs ciblés avec une grande certitude (Figure 3). Cette simplification est donc très utile pour la mise en place de normes de modélisation et de principes de bonnes pratiques.

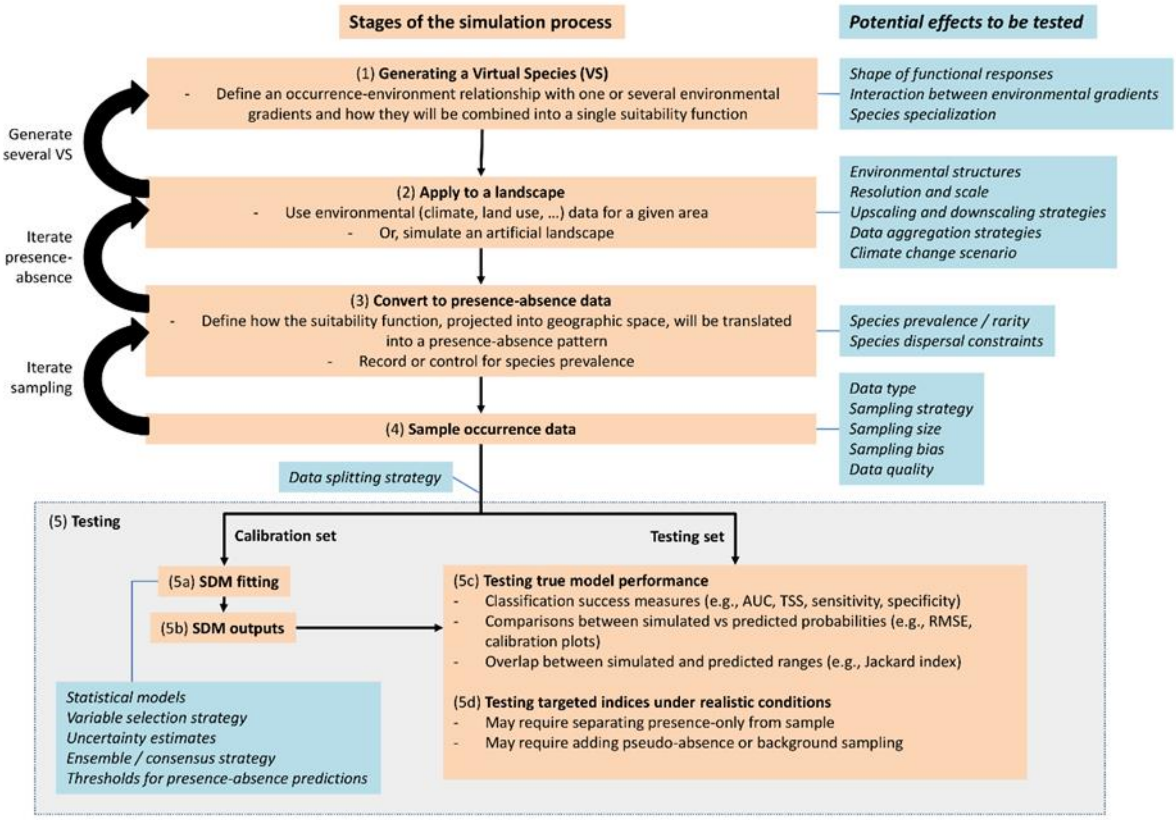


Figure 3: Différentes étapes de la génération d'une espèce virtuelle, avec les questions qui peuvent être étudiées à chaque phase de la modélisation à l'aide de la stratégie de l'écologie virtuelle. Figure extraite de Meynard et al. 2019 dans Ecography.

Ma contribution dans ce domaine a commencé avec une étude de l'influence du type et complexité de la relation occurrence-environnement sur la performance prédictive des modèles (Meynard and Quinn 2007). Dans ce contexte, j'ai généré plusieurs types d'espèces artificielles qui répondaient à l'environnement avec différentes courbes fonctionnelles. Cette approche, qui rentre dans la logique plus large de l'approche de l'écologie virtuelle (Zurell et al. 2010), a l'avantage de simuler une situation tout en contrôlant les facteurs qui pourraient déterminer la performance des modèles statistiques, ce qui ne serait pas possible sur le terrain. Ces espèces artificielles étaient donc « semées » dans un paysage réel, celui de la Californie, sous un environnement contrôlé (Figure 4). J'ai ensuite échantillonné (artificiellement) le paysage d'une façon aléatoire pour tester quel modèle statistique pouvait reconstituer les patterns de distribution avec le plus de succès pour les divers types d'espèces. Cette stratégie m'a permis de montrer qu'il n'y a pas un modèle statistique qui soit le meilleur dans toutes les circonstances. Au contraire, les modèles basés sur des relations linéaires type GLM et GAM démontrent une meilleure performance sur des espèces qui ont des relations occurrence-environnement qui se conforment à ce genre de relations, alors que les arbres de classification (CART) et ceux basés sur l'intelligence artificielle (GARP) sont plus performants quand il s'agit de caractériser des relations seuil ou avec beaucoup d'interactions (quoi que, dans le contexte de cette étude finalement GARP ne démontrait pas vraiment d'avantages par rapport aux autres modèles testés, voir Meynard & Quinn, 2007).

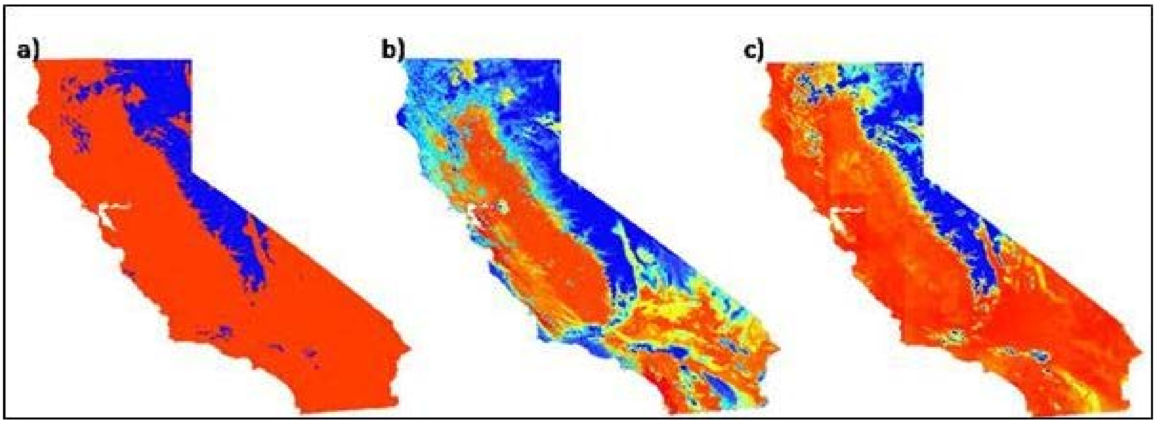


Figure 4: Comparaison de la probabilité d'occurrence d'une espèce artificielle (a) avec les prédictions générées avec deux modèles d'enveloppe climatique: (b) GARP; (c) Modèle Linéaire Généralisé (GLM). Les couleurs rouges indiquent une grande probabilité d'occurrence, alors que les couleurs froides indiquent une faible probabilité d'occurrence. Les résultats indiquent que les GLM et les GAM sont en général beaucoup plus performants que les arbres de régression et que GARP (voir Meynard & Quinn 2007).

Cette étude s'en ai suivi avec un article publié en 2012, où nous avons exploré l'idée qu'une réponse du type seuil permettrait de prévoir avec bien plus de certitudes l'aire de répartition d'une espèce comparé avec une espèce qui aurait une réponse graduelle (Meynard and Kaplan 2012). Cette série de simulations nous ont permis surtout de révéler que l'un des principaux indices utilisés pour mesurer la capacité prédictive des SDMs, le AUC, n'est pas adapté à des situations dans lesquelles la réponse environnement-occurrence est graduelle plutôt que seuil. En effet, quand la réponse est graduelle, la sortie du modèle devrait être interprétée dans un contexte probabilistique : si la probabilité d'occurrence sur un site est de 0,1, on retrouvera 1 site sur 10 de caractéristiques environnementales identiques qui sera occupé, et les 9 autres seront vides. Un modèle qui serait donc parfait théoriquement pourrait prédire très bien la probabilité d'occurrence sur ce site. Par contre, si on veut prédire la présence ou absence, on aura toujours une chance de nous tromper (Figure 5). Aussi, la performance des modèles n'est pas aussi dépendante de la prévalence de l'espèce modélisée comme les études antérieures laissent entendre, mais surtout dépend de la correspondance entre la prévalence réelle de l'espèce modélisée et la prévalence sur l'échantillon utilisé pour la modélisation (Meynard and Kaplan 2012).

Finalement, en écrivant ce manuscrit, nous avons détecté un problème assez fondamental dans la façon dans laquelle les simulations d'espèces virtuelles étaient faites dans un bon nombre de publications récentes. Ce constat, avec un commentaire des principes fondamentaux des méthodes de simulation dans ce domaine, ont fait l'objet d'un article éditorial au *Journal of Biogeography* (Meynard and Kaplan 2013) qui souligne les avantages et problèmes liés à cette approche de façon très synthétique. Une collaboration avec Boris Leroy (MNHN, Paris) a ensuite permis de mettre en place un package pour le logiciel R qui facilite la simulation des espèces virtuelles (Leroy et al. 2016), ainsi que de pointer vers d'autres indices de succès prédictif, notamment ceux basés sur la similarité des distributions, ainsi que l'importance d'avoir de bonnes données d'absences pour évaluer les SDMs (Leroy et al. 2018). Malgré ceci, la stratégie de simulation continue à poser des problèmes d'interprétation , et c'est un domaine qui est en développement constant.

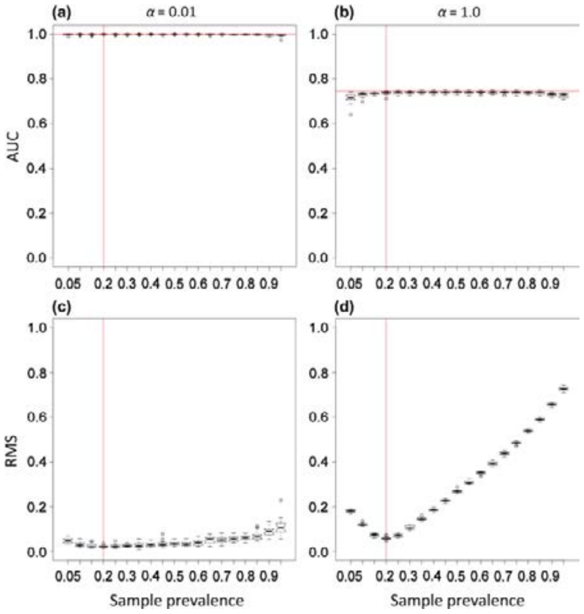


Figure 5: Capacité prédictive en terme de classification de présences-absences (AUC) ou probabilités d'occurrence (RMS) au dépend de si l'espèce présente une réponse seuil (alpha = 0.01, colonne de gauche) ou graduelle (alpha = 1, colonne de droite) face au gradient environnemental. Quand la réponse est de type seuil, on arrive à prédire parfaitement bien les présences absences, aussi bien que les probabilités d'occurrence. Quand la réponse est graduelle, on arrive à prédire très bien les probabilités d'occurrence (RMS proche de 0), surtout si la prévalence de l'échantillon utilisé pour la modélisation correspond à la prévalence réelle de l'espèce. Par contre, le pattern de présence-absence ne peut pas être récupéré à la perfection, et la valeur de AUC (succès de classification) a une valeur maximale théorique qui est inférieure à 1.

Le volet « espèces virtuelles » est un volet qui est toujours en développement et continuera à l'être dans ma recherche future. Dans un de mes articles les plus récent (Meynard et al. 2019) nous révisons ce que l'approche a contribué et peut encore contribuer dans ce domaine, et nous donnons des recommandations concrètes pour standardiser les méthodes de simulation. Il s'agit d'un article qui a été choisi pour apparaitre dans un numéro spécial des E4 Awards de *Ecography*. Aussi, dans une collaboration avec David Kaplan (MARBEC, Sète) nous préparons un article sur le problème des échelles spatiales dans la modélisation des répartitions, à l'aide d'une approche d'espèces virtuelles. Finalement, dans le contexte de prévisions de risques liés aux ravageurs agricoles, je développe une méthode qui combine simulations et données réelles, pour optimiser la valeur prédictive des modèles construits avec des données typiquement disponibles dans le contexte agricole.

En résumé, l'utilisation des espèces virtuelles est un axe prometteur qui permet de développer des méthodes et répondre à des questions théoriques en lien avec les SDMs.

Volet appliqué

En ce qui concerne l'application des SDMs, depuis mon recrutement à l'INRA en 2010 j'ai travaillé sur ce volet pour répondre à des questions biogéographiques aussi bien qu'agricoles. Les publications associées incluent des questions de différenciation de la niche environnementale entre espèces ou sous-espèces phylogénétiquement proches (Ganem et al. 2012, Meynard et al. 2012a, 2013a, Latinne et al. 2015, Meynard et al. 2017), des questions sur la biogéographie et conservation de certaines espèces (Meynard et al. 2009, Monsarrat et al. 2015, 2016, Latinne et al. 2015), sur les effets du changement climatique sur la diversité

(Albouy et al. 2015, Iturralde-Pólit et al. 2017), et des efforts de modélisation pour étudier le risque agricole (Meynard et al. 2013a, 2017). Ces publications incluent des co-auteurs d'origines diverses, aussi bien que des régions et systèmes d'étude assez différents.

Je développerai en un peu plus en détail l'exemple du criquet pèlerin, qui, me semble, touche plusieurs de ces domaines. Il s'agit d'un travail qui est le fruit d'une collaboration, avec Marie-Pierre Chapuis (Cirad, CBGP), ainsi qu'avec un réseau d'experts acridiens qui travaillent sur la gestion des pullulations de criquets en Afrique du Nord. Dans un premier temps nous avons cherché à modéliser la répartition actuelle des deux sous-espèces connues de nos jours pour prévoir les changements potentiels de répartition sous différent scénarios de changements climatiques pour cette espèce qui peut générer des dégâts agricoles très conséquents (Meynard et al. 2017). Ceci nous a permis d'évaluer le risque potentiel au futur lié à ce ravageur de cultures.

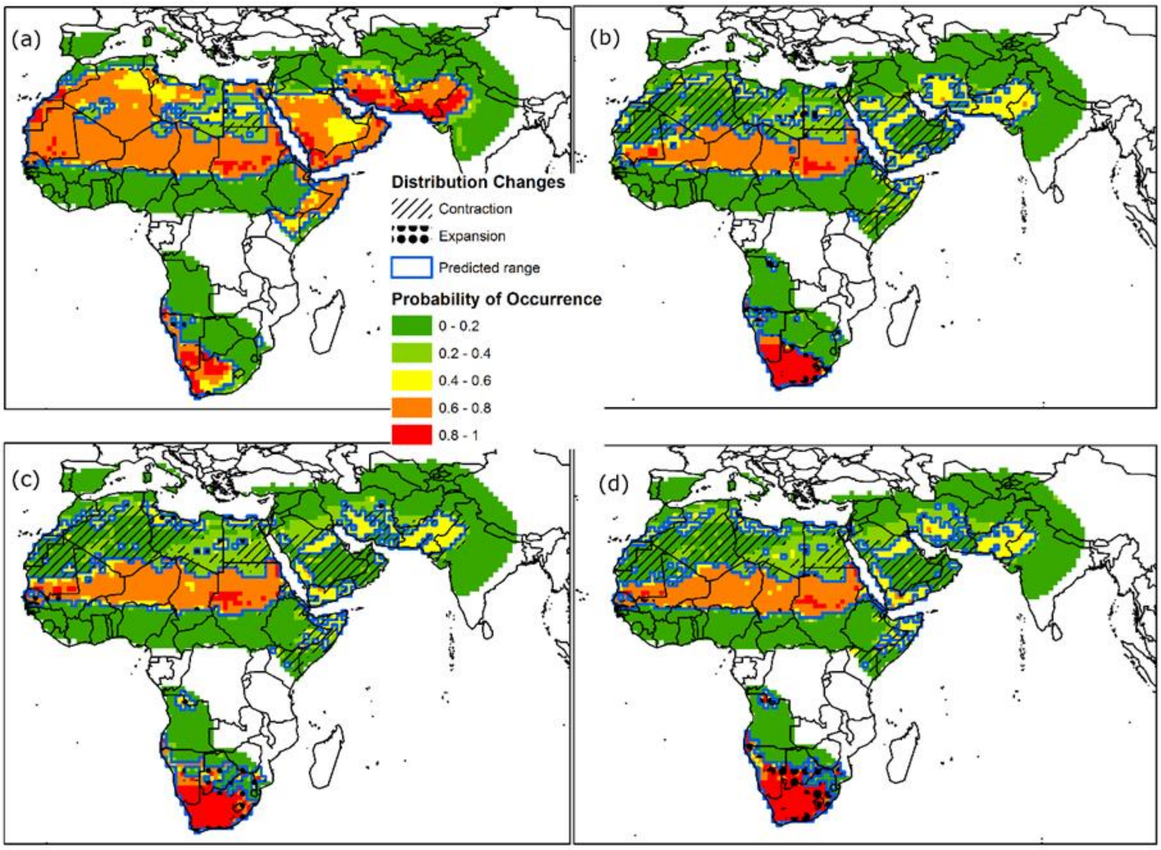


Figure 6: Prédictions des changements de répartition sous deux scenarios de changements climatiques (A1B à gauche, A2 à droite), pour deux horizons temporels (2050 ligne supérieure, 2090 ligne inférieure). Le contour bleu représente la répartition prédite pour chaque scénario; les régions striées correspondent à des zones de contraction (l'espèce disparaît) par rapport aux conditions actuelles; les pointillés sont des zones d'expansion par rapport aux conditions actuelles. Au nord, S. g. gregaria; au sud S. g. flaviventris. Figure prise de Meynard et al (2017).

L'un des résultats de ce travail a été de porter attention sur la sous-espèce sud-africaine, *Schistocerca gregaria flaviventris*, qui n'est pas aujourd'hui problématique dans le contexte agricole, mais qui risque d'étendre son aire de répartition au futur (Figure 6). Mais cet effort nous a permis aussi de nous poser la question de différentiation de niches environnementaux entre les deux sous-espèces. En effet, des analyses de superposition et différentiation de niche (Broennimann et al. 2012) suggèrent qu'il n'y a pas eu de différentiation de niche entre les deux sous-espèces, et que les différences observées dans les climats occupés entre les deux clades sont très probablement le résultat de la disponibilité différentielle de climats similaires dans les deux régions (l'aire de répartition pour la sous-espèces au sud représentant un sous-ensemble des conditions climatiques disponibles pour la sous espèce du nord). En continuation avec cette collaboration, une analyse plus approfondie de la différenciation moléculaire, ainsi que des projections d'aires de répartition dans le passé (Holocene et dernier maximum glaciaire) suggèrent que la différentiation entre ces deux clades est assez récente (~6000 BP), et qu'elle a pu être le résultat d'un évènement de dispersion isolé d'une population du nord vers le sud, plutôt qu'une fragmentation d'une espèce qui aurait été connectée au sud et au nord pendant des périodes de changements climatiques passés (Chapuis et al, soumis à PCI). Ici donc, l'application de la stratégie de SDM a permis de répondre à une question appliquée (risque agricole sous des scénarios de changement climatique) mais aussi de mieux comprendre l'origine biogéographique des deux clades.

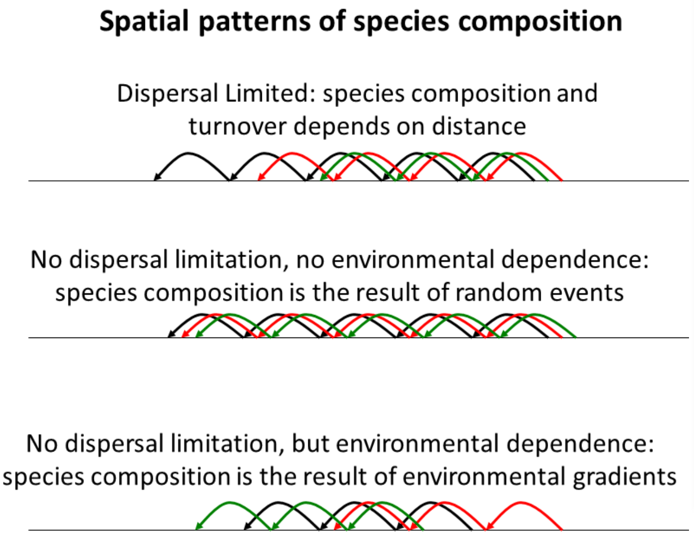
Ce volet de ma recherche a donc fait partie centrale, et restera centrale, dans ma recherche à futur. La gamme de publications montre bien la diversité de systèmes étudiés, de collaborations au niveau national et international, et du développement au niveau théorique et appliqué de ma recherche. Parmi les projets de collaboration en cours, je travaille par exemple, avec Nicolas Sauvion (BGPI, Montpellier) pour modéliser la répartition de différentes plantes hôtes de la famille *Prunus* (ex. prûnier, arbricotier), des arbres frutiers de grande importance économique en Europe, et de deux espèces de psylles, insectes hémiptères qui transmettent une maladie bactérienne (jaunisse des fruit). La modélisation conjointe de la plante hôte et du vecteur permettra alors de mieux évaluer la vulnérabilité des cultures faces aux changements climatiques.

II- Biodiversité

Comprendre comment se distribue la diversité biologique à grandes échelles est une question intéressante et parfois centrale sous au moins deux points de vue.

Tout d'abord, sous un point de vue biogéographique, c'est une question centrale pour comprendre les origines de la biodiversité (voir par exemple Hutchinson 1959). S'il y a plus d'espèces sous les tropiques que vers les pôles, s'agit-il d'une limitation métabolique ou évolutive liée à l'adaptation au froid, ou plutôt à un manque de stabilité environnementale plus importante à travers les temps géologiques dans les régions froides ? Hawkins, en faisant la révision des théories qui avaient été publiées pour expliquer ce gradient de diversité latitudinal en a dénommé plus d'une vingtaine d'hypothèses (Hawkins 2004), souvent alliant l'aléatoire aux explications liées aux gradients environnementaux, les taux évolutifs, la compétition et les dynamiques de dispersion et isolement. En parallèle, un gros corps de littérature s'est développé en écologie des communautés en essayant d'identifier des règles d'assemblage (Keddy and Weiher 1999) : est-ce que les communautés dans les tropiques ont quelque chose en commun avec les communautés dans les zones tempérées, par exemple ? Ce corps de littérature a, lui aussi, allié des processus aléatoire, compétitifs et de filtres environnementaux, mais a mis l'accent sur les contraintes écologiques, laissant de côté les aspects évolutifs. Dans l'esprit de la réflexion de Levin (Levin 1992), commencent ensuite à surgir des corps conceptuels essayant d'unir petites et larges échelles temporelles et spatiales, notamment avec la théorie neutre de la biodiversité (Hubbell 2001) et la théorie des métacommunautés (Holyoak et al. 2005). Dans ce contexte, l'un des grands défis pour appliquer ce cadre théorique est de relier les paradigmes écologiques à des données empiriques qui sont souvent moins que parfaites (Logue et al. 2011). Les approches le plus souvent utilisées dans ce domaine combinent des analyses de la structure spatiale des patterns de diversité (Figure 7), avec l'analyse de structure de la diversité phylogénétique ou fonctionnelle (Figure 8).

Le deuxième point de vu pour lequel la cartographie de la biodiversité peut être intéressant c'est celui de la conservation. En effet, connaître la répartition des zones les plus riches en espèces est une donnée initiale importante pour planifier la conservation à grandes échelles (Mittermeier et al. 2003). Les efforts initiaux dans cette direction ne considéraient que le nombre d'espèces (protection des « hotspots ») et leur complémentarité (il faut protéger des espèces qui ne sont pas encore représentées dans les réseaux de conservation). A partir des années 90s, il y a aussi une constatation qui est encore aujourd'hui en train de bouleverser l'écologie de la conservation. C'est le fait que les espèces sont différentes entre elles, certaines peuvent avoir un rôle fondamental sur un processus écosystémique ou être uniques du point de vue évolutif. La disparition d'une telle espèce n'est donc pas équivalente à la disparition d'autres espèces qui sont plus communes ou qui se trouvent dans des familles diverses avec multiples représentants, et la richesse spécifique se révèle donc insuffisante pour caractériser la biodiversité dans des buts de conservation. C'est ainsi que, de plus en plus, aujourd'hui les efforts de conservation de la biodiversité cherchent à intégrer la diversité en termes de nombre d'espèces (diversité taxonomique ou richesse spécifique), la diversité phylogénétique (représentation de différents clades ou branches évolutives) et la diversité fonctionnelle (représentant différents traits d'histoire de vie ou stratégies écologiques).



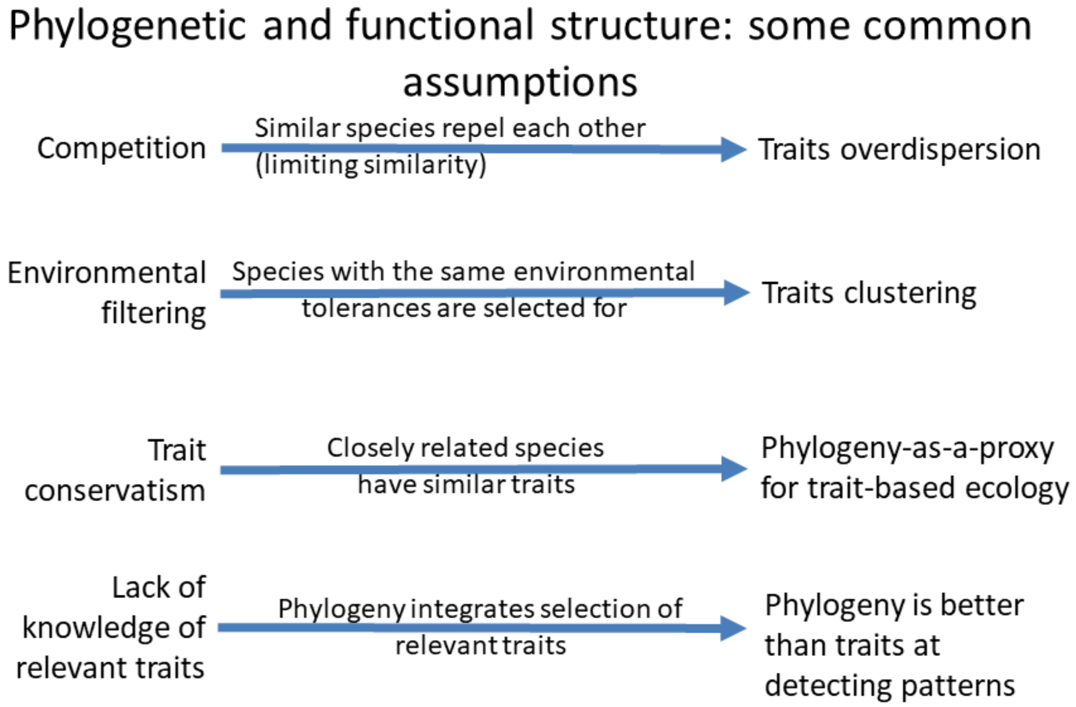
Spatial patterns of species composition

Dispersal Limited: species composition and turnover depends on distance

No dispersal limitation, no environmental dependence: species composition is the result of random events

No dispersal limitation, but environmental dependence: species composition is the result of environmental gradients

Figure 7 *: Analyse des patterns spatiaux pour déterminer le rôle des filtres environnementaux versus la dispersion dans la composition des communautés. Les fleches de chaque couleur représentent des espèces qui ont une capacité de dispersion plus ou moins fortes. Dans les trois cas de figure, on suppose que le pattern d'autocorrélation spatiale dans la composition des communauté peut être due à des limitations de dispersion (premier cas), il y a absence de structure spatiale (deuxième cas), ou elle est due à la similarité des environnements (troisième cas)*



Phylogenetic and functional structure: some common assumptions

Competition — Similar species repeal each other (limiting similarity) → Traits overdispersion

Environmental filtering — Species with the same environmental tolerances are selected for → Traits clustering

Trait conservatism — Closely related species have similar traits → Phylogeny-as-a-proxy for trait-based ecology

Lack of knowledge of relevant traits — Phylogeny integrates selection of relevant traits → Phylogeny is better than traits at detecting patterns

Figure 8: *Suppositions et analyses liées à la structure phylogénétique et fonctionnelle des communautés.*

Dans ce qui suit, je présenterai ma recherche d'abord en ce qui concerne les patterns de diversité à grande échelle, puis, dans un deuxième temps, je parlerai des métacommunautés.

Diversité

Dans mes premières études en lien avec la diversité à grandes échelles, mon intérêt principal était la conservation. C'est ainsi que pendant ma thèse j'ai cherché à modéliser la répartition d'oiseaux de la forêt tempérée du Chili, pour ensuite générer des alternatives de conservation basées sur une stratégie d'optimisation : choisir un réseau d'aires pour la conservation dont l'aire totale est minimisée tout en protégeant toutes les espèces d'intérêt. Cet exercice de planification de la conservation (sensu Pressey 2004) a montré qu'une limitante importante pour la protection des oiseaux dans cette région est liée à la protection de la végétation méditerranéenne, en particulier dans la zone centrale du pays où le développement économique est le plus concentré (Figure 9). En effet, les aires de conservation sont pratiquement inexistants dans la région méditerranéenne du pays, alors que les zones tempérées sont bien mieux couvertes par le système national de protection (Meynard et al. 2009). Dans un travail postérieur, en étudiant les communautés de chauve-souris dans les forêts tempérées, nous avons à nouveau montré que l'une des limitantes les plus importantes pour la conservation dans cette région est liée à l'exploitation des forêts. Il s'avère donc fondamental d'allier stratégies de développement économique avec les stratégies de conservation (Meynard et al. 2007).

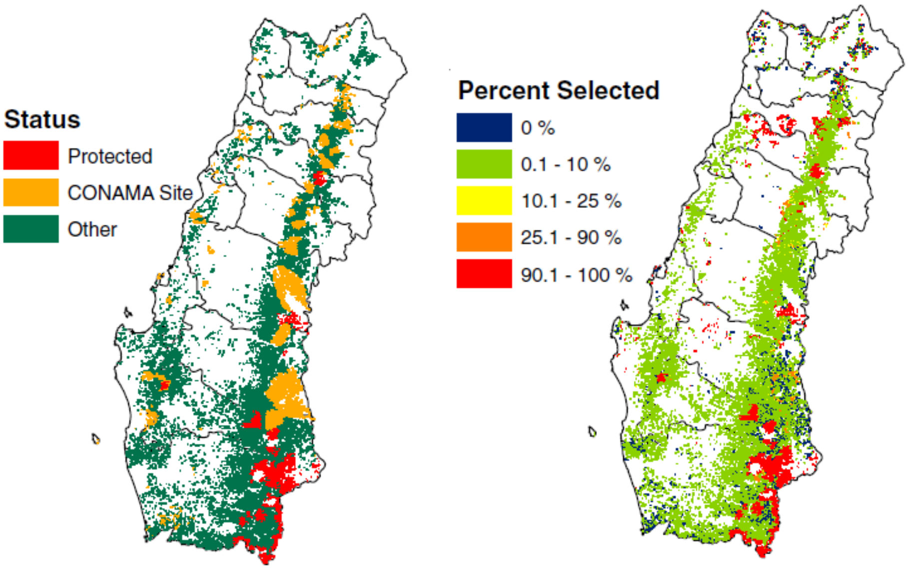


Figure 9 : Exercice de planification systématique de la conservation au centre-sud du Chili. A gauche, une carte des forêts existantes en dehors du réseau de conservation (vert), dans le système d'aires protégées de l'état (rouge) ou dans des sites qui avaient été désignés comme prioritaires pour la conservation par la commission nationale de l'environnement (jaune) ; à droite, le résultat de l'un des exercices de planification systématique qui montre en rouge les sites qui sont irremplaçables et qu'il faudrait donc prioriser pour la conservation. Les quelques rémanents de forêt dans la vallée centrale au nord de la zone d'étude ressortent comme particulièrement importants dans ce contexte.

Au-delà de ces efforts de conservation localisés au sud du Chili, mes études sur les oiseaux de France (Devictor et al. 2010, Meynard et al. 2011, Monnet et al. 2014), des poissons de la Mer Méditerranée (Meynard et al. 2012b, Albouy et al. 2015, Granger et al. 2015a) des mammifères marin au niveau global (Albouy et al. 2017), et d'amphibiens en Amazonie (Ouchi-Melo et al. 2018) ont montré que de façon assez générale la diversité taxonomique, phylogénétique et fonctionnelle ne se répartissent pas tout à fait de la même façon, même si les corrélations peuvent être souvent assez fortes entre ces trois facettes. Par exemple, une collaboration avec une étudiante au Brésil a permis de montrer que les zones prioritaires pour la conservation des amphibien au Cerrado du Brésil n'incluent pas des sites qui abritent des espèces qui sont uniques du point de vue phylogénétique et fonctionnel, démontrant une fois encore l'importance de considérer les trois facettes de la diversité dans les efforts de planification de la conservation au niveau national (Ouchi-Melo et al. 2018).

Dans le contexte macroécologique, le cas des études des communautés d'oiseaux de France peut démontrer comment, en ayant un jeu de donné de longue durée et de qualité pour une région assez large, on peut étudier plus en profondeur les relations entre différentes facettes de la diversité et les gradients environnementaux. Dans un premier travail en collaboration avec Vincent Devictor, entre autres, nous avons utilisé des données à haute résolution sur la distribution spatiale des oiseaux à l'échelle du pays pour analyser la répartition des trois facettes de la diversité. Nous avons constaté une importante discordance spatiale entre chaque composante de la biodiversité (diversité taxonomique, phylogénétique et fonctionnelle). Nous avons en outre révélé une représentation inégale de chaque composante dans les aires protégées: la diversité fonctionnelle était nettement sous-représentée, tandis que la diversité taxonomique était nettement surreprésentée dans les aires protégées (Devictor et al. 2010). Nos résultats remettent en cause l'utilisation d'une composante de la diversité en tant que substitut d'autres composantes et soulignent la nécessité d'adopter une approche intégrative de la conservation. Dans une deuxième étude (Meynard et al. 2011), nous avons utilisé les même données pour tester dans quelle mesure les hypothèses macroécologiques reliant la diversité aux facteurs environnementaux peuvent être extrapolées aux diversités fonctionnelles et phylogénétiques, c'est-à-dire dans quelle mesure les traits fonctionnels et les contextes évolutifs varient selon les espèces dans une communauté ou une région. Nous avons donc utilisé une partition spatiale de la diversité où la diversité régionale ou γ est calculée en agrégeant des informations sur les communautés locales, la diversité locale ou α correspond à la diversité d'une localité, et le turnover ou diversité β correspond au turnover moyen entre les localités et la région. Nos résultats soutiennent généralement l'idée que les hypothèses macroécologiques précédemment appliquées à la diversité taxonomique, aux niveaux local et régional, peuvent être étendues à la diversité phylogénétique et fonctionnelle, avec des stratégies d'analyses similaires qui peuvent être adaptées aux nouvelles facettes (Figure 10). Aussi, les changements dans la diversité régionale résultent de changements dans les diversités locales et sont liées au turnover. On révèle que certaines conditions environnementales, telles que l'utilisation des sols liés au développement humain, ont un impact considérable sur les niveaux de diversité, et les paysages hétérogènes ont tendance à avoir des niveaux de diversité plus élevés. Finalement, ce travail a été poursuivi à travers une collaboration avec une étudiante de doctorat, qui a montré que les trois facettes de la diversité évoluaient de façon différente à travers le temps (Monnet et al. 2014). En effet, ces résultats suggèrent que la diversité taxonomique a augmenté au niveau régional, principalement dû à l'homogénéisation des communautés grâce à quelques espèces qui sont bien adaptées aux activités humaines et deviennent donc cosmopolites. Par contre, en regardant la diversité fonctionnelle, on constate un turnover fonctionnel qui a tendance à diminuer dans le temps.

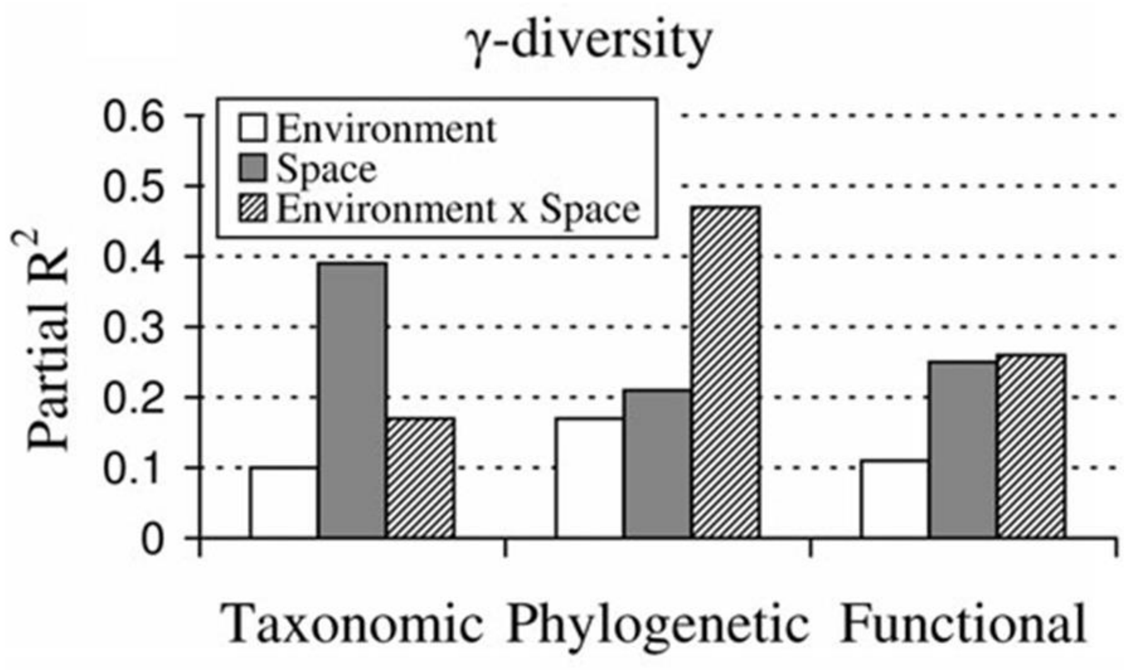


Figure 10 : Stratégie de partition de la variance appliquée aux trois facettes de la diversité. Dans tous les cas, l'interaction entre environnement et structure spatiale est importante, mais la portion varie d'après la facette considérée. Figure prise de Meynard et al (2011).

Ces études m'ont souvent amenée à poser des questions sur l'efficacité et la pertinence des indices de diversité qui sont utilisés dans ce contexte. C'est ainsi que, en collaboration avec Nicolas Mouquet et Vincent Devictor, nous avons rassemblé en 2010 une vingtaine d'experts dans cette thématique pour un atelier de travail sur la diversité phylogénétique. Cet effort s'est culminé par un colloque qui a duré une journée et a rassemblé presque 200 participants, mais aussi avec la rédaction d'un article de révision sur les applications et perspectives de la diversité phylogénétique (Mouquet et al. 2012). Par ailleurs, en collaboration avec Bastien Mérigot et son étudiante, Victoria Granger, nous avons étudié la pertinence des stratégies de cartographie des différents indices sur les poissons de la mer Méditerrannée. Et, en collaboration avec Francesco de Bello nous avons montré des problèmes conceptuels liés à la partition de la diversité en α, β, et γ (de Bello et al. 2010). Toutes ces études montrent que, globalement, il reste encore beaucoup à faire pour développer des indices de diversité qui soient adaptés à la fois à la théorie écologique et aux données récoltées sur le terrain.

Finalement, un dernier volet de mes études de diversité à cette échelle est en lien avec les prévisions face aux changements globaux. En effet, les modèles de distribution présentés dans la première partie peuvent être utilisés pour générer des prévisions face à différent scenarios de changements. Ensuite, les prévisions de répartition pour chacune de ces espèces peuvent être superposées dans une région et combinées avec des informations phylogénétiques ou fonctionnelles pour générer des cartes de répartition de la diversité taxonomique, phylogénétique et fonctionnelles sous différents scenarios. C'est ainsi que, par exemple, une de mes étudiantes de M2 a rassemblé des informations d'occurrence des mammifères en Equateur à partir de données de muséum. Elle a ensuite modélisé la répartition potentielle de 230 espèces, puis projeté leur répartition sous différents scenarios de changement climatique. Toutes les prédictions, y compris les scénarios les plus conservateurs en termes de dispersion et de changement climatique, incluent des changements majeurs prévus dans la répartition de la diversité des espèces de mammifères en Equateur. Les primates pourraient être les plus gravement touchés car ils auraient moins de zones convenables que d'autres mammifères (Iturralde-Pólit et al. 2017). Dans un esprit similaire, mais en alliant données phylogénétiques et fonctionnelles aux cartes de répartition, une collaboration avec Camille Albouy, entre autres, a montré le potentiel de l'approche pour révéler des patterns de changements différentiels entre les facettes de diversité.

Toutes ces études montrent qu'il est important, du point de vu de la conservation, de considérer la répartition des trois facettes indépendamment, même si les corrélations entre diversités taxonomique, fonctionnelles et phylogénétiques sont parfois fortes.

Métacommunautés

Les métacommunautés sont définies comme des communautés qui sont plus ou moins connectées à travers la dispersion entre elles. Le concept est apparu dans les années 2000 comme une stratégie pour relier les échelles locales aux échelles moyennes ou régionales, et comme une extension multi-espèce du concept de métapopulations. Pour la plupart des organismes macroscopiques il s'agirait donc d'expliquer les patterns de diversité à des échelles qui vont de quelques dizaines de km jusqu'à quelques milliers de km[3]. Dans un premier temps, il y a eu quatre paradigmes qui étaient amplement acceptés comme dominant les métacommunautés, et donc qui pouvaient expliquer la répartition de la biodiversité à ces échelles intermédiaires. Ces paradigmes étaient surtout le produit de la combinaison de 4 processus fondamentaux : dispersion, filtres environnementaux, interactions biologiques (telles que compétition), et processus aléatoires (souvent réduits aux dynamiques de colonisation et extinction) (Leibold et al. 2004, Holyoak et al. 2005). De nos jours, il est plutôt accepté que les patterns de diversité observés sont le résultat de ces 4 processus, et que donc, les quatre paradigmes originaux ne sont pas exclusifs les uns des autres (Vellend 2010, Brown et al. 2017). Les questions peuvent être recadrées donc dans un continuum où l'on cherche à démontrer comment ces 4 processus interagissent à différentes échelles pour déterminer la diversité observée.

Mes explorations à ce sujet ont commencé pendant ma thèse avec l'étude des patterns de diversité des métacommunautés d'oiseaux dans la forêt tempérée chilienne (Meynard and Quinn 2008). Dans ce travail, j'ai effectué des relevés d'oiseaux et de végétation dans les forêts tempérées d'Amérique du Sud sur 147 sites situés dans neuf zones protégées différentes du centre-sud du Chili. J'ai également collecté des données climatiques et de productivité pour ces localités. Cinq indices de diversité locale ont été calculés: la richesse spécifique observée, les estimations de la richesse par ACE et Chao, et les indices de diversité de Shannon et Simpson. Une combinaison de modèles de régression multiple et de modèles autorégressifs spatiaux simultanés nous a permis de sélectionner un petit nombre de facteurs environnementaux qui semblent influencer la diversité des espèces d'oiseaux. Nous avons ensuite proposé une hypothèse complexe sur les interactions climat, végétation et diversité

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[3] Ceci dit, une metacommunauté peut concerner des echelles bien différentes au dépend des échelles de dispersion des organismes concernés. Voir par ex Venail et al. 2010 pour une métacommunauté expérimentale crée à partir de bactéries sur des plaques de laboratoire.

aviaire, que nous avons testé avec une approche de modélisation par équations structurelles (SEM). Cette analyse a montré qu'il existe des effets directs et indirects du climat et de la superficie des fragments sur la diversité aviaire, ainsi que des effets directs de la structure de la végétation. Dans l'ensemble, la faible structure spatiale du turnover des espèces ainsi que les effets environnementaux importants sur la diversité des oiseaux confortent l'idée selon laquelle les filtres environnementaux jouent un rôle prépondérant dans la structuration des assemblages aviaires dans la région.

Cette thématique a continué à être centrale dans ma recherche à travers plusieurs collaborations importantes. En collaboration avec Wilfried Thuiller (LECA, Grenoble), nous avons étudié l'importance relative des différents processus (filtres environnementaux, dispersion, interactions, aléatoire) sur les métacommunautés de plantes alpines à différentes échelles spatiales (Meynard et al. 2013b). Nous avons ainsi montré que les filtres environnementaux expliquent une part de plus en plus importante de la variance de la diversité lorsque l'échelle d'étude devient plus large. Aussi, la stratégie d'analyse proposée, qui combine des approches complémentaires, permet d'avoir une meilleure vision de l'importance de chaque processus pour déterminer la structure des communautés actuelles. Dans le cadre de la même collaboration, nous avons étudié, avec Tamara Munkemuller et Francesco de Bello, quelle combinaison d'indices serait la meilleure pour révéler l'existence de différentes combinaisons de processus dans cette détermination de la biodiversité. Les résultats de cette étude de simulations montrent que l'utilisation de plusieurs indices, notamment des indices de turnover spatial et des indices qui incorporent diversité phylogénétique et fonctionnelle, peuvent augmenter significativement notre capacité de reconnaître correctement les processus qui sont à l'origine de la diversité observée. Finalement, une collaboration avec Vincent Bretagnolle à travers une étudiante de doctorat a permis d'appliquer ce genre de stratégie d'analyse sur les communautés d'oiseaux en milieu agricole. Cette étude a permis de révéler l'importance de la structure du paysage, notamment la composition des haies en bordure de champs agricoles, ainsi que de révéler des réponses différentielles des oiseaux au dépend des groupes fonctionnels concernés (Henckel et al. 2019).

C'est aussi dans cette perspective qui se situe la thèse doctorale de Simon Roy que je co-encadre actuellement avec Guillaume Fried, où nous cherchons à comprendre le rôle des pratiques agricoles sur la diversité des bordures de champs en utilisant une approche de métacommunautés (thèse financée INRA-ANSES, commencée en octobre 2019, voir perspectives).

Conclusions et perspectives

Les deux axes de recherche présentés ci-dessus ont été présents depuis le début de ma recherche, mais les approches et applications ont évolués avec le temps. Aujourd'hui je me retrouve de plus en plus à appliquer le genre d'approche macroécologique à l'analyse de données dans un contexte agricole et de changements climatiques, pour répondre à des enjeux sociétaires importants. C'est dans ce contexte que je compte continuer à travailler autour de la modélisation de la répartition des espèces et autour de l'étude des métacommunautés, en combinant des approches de l'écologie virtuelle, des analyses de données réelles, et des projections sous des scénarios climatiques.

Répartition des espèces

En ce qui concerne la répartition des espèces, à travers mes études antérieures et mes collaborations en cours, je commence à accumuler un nombre considérable d'études individuelles sur la répartition potentielle de divers ravageurs de cultures et d'espèces d'intérêt agricole, y-inclus sous des scénarios de changements climatiques : répartitions de 15 espèces dans la familles de Tetranychidae (dont la plupart sont des ravageurs de culture) et deux Phytoseiidae (prédateurs utilisés comme agents de lutte biologique contre les tétraniques) –collaboration avec Maria Navajas, Marie-Stéphane Tixier et Alain Migeon (UMR CBGP, Montpellier) ; répartitions de *Cacopsylla pruni*, des psylles vecteurs d'une maladie bactérienne (European Stone Fruit Yellows -ESFY), et leur plantes hôtes d'importance économique - collaboration avec Nicolas Sauvion (UMR BGPI, Montpellier) et Virginie Ravigné (UMR PVBMT, La Réunion) ; répartition des criquets pèlerins et autres criquets problématiques du point de vue agricole - collaborations avec Marie Pierre Chapuis et Cyril Piou (UMR CBGP, Montpellier), ainsi qu'avec Eduardo Trumper (INTA, Argentine) ; répartition d'une variété de la plante de café en Afrique, y-inclus plusieurs clusters génétiques- collaboration avec Valérie Poncet (UMR DIADE, Montpellier) et Stéphanie Manel (CEFE, Montpellier) ; répartition de divers haplotypes de *Spodoptera frugiperda* en Afrique de l'ouest- collaboration avec Nathalie Gauthier (UMR CBGP, Montpellier), répartition des *Sesamia sp* en Afrique – collaboration avec Gael Kergoat (UMR CBGP, Montpellier) et Bruno Le Ru (anciennement UMR EDGE, Bretagne).

Sur mes projets en cours, je cherche donc à intégrer les patterns qui s'en dégagent au-delà des cas particuliers. Par exemple, un projet financé par l'INRA (projet NicoTools) en collaboration avec Gael Kergoat a permis de financer une étudiante de master 2, Livia Rodrigues de Sa, qui a étudié le lien entre les traits d'histoires de vie et la capacité des espèces de devenir ravageurs de culture. Dans cette étude préliminaire nous avons analysé les différences entre traits d'histoire de vie et l'état ravageur ou non ravageur à l'intérieur des Sesamiina (Noctuidae: Apaeminii), un groupe avec plus de 200 espèces pour lequel nous avons rassemblé des données d'occurrence, de traits d'histoire de vie, et une phylogénie calibrée. Ce jeu de données peut donc être utilisé pour analyser les patterns d'évolution des traits en lien avec des problématiques agricoles. Le travail commencé par l'étudiante fera sûrement partie d'une publication dans un futur proche.

Par ailleurs, l'accumulation de cas particuliers de ravageurs sous différents scénarios de changement climatique fera partie d'un effort de synthèse que je compte entamer une fois les publications liées à chacun de ces cas d'étude seront finalisées. Cette synthèse cherchera donc à identifier le type d'espèces qui risque de poser plus de problèmes, ainsi que des régions géographiques qui risquent d'être le plus vulnérables. Je compte, dans cet effort, utiliser la superposition de changements de répartitions sur les espèces les plus emblématiques, mais aussi une exploration en utilisant des espèces virtuelles, pour identifier les gradients et les réponses à rechercher sur les ravageurs les plus importants.

Diversité et métacommunautés

Dans cet axe, la collaboration actuelle la plus importante de mon point de vue c'est le travail que je réalise avec Guillaume Fried (LSV-ANSES, Montpellier), et qui risque de prendre une place plus importante dans ma recherche à futur. En effet, cette collaboration nous a permis de financer une thèse qui a démarré en octobre 2019 où nous cherchons à appliquer les principes de métacommunautés pour comprendre la part des pratiques agricoles sur la détermination de la diversité en bordure de champs agricoles. Le but principal de ce projet est de valoriser des jeux de données existants à l'échelle nationale pour comprendre les dynamiques des communautés de plantes et coléoptères en bordure de champs agricole. Nous voulons, en particulier, faire le lien entre pratiques agricoles et composition des communautés des bordures des champs, tout en incorporant d'autres facteurs écologiques qui risquent d'influencer ces communautés (filtres environnementaux, dispersion, interactions biologiques) à plusieurs échelles spatiales. Pour ce faire, nous utiliseront des données issues de deux jeux de données à niveau national (le réseau Biovigilance Flore, 2002-2012; et le réseau 500 ENI, 2012-présent), en nous concentrant sur les données collectées de plantes adventices et de coléoptères. Ce réseau couvre toute la France, sur plusieurs types de cultures et inclue des informations détaillées sur des traits fonctionnels, sur les pratiques agricoles des champs adjacents, et sur des données environnementales locales. Nous utiliserons une combinaison d'analyses spatiales et multivariées à l'échelle nationale, régionale, de paysage et locale pour comprendre le rôle de chaque processus écologique à chaque niveau, et le potentiel de gestion qui puisse être lié. Ces analyses incluront une analyse par groupe fonctionnel, des analyses de cooccurrences, ainsi que des analyses de partition de variance et de modèles nuls. Globalement, ce travail nous permettra d'avoir une première évaluation à l'échelle nationale des effets non intentionnels des pratiques agricoles sur la composition et la diversité des communautés des bordures de champs, ainsi que de proposer de nouveaux indicateurs et outils de suivi de ces milieux.

Par ailleurs, j'ai commencé à participer dans le réseau du GT 500 ENI en fin 2019, ce qui me permets aujourd'hui de porter un sous-groupe de travail où nous cherchons à comprendre les corrélations entre les différents groupes taxonomiques suivis dans les parcelles ENI (plantes, coléoptères, oiseaux, verres de terre), pour éventuellement essayer de comprendre les facteurs qui déterminent la diversité dans leur ensemble, et proposer des stratégies de gestion agricole qui soient en accord avec les objectifs de diminution d'utilisation de pesticides et la conservation de la biodiversité.

Cette nouvelle collaboration a aussi donné naissance à de nouveaux projets. Nous avons, par exemple, déposé un préprojet ANR qui cherche à allier les forces présentes au CBGP au niveau taxonomique pour mieux valoriser les données du réseau 500 ENI. Dans ce projet nous proposons donc de créer une librairie de base pour un barcoding des coléoptères présents en milieu agricole, ce qui permettra de raffiner et standardiser les données collectées dans le réseau, ainsi que d'étudier des liens fonctionnels entre plantes et coléoptères. Nous créons aussi de nouveaux liens entre plusieurs taxonomistes de notre unité avec qui je n'ai pas encore collaboré (par ex. Julien Haran, Bruno Michel, Laurent Soldati, entre autres), des chercheurs au muséum d'histoire naturelle qui participent dans le réseau (Emannuelle Porsche et Camila Andrade), et avec d'autres unités INRA et le ministère de l'agriculture, qui sont eux participants actifs du réseau 500 ENI.

J'espère donc avoir montré à travers ces projets, le fait que ma recherche continuera à se placer autour des deux axes que j'ai présentés dans l'analyse de ma recherche antérieure. Cependant, l'expérience acquise par le passé me permet de pousser plus loin dans les démarches de synthèses, en particulier sur les problèmes appliqués en milieu agricole.

Références

Albouy, C. et al. 2015. Projected impacts of climate warming on the functional and phylogenetic components of coastal Mediterranean fish biodiversity. - Ecography 38: 681–689.

Albouy, C. et al. 2017. Multifaceted biodiversity hotspots of marine mammals for conservation priorities. - Divers. Distrib. 23: 615–626.

Araújo, M. B. and Rahbek, C. 2006. How does climate change affect biodiversity? - Science 313: 1396–1397.

Araújo, M. B. et al. 2004. Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. - Glob. Change Biol. 10: 1618–1626.

Begon, M. et al. 1996. Ecology. - Blackwell Science.

Bellard, C. et al. 2012. Impacts of climate change on the future of biodiversity. - Ecol. Lett. 15: 365–377.

Broennimann, O. et al. 2012. Measuring ecological niche overlap from occurrence and spatial environmental data. - Glob. Ecol. Biogeogr. 21: 481–497.

Brown, J. H. 1995. Macroecology. - Chicago University Press.

Brown, J. H. and Lomolino, M. V. 1998. Biogeography. - Sinauer.

Brown, B. L. et al. 2017. Making sense of metacommunities: dispelling the mythology of a metacommunity typology. - Oecologia 183: 643–652.

Chave, J. 2013. The problem of pattern and scale in ecology: what have we learned in 20years? - Ecol. Lett. 16: 4–16.

Dawson, T. P. et al. 2011. Beyond Predictions: Biodiversity Conservation in a Changing Climate. - Science 332: 53–58.

de Bello, F. et al. 2010. The spatial partitioning of diversity: showing Theseus a way out of the labyrinth. - J. Veg. Sci. 21: 992–1000.

Devictor, V. et al. 2010. Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: the need for integrative conservation strategies in a changing world. - Ecol. Lett. 13: 1030–1040.

Dufour, C. M. S. et al. 2015. Space Use Variation in Co-Occurring Sister Species: Response to Environmental Variation or Competition? - PLOS ONE 10: e0117750.

Gallien, L. et al. 2010. Predicting potential distributions of invasive species: where to go from here? - Divers. Distrib. 16: 331–342.

Ganem, G. et al. 2012. Presence of three mitochondrial lineages of striped mice (Rhabdomys) in the Free-State (South Africa): factors that may promote their co-occurrence. - Acta Oecologica 42: 30–40.

Granger, V. et al. 2015a. Large-scale spatio-temporal monitoring highlights hotspots of demersal fish diversity in the Mediterranean Sea. - Prog. Oceanogr. 130: 65–74.

Granger, V. et al. 2015b. Mapping diversity indices: not a trivial issue. - Methods Ecol. Evol. 6: 688–696.

Guisan, A. and Thuiller, W. 2005. Predicting species distribution: offering more than simple habitat models. - Ecol. Lett. 8: 993–1009.

Hawkins, B. A. 2004. Are we making progress toward understanding the global diversity gradient? - Basic Appl. Ecol. 5: 1–3.

Henckel, L. et al. 2019. On the relative importance of space and environment in farmland bird community assembly. - Plos One 14: e0213360.

Hijmans, R. J. et al. 2005. Very High Resolution interpolated climate surfaces for global land areas. - Int. J. Climatol. 25: 1965–1978.

Holyoak, M. et al. 2005. Metacommunities: a Framework for Large-Scale Community Ecology. - In: Holyoak, M. et al. (eds), Metacommunities: Spatial Dynamics and Ecological Communities. The University of Chicago Press, pp. 1–31.

Hubbell, S. P. 2001. The Unified Neutral Theory of Biodiversity and Biogeography. - Princeton University Press.

Hutchinson, G. E. 1959. Homage to Santa Rosalia, or why are there so many kinds of species. - Am. Nat. 93: 145–159.

Iturralde-Pólit, P. et al. 2017. The effects of climate change on a mega-diverse country: predicted shifts in mammalian species richness and turnover in continental Ecuador. - Biotropica 49: 821–831.

Keddy, P. and Weiher, E. 1999. The scope and goals of research on assembly rules. - In: Weiher, E. and Keddy, P. (eds), Ecological Assembly Rules: Perspectives, advances, retreats. First. Cambridge University Press, pp. 1–20.

Kriticos, D. J. et al. 2012. CliMond: global high-resolution historical and future scenario climate surfaces for bioclimatic modelling. - Methods Ecol. Evol. 3: 53–64.

Latinne, A. et al. 2015. Influence of past and future climate changes on the distribution of three Southeast Asian murine rodents. - J. Biogeogr. 42: 1714–1726.

Leibold, M. A. et al. 2004. The metacommunity concept: a framework for multi-scale community ecology. - Ecol. Lett. 7: 601–613.

Leroy, B. et al. 2016. virtualspecies, an R package to generate virtual species distributions. - Ecography 39: 599–607.

Leroy, B. et al. 2018. Without quality presence-absence data, discrimination metrics such as TSS can be misleading measures of model performance. - J. Biogeogr. 45: 1994–2002.

Levin, S. 1992. The Problem of Pattern and Scale in Ecology. - Ecology 73: 1943–1967.

Logue, J. B. et al. 2011. Empirical approaches to metacommunities: a review and comparison with theory. - Trends Ecol. Evol. 26: 482–491.

MacArthur, R. H. and Wilson, E. O. 2016. The Theory of Island Biogeography. - Princeton University Press.

Meynard, C. N. and Quinn, J. F. 2007. Predicting species distributions: a critical comparison of the most common statistical models using artificial species. - J. Biogeogr. 34: 1455–1469.

Meynard, C. N. and Quinn, J. F. 2008. Bird metacommunities in the temperate forests of South America: direct and indirect effects of vegetation structure, area and climate. - Ecology 89: 981–990.

Meynard, C. N. and Kaplan, D. M. 2012. The effect of a gradual response to the environment on species distribution modeling performance. - Ecography 35: 499–509.

Meynard, C. N. and Kaplan, D. M. 2013. Using virtual species to study species distributions and model performance. - J. Biogeogr. 40: 1–8.

Meynard, C. N. et al. 2004. Biogeografìa de Aves Rapaces de Chile. - In: Muñoz, A. et al. (eds), Aves Rapaces de Chile. First Edition. CEA Ediciones, pp. 129–144.

Meynard, C. N. et al. 2007. Integrando ciencia, economía y sociedad: servicios ecosistémicos en la ecoregión de bosques lluviosos valdivianos. - Gac. Ecológica México 84–85: 29–38.

Meynard, C. N. et al. 2009. Comparing alternative systematic conservation planning strategies against a politically driven conservation plan. - Biodivers. Conserv. 18: 3061–3083.

Meynard, C. et al. 2011. Beyond taxonomic diversity patterns: how do α, β and γ components of bird functional and phylogenetic diversity respond to environmental gradients across France? - Glob. Ecol. Biogeogr. 20: 893–903.

Meynard, C. N. et al. 2012a. Assessment of environmental differentiation in the striped mouse (Rhabdomys sp.) over southern Africa: the influence of past climate change on current distributions. - Ecol. Evol. 2: 1008–1023.

Meynard, C. N. et al. 2012b. A phylogenetic perspective on the evolution of Mediterranean teleost fishes. - Plos One 7: e36443.

Meynard, C. N. et al. 2013a. Uncertainties in predicting species distributions under climate change: a case study using Tetranychus evansi (Acari: Tetranychidae). - PLoS ONE 8: e66445.

Meynard, C. N. et al. 2013b. Disentangling the drivers of metacommunity structure across spatial scales. - J. Biogeogr. 40: 1560–1571.

Meynard, C. N. et al. 2017. Climate-driven geographic distribution of the desert locust during recession periods: Subspecies' niche differentiation and relative risks under scenarios of climate change. - Glob. Change Biol. 23: 4739–4749.

Meynard, C. N. et al. 2019. Testing methods in species distribution modelling using virtual species: what have we learnt and what are we missing? - Ecography in press.

Mittermeier, R. A. et al. 2003. Hotspots and coldspots. - Am. Sci. 91: 384–384.

Monnet, A.-C. et al. 2014. Asynchrony of taxonomic, functional and phylogenetic diversity in birds. - Glob. Ecol. Biogeogr. 23: 780–788.

Monsarrat, S. et al. 2015. Historical summer distribution of the endangered North Atlantic right whale (Eubalaena glacialis): a hypothesis based on environmental preferences of a congeneric species. - Divers. Distrib. 21: 925–937.

Monsarrat, S. et al. 2016. A spatially explicit estimate of the prewhaling abundance of the endangered North Atlantic right whale. - Conserv. Biol. 30: 783–791.

Mouquet, N. et al. 2012. Ecophylogenetics: advances and perspectives. - Biol. Rev. 87: 769–785.

Ouchi-Melo, L. S. et al. 2018. Integrating phylogenetic and functional biodiversity facets to guide conservation: a case study using anurans in a global biodiversity hotspot. - Biodivers. Conserv. 27: 3247–3266.

Pressey, R. L. 2004. Conservation Planning and Biodiversity: Assembling the best data for the job. - Conserv. Biol. 18: 1677–1681.

Soberón, J. M. 2010. Niche and area of distribution modeling: a population ecology perspective. - Ecography 33: 159–167.

Vellend, M. 2010. Conceptual Synthesis in Community Ecology. - Q. Rev. Biol. 85: 183–206.

Venail, P. A. et al. 2010. Dispersal scales up the biodiversity-productivity relationship in an experimental source-sink metacommunity. - Proc. R. Soc. B-Biol. Sci. 277: 2339–2345.

Zurell, D. et al. 2010. The virtual ecologist approach: simulating data and observers. - Oikos 119: 622–635.

Annexes

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Disentangling the role of connectivity, environmental filtering, and spatial structure on metacommunity dynamics

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Dispersal is a key process in metacommunity dynamics, allowing the maintenance of diversity in complex community networks. Geographic distance is usually used as a surrogate for connectivity implying that communities that are closely located are considered more prone to exchange individuals than distant communities. However, in some natural systems, organisms may be subjected to directional dispersal (air or water flows, particular landscape configuration), possibly leading close communities to be isolated from each other and distant communities to be connected. Using geographic distance as a proxy for realised connectivity may then yield misleading results regarding the role of dispersal in structuring communities in such systems. Here, we quantified the relative importance of flow connectivity, geographic distance, and environmental gradients to explain polychaete metacommunity structure along the coasts of the Gulf of Lions (northwest Mediterranean Sea). Flow connectivity was estimated by Lagrangian particle dispersal simulations. Our results revealed that this metacommunity is strongly structured by the environment at large spatial scales, and that both flow connectivity and geographic distance play an important role within homogeneous environments at smaller spatial scales. We thus strongly advocate for a wider use of connectivity measures, in addition to geographic distance, to study spatial patterns of biological diversity (e.g. distance decay) and to infer the processes behind these patterns at different spatial scales.

Synthesis

Everything is connected, but connections are seldom accurately quantified. Biological communities are often studied separately, using observations, experiments and models to unravel local dynamics of organisms interacting with each other. However, regional processes such as dispersal through ocean and air circulation, likely to connect distant communities and influence their local dynamics, are not always accounted for, or, at best, used as an homogeneous and distance-related factor. Ocean models have being extensively developed and validated during the past decades with the increasing availability of accurate meteorological data. Using such model outputs, precise quantification of exchange rates of organisms between communities was performed in a marine Mediterranean coastal area. Jointly with local environmental and biological data, these results were used to quantify the effects of realistic connectivity on local and regional polychaete community structure, and revealed that the environmental gradient, geographic distance, and connectivity were responsible for community structure at different spatial scales.

The concept of metacommunity, defined as a set of distinct communities connected by dispersal, has marked a turning point in community ecology in shifting the focus from biological interactions to a more complex vision including environmental filtering, dispersal or random effects (Leibold et al. 2004, Holyoak et al. 2005, Logue et al. 2011). While the initial metacommunity frameworks (i.e. neutrality, patch dynamics, species sorting, and mass effect) were intentionally oversimplified, they helped to build a more process-based large-scale ecology (Leibold et al. 2004, McGill 2010, Massol et al. 2011). For example, the neutral theory, which assumes ecological equivalence between species, has helped defining the role of dispersal and stochastic processes in structuring ecological communities (Bell 2001, Hubbell 2001, Chave 2004). Similarly, niche-based studies recognising ecological differences between species have emphasized the influence of environmental heterogeneity and patch extinction–colonisation dynamics (Tilman 1994, Mouquet and Loreau 2002). It is now accepted that communities are structured by a combination of these processes to different degrees (Hubbell 2001, Holyoak et al. 2005, Cavender-Bares et al. 2009). The potential of adopting a more integrated approach in which the relative influences of environmental gradients, dispersal, and biological interactions on different types of metacommunities are all quantified is now widely recognised (Logue et al. 2011). In other words, under the current metacommunity framework, these mechanisms are not exclusive, but rather complementary (Tuomisto et al. 2003, Cottenie 2005, Ellis et al. 2006, Meynard and Quinn 2008, Drakou et al. 2009, Zhang et al. 2010, Meynard et al. 2011). Therefore, rather than trying to define which is the single most important structuring force, the focus is now on understanding their relative importance, or what proportion of the overall variance in community structure can be explained by each process.

Among the patterns that have been used to explain community composition, community similarity ('beta diversity') has been widely documented (Cottenie 2005, Tuomisto and Ruokolainen 2006). In particular, the decrease in community similarity with geographic distance, the so-called 'distance decay', has proven to be common to different groups of organisms (Soininen et al. 2007): closely-located communities are generally more similar in terms of species composition than those located further apart (Tuomisto et al. 2003). This pattern is expected if dispersal is an important limiting factor in structuring ecological communities. However, spatial autocorrelation in biological data can also arise from environmental filtering: sites that are located at short distances are more likely to be environmentally similar and thus suitable for the same species (Legendre and Legendre 1998, Lichstein et al. 2002). These two different mechanisms (dispersal and environmental filtering) will therefore produce similar predictions regarding distance decay, and are therefore difficult to separate in empirical studies (Meynard et al. 2011).

It may nevertheless be possible to disentangle the relative roles of dispersal and environmental filtering in particular natural systems where each one of these produces different spatial structures. In many ecological systems, dispersal is likely to be influenced not only by geographic distance but also by its direction. For example, dispersal of seeds in some terrestrial plants (Minami and Azuma 2003) and dispersal of freshwater invertebrates in some aquatic systems (Vanschoenwinkel et al. 2009) are driven by winds, and larval dispersal of marine organisms is influenced by oceanic currents and, to some lesser extent, by larval behaviour (Cowen et al. 2007). In these systems, the directionality of dispersal influences connectivity between communities, which prevents the latter to be fully overlapping with environmental gradients. In such cases, comparing changes in community composition with geographic distance does not account for directional dispersal. Instead, a connectivity measure based on landscape properties (e.g. hydrodynamic, aerodynamic or vector-mediated processes) and the biology of the dispersing organisms should be more relevant to test the relative effects of dispersal and environmental filtering in shaping community structure and composition.

Marine environments are ideal systems in which to implement such analyses. In these systems, connectivity is an important determinant of marine community structure (Kinlan et al. 2005, Watson et al. 2010) and can limit population abundances (Bode et al. 2006, Guizien et al. 2006). Moreover, marine organisms are strongly influenced by asymmetric dispersal (i.e. where connectivity between communities A to B differs from connectivity between B to A, Salomon et al. 2010), and water flows in the ocean create highly complex structures, generating gyres favouring retention in some areas (Hill et al. 1996), or streams favouring long-distance routes (Botsford et al. 2003). In such complex systems, connectivity between communities will thus not be a simple linear, Gaussian or exponential function of geographic distance but, rather, will be influenced by the characteristics (e.g. speed, direction) of the medium transporting organisms (Sammarco and Andrews 1988, Cowen et al. 2000). Although the importance of local biotic and abiotic conditions in the maintenance of marine organisms has been demonstrated (Galeron et al. 2000, Gogina et al. 2010), quantifying the relative effects of realised flow connectivity (effective links between communities and their strengths) versus environmental filtering in the recruitment success of benthic organisms has rarely been achieved (Scheltema 1986, Roughgarden et al. 1988, Caley et al. 1996, Connolly and Roughgarden 1999).

Here, we account for both flow connectivity (hydrodynamically-driven exchange of individuals between different locations) and geographic distance (linear representation of connectivity) to better understand the spatial structure of a marine invertebrate metacommunity along the coastline of the northwest Mediterranean Sea. The data set used consists of 21 transects, perpendicular to the shore, along the coastline of the Gulf of Lions, where geostrophic currents display a typical directional wind-induced regime (Millot 1990). We focused on the polychaetes, which are a highly diverse group, both taxonomically and functionally (McHugh and Fong 2002). In the Gulf of Lions, polychaetes make up a large part of the abundance and biomass of the benthos and are strongly structured along environmental gradients (Grémare et al. 1998, Labrune et al. 2007). A measure of connectivity that estimates larval dispersal based on ocean current simulations was used as an alternative and more realistic measure of dispersal than that predicted by geographic distance. Note that as we explicitly account for space and the environment, our statistical approach can be related to the variation partitioning strategy outlined and discussed against other approaches in Logue et al. (2011). We tested how much the environmental gradient was structuring community composition and how much of the remaining variation was explained by geographic distance and our measure of flow connectivity. We used the correlation between species turnover (beta diversity) and flow connectivity as an estimation of dispersal limitation in structuring the polychaete metacommunity at different spatial scales. If dispersal is dominant, and spatial autocorrelation is only reflecting dispersal limitations, we would expect beta diversity to be strongly correlated with flow connectivity. On the contrary, if environmental filtering is dominant, and spatial autocorrelation is reflecting environmental structure rather than dispersal limitations, we would expect communities to be strongly correlated with the environment.

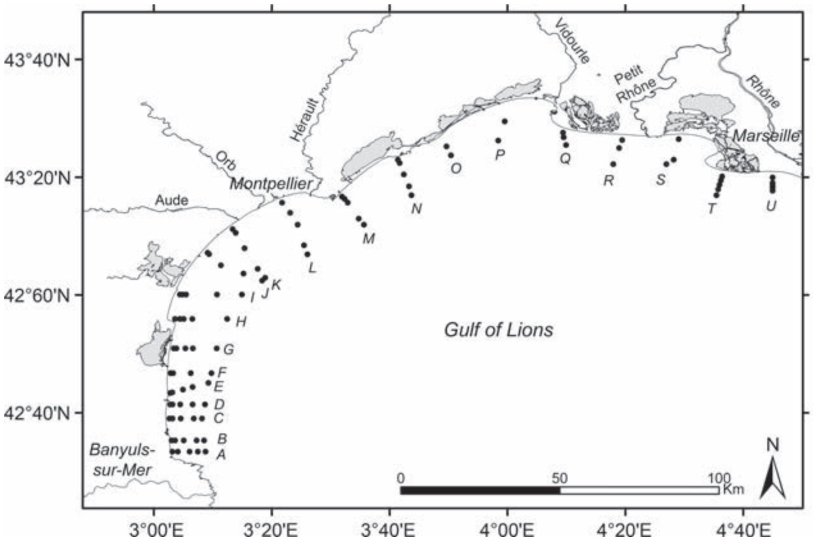

Figure 1. Location of the 92 sites sampled during the oceanographic campaign in 1998. Transects were located along the Gulf of Lions, between the French-Spanish border and the eastern part of the Rhône River. Stations were located between 10 and 50 m water depth. Adapted from Labrune et al. (2007).

Methods

Study area

The Gulf of Lions (Fig. 1) is located in the north-western part of the Mediterranean Sea, between Cape Creus (Spain) and Cape Croisette (Marseille, France). It is characterised by a large continental shelf, up to 80 km wide at Cape Agde (France), with a mean depth of approximately 76 m. At the boundary of the continental shelf, the shelf break is crossed by submarine canyons. Towards the continent, the local orography plays a key role on the main wind regimes: the Tramontane wind blows from north–northwest between the Pyrenees and the Massif Central (western side of the Gulf), and the Mistral wind blows from the north in the Rhône valley between the Massif Central and the Alps (eastern side of the Gulf). Since the Mediterranean Sea has a microtidal regime (tidal amplitudes lower than 0.5 m), the coastal circulation mainly results from the interaction of these winds at regional scale, river inputs, and a large scale thermo-haline northern current flowing from east to west along the continental shelf break (Millot 1990, Estournel et al. 2003).

Polychaete survey and environmental data

Between 19 and 29 September 1998, sampling was conducted in the Gulf of Lions along the portion of coast between the French–Spanish border and the mouth of the Rhône River to collect benthic samples from soft bottoms. This section of coast is approximately 110 km from south to north and 140 km from west to east (Fig. 1). Twenty-one cross-shore transects were sampled at two to five stations (five stations on 15 transects, four stations on one transect, three stations on three transects, two stations on two transects, 92 stations in total), with similar sampling protocol. At each station, four sediment samples were collected using a 0.1 m^2 van Veen grab, from which three were taken for benthic macrofauna identification to the species level, and one for granulometric and organic content analysis. Macrofauna samples were immediately sieved with a 1 mm mesh and the fauna retained was fixed in 5% formalin. Samples were then sorted at the laboratory to separate polychaetes from the remaining macrofauna. Identification of polychaete species was done as described in Labrune et al. (2007). Polychaetes were identified to the lowest practical taxonomic level and counted. Unidentified taxa were only counted when they could not be mistaken for other identified taxa and counted as separate species. Sediment granulometry analysis showed that the marine sea floor is composed of several sediment types stretching along the coast, ranging cross-shore from sandy to muddy sediments (Labrune et al. 2007).

Spatial and environmental data analysis

Geographic distance, flow connectivity, and environmental distance between each pair of stations were calculated. Geographic distance between each pair of stations was calculated using latitudinal and longitudinal WGS84 coordinates of each station. Transforming this linear geographic distance matrix to a Gaussian or exponential connectivity matrix was not performed here, contrary to other studies because it would intensify connectivity between close sites and reduce connectivity between distant sites, patterns that are already captured, more accurately, in the flow connectivity matrix. Flow connectivity was assessed using numerical simulations of larval dispersal in the Gulf of Lions including realistic hydrodynamic forcing of 2004. Hydrodynamic simulations (using the SYMPHONIE computer code: Johns et al. 1992, Marsaleix 1993, Estournel et al. 2003) have been validated in a number of studies in this area using in situ and satellite observations (e.g. Rhône river plume, Estournel et al. 1997, Marsaleix et al. 1998, Estournel et al. 2001; northern current inflow, Auclair et al. 2001; wind-induced currents, Estournel et al. 2003).

Dispersal of virtual active larvae released from spawning points situated along the coasts of the Gulf of Lions was calculated using the Lagrangian procedure described in Guizien et al. (2006). Flow connectivity among the sampling stations was quantified by counting the number of virtual larvae coming from the spawning points and reaching areas delimited around the stations, between 5 and 50 m depth, after four weeks of dispersal (Supplementary material Appendix 1 and Fig. A1 for details).

An environmental Euclidian distance matrix was calculated between each pair of stations using field environmental measurements directly related to the sediment: depth, grain size (median particle diameter: d50), total carbon and nitrogen content in sediment, organic carbon in sediment, organic carbon to nitrogen ratio in the sediment. We also used other environmental variables, namely chlorophyll a (chl a) and sea surface temperature (SST), that are known to affect water column properties and thus indirectly sediment properties (e.g. through organic matter enrichment). Estimates of these two variables were derived from MODIS imagery (<http://modis.gsfc.nasa.gov/>) as seasonal averages for 2006. All these environmental variables were scaled to have a mean equal to 0 and a variance equal to 1 prior to distance calculation.

Estimating beta diversity

Similarity between each pair of polychaete communities was assessed using the Simpson beta-diversity index calculated as $\beta_{sim} = \min(b, c)/(\min(b, c) + a)$, where *a* represents the total number of species occurring in both communities, *b* represents the total number of species that occur in the neighbouring community but not in the focal one, and *c* represents the total number of species that occur in the focal community but not in the neighbouring one (Koleff et al. 2003). This index focuses on species turnover between sites while standardizing the effects of changes in species richness between these sites (Koleff et al. 2003). It is related to the Jaccard and Sorensen indices, but is less sensitive to sample size, and generally performs better than other beta diversity indices (Koleff et al. 2003, Baselga 2010). We used this index because of large differences in polychaete species richness among the communities sampled, with a few species (e.g. *Ditrupa arietina*) that largely dominated in some places. This index reaches a maximum when the proportion of species shared in two communities (*a*) is small, and when the proportion of species gained and lost when moving from the focal (*b*) to the neighbouring (*c*) community is similar.

Statistical analysis

We assessed whether and how similarity in species composition among stations was related to environmental gradients, flow connectivity, and geographic distance. Significance of the Pearson product-moment correlations was computed using Mantel tests (Mantel 1967) and partial Mantel tests (Smouse et al. 1986) using the vegan library (Oksanen 2011) in the statistical package R ver. 2.13.0 (R Development Core Team). These tests used a modified regression analysis between two (Mantel test) or three (partial Mantel tests) matrices. The rows and the columns of the matrices were randomly permuted 10 000 times to calculate the correlation coefficient *r*. Finally, a Monte Carlo simulation method was used to estimate the statistical significance of each test. The Mantel tests were used to assess which component, among the environment, geographic distance and connectivity, was best correlated with beta diversity. The partial Mantel tests were complementary of the Mantel tests to further determine if the effects of one of the components were hidden behind the effects of another. For instance, if the environment is spatially autocorrelated, partialing out geographic distance in a Mantel test using the environment should remove significance of the environment.

Scale of the analysis

Depth can be an important factor determining benthic community structure (Garrabou et al. 2002, Wei et al. 2010). All Mantel and partial Mantel tests were thus performed for all stations, and separately for three groups of stations sampled at depths of 1) 10 and 20 m, 2) 30 m, and 3) 40 and 50 m. This division corresponds roughly to sediment layout (bands of similar sediment types stretching along the coastline) and to the four clusters of polychaete assemblages previously defined in Labrune et al. (2007). These bands of stations are relatively homogeneous environmentally, particularly with respect to sediment and depth, allowing us to decouple the effects of environment and both connectivity and geographic distance while controlling for the influence of depth.

Results

Both environment and flow connectivity were spatially structured (Fig. 2). When all environmental properties were considered, environmental differences increased with geographic distance, i.e. closer sites were more similar between them than sites located far apart (Fig. 2A). This pattern was reinforced when stations of the same depth were considered (30 m Fig. 2B, and see Fig. A2 for other depths), i.e. environmental similarity among closely located sites was stronger when looking within a depth band. Mantel tests showed that connectivity was not significantly correlated with geographic distance (Table 1, Mantel test). We noted nonetheless a triangular relationship between connectivity and geographic distance (Fig. 2C–D). This reveals that 1) sites far away from each other have weaker chances to be connected, even if they are on the same pathway in terms of hydrodynamics, and that 2) exchange rates of closely located sites can vary from small to large values, likely because of hydrodynamics directionality. Retention (within-community connectivity) reached 4% and occurred for nearly every site during the elapsed time of four week-dispersal, which means that each local community is partly supported by self-recruitment (Fig. A1). Inter-community connectivity rates varied from 0 (absolutely no connectivity) to 3%, and connectivity was greater below the retention diagonal than above, meaning that the flow was predominantly oriented along the coast from east to west (Supplementary material Appendix 1

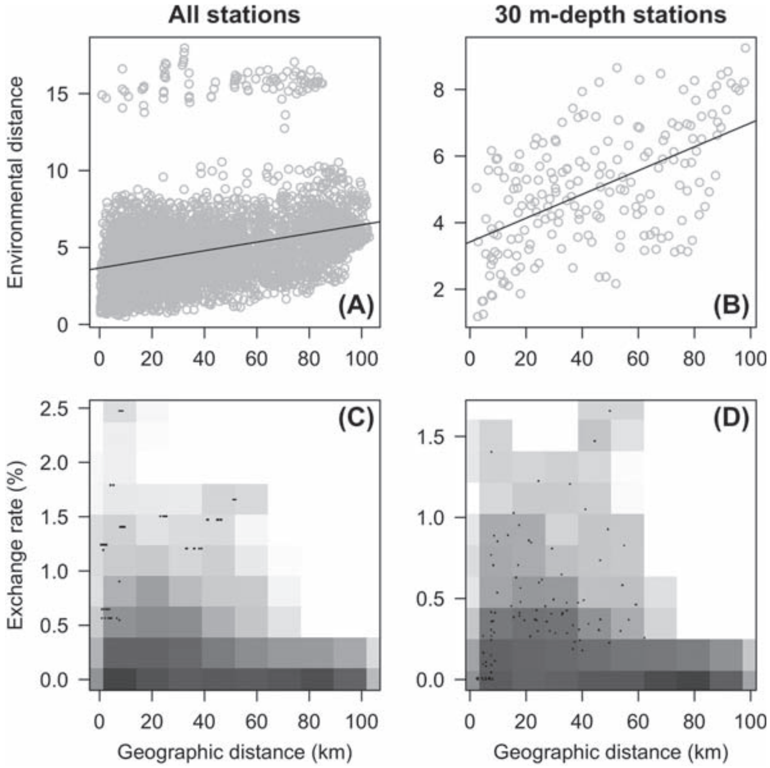

Figure 2. Relationships between geographic distance and environmental distance (A): $R^2 = 0.11$, $p < 0.001$; (B): $R^2 = 0.30$, $p < 0.001$ and flow connectivity measured as exchange rates (C, D) for all stations and for stations located at 30 m-depth. The shading of each square is proportional to the density of dots in that square.

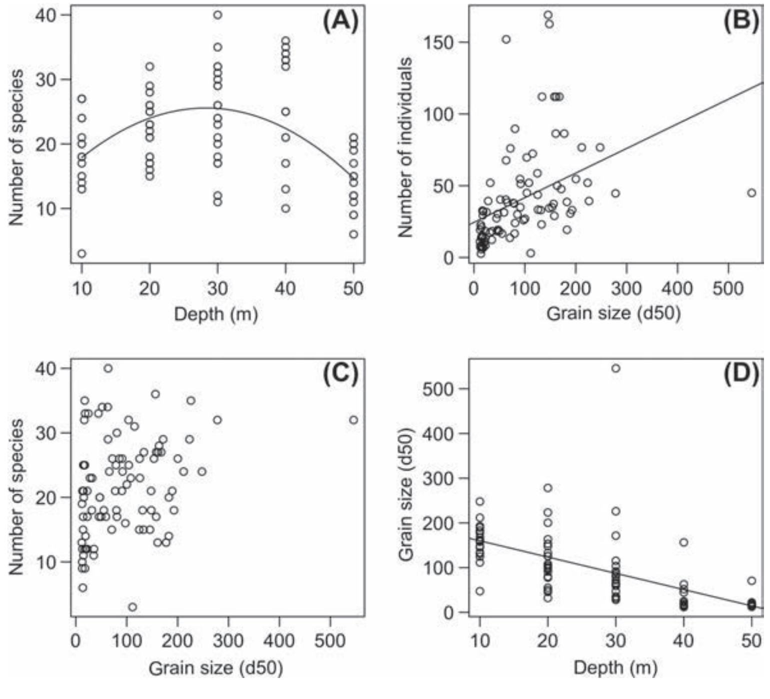

Figure 3. Relationships between environmental and community characteristics (number of individuals and number of species, A, B, C) and between the main environmental characteristics (grain size and depth, D). Hump-shaped correlation was found between depth and number of species (A): polynomial model with $\text{richness} = -0.023 \times \text{depth}^2 + 1.3 \times \text{depth} + 7.29$, $p(\text{depth}^2) < 0.001$; significant linear correlations were found between grain size and number of individuals (B): $R^2 = 0.17$, $p < 0.001$ and depth (D): $R^2 = 0.37$, $p < 0.001$; no significant correlation was found between grain size and the number of species (C).

Table 1. Correlations of species distance with environment, geographic distance, and connectivity, and correlation of geographic distance with connectivity, for all sites (92) and 30 m-deep sites measured using Mantel and partial Mantel tests. The tests were based on Pearson's product-moment correlation (10000 permutations) for species distance matrix against matrices of environmental distance, geographic distance, and connectivity.

Mantel	r (p value)		Partial Mantel	r (p value)	
Simpson beta diversity vs	all	30 m	Simpson beta diversity vs	all	30 m
Environment	0.328 (< 0.001)	0.254 (0.013)	Environment | geographic distance	0.34 (< 0.001)	0.067 (0.274)
Geographic distance	0.023 (0.14)	0.367 (< 0.001)	Environment | connectivity	0.329 (< 0.001)	0.292 (0.004)
Connectivity	0.005 (0.428)	0.192 (0.023)	Geographic distance | environment	−0.098 (1)	0.282 (0.002)
Geographic distance vs connectivity	−0.333 (1)	−0.383 (1)	Connectivity | environment	0.029 (0.101)	0.242 (0.006)

Fig. A1). This pattern indicates that connectivity is unevenly distributed over the study area. Overall, flow connectivity and geographic distance provided complementary information about spatial structure of the metacommunity.

We found a hump-shaped relationship between species richness and depth (p(depth^2) < 0.001, Fig. 3A; see also Labrune et al. 2007), with species richness peaking at 30 m (Fig. 3A). Coarse sediments found in most 10 to 30 m-depth stations also tended to host more individuals ($R^2 = 0.17$, $p < 0.001$, Fig. 3B). This abundance effect was driven by one dominant species, *Ditrupa arietina*, at these stations, but not by a change in the number of species present (Fig. 3C). As expected, depth and grain size were correlated ($R^2 = 0.37$, $p < 0.001$, Fig. 3D): coarse (sandy) sediment dominated in shallow water, whereas the mud content of sediments increased with depth. The environmental gradient was therefore stronger when all stations (thus all depths) were included in the analysis, and weaker when each depth was considered separately, except around the mouth of the Rhône River, due to river particle deposits during flooding events (Marion et al. 2010) allowing muddy sediments to be mixed with sandy sediments at shallow depths (Labrune et al. 2007).

Mantel and partial Mantel tests of the relationships between environmental properties and connectivity and geographic distance revealed the complexity of the spatial organisation of these communities. When all stations were considered, beta diversity was significantly correlated with environmental variations (Table 1, Mantel test). This was confirmed by partial Mantel tests which revealed that, when geographic distance or flow connectivity were taken into account, beta diversity was still significantly correlated to the environment (Table 1, partial Mantel tests). Conversely, when the environment was taken into account, beta diversity was neither significantly correlated with geographic distance nor with flow connectivity (Table 1). This suggests that, at least at this scale, the environment was the most important driver of community composition. When the same analysis was performed within depth bands, results showed that the environment, geographic distance and flow connectivity were all significantly correlated with beta diversity (Table 1 and Fig. 4 for 30 m depth; other depth analyses can be found in the Supplementary material Appendix 1 Table A1 and Fig. A3). When the environment was controlled for in the partial Mantel tests (Table 1), both geographic distance and flow connectivity remained significantly correlated with beta diversity. When geographic distance was partialed out, the environment was no longer correlated with beta diversity. On the contrary, when flow connectivity was partialed out, the environment remained significantly correlated to beta diversity. This suggests that the effect of the environmental filtering on species turnover depends on its spatial structure (e.g. the environment is strongly interrelated to geographic distance), but is independent of connectivity.

Discussion

This study provides an example of how the spatial structure of environmental variability can be partially decoupled from connectivity when studying their effects on community composition in dispersive environments. The patterns of spatial structure and connectivity, both when all sites are considered together and when depth bands are separated, reveal an important role of environmental gradients in shaping polychaete communities. Geographic distance per se and flow connectivity appear to be important drivers determining the composition of these communities when patterns of diversity are considered within depth bands, i.e. within more homogeneous environments.

A first important result is that the spatial scale considered influences the most relevant factors determining community structure. We found that alongshore flow connectivity was important when environmental heterogeneity was low, i.e. within depth bands, but that cross-shore environmental gradients were preponderant over connectivity when including all depth bands. This predominant role of the environmental filtering on polychaetes, previously highlighted in empirical studies from Labrune et al. (2007, 2008), suggests that community composition arises partly from species sorting (Holyoak et al. 2005). In marine environments, depth and associated characteristics such as sediment layout and grain size are believed to strongly influence the composition of benthic communities (Garrabou et al. 2002, Labrune et al. 2007, 2008), setting distinct niches for the organisms, hence driving dissimilarities between communities.

Nevertheless, and consistent with our results, recent theoretical and empirical studies have demonstrated that dispersal is also a significant process whose strength can strongly impact community structure (Mouquet et al.

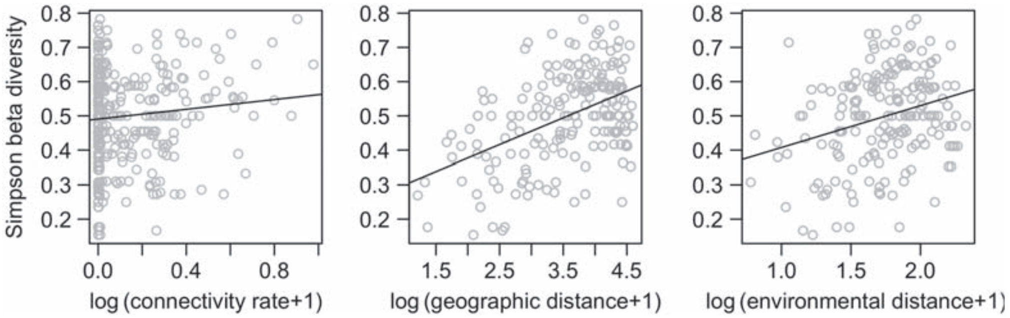

Figure 4. Relationships between beta diversity and flow connectivity, geographic and environmental distances for 30 m-depth sites. Logarithm added of one for exchange rate (in percent), geographic distance (in km) and Euclidian environmental distance is given.

2004, Cadotte and Fukami 2005, Venail et al. 2008). For instance, the laboratory experimental study carried out by Venail et al. (2008) highlighted that different levels of dispersal could induce changes of diversity in a bacterial metacommunity, and Cadotte and Fukami (2005) found that community structure changed over time and space when dispersal occurred at different spatial scales. In our study area, the decoupled effect of environment and flow connectivity on polychaete community structure may be due to the specific ocean current regime occurring in the area, which is partly uncorrelated with environmental patterns (sediment layout especially). Two nearby sites (i.e. in the same transect perpendicular to the coast, at different depths) may not be strongly connected when the water flow is parallel to the coast (Guizien et al. 2006), although some of them may be similar in terms of their physical properties (e.g. granulometry, Labrune et al. 2007). Exceptions may be encountered in specific areas such as towards the middle of the Gulf, where gyres and cross-shore connectivity may occur, allowing stronger connectivity between sites at different depths in this region.

This decoupling between environmental variability and connectivity is also consistent with empirical results in other systems. For example, Laliberté et al. (2009) found that the abundance of tree seedlings was first controlled by a broad environmental gradient, and then, within this gradient, by other spatial processes such as dispersal occurring at smaller scales. Another theoretical study pointed out that different levels of dispersal and regional environmental heterogeneity combined could affect community structure (Mouquet et al. 2006). Overall, our results provide empirical support for considering that metacommunity structure results from a combination of several mechanisms interacting at different spatial scales (Cadotte and Fukami 2005, Logue et al. 2011): environmental filtering predominating large scales, and dispersal being more important within similar environments. The possible existence of decoupling between spatial autocorrelation, environmental heterogeneity and connectivity needs to be further integrated using linear (e.g. this study) and non-linear methods to assess whether community structure, spatial structure, and connectivity interact non-linearly (Bode et al. 2011).

Patterns of similarity decay with geographic distance are not sufficient to study the influence of dispersal on metacommunity structure or dynamics since they can be linked to each asset of connectivity, environmental similarity and geographic distance. Decay of similarity is often examined using geographic distance (Soininen et al. 2007), as in our analysis, but it has also been found with other distance measures (e.g. environmental distance, Tuomisto et al. 2003; stream distance, Maloney and Munguia 2011). In the Gulf of Lions, we observed that environmental distance increased with geographic distance, so we used this environmental distance to perform tests on community similarity matrices, and found a decay of polychaete community similarity with increasing environmental distance. Other studies support this idea (Tuomisto et al. 2003, Duque et al. 2009, Maloney and Munguia 2011). For instance, Tuomisto et al. 2003 found an increase in environmental distance with geographic distance and a decay of similarity both with geographic and environmental distances. A recent study of Maloney and Munguia (2011) also reported different rates of decay with both environmental and geographic distances, suggesting that global decay patterns can emerge from a combination of different factors. These authors also found different rates of decay for the different regions they considered. Our analyses provide similar results, i.e. decay rates varied when different depth bands were considered. This decay within specific subscales demonstrates that complex community dynamics need to be investigated not only at large regional scale but also within specific environments to account for structural factors of community composition. To refine the results, analysis including more specific sediment types within depth bands could be conducted, especially in the region of the mouth of the Rhône River which displays a complex sediment layout and where mud is found at shallower depths than in the rest of the Gulf.

Beyond the particular marine system studied, dispersal of propagules also occurs for terrestrial organisms, either through vectors (e.g. vertebrates transporting seeds: Howe and Smallwood 1982) or trough atmospheric (seeds transported by wind: Nathan et al. 2011) and oceanographic processes (seed water-dispersal in coastal areas: Brunbjerg et al. 2012). On land, some of these processes might be directional, but may probably be more variable due to smaller inertia in air than in water (Gaylord et al. 2006) and to the vectors' behaviour (e.g. plants: Ozinga et al. 2004). In marine ecosystems, dispersal resulting in connectivity between regions can play a major role on community dynamics because it enables the colonisation of distant areas by marine species and favours their mixing at large scales (Caley et al. 1996, Bode et al. 2006, Guizien et al. 2006). However, the exact role of connectivity vs environmental gradients or local environments leading to recruitment success remains difficult to assess because of a temporal decoupling of these two factors: larvae are transported by currents and settle when competent, and only after that their chances of developing into adults will depend on the environmental conditions found on their settling site (Butman 1987). Conversely, currents, if too strong, may prevent some organisms from being transported to a suitable habitat or settlement site (Guizien et al. 2006).

Our study illustrates the importance of another potential caveat concerning connectivity issues in marine environments, which is the lack of accurate estimate of flow connectivity itself. Indeed, empirical studies trying to measure connectivity have only been conducted at small or large spatial scales, for particular species and with specific methods (Incze et al. 2000, Carson et al. 2011, Saenz-Agudelo et al. 2011), but no synthetic connectivity index exists to date. Numerical simulations applied to different areas of the globe have allowed approximations of connectivity patterns for local populations (James et al. 2002, Bode et al. 2006, Marinone et al. 2008, Ayata et al. 2010), but constructing accurate hydrodynamic models coupled to particle dispersal is demanding in terms of their design, parameterisation, and computer resources needed to run them, especially when designed at fine resolution or close to the coast where fine-scale physical processes occur. Here, connectivity was determined using a realistic 3D hydrodynamical model with a simulation resolution and coverage adapted to study dispersal at large scale (Guizien et al. 2006). Because the coupling with a species-specific larval behaviour may not account for the different behaviours and pelagic larval duration (PLD) of all the polychaete species present in the Gulf, we calculated exchange rates using a four-week PLD, which is a good estimate of mean PLD for benthic invertebrates (McEdward 1995). Subsequently incorporating different types of larvae in the model (active, passive, and with different PLD) was not possible in our simulations, but attempts to do so were achieved in Guizien et al. (2012). The difficulty to account for these discrepancies lies in calculating a final connectivity matrix that incorporates appropriate proportions of all larval species, which first implies running separate simulations, species by species. Only this could lead to more realistic estimations of flow connectivity, and consequently, of connectivity effects on metacommunity structure. This could at the same time allow assessing the importance of connectivity on particular species of interest (Treml et al. 2012). Another limitation might come from having used a flow connectivity matrix estimated for 2004 and a one-year regional diversity survey in 1998: coastal circulation and diversity temporal variability may partly blur the correlation between the average connectivity matrix and the diversity survey, even if interannual variability of the average connectivity matrix can be ignored. Moreover, the single year diversity survey may have been partly biased by peculiar connectivity in the years before diversity assessment for short-lived species. It would therefore be beneficial to gather connectivity matrices for different years, especially around the year of diversity surveys.

Metacommunities are structured by a number of processes, in particular by environmental and dispersal filters (Leibold et al. 2004, Holyoak et al. 2005), which ecologists have mostly studied as separate paradigms (Logue et al. 2011). Here, by using a measure of connectivity decoupled from geographic distance, we have shown than these paradigms may be spatially interlocked, leading to a more comprehensive understanding of metacommunity dynamics in this region and allowing to sort out the importance and scale of action of environmental and dispersal processes. Incorporation of connectivity estimates in the analysis, a characteristic that few studies have done to date, rendered the study more realistic concerning the processes occurring in dispersive environments. Environmental properties that were used in this study are known to influence polychaete communities (Arvanitidis et al. 2002, Labrune et al. 2007), but other variables may be taken into account in further analysis (e.g. oxygen, phosphate and silicate). Further work and other methods should be implemented to capture more precisely the effects of dispersal only on community structure, and assess in which type of marine ecosystem dispersal is a critical process. The approach presented here could also be applied to other freshwater and terrestrial ecosystems in which connectivity is known, and displaying complex or unusual dispersal patterns (e.g. asymmetric, oriented, gyres), and to other organisms dispersing particles (e.g. seeds for plants). Our results may also be useful for diversity conservation since the design of marine protected areas and terrestrial natural reserves requires a sound understanding of community dynamics, its dispersal patterns and its interaction with habitats to protect, at both local and regional scales (Economo 2011). New analyses will be needed to meet these requirements, including elements of mechanistic landscape ecology and statistical analysis of biogeographic patterns within the same framework.

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References

Arvanitidis, C. et al. 2002. Seascape biodiversity patterns along the Mediterranean and the Black Sea: lessons from the biogeography of benthic polychaetes. – Mar. Ecol. Prog. Ser. 244: 139–152.

Auclair, F. et al. 2001. The penetration of the Northern Current over the Gulf of Lions (Mediterranean) as a downscaling problem. – Oceanol. Acta 24: 529–544.

Ayata, S. D. et al. 2010. How does the connectivity between populations mediate range limits of marine invertebrates? A case study of larval dispersal between the Bay of Biscay and the English Channel (northeast Atlantic). – Prog. Oceanogr. 87: 18–36.

Baselga, A. 2010. Partitioning the turnover and nestedness components of beta diversity. – Global Ecol. Biogeogr. 19: 134–143.

Bell, G. 2001. Neutral macroecology. – Science 293: 2413–2418.

Bode, M. et al. 2006. Larval dispersal reveals regional sources and sinks in the Great Barrier Reef. – Mar. Ecol. Prog. Ser. 308: 17–25.

Bode, M. et al. 2011. Different dispersal abilities allow reef fish to coexist. – Proc. Natl Acad. Sci. USA 108: 16317–16321.

Botsford, L. W. et al. 2003. Principles for the design of marine reserves. – Ecol. Appl. 13: S25–S31.

Brunbjerg, A. K. et al. 2012. Species sorting dominates plant metacommunity structure in coastal dunes. – Acta Oecol. 39: 33–42.

Butman, C. A. 1987. Larval settlement of soft-sediment invertebrates: the spatial scale of pattern explained by active habitat selection and the emerging role of hydrodynamical processes. – Oceanogr. Mar. Biol. 25: 113–165.

Cadotte, M. W. and Fukami, T. 2005. Dispersal, spatial scale, and species diversity in a hierarchically structured experimental landscape. – Ecol. Lett. 8: 548–557.

Caley, M. J. et al. 1996. Recruitment and the local dynamics of open marine populations. – Annu. Rev. Ecol. Syst. 27: 477–500.

Carson, H. S. et al. 2011. Evaluating the importance of demographic connectivity in a marine metapopulation. – Ecology 92: 1972–1984.

Cavender-Bares, J. et al. 2009. The merging of community ecology and phylogenetic biology. – Ecol. Lett. 12: 639–715.

Chave, J. 2004. Neutral theory and community ecology. – Ecol. Lett. 7: 241–253.

Connolly, S. R. and Roughgarden, J. 1999. Theory of marine communities: competition, predation, and recruitment-dependant interaction strength. – Ecol. Monogr. 69: 277–296.

Cottenie, K. 2005. Integrating environmental and spatial processes in ecological community dynamics. – Ecol. Lett. 8: 1175–1182.

Cowen, R. K. et al. 2000. Connectivity of marine populations: open or closed? – Science 287: 857–859.

Cowen, R. K. et al. 2007. Population connectivity in marine systems: an overview. – Oceanography 20: 14–21.

Drakou, E. G. et al. 2009. Freshwater fish community structured more by dispersal limitation than by environmental heterogeneity. – Ecol. Freshwater Fish 18: 369–379.

Duque, A. et al. 2009. Distance decay of tree species similarity in protected areas on Terra Firme forests in Colombian Amazonia. – Biotropica 41: 599–607.

Economo, E. P. 2011. Biodiversity conservation in metacommunity networks: linking pattern and persistence. – Am. Nat. 177: E167–E180.

Ellis, A. M. et al. 2006. Evaluating the long-term metacommunity dynamics of tree hole mosquitoes. – Ecology 87: 2582–2590.

Estournel, C. et al. 1997. The plume of the Rhône: numerical simulation and remote sensing. – Continental Shelf Res. 17: 899–924.

Estournel, C. et al. 2001. The Rhône River plume in unsteady conditions: numerical and experimental results. – Estuar. Coast. Shelf Sci. 53: 25–38.

Estournel, C. et al. 2003. Observation and modeling of the winter coastal oceanic circulation in the Gulf of Lions under wind conditions influenced by continental orography (FETCH experiment). – J. Geophys. Res. 108 (C3).

Galeron, J. et al. 2000. Variation in structure and biomass of the benthic communities at three contrasting sites in the tropical northeast Atlantic. – Mar. Ecol. Prog. Ser. 197: 121–137.

Garrabou, J. et al. 2002. Structure and dynamics of north-western Mediterranean rocky benthic communities along a depth gradient. – Estuar. Coast. Shelf Sci. 55: 493–508.

Gaylord, B. et al. 2006. Macroalgal spore dispersal in coastal environments: mechanistic insights revealed by theory and experiment. – Ecol. Monogr. 76: 481–502.

Gogina, M. et al. 2010. Distribution of benthic macrofaunal communities in the western Baltic Sea with regard to near-bottom environmental parameters. 2. Modelling and predictions. – J. Mar. Syst. 80: 57–70.

Grémare, A. et al. 1998. Long-term comparison of macrobenthos within the soft bottoms of the Bay of Banyuls-sur-mer (northwestern Mediterranean Sea). – J. Sea Res. 40: 281–302.

Guizien, K. et al. 2006. Dispersal of *Owenia fusiformis* larvae by wind-driven currents: turbulence, swimming behaviour and mortality in a three-dimensional stochastic model. – Mar. Ecol. Prog. Ser. 311: 47–66.

Guizien, K. et al. 2012. Using realistic Lagrangian larval dispersal simulations for marine protected area design: application to the Gulf of Lions (northwest Mediterranean). – Limnol. Oceanogr. 57: 1099–1112.

Hill, A. E. et al. 1996. The western Irish Sea gyre: a retention system for Norway lobster (*Nephrops norvegicus*)? – Oceanol. Acta 19: 357–368.

Holyoak, M. et al. 2005. Metacommunities: a framework for large-scale community ecology. – In: Holyoak, M. et al. (eds), Metacommunities, spatial dynamics and ecological communities. Univ. of Chicago Press, pp. 1–31.

Howe, H. F. and Smallwood, J. 1982. Ecology of seed dispersal. – Annu. Rev. Ecol. Syst. 13: 201–228.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. – Princeton Univ. Press.

Incze, L. S. et al. 2000. Neustonic postlarval American lobsters, *Homarus americanus*, in the western Gulf of Maine: spatial and interannual variations. – Can. J. Fish. Aquat. Sci. 57: 755–765.

James, M. K. et al. 2002. The structure of reef fish metapopulations: modelling larval dispersal and retention patterns. – Proc. R. Soc. B 269: 2079–2086.

Johns, B. et al. 1992. On the wind-driven coastal upwelling in the Gulf of Lions. – J. Mar. Syst. 3: 309–320.

Kinlan, B. P. et al. 2005. Propagule dispersal and the scales of marine community process. – Divers. Distrib. 11: 139–148.

Koleff, P. et al. 2003. Measuring beta diversity for presence–absence data. – J. Anim. Ecol. 72: 367–382.

Labrune, C. et al. 2007. Assessment of soft-bottom polychaete assemblages in the Gulf of Lions (NW Mediterranean) based on a mesoscale survey. – Estuar. Coast. Shelf Sci. 71: 133–147.

Labrune, C. et al. 2008. Structure and diversity of shallow soft-bottom benthic macrofauna in the Gulf of Lions (NW Mediterranean). – Helgoland Mar. Res. 62: 201–214.

Laliberté, E. et al. 2009. Assessing the scale-specific importance of niches and other spatial processes on beta-diversity: a case study from a temperate forest. – Oecologia 159: 377–388.

Legendre, P. and Legendre, L. 1998. Numerical ecology, 2nd English edn. – Elsevier.

Leibold, M. A. et al. 2004. The metacommunity concept: a framework for a multi-scale community ecology. – Ecol. Lett. 7: 601–613.

Lichstein, J. W. et al. 2002. Spatial autocorrelation and autoregressive models in ecology. – Ecol. Monogr. 72: 445–463.

Logue, J. B. et al. 2011. Empirical approaches to metacommunities – a review and comparison to theory. – Trends Ecol. Evol. 26: 482–491.

Maloney, K. O. and Munguia, P. 2011. Distance decay of similarity in temperate aquatic communities: effects of environmental transition zones, distance measures and life histories. – Ecography 34: 287–295.

Mantel, N. 1967. Detection of disease clustering and a generalized regression approach. – Cancer Res. 27: 209–220.

Marinone, S. G. et al. 2008. Connectivity in the northern Gulf of California from particle tracking in a three-dimensional numerical model. – J. Mar. Syst. 71: 149–158.

Marion, C. et al. 2010. In situ record of sedimentary processes near the Rhône River mouth during winter events (Gulf of Lions, Mediterranean Sea). – Continental Shelf Res. 30: 1095–1107.

Marsaleix, P. 1993. Modélisation tridimensionnelle de la circulation océanique dans le Golfe du Lion. – PhD thesis, Univ. Paul Sabatier de Toulouse.

Marsaleix, P. et al. 1998. A numerical study of the formation of the Rhône River plume. – J. Mar. Syst. 14: 99–115.

Massol, F. et al. 2011. Linking community and ecosystem dynamics through spatial ecology. – Ecol. Lett. 14: 313–323.

McEdward, L. 1995. Ecology of marine invertebrate larvae. – CRC Press.

McGill, B. 2010. Towards a unification of unified theories of biodiversity. – Ecol. Lett. 13: 627–642.

McHugh, D. and Fong, P. P. 2002. Do life history traits account for diversity of polychaete annelids? – Invertebr. Biol. 121: 325–338.

Meynard, C. N. and Quinn, J. F. 2008. Bird metacommunities in temperate South American forest: vegetation structure, area and climate effects. – Ecology 89: 981–990.

Meynard, C. N. et al. 2011. Beyond taxonomic diversity patterns: how do α, β and γ components of bird functional and phylogenetic diversity respond to environmental gradients across France? – Global Ecol. Biogeogr. 20: 893–903.

Millot, C. 1990. The Gulf of Lions' hydrodynamics. – Continental Shelf Res. 10: 885–894.

Minami, S. and Azuma, A. 2003. Various flying modes of wind-dispersal seeds. – J. Theor. Biol. 225: 1–14.

Mouquet, N. and Loreau, M. 2002. Coexistence in metacommunities: the regional similarity hypothesis. – Am. Nat. 159: 420–426.

Mouquet, N. et al. 2004. Immigration and local competition in herbaceous plant communities: a three-year seed-sowing experiment. – Oikos 104: 77–90.

Mouquet, N. et al. 2006. Consequences of varying regional heterogeneity in source-sink metacommunities: a mechanistic model. – Oikos 113: 481–488.

Nathan, R. et al. 2011. Mechanistic models of seed dispersal by wind. – Theor. Ecol. 4: 113–132.

Oksanen, J. 2011. vegan: community ecology package. R package ver. 1.17-10. (<http://CRAN-R-project.org/package=vegan>).

Supplementary material (Appendix oik-00377 at <www.oikosoffice.lu.se/appendix>). Appendix 1.

Ozinga, W. A. et al. 2004. Dispersal potential in plant communities depends on environmental conditions. – J. Ecol. 92: 767–777.

Roughgarden, J. et al. 1988. Recruitment dynamics in complex life cycles. – Science 241: 1460–1466.

Saenz-Agudelo, P. et al. 2011. Connectivity dominates larval replenishment in a coastal reef fish metapopulation. – Proc. R. Soc. B 278: 2954–2961.

Salomon, Y. et al. 2010. Effects of asymmetric dispersal on the coexistence of competing species. – Ecol. Lett. 13: 432–441.

Sammarco, P. W. and Andrews, J. C. 1988. Localized dispersal and recruitment in Great Barrier Reef corals: the Helix experiment. – Science 239: 1422–1424.

Scheltema, R. S. 1986. On dispersal and planktonic larvae of benthic invertebrates: an eclectic overview and summary of problems. – Bull. Mar. Sci. 39: 290–322.

Smouse, P. E. et al. 1986. Multiple regression and correlation extensions of the Mantel test of matrix correspondence. – Syst. Zool. 35: 627–632.

Soininen, J. et al. 2007. The distance decay of similarity in ecological communities. – Ecography 30: 3–12.

Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. – Ecology 75: 2–16.

Treml, E. A. et al. 2012. Reproductive output and duration of the pelagic larval stage determine seascape-wide connectivity of marine populations. – Integr. Compar. Biol. 52: 525–537.

Tuomisto, H. and Ruokolainen, K. 2006. Analyzing or explaining beta diversity? Understanding the targets of different methods of analysis. – Ecology 87: 2697–2708.

Tuomisto, H. et al. 2003. Dispersal, environment and floristic variation of western Amazonian forests. – Science 299: 241–244.

Vanschoenwinkel, B. et al. 2009. Wind mediated dispersal of freshwater invertebrates in a rock pool metacommunity: differences in dispersal capacities and modes. – Hydrobiologia 635: 363–372.

Venail, P. A. et al. 2008. Diversity and productivity peak at intermediate dispersal rate in evolving metacommunities. – Nature 452: 210–214.

Watson, J. R. et al. 2010. Realized and potential larval connectivity in the southern California Bight. – Mar. Ecol. Prog. Ser. 401: 31–48.

Wei, C.-L. et al. 2010. Global patterns and predictions of seafloor biomass using random forests. – PLOS ONE 5: e15323. doi: 10.1371/journal.pone.0015323.

Zhang, C. et al. 2010. Partitioning temperate plant community structure at different scales. – Acta Oecol. 36: 306–313.

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RESEARCH ARTICLE

Space Use Variation in Co-Occurring Sister Species: Response to Environmental Variation or Competition?

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Abstract

Coexistence often involves niche differentiation either as the result of environmental divergence, or in response to competition. Disentangling the causes of such divergence requires that environmental variation across space is taken into account, which is rarely done in empirical studies. We address the role of environmental variation versus competition in coexistence between two rodent species: *Rhabdomys bechuanae* (*bechuanae*) and *Rhabdomys dilectus dilectus* (*dilectus*) comparing their habitat preference and home range (HR) size in areas with similar climates, where their distributions abut (allopatry) or overlap (sympatry). Using Outlying Mean Index analyses, we test whether habitat characteristics of the species deviate significantly from a random sample of available habitats. In allopatry, results suggest habitat selection: *dilectus* preferring grasslands with little bare soil while *bechuanae* occurring in open shrublands. In sympatry, shrubland type habitats dominate and differences are less marked, yet *dilectus* selects habitats with more cover than *bechuanae*. Interestingly, *bechuanae* shows larger HRs than *dilectus*, and both species display larger HRs in sympatry. Further, HR overlaps between species are lower than expected. We discuss our results in light of data on the phylogeography of the genus and propose that evolution in allopatry resulted in adaptation leading to different habitat preferences, even at their distribution margins, a divergence expected to facilitate coexistence. However, since sympatry occurs in sites where environmental characteristics do not allow complete species separation, competition may explain reduced inter-species overlap and character displacement in HR size. This study reveals that both environmental variation and competition may shape species coexistence.

Introduction

The concept of character displacement is the subject of regular debate in ecology [1–4]. Ecological character displacement is defined as a process where populations respond to competition by modifying their resource-use traits through phenotypic plasticity or genetic adaptation [5]. This response to competition plays an important role in generating and maintaining biodiversity as well as shaping the mechanisms of coexistence [1,6,7], particularly between species sharing similar niches [8]. However, solid empirical evidence demonstrating the process of character displacement is rare (shown in only 9 out of 144 studies reviewed in [4]), partly due to confusion between character variation and character displacement [4,9]. Character variation due to ecological heterogeneity could occur when species adapt to distinct environments in allopatry, and may not be interpreted as character displacement when the same species are found to be divergent in sympatry [9]. Moreover, when species occur along a gradient of environmental conditions, their traits may converge in sympatry despite competition [10]. In such conditions, ecological heterogeneity across space has been argued to be a more convincing cause of character variation than competition [4].

Our study aims to test the role of adaptation to distinct environments versus competition leading to character displacement in shaping coexistence between two sister species of the African four striped mouse: *Rhabdomys bechuanae* (sensu [11], hereafter *bechuanae*) and *Rhabdomys dilectus dilectus* (sensu [12], hereafter *dilectus*). We focus here on space use, an important dimension of the niche [13] because it determines access to resources, and hence could directly influence reproductive success and survival [14]. Further, the evolution of this complex trait could be shaped both by environmental conditions [15,16] and competitive interference in areas of coexistence [17,18].

Space use, or the spatial dimension of a species niche, can be described at beta and alpha scales [19]. The beta scale considers the climate and environmental conditions over the entire range of the species defining its environmental niche. The alpha scale considers niche variation between individuals and populations (i.e. "the niche variation hypothesis", [20]) and allows for a more detailed assessment of niche characteristics.

We studied the spatial niche of the two striped mouse species at an alpha scale by analyzing their habitat use and home range (HR) characteristics. The striped mouse shows marked differentiation across climate and vegetation along an east-to-west gradient in southern Africa [11,21]. Large scale studies, modelling the two species' niches over South Africa and Namibia suggested environmental divergence, *dilectus* being found in the wetter areas of the north-eastern parts of South Africa where grassland vegetation dominates, while *bechuanae* occupies warmer and drier regions and penetrates into the more mesic central part of South Africa within areas where open shrubland vegetation dominates [11,21]. Such a divergence could either be the result of adaptation in distinct environmental conditions, or reflect a large range of plastic responses to the environmental gradient occupied by the two species. Here, we test the role of adaptation versus plasticity in this divergence and disentangle the role of ecological heterogeneity versus competition in shaping species coexistence in the field.

The distribution of the two species abuts in areas with similar environmental conditions, where pockets of sympatric populations exist [22]. To distinguish habitat selection from character displacement, we compared habitat preference and HR characteristics of the two species at their distribution margins where allopatric and sympatric populations are found. We made the following predictions: first, if environmental niche divergence resulted from adaptation in allopatry, as suggested by the beta scale study, populations at the margins of the two species distribution, occurring in similar environments, would select different habitats. Second, if environmental heterogeneity in areas of sympatry is sufficient to allow species segregation, we would expect little competition, if any, on the spatial dimension of the species niche. Alternatively, if environmental heterogeneity does not allow complete habitat separation, competition is expected to induce character displacement, even if sympatry is only temporary, because the trait studied here, HR size, is expected to respond rapidly to interference competition [23].

Material and Methods

Ethics statement

Permits to work and handle animals in the field were obtained from the Free State and North West Province reserve ethics authorities (n°01/15700, 01/11262). Animals handling was performed under permissions from the French agriculture ministry to GG (C34–265), and Wits university ethics committee for CMSD (AESC n°: 2012/13/2A).

Study species

Rhabdomys sp. individuals forage alone during the day and rest at night in a nest either alone or in groups [24]. All *Rhabdomys* species are morphologically very similar, requiring genotyping for their identification. In our study, species identity was assessed by genotyping their Cytochrome Oxydase I mitochondrial gene (described in [22]).

Study area

Mice were studied in four nature reserves located within the savanna and grassland biomes (sensu [25]) of central South Africa: three reserves in the Free State Province and one at its boundary with the North West Province (Fig. 1). The reserves occur along a north-south axis, from Bloemhof Dam (BLH; S27° 38' E25° 40') and Sandveld (SA; S27° 43' E25° 45'), to Soetdoring (SO; S28° 50' E26° 03') and Tussen die Riviere (TDR; S30° 28' E26° 09'). In these reserves, *dilectus* and *bechuanae* occur in different geographic settings, either as monospecific populations (hereafter: allpatric sites) or as regular but temporary mixed species populations (hereafter: sympatric sites, S1 Fig.). In sympatric sites mice of the two species could be trapped in the same traps (although not together).

We sampled a total of 22 sites across the four reserves, among which 11 were sampled at 2 to 3 occasions (Table 1). The HRs of the mice studied never overlapped between sites during the study period (which lasted roughly two weeks per site).

Although we did not monitor predation and competition with other species, we observed the presence of snakes, birds of prey and carnivore small mammals in all sites. Other rodent species were present in the trapping sites: the most frequent ones were *Gerbiliscus sp*. and *Nannomys minutoides*.

Trapping procedure

Trapping took place during the austral spring: October-November 2011 (SA), October-November 2012 (SA, SO, TDR, BLH), and autumn: April-May 2012 (SA, SO) and April-May 2013 (SA, TDR, BLH). Our trapping strategy aimed to sample most vegetation types available within the area. Small mammal live traps (Sherman and PVC traps of equivalent size) were baited with a mixture of oats, salt and peanut butter, and were provided with a piece of cotton wool as bait and to reduce thermal stress. The number of trap lines varied with the site size, and distance between traps was roughly 10m (10 to 30 traps/line). Traps were checked 2–3 times a day regularly between 7am and 7pm (mean±SD: 79.5±50.89 traps per day per site). Upon capture, each mouse was sexed, weighed, measured (body length) and individually marked with two ear tags (7mm, 0.17g; National Band and Tag Co., Newport, KY-USA). We

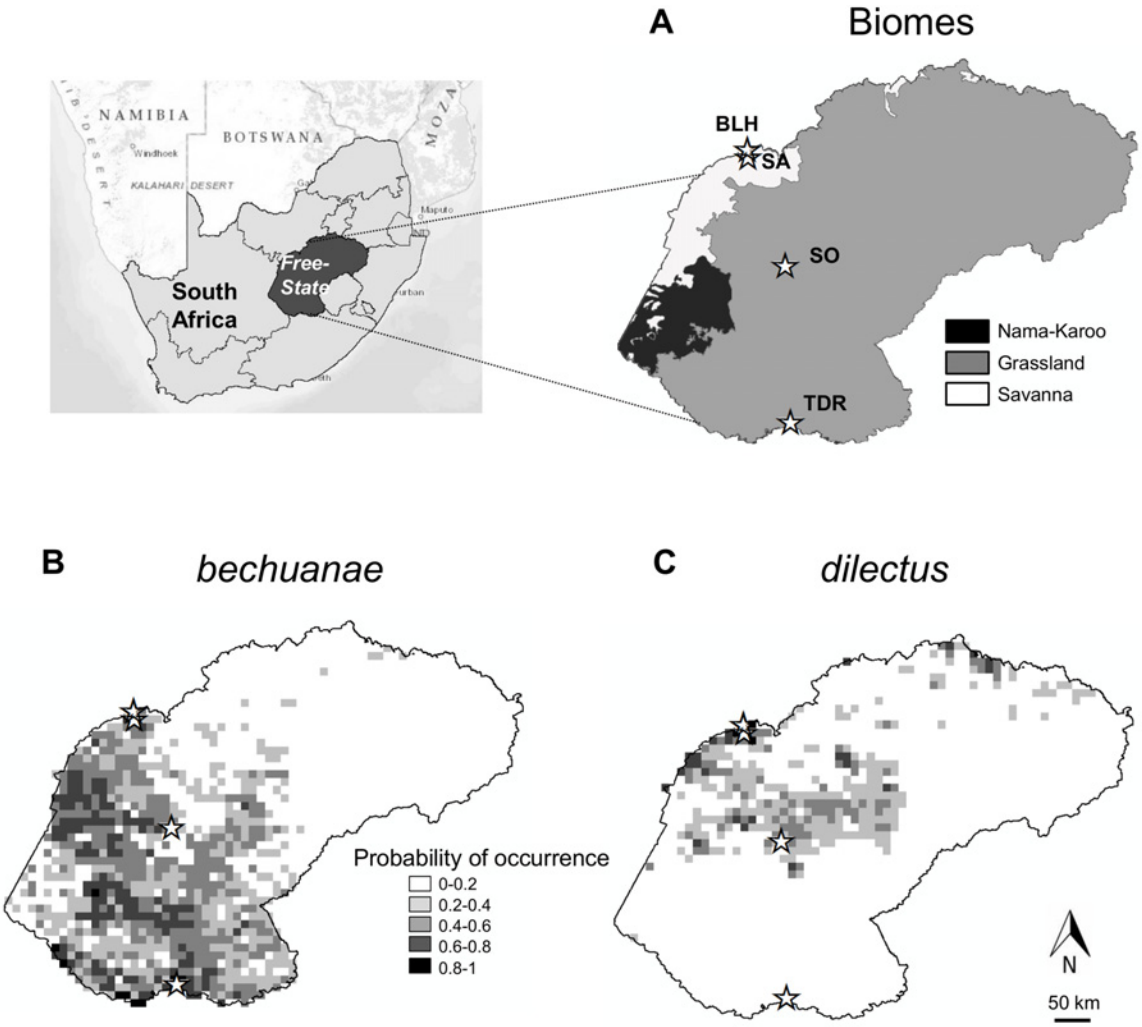

Fig 1. Study area and species occurrence probability. Details on biomes (A) and probabilities of occurrence of *dilectus* and *bechuanae* (B, C) (modified from Ganem *et al*. 2012). Star symbols indicate position of Bloemhof (BLH), Sandveld (SA), Soetdoring (SO) and Tussen die Riviere (TDR) Nature reserves.

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also collected a piece of tail (≈1cm) for species identification. Overall, we trapped and genotyped 599 mice. Following [26], we estimated relative density within each site by computing the total number of striped mice captured during the first five trapping days divided by the total length of trap lines accounting for a 60 m buffer around the trap lines (roughly the average diameter of a mouse HR, Table 1).

Habitat characterization

Earlier studies addressing beta scale niche analysis [21,22] suggested that the two species could have different requirements in terms of vegetation cover and structure (i.e. grass versus woody vegetation). Here we aimed to test this hypothesis at an alpha scale, and characterized the vegetation structure of mouse habitats by measuring the percentage of trees, bushes, grass and bare soil over 60x60m quadrats, centred on a trap line (the first and last traps were at the centre of, respectively, the first and last quadrats on a given trap line). Furthermore, vegetation cover was determined within 1x1m metal square thrown to the right and left of a trap line at every second trap. Within these 1x1m quadrats, we evaluated the percentage of grass versus woody plants (small

Table 1. Characteristics of studied sites across the four nature reserves.

Reserve	Year	Season	Site	Geography	Radio-tracking	Total number of		Area (m^2)	Percentage of area characterized with the 60x60 quadrats	Density index
						Bechuanae	*dilectus*			
BLH	2012	spring	BLH1	allopatry	yes	0	8	30113	75	0.03
BLH	2012	spring	BLH2	allopatry	yes	0	17	50319	31	0.04
BLH	2012	spring	BLH3	allopatry	yes	0	13	85622	20	0.01
SA	2012	spring	SA1	allopatry	yes	18	0	193027	49	0.01
SA	2011	spring	SA1	sympatry	yes	96	43	193027	49	0.06
SA	2011	spring	SA2	sympatry	yes	7	10	45531	19	0.05
SA	2012	spring	SA3	allopatry	yes	4	0	44151	31	0.01
SO	2012	spring	SO1	allopatry	yes	14	0	28150	52	0.02
SO	2012	spring	SO2	allopatry	yes	4	0	17907	53	0.01
SO	2012	spring	SO3	allopatry	yes	0	51	88514	64	0.05
SO	2012	spring	SO4	sympatry	yes	1	10	107895	42	0.01
TDR	2012	spring	TDR1	allopatry	yes	68	0	119527	48	0.07
BLH	2013	autumn	BLH3	allopatry	no	0	3	85622	20	
BLH	2012	spring	BLH4	allopatry	no	0	3	16763	52	
SA	2012	autumn	SA1	sympatry	no	25	8	193027	49	
SA	2012	autumn	SA3	allopatry	no	12	0	44151	31	
SA	2013	autumn	SA3	allopatry	no	8	0	44151	31	
SA	2013	autumn	SA4	allopatry	no	0	1	37110	48	
SA	2012	autumn	SA4	sympatry	no	4	7	37110	48	
SA	2012	spring	SA4	sympatry	no	1	2	37110	48	
SA	2012	autumn	SA5	allopatry	no	17	0	19462	45	
SA	2012	spring	SA5	allopatry	no	1	0	19462	45	
SA	2013	autumn	SA5	allopatry	no	1	0	19462	45	
SA	2012	autumn	SA6	allopatry	no	8	0	12751	71	
SA	2012	autumn	SA7	sympatry	no	7	6	124315	29	
SA	2012	spring	SA7	sympatry	no	5	1	124315	29	
SA	2012	autumn	SA8	allopatry	no	4	0	7659	70	
SA	2012	autumn	SA9	allopatry	no	18	0	43011	34	
SA	2013	autumn	SA9	allopatry	no	5	0	43011	34	
SO	2012	autumn	SO1	allopatry	no	4	0	28150	52	
SO	2012	autumn	SO3	allopatry	no	0	52	88514	64	
SO	2012	autumn	SO4	allopatry	no	0	11	107895	42	
SO	2012	autumn	SO5	allopatry	no	7	0	18942	33	
SO	2012	autumn	SO6	allopatry	no	0	1	6537	47	
SO	2012	autumn	SO7	sympatry	no	1	1	9503	64	
TDR	2013	autumn	TDR1	allopatry	no	4	0	119527	48	
TDR	2012	spring	TDR2	allopatry	no	3	0	17701	57	

BLH: Bloemof, SA: Sandveld, SO: Soetdoring and TDR: Tussen Die Riviere nature reserves.

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shrubs), the percentage of bare soil and an estimate of mouse visibility (an index ranging from 1, i.e. completely visible, to 5, i.e. completely hidden, a value determined by averaging the visibility of a dummy mouse that we placed in four different locations inside the metal square). Altogether we used 136 60x60m quadrats (5.9±6.31 per site) and 229 1x1m quadrats (10.4±15.37 per site).

Radiotracking

A total of 101 adult mice (body mass ≥ 23 grams), were equipped with VHF collars (MD 2C Holohil, Carp, Ontario, Canada) in October-November 2011 and 2012 in 11 distinct sites on the four reserves. Radiotracking was performed on foot with a wide-range receiver (AOR 8000) and a hand-held Telonics R4–14K antenna. Localization of a collared mouse followed the standard triangulation technique and its precise location was confirmed with the receiver cable used without the antenna. The receiver volume was set to 0 during the triangulation to reduce mice disturbance. The GPS coordinates of radio-collared individuals were recorded five times during the day (at about 7, 9, 11am and 2 and 4pm) and once at sunset (roughly 7pm).

Home range size and overlap estimations

HRs were defined as the areas encompassed within the 0.95 cumulative isopleth of the Utilization Distributions (UDs), estimated using the fixed kernel method with the reference smoothing parameter [27]. Our sampling regime was chosen after a calibration session where we followed 30 individuals for more than seven days (from 40 to 69 relocations). The estimated HR size of our controls stabilized after 27 relocations and a paired comparison of the HR size at 27 and 41 regular relocations did not show a significant difference (Wilcoxon test, V = 306, p = 0.14). Following [28], we chose a strategy maximizing the number of mice radiotracked with a sampling regime standardized to a minimum of 27 independent relocations, collected over five consecutive days.

We compared HR overlaps in a sympatric site between pairs of mice of the same species versus different species. We computed the overlap between each pair of HRs using their UD-based volume of intersection [29]. Because UDs are truncated at the 0.95 cumulative isopleth (excluding the poorly estimated UD tails), overlap values were normalized to 1 by dividing them by 0.95 (see [30] for details).

Statistical analyses

Statistical analysis was conducted with R-v2.15 [31]. Normality and heteroscedasticity of distributions were checked with a Shapiro test and visualized with the plot of the model's residuals. When these conditions were not met even after data transformation, non-parametric tests were used. Significance level was set to 0.05, and adjusted for multiple comparisons with the sequential Bonferroni procedure when necessary. UD, overlap computations, and permutation tests (see below) were performed using home-made programs in Pascal.

Mice-habitat relationship assessed with trapping data

A total of 599 trapped mice were used in these analyses. A mouse was considered as potentially using a 60x60m quadrat when it was trapped within it, and a 1x1m quadrat when it was trapped less than 10m from it. Each quadrat was then assigned to one or the other species, to both species, or to none. A total of 89 60x60m quadrats and 227 1x1m quadrats were assigned to one or the two species.

We performed an Outlying Mean Index multivariate analysis to characterize the environmental niche of each species (i.e. OMI) [32]. Briefly, the OMI procedure generates ordination axes corresponding to the combination of environmental variables (here vegetation structure and cover) that are most relevant for the species under study, and provides a measure of the habitat conditions occupied by the species. Our two habitat parameters (vegetation structure and cover) were obtained at different sampling scales, hence, we carried out an OMI analysis at each scale (i.e. 60x60m and 1x1m). Each analysis produced a habitat niche position value (i.e. the mean habitat characteristics of species occurrence) and breadth (i.e. variance) for each of the four categories studied here, i.e. the two species in allopatric versus sympatric sites. We assessed marginality (i.e. deviation from a random sample of available conditions) of niche position and breadth of a given category on an OMI axis through comparisons with distributions obtained performing 1000 random permutations followed by bootstrap two-tailed tests.

The niche positions of the four population categories (two species in allopatry versus in sympatry) on the first OMI axis (OMI1) were compared with linear mixed ANOVAs (package nlme), with the category as a fixed effect and site as a random effect, followed by Tukey post-hoc tests when relevant (package mulcomp, glht function). The same procedure was applied on a subsample of the data comprised of only sympatric sites, to test whether excluding allopatric habitats from the analyses would detect species divergence in sympatry.

Mice-habitat relationships assessed with home range data

Habitat at the HR scale was characterized with the 60x60m quadrats that covered an area corresponding to at least 70% of the HR. Such a coverage was reached for 80 of the estimated HRs (S1 Table). The four vegetation structure variables measured within a quadrat were weighted by the relative proportions of the HR UD covered. These data were then analyzed following the same procedure as described above.

Determinants of home range size variation

For the purpose of this analysis, we reduced the four variables describing vegetation structure into one corresponding to the first axis of a Principal Component Analysis (PCA). This axis represented 76% of total variance. We tested the influence of body size, sex, population density, habitat (i.e. PCA1), geography (i.e. allopatry vs sympatry) and species on log-transformed HR size. Our data showed spatial autocorrelation (Moran test, $p<0.001$, library "spdep"), hence we applied the spatial simultaneous autoregressive error model estimation (sarlm model) in subsequent ANCOVA analyses. Our initial ANCOVA model comprised all factors as main effects and second and third order interactions with "species", except for density which was included as a co-variable in the model. Preliminary analyses showed that density did not vary between species (KW, DF = 2, $\chi^2 = 1.72$, p = 0.42) or with the habitat parameter of the model (Spearman, $\rho = 0.06$, p = 0.58), and that body size did not differ between our sample of males and females (Anova, DF = 1,97, F = 0.61 p = 0.44). The most parsimonious model was obtained after sequential elimination of factors with non-significant effects (following [33]), and post-hoc checking that its AICc was significantly smaller to that of the initial model.

HR overlaps in a sympatric site

Because we did not know the species identity of mice during our field study, our selection of radiotracked mice could not be balanced. The between-species HR overlap analysis could eventually be performed for only one sympatric site (SA1), in which 6 *dilectus* (3 females and 3 males) and 14 *bechuanae* (9 females and 5 males) were radiotracked. Other sympatric sites contained too few radiotracked individuals of one species or the other to enable us to perform statistical tests. We computed three observed values: the mean overlap between any two *dilectus* HRs, the mean overlap between any two *bechuanae* HRs and the mean overlap between HRs of any two mice belonging to different species. To test the null hypothesis: "random overlap between species", we determined all the possible partitions of 20 mice in a group of 6 (G6) and a group of 14 (G14). Because the degree of HR overlap between two mice could also depend on sex, we kept only the 12320 partitions (out of 38760) showing the observed sex ratios (i.e. 3 females and 3 males in G6 and 9 females and 5 males in G14). For each partition, we computed the mean overlap between two mice belonging to the same group (G6xG6 and G14xG14) or to different groups (G6xG14). Mean values are based on 15 (G6xG6), 91 (G14xG14) or 84 (G6xG14) observations. In this way, by considering the whole set of partitions, we built up three theoretical distributions expected under the null hypothesis, to which we compared the three observed values mentioned above. As in any permutation test, the probability to reject the null hypothesis, i.e. obtaining a value equal to or more extreme than the observed value in each of the three tests, was computed as $P = 2(n_e+1)/n$ (bilateral test), where n_e is the number of these most extreme values and n is the total number of values ($n = 12320$).

Results

Variation of habitat preference within and between species

We compared the habitat characteristics of allopatric and sympatric mice of the two species at the population (site) and individual (HR) levels with three distinct OMI analyses. The first axes (i.e OMI1) always captured a significant proportion of the habitat variation (>94%, Fig. 2), and results were consistent across analyses. These three axes had positive values for presence of grass and mouse visibility, and negative values for the presence of woody type vegetation and bare soil (Fig. 2). The habitat niche positions of the two species in allopatric sites were significantly different from a random sample of available habitats ($p<0.05$), and from each other (respectively, at the site level, vegetation structure and cover, and at the HR level vegetation structure: $z = -4.41$, $z = -7.69$ and $z = 5.28$, $p<0.001$). The niche position of allopatric *bechuanae* showed significant negative values (i.e. habitat characterized by more woody vegetation and presence of bare soil than that in a random sample of available habitats), while those of *dilectus* were significantly positive (i.e. habitats characterized by the presence of more grass and cover than in a random sample). Unlike allopatric sites, the niche position of individuals of the two species in sympatry did not differ from random expectations ($p>0.05$). However, their positions differed from that of their allopatric counterparts. Indeed, in sympatry, *bechuanae* occurred in a habitat with higher mouse visibility and cover values (vegetation cover, $z = 3.39$, $p = 0.003$), but with similar values of vegetation structure (at the site and HR levels, Fig. 2) compared to its habitat in allopatry. In contrast, habitat characteristics of *dilectus* in allopatry and sympatry differed in the three analyses, as its habitat in sympatry was characterized by lower values of mouse visibility, cover and presence of grass than in allopatry (respectively, at the site level the vegetation structure and cover, at the HR level the vegetation structure: $z = -3.88$ $z = -3.84$ $z = -4.29$ $p<0.001$, Fig. 2).

Considering only sympatric sites, the first OMI axes captured most of the data variation (>88%), and described a habitat gradient ranging from high values of bare soil and presence of trees (negative values of OMI1) to high values of grass, mouse visibility and presence of bushes (positive values of OMI1, Fig. 3). Despite the reduced power due to a smaller sample size (particularly for the HR level analysis), the results indicate that *bechuanae* occurs in micro-habitats characterized by more bare soil, woody vegetation and less mouse visibility than that of *dilectus*, although these differences (respectively at the site level, the vegetation structure and cover: $p = 0.03$ $p = 0.05$) were not strong (significance level adjusted for multiple testing $\alpha' = 0.025$; Fig. 3).

Variation of HR size within and between species

None of the first and second order interactions with species were significant predictors of HR size variation, indicating that the patterns described below were consistent across species. Males had larger HRs than females ($z = 2.37$, $p = 0.02$, Fig. 4, S2 Table) and population density and habitat did not significantly affect HR size (respectively, $z = -0.89$, $p = 0.37$ and $z = 1.66$, $p = 0.10$, S2 Table). Further, *bechuanae* had larger HRs than *dilectus* ($z = 3.40$, $p<0.001$) both in allopatry and sympatry, although the HRs of both species were smaller in allopatry than in sympatry ($z = 2.82$, $p<0.01$, Fig. 4, S2 Table).

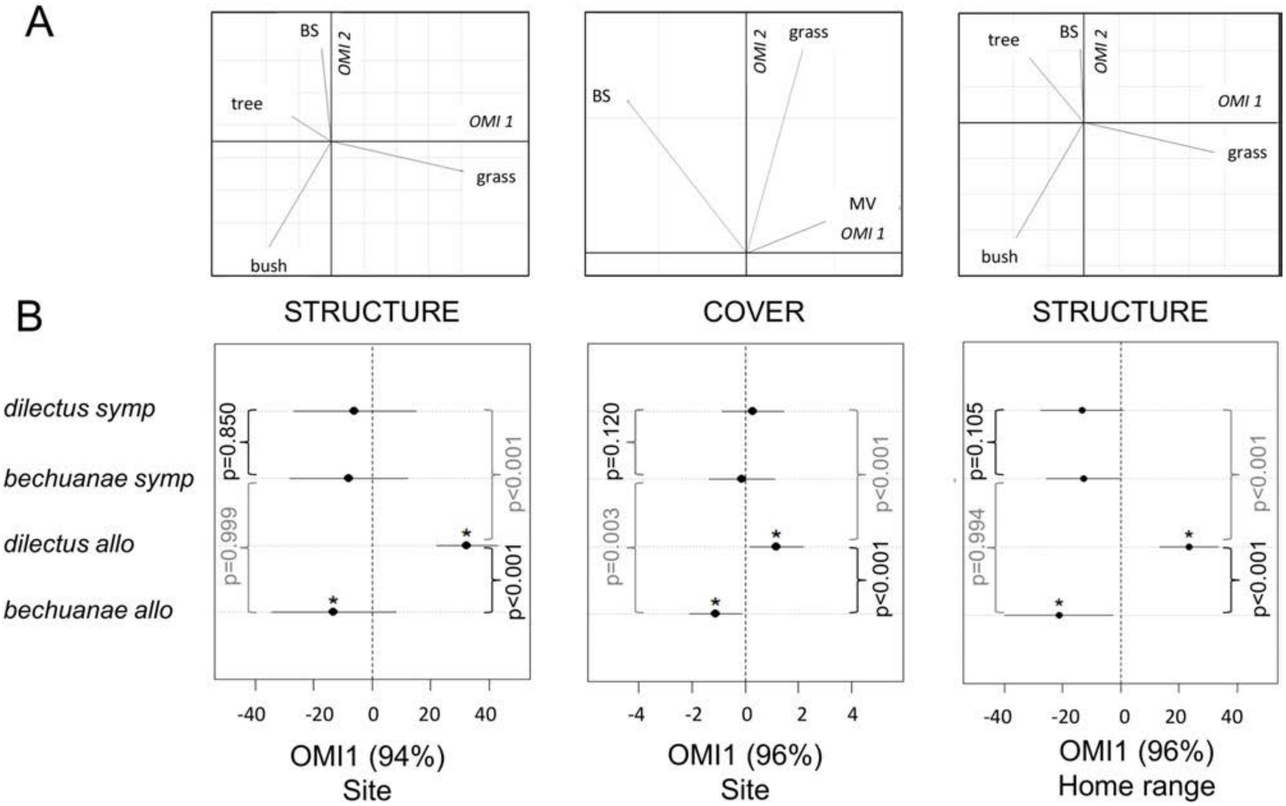

Fig 2. Habitat niche divergence in sympatry and allopatry. Habitat divergence between allopatric (allo) and sympatric (symp) populations of the two species as assessed with Outlying Mean Index (OMI) analyses. The upper row (A) shows the relative contribution of the different habitat variables: vegetation structure (tree, grass, bush and bare soil (BS)) and cover (bare soil (BS), grass and mouse visibility (MV)) to the first two OMI axes. The lower row (B) indicates the position (dot) and breadth (line) of each species niche along the first OMI axis (* when significantly different from random expectation). The p-values of Tukey tests are given for every pair comparison (black: inter-specific, grey: intra-specific).

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Patterns of overlap in a sympatric site

Overlaps of HRs between the two species were significantly lower than random expectations (observed value: 0.011±0.048; permutation test $p<0.01$), while they were higher than expected within *bechuanae* (observed value: 0.057±1.265; $p<0.01$), and not different from random within *dilectus* (observed value: 0.023±0.052; $p>0.5$, S2 Fig.).

Discussion

Our study is among very few that attempted to disentangle the complex interaction between environment and competition in shaping character variation [23]. We focused on the spatial niche (i.e. habitat selection and HR size) of two sister species of striped mice whose distributions are mostly allopatric and characterized by distinct environmental conditions [11,12]. We assessed the influence of environmental variation and competition on habitat selection and HR size variation in an area where the distributions of the two species abut and where allopatric and sympatric populations can be compared under similar climatic conditions [22].

Earlier large scale investigations indicated that the environmental niche of the two studied species diverged: the habitats of *bechuanae* are dominated by warmer climates and drier open shrubland vegetation, while those of *dilectus* are characterized by wetter climates and grassland

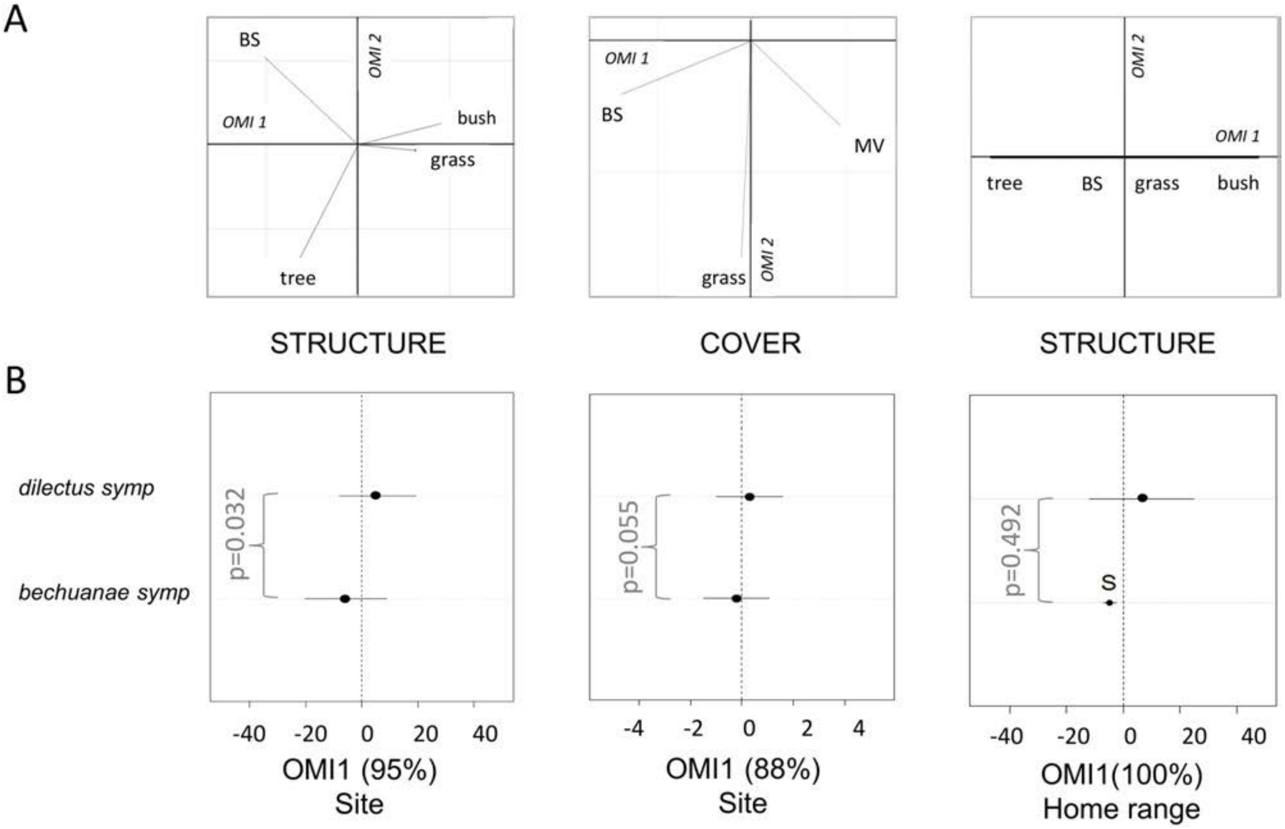

Fig 3. Details on habitat niche divergence in sympatry. Habitat divergence of the two species in sympatric sites assessed with Outlying Mean Index (OMI) analyses. See legend in Fig. 2. The p-values follow Wilcoxon tests.

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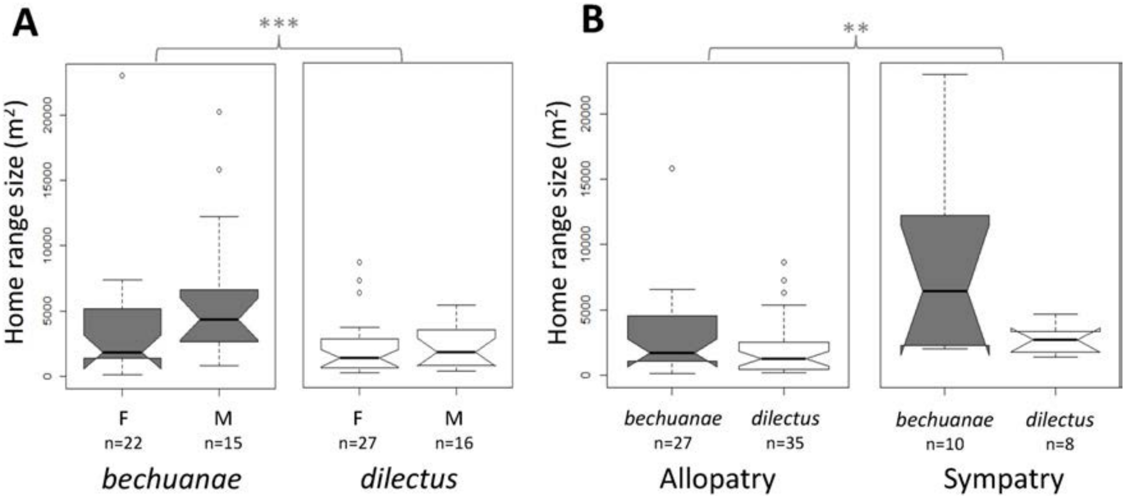

Fig 4. Home range size estimates. Home range size estimates (isopleth 0.95) across species (grey: *bechuanae*, white: *dilectus*), A: sex (F females and M males) and B: "geography" (** $p<0.01$, *** $p<0.001$ refers to Ancova results in S2 Table). Box-plots show the median (thick line), first and third quartiles. Non-overlapping notches are roughly equivalent to 95% confidence intervals.

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type vegetation, providing more cover [11,21,22]. Such beta scale studies are particularly relevant to address species niche characteristics over their entire range; however, they could suffer from confounding effects due to spatial autocorrelation of large scale environmental variables and are not expected to reveal micro-environmental heterogeneity [34], but see [35]. Nevertheless, using an alpha approach, the present study confirms habitat niche divergence at a fine scale and highlights a role for both environmental variation and competition in shaping the spatial niche of *bechuanae* and *dilectus* in sympatry.

Niche divergence

Habitat

Sister species are expected to have similar niches if they retain ancestral characteristics (niche conservatism, [36]), or when they evolve under similar conditions [37]. In all cases, contact or secondary sympatry between species sharing similar niches are expected to trigger character displacement [8,35]. Earlier studies of the striped mouse environmental niche indicated that evolution in allopatry took place under different environmental conditions [11,21], and that divergent adaptation may facilitate coexistence. The present study confirms divergence in habitat selection by the two species at the margins of their distributions but also indicates that the available habitat in sympatry is more similar to that of *bechuanae* in allopatry (i.e. less cover and more woody vegetation) than that of *dilectus*. Nevertheless, the latter still selects micro-habitats with more cover and less woody vegetation than *bechuanae*, confirming micro-habitat partitioning in sympatry as suggested by preliminary observations [22]. Such differences in habitat preference, consistent over the entire species range including its margins and sympatric zones, together with the largely allopatric distribution of the species, support evolution under different selective pressures in allopatry (i.e. adaptation), and a more recent secondary contact where these preferences are still expressed. Partition of the habitat niche could thus result in lower interspecific competition pressures facilitating co-existence [38,39]. Nevertheless our study indicates that habitat divergence in sympatry is tenuous compared to that in allopatry. Further, the habitat available in sympatry differed significantly from that in allopatry for *dilectus*, suggesting that the latter invaded the range of *bechuanae* and that coexistence occurs in areas to which *dilectus* might be less adapted.

Home Range

Lesser habitat partition in sympatry is expected to induce competition which we assessed comparing HR size variation, a trait known to be influenced by habitat features [16] and interspecific interference [40]. We found differences in HR size between the species: *dilectus* having smaller HRs than *bechuanae*. These differences exist despite sexual dimorphism in HR size (i.e larger in males than females), in both species, that could relate to behavioural [41,42] and physiological [16,43] sex differences.

Our study did not address the precise mechanisms of HR divergence; however, based on inference from the literature, we may expect that, like other species, striped mice adjust their HR size to available cover or shelter (e.g. [16] on the wood mouse) or to visibility of potential predators (e.g. [44] on roe deer). Such patterns are consistent with our observations that, the species showing preference for habitats with cover, *dilectus*, also has smaller HRs compared to *bechuanae* which selects habitats with more wood and less cover. Larger HRs may also provide access to patchily located shelters from predators [45], which may be the case for *bechuanae* which selects open shrubland type habitats. Differences in HR size may also indicate differences in food distribution, since smaller HRs were proposed to reflect more concentrated food distribution in other studies [44,46–49]. Surprisingly, we did not detect a significant influence of vegetation structure on HR size variation. Possible explanations might be that, either this variable only has an indirect effect on HR size (see above), or to lower resolution due to small sample size.

Character displacement

Differences in habitat preferences may facilitate coexistence between *bechuanae* and *dilectus*. However, as indicated above, sympatry occurs in habitats that are less favorable for *dilectus* and our study suggests that species segregation in sympatry may not be complete. Patterns of HR size variation in allopatry versus sympatry also suggest that competition may occur. Indeed, both species had a significant increase in their HR size in sympatry as compared to allopatry. Although we cannot exclude that such variation could be consistent with habitat variation as far as *dilectus* is concerned, this argument may not hold for *bechuanae* whose preferred habitat in allopatry and sympatry is similar.

A larger HR size in sympatry may reveal inter-species intolerance and competition [17,23,40]. In our study, larger HRs in sympatry compared to allopatry, at least in *bechuanae*, could be a response to competition and a strategy aimed at limiting costly interactions with the other species through character displacement [40]. Alternatively, it could be a strategy to occupy most of the available resources (e.g. nest sites). Patterns of HR overlap in our study suggest that our first hypothesis may be true, as *bechuanae* showed more HR overlaps than expected with members of the same species, while between species overlaps were lower than expected under random predictions.

Micro-habitat selection and space partition are expected to be adaptive responses to reduce competition [17,18,50]. Here, despite different habitat preferences, habitat segregation is tenuous in sympatry, resulting in *bechuanae* enlarging its HR possibly to avoid *dilectus*, making detours, or to control a larger number of shelters to outcompete *dilectus*.

Conclusion

It was argued that ecological complexity was not considered often enough in assessments of mechanisms of coexistence [9], and that evidence for character displacement resulting from species interference is rare [4]. Our study provides valuable field data in an interesting study model allowing to compare the spatial niche characteristics of two species in a relatively homogeneous sympatric and allopatric environment (a common garden setting). Furthermore, the alpha scale investigation, together with an earlier beta scale one [11,21,22], provides a comprehensive picture of how environmental heterogeneity and interference competition could shape the spatial niche of two sister species and influence patterns of coexistence. Future studies should include mechanistic experimental approach to address competition between the two species and determine the proximal mechanisms (e.g. the impact of competition on the species fitness) shaping the species range limits and patterns of co-existence.

Supporting Information

S1 Fig. Experimental design. A: An example of distribution of allopatric and sympatric sites (SO1-SO6) within Soetdoring Nature Reserve. B: Distribution of the quadrats used for habitat assessment (vegetation structure and cover) around the trap lines.
(TIF)

S2 Fig. Three theoretical distributions of the mean volumes of interaction within HR overlaps. From left to right: distributions of intra-species overlap values within *dilectus* (A) and *bechuanae* (B) and between the species (C). The red lines indicate position of observed mean values.
(TIF)

S1 Table. HR estimates sample size. Number of HR estimates per species and sex in allopatric and sympatric sites, and size of the subsample for which the habitat was characterized.
(XLSX)

S2 Table. Factors influencing HR size variation. Results of the initial and minimal ANCOVA models. The models (sarlm residual, see text), testing factors that may influence HR size variation: habitat (PCA 1), sex, geography (allopatry vs sympatry), body size and population density. Bold p-values indicate significant effects.
(XLSX)

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Author Contributions

Conceived and designed the experiments: CMSD GG. Performed the experiments: CMSD GG JW CR JP JJP NA. Analyzed the data: CMSD GG CM SB. Contributed reagents/materials/analysis tools: CMSD GG NP JW NA. Wrote the paper: CMSD GG CM NP. Conceived and wrote the general project and raised funding: NP GG.

References

1. Dayan T, Simberloff D (2005) Ecological and community-wide character displacement: the next generation. Ecology Letters 8: 875–894. Available: http://doi.wiley.com/10.1111/j.1461-0248.2005.00791.x. Accessed 2013 August 6.
2. Brown W, Wilson E (1956) Character displacement. Systematic Zoology 5: 49–64.
3. Grant PR (1972) Convergent and divergent character displacement. Biological Journal of the Linnean Society 4: 39–68.
4. Stuart YE, Losos JB (2013) Ecological character displacement: glass half full or half empty? Trends in Ecology & Evolution 28: 402–408. Available: http://www.ncbi.nlm.nih.gov/pubmed/23537690. Accessed 7 August 2013. doi: 10.1111/1365-2656.12336 PMID: 25637388
5. Pfennig DW, Pfennig KS (2012) Evolution's wedge competition and the origins of diversity Berley, California. doi: 10.1016/S2214-109X(15)70024-0 PMID: 25638812
6. Grant PR, Grant BR (2006) Evolution of character displacement in Darwin's finches. Science 313: 224–226. Available: http://www.ncbi.nlm.nih.gov/pubmed/16840700. Accessed 2012 November 6. PMID: 16840700
7. Chesson P (2000) Mechanisms of maintenance of species diversity. Annual review of Ecology and Systematics 31: 343–358. Available: http://www.jstor.org/stable/10.2307/221736. Accessed 2013 August 23.
8. Violle C, Nemergut DR, Pu Z, Jiang L (2011) Phylogenetic limiting similarity and competitive exclusion. Ecology Letters 14: 782–787. Available: http://www.ncbi.nlm.nih.gov/pubmed/21672121. Accessed 2013 December 14. doi: 10.1111/j.1461-0248.2011.01644.x PMID: 21672121
9. Goldberg EE, Lande R (2006) Ecological and reproductive character displacement on an environmental gradient. Evolution 60: 1344–1357. Available: http://www.ncbi.nlm.nih.gov/pubmed/16929652. PMID: 16929652
10. Case TJ, Taper ML (2000) Interspecific competition, environmental gradients, gene flow, and the coevolution of species' borders. The American Naturalist 155: 583–605. PMID: 10777432
11. Du Toit N, van Vuuren BJ, Matthee S, Matthee CA (2012) Biome specificity of distinct genetic lineages within the four-striped mouse Rhabdomys pumilio (Rodentia: Muridae) from southern Africa with implications for taxonomy. Molecular Phylogenetics and Evolution 65: 75–86. Available: http://www.ncbi.

nlm.nih.gov/pubmed/22728170. Accessed 2012 November 7. doi: 10.1016/j.ympev.2012.05.036 PMID: 22728170

12. Rambau RV, Robinson TJ, Stanyon R (2003) Molecular genetics of Rhabdomys pumilio subspecies boundaries: mtDNA phylogeography and karyotypic analysis by fluorescence in situ hybridization. Molecular Phylogenetics and Evolution 28: 564–575. Available: http://linkinghub.elsevier.com/retrieve/pii/S1055790303000587. Accessed 2012 November 16. PMID: 12927139
13. Lopez-Darias M, Schoener TW, Spiller DA, Losos JB (2012) Predators determine how weather affects the spatial niche of lizard prey: exploring niche dynamics at a fine scale. Ecology 93: 2512–2518. Available: http://www.ncbi.nlm.nih.gov/pubmed/23431582. PMID: 23431582
14. Powell RA, Mitchell MS (2012) What is a home range? Journal of Mammalogy 93: 948–958. Available: http://www.bioone.org/doi/abs/10.1644/11-MAMM-S-177.1. Accessed 2012 November 4.
15. Schoener T (1974) Resource partitioning in ecological communities. Science 185: 27–39. PMID: 17779277
16. Godsall B, Coulson T, Malo AF (2013) From physiology to space use: energy reserves and androgenization explain home-range size variation in a woodland rodent. Journal of Animal Ecology 83: 126–135. Available: http://www.ncbi.nlm.nih.gov/pubmed/23931095. Accessed 2013 December 16. doi: 10.1111/1365-2656.12116 PMID: 23931095
17. Arakaki S, Tokeshi M (2011) Analysis of spatial niche structure in coexisting tidepool fishes: null models based on multi-scale experiments. Journal of Animal Ecology 80: 137–147. doi: doi:10.1111/j.1365–2656.2010.01749.x PMID: 20796205
18. MacArthur R, Recher H, Cody M (1966) On the relation between habitat selection and species diversity. The American naturalist 100: 319–332.
19. Ackerly D, Schwilk D., Webb C. (2006) Niche evolution and adaptive radiation: testing the order of trait divergence. Ecology 87: 50–61. Available: http://www.ncbi.nlm.nih.gov/pubmed/16922302.
20. Van Valen L (1965) Morphological variation and width of ecological niche. The American Naturalist 99: 377–390.
21. Meynard CN, Pillay N, Perrigault M, Caminade P, Ganem G (2012) Evidence of environmental niche differentiation in the striped mouse (Rhabdomys sp.): inference from its current distribution in southern Africa. Ecology and Evolution 2: 1008–1023. Available: http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=3399166&tool = pmcentrez&rendertype = abstract. Accessed 2012 November 26. doi: 10.1002/ece3.219 PMID: 22837845
22. Ganem G, Meynard CN, Perrigault M, Lancaster J, Edwards S, et al. (2012) Environmental correlates and co-occurrence of three mitochondrial lineages of striped mice (Rhabdomys) in the Free State Province (South Africa). Acta Oecologica 42: 30–40. Available: http://linkinghub.elsevier.com/retrieve/pii/S1146609X12000045. Accessed 2012 December 19.
23. Mikami OK, Kawata M (2002) The effects of individual interactions and habitat preferences on spatial structure in a grassland bird community. Ecography 25: 200–214. Available: http://www.blackwell-synergy.com/links/doi/10.1034/j.1600-0587.2002.250208.x.
24. Schradin C (2004) Territorial defense in a group-living solitary forager: who, where, against whom? Behavioral Ecology and Sociobiology 55: 439–446. Available: http://www.springerlink.com/openurl.asp?genre = article&id = doi:10.1007/s00265-003-0733-x. Accessed 2012 November 2.
25. Mucina L, Rutherford M (2006) The Vegetation of South Africa, Lesotho and Swaziland. South African National Biodiversity Institute, Pretoria, South Africa.
26. Stapp P, Van Horne B (1997) Response of Deer Mice (Peromyscus maniculatus) to shrubs in shortgrass prairie: linking small-scale movements and the spatial distribution of individuals. Functional Ecology 11: 644–651.
27. Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70: 164–168.
28. Börger L, Franconi N, De Michele G, Gantz A, Meschi F, et al. (2006) Effects of sampling regime on the mean and variance of home range size estimates. Journal of Animal Ecology 75: 1393–1405. Available: http://www.ncbi.nlm.nih.gov/pubmed/17032372. Accessed 2013 August 8. PMID: 17032372
29. Seidel K (1992) Statistical properties and applications of a new measure of joint space use for wildlife. University of Washington, Seattle, USA.
30. Benhamou S, Valeix M, Chamaillé-Jammes S, Macdonald DW, Loveridge AJ (2014) Movement-based analysis of interactions in African lions. Animal Behaviour 90: 171–180. Available: http://linkinghub.elsevier.com/retrieve/pii/S0003347214000645. Accessed 2014 March 21.
31. R Development Core Team. 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. doi: 10.1016/j.neuroimage.2011.01.013 PMID: 21238596

32. Doledec S, Chessel D, Gimaret-Carpentier C (2000) Niche separation in community analysis: a new method. Ecology 81: 2914–2927.

33. Zar J (1999) Biostatistical Analysis. 4th ed. Ryu T, Snavely S, editors Prentice-Hall. Upper Saddle River, USA.

34. Soberón J (2007) Grinnellian and Eltonian niches and geographic distributions of species. Ecology Letters 10: 1115–1123. Available: http://www.ncbi.nlm.nih.gov/pubmed/17850335. Accessed 2014 May 23. PMID: 17850335

35. McCormack JE, Zellmer AJ, Knowles LL (2010) Does niche divergence accompany allopatric divergence in Aphelocoma jays as predicted under ecological speciation? Insights from tests with niche models. Evolution 64: 1231–1244. Available: http://www.ncbi.nlm.nih.gov/pubmed/19922442. Accessed 2014 May 23. doi: 10.1111/j.1558-5646.2009.00900.x PMID: 19922442

36. Peterson AT, Soberon J, Sanchez-Cordero V (1999) Conservatism of ecological niches in evolutionary time. Science 285: 1265–1267. Available: http://www.sciencemag.org/cgi/doi/10.1126/science.285.5431.1265. Accessed 2014 May 26. PMID: 10455053

37. Losos JB (2011) Convergence, adaptation, and constraint. Evolution 65: 1827–1840. Available: http://www.ncbi.nlm.nih.gov/pubmed/21729041. Accessed 2014 June 3. doi: 10.1111/j.1558-5646.2011.01289.x PMID: 21729041

38. Schluter D, Mcphail JD (1992) Ecological character displacement and speciation in sticklebacks. The American naturalist 140: 85–108. doi: 10.1086/285404 PMID: 19426066

39. Lira A, Souza A, Silva Filho A, Albuquerque C (2013) Spatio-temporal microhabitat use by two co-occurring species of scorpions in Atlantic rainforest in Brazil. Zoology 116: 182–185. Available: http://www.ncbi.nlm.nih.gov/pubmed/23664851. Accessed 2013 November 1. doi: 10.1016/j.zool.2013.01.002 PMID: 23664851

40. Trombulak SC (1985) The influence of interspecific competition on home range size in chipmunks (Eutamias). Journal of Mammalogy 66: 329–337.

41. Clutton-Brock TH (1989) Mammalian mating systems. Proceedings of the Royal Society of London 236: 339–372. Available: http://www.ncbi.nlm.nih.gov/pubmed/2567517. PMID: 2567517

42. Schradin C (2006) Whole-day follows of striped mice (Rhabdomys pumilio), a diurnal murid rodent. Journal of Ethology 24: 37–43. Available: http://www.springerlink.com/index/10.1007/s10164-005-0158-2. Accessed 2012 December 19.

43. Schradin C, Scantlebury M, Pillay N, König B (2009) Testosterone levels in dominant sociable males are lower than in solitary roamers: physiological differences between three male reproductive tactics in a sociably flexible mammal. The American Naturalist 173: 376–388. Available: http://www.ncbi.nlm.nih.gov/pubmed/19199528. Accessed 2012 November 12. doi: 10.1086/596535 PMID: 19199528

44. Tufto J, Andersen R, Linnell J (1996) Habitat use and ecological correlates of home range size in a small cervid: the roe deer. Journal of Animal Ecology 65: 715–724.

45. Holmes W (1991) Predator risk affects foraging behaviour of pikas: observational and experimental evidence. Animal Behaviour 42: 111–119.

46. Schradin C, Pillay N (2005) Intraspecific variation in the spatial and social organization of the african striped mouse. Journal of Mammalogy 86: 99–107.

47. Schradin C, Schmohl G, Rödel HG, Schoepf I, Treffler SM, et al. (2010) Female home range size is regulated by resource distribution and intraspecific competition: a long-term field study. Animal Behaviour 79: 195–203. Available: http://linkinghub.elsevier.com/retrieve/pii/S0003347209004965. Accessed 2012 November 4.

48. Stradiotto A, Cagnacci F, Delahay R, Tioli S, Nieder L, et al. (2009) Spatial organization of the yellow-necked mouse: effects of density and resource availability. Journal of Mammalogy 90: 704–714.

49. Jonsson P, Hartikainen T, Koskela ESA (2002) Determinants of reproductive success in voles: space use in relation to food and litter size manipulation. Evolutionary Ecology 16: 455–467.

50. Hawes ML (1977) Home range, territoriality, and ecological separation in sympatric shrews, Sorex vagrans and Sorex obscurus. Journal of Mammalogy 58: 354–367.

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ORIGINAL ARTICLE

Influence of past and future climate changes on the distribution of three Southeast Asian murine rodents

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ABSTRACT

Aim We tested the influence of Pleistocene climatic fluctuations and the potential effect of future climate change on Southeast Asian small mammal distributions using two forest-dwelling (*Leopoldamys herberti* and *Leopoldamys sabanus*) and one karst (*Leopoldamys neilli*) endemic rodent species as models.

Location Southeast Asia.

Methods We used presence–absence data of genetically identified individuals, bioclimatic variables and species distribution modelling techniques to predict potential distributions of the three studied species under current, past [Last Interglacial (LIG) and Last Glacial Maximum (LGM)] and future conditions. We applied a variety of modelling techniques and then used consensus techniques to draw up robust maps of potential distribution ranges at all stages.

Results According to our models, these three *Leopoldamys* species did not experience significant range contraction during the LGM. Our models revealed substantial range contraction during the LIG for *L. herberti* in northern Indochina, while its distribution expanded in southern Indochina. Evidence of a southward range expansion during that period was also obtained for *L. neilli*, whereas *L. sabanus* remained widely distributed in insular Southeast Asia but experienced a range contraction on the Thai-Malay Peninsula. The two future climate change scenarios used predicted that large climatically suitable areas would still be available in the future for the three species.

Main conclusions Our model predictions contradict the well-established hypothesis that Southeast Asian forest-dwelling species were confined to small refugia during the LGM. Moreover, our results suggest that some Southeast Asian taxa may have been distributed in their refugial state during the LIG rather than the LGM. This could be because of vegetation changes that may have occurred at that time as a result of the increased seasonality observed during the LIG. These Pleistocene refugia may have been localized in northern Indochina but our study also revealed that southern Indochina could provide major potential refugia.

Keywords

Climate change, Last Glacial Maximum, Last Interglacial, *Leopoldamys*, Murinae, Pleistocene, rodents, Southeast Asia, species distribution modelling.

INTRODUCTION

The distributional response of plant and animal species to Pleistocene climate changes has been studied widely in Europe and North America. In these temperate regions, the contraction of the northern range of many species during glacial periods, followed by northward recolonizations from southern refugia during interglacial periods, has been frequently documented (Hewitt, 2004; Michaux *et al.*, 2005; and references therein). However, recent studies have demonstrated that this pattern does not always apply. For example, northern regions of central and eastern Europe have also acted as

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refugia for some temperate plant and animal species (Kotlík *et al.*, 2006; Stewart *et al.*, 2010). In the tropics, the effects of the Pleistocene cyclic glaciations were less intense than in temperate regions but it has been suggested that the cooler arid climate during glacial periods led to the formation of isolated rain forest refugia in mountainous areas (Brandon-Jones, 1996; Haffer, 1997). However, little is currently known regarding the distributional consequences of Pleistocene climatic fluctuations for tropical species, especially in Southeast Asia.

Southeast Asia encompasses four biogeographical subregions that host around 18% of all plant and animal species on Earth (Myers *et al.*, 2000). A complex geological history and repeated climatic fluctuations over the last few million years have influenced the biogeographical patterns of many species in the region and created a unique fauna characterized by high levels of endemism (Woodruff, 2010). In Asia, the glacial advance was less extensive than in Europe or North America. Two main climate-related events may have contributed to diversification and population divergence during the Pleistocene in Southeast Asia. First, drastic changes in the Southeast Asian landscape occurred throughout the Pleistocene as a result of sea-level variations. Parts of the Sunda shelf were repeatedly exposed and submerged during this time period (Voris, 2000). Consequently, temporary land bridges were frequently created between the mainland and insular regions of Sundaland, possibly enabling biotic migrations from the mainland to the archipelago (Heaney, 1986). Second, Pleistocene climatic fluctuations also contributed to vegetation changes in Southeast Asia. However, the Quaternary distribution of forest types in this region is still uncertain and highly debated (Hope *et al.*, 2004; Bird *et al.*, 2005; Cannon *et al.*, 2009; Wurster *et al.*, 2010).

Many Sundaic bird and mammal species did not seem to experience significant population fragmentation during the Last Glacial Maximum (LGM; 19–26.5 ka; Peltier & Fairbanks, 2006) (Gorog *et al.*, 2004; Lim *et al.*, 2010; Lim & Sheldon, 2011) but Indochinese forest-dwelling mammals (Brandon-Jones, 1996; Luo *et al.*, 2004; Patou *et al.*, 2010), birds (Fuchs *et al.*, 2008) and insects (Morgan *et al.*, 2011) may have been restricted to allopatric rain forest refugia in some northern Southeast Asian mountain ranges during Pleistocene glacial periods before expanding southwards during interglacial periods. However, recent studies combining phylogeographical analyses and species distribution modelling (SDM) have revealed, surprisingly, a severe range contraction for several bird species in southern China during the Last Interglacial (LIG; 116–130 ka; Shackleton *et al.*, 2003), while similar distributions have been noted for these species when comparing present-day and LGM patterns (Dai *et al.*, 2011; Zhao *et al.*, 2012; Wang *et al.*, 2013). The invasive mosquito, *Aedes albopictus*, was also distributed widely in Southeast Asia during the LGM according to SDM projections (Porretta *et al.*, 2012). However, SDM approaches have never been applied to past distributions of Southeast Asian forest mammals, and the effects of Quaternary climate changes on mammal distributions in Southeast Asia are not yet clearly understood.

In this study, we selected three long-tailed giant rat species belonging to the genus *Leopoldamys* (Rodentia, Muridae) to assess the influence of Pleistocene climatic fluctuations and the potential effect of future climate change on small forest mammal distributions in Southeast Asia using SDMs. These are interesting model species because their distinct distributions span a large portion of Southeast Asia and they have contrasting ecological and forest habitat requirements. *Leopoldamys sabanus* (Thomas, 1887) (lineage L5 in Balakirev *et al.*, 2013) is semi-arboreal and found in lowland Sundaic forest habitats. *Leopoldamys herberti* (Kloss, 1916) (lineage L1) occurs in primary and secondary evergreen lowland and montane forests of Indochina. *Leopoldamys neilli* (Marshall, 1977) (lineage L2) is endemic to limestone karsts of Indochina. These giant rats may also play an important role in forest regeneration as they are better seed dispersers than many other rodent species in Southeast Asia and China (Wells *et al.*, 2009; Chang & Zhang, 2011).

The taxonomy of *Leopoldamy*s species has been reviewed recently and is now better understood. Six species were recognized by Musser & Carleton (2005). Balakirev *et al.* (2013) and Latinne *et al.* (2013a), however, suggested that an additional species existed in the Indochinese region, i.e. *L. herberti*, a phylogenetic lineage that was previously thought to belong to *Leopoldamy*s *edwardsi* (Pagès *et al.*, 2010). Evidence of *L. herberti* has been found in northern Thailand, Laos, Vietnam and Cambodia, but its occurrence in neighbouring countries has not been documented. *Leopoldamys neilli* has been described in Thailand but has also recently been discovered in northern Laos and Vietnam (Balakirev *et al.*, 2013; Latinne *et al.*, 2013a). The distribution of *L. sabanus* was previously thought to encompass both the Indochinese and Sundaic subregions, but Balakirev *et al.* (2013) and Latinne *et al.* (2013b) have shown that it is probably a Sundaic species with southern Thailand the northern limit of its range: it does not occur further north in Indochina. These molecular studies have therefore revealed important misclassification errors in previous studies, showing that current knowledge of these species distributions is uncertain, as is the conservation status of the three species. *Leopoldamys neilli* was previously classified as Endangered on the IUCN Red List but is now considered Data Deficient because of the lack of knowledge regarding its distribution and ecological requirements (Lunde & Aplin, 2008). *Leopoldamys sabanus* is listed as Least Concern because of its presumed large distribution and populations (Lunde *et al.*, 2008). The conservation status of *L. herberti* has never been assessed separately because this lineage was previously thought to belong to *L. edwardsi*.

Our study, involving SDM techniques, had two main objectives. First, we wanted to assess the influence of Pleistocene climatic fluctuations on *L. neilli*, *L. herberti* and *L. sabanus* distributions. The aim was to determine whether they were confined to small forest refugia during the Pleistocene glacial or interglacial periods and, if so, to localize these potential refugia. Maps of projected past and current distributions of these species provide a link between current environmental occupancy and biogeographical hypotheses based on molecular data that have been proposed in previous studies. Our second objective was to assess the potential impact of future climate change on the distribution of the three species.

MATERIALS AND METHODS

Species occurrence data

We focused only on occurrence data of genetically identified specimens because of the identification problems described above. We used a combination of locality points that we gathered during several field surveys and additional records from previous studies for which sequences were available. Field surveys in Thailand, Laos and Cambodia were carried out between 2002 and 2012. Most of the surveyed regions were sampled at least twice (during dry and rainy seasons), 1 or 2 years apart. Several habitat types, including human settlements, forests, cultivated areas and limestone karsts, were surveyed using georeferenced lines of live-capture cage traps during three consecutive nights. The cytochrome *b* gene (*cytb*) and/or the cytochrome *c* oxidase subunit I gene (*COI*) were amplified for all *Leopoldamys* samples, as described in Pagès *et al.* (2010) and Latinne *et al.* (2013b). Besides our own sampling, we added five Laotian *L. herberti* specimens from the Australian National Wildlife Collection (CSIRO, Canberra, ACT) and two *L. sabanus* specimens from Borneo collected by Wells *et al.* (2007), as well as GenBank records for which geographical coordinates or a precise geographical locality were specified (as of 15 June 2013). These GenBank sequences included those published in Gorog *et al.* (2004) and Balakirev *et al.* (2013) as well as three unpublished sequences of specimens from the Royal Ontario Museum (Toronto, ONT) (see Appendix S1 in the Supporting Information for GenBank accession numbers of all sequences).

Phylogenetic analyses were then performed on the complete dataset using Bayesian inference and maximum likelihood approaches (see Appendix S1 for more details). These phylogenetic analyses allowed us to assign each individual unambiguously to one of the genetic lineages defined in Balakirev *et al.* (2013) and Latinne *et al.* (2013a). All samples belonging to the lineages L1 (*L. herberti*), L2 (*L. neilli*) and L5 (*L. sabanus*) were included.

The data were represented in a geographical information system using ArcGIS 9.3 (ESRI, Redlands, CA, USA). They included 42 positive records for *L. neilli* (31 in Thailand, five in Laos, five in Vietnam and one in China), 42 for *L. herberti* (25 in Thailand, eight in Laos, seven in Vietnam and two in Cambodia), 25 for *L. sabanus* (17 in Thailand, one in Malay Peninsula, six in Borneo and one in Sumatra) and a total of 428 surveyed sites (268 in Thailand, 72 in Laos, 11 in Vietnam, 68 in Cambodia, one in China, one in Malay Peninsula, one in Sumatra and six in Borneo). These localities were overlaid on a 10′-resolution grid corresponding to the environmental data resolution (see below). Any points falling within the same grid cell were coded as a single presence or absence location. Absence records corresponded to the surveyed sites where the *Leopoldamys* species were not encountered. After the overlay, we were left with 31, 32 and 20 presence records for *L. neilli*, *L. herberti* and *L. sabanus*, respectively, with 122 grid cells overall having a presence or absence record (Fig. 1).

Environmental variables and climatic scenarios

For potential distribution projections, we considered an area including the Indochinese and Sundaic subregions, as well as Bangladesh and north-eastern India (Fig. 1a). This area encompasses two relevant biogeographical regions where the genus *Leopoldamys* is currently distributed and where fossils of this genus have been discovered (Medway, 1977; Zheng, 1993; Chaimanee, 1998; Storm *et al.*, 2005; Bacon *et al.*, 2006).

Current, past and future climatic scenarios were downloaded from the WorldClim database (Hijmans *et al.*, 2005; http://www.worldclim.org). Past scenarios were those of the LGM (19–26.5 ka) and LIG (116–130 ka). These two time periods correspond to two opposite climatic extremes during the Pleistocene that may represent key events in the evolutionary history of forest-dwelling species in Southeast Asia and may have strongly affected their distribution.

We selected future climate projections for the end of the century (data centred on 2080 and averaged across a decade), when several studies have predicted that the impacts of climate change will be more pronounced than earlier in the century (e.g. Butler *et al.*, 2012; Bertelsmeier *et al.*, 2013), in order to explore potential long-term range shifts of the species. To explore uncertainties related to future climate projections, we compared two scenarios from the Canadian Center for Climate Modeling and Analysis (Gatineau, QC) repository, i.e. B2A and A1B, which cover a moderate to medium range of future greenhouse gas emissions and socio-economic developments. The A1B scenario is one of very rapid economic growth associated with a projected global average surface warming of 2.8 °C (1.7–4.4 °C) and an estimated sea level rise of 0.21–0.48 m for the end of 21st century. The B2A scenario is more conservative and based on local environmental sustainability: it produces a less dramatic climate change projection, with an estimated warming of 2.4 °C (1.4–3.8 °C) and an estimated sea level rise of 0.20–0.43 m (IPCC, 2007).

Nineteen bioclimatic variables representing annual trends, seasonality and extreme or limiting environmental factors were used (http://worldclim.org/bioclim). Data were downloaded and used at 10′ resolution or resampled at that resolution (in the case of the LGM and LIG) by using block statistics in ArcGIS.

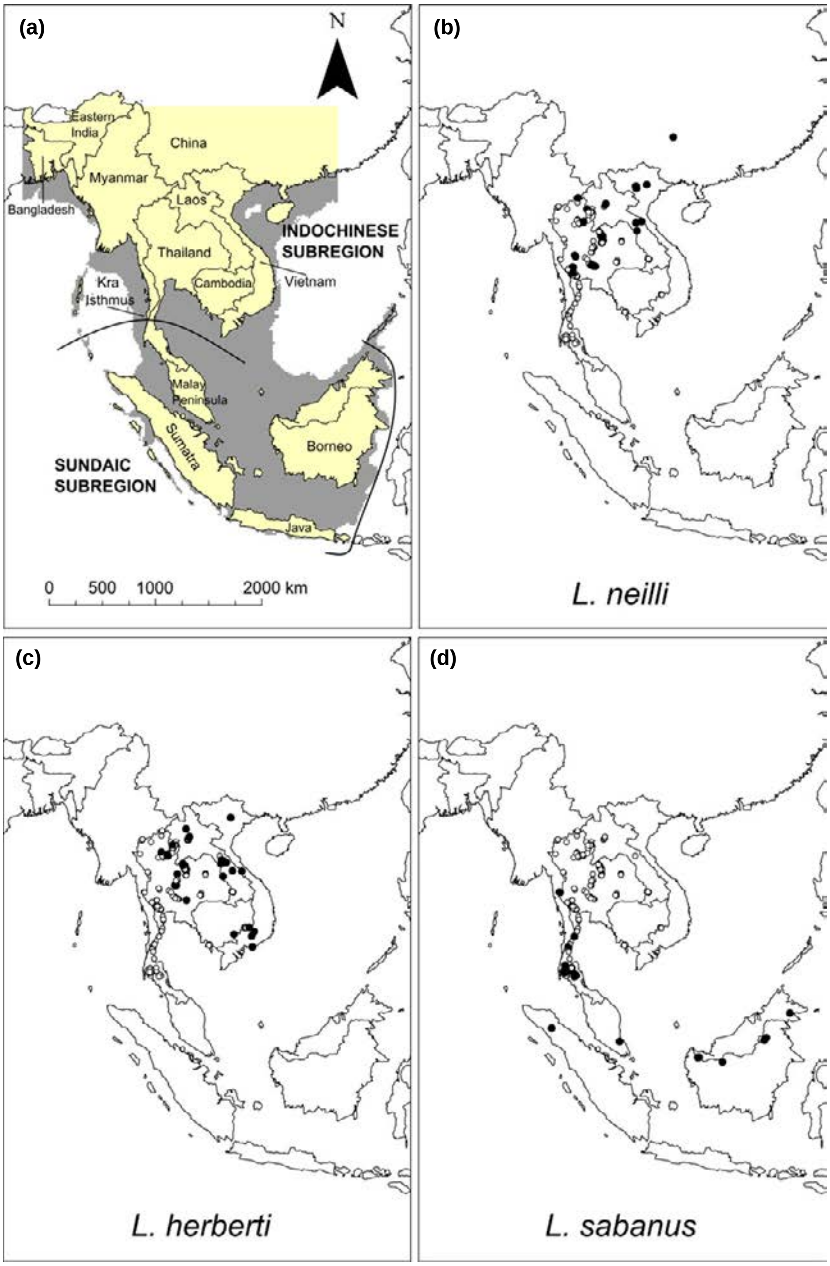

Figure 1 (a) The study area used to investigate the effect of past and future climate changes on the distribution of three Southeast Asian murids: the yellow area represents the projection zone of the potential distributions of the study species under current conditions and during the Last Interglacial (LIG). The grey area corresponds to the exposed Sunda shelf during the Last Glacial Maximum (LGM), when the sea level was 120 m below the current level (sea level representation from WorldClim; Hijmans *et al.*, 2005; http://www.worldclim.org). The Kra Isthmus represents the approximate northern limit of the Sundaic region. (b, c, d) Presence–absence (black/white dots, respectively) data for the three study species, *Leopoldamys neilli*, *L. herberti* and *L. sabanus*.

Species distribution modelling

We built SDMs using present-day environmental variables before projecting the best models to past (hindcasting) and future (forecasting) climate scenarios. We started by carrying out a principal components analysis (PCA) with all WorldClim variables under present-day conditions, to choose a subset of environmental variables that explained the most variability in environmental gradients in the study region. This variable selection was carried out independently of the presence–absence data, in order to select environmental variables that represented meaningful gradients across the study region. The first three PCA axes explained 98% of the variance in the 19 bioclimatic variables used as predictors. We examined further the variables that contributed the most to these three axes and eliminated those that were highly correlated between them (Pearson's $r > 0.8$). This left the following list of predictors: temperature seasonality (BIO4), annual precipitation (BIO12), precipitation of the warmest quarter (BIO18) and precipitation of the coldest quarter (BIO19). The functional responses of the study species to these four environmental predictors and the variations of these bioclimatic variables during the LIG and the LGM are depicted in Appendix S2.

We then ran a variety of models in the R 3.0.1 statistical package (R Core Team, 2013) to predict the current distribution of the three species using the four environmental predictors. We used seven different statistical models to include variability between strategies within an ensemble forecasting framework (Araújo & New, 2007). These models included regression-like techniques [generalized linear regression (GLM) and generalized additive models (GAM) (mgcv package)], tree-like techniques [classification trees (CART) (rpart package) and boosted regression trees (BRT) (gbm package)] and presence-only methods. Two of the presence-only methods [DOMAIN and BIOCLIM (dismo package)] rely on statistical characterizations of the environment occupied by the species, while Maxent 3.3.3k (downloaded from http://www.cs.princeton.edu/~schapire/maxent/ and run using the dismo package) relies on maximum entropy.

We assessed the model performance by calculating classification errors for each model using the area under the receiver operating characteristic curve (AUC), sensitivity, specificity and true skill statistic (TSS; sensitivity + specificity − 1) and a cross-validation strategy. We used 90% of the data to calibrate the models and 10% to calculate performance measures. This provided a reasonable trade-off between having enough testing points and not eliminating a number of occurrences from the calibration set that would be limiting for model calibration, particularly when there was a scant number of occurrences. All performance measures (including those for Maxent) were calculated within R. AUC is an overall performance measure that takes both the presence and absence classification errors into account (Fielding & Bell, 1997). Sensitivity represents the success rate for classifying presences, whereas specificity indicates absence classification success (Fielding & Bell, 1997). While AUC is threshold-independent, sensitivity and specificity require a fixed threshold on the predicted probability of occurrence above which all sites are predicted as presences and below which absences are predicted. We used the threshold that maximized sensitivity + specificity (maximizing sum threshold, MST), as recommended in previous studies (Liu *et al.*, 2005a; Jimenez-Valverde & Lobo, 2007).

Finally, models with high classification rates (AUC > 0.8 and TSS > 0.6) were used to draw up consensus maps for each species under current, past and future climatic conditions, while other models were discarded. We calculated mean, median and the first PCA axis in a PCA of predicted values for all the best models (Marmion *et al.*, 2009). These different consensus strategies generated similar distributions, so we only present the median results.

RESULTS

The models varied greatly in their classification performance but there were three to five models for each species that had an AUC > 0.8 and TSS > 0.6 (Table 1) and were therefore used for drawing up the consensus distribution maps.

Current and past projections

Besides central and northern Thailand, large areas of presence were predicted for *L. neilli* in Laos, Vietnam, central

Table 1 Classification performance measures resulting from fitting the distribution models of three Southeast Asian murids under current climatic conditions with 90% of the data, and calculating the classification error with the other 10%. For Maxent, the data were subsampled in R, exported to Maxent, and then the results re-imported into R in order to calculate the statistics using the same strategy as for the other models. Models with high classification rates [area under the receiver operating characteristic curve (AUC) > 0.8 and true skill statistic (TSS) > 0.6] are in bold. MST, maximizing sum threshold.

Species	Model	AUC	TSS	Sensitivity (MST)	Specificity (MST)
Leopoldamys neilli	BIOCLIM	0.703 ± 0.018	0.5 ± 0.064	0.7 ± 0.104	0.8 ± 0.02
	BRT	**0.856 ± 0.009**	**0.71 ± 0.031**	**0.967 ± 0.010**	**0.743 ± 0.025**
	CART	0.793 ± 0.019	0.569 ± 0.09	0.75 ± 0.092	0.819 ± 0.04
	DOMAIN	0.693 ± 0.013	0.469 ± 0.056	0.85 ± 0.041	0.619 ± 0.075
	GAM	**0.8 ± 0.016**	**0.644 ± 0.038**	**0.85 ± 0.041**	**0.793 ± 0.032**
	GLM	**0823 ± 0.019**	**0.662 ± 0.045**	**0.9 ± 0.025**	**0.762 ± 0.039**
	Maxent	**0.894 ± 0.011**	**0.79 ± 0.02**	**0.983 ± 0.005**	**0.806 ± 0.017**
Leopoldamys herberti	BIOCLIM	0.711 ± 0.011	0.472 ± 0.04	0.733 ± 0.089	0.667 ± 0.032
	BRT	0.776 ± 0.014	0.622 ± 0.036	0.867 ± 0.04	0.694 ± 0.022
	CART	0.737 ± 0.016	0.439 ± 0.105	0.65 ± 0.099	0.706 ± 0.052
	DOMAIN	0.638 ± 0.009	0.267 ± 0.076	0.817 ± 0.087	0.483 ± 0.076
	GAM	**0.806 ± 0.017**	**0.667 ± 0.052**	**0.917 ± 0.022**	**0.739 ± 0.031**
	GLM	**0.837 ± 0.016**	**0.75 ± 0.034**	**0.917 ± 0.022**	**0.789 ± 0.021**
	Maxent	**0.867 ± 0.016**	**0.744 ± 0.05**	**0.967 ± 0.01**	**0.783 ± 0.035**
Leopoldamys sabanus	BIOCLIM	0.746 ± 0.024	0.54 ± 0.096	0.675 ± 0.112	0.865 ± 0.013
	BRT	**0.96 ± 0.003**	**0.935 ± 0.008**	**1.000 ± 0.000**	**0.935 ± 0.008**
	CART	0.775 ± 0.03	0.525 ± 0.142	0.600 ± 0.147	0.925 ± 0.01
	DOMAIN	**0.852 ± 0.013**	**0.805 ± 0.019**	**1.000 ± 0.000**	**0.805 ± 0.019**
	GAM	**0.942 ± 0.004**	**0.865 ± 0.024**	**0.975 ± 0.012**	**0.89 ± 0.018**
	GLM	**0.962 ± 0.003**	**0.93 ± 0.009**	**1.000 ± 0.000**	**0.93 ± 0.008**
	Maxent	**0.95 ± 0.004**	**0.9 ± 0.017**	**1.000 ± 0.000**	**0.9 ± 0.017**

BRT, boosted regression trees; CART, classification trees; GAM, generalized additive models; GLM, generalized linear regression.

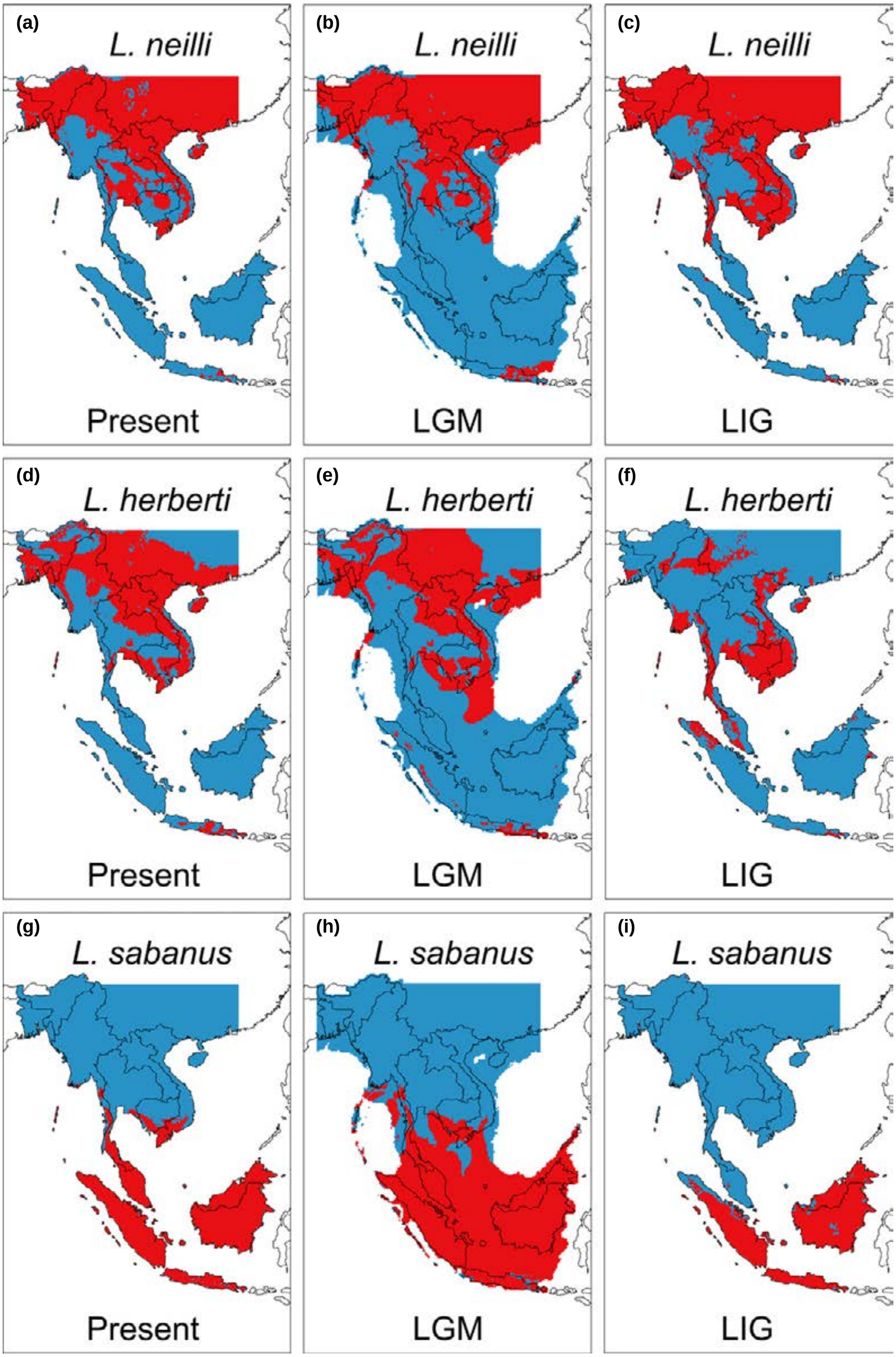

Figure 2 Consensus maps among the best performing models of the predicted distributions of three Southeast Asian murids (in red): *Leopoldamys neilli* (a, b, c), *L. herberti* (d, e, f) and *L. sabanus* (g, h, i) under current, Last Glacial Maximum (LGM) and Last Interglacial (LIG) conditions. The representation of sea level during the LGM is from WorldClim (Hijmans *et al.*, 2005; http://www.worldclim.org).

Cambodia, southern China, northern Myanmar and eastern India under current conditions (Fig. 2a). The consensus distribution under LGM conditions for this species was mostly similar to its present-day distribution (Fig. 2b, Appendix S3). Moreover, a small potentially suitable area for *L. neilli* was predicted during the LGM on the exposed Sunda shelf, in the northern portion of the current South China Sea. The projection at the LIG predicted a range contraction for *L. neilli* in central Thailand and a range expansion in the southern part of the Indochinese region compared with its potential current and LGM distributions (Fig. 2c, Appendix S3).

For *L. herberti*, large continuous tracts of potential occurrence were predicted under current conditions in northern Thailand, Laos, northern Vietnam, southern China, northern and eastern Myanmar and eastern India, as well as in central Thailand, southern Cambodia and southern Vietnam (Fig. 2d). No major changes were observed between the potential distributions of this species under current and LGM climatic conditions, with the exception of small range expansions in some parts of the emerged Sunda shelf during the LGM (Fig. 2e, Appendix S3). However, a marked contraction of climatically suitable area for *L. herberti* in the northern part of the Indochinese region during the LIG was observed while it expanded southwards (Fig. 2f, Appendix S3).

The current potential range of *L. sabanus* included southern Thailand and the Malay Peninsula, in addition to the islands of Sumatra, Java and Borneo (Fig. 2g). Small regions of climatically suitable habitat were also predicted for this species in western Thailand, southern Cambodia and Vietnam. The predicted distribution of *L. sabanus* during the LGM also encompassed the Thai–Malay Peninsula, some areas of southern Cambodia and Vietnam as well as a large part of the exposed Sundaland (Fig. 2h,i, Appendix S3). During the LIG, climatically suitable areas for *L. sabanus* were restricted to Borneo, Sumatra and Java.

Climate change scenarios for 2080

Overall, an expansion of the potential distributional range of *L. neilli* was predicted for many areas of the Indochinese subregion under the A1B scenario for 2080 (Fig. 3a). However, its predicted distribution under the B2A scenario showed more conservative expansions and a range reduction in areas of central Thailand, northern Laos and south-western China (Fig. 3b).

For *L. herberti*, the main distributional changes under the A1B scenario were predicted in northern and central Thailand, where the species was more likely be found in 2080 (Fig. 3c). In contrast, under the B2A scenario, the predicted distributional range of *L. herberti* decreased in northern and north-eastern Thailand and south-western China, while it slightly increased in southern China (Fig. 3d).

Neither A1B nor B2A scenarios predicted any future distributional change for *L. sabanus* in the Sundaic subregion. Only minor changes were predicted in the Indochinese subregion, close to the northern limit of its potential range (Fig. 3e,f).

DISCUSSION

Current distribution of the three *Leopoldamys* species

Our maps contribute to a better understanding of the potential current range of the study species and provide a working hypothesis for further evaluation in the field. Our results confirmed the Indochinese distribution of *L. herberti*, while *L. sabanus* was confined to the Sundaic subregion, with the exception of a patch of suitable habitat in southern Vietnam and southern Cambodia, where the two species could occur in sympatry. However, no genetically identified *L. sabanus* specimens have ever been recorded in this area so the presence of *L. sabanus* in the south-eastern part of the Indochinese region remains hypothetical; dispersal limitations as well as possible competition with other species could explain its absence there.

The potential distribution of *L. neilli* was quite similar to that of *L. herberti* but extended further in eastern India and southern China. However, the distribution of *L. neilli* is dependent on the presence of limestone karsts. Therefore the exact distribution of this species would probably be more fragmented than indicated by our distribution maps, and climatically suitable areas predicted in our study area should be viewed with caution for this species and reviewed in light of the availability of karsts in different areas. Large tracts of climatically suitable habitat for *L. neilli* and *L. herberti* were predicted in Bangladesh, eastern India and northern Myanmar. No genetic data on *Leopoldamys* specimens from these areas are currently available, but the presence of *L. edwardsi* in these regions has been reported in the literature (Musser & Carleton, 2005). Further genetic studies in the Bangladesh, India and Myanmar regions mentioned above could therefore be useful for fine-tuning the distribution maps presented here. A few patches of climatically suitable habitat for *L. herberti* and *L. neilli* were also predicted on Java, in the Sundaic region. However, these species have never been recorded on Java or neighbouring islands, and their presence in this region would be highly unlikely.

Influence of the Pleistocene climatic fluctuations on the distribution of *Leopoldamys* species

Climatic variables such as temperature and precipitation are major determinants of vegetation types, and major changes in vegetation cover in Southeast Asia occurred during the Pleistocene as a result of climatic oscillations. These vegetation changes may have played a major role in shaping the phylogeographical structure of Southeast Asian fauna (Luo *et al.*, 2004; Fuchs *et al.*, 2008; Lim & Sheldon, 2011; Morgan *et al.*, 2011). However, there is no firm consensus on the Quaternary distribution of vegetation types in this region. During the Pleistocene glacial periods, it has been suggested

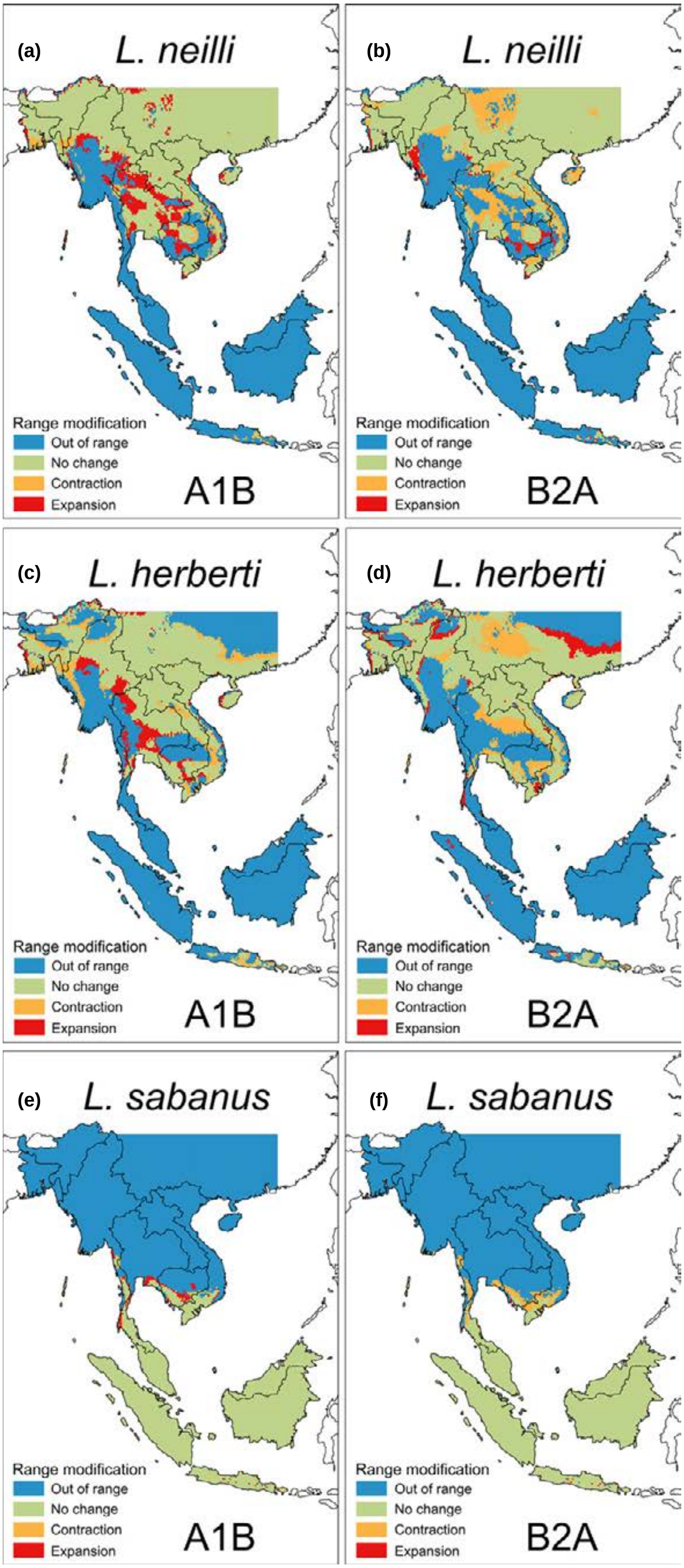

Figure 3 Consensus distribution maps among the best performing models of the predicted future range modifications of three Southeast Asian murids: *Leopoldamys neilli* (a, b), *L. herberti* (c, d), *L. sabanus* (e, f) under A1B and B2A climate change scenarios for 2080.

that Southeast Asian tropical rain forests retracted with only a few subsisting refugia, and that they were replaced by seasonal forests and savanna (Hope *et al.*, 2004; Bird *et al.*, 2005; Wurster *et al.*, 2010). Alternatively, some studies have indicated that during the LGM a large and continuous tract of tropical lowland rain forest persisted on the Sundaland (Cannon *et al.*, 2009; Wang *et al.*, 2009).

As a forest-dwelling rodent living in evergreen and montane forests of the Indochinese region, the distribution of *L. herberti* could have been influenced by Pleistocene changes in vegetation cover. However, according to our models based on climatic variables, the potential LGM distributional range of this species was unexpectedly similar to its present-day distribution. More surprisingly, our models revealed a substantial range contraction for *L. herberti* during the LIG in northern Indochina, while its distribution expanded in southern Indochina. Therefore, *L. herberti* populations could have been isolated in these northern and southern Indochinese refugia during the LIG. This interglacial fragmentation could have been responsible for the southern (L1a) and northern (L1b) Indochinese lineages observed within *L. herberti* (Balakirev *et al.*, 2013).

Range expansion in southern Indochina during the LIG was also observed for *L. neilli* in our model projections but, in contrast to *L. herberti*, *L. neilli* did not seem to experience any range contraction in northern Indochina from the LIG to present day. However, the predicted LIG distribution of *L. neilli* in Thailand was much more reduced than today and during the LGM, which may have contributed to the high genealogical divergence observed among *L. neilli* lineages in Thailand (Latinne *et al.*, 2011, 2012).

Our study of the potential distribution of *L. sabanus* clearly suggests that suitable habitats for this species subsisted on each Sunda island and the Thai–Malay Peninsula during the LGM. Gorog *et al.* (2004) reached similar conclusions and found a lack of phylogeographical structure for *L. sabanus* in Borneo, indicating that either the species survived in a single Bornean refugium from which it subsequently recolonized the rest of the island, or it occupied a large portion of Borneo during the LGM. Our models favour the latter hypothesis and also indicate that the exposed Sunda shelf during the LGM was a climatically suitable area for *L. sabanus*. These results support those of Cannon *et al.* (2009), who argue that rain forests would have been at their maximum on the Sunda shelf during the LGM. However, according to available genetic data, extensive migration of *L. sabanus* among the mainland and the Sunda islands did not seem to occur during the LGM. Three allopatric phylogenetic lineages corresponding to the Thai–Malay Peninsula, Borneo and Sumatra were observed within *L. sabanus* and their divergence largely pre-dated the LGM (Gorog *et al.*, 2004). Two factors may explain this apparent lack of migration of *L. sabanus* across the Sunda shelf when our models indicated that the region was climatically suitable for this species. First, the existence of a north–south savanna corridor that may have acted as a dispersal barrier for forest-dwelling species has been suggested (Heaney, 1991; Penny, 2001; Bird *et al.*, 2005; Wurster *et al.*, 2010), although this has been refuted in other studies (Cannon *et al.*, 2009; Wang *et al.*, 2009; Slik *et al.*, 2011). Second, the influence of abiotic factors such as soil conditions that may have limited plant growth has also been proposed to explain the absence or low level of cross-shelf migration observed for numerous taxa in the Sundaic region (Lim & Sheldon, 2011; Slik *et al.*, 2011).

In an attempt to explain our results that contradict the well-established hypothesis that the LIG distribution of Southeast Asian forest-dwelling species was similar to their present-day distribution while these species were confined to small refugia during the LGM, we explored the past fluctuations of the four bioclimatic variables used in our models (Appendix S2). The most striking variation was observed for temperature seasonality (BIO4), which was consistently increased in Southeast Asia during the LIG compared with current conditions, while it did not vary greatly during the LGM. The three other bioclimatic predictors varied more heterogeneously in our study area. We noticed a stronger decrease in the precipitation of the coldest quarter of the year (BIO19) during the LIG than during the LGM in the Indochinese region, while the precipitation of the warmest quarter (BIO18) increased in southern Indochina and in the Sundaic region during the LIG. These increased seasonal contrasts of temperature and precipitation in Asia during the LIG were the result of higher insolation received during the boreal summer (Wang *et al.*, 2008; Nikolova *et al.*, 2013).

The seasonality of both temperature and precipitation is a major determinant of vegetation distribution and richness in Asia (Fang *et al.*, 1996; Sang, 2009; Chiu *et al.*, 2012) and its variation led to a modification of the relative abundance of C_3 and C_4 plants during the Pleistocene (Liu *et al.*, 2005b; Yang *et al.*, 2012). Therefore, as a result of this increased climatic seasonality during the LIG compared with the current or LGM climatic conditions, important changes in the vegetation cover may have occurred at that time and caused the range modifications predicted for *L. herberti* and, to a lesser extent, for *L. neilli* and *L. sabanus* during the LIG. These changes in environmental conditions affected some *Leopoldamys* species more severely than others because of their specific responses to each of these environmental drivers (Appendix S2).

Fossil records could be an interesting tool for testing the validity of our models. Numerous fossil teeth attributed to *L. sabanus* and dated from the middle to late Pleistocene have been discovered in Southeast Asia (Medway, 1977; Chaimanee, 1998; Storm *et al.*, 2005; Bacon *et al.*, 2006) but only a few of them have been given an absolute age. Two Indochinese sites, Snake Cave in north-eastern Thailand (one fossiliferous level older than 160 ka; Esposito *et al.*, 2002) and Ma U'Oi Cave in northern Vietnam (two fossiliferous levels dated to 193 ± 17 ka and 49 ± 4 ka; Bacon *et al.*, 2006), do not correspond with the periods studied (LIG and LGM) but have been attributed to other Pleistocene glacial periods. Their usefulness for validating our predictions is thus very limited. Moreover, although these teeth probably belong to *Leopoldamys*, their identification at the species level remains uncertain because of the recent taxonomic changes introduced within that genus and described in the Introduction. These fossil teeth need to be re-examined and identified on the basis of the latest taxonomic revisions of the genus *Leopoldamys* (Musser *et al.*, 2006). Our past potential distribution maps predicted the presence of both *L. herberti* and *L. neilli* in northern Thailand and northern Vietnam during the LGM and are concordant with the available fossil data if we consider their LGM distribution as representative of their distribution during other Pleistocene glacial periods and that the fossil teeth from Chaimanee (1998) and Bacon *et al.* (2006) belong to a *Leopoldamys* species other than *L. sabanus*. *Leopoldamys sabanus* teeth have also been identified in eastern Java and are representative of the Punung fauna of early LIG age (between 118 ± 3 ka and 128 ± 15 ka) (Storm *et al.*, 2005; Westaway *et al.*, 2007), thus corroborating our predicted LIG distribution for *L. sabanus*.

Impact of future climate changes on *Leopoldamys* species

Although the two future climate change scenarios used in this study showed contrasting results, large areas of predicted presence will subsist in the future for the three *Leopoldamys* species under both scenarios. The A1B scenario, which is now considered more plausible than the B2A scenario (Kriticos *et al.*, 2012), predicted a range expansion in several areas for the three species. However, the subsistence of these species will depend on the availability and long-term maintenance of suitable habitats: limestone karsts for *L. neilli* and forests for *L. herberti* and *L. sabanus*. These habitats are highly threatened and both the annual limestone quarrying rate and the relative deforestation rate are higher in Southeast Asia than in other tropical regions of the world (Achard *et al.*, 2002; Clements *et al.*, 2006). Therefore, habitat loss as a result of direct anthropogenic causes rather than climate change appears to be the major threat these three species will face in the future. However, climate change may also negatively impact tropical tree growth and consequently affect the future survival of rain forests and their fauna (Feeley *et al.*, 2007).

CONCLUSIONS

Overall, our model predictions for *L. neilli, L. herberti* and *L. sabanus* contradict the well-established hypothesis that Southeast Asian forest-dwelling species were confined to small refugia during Pleistocene glacial periods. Moreover, our model results contribute to a growing body of literature suggesting that the distribution of several East and Southeast Asian taxa were in their refugial state during Pleistocene interglacial periods rather than during glacial periods (Dai *et al.*, 2011; Zhao *et al.*, 2012; Peterson & Ammann, 2013; Wang *et al.*, 2013). The LIG has thus played a more important role than the LGM in isolating populations of these taxa and shaping their phylogeographical patterns. We hypothesize that this could be because of the important vegetation changes that may have occurred at that time as a result of the increased seasonality of both temperature and precipitations observed during the LIG.

Our study revealed a southward range expansion of *L. herberti* and *L. neilli* during the LIG and the probable importance of southern Indochina as providing refugia for *L. herberti* during Pleistocene climatic fluctuations. In contrast to the mountain ranges of northern Indochina, where *L. herberti* could also have subsisted during the LIG, southern Indochina has never been identified as potential Pleistocene refugia for forest-dwelling species in Southeast Asia. This region may host particular phylogeographical lineages of several forest-dwelling taxa, as observed for *L. herberti*, and deserves the attention of future phylogeographical studies in Indochina.

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REFERENCES

Achard, F., Eva, H.D., Stibig, H.J., Mayaux, P., Gallego, J., Richards, T. & Malingreau, J.P. (2002) Determination of deforestation rates of the world's humid tropical forests. *Science*, **297**, 999–1002.

Araújo, M.B. & New, M. (2007) Ensemble forecasting of species distributions. *Trends in Ecology and Evolution*, **22**, 42–47.

Bacon, A.M., Demeter, F., Rousse, S., Long, V.T., Duringer, P., Antoine, P.O., Thuy, N.K., Mai, B.T., Huong, N.T.M., Dodo, Y., Matsumura, H., Schuster, M. & Anezaki, T. (2006) New palaeontological assemblage, sedimentological and chronological data from the Pleistocene Ma U'Oi cave (northern Vietnam). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **230**, 280–298.

Balakirev, A.E., Abramov, A.V. & Rozhnov, V.V. (2013) Revision of the genus *Leopoldamys* (Rodentia, Muridae) as inferred from morphological and molecular data, with a special emphasis on the species composition in continental Indochina. *Zootaxa*, **3640**, 521–549.

Bertelsmeier, C., Guénard, B. & Courchamp, F. (2013) Climate change may boost the invasion of the Asian needle ant. *PLoS ONE*, **8**, e75438.

Bird, M.I., Taylor, D. & Hunt, C. (2005) Palaeoenvironments of insular Southeast Asia during the Last Glacial Period: a savanna corridor in Sundaland? *Quaternary Science Reviews*, **24**, 2228–2242.

Brandon-Jones, D. (1996) The Asian Colobinae (Mammalia: Cercopithecidae) as indicators of Quaternary climatic change. *Biological Journal of the Linnean Society*, **59**, 327–350.

Butler, C.J., Wheeler, E.A. & Stabler, L.B. (2012) Distribution of the threatened lace hedgehog cactus (*Echinocereus reichenbachii*) under various climate change scenarios. *The Journal of the Torrey Botanical Society*, **139**, 46–55.

Cannon, C.H., Morley, R.J. & Bush, A.B.G. (2009) The current refugial rainforests of Sundaland are unrepresentative of their biogeographic past and highly vulnerable to disturbance. *Proceedings of the National Academy of Sciences USA*, **106**, 11188–11193.

Chaimanee, Y. (1998) Plio-Pleistocene rodents of Thailand. *Thai Studies in Biodiversity*, **3**, 1–303.

Chang, G. & Zhang, Z. (2011) Differences in hoarding behaviors among six sympatric rodent species on seeds of oil tea (*Camellia oleifera*) in Southwest China. *Acta Oecologica*, **37**, 165–169.

Chiu, C.-A., Lin, P.-H., Hsu, C.-K. & Shen, Z.-H. (2012) A novel thermal index improves prediction of vegetation zones: associating temperature sum with thermal seasonality. *Ecological Indicators*, **23**, 668–674.

Clements, R., Sodhi, N.S., Schilthuizen, M. & Ng, P.K.L. (2006) Limestone karsts of southeast Asia: imperiled arks of biodiversity. *BioScience*, **56**, 733–742.

Dai, C., Zhao, N., Wang, W., Lin, C., Gao, B., Yang, X., Zhang, Z. & Lei, F. (2011) Profound climatic effects on two East Asian black-throated tits (Ave: Aegithalidae), revealed by ecological niche models and phylogeographic analysis. *PLoS ONE*, **6**, e29329.

Esposito, M., Reyss, J.-L., Chaimanee, Y. & Jaeger, J.-J. (2002) U-series dating of fossil teeth and carbonates from Snake Cave, Thailand. *Journal of Archaeological Science*, **29**, 341–349.

Fang, J.-Y., Ohsawa, M. & Kira, T. (1996) Vertical vegetation zones along 30° N latitude in humid East Asia. *Vegetatio*, **126**, 135–149.

Feeley, K.J., Wright, S.J., Supardi, M.N.N., Kassim, A.R. & Davies, S.J. (2007) Decelerating growth in tropical forest trees. *Ecology Letters*, **10**, 461–469.

Fielding, A.H. & Bell, J.F. (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, **24**, 38–49.

Fuchs, J., Ericson, P.G.P. & Pasquet, E. (2008) Mitochondrial phylogeographic structure of the white-browed piculet (*Sasia ochracea*): cryptic genetic differentiation and endemism in Indochina. *Journal of Biogeography*, **35**, 565–575.

Gorog, A.J., Sinaga, M.H. & Engstrom, M.D. (2004) Vicariance or dispersal? Historical biogeography of three Sunda shelf murine rodents (*Maxomys surifer*, *Leopoldamys sabanus* and *Maxomys whiteheadi*). *Biological Journal of the Linnean Society*, **81**, 91–109.

Haffer, J. (1997) Alternative models of vertebrate speciation in Amazonia: an overview. *Biodiversity and Conservation*, **6**, 451–476.

Heaney, L.R. (1986) Biogeography of mammals in SE Asia: estimates of rates of colonization, extinction and speciation. *Biological Journal of the Linnean Society*, **28**, 127–165.

Heaney, L.R. (1991) A synopsis of climatic and vegetational change in Southeast Asia. *Climatic Change*, **19**, 53–61.

Hewitt, G.M. (2004) Genetic consequences of climatic oscillations in the Quaternary. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **359**, 183–195.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.

Hope, G., Kershaw, A.P., van der Kaars, S., Xiangjun, S., Liew, P.M., Heusser, L.E., Takahara, H., McGlone, M., Miyoshi, N. & Moss, P.T. (2004) History of vegetation and habitat change in the Austral-Asian region. *Quaternary International*, **118**, 103–126.

IPCC (2007) *Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK.

Jimenez-Valverde, A. & Lobo, J.M. (2007) Threshold criteria for conversion of probability of species presence to either–or presence–absence. *Acta Oecologica*, **31**, 361–369.

Kotlík, P., Deffontaine, V., Mascheretti, S., Zima, J., Michaux, J.R. & Searle, J.B. (2006) A northern glacial refugium for bank voles (*Clethrionomys glareolus*). *Proceedings of the National Academy of Sciences USA*, **103**, 14860–14864.

Kriticos, D.J., Webber, B.L., Leriche, A., Ota, N., Macadam, I., Bathols, J. & Scott, J.K. (2012) CliMond: global high-resolution historical and future scenario climate surfaces for bioclimatic modelling. *Methods in Ecology and Evolution*, **3**, 53–64.

Latinne, A., Waengsothorn, S., Herbreteau, V. & Michaux, J.R. (2011) Evidence of complex phylogeographic structure for the threatened rodent *Leopoldamys neilli*, in Southeast Asia. *Conservation Genetics*, **12**, 1495–1511.

Latinne, A., Waengsothorn, S., Rojanadilok, P., Eiamampai, K., Sribuarod, K. & Michaux, J.R. (2012) Combined mitochondrial and nuclear markers revealed a deep vicariant history for *Leopoldamys neilli*, a cave-dwelling rodent of Thailand. *PLoS ONE*, **7**, e47670.

Latinne, A., Chaval, Y., Waengsothorn, S., Rojanadilok, P., Eiamampai, K., Sribuarod, K., Herbreteau, V., Morand, S. & Michaux, J.R. (2013a) Is *Leopoldamys neilli* (Rodentia, Muridae) a synonym of *Leopoldamys herberti*? A reply to Balakirev *et al.* (2013). *Zootaxa*, **3731**, 589–598.

Latinne, A., Waengsothorn, S., Rojanadilok, P., Eiamampai, K., Sribuarod, K. & Michaux, J.R. (2013b) Diversity and endemism of Murinae rodents in Thai limestone karsts. *Systematics and Biodiversity*, **11**, 323–344.

Lim, H.C. & Sheldon, F.H. (2011) Multilocus analysis of the evolutionary dynamics of rainforest bird populations in Southeast Asia. *Molecular Ecology*, **20**, 3414–3438.

Lim, H.C., Zou, F., Taylor, S.S., Marks, B.D., Moyle, R.G., Voelker, G. & Sheldon, F.H. (2010) Phylogeny of magpie-robins and shamas (Aves: Turdidae: *Copsychus* and *Trichixos*): implications for island biogeography in Southeast Asia. *Journal of Biogeography*, **37**, 1894–1906.

Liu, C.R., Berry, P.M., Dawson, T.P. & Pearson, R.G. (2005a) Selecting thresholds of occurrence in the prediction of species distributions. *Ecography*, **28**, 385–393.

Liu, W., Huang, Y., An, Z., Clemens, S.C., Li, L., Prell, W.L. & Ning, Y. (2005b) Summer monsoon intensity controls C_4/C_3 plant abundance during the last 35 ka in the Chinese Loess Plateau: carbon isotope evidence from bulk organic matter and individual leaf waxes. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **220**, 243–254.

Lunde, D.P. & Aplin, K. (2008) *Leopoldamys neilli. IUCN Red List of Threatened Species*. Version 2014.2. Available at: http://www.iucnredlist.org.

Lunde, D.P., Aplin, K., Ruedas, L.A. & Molur, S. (2008) *Leopoldamys sabanus. IUCN Red List of Threatened Species*. Version 2014.2. Available at: http://www.iucnredlist.org.

Luo, S.-J., Kim, J.-H., Johnson, W.E. *et al.* (2004) Phylogeography and genetic ancestry of tigers *Panthera tigris*. *PLoS Biology*, **2**, e442.

Marmion, M., Parviainen, M., Luoto, M., Heikkinen, R.K. & Thuiller, W. (2009) Evaluation of consensus methods in predictive species distribution modelling. *Diversity and Distributions*, **15**, 59–69.

Medway, L. (1977) The Niah excavations and an assessment of the impact of early man on mammals in Borneo. *Asian Perspectives*, **20**, 51–69.

Michaux, J.R., Libois, R. & Filippucci, M.G. (2005) So close and so different: comparative phylogeography of two small mammal species, the yellow-necked fieldmouse (*Apodemus flavicollis*) and the woodmouse (*Apodemus sylvaticus*) in the western Palearctic region. *Heredity*, **94**, 52–63.

Morgan, K., O'Loughlin, S.M., Chen, B., Linton, Y.M., Thongwat, D., Somboon, P., Fong, M.Y., Butlin, R., Verity, R., Prakash, A., Htun, P.T., Hlaing, T., Nambanya, S., Socheat, D., Dinh, T.H. & Walton, C. (2011) Comparative phylogeography reveals a shared impact of Pleistocene environmental change in shaping genetic diversity within nine *Anopheles* mosquito species across the Indo-Burma biodiversity hotspot. *Molecular Ecology*, **20**, 4533–4549.

Musser, G.G. & Carleton, M. (2005) Superfamily Muroidea. *Mammal species of the world: a taxonomic and geographic reference* (ed. by D.E. Wilson and D.M. Reeder), pp. 894–1531. Johns Hopkins University Press, Baltimore, MD.

Musser, G.G., Lunde, D.P. & Son, N.T. (2006) Description of a new genus and species of rodent (Murinae, Muridae, Rodentia) from the tower karst region of northeastern Vietnam. *American Museum Novitates*, **3517**, 1–41.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853–858.

Nikolova, I., Yin, Q., Berger, A., Singh, U.K. & Karami, M.P. (2013) The last interglacial (Eemian) climate simulated by LOVECLIM and CCSM3. *Climate of the Past*, **9**, 1789–1806.

Pagès, M., Chaval, Y., Herbreteau, V., Waengsothorn, S., Cosson, J.F., Hugot, J.P., Morand, S. & Michaux, J. (2010) Revisiting the taxonomy of the Rattini tribe: a phylogeny-based delimitation of species boundaries. *BMC Evolutionary Biology*, **10**, 184.

Patou, M.L., Wilting, A., Gaubert, P., Esselstyn, J.A., Cruaud, C., Jennings, A.P., Fickel, J. & Veron, G. (2010) Evolutionary history of the *Paradoxurus* palm civets: a new model for Asian biogeography. *Journal of Biogeography*, **37**, 2077–2097.

Peltier, W.R. & Fairbanks, R.G. (2006) Global glacial ice volume and Last Glacial Maximum duration from an extended Barbados sea level record. *Quaternary Science Reviews*, **25**, 3322–3337.

Penny, D. (2001) A 40,000 year palynological record from north-east Thailand; implications for biogeography and palaeo-environmental reconstruction. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **171**, 97–128.

Peterson, A.T. & Ammann, C.M. (2013) Global patterns of connectivity and isolation of populations of forest bird species in the late Pleistocene. *Global Ecology and Biogeography*, **22**, 596–606.

Porretta, D., Mastrantonio, V., Bellini, R., Somboon, P. & Urbanelli, S. (2012) Glacial history of a modern invader: phylogeography and species distribution modelling of the Asian Tiger mosquito *Aedes albopictus*. *PLoS ONE*, **7**, e44515.

R Core Team (2013) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Sang, W. (2009) Plant diversity patterns and their relationships with soil and climatic factors along an altitudinal gradient in the middle Tianshan Mountain area, Xinjiang, China. *Ecological Research*, **24**, 303–314.

Shackleton, N.J., Sánchez-Goñi, M.F., Pailler, D. & Lancelot, Y. (2003) Marine isotope substage 5e and the Eemian interglacial. *Global and Planetary Change*, **36**, 151–155.

Slik, J.W.F., Aiba, S.I., Bastian, M. *et al.* (2011) Soils on exposed Sunda Shelf shaped biogeographic patterns in the equatorial forests of Southeast Asia. *Proceedings of the National Academy of Sciences USA*, **108**, 12343–12347.

Stewart, J.R., Lister, A.M., Barnes, I. & Dalén, L. (2010) Refugia revisited: individualistic responses of species in space and time. *Proceedings of the Royal Society B: Biological Sciences*, **277**, 661–671.

Storm, P., Aziz, F., de Vos, J., Kosasih, D., Baskoro, S., Ngaliman & van den Hoek Ostende, L.W. (2005) Late Pleistocene *Homo sapiens* in a tropical rainforest fauna in East Java. *Journal of Human Evolution*, **49**, 536–545.

Voris, H.K. (2000) Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems and time durations. *Journal of Biogeography*, **27**, 1153–1167.

Wang, Y., Cheng, H., Edwards, R.L., Kong, X., Shao, X., Chen, S., Wu, J., Jiang, X., Wang, X. & An, Z. (2008) Millennial- and orbital-scale changes in the East Asian monsoon over the past 224,000 years. *Nature*, **451**, 1090–1093.

Wang, X., Sun, X., Wang, P. & Stattegger, K. (2009) Vegetation on the Sunda Shelf, South China Sea, during the Last Glacial Maximum. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **278**, 88–97.

Wang, W., McKay, B.D., Dai, C., Zhao, N., Zhang, R., Qu, Y., Song, G., Li, S.-H., Liang, W., Yang, X., Pasquet, E. & Lei, F. (2013) Glacial expansion and diversification of an East Asian montane bird, the green-backed tit (*Parus monticolus*). *Journal of Biogeography*, **40**, 1156–1169.

Wells, K., Kalko, E.K.V., Lakim, M.B. & Pfeiffer, M. (2007) Effects of rain forest logging on species richness and assemblage composition of small mammals in Southeast Asia. *Journal of Biogeography*, **34**, 1087–1099.

Wells, K., Corlett, R.T., Lakim, M.B., Kalko, E.K.V. & Pfeiffer, M. (2009) Seed consumption by small mammals from Borneo. *Journal of Tropical Ecology*, **25**, 555–558.

Westaway, K.E., Morwood, M.J., Roberts, R.G., Rokus, A.D., Zhao, J.X., Storm, P., Aziz, F., van den Bergh, G., Hadi, P., Jatmiko & de Vos, J. (2007) Age and biostratigraphic significance of the Punung Rainforest Fauna, East Java, Indonesia, and implications for *Pongo* and *Homo*. *Journal of Human Evolution*, **53**, 709–717.

Woodruff, D.S. (2010) Biogeography and conservation in Southeast Asia: how 2.7 million years of repeated environmental fluctuations affect today's patterns and the future of the remaining refugial-phase biodiversity. *Biodiversity and Conservation*, **19**, 919–941.

Wurster, C.M., Bird, M.I., Bull, I.D., Creed, F., Bryant, C., Dungait, J.A.J. & Paz, V. (2010) Forest contraction in north equatorial Southeast Asia during the Last Glacial Period. *Proceedings of the National Academy of Sciences USA*, **107**, 15508–15511.

Yang, S., Ding, Z., Wang, X., Tang, Z. & Gu, Z. (2012) Negative $\delta^{18}O$–$\delta^{13}C$ relationship of pedogenic carbonate from northern China indicates a strong response of C_3/C_4 biomass to the seasonality of Asian monsoon precipitation. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **317–318**, 32–40.

Zhao, N., Dai, C., Wang, W., Zhang, R., Qu, Y., Song, G., Chen, K., Yang, X., Zou, F. & Lei, F. (2012) Pleistocene climate changes shaped the divergence and demography of Asian populations of the great tit *Parus major*: evidence from phylogeographic analysis and ecological niche models. *Journal of Avian Biology*, **43**, 297–310.

Zheng, S. (1993) *Quaternary rodents of Sichuan-Guizhou area*. Science Press, Beijing, China.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 GenBank accession numbers and phylogenetic tree including all the samples used in this study.

Appendix S2 Responses of the three study species to the four selected bioclimatic predictors and variations of these bioclimatic variables during the LIG and the LGM.

Appendix S3 Maps of predicted range modifications in the past for the three study species.

DATA ACCESSIBILITY

DNA sequences generated for this study were deposited in GenBank under accession numbers KM262595–KM262621. GenBank accession numbers of all other sequences used in this study are available in Appendix S1 in Supporting Information.

BIOSKETCH

Alice Latinne is interested in the evolution and diversity of murine rodents in Southeast Asia. She studies the evolutionary history of several murine species using phylogeographical and population genetic tools. She is currently working on the evolutionary dynamics of rodent–parasite interactions and uses parasites as markers of their host evolution.

Author contributions: A.L., C.N.M. and J.R.M. conceived the study; A.L., V.H., S.W. and S.M. collected data in the field; A.L. gathered the data and carried out the phylogenetic analyses; C.N.M. carried out the modelling; A.L. and C.N.M. wrote the paper.

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The effects of climate change on a mega-diverse country: predicted shifts in mammalian species richness and turnover in continental Ecuador

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ABSTRACT

Ecuador has some of the greatest biodiversity in the world, sheltering global biodiversity hotspots in lowland and mountain regions. Climate change will likely have a major effect on these regions, but the consequences for faunal diversity and conservation remain unclear. To address this issue, we used an ensemble of eight species distribution models to predict future shifts and identify areas of high changes in species richness and species turnover for 201 mammals. We projected the distributions using two different climate change scenarios at the 2050 horizon and contrasted two extreme dispersal scenarios (no dispersal vs. full dispersal). Our results showed extended distributional shifts all over the country. For most groups, our results predicted that the current diversity of mammals in Ecuador would decrease significantly under all climate change scenarios and dispersal assumptions. The Northern Andes and the Amazonian region would remain diversity hotspots but with a significant decrease in the number of species. All predictions, including the most conservative scenarios in terms of dispersal and climate change, predicted major changes in the distribution of mammalian species diversity in Ecuador. Primates might be the most severely affected because they would have fewer suitable areas, compared with other mammals. Our work emphasizes the need for sound conservation strategies in Ecuador to mitigate the effects of climate change

Abstract in Spanish is available with online material.

Key words: climate change scenarios; CliMond; conservation assessment; ensemble forecasting; species range; species richness; species turnover.

Continental Ecuador covers a small area of 253,370 km^2, yet it shelters a vast diversity of plants and animals. Biodiversity studies have reported 422 mammalian species in Ecuador (Tirira 2014), and continually add new species to this list. For example, the western Andes remain a *terra incognita* where new species and records are frequently reported, making Ecuador a mega-diverse country (Mittermeier *et al.* 1997). Such diversity is primarily related to the confluence of three biogeographic regions and their environmental variability (Dangles & Nowicki 2010): the Amazon basin, the Tumbes-Chocó-Magdalena region, and the Tropical Andes (Fig. 1A). Two of these regions are considered biodiversity hotspots due to their high density of endemic species and threats these species face (Mittermeier *et al.* 1999). Mammals, in particular, are highly threatened, with 26 percent of species classified as vulnerable, endangered, or critically endangered in continental Ecuador (Tirira 2011).

Habitat destruction and climate change pose serious threats to biodiversity in the region, with likely consequences for species ranges (Chen *et al.* 2011). Climate models predict temperature increases between 2 and 7°C in tropical South America by the end of the 21st century (Urrutia & Vuille 2009). Both tropical and mountain regions are expected to show no-analog environmental conditions under climate change scenarios, including higher maximum temperatures (Bradley *et al.* 2006) and drier conditions (Lapola *et al.* 2009). Birds (Barbet-Massin *et al.* 2012, Tingley *et al.* 2012), nonvolant mammals (Levinsky *et al.* 2007) and amphibians (Pounds *et al.* 2006), among others, have already been shown to respond to climate change by shifting their ranges. With environmental gradients shifting geographically, species may move out of protected areas, causing the reserve network to become ineffective (Burns *et al.* 2003, Hannah *et al.* 2007). Changes in the distributions of species in mountain areas will likely be more complex than usually hypothesized at broad spatial scales. For example, the interactions between precipitation and temperature changes are not always in the same direction through the altitudinal gradient, producing pockets of downward shifts in distributions (Pounds *et al.* 1999, Jacobsen *et al.* 2014, Crespo-Pérez *et al.* 2015). This complexity highlights the importance of considering multiple abiotic factors at finer spatial scales (Tingley *et al.* 2012, Anderson 2013).

These factors taken together—Ecuador being in a mountainous region, harboring high biodiversity in a small area, and

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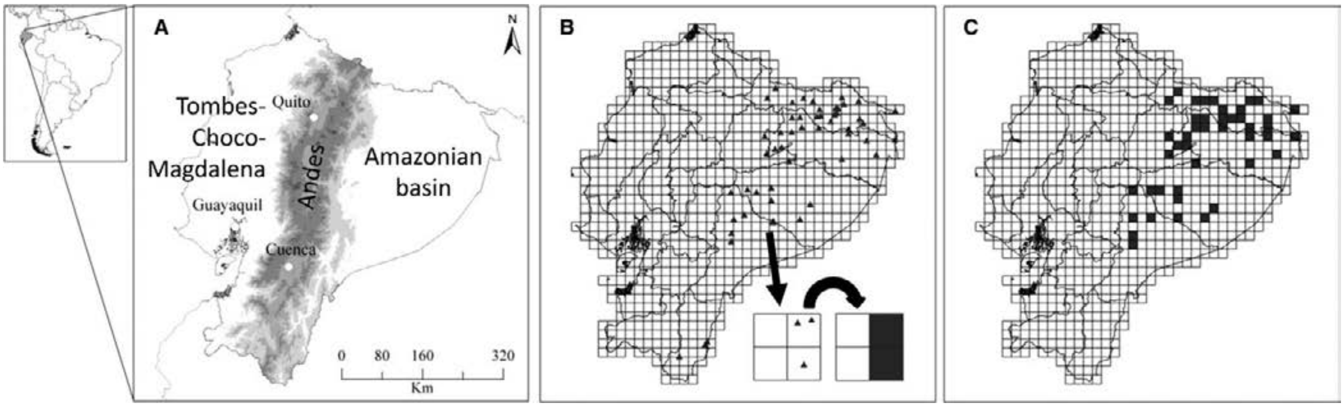

FIGURE 1. Study area and occurrence data aggregation strategy. (A) The study area showing the three main biogeographic regions and the Andean range; (B) Individual occurrence data were overlaid over an 18-km resolution grid; occurrences falling in the same grid cell were aggregated as a single occurrence, whereas cells containing no occurrence record for the focal species were subsequently considered in the random draw of background sites; (C) the same occurrence data shown in (B) but after aggregation at the resolution of the grid.

presenting a high habitat reduction rate—put its biodiversity at high risk under climate change scenarios. Studies related to climate change in the region have focused on the current status of glaciers and water availability (Buytaert & De Bièvre 2012, Rabatel *et al.* 2013, Michelutti *et al.* 2015), and on paleo changes in hydrology and climate in the Amazon (Cheng *et al.* 2013). One exception is Garavito *et al.* (2015), who investigated the effects of climate change on 129 tree species endemic to the upper mountains of the tropical Andes, and found that the risk of extinction of different species would increase an average of 18–20 percent. However, we lack information on the potential effects of climate change on mammal biodiversity in Ecuador.

We explored potential effects of climate change on the distribution of Ecuadorian mammals by comparing two different climate change scenarios for the year 2050. We aimed to analyze changes in species richness and turnover rates caused by future climate change. We used species distribution modeling with an ensemble forecasting strategy considering eight different modeling techniques and three levels of presumed species prevalence. We contrasted two extreme dispersal scenarios (no-dispersal vs. full dispersal) to calculate changes in species richness and species turnover over time, and analyzed the potential future impacts on mammalian species diversity in Ecuador. Our study analyzed the existing and potential effects of climate change on tropical mammals, and examined which species and areas would be more susceptible to climate change, to improve recommendations for the conservation and management of target species.

METHODS

Species occurrence data.—To forecast species distributions, we obtained occurrence records from the Mammalogy Section of the Museum of Zoology (QCAZ-M) at the *Pontificia Universidad Católica del Ecuador* and from the *Red Noctilio* database, which gathers information of mammal collections from 75 museums of natural history around the world (Tirira 2013).

We focused on the biodiversity of mammalian species in continental Ecuador. Our study area had a total of 9,183 available records with revised geographic coordinates for 236 species. However, 35 species had <10 records after spatial aggregation of the data (see below). We therefore modeled 201 species, representing 58 percent of the mammals known to occur in continental Ecuador, and including twelve orders and 37 families *sensu* Wilson and Reeder (2005).

Environmental data.—We obtained climate variables from CliMond (Kriticos *et al.* 2011), a data base that was generated with input from WorldClim (Hijmans *et al.* 2005) and the Climatic Research Unit (CRU) datasets (New *et al.* 2002). CliMond includes basic climatological variables related to precipitation and temperature, as well as additional composite variables indicating humidity and productivity. CliMond was designed for large-scale studies, including variables that are widely recognized as limiting species distributions (Watling *et al.* 2012), and are relevant biologically for characterizing species ranges (Nix & Busby 1986). Since the release of CliMond, a new set of CRU simulations includes more recent climatological and socio-economic data, and describes four pathways of greenhouse gas emissions and atmospheric concentrations (Pachauri *et al.* 2014). Unfortunately, these updates were not available in CliMond at the time of our study and the latest database of Worldclim does not include radiation and moisture indices we considered important to characterize environmental gradients in Ecuador. The previous simulations remain valid and are supported by a recent study, which showed that the new models and those released in 2007 produce similar projected global temperature changes, and projection uncertainties have been similar over successive IPCC reports (Knutti & Sedláček 2013). We therefore decided to use CliMond for our projections.

Our climate change scenarios include socio-economic scenarios released in 2007 (Pachauri & Reisinger 2007). We divided the list of 35 CliMond bioclimatic variables into four groups: temperature (11 variables), precipitation, radiation, and moisture (8 variables in each group). We obtained the environmental variables at a resolution of 10-min (~18.6 km × 16.6 km on the equator). To minimize multicollinearity between predictors, we selected eight minimally correlated variables based on the following procedure. First, we carried out a Principal Component Analysis (PCA), which allowed us to select variables that represent the major axes of environmental gradients in the study region; the first three principal components summarized more than 80 percent of the total variance in the environmental data and, consequently, we retained these components. In the following steps, we tried to represent these axes by using the raw variables that (i) most influence each PCA axis, (ii) are minimally correlated between them (Pearson correlation <0.75), and (iii) represent the four environmental groups among CliMond variables. We selected these eight variables for the final analysis: BIO001—Annual mean temperature, BIO02—Mean diurnal temperature range, BIO03—Isothermality (diurnal/annual temperature range), BIO12—Annual precipitation, BIO18—Precipitation of warmest quarter, BIO20—Annual mean radiation, BIO23—Radiation seasonality, and BIO31—Moisture index seasonality.

Climate forecasts predict plausible future climates that result from a combination of a particular General Circulation Model (GCM) describing the physical processes, and a particular Special Report on Emissions Scenario (SRES) that describes the socio-economic processes. Here we considered two GCMs: CSIRO-MK (Centre for Australian Weather and Climate Research) and MIROC-H (Centre of Climate Research, Japan). Kriticos *et al.* (2011) argued that these two GCMs have a good representation of the observed climate at a regional scale. For each GCM, we chose two SRES families: A1 and A2. Family A1 assumes a world of very rapid economic growth, and family A2 assumes a world of slow economic growth. We did not consider conservative carbon emission scenarios because previous work suggested that they are no longer plausible (Kriticos *et al.* 2011). In fact, the latest CRU simulations showed that the conservative pathway is an unrealistic stringent mitigation scenario (Pachauri *et al.* 2014), where emissions would need to decline substantially in the very short term, including major coordination between multiple countries worldwide (Van Vuuren *et al.* 2011).

To process the environmental and occurrence data, we generated a regular grid of 18-km resolution for continental Ecuador (872 grid cells). We included the occurrence records of species distributed across the study area into the grid using a spatial aggregation strategy, which recorded any number of occurrences within a single grid cell as a presence record (Fig. 1B and C). This procedure eliminates pseudo-replication and brings environmental and occurrence data to the same resolution.

MODELING METHODS.—SDMs describe the relationship between species occurrences and environmental conditions (Elith & Leathwick 2009) to define suitable conditions for species (Anderson 2013). Some of them use presence-only data, while others require presence-absence data. Here we used presence-only records and generated background data to create a contrast between occupied sites and the overall available environment. We randomly selected 200 background sites for each species across all available environments, excluding grid cells that were already marked as present. We selected background sites independently for each individual model run and species, to represent a subset of the environmental space where the species of interest has never been recorded. These background data served as pseudo-absences in the modeling efforts that required presence-absence data, as well as for the calculation of classification rates during model evaluation (see below). We used the R statistical software (v.2.15.3, R CORE TEAM 2012) to build and calibrate all models.

We used eight modeling methods based on logistic regression and machine learning approaches (Segurado & Araújo 2004, Elith *et al.* 2006, Phillips & Dudik 2008). Presence-only methods included BIOCLIM (Busby 1991), DOMAIN (Carpenter *et al.* 1993), and Mahalanobis distances (Farber & Kadmon 2003), which use presence records to describe the multivariate environmental space where a species is found, and the Maximum Entropy method (MaxEnt) which finds a distribution closest to uniform within the environmental space of occurrence sites (Phillips *et al.* 2006). Presence-absence methods included Generalized Linear Models (GLM) and Generalized Additive models (GAM), which are regression-based methods that model ecological relationships allowing for a binomial response (Austin 2002). We also included decision tree-based methods like classification trees (CART) and boosted regression trees (BTR), which identify environmental breaks that produce homogeneous groups in an iterative procedure (Friedman *et al.* 2000, Elith *et al.* 2008). These presence-absence methods allow us to change the expected species prevalence by using different weights on presences and background data, taking into account the uncertainty related to the expected species frequency when presence-only data are used (Meynard *et al.* 2013) and controlling for the effect of including a disproportionate number of absences when only a few presences are recorded. Here we used three levels of prevalence: 0.2, 0.5, and 0.8. This procedure resulted in 16 predicted probabilities of occurrence per species under current climatic conditions and under each climate change scenario.

We adopted a leave-one-out jackknife approach to calculate different classification success metrics for each model (Fielding & Bell 1997) because this is most appropriate for species with a small number of records. Notice that while presence records are fixed (*i.e.,* all available records are used) during this evaluation procedure, pseudo-absences were redrawn for each new jackknife iteration. We evaluated model projections by calculating sensitivity, specificity, the area under the receiver operating characteristic (ROC) curve (AUC), and the True Skill Statistic (TSS). In a ROC plot, the true positive rate (sensitivity) is plotted against the false positive rate (1-specificity) at all possible thresholds of presence–absence classification as the threshold varies from 0 to 1. We defined the area under this curve (AUC) as the probability at which presences and absences are accurately classified. Prediction accuracy is considered to be good for AUC values >0.8 (Fielding & Bell 1997). We also calculated the true skill statistic (TSS), which represents a better balance when species prevalence is very high or very low (Allouche *et al.* 2006). We calculated this as TSS = sensitivity + specificity − 1, and it ranges from -1 (poor) to 1 (perfect classification). We considered values >0.6 as appropriate (Coetzee *et al.* 2009).

To draw the consensus distribution for each species, we selected the five models that performed best in terms of AUC and TSS and then used these models to make a unique consensus prediction using a mean between predicted probabilities of occurrence (Marmion *et al.* 2009). This ensemble forecasting strategy has been recommended to take into account variability between models (Araújo & New 2007, Franklin 2009), and usually reduces uncertainty and increases accuracy by selecting the most consensual projections (Araújo *et al.* 2005, Coetzee *et al.* 2009). Because of the broad diversity of SDMs used here, the consensus predictions could contain a mixture of results from presence-only and presence-absence models, depending on model performance. Consensus predictions were then transformed to presence-absence (binary response) by using the threshold value that maximizes the sum of sensitivity plus specificity (Liu *et al.* 2005). The final projections of species distributions were based on the final runs of the models using all the occurrence data (Araújo *et al.* 2005).

For each climate change scenario, we calculated species richness per grid cell by stacking projections for individual species (Dubuis *et al.* 2011). Although this method may overestimate species richness in general, it has the advantage of allowing the analysis of species composition at the same time as species richness. Also, it may have higher correlations between observed and predicted values, as compared to a multiple regression approach where species richness would be modeled directly as the response variable (Dubuis *et al.* 2011). Since we were interested in analyzing changes in individual species ranges, as well as overall species compositional turnover across the study area, we adopted the stacking method. Some areas in Ecuador have not been surveyed thoroughly or even at all, so using the observed species richness as the response variable in a modeling effort will likely underestimate species richness in these areas (see Appendix S1 for more details).

For prediction into future scenarios, we adopted two extreme dispersal scenarios. The first was an unlimited dispersal scenario, whereby we assumed that species would track suitable climate over the entire study area. We also used a no-dispersal scenario (species would not be able to disperse at all), so that any future range will only include the overlap between the current potential range and the future potential range. Realistic future range shifts will likely fall between these extremes. We therefore represented a conservative and a pessimistic scenario in terms of area expansions and reductions, as well as in terms of compositional turnover.

RANGE SHIFTS UNDER CLIMATE CHANGE.—We used the consensus forecast to estimate the climatically suitable space for current and future distributions for each species from predicted binary responses. We then calculated the percentage of area gained or lost for each species, the number of species predicted to occur in each grid cell, the difference in species richness and the compositional turnover between now and 2050. We calculated the Species Temporal Turnover (STT) for each grid cell as STT = 100 x (L+G)/(SR+G); where STT is the species temporal turnover, L is the number of species lost in each grid cell, G is the number of species gained and SR is the current species richness of the target grid cell (Thuiller *et al.* 2005). A turnover value of 0 indicates that the assemblage of species is predicted to remain the same in the future, and a value of 100 percent indicates that the assemblage of species is completely different. Notice that turnover can be high in regions where species are lost as well as in places where species are gained.

RESULTS

Most variability between predictions of species richness came from the particular GCM used rather than from the SRES scenario, although the general geographic trends in species diversity remained the same across scenarios (see Appendix S2). The combination of MIROC with A1B produced the most conservative climate scenario (*i.e.,* the one that predicts the least changes in species richness and turnover) and the combination of CSIRO with A2 produced the most pessimistic scenario. For simplicity, here we focus on these two extreme scenarios for 2050 to analyze shifts in diversity. Supplementary materials S2 and S3 contain further comparisons between different combinations of GCM x SRES.

All scenarios predicted that climate change will have effects on species richness distribution patterns. First, we found that species richness per grid cell would generally decrease (Fig. 2). Currently, mammal species richness is concentrated in the northern tropical Andes of Ecuador and in the western Amazon basin (Fig. 2A), representing the greatest species richness (123 species) recorded anywhere within the drainage. Under all scenarios (Fig. 2B–E) this maximum richness is expected to drop by 2050 (compare in Fig. 2, red and light orange areas for example). As expected, the no-dispersal scenario (lower row in Fig. 2) produces a more-pessimistic prediction than the full-dispersal scenario (upper row in Fig. 2), with large reductions in species richness all over Ecuador. Hotspots move little from their present locations, although the models predict a slight shift to the southeast for the Amazon basin and to the north for the Andes, due to individual species shifting in the same direction. This shift is logically seen for the full-dispersal scenario but not for the no-dispersal scenario.

As previously noted, these changes reflect extreme-case scenarios (Fig. 3, see also Appendix S2 and S3). For example, the climate scenario CSIRO-A2, which represents the most pessimistic extreme, predicts a maximum species richness per grid cell by 2050 of 75 species under the full-dispersal scenario and 58 under the no-dispersal scenario (Fig. 3C and E), whereas MIROC-A1B predicts 92 and 77 species, respectively (Fig. 3B and D). Half of grid cells have fewer than 40 and 30 species for MIROC-A1B and CSIRO-A2 respectively under the full-dispersal scenario (Fig. 3B and D), but species richness in the same grid

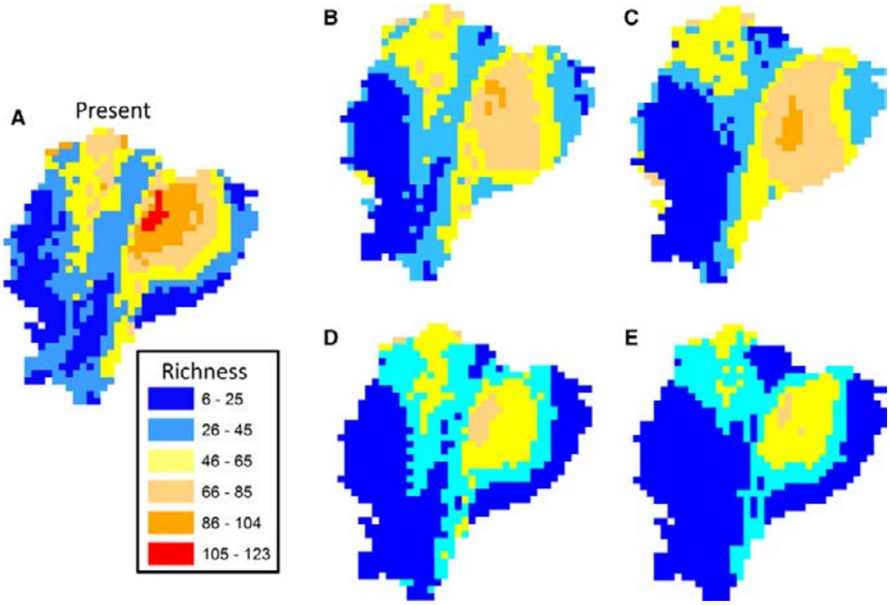

FIGURE 2. Comparison of species richness: (A) under current conditions; 2050 conditions for (B) MIROC—A1B, full dispersal hypothesis; (C) CSIRO—A2, full dispersal hypothesis; (D) MIROC—A1B, no dispersal hypothesis; and (E) CSIRO—A2, no dispersal hypothesis. Shown color codes at the left lower corner are the same for all maps.

cells would drop to 20 and 15 species, respectively, under the no-dispersal scenario (Fig. 3C and E).

Comparing the difference in species richness and species turnover between full-dispersal and no-dispersal scenarios provides complementary information on the potential changes in diversity (Fig. 4). For both scenarios, when the difference in species richness is large, the turnover rate is also large, independently of whether this represents species losses or gains. Notably, some of the areas that are predicted to gain species under the full-dispersal scenario are also predicted to suffer the highest compositional turnover.

Concerning range shifts for individual species, changes in suitable area will likely be important within Ecuador. Roughly 35 percent of the species would lose some area of their range in the country under the full-dispersal hypothesis and the MIROC-A1B scenario, and 30 percent of the species would lose more than half of their current potential range in Ecuador (Fig. 5). Under the most pessimistic scenario (CSIRO-A2), 40 percent of species would lose more than half of their range under full dispersal.

When analyzing the percentage of area change for individual species in six different mammal groups, we found that the majority of species (58%) would reduce their potential distribution area, even when allowing full dispersal (Fig. 6). Primates and bats would be most affected; about 30 percent of primate species and 23 percent of bat species would experience severe reductions (≥50%) of their potential distribution ranges followed by rodents, carnivores, and species classified as 'others'. Those three groups would be equally affected (18% of species in each group will lose more than 50% of their potential distribution). The group least influenced by future climate change is the ungulates (<14% of species will lose more than 50% of their potential distribution). The model predicted that twelve species would lose almost all their area at the 2050 horizon under both climate change scenarios; most of them are bats (*Chiroderma salvini*, *Platyrrhinus brachycephalus*, *Rhinophylla alethina*, *Sturnira ludovici*, *Sturnira magna*, *Trachops cirrhosus*, and *Tadarida brasiliensis*). Eight species in four taxa could double their potential distribution range; most of them are rodents (*e.g.*, *Akodon aerosus*, *Scolomys melanops*, and *Dactylomys dactylinus*).

In general, the models predicted that species would lose a greater percentage of their potential distribution range under the less conservative climate change scenario (CSIRO-A2), while the 67 percent of species that would experience an increase in their potential distribution area would also gain a greater percentage of area under this scenario. For example, the giant otter, *Pteronura brasiliensis* (Carnivora) is expected to increase its potential distribution area by 150 percent at the horizon 2050 under the MIROC-A1B scenario, and by >160 percent for the CSIRO-A2 scenario. The same happens with other species like *Anoura cultrata* (Chiroptera) and *Coendou rothschildi* (Rodentia), which are expected to increase their potential distribution area by 134 and 117, and >160 percent each, for the MICROC-A1B and CSIRO-A2 scenarios, respectively. In total, 17 species would be able to increase their suitable area by more than 80 percent, assuming full dispersal.

Finally, the frequency of species and percentage of area lost in the future due to climate change (Fig. 7) is expected to result in a decrease in the number of species as the area lost increases. A large number of species will lose more than 80 percent of their potential distribution range.

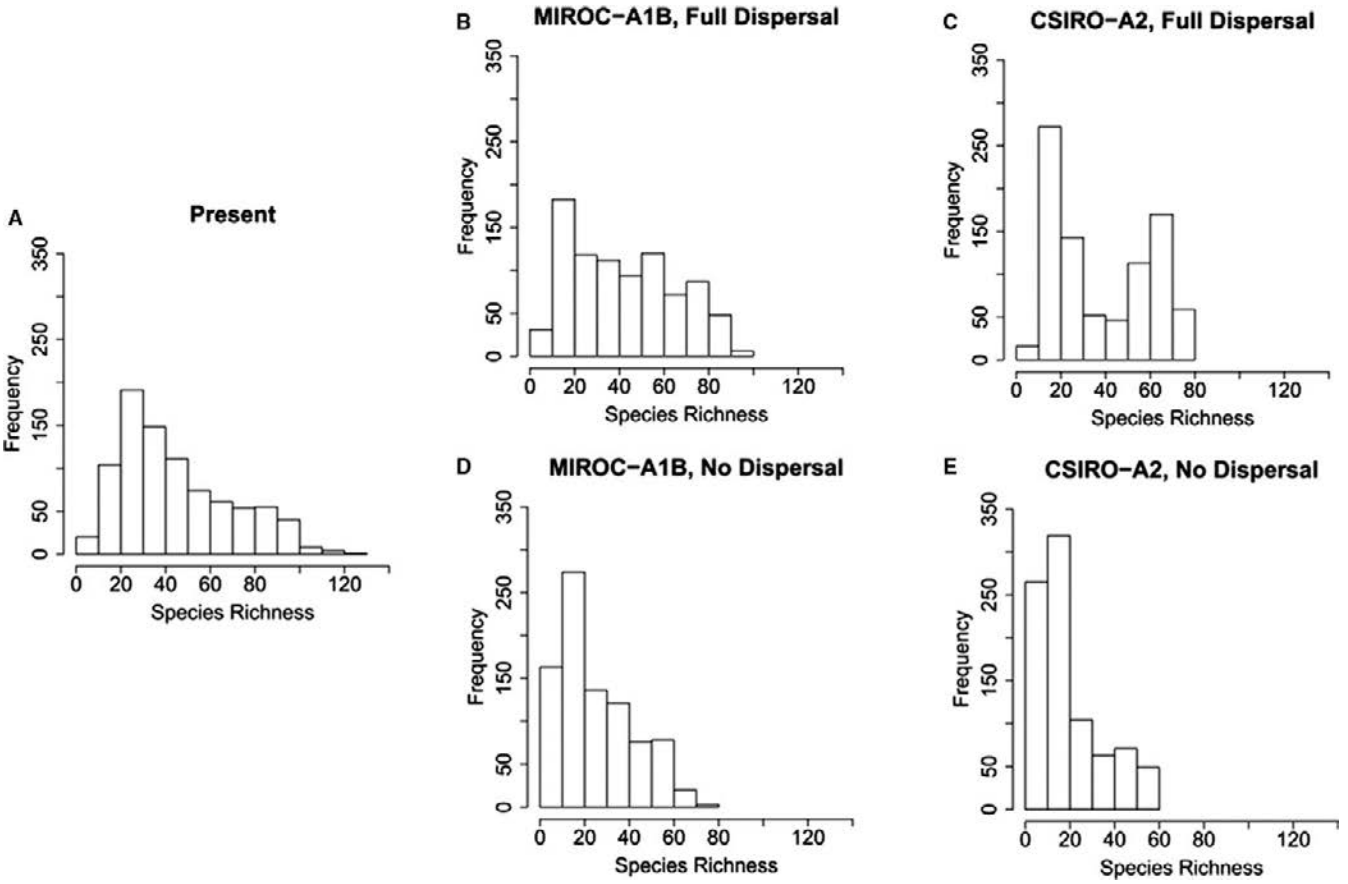

FIGURE 3. Histograms showing the distribution of species richness (frequency of species per grid cell) for current conditions, as well as for the two extreme scenarios and the two dispersal hypothesis: (B) and (D) correspond to MIROC-A1B, which is the most conservative scenario, whereas (C) and (E) correspond to CSIRO-A2, which is the most pessimistic scenario. The upper row (B and C) represents full dispersal scenarios, while the lower row (D and E) represents no-dispersal scenarios.

DISCUSSION

General distribution changes.—Species richness obtained from current models is expected to decrease in all climate change scenarios and dispersal assumptions, even under a full-dispersal scenario where species would be perfectly capable of tracking their preferred environments. Our results show that, although the no-dispersal scenario produces more important changes in species richness, spatial patterns of shifts remain similar across all models. As an example, the no-dispersal scenario predicted richness patterns similar to those obtained with a full-dispersal scenario (Fig. 2). Regions such as the Northern Andes and Amazonia would remain hotspots, but with fewer species. Amazonia would also present a low species turnover, probably because both climatic models (CSIRO and MIROC) predicted the entire country to become warmer, but with a slight increase in precipitation in the east. Shifts in precipitation patterns could affect potential species distributions in tropical forests more than changes in temperature (Condit 1998), and precipitation would explain a greater proportion of range limit movements than temperature in some areas (Tingley *et al.* 2012). Understanding this precipitation-richness relationship therefore remains pivotal to forecasting the potential effects of climate change in the area.

Predictions for different groups and species.—Since our modeling effort is based on presence-only data and we do not have an independent dataset to evaluate model results, our projections must be interpreted with caution. For example, some grid cells have been better surveyed than others across Ecuador, and we do not have an independent estimate of sampling effort. This means that some of the background data might include sites where the target species is actually present but has not been recorded. However, we designed our pseudo-absence selection strategy to minimize the effect that a wrong absence could have in modeled distributions because (1) background data were randomly selected and changed from one model and species to the next; (2) the calculation of classification metrics was iterated over the equivalent number of presences during the jackknife procedure and for each model and species, randomly selecting new sites at each iteration; (3) the weighting scheme when using

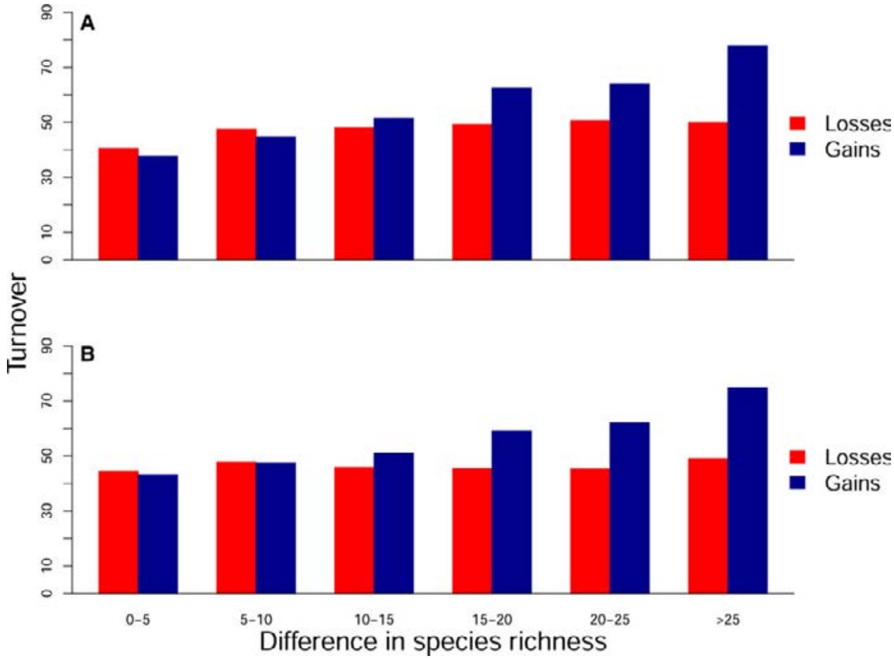

FIGURE 4. A comparison between ranges of difference species richness (losses and gains) and the average of turnover for each of those ranges in 2050 for (A) Scenario MIROC– A1B; and (B) CSIRO– A2.

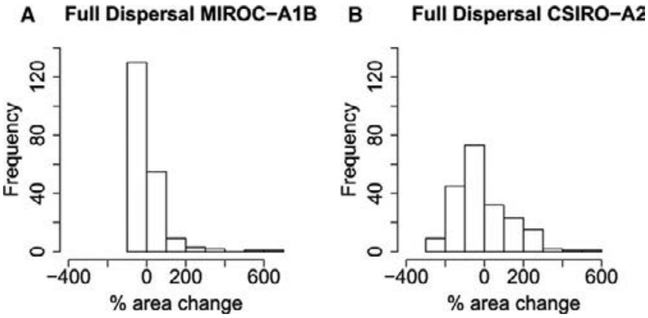

FIGURE 5. Change in species suitable area within Ecuador expressed in terms of a percentage of the current potential range in the country with respect to future projections. (A) MIROC-A1B; (B) CSIRO-A2, both represent a full dispersal hypothesis.

presence-absence methods will control the relative influence of pseudo-absences with respect to the available occurrences; (4) the ensemble forecasting strategy adopted here will consider only the best models and will tend to capture the consensus between them (Araújo *et al.* 2005, Coetzee *et al.* 2009); and (5) we used a combination of presence-only and presence-absence models to draw the consensus projections. All of this makes it extremely unlikely that a particular pseudo-absence has a major influence on the final projections of species distributions. Moreover, a preliminary comparison of the richness patterns in well-sampled areas suggests that our predictions are a good first approximation of reality (see Appendix S1). Gathering more extensive biodiversity data across highly diverse and vulnerable regions such as those represented in Ecuador should be of high priority to preserve global diversity. However, in the absence of better data, the modeling approach presented here represents a systematic method to fill in knowledge gaps and prepare for the future.

Coastal regions and mid-elevation Andean slopes have historically been the most disturbed by human activities in Ecuador. According to Tirira (2011), species like *Tremarctos ornatus* (Carnivora) in the Andes and *Ateles fusciceps* (Primates) in the coastal region are critically endangered species mainly because of habitat fragmentation. Our results showed that *Ateles fusciceps* would lose 62 percent of its current range due to climate change. Given the magnitude of these potential changes, it would be advisable to incorporate both habitat fragmentation and vulnerability to climate change when evaluating species threats (Bomhard *et al.* 2005).

Primates assessed here might be the most severely affected group because they would have fewer suitable areas as compared to other mammals. In contrast, the models predicted that carnivores and ungulates would be less affected by changes. These orders are the least dispersal-limited and the distances they need to disperse might be shorter, relative to the distances required for species of other orders (Schloss *et al.* 2012). The assumption of no-dispersal could be more appropriate for conservation assessments since many other factors affect dispersal abilities of species and most of the reductions in range for mammals are due to dispersal limitations rather than a reduction in the area that is climatically suitable.

CONSERVATION ISSUES.—With the full-dispersal scenario, we expect species to be able to colonize new suitable sites, but in reality

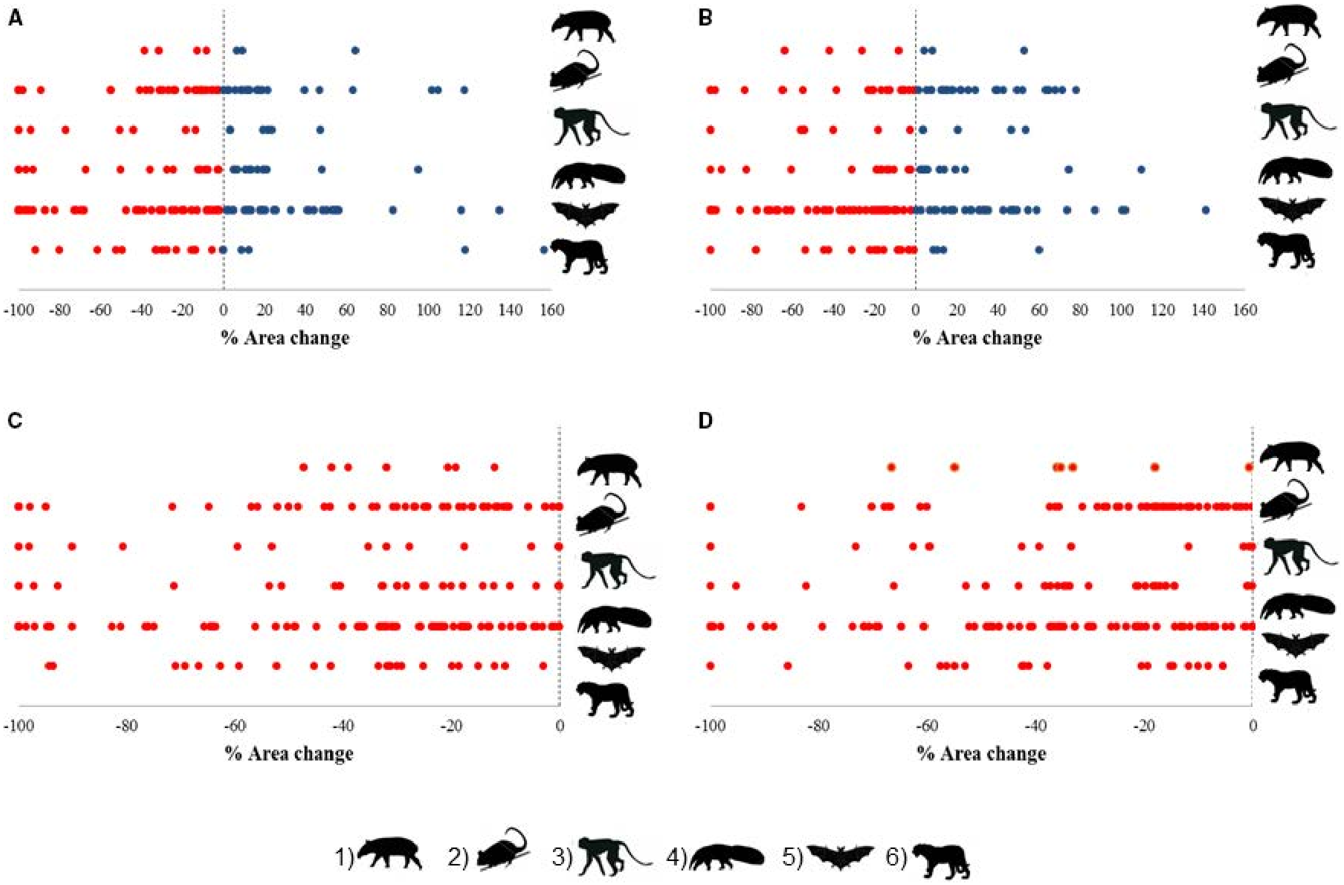

FIGURE 6. Percentage of area change for each species divided in six groups of mammals (each point represents one species): (1) ungulates, (2) rodents, (3) primates, (4) bats, (5) carnivores, and (6) others. Comparison under future conditions for 2050 for conservative and pessimistic scenarios. MIROC—A1B (A and C) and CSIRO—A2 (B and D) under the full dispersal hypothesis (A and B) and no-dispersal scenario (C and D).

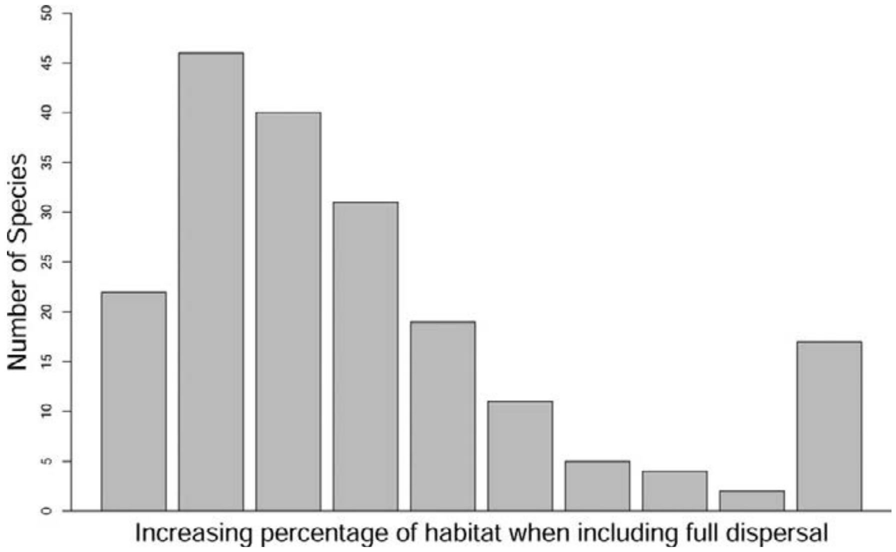

FIGURE 7. Histogram of percent of habitat lost per species under a full dispersal MIROC– A1B scenario.

some species may not be able to shift their ranges fast enough to track their suitable climates. Primates, for example, are more dispersal-limited than other taxa and may need to expand their ranges over longer distances to reach suitable climates (Schloss *et al.* 2012). In fact, survival of species in the future would depend on their abilities to track changes in suitable climates relative to the velocity at which climate changes in space (Loarie *et al.* 2009). For example, in some locations in Amazonia, average dispersal velocity for a subset of mammal species is about 1 km/yr, but the average velocity of climate change experienced can be as high as 8 km/yr (Schloss *et al.* 2012). In tropical regions, species generally have more restricted physiological tolerances and are expected to be more sensitive to climate change (Deutsch *et al.* 2008). The inability to keep pace with climate change may be due to narrower climatic niches of tropical species (Schloss *et al.* 2012). We predict an important loss of species in the Ecuadorian Andes, since some species living in this region could already be near their critical thermal maximum. Other approaches have documented a rapid loss of climatically suitable space for species of different taxa, and greater shifts are restricted to the mountains (Parmesan 2006, Tingley *et al.* 2012). According to Janzen (1967), tropical mountain passes should act as effective dispersal barriers. Also, dispersal ability of mammals could be higher or lower, depending on the species and the degree of fragmentation of their habitat.

Habitat loss and fragmentation are among the most important threats to global diversity (Laurance & Cochrane 2001), making it important to evaluate the synergistic effects of climate change and habitat fragmentation (Drake *et al.* 2005, Mantyka-Pringle *et al.* 2012). In Ecuador, deforestation rate is of 77,647 ha per year. The coast is the most disturbed area and has only 28 percent of the original forest cover remaining. Amazonia still has 89 percent of its original vegetative cover. The coast has an annual rate change of −2.49 percent, while the Tropical Andes has a −1 percent, and Amazonia a −0.3 percent (MAE 2012). Therefore, to ensure mammal species survival into the near future, it is necessary to include the effects of habitat loss and dispersal limitations.

CONCLUSIONS

A combination of distribution modeling techniques can be a useful methodology for data exploration to identify potential knowledge gaps, provide direction to fieldwork design, and guide conservation assessments incorporating climate change impacts on species' potential distribution (Elith *et al.* 2006, Hernandez *et al.* 2006). Although species distribution modeling is widely used for conservation planning, it is also necessary to continue collecting data on species for reliable assessments of the effects of climate on biodiversity and for the formation of sound management policies. SDMs ignore many potentially important ecological processes, such as biological interactions and dispersal mechanisms. Given the constraints of these models, results need to be taken with caution. However, their consistency across model types and extreme dispersal scenarios in this study provide a strong indication of potentially important shifts in diversity in this megadiverse area. Our results show that even under conservative climate change and full-dispersal scenarios, diversity patterns in Ecuadorian mammals are likely to undergo considerable changes. Future research should therefore aim at understanding how these effects of climate change will interact with habitat degradation, and reinforce conservation efforts that take these effects into account.

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DATA AVAILABILITY

Data available in the Dryad Repository: http://dx.doi.org/10.5061/dryad.4v52c (Iturralde-Pólit *et al.* 2017).

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

APPENDIX S1. Richness and predictive success.

APPENDIX S2. Geographic distribution and sources of uncertainties.

APPENDIX S3. Consistency of diversity projections under different climate change scenarios over time and space.

LITERATURE CITED

Allouche, O., A. Tsoar, and R. Kadmon. 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). J. Appl. Ecol. 43: 1223–1232.

Anderson, R. P. 2013. A framework for using niche models to estimate impacts of climate change on species distributions. Ann. N. Y. Acad. Sci. 1297: 8–28.

Araújo, M. B., and M. New. 2007. Ensemble forecasting of species distributions. Trends Ecol. Evol. 22: 42–47.

Araújo, M. B., R. J. Whittaker, R. J. Ladle, and M. Erhard. 2005. Reducing uncertainty in projections of extinction risk from climate change. Glob. Ecol. Biogeogr. 14: 529–538.

Austin, M. P. 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. Ecol. Model. 157: 101–118.

Barbet-Massin, M., W. Thuiller, and F. Jiguet. 2012. The fate of European breeding birds under climate, land-use and dispersal scenarios. Glob. Change Biol. 18: 881–890.

Bomhard, B., D. M. Richardson, J. S. Donaldson, G. O. Hughes, G. F. Midgley, D. C. Raimondo, A. G. Rebelo, M. Rouget, and W. Thuiller. 2005. Potential impacts of future land use and climate change on the

Red List status of the Proteaceae in the Cape Floristic Region, South Africa. Glob. Change Biol. 11: 1452–1468.

Bradley, R. S., M. Vuille, H. F. Diaz, and W. Vergara. 2006. Threats to water supplies in the tropical andes. Science 312: 1755–1756.

Burns, C. E., K. M. Johnston, and O. J. Schmitz. 2003. Global climate change and mammalian species diversity in US national parks. Proc. Natl Acad. Sci. USA 100: 11474–11477.

Busby, J. R. 1991. BIOCLIM-a bioclimate analysis and prediction system. Plant Prot. Q. 6: (Australia) pp. 64–68.

Buytaert, W., and B. De Bièvre. 2012. Water for cities: The impact of climate change and demographic growth in the tropical Andes. Water Resour. Res. 48: 8.

Carpenter, G., A. N. Gillison, and J. Winter. 1993. DOMAIN: a flexible modelling procedure for mapping potential distributions of plants and animals. Biodivers. Conserv. 2: 667–680.

Chen, S., G. Jiang, J. Zhang, Y. Li, and H. Qian. 2011. Species turnover of amphibians and reptiles in eastern China: disentangling the relative effects of geographic distance and environmental difference. Ecol. Res. 26: 949–956.

Cheng, H., A. Sinha, F. W. Cruz, X. Wang, R. L. Edwards, F. M. d'Horta, C. C. Ribas, M. Vuille, L. D. Stott, and A. S. Auler. 2013. Climate change patterns in Amazonia and biodiversity. Nat. Commun. 4: 1411.

Coetzee, B. W., M. P. Robertson, B. F. Erasmus, B. J. Van Rensburg, and W. Thuiller. 2009. Ensemble models predict Important Bird Areas in southern Africa will become less effective for conserving endemic birds under climate change. Glob. Ecol. Biogeogr. 18: 701–710.

Condit, R. 1998. Ecological implications of changes in drought patterns: shifts in forest composition in Panama. Clim. Change. 39: 413–427.

Crespo-Pérez, V., J. Régnière, I. Chuine, F. Rebaudo, and O. Dangles. 2015. Changes in the distribution of multispecies pest assemblages affect levels of crop damage in warming tropical Andes. Glob. Change Biol. 21: 82–96.

Dangles, O., and F. Nowicki. 2010. Biota Máxima. Ecuador Biodiverso. Pontificia Universidad Catolica del Ecuador (PUCE). Institut de Recherche pour le Développment, Quito, Ecuador.

Deutsch, C. A., J. J. Tewksbury, R. B. Huey, K. S. Sheldon, C. K. Ghalambor, D. C. Haak, and P. R. Martin. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. Proc. Natl Acad. Sci. USA 105: 6668–6672.

Drake, B. G., E. A. Johnson, B. A. Seibel, M. A. Cochrane, V. J. Farby, D. Rasse, and L. Hannah. 2005. Synergistics effects. Climate change and biodiversity. *In* T. E. Lovejoy, and L. Hannah (Eds.). pp. 296–316. Yale University, Ann Arbor, Michigan.

Dubuis, A., J. Pottier, V. Rion, L. Pellissier, J. P. Theurillat, and A. Guisan. 2011. Predicting spatial patterns of plant species richness: a comparison of direct macroecological and species stacking modelling approaches. Divers. Distrib. 17: 1122–1131.

Elith, J., C. H. Graham, R. P. Anderson, M. Dudík, S. Ferrier, A. Guisan, R. J. Hijmans, F. Huettmann, J. R. Leathwick, and A. Lehmann. 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29: 129–151.

Elith, J., and J. R. Leathwick. 2009. Species distribution models: ecological explanation and prediction across space and time. Annu. Rev. Ecol. Evol. Syst. 40: 677–697.

Elith, J., J. R. Leathwick, and T. Hastie. 2008. A working guide to boosted regression trees. J. Anim. Ecol. 77: 802–813.

Farber, O., and R. Kadmon. 2003. Assessment of alternative approaches for bioclimatic modeling with special emphasis on the Mahalanobis distance. Ecol. Model. 160: 115–130.

Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Found. Environ. Conserv. 24: 38–49.

Franklin, J. 2009. Mapping species distributions. Spatial inference and prediction. Cambridge University Press, Cambridge, UK.

Friedman, J., T. Hastie, and R. Tibshirani. 2000. Additive logistic regression: a statistical view of boosting (With discussion and a rejoinder by the authors). Ann. Stat. 28: 337–407.

Garavito, N. T., A. C. Newton, D. Golicher, and S. Oldfield. 2015. The relative impact of climate change on the extinction risk of tree species in the montane tropical andes. PLoS ONE 10: e0131388.

Hannah, L., G. Midgley, S. Andelman, M. Araújo, G. Hughes, E. Martinez-Meyer, R. Pearson, and P. Williams. 2007. Protected area needs in a changing climate. Front. Ecol. Environ. 5: 131–138.

Hernandez, P. A., C. H. Graham, L. L. Master, and D. L. Albert. 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. Ecography 29: 773–785.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25: 1965–1978.

Iturralde-Pólit, P., O. Dangles, S. F. Burneo, and C. N. Meynard. 2017. Data from: The effects of climate change on a mega-diverse country: predicted shifts in mammalian species richness and turnover in continental Ecuador. Dryad Digital Repository. http://dx.doi.org/10.5061/dryad.4v52c

Jacobsen, D., S. Cauvy-Fraunie, P. Andino, R. Espinosa, D. Cueva, and O. Dangles. 2014. Runoff and the longitudinal distribution of macroinvertebrates in a glacier-fed stream: implications for the effects of global warming. Freshw. Biol. 59: 2038–2050.

Janzen, D. H. 1967. Why mountain passes are higher in the tropics. Am. Nat. 101: 233–249.

Knutti, R., and J. Sedláček. 2013. Robustness and uncertainties in the new CMIP5 climate model projections. Nat. Clim. Chang. 3: 369–373.

Kriticos, D. J., B. L. Webber, A. Leriche, N. Ota, I. Macadam, J. Bathols, and J. K. Scott. 2011. CliMond: global high-resolution historical and future scenario climate surfaces for bioclimatic modelling. Methods Ecol. Evol. 3: 53–64.

Lapola, D. M., M. D. Oyama, and C. A. Nobre. 2009. Exploring the range of climate biome projections for tropical South America: the role of CO2 fertilization and seasonality. Global Biogeochem. Cycles 23: GB3003.

Laurance, W. F., and M. A. Cochrane. 2001. Synergistic effects in fragmented landscapes. Conserv. Biol. 15: 1488–1489.

Levinsky, I., F. Skov, J. C. Svenning, and C. Rahbek. 2007. Potential impacts of climate change on the distributions and diversity patterns of European mammals. Biodivers. Conserv. 16: 3803–3816.

Liu, C., P. M. Berry, T. P. Dawson, and R. G. Pearson. 2005. Selecting thresholds of occurrence in the prediction of species distributions. Ecography 28: 385–393.

Loarie, S. R., P. B. Duffy, H. Hamilton, G. P. Asner, C. B. Field, and D. D. Ackerly. 2009. The velocity of climate change. Nature 462: 1052–1055.

Mantyka-Pringle, C. S., T. G. Martin, and J. R. Rhodes. 2012. Interactions between climate and habitat loss effects on biodiversity: a systematic review and meta-analysis. Glob. Change Biol. 18: 1239–1252.

Marmion, M., M. Parviainen, M. Luoto, R. K. Heikkinen, and W. Thuiller. 2009. Evaluation of consensus methods in predictive species distribution modelling. Divers. Distrib. 15: 59–69.

Meynard, C. N., A. Migeon, and M. Navajas. 2013. Uncertainties in predicting species distributions under climate change: A case study using *Tetranychus evansi* (Acari: Tetranychidae), a widespread agricultural pest. PLoS ONE 8: e66445.

Michelutti, N., A. P. Wolfe, C. A. Cooke, W. O. Hobbs, M. Vuille, and J. P. Smol. 2015. Climate change forces new ecological states in tropical Andean lakes. PLoS ONE 10: e0115338.

Miniterio del Ambiente. 2012. Línea base de deforestación del Ecuador Continental. Ministerio del Ambiente, Quito - Ecuador.

Mittermeier, R. A., C. G. Mittermeier, and P. R. Gil. 1997. Megadiversity: Earth's biologically wealthiest nations. Cemex México, Distrito Federal, Brazil.

Mittermeier, R. A., N. Myers, C. G. Mittermeier, and P. R. Gil. 1999. Hotspots: Earth's biologically richest and most endangered terrestrial ecoregions. CEMEX, SA, Agrupación Sierra Madre, SC, Mexico.

New, M., D. Lister, M. Hulme, and I. Makin. 2002. A high-resolution data set of surface climate over global land areas. Clim. Res. 21: 1–25.

Nix, H., and J. Busby. 1986. BIOCLIM, a bioclimatic analysis and prediction system. Annual report CSIRO. CSIRO Division of Water and Land Resources, Canberra, ACT.

Pachauri, R. K., M. Allen, V. Barros, J. Broome, W. Cramer, R. Christ, J. Church, L. Clarke, Q. Dahe, and P. Dasgupta. 2014. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.

Pachauri, R. K., and A. Reisinger. 2007. Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Intergovernmental Panel on Climate Change.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annu. Rev. Ecol. Evol. Syst. 37: 669.

Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy Modeling of species geographic distributions. Ecol. Model. 190: 231–259.

Phillips, S. J., and M. Dudik. 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography 31: 161–175.

Pounds, J. A., M. R. Bustamante, L. A. Coloma, J. A. Consuegra, M. P. L. Fogden, P. N. Foster, E. La Marca, K. L. Masters, A. Merino-Viteri, and R. Puschendorf. 2006. Widespread amphibian extinctions from epidemic disease driven by global warming. Nature 439: 161–167.

Pounds, J. A., M. P. Fogden, and J. H. Campbell. 1999. Biological response to climate change on a tropical mountain. Nature 398: 611–615.

R CORE TEAM. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0

Rabatel, A., B. Francou, A. Soruco, J. Gomez, B. Cáceres, J. Ceballos, R. Basantes, M. Vuille, J.-E. Sicart, C. Huggel, M. Scheel, Y. Lejeune, Y. Arnaud, M. Collet, T. Condom, G. Consoli, V. Favier, V. Jomeli, R. Galarraga, P. Ginot, L. maisincho. J. Mendoza, M. Menegoz, E. Ramírez, P. Ribstein, W. Suárez, M. Villacís, and P. Wagnon. 2013. Current state of glaciers in the tropical Andes: a multi-century perspective on glacier evolution and climate change. The Cryosphere 7: 81–102.

Schloss, C. A., T. A. Nuñez, and J. J. Lawler. 2012. Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. Proc. Natl Acad. Sci. USA 109: 8606–8611.

Segurado, P., and M. B. Araújo. 2004. An evaluation of methods for modelling species distributions. J. Biogeogr. 31: 1555–1568.

Thuiller, W., S. Lavorel, M. B. Araújo, M. T. Sykes, and I. C. Prentice. 2005. Climate change threats to plant diversity in Europe. Proc. Natl Acad. Sci. USA 102: 8245.

Tingley, M. W., M. S. Koo, C. Moritz, A. C. Rush, and S. R. Beissinger. 2012. The push and pull of climate change causes heterogeneous shifts in avian elevational ranges. Glob. Change Biol. 18: 3279–3290.

Tirira, D. (Ed.) 2011. Libro Rojo de los Mamíferos del Ecuador. Fundación Mamíferos y Conservación, Pontificia Universidad Católica del Ecuador y Ministerio del Ambiente del Ecuador, Quito, Ecuador.

Tirira, D. 2013. Red Noctilio. Base de información no publicada sobre los mamíferos del Ecuador. Murciélago Blanco, Ecuador.

Tirira, D. 2014. Mamíferos del Ecuador: Lista Actualizada de especies. Asociación Ecuatoriana de Mastozoología y Fundación Mamíferos y Conservación, Quito, Ecuador.

Urrutia, R., and M. Vuille. 2009. Climate change projections for the tropical Andes using a regional climate model: Temperature and precipitation simulations for the end of the 21st century. J. Geophys. Res. Atmos. 114: 2108.

Van Vuuren, D. P., E. Stehfest, M. G. den Elzen, T. Kram, J. van Vliet, S. Deetman, M. Isaac, K. K. Goldewijk, A. Hof, and A. M. Beltran. 2011. RCP2. 6: exploring the possibility to keep global mean temperature increase below 2°C. Clim. Change. 109: 95–116.

Watling, J. I., S. S. Romanach, D. N. Bucklin, C. Speroterra, L. A. Brandt, L. G. Pearlstine, and F. J. Mazzotti. 2012. Do bioclimate variables improve performance of climate envelope models? Ecol. Model. 246: 79–85.

Wilson, D. E., and D. A. M. Reeder. 2005. Mammal species of the world: A taxonomic and geographic reference. Johns Hopkins Univ Pr, Baltimore.

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ORIGINAL PAPER

Integrating phylogenetic and functional biodiversity facets to guide conservation: a case study using anurans in a global biodiversity hotspot

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Abstract

The Cerrado is one of the most threatened biomes in Brazil, with little spatial representation within the Protected Area network. Recently, proposed conservation plans worldwide have advocated for the use of multiple biodiversity facets to protect unique evolutionary and functional processes. Our aim was to identify areas with high biodiversity representativeness applying this multifaceted perspective, and propose conservation plans based on the joint analysis of taxonomic, functional and phylogenetic diversity. We used a database of the Brazilian National Program for Research in Biodiversity, which employs a standard protocol for sampling tadpoles. The Cerrado database includes samples from 165 water bodies spread over 15 localities, covering most of the Central Brazilian Cerrado. We selected four morphological traits to calculate functional diversity and used a dated phylogeny available in the literature to compute phylogenetic diversity. Our approach selected five priority areas for conservation, one of which is already protected. Our results highlighted the importance of four new areas which show high values of diversity, including original lineages and traits, and urgently need conservation prioritization. Furthermore, unlike the current protected network, our approach performs significantly better than random at protecting sites with high phylogenetic and functional diversity. We therefore discuss how the multifaceted indices considered can help protect key ecosystem functions and evolutionary legacy in anuran communities of the Brazilian Cerrado.

Keywords Cerrado hotspot · Multifaceted analysis · Tadpoles · Functional and phylogenetic diversity

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Introduction

Since the early 80' s, different strategies have been applied to guide conservation decisions in a rational and systematic process, to conserve as much biological diversity as possible (Pressey et al. 2007). However, these approaches have been largely based on taxonomic diversity, namely the protection of individual species or the protection of hotspots of species richness (Margules and Pressey 2000; Myers et al. 2000; Rodrigues et al. 2006). While these approaches have certainly advanced greatly the field of conservation biology, they usually implicitly assume that the extinction or decline of one species or the other are equivalent (i.e., all species are phylogenetically and functionally equivalent) (Iknayan et al. 2014), and they usually focus on endemic and rare species as units of conservation (e.g., IUCN conservation categories; IUCN 2017). These simplifications may be problematic for two reasons. First, abundant and widespread species sometimes perform key or unique ecosystem functions or represent highly distinct evolutionary lineages (Lavorel et al. 1997; Devictor et al. 2010; Mouquet et al. 2012). Their decline or extinction would therefore have disproportionately important consequences for ecosystem function or for evolutionary distinctiveness. In this context, focusing solely on rarity, range size or population decline as criteria for prioritization may lead us to ignore potential tipping points for ecosystem functions. Second, regardless of the species range or abundance, not all species are equivalent. For example, keystone species may cause large shifts in ecosystem functions (Hooper et al. 2005). A growing body of literature suggests that species with different life history traits and ecological properties complement each other providing different ecosystem functions (i.e., the niche complementarity hypothesis: Cadotte 2017; Hautier et al. 2018). Conversely, the insurance hypothesis within the biodiversity ecosystem-function (BEF) framework predicts that some level of redundancy guarantees that the system resists to individual extinctions without compromising ecosystem processes (Reiss et al. 2009; Isbell et al. 2018). Furthermore, recent studies have shown that species that seem redundant when looking at one particular function, are not redundant when analyzing multiple functions at the same time (Reiss et al. 2009; Cadotte 2017; Hautier et al. 2018) or when compared through time (Loreau et al. 2003). All these lines of evidence point to the need to consider the maximization of species differences within an ecosystem as a suitable conservation goal if we are interested in the maintenance of ecosystem functions (e.g., Mace et al. 2012; Trindade-Filho et al. 2012).

Along the same lines, phylogenetic considerations may be relevant in conservation biology for several reasons (Mouquet et al. 2012). First, traits are sometimes highly conserved along evolutionary lineages. Because of this, phylogenies have been advocated as a proxy for functional composition (Cadotte et al. 2010; but see Venail et al. 2015). Indeed, given that we lack complete knowledge regarding the functional traits that are relevant for particular ecosystem functions, and given recent advances in molecular biology, phylogenies are sometimes more complete and of easier access than functional traits (Mouquet et al. 2012). Second, phylogenetic diversity and distinctiveness may be considered as conservation goals per se (Pavoine et al. 2005; Mouquet et al. 2012). For example, the extinction of a species from an old, species-poor clade will result in a greater loss of evolutionary information than the extinction of a less distinct species from a young and species-rich clade (Redding and Mooers 2006; Winter et al. 2013). On top of that, some species' extinctions can also cause evolutionary cascades, implying changes in the evolutionary paths of the remaining species (Dirzo et al. 2014). Finally, and more speculatively, it has also been proposed that phylogenetic diversity represents evolutionary potential during episodes of rapid environmental change, such as the one current climate change is imposing on ecosystems (Forest et al. 2007).

These recent developments also highlight the fact that there are at least four different dimensions of phylogenetic and functional composition that need to be considered to fully characterize the conservation value of a site within each facet. We will call them here functional or phylogenetic richness, divergence, regularity and originality (Table 1). Richness refers to the total number of species, or the total accumulated functional traits and evolutionary history represented in a community (Mason et al. 2005; Tucker et al. 2016); divergence refers to the average or overall phylogenetic or functional separation between species (Mason et al. 2003; Tucker et al. 2016); regularity is another type of divergence that focuses on how evenly spaced (phylogenetically or functionally) species within a community are (Mason et al. 2005; Tucker et al. 2016); and finally originality refers to how different one particular species is from all others (Pavoine et al. 2005). Notice that while richness, divergence and regularity are diversity measures and apply to the full community represented in a site, originality is species-specific and allows identifying species that are unique in either their functional or phylogenetic identities. Recent studies have shown that including functional and phylogenetic approaches into ecological studies ensure predictability on communities' sensitivity and resilience (e.g., Balvanera et al. 2006; Srivastava and Bell 2009; Mace et al. 2012). However, they have also shown that phylogenetic and functional diversity measures are often very highly correlated to taxonomic diversity (Meynard et al. 2011; Mouquet et al. 2012; Pardo et al. 2017). Therefore, the analysis of functional and phylogenetic diversity often requires comparing the observed diversity value to what would be expected solely from species richness (Laliberté and Legendre 2010; Vellend et al. 2011; Pardo et al. 2017). In other words, the conservation value of multiple sites need to be evaluated against what would be expected based on a random draw of the same number of species, potentially revealing areas with more trait functions or phylogenetic history than expected solely by the number of species present in that site.

The Cerrado biome is the richest savanna region in the world (Silva and Bates 2002; Silva et al. 2006) and comprises high species richness and endemism, therefore being considered as a global biodiversity hotspot (Myers et al. 2000). It is also one of the most endangered biomes of the world, threatened mainly by the expansion of the agricultural frontier (Strassburg et al. 2017). Amphibians, to which anurans belong, show a higher proportion of threatened species compared to other vertebrates, with 32.4% of all known species being in either the "threatened" or "extinct" categories (2030 species out of 6260 amphibians) (IUCN 2016). Large declines of amphibian populations have been documented, demanding urgent public and governmental efforts for effective amphibian conservation in Brazil (Becker and Loyola 2008). Anurans are highly dependent on the existence of high humidity and the persistence of water sources throughout their life cycles, resources that are limited in the Cerrado during the dry season. On top of their ecological vulnerabilities, adult anurans and tadpoles may fulfill important ecosystem functions in natural communities. For example, adult anurans and tadpoles feed on eggs (Bowatte et al. 2013), larval stages (Mokany 2007) and adult mosquitos (Raghavendra et al. 2008), some of which are important vectors of tropical diseases (e.g., *Aedes spp.*, *Anopheles spp.* and *Lutzomyia spp.*). They can therefore play a role controlling obnoxious populations and can help disease control (e.g., yellow fever, dengue fever, zika virus, malaria, leishmaniases; Raghavendra et al. 2008), especially in tropical areas. Most tadpoles also feed on microalgae, therefore playing an important role in the maintenance of water quality of ponds and streams by preventing water eutrophication (Ranvestel et al. 2004). Given this evidence, and although anuran functional roles have not been thoroughly studied and quantified, there is no question

Table 1 Dimensions of diversity (biodiversity facets), respective definition and diversity metrics used to quantify them

Facet	Diversity			Originality
	Richness	Divergence	Regularity	
Taxonomic	Number of species: SR	The degree of species similarities in a community: TD_{RAO} (Rao 1982)	The regularly distribution of species abundances in a community: TD_{RAO} (Rao 1982)	–
Phylogenetic	Total evolutionary history accumulated in a community: PD_F (Faith 1992)	Mean phylogenetic distance of all species in a community: PD_{RAO} (Rao 1982) MPD (Webb et al. 2002)	The regularly distribution of species in the phylogenetic tree in a community: Rao’s functional entropy (Rao 1982) Hed and Haed (Cadotte et al. 2010)	How unique a species is according to its evolutionary history: Phylogenetic Originality (Pavoine et al. 2005)
Functional	Total trait space accumulated in a community: FRic (Villéger et al. 2008)	Mean divergence of functional characters in a community: FD_{RAO} (Rao 1982) FDiv (Mason et al. 2003)	The regularly distribution of species traits abundances in a community: FD_{RAO} (Rao 1982)	How unique a species is according to its functional traits: Functional Originality (Pavoine et al. 2005)

SR Species richness, TD_{RAO} Rao’s taxonomic diversity, *FRic* Functional richness, *FDiv* functional divergence, FD_{RAO} Rao’s functional diversity, PD_F Faith’s phylogenetic diversity, *MPD* mean pairwise phylogenetic distance, PD_{RAO} Rao’s phylogenetic diversity, *Hed and Haed* evolutionary distinctiveness that their conservation has also functional implications at the ecosystem level. Loyola et al. (2008) identified priority areas for the conservation of endangered anurans in the Neotropics and found that species with an aquatic reproductive mode are often underrepresented in the conservation planning process. In fact, many protected forest remnants are isolated, meaning that forest habitats where adults spend most of their life, and water bodies where they reproduce, are often disconnected, a process called habitat splitting and which constitutes one of the greatest threats to amphibians (Becker et al. 2007). This makes anurans in the Cerrado a very highly vulnerable group of species.

In this study, we aimed at applying a taxonomic, phylogenetic and functional approach including as many of these different facets as possible to a highly vulnerable group of species, anurans, in a global biodiversity hotspot, the Cerrado biome in Brazil, to prioritize sites for conservation of water-dependent anurans. To our knowledge, this is the first integrative study using anurans' taxonomic, phylogenetic and functional components to consider conservation recommendations in the Cerrado. We derive recommendations on highly valuable sites for conservation as well as focal species, highlighting the advantages and shortcoming of the multifaceted approach.

Methodology

Study area

The Cerrado is a Savannah biome, with a mosaic of savanna, grasslands and forests (Eiten 1972). The climate is tropical, with precipitation varying between 800 and 2000 mm/year, with a pronounced dry season from April to September (Peel et al. 2007), and average temperatures between 18 °C to 28 °C (Dias 1992). The Brazilian Cerrado is the second largest biome in South America, covering 2036.448 km^2 (Ministério do Meio Ambiente 2017). Despite its biological importance, the Cerrado is the hotspot with the lowest percentage of fully protected areas in Brazil (Ministério do Meio Ambiente 2017). Although 8.21% of its territory is currently under some kind of legal protection, only 2.85% is under full protection, the other 5.36% being designated under sustainable use conservation units, including private reserves (Ministério do Meio Ambiente 2017).

Database

We used the database of the Brazilian National Program for Research in Biodiversity (SISBIOTA-Brazil) project that employed a standard protocol for sampling tadpoles in five Brazilian biomes. The Cerrado biome database gathers information on tadpoles from 165 waterbodies (ponds and streams), located in 15 distinct areas (Fig. 1). The sampling effort of the SISBIOTA focused on filling the gaps in tadpole inventories that were already existent, and is therefore appropriate to focus on the most vulnerable species, the ones that depend on waterbodies for reproduction (Lips et al. 2003; Bustamante et al. 2005). Additionally, to standardize and allow comparisons at large spatial scales from the SISBIOTA database, we considered only isolated lentic and lotic waterbodies, i.e., those without communication among them or with other types of waterbodies. The standard protocol consisted of sampling tadpoles with a hand dipnet (32 cm diameter and 1.5 mm^2 mesh) through all surface of each pond (Skelly and Richardson 2010) and along a 100 m transect in streams between November 2011 and May 2014. We sampled each water body during

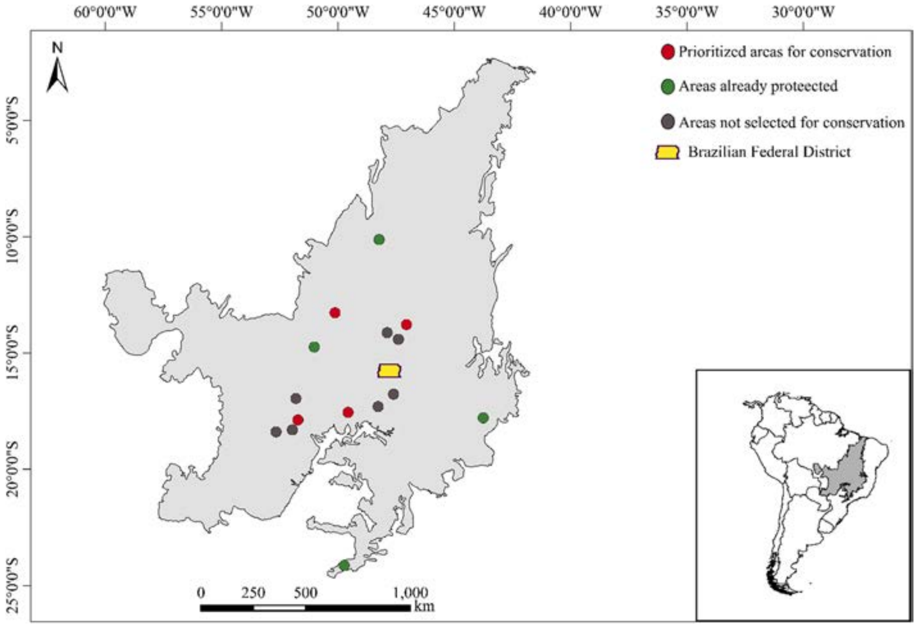

Fig. 1 Distribution of 15 sampled areas in Brazilian Cerrado. Green dots represent already protected areas. Red dots are the areas selected by us as the priorities for conservation of multiple dimension of diversity. Gray dots are areas not selected as a priority in our conservation approach

1 h, trying to maximize the total area covered as well as representing all types of microhabitats in each survey (Skelly and Richardson 2010). The total number of tadpoles per species for each water body was then considered as a reliable abundance estimate, which was subsequently used for the calculation of diversity indices requiring relative abundances. All the species included in our study present direct dependence of water bodies during some part of their life cycle. In our dataset there are two species that are generally considered as terrestrial or semi-terrestrial that are in fact dependent of water: *Ameerega flavopicta*, which exhibits parental care of the eggs, but where the adult males need to take the hatched tadpoles to nearby ponds associated to streams to complete their metamorphosis (Haddad and Martins 1994; Toledo et al. 2004); and *Thoropa* tadpoles, which present a semi-terrestrial development, but can only occur in rocks within or at the immediate proximity of streams (Caramaschi and Sazima 1984; Eterovick and Barros 2003).

Functional traits

We chose four morphological traits (total length, body compression, number of teeth rows and reproductive mode) available in the SISBIOTA database, which represent good predictors of the functional role of tadpoles on water ecosystems (Table S1). This database holds categorical and continuous morphological traits, determined in five to ten tadpoles per species, between 33 to 38 developmental stages (Gosner 1960). For species sampled out of this interval, we consulted the respective description papers or we made the measurements in tadpoles deposited in Brazilian scientific collections ("Coleção do Departamento de Zoologia e Botânica da UNESP de São José do Rio Preto", "Museu de Zoologia da

Universidade Estadual de Campinas”,”Coleção Célio F. B. Haddad”, “Coleção Zoológica da Universidade Federal de Goiás”). We excluded three species of our functional analysis because of the lack of information on all the four traits. The remaining species have complete information for all trait values.

Phylogeny

We constructed the phylogenetic topology for anuran species of the Cerrado based on Pyron (2014)’s dated phylogeny. Species unrepresented on that phylogeny were replaced with a congeneric species for which the same age was assumed. If no congeneric species was represented, we bound the species on the likely phylogenetic placement based on cladistics literature (Faivovich 2002; Faivovich et al. 2005, see topology in Fig. S1). Of the 67 species included in the analysis, 88% were represented in Pyron’s phylogeny, 9% were added at the congeneric level, and 3% were bound based on the cladistics literature. We then used *bladj* (Branch Lenght Adjuster) on the software Phylocom 4.2 (Webb et al. 2008) to estimate the age of taxa that were bound on the Pyron’s dated phylogeny. *bladj* sets the age of the nodes of unknown age by estimating the age of clade diversification from the branches of known age (see also Chamberlain et al. 2012). To calculate phylogenetic diversity, we considered the distance between species in millions of years.

Functional, phylogenetic and species diversity

We chose a variety of diversity indices to represent taxonomic, functional and phylogenetic richness, divergence and regularity, for the 15 sites studied, plus an index of species originality to identify functionally or phylogenetically unique species (Table 1). Among the indices considered, the Rao diversity index is the only one that can be calculated for taxonomic (TD), functional (FD) and phylogenetic diversity (PD), allowing comparisons between these three facets. All other indices are specific to either the taxonomic, functional or phylogenetic components (see Table 1, Fig. 2, for details).

For functional and phylogenetic originality of species, we used the originality index proposed by Pavoine et al. (2005). This index is also based on the Rao quadratic entropy (QE), but specifically weights in the uniqueness of each species in different communities. We selected the top 5% of species with the highest originality values for further discussions.

Defining conservation priorities for protected areas

To identify priority areas for conservation of anuran species, we used a ranking method that integrates the different facets of diversity mentioned above. We did not consider spatial prioritization methods, such as systematic conservation planning, because we do not have continuous distribution information for the species or their habitats at the scale and resolution required, and optimization software commonly used to implement it are not currently well adapted to incorporate phylogenetic and functional diversity and their different variants. However, our dataset is the most complete in the region to include representation of early life-stages of anurans and evaluate important independent waterbodies. A score-based ranking method therefore seemed like a sensitive choice, given the good response regarding conservation prioritization in particular contexts (Volkmann et al. 2014; Chen et al. 2017). The ranking followed these steps:

(1) We computed Pearson's correlation among diversity indices, using the Bonferroni correction for significance levels (Table S2). When the indices were correlated to >0.8, we eliminated from further analysis one of them, prioritizing the index that represented more diversity dimensions and that was most used in the literature. A Principal Components Analysis (Legendre and Legendre 2012) complemented this analysis to visually assess the relationship among indices and the evidence of which one is representing the same diversity component (Fig. 3). This led us to remove four correlated diversity indices. Therefore, the rest of the ranking was carried out considering the remaining six diversity indices: Rao's Functional, Phylogenetic and Taxonomic diversities, species richness, functional divergence and evolutionary distance (Hed).

(2) We standardized each selected index with the following formula proposed by Maire et al. (2013):

$$Div_{stand} = \frac{\alpha_x - \alpha_{\min x}}{\alpha_{\max x} - \alpha_{\min x}}$$

where α is the value of the index in each area x, and $\alpha_{\min x}$ and $\alpha_{\max x}$ are the lowest and highest values of the index α in the area x. Therefore, the standardized indices $Div_{stand(\alpha)}$ vary between 0 and 1 with in each of the 15 sampled areas.

(3) We calculated a synthetic index (SI) of conservation prioritization by summing up each of the standardized indices in each site (Maire et al. 2013). SI varies from a minimum value (different from zero, that represents the area with the lowest values for all indices) to six (the maximum value obtained if one area has the highest value for all indices).

(4) Finally, we ranked the areas based on their SI values. Sites with $SI > 3.0$ were considered as high priority, since those represent the highest diversity values for at least four of the six indices.

To ensure that the areas for conservation prioritization are representing singular sites that add new diversity to the previously selected ones, we estimated the cumulative percentage of Rao's functional and phylogenetic diversity when adding new sites. We implemented this by ranking the sites from the most to the least diverse (in terms of Rao FD and PD), and vice versa, and calculated the pulled Rao FD and PD by aggregating the sites in order along the diversity gradient (Devictor et al. 2010). We compared these curves to a Whisker plot that represents the random expectation given the same species richness by randomly selecting areas for protection and calculating the accumulation of diversity sorting three sites each time and repeating the process 20 times.

Finally, we performed a sample-based rarefaction analysis to verify if sample effort influenced our synthetic metric for prioritization of sites (Fig. S2). The classic rarefaction of species richness (Gotelli and Colwell 2001) has only been implemented to Rao's FD and PD (Ricotta et al. 2012), so we based this analysis only using Rao in all three facets.

Spatial autocorrelation

We tested spatial autocorrelation using Moran's I correlograms for all biodiversity facets (Legendre and Legendre 2012). We choose a priori six distance classes, each one composed by similar number of samples and the significance test for autocorrelation was based in 1000 randomizations. Moran's I correlogram was calculated in the software *Spatial Analysis in Macroecology* (SAM; Rangel et al. 2006, 2010).

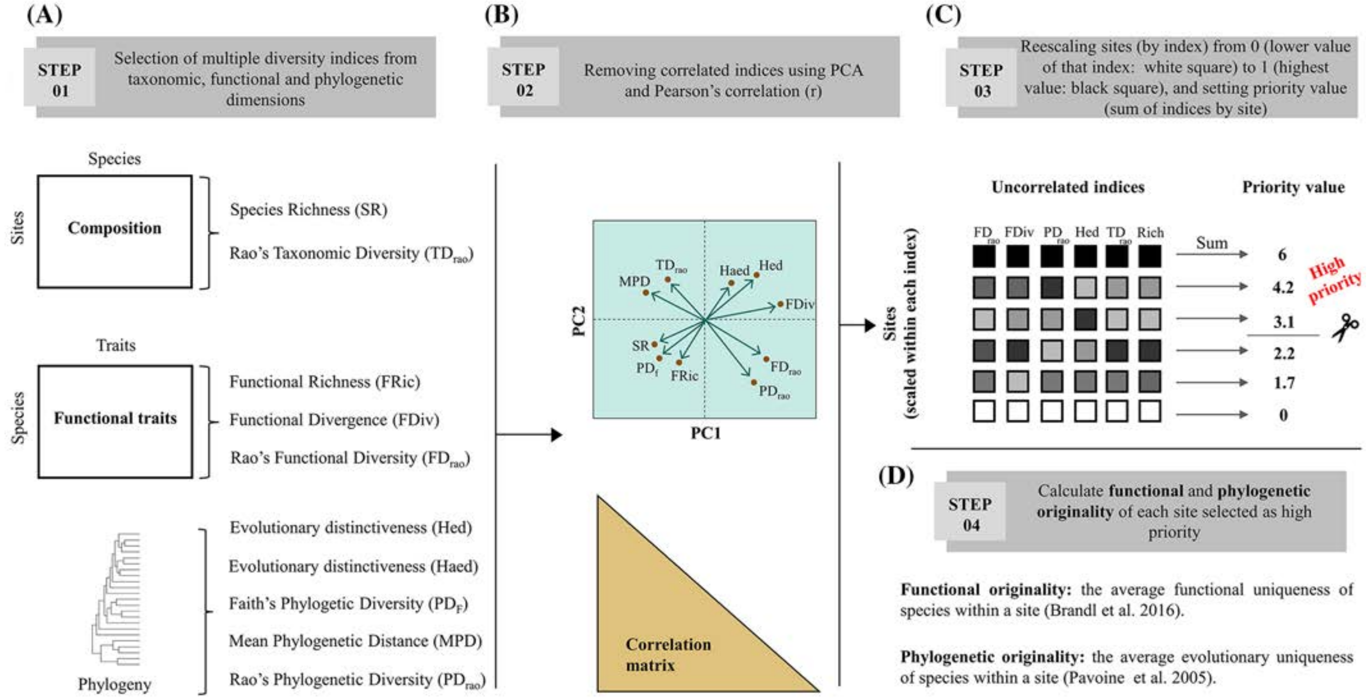

Fig. 2 Main steps used in the prioritization for conservation in the Cerrado. First, we performed the selection of multiple diversity indices using PCA (Fig. 3) and Pearson's correlation corrected by Bonferroni criteria (Table S2). Second, we tested and removed the correlated indices. Third, we standardized and summed up the six indices selected for each area to obtain a synthetic index (SI) of conservation prioritization (Maire et al. 2013). SI varies from a minimum value (different from zero, that represents the area with the lowest values for all indices) to six (the maximum value obtained if one area has the highest value for all indices). We rank the areas based on their SI values and considered as areas with high priority for conservation those with SI > 3.0. Last, we calculated functional and phylogenetic originality

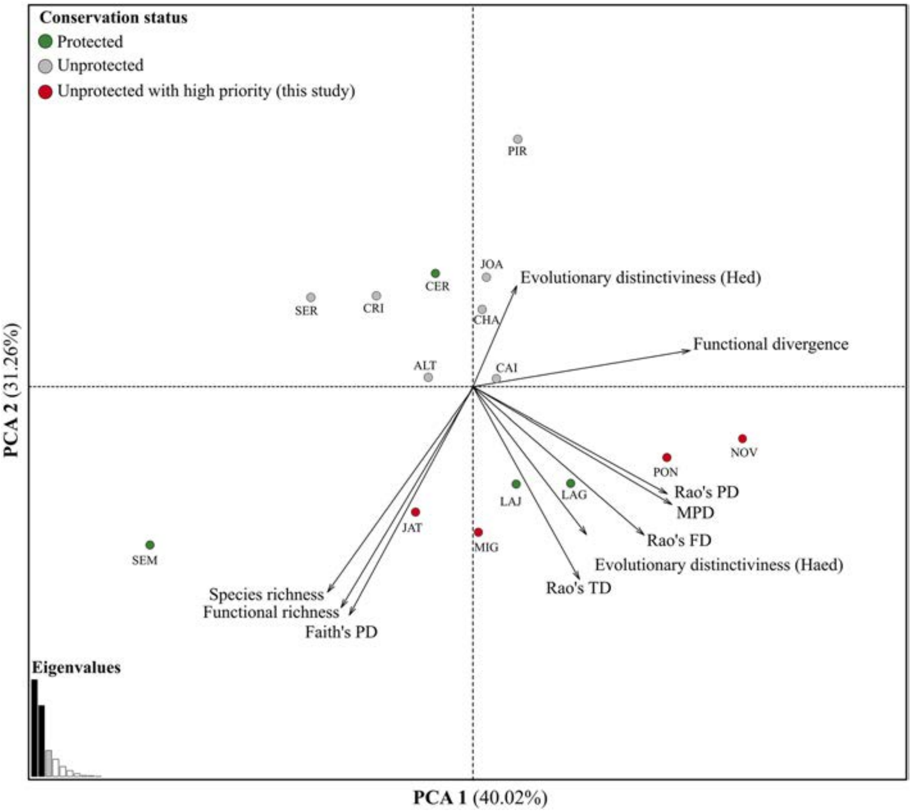

Fig. 3 Principal component analysis of biodiversity indices. First axis explained 40.02% and second axis 31.26% of all data variation. Red circles represent sites with the lowest biodiversity values of all indices, excepted evolutionary distinctiveness (Hed). Abbreviations: CER (Cerrado State Park), LAJ (Lajeado State Park), LAG (Lago Cedro Extractive Reserve), SEM (Sempre Vivas State Park), JAT (Jataí), MIG (São Miguel do Araguaia), NOV (Nova Roma), PON (Pontalina), ALT (Alto Paraíso de Goiás), CAI (Caiapônia), CHA (Chapadão do Céu), CRI (Cristalina),JOA (São João da Aliança), SER (Serranópolis) and, PIR (Pires do Rio)

Results

We found 70 species of anurans distributed on 15 areas in the Brazilian Cerrado, but we eliminated three of them from the analysis because of lack of information on their functional traits (Table S3). Only the last distance class (around 850 km) presents a low negative autocorrelation in functional diversity (FD), indicating that distant sites have different patterns of FD (Fig. S3). For the other five diversity indices, we found no spatial autocorrelation (Fig. S3).

The most phylogenetically original species was *Chiasmocleis albopunctata*, followed by two other Microhylidae frogs (*Dermatonotus muelleri* and *Elachistocleis cesarii*, Table S4). In fact, the originality analyses gave higher weights to Microhylidae species, which constitutes a largely isolated clade on our tree (Fig. S1). In terms of functional originality, the most original species was *Leptodactylus labyrinthicus*, followed by *Physalaemus marmoratus*, *L. gr. labyrinthicus* and *Physalaemus centralis* (Table S4). The functional originality analysis gave higher weights to Leptodactylidae frogs (the four most functionally original species).

Five areas presented high priority values according to the synthetic index. One of them, Lago Cedro Extractive Reserve (LAG, Table 2, Fig. 2), is already protected. The remaining four areas are not currently protected: Nova Roma (NOV), São Miguel do Araguaia (MIG), Pontalina (PON) and Jataí (JAT, Table 2, Fig. 2). The sample-based rarefaction analysis showed that the recommendation of JAT as high priority area was partly driven by sampling bias, whereas the other sites were robust to such biases. Indeed, when we rarefied the species richness, Rao's FD and PD, JAT did not have the highest value of functional and phylogenetic diversity (Fig. S2). Conversely, even after rarefying these diversity dimensions, the other three areas still have the highest diversity values.

Related to the accumulation of functional and phylogenetic diversity, we found that our prioritization approach always does significantly better at representing the diversity facets as compared to choosing the sites randomly (Fig. 4). We also found that areas already protected fall within the range of the random selection, which means that those sites do not protect functionally and phylogenetically diverse sites more efficiently than a random draw of sites (Fig. 4).

Discussion

As hotly debated in the last decade (Mason et al. 2005; Tucker et al. 2016), we demonstrated that the use of species richness is not necessarily a good proxy for other biodiversity dimensions. Here, by combining different biodiversity dimensions into a synthetic metric,

Table 2 Conservation priority values for each area in the Brazilian Cerrado

Areas	Synthetic index
Nova Roma	4.11
São Miguel do Araguaia	4.07
RESEX Lago Cedro	4.07
Pontalina	3.41
Jataí	3.19
PE Lajeado	3.00
Alto Paraíso de Goiás	2.52
Pires do Rio	2.35
São João da Aliança	2.15
Caiapônia	2.08
Chapadão do Céu	1.76
Cristalina	1.52
PE Cerrado	1.43
PE Sempre Vivas	1.42
Serranópolis	1.14

Those in italic are already included in the Brazilian protected areas network and in bold are the areas identified as priorities for conservation

RESEX extractive reserve, *PE* state park we were able to select five areas deserving high conservation priority for anurans in the Cerrado biodiversity hotspot. More importantly, four of these areas (Nova Roma—NOV, São Miguel do Araguaia—MIG, Pontalina—PON and Jataí—JAT: Figs. 1 and 2) are not included in the current network of Brazilian protected areas (Ministério do Meio Ambiente 2004), highlighting the under-representation of phylogenetic and functional composition in the current protected area planning. Our results fall in line with other regions and taxonomic groups, such as birds (Devictor et al. 2010), fishes (Strecker et al. 2011), spiders (Gonçalves-Souza et al. 2015) and plants (Pardo et al. 2017), reinforcing the idea that there is a strong mismatch among different biodiversity facets, and that our current conservation planning system focusing on taxonomic units disregards the importance of community properties. This is well illustrated in our Fig. 4, which shows that by considering 4–9 sites for conservation (depending on the facet, Fig. 4a vs. b), we would be doing a significantly better job than a random draw by systematically using a compound index such as the one used here. Conversely, that same analysis also shows that the areas that are currently protected do not do a better job as compared to a random selection, when considering functional and phylogenetic diversity.

The mismatch between taxonomic diversity, which is usually the only facet considered in conservation planning, and the other facets of diversity, can have important consequences in terms of the selection of sites of high priority (Devictor et al. 2010; Gonçalves-Souza et al. 2015). For instance, some areas could have high species richness but low phylogenetic diversity when there is geographic isolation and recent colonization with fast in situ diversification. Similarly, when species are functionally redundant, there is an incongruence between species richness and functional diversity (Gillespie 2004; Weinstein et al. 2014). Furthermore, phylogenetic and functional originality could also affect whether species richness will work properly as a proxy for other diversity dimensions (Swenson et al. 2007). When there is strong trait conservatism, sister groups will show similar traits; conversely, under low conservatism, traits can be more labile within a group of species. It is therefore the combination of evolutionary history as well as ecological mechanisms currently affecting community assembly, which will determine the interplay and relevance of taxonomic, phylogenetic and functional components in a conservation context. Therefore, and as others have done before us (Devictor et al. 2010; Gonçalves-Souza et al. 2015), we also recommend the use of complementary indices in conservation decisions. Our arguments are further reinforced by the recent study by Pollock et al. (2017), in which they demonstrated, at a global scale, that linking multifaceted biodiversity provides large conservation gains for birds and mammals by ensuring a rich array of further effects for the ecosystem functioning and human well-being.

Implications for the Brazilian protected network: the case of the Cerrado hotspot

Limited funding available for nature conservation usually jeopardizes our ability to protect biodiversity over large areas (Bruner et al. 2004). By using different approaches, and different diversity measures, we may avoid overlooking important features in deciding conservation prioritization. However, increasing human, social and academic effort to cover different conservation approaches is a double-edged sword, because it improves information assessment, but it increases conservation costs. The most common approach to identify conservation priority areas is to try to represent the maximum biodiversity while minimizing the total cost or area allocated to protected areas (Margules and Pressey 2000). Our

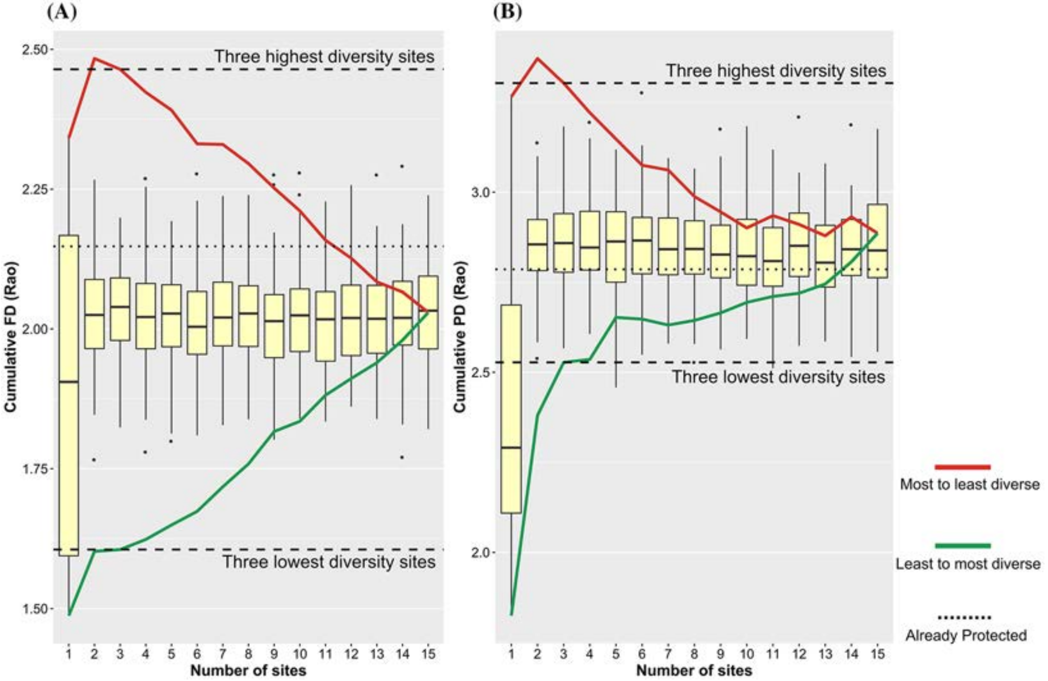

Fig. 4 Diversity accumulation curves for **a** Functional diversity (FD) and **b** Phylogenetic diversity (PD) as calculated with Rao's index. Whisker boxes represent FD or PD for the same number of randomly selected sites. The red line represents the strategy where sites are added in order, from the most diverse to the least diverse. The green line represents the diversity if we added sites in the opposite order (from the least to the most diverse). The dotted line represents diversity in the sites already protected, and the two dashed lines represent cumulative diversity in the three sites containing either the highest or the lowest diversity. Therefore, the green line would represent adding sites in the least efficient possible way, whereas the red line is the most efficient way. Notice that the red line is above the whisker boxes (random expectation) and above the dotted line (already protected) until we have added almost all the sites to the protected area network, meaning that our strategy would, for any given number of protected sites, protect more functional and phylogenetic diversity than either the current protected areas or the least-to-most diversity strategy

approach uses different diversity facets, such as evolutionary history and functional traits, to increase the robustness of the selection of priority areas without significantly increasing conservation costs.

There are good reasons to create new protected areas in the Cerrado hotspot, including the small percent of land currently protected (only 2.85% of the Cerrado hotspot in integral protection conservation units) (Ministério do Meio Ambiente 2017) and the high deforestation rates, which make it one of the most threatened biomes on the South American continent (Silva and Bates 2002; Klink and Machado 2005). Interestingly, the areas JAT and NOV, were already defined as high priority areas for conservation in 2016 by the Brazilian Ministry of the Environment. These areas should be urgently protected because they have high anuran diversity in multiple facets (this study), as well as presence of traditional human communities, high esthetic value given by the caverns in the region, and presence of dry forests (Ministério do Meio Ambiente 2017). The other two areas, MIG and PON, were not included in this government document, and we argue that they should be added. On top of their high multifaceted biodiversity value, these two sites are located in areas under high agriculture and pasture pressure (Ministério do Meio Ambiente 2017), which cause water silting by soil erosion and contamination of water bodies, increasing the threats to anuran species.

Implications for anuran conservation

According to the IUCN red list (IUCN 2017), most of the anuran species present in our study area are not under any type of threat (excepted *Hypsiboas cipoensis*, which is considered “near threatened”). Thus, even if red lists are a useful and effective tool for conservation of vertebrates in general at large scales (Rodrigues et al. 2006), here they would not have added any useful insights regarding the conservation of anuran biodiversity. As Hidasi-Neto et al. (2013) have demonstrated, IUCN red lists are not able to capture on their own the ecological and evolutionary importance of species. This emphasizes the need of adding additional criteria to the IUCN red lists. Here, we argue that those lists should systematically include, both at the site level and at the species level, the value of phylogenetic and functional differences between species in reinforcing ecological processes.

In that context, an important criterion is species originality, which prioritizes species based on unique functional traits or evolutionary history (Pavoine et al. 2005). The pattern we have found suggests that some species contributing disproportionately to the functional or phylogenetic originality pattern of some areas deserve conservation attention, even if some of them are widespread. In the Cerrado hotspot, Microhylidae frogs, *Chiasmocleis albopunctata*, *Dermatonotus muelleri*, and *Elachistocleis cesarii* showed the most distinctive evolutionary history, which goes along the lines of Silvano et al. (2016) who had already characterized this group as evolutionary distinct in the Cerrado. This clade diversified about 70 million years ago during the late Cretaceous and early Tertiary, and has been an important source of diversification ever since (Roelants et al. 2007). Microhylidae frogs are fossorial species, and many of them present explosive breeding. Thus, these frogs only get out of the ground for reproduction, which occurs just once in a year (Wells 1977). These biological and behavioral characteristics allow them to deal with the severe dry season and frequent fires occurring in the Cerrado.

Opposite arguments regarding phylogenetically distinctiveness of groups have been made in the literature. On one hand it has been argued that recently diversified clades represent taxonomic groups that have higher evolutionary potential to adapt quickly to environmental changes, because they already show quick adapted evolutionary history (Erwin 1991; Mace et al. 2003). This would mean little phylogenetic originality at the species level would be compensated by high functional originality within a group and/or high phylogenetic and functional diversity at the community level. On the other hand, it has also been argued that older and more distinct clades carry high evolutionary potential to deal with stressful and stochastic events because of the accumulation of genetic diversification through time (Sgrò et al. 2011; Mouquet et al. 2012). This would mean that we should value phylogenetic originality over other diversity considerations. Despite these contradictions, two facts remain clear throughout both arguments. First, losing a species that represents an old and unique lineage is of conservation concern on itself, since its disappearance will eliminate a branch of evolutionary history that will remain unrepresented. In that context, highlighting the phylogenetic originality of these Microhylidae frogs can help us consider their conservation under a new perspective. And second, whether phylogenetic diversity represents on itself a desirable quality in conservation sites will depend on its relationship to functional properties of the ecosystems.

The four new areas identified here have at least one of these phylogenetic original species in their composition: *D. muelleri* (Microhylidae) and *E. cesarii* (Microhylidae) in NOV, *E. cesarii* in MIG, *D. muelleri* and *E. cesarii* in PON, and *E. cesarii* in JAT. Despite their functional originality, *L. labyrinthicus* and *P. centralis* were the only two functionally original species present in the selected areas, both were found in MIG, and *P. centralis* in JAT. These species exhibit traits that are making them unique in the sampled areas: the type of reproductive mode, the ability of their tadpoles to live in the bottom of ponds, and, in the case of *L. labyrinthicus*, reduced labial tooth rows (de Sousa et al. 2014). Their eggs are embedded in a foam nest, avoiding their desiccation (Zina 2006). The benthonic foraging of their free-living tadpoles and the foam nests of both species allow them to survive even when water volume decreases, a common event in a savanna biome. Although the functional roles of these species have not been thoroughly quantified in these ecosystems, tadpoles in general are crucial for nutrient cycling in water bodies because they affect the abundance and diversity of basal resources and primary consumers (Ranvestel et al. 2004), and abundant species are particularly important in influencing trophic links. Benthic tadpoles facilitate periphyton production by grazing, being key organisms for the food web dynamics and energy flow (Ranvestel et al. 2004). These kinds of traits seem to be associated with idiosyncratic functions that increase ecosystem functioning. Furthermore, as either functionally or phylogenetically original species have a significant contribution to the diversity of these high priority areas, losing these species in still unprotected areas could erode regional biodiversity. We therefore believe that future studies should focus on the role of these functionally unique species in maintaining water ecosystem health in the region.

Conclusions

In November 2016, the Brazilian Ministry of the Environment published a guide to enlarge, implement and consolidate the Brazilian national system of conservation units (SNUC) aiming to include new areas in the conservation system. Here we recommend that in a near future four areas in the Cerrado hotspot should be legally protected by Brazilian laws. More broadly, we strongly argue for the inclusion of phylogenetic and functional considerations in conservation planning. Selecting protected areas based on traditional biodiversity metrics that ignore the uniqueness of each species, such as species richness and endemism, disregards evolutionary and functional considerations that may be key for ecosystem resilience. Taxonomic criteria can be misleading because (i) they usually ignore evolutionary patterns, (ii) they do not ensure community persistence in the long term (Forest et al. 2007; Faith 2008) and, (iii) they do not allow us to make predictions about functional consequence of environmental changes (Díaz et al. 2007; Reiss et al. 2009). Ultimately, we can only guarantee the long-term maintenance of the community if we can protect key ecosystem functions, rather than species or sites selected at random or through rarity criteria, and we have to admit that species that are sometimes abundant or widespread may play key roles in the maintenance of ecosystems functions. One of the key advantages of our approach is that it allows incorporating such criteria, even without a full understanding of species evolutionary and functional roles within the community. One could argue that allocating limited conservation funds to species and sites that are unique on either one of these dimensions is a sensible investment for future resilience of ecosystems.

In addition, it is important to highlight that our study tried to fill the gap existing in anuran conservation regarding water-dependent larval stages. By conserving early developmental stages, we are increasing the probability that anurans reach their adult phase. Adult anurans exhibit an important role in mosquito control, the most common vectors of diseases in tropical systems.

Our study certainly has some potential limitations, such as the fact that we cannot tease apart the contribution of terrestrial, semi-terrestrial, and phytotelma species to ecosystem functioning, or how do species (and lineages) respond to different environmental habitats (e.g. ponds, streams). Thus, we encourage future studies to expand this approach to terrestrial and aquatic habitats. Also, there might be other more efficient ways to combine phylogenetic and functional information into a compound index, or even specific situations under which we might want to consider one or the other facet as more important for prioritization. However, this case study clearly demonstrates that the establishment of conservation strategies for anurans in the Cerrado can be improved by considering multiple biodiversity facets to maximize anuran protection. A major field that remains to be explored for a better assessment of the functional approach is the quantification of ecosystem services that are performed by anurans, including the key links to other trophic levels (e.g., how many mosquitos do they eat and what would happen with certain diseases if anurans disappear).

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References

Balvanera P, Pfisterer AB, Bucmann N et al (2006) Quantifying the evidence for biodiversity effects on ecosystem functioning and services. Ecol Lett 9:1146–1156

Becker CG, Loyola RD (2008) Extinction risk assessments at the population and species level: implications for amphibian conservation. Biodivers Conserv 17:2297–2304. https://doi.org/10.1007/s10531-007-9298-8

Becker CG, Fonseca CR, Haddad CFB et al (2007) Habitat split and the global decline of amphibians. Science 318:1775–1777. https://doi.org/10.1126/science.1149374

Bowatte G, Perera P, Senevirathne G et al (2013) Tadpoles as dengue mosquito (*Aedes aegypti*) egg predators. Biol Control 67:469–474. https://doi.org/10.1016/j.biocontrol.2013.10.005

Bruner AG, Gullison RE, Balmford A (2004) Financial costs and shortfalls of managing and expanding preotected-area systems in developing countries. Bioscience 54:1119–1126. https://doi.org/10.1641/0006-3568(2004)054

Bustamante MR, Ron SR, Coloma LA (2005) Changes in diversity of seven anuran communities in the Ecuadorian Andes. Biotropica 37:180–189. https://doi.org/10.1111/j.1744-7429.2005.00025.x

Cadotte MW (2017) Functional traits explain ecosystem function through opposing mechanisms. Ecol Lett 20:989–996. https://doi.org/10.1111/ele.12796

Cadotte MW, Jonathan Davies T, Regetz J et al (2010) Phylogenetic diversity metrics for ecological communities: integrating species richness, abundance and evolutionary history. Ecol Lett 13:96–105. https://doi.org/10.1111/j.1461-0248.2009.01405.x

Caramaschi U, Sazima I (1984) Uma nova espécie deThoropa da Serra do Cipó, Minas Gerais, Brasil (Amphibia, Leptodactylidae). Rev Bras Zool 2:139–146. https://doi.org/10.1590/S0101-81751983000300004

Chamberlain SA, Hovick SM, Dibble CJ et al (2012) Does phylogeny matter? Assessing the impact of phylogenetic information in ecological meta-analysis. Ecol Lett 15:627–636. https://doi.org/10.1111/j.1461-0248.2012.01776.x

Chen Y, Zhang J, Jiang J et al (2017) Assessing the effectiveness of China's protected areas to conserve current and future amphibian diversity. Divers Distrib 23:146–157. https://doi.org/10.1111/ddi.12508

de Dias BFS (1992) Cerrados: uma caracterização. In: Alternativas de desenvolvimento dos Cerrados: manejo e conservação dos recursos naturais renováveis, pp 11–25

de Sousa VTT, Nomura F, Venesky MD et al (2014) Flexible feeding kinematics of a tropical carnivorous anuran tadpole. J Zool 293:204–2010. https://doi.org/10.1111/jzo.12135

Devictor V, Mouillot D, Meynard C et al (2010) Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: the need for integrative conservation strategies in a changing world. Ecol Lett 13:1030–1040. https://doi.org/10.1111/j.1461-0248.2010.01493.x

Díaz S, Lavorel S, de Bello F et al (2007) Incorporating plant functional diversity effects in ecosystem service assessments. Proc Natl Acad Sci 104:20684–20689. https://doi.org/10.1073/pnas.0704716104

Dirzo R, Young HS, Galetti M et al (2014) Defaunation in the anthropocene. Science 345:401–406. https://doi.org/10.1126/science.1251817

Eiten G (1972) The Cerrado vegetation of Brazil. Bot Rev 38:201–338. https://doi.org/10.1007/BF02859158

Erwin TL (1991) An evolutionary basis for conservation strategies. Science 253:750–752. https://doi.org/10.1126/science.253.5021.750

Eterovick PC, Barros IS (2003) Niche occupancy in south-eastern Brazilian tadpole communities in montane-meadow streams. J Trop Ecol 19:439–448. https://doi.org/10.1017/S026646740300347X

Faith DP (1992) Conservation evaluation and phylogenetic diversity. Biol Conserv 61:1–10. https://doi.org/10.1016/0006-3207(92)91201-3

Faith DP (2008) Threatened species and the potential loss of phylogenetic diversity: conservation scenarios based on estimated extinction probabilities and phylogenetic risk analysis. Conserv Biol 22:1461–1470. https://doi.org/10.1111/j.1523-1739.2008.01068.x

Faivovich J (2002) A cladistic analysis of Scinax (Anura: Hylidae). Cladistics 18:367–393

Faivovich J, Haddad CFB, Garcia PCA et al (2005) Systematic review of the frog family Hylidae, with special reference to Hylinae: phylogenetic analysis and taxonomic revision. Bull Am Museum Nat Hist 294:1–240

Forest F, Grenyer R, Rouget M et al (2007) Preserving the evolutionary potential of floras in biodiversity hotspots. Nature 445:757–760. https://doi.org/10.1038/nature05587

Gillespie R (2004) Community assembly through adaptive radiation in Hawaiian spiders. Science (80-) 303:356–359.

Gonçalves-Souza T, Santos AJ, Romero GQ, Lewinsohn TM (2015) Conservation along a hotspot rim: spiders in Brazilian coastal restingas. Biodivers Conserv 24:1131–1146. https://doi.org/10.1007/s10531-014-0846-8

Gosner KL (1960) A simplified table for staging anuran embryos larvae with notes on identification. Herpetodologists' Leag 16:183–190. https://doi.org/10.2307/3890061

Gotelli NJ, Colwell RK (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecol Lett 4:379–391. https://doi.org/10.1046/j.1461-0248.2001.00230.x

Haddad CFB, Martins M (1994) Four Species of Brazilian Frogs Related to Epipedobates pictus (Dendrobatidae): Taxonomy and Natural History Observations. Herpetologica 50:282–295

Hautier Y, Isbell F, Borer ET et al (2018) Local loss and spatial homogenization of plant diversity reduce ecosystem multifunctionality. Nat Ecol Evol 2:50–56. https://doi.org/10.1038/s41559-017-0395-0

Hidasi-Neto J, Loyola RD, Cianciaruso MV (2013) Conservation actions based on red lists do not capture the functional and phylogenetic diversity of birds in Brazil. PLoS ONE 8:e73431. https://doi.org/10.1371/journal.pone.0073431

Hooper DU, Chapin FS, Ewel JJ et al (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol Monogr 75:3–35

Iknayan KJ, Tingley MW, Furnas BJ, Beissinger SR (2014) Detecting diversity: emerging methods to estimate species diversity. Trends Ecol Evol 29:97–106. https://doi.org/10.1016/j.tree.2013.10.012

Isbell F, Cowles J, Dee LE et al (2018) Quantifying effects of biodiversity on ecosystem functioning across times and places. Ecol Lett 21:763–778. https://doi.org/10.1111/ele.12928

IUCN (2016) The IUCN red list of threatened species. http://www.iucnredlist.org. Accessed 7 Dec 2016

IUCN (2017) The IUCN red list of threatened species. http://www.iucnredlist.org. Accessed 11 Nov 2017

Klink CA, Machado RB (2005) Conservation of the Brazilian Cerrado. Conserv Biol 19:707–713. https://doi.org/10.1111/j.1523-1739.2005.00702.x

Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. Ecology 91:299–305

Lavorel S, McIntyre S, Landsberg J, Forbes TDA (1997) Plant functional classifications: from general groups to specific groups based on response to disturbance. Trends Ecol Evol 12:474–478. https://doi.org/10.1016/S0169-5347(97)01219-6

Legendre P, Legendre L (2012) Numerical Ecology, 3rd edn. Elsevier, Amsterdam

Lips KR, Reeve JD, Witters LR (2003) Population declines in Central America. Conserv Biol 17:1078–1088. https://doi.org/10.1046/j.1523-1739.2003.01623.x

Loreau M, Mouquet N, Gonzalez A (2003) Biodiversity as spatial insurance in heterogeneous landscapes. Proc Natl Acad Sci 100:12765–12770

Loyola RD, Becker CG, Kubota U et al (2008) Hung out to dry: choice of priority ecoregions for conserving threatened neotropical anurans depends on life-history traits. PLoS ONE 3:e2120. https://doi.org/10.1371/journal.pone.0002120

Mace GM, Gittleman JL, Purvis A (2003) Preserving the tree of life. Science 300:1707–1709. https://doi.org/10.1126/science.1085510

Mace GM, Norris K, Fitter AH (2012) Biodiversity and ecosystem services: a multilayered relationship. Trends Ecol Evol 27:19–26. https://doi.org/10.1016/j.tree.2011.08.006

Maire A, Buisson L, Biau S et al (2013) A multi-faceted framework of diversity for prioritizing the conservation of fish assemblages. Ecol Indic 34:450–459. https://doi.org/10.1016/j.ecolind.2013.06.009

Margules CR, Pressey RL (2000) Systematic conservation planning. Nature 405:243–253. https://doi.org/10.1038/35012251

Mason NWH, MacGillivray K, Steel JB, Wilson JB (2003) An index of functional diversity. J Veg Sci 14:571–578

Mason NWH, Mouillot D, Lee WG, Wilson JB (2005) Functional richness, functional evenness and functional divergence: the primary of functional components diversity. Oikos 111:112–118. https://doi.org/10.1111/j.0030-1299.2005.13886.x

Meynard CN, Devictor V, Mouillot D et al (2011) Beyond taxonomic diversity patterns: How do α, β and γ components of bird functional and phylogenetic diversity respond to environmental gradients across France? Glob Ecol Biogeogr 20:893–903. https://doi.org/10.1111/j.1466-8238.2010.00647.x

Ministério do Meio Ambiente (2004) Portaria 126

Ministério do Meio Ambiente (2017) Biomas. http://www.mma.gov.br/biomas. Accessed 15 Dec 2017

Mokany A (2007) Impact of tadpoles and mosquito larvae on ephemeral pond structure and processes. Mar Freshw Res 58:436–444

Mouquet N, Devictor V, Meynard CN et al (2012) Ecophylogenetics: advances and perspectives. Biol Rev Camb Philos Soc 87:769–785. https://doi.org/10.1111/j.1469-185X.2012.00224.x

Myers N, Mittermeier RA, Mittermeier CG et al (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858. https://doi.org/10.1038/35002501

Pardo I, Roquet C, Lavergne S et al (2017) Spatial congruence between taxonomic, phylogenetic and functional hotspots: true pattern or methodological artefact? Divers Distrib 23:209–220. https://doi.org/10.1111/ddi.12511

Pavoine S, Ollier S, Dufour A-B (2005) Is the originality of a species measurable? Ecol Lett 8:579–586. https://doi.org/10.1111/j.1461-0248.2005.00752.x

Peel MC, Finlayson BL, Mcmahon TA (2007) Updated world map of the Köppen-Geiger climate classification. Hydrol Earth Syst Sci 11:1633–1644

Pollock LJ, Thuiller W, Jetz W (2017) Large conservation gains possible for global biodiversity facets. Nature 546:141–144. https://doi.org/10.1038/nature22368

Pressey RL, Cabeza M, Watts ME et al (2007) Conservation planning in a changing world. Trends Ecol Evol 22:583–591. https://doi.org/10.1016/j.tree.2007.10.001

Pyron RA (2014) Biogeographic analysis reveals ancient continental vicariance and recent oceanic dispersal in amphibians. Syst Biol 63:779–797. https://doi.org/10.1093/sysbio/syu042

Raghavendra K, Sharma P, Dash AP (2008) Biological control of mosquito populations through frogs: opportunities & constrains. Indian J Med Res 128:22–25

Rangel TFLVB, Diniz-Filho JAF, Bini LM (2006) Towards an integrated computational tool for spatial analysis in macroecology and biogeography. Glob Ecol Biogeogr 15:321–327. https://doi.org/10.1111/j.1466-822X.2006.00237.x

Rangel TF, Diniz-Filho JAF, Bini LM (2010) SAM: a comprehensive application for spatial analysis in macroecology. Ecography (Cop) 33:46–50. https://doi.org/10.1111/j.1600-0587.2009.06299.x

Ranvestel AW, Lips KR, Pringle CM et al (2004) Neotropical tadpoles influence stream benthos: evidence for the ecological consequences of decline in amphibian populations. Freshw Biol 49:274–285. https://doi.org/10.1111/j.1365-2427.2004.01184.x

Rao CR (1982) Diversity and dissimilarity coefficients: a unified approach. Theor Popul Biol 21:24–43

Redding DW, Mooers AØ (2006) Incorporating evolutionary measures into conservation prioritization. Conserv Biol 20:1670–1678. https://doi.org/10.1111/j.1523-1739.2006.00555.x

Reiss J, Bridle JR, Montoya JM, Woodward G (2009) Emerging horizons in biodiversity and ecosystem functioning research. Trends Ecol Evol 24:505–514. https://doi.org/10.1016/j.tree.2009.03.018

Ricotta C, Bacaro G, Marignani M et al (2012) Computing diversity from dated phylogenies and taxonomic hierarchies: does it make a difference to the conclusions? Oecologia 170:501–506. https://doi.org/10.1007/s00442-012-2318-8

Rodrigues ASL, Pilgrim JD, Lamoreux JF et al (2006) The value of the IUCN Red List for conservation. Trends Ecol Evol 21:71–76. https://doi.org/10.1016/j.tree.2005.10.010

Roelants K, Gower DJ, Wilkinson M et al (2007) Global patterns of diversification in the history of modern amphibians. Proc Natl Acad Sci 104:887–892

Sgrò CM, Lowe AJ, Hoffmann AA (2011) Building evolutionary resilience for conserving biodiversity under climate change. Evol Appl 4:326–337. https://doi.org/10.1111/j.1752-4571.2010.00157.x

Silva JMC, Bates JM (2002) Biogeographic patterns and conservation in the South American Cerrado: a tropical savanna hotspot. Bioscience 52:225–233. https://doi.org/10.1641/0006-3568(2002)052[0225:BPACIT]2.0.CO;2

Silva JF, Farinas MR, Felfili JM, Klink CA (2006) Spatial heterogeneity, land use and conservation in the Cerrado region of Brazil. J Biogeogr 33:536–548. https://doi.org/10.1111/j.1365-2699.2005.01422.x

Silvano DL, Valdujo PH, Colli GR (2016) Priorities for conservation of the evolutionary history of amphibian in the Cerrado. In: Pellens R, Grandcolas P (eds) Biodiversity conservation and phylogenetic systematics. Springer International Publishing, Berlin, pp 287–304

Skelly DK, Richardson JL (2010) Larval sampling. In: Kenneth Dodd (Ed) Amphibian ecology and conservation: a handbook of techniques. Oxford University Press, Oxford, pp 55–70

Srivastava DS, Bell T (2009) Reducing horizontal and vertical diversity in a foodweb triggers extinctions and impacts functions. Ecol Lett 12:1016–1028. https://doi.org/10.1111/j.1461-0248.2009.01357.x

Strassburg BBN, Brooks T, Feltran-Barbieri R et al (2017) Moment of truth for the Cerrado. Nature 1:1–3. https://doi.org/10.1038/s41559-017-0099

Strecker ALS, Olden JD, Whittier JB, Paukert CP (2011) Defining conservation priorities for freshwater fishes according to taxonomic, functional, and phylogenetic diversity. Ecol Appl 21:3002–3013

Swenson NG, Enquist BJ, Thompson J, Zimmerman JK (2007) The influence of spatial and size scale on phylogenetic relatednesss in tropical forest communities. Ecology 88:1770–1780. https://doi.org/10.1890/06-1499.1

Toledo LF, Guimarães LDA, Lima LP et al (2004) Notes on courtship, egg-laying site, and defensive behavior of Epipedobates flavopictus (Anura, Dendrobatidae) from two mountain ranges of central and southeastern Brazil. Phyllomedusa 3:145–147

Trindade-Filho J, Landa Sobral F, Cianciaruso MV, Loyola RD (2012) Using indicator groups to represent bird phylogenetic and functional diversity. Biol Conserv 146:155–162. https://doi.org/10.1016/j.biocon.2011.12.004

Tucker CM, Cadotte MW, Carvalho SB et al (2016) A guide to phylogenetic metrics for conservation, community ecology and macroecology. Biol Rev 92:698–715. https://doi.org/10.1111/brv.12252

Vellend M, Cornwell WK, Magnuson-Ford K, Mooers AØ (2011) Measuring phylogenetic biodiversity. In: Magurran AE, Mcgill BJ (eds) Biological diversity. Columbia University Press, New York

Venail P, Gross K, Oakley TH et al (2015) Species richness, but not phylogenetic diversity, influences community biomass production and temporal stability in a re-examination of 16 grassland biodiversity studies. Funct Ecol 29:615–626. https://doi.org/10.1111/1365-2435.12432

Villéger S, Mason H, Mouillot D (2008) New multidimensional functional diversity indices for a multifaceted framework. Ecology 89:2290–2301

Volkmann L, Martyn I, Moulton V et al (2014) Prioritizing populations for conservation using phylogenetic networks. PLoS ONE. https://doi.org/10.1371/journal.pone.0088945

Webb CO, Ackerly DD, McPeek MA, Donoghue MJ (2002) Phylogenies and community ecology. Annu Rev Ecol Syst 33:475–505. https://doi.org/10.1146/annurev.ecolsys.33.010802.150448

Webb CO, Ackerly DD, Kembel SW (2008) Phylocom: software for the analysis of phylogenetic community structure and trait evolution. Bioinformatics 24:2098–2100. https://doi.org/10.1093/bioinformatics/btn358

Weinstein BG, Tinoco B, Parra JL et al (2014) Taxonomic, phylogenetic, and trait beta diversity in South American hummingbirds. Am Nat 184:211–224. https://doi.org/10.1086/676991

Wells KD (1977) The social behaviour of anuran amphibians. Anim Behav 25:666–693. https://doi.org/10.1016/0003-3472(77)90118-X

Winter M, Devictor V, Schweiger O (2013) Phylogenetic diversity and nature conservation: where are we? Trends Ecol Evol 28:199–204. https://doi.org/10.1016/j.tree.2012.10.015

Zina J (2006) Communal nests in Physalaemus pustulosus (Amphibia: Leptodactylidae): experimental evidence for female oviposition preferences and protection against desiccation. Amphibia-Reptilia 27:148–150. https://doi.org/10.1163/156853806776052092

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RESEARCH ARTICLE

On the relative importance of space and environment in farmland bird community assembly

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Abstract

The relative contribution of ecological processes in shaping metacommunity dynamics in heavily managed landscapes is still unclear. Here we used two complementary approaches to disentangle the role of environment and spatial effect in farmland bird community assembly in an intensive agro-ecosystem. We hypothesized that the interaction between habitat patches and dispersal should play a major role in such unstable and unpredictable environments. First, we used a metacommunity patterns analysis to characterize species co-occurrences and identify the main drivers of community assembly; secondly, variation partitioning was used to disentangle environmental and geographical factors (such as dispersal limitation) on community structure and composition. We used high spatial resolution data on bird community structure and composition distributed among 260 plots in an agricultural landscape. Species were partitioned into functional classes, and point count stations were classified according to landscape characteristics before applying metacommunity and partitioning analyses within each. Overall we could explain around 20% of the variance in species composition in our system, revealing that stochasticity remains very important at this scale. However, this proportion varies depending on the scale of analysis, and reveals potentially important contributions of environmental filtering and dispersal. These conclusions are further reinforced when the analysis was deconstructed by bird functional classes or by landscape habitat classes, underlining trait-related filters, thus reinforcing the idea that wooded areas in these agroecosystems may represent important sources for a specific group of bird species. Our analysis shows that deconstructing the species assemblages into separate functional groups and types of landscapes, along with a combination of analysis strategies, can help in understanding the mechanisms driving community assembly.

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Introduction

Understanding the mechanisms involved in community assembly is a major challenge for ecologists. Meta-community theory suggests that the composition of a community results from four kinds of mechanisms: biotic interactions, environmental filtering, dispersal and demographic stochasticity [1–3]. Since ecological parameters (e.g., demography or dispersal) are often extremely difficult to estimate, indirect methods consisting of analyzing spatial patterns of species distributions have often been used to disentangle these mechanisms in the field [4]. However, interpreting the results of these analyses is still challenging because several mechanisms can lead to the same spatial distribution patterns [5]. For instance, some biotic interactions (such as facilitation) may lead to aggregation of individuals, resulting in a positive spatial autocorrelation; on the contrary, competition may lead to overdispersion between closely related species, which would exclude each other in close proximity [6]. Other mechanisms that can generate spatial autocorrelation include population dynamics (reproduction and mortality), local dispersal [7], and environmental filtering [8]. When environmental variables are themselves spatially structured, and species with similar functional traits are likely to be found in similar habitats, disentangling the share of exogenous autocorrelation (spatial auto-correlation due to the spatial distribution of habitats) and endogenous autocorrelation (due to population dynamic and dispersal) is often difficult [7]. Even so, recent studies have suggested that models including spatial autocorrelation due to dispersal, as well as stochastic events of colonization and extinction, can better represent metacommunity structure and species distribution ranges as compared to models based on environmental variation only [9,10]. Hence, the study of the spatial structure of community composition is useful in disentangling community drivers, but it is not sufficient to distinguish between mechanisms driving community assembly.

Adding to this difficulty, there is an increasing recognition that all these processes (dispersal, demography, biological interactions and environmental filtering) seem to be complementary rather than exclusive [11,12], and their relative contribution varies between communities and ecosystems, and across spatial scales [13,14]. For example, environmental filtering may generally account for species distributions at large scales, but this effect varies strongly between taxa and ecosystems [14]. In addition, spatial or temporal environmental heterogeneity [9,15], as well as dispersal under certain conditions, may allow species coexistence despite environmental filtering [10]. These findings point to the need to consider the particularities of scales and taxa when trying to understand community assembly.

One complementary solution to link empirical observations to mechanisms in community ecology has involved the incorporation of functional traits, which can help to distinguish different types of mechanisms related to competition and environmental filtering among others [9,15]. Indeed, since ecological communities can host a large number of species with different life history traits, partitioning coexistence using global statistical partitioning might lead to results that are difficult to interpret. An appealing solution is to divide communities into smaller clusters of ecologically similar species, using a deconstruction approach [16–18]. The deconstruction approach is meant to identify key groups of species that respond similarly to major variables, and therefore allow a better understanding of the variability observed when all species are considered together. This would ensure that the observed spatial patterns are the result of similar species responding to similar drivers, as opposed to different species having opposing responses that will blur the global patterns and impede the finding of clear explanations. While studies that combine different community assembly mechanisms are becoming more common, (e.g., [19,20]), very few have tried to disentangle the relative contribution of these processes depending on habitat characteristics or species ecology, and most have been conducted in aquatic ecosystems, while studies on terrestrial ecosystems focus mainly on plants [14]. Largely missing from this literature is the study of animal communities in terrestrial ecosystems, especially in human-dominated or managed ones [14].

Here we applied a methodology to disentangle community assembly processes including a clustering by habitat and species groups. This study focuses on highly disturbed ecosystems that are managed for resource production (farmland landscapes), in which species may further depend on local source-sink dynamics to subsist in an environment that is highly variable and constantly perturbed (e.g., seasonality of farming practices, crop rotation). Our case study is a fairly rich farmland bird metacommunity of 40 species, in a cereal agro-ecosystem in the west of France. This biological system is characterized by a high functional diversity of species coexisting in highly heterogeneous and changing habitats. Intensive sampling during 5 years allowed fine scale analysis of species distributions. Contrary to the majority of studies that analyzed species distribution patterns at broad scales [21–23], we used a scale of analysis that matches the size of the breeding territory of most farmland bird species [24–26], as well as complementary methods allowing testing different processes simultaneously.

Our methodology involves a functional and landscape deconstruction strategy, along with spatial and partial regression analyses, to understand the relative contributions of environmental filtering, dispersal and neutral processes (demographic stochasticity). We used three complementary approaches. First, metacommunity patterns sensu Presley et al. [5,27] were analyzed to characterize the global patterns of co-occurrence and identify the most important environmental gradients and coherent groups of species. This approach allows distinguishing patterns resulting from species sorting, biotic interactions (competition) and random assembly processes [19]. Second, a variation partitioning approach was used to disentangle the relative contributions of environment (exogenous autocorrelation) and neutral processes (endogenous autocorrelation) in community composition, see [19]. Third, the two approaches were combined with a deconstruction approach (by species group and landscape type) to see if different groups of species or landscapes presented a different influence of community assembly drivers. Finally, as these processes can be highly scale-dependent, analyses were conducted at various spatial grains.

Materials and methods

Study area

The study site was the Zone Atelier Plaine & Val de Sèvre, an area of 429 km^2 which is part of the French Long Term Ecological Research network, see [28], located in central western France, in the Poitou-Charentes Region (France; 46.23˚N, 0.41˚W, Fig 1). It is an intensive farming system, where cereal crops are dominant (e.g., on average during the 5-year period included in this study, 36.8% of the surface was occupied by winter cereals, with 33.3% represented by wheat and 3.1% by barley). Other main crops include rapeseed (8.7%), maize (8.6%), sunflower (10.7%), grassland (7.8%) and alfalfa (3.9%). The mean field size (11,000 fields) was 3.7 ha.

Point counts

Breeding birds were surveyed on a total of 260 locations (approximately one per square kilometer) using point counts spread over the whole study area (Fig 1). For each point count, we recorded all birds seen or heard during 5 minutes in a 200 meter radius. All individuals were located on a map by the observer to avoid double counting. The same point counts were surveyed twice during the breeding season (mean range date 22/04-16/05 for session 1 and 24/05–28/06 for session 2), and every year from 2009 to 2013. These survey dates allow to take

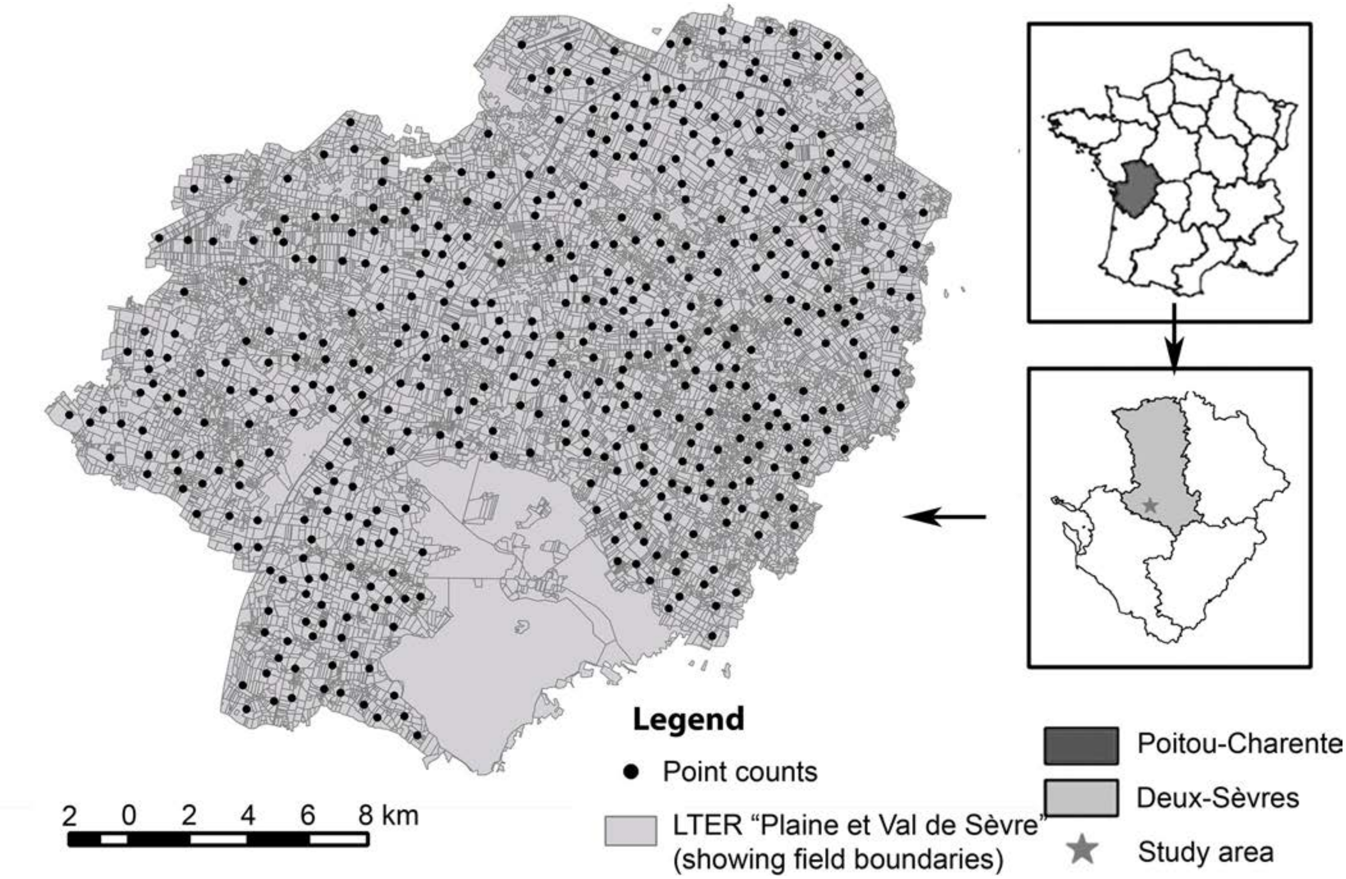

Fig 1. Location of the LTER Plaine et Val de Sèvre (study area) and positions of the 260 point count stations. These stations are distributed fairly evenly over the whole study area.

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into account both early and late migrants. Five minute point counts are appropriate to have a good estimate of the community composition [29,30], allowing to cover more points while limiting the risk of double counts. In total, 95 bird species were recorded. However, here we only considered species breeding locally, which are more likely to be affected by local environmental conditions. After eliminating rare species (representing less than 1% of the total counts), non-breeding species (migrants), raptors (which have large territories) and gregarious feeding species that breed in towns and villages but feed in farmland landscapes (e.g., common swift *Apus apus*; see S1Appendix. for detailed species selection), 40 species were left for the rest of the analysis.

Landscape characterization

The land use of the study area was surveyed twice a year from 2009 to 2013 corresponding to the periods for early harvesting and late sowing of crops. All data were geo-referenced and mapped into a GIS geodatabase. Spatial data were processed using Quantum GIS version 1.7.3 (Development Team 2002–2010). We identified 37 land use types based on the field survey (33 agricultural, 3 urban and 1 forest). These land uses were regrouped into 11 categories: alfalfa, grassland, ryegrass, sunflower, spring crops of pea-flax-field beans, rapeseed, cereals, maize, other crops (e.g. mustard, sorghum, millet and tobacco, representing less than 2% of crops), urban, and forest. This clustering was based on expert opinion to allow simplifying the analysis and obtaining a more functional classification according to species preferences. Two linear components (roads and hedgerows) were added to these categories, as we suspected that these played an important role structuring bird communities in an agricultural landscape. For each point count station, we recorded the area occupied by each land use category as well as the length of hedgerows and roads or paths within a buffer area around it. A previous study [31] found that the best scale for assessing the environmental effect on farmland birds at this study site, during the breeding season, was an average of 300 meters. However, this scale varied slightly between species; we therefore choose to assess the effect of environmental variables at various radii ranging from 200m to 1400m in 200m intervals (resulting in 7 grains of analysis).

Statistical analyses

Step 1: Farmland bird metacommunity patterns. The distribution patterns of species within the metacommunity were first analyzed using the methods described by Leibold and Mikkelson and Presley et al. [5,27]. This method characterizes metacommunities using a site-by-species matrix, to identify particular idealized metacommunity patterns that can be related to the underlying assembly mechanisms (biotic interactions, environment or random assembly). Note, however, that this method cannot assess the potential role of dispersal, which is central to metacommunity dynamics [19].

First, we ordered the site-by-species matrix according to the first or second axes obtained after a correspondence analysis (using a reciprocal averaging algorithm). This analysis maximizes the proximity of sites with similar species composition and the proximity of species sharing the same sites. The reordered matrix thus maximizes the coherence of the species distribution prior to assessing the deviation from a null model [5]. Then, the ordered matrix was used to calculate three indices to characterize the metacommunity structure: coherence, species range turnover, and boundary clumping (Fig 2), (see [5] for a full description of the method to compute these indices). First, coherence indicates whether the various species are non-randomly distributed along a particular gradient (positive coherence), are mutually excluded owing, for example, to interspecific competition (negative coherence, with a characteristic checkerboard pattern) or are randomly assembled (coherence close to zero, i.e., non-significant). When coherence is positive, two further indices need to be calculated. The second index corresponds to the spatial species turnover, which measures the number of times one species replaces another one between two sites. The number of replacements is calculated for each pair of sites and each pair of species. A negative turnover, characterized by less replacement than expected to occur by chance, suggests a nested structure. If the turnover is positive, a third index is calculated: the boundary clumping. This indicates the aggregation of the distribution ranges between species. When positive, the pattern is Clementsian, i.e., different groups of species share the same ecological boundaries (indicating species that have the same environmental tolerances). When not significant, the pattern is Gleasonian, i.e., each species has its own ecological boundaries so the species differ in their environmental tolerances. A negative value indicates an evenly spaced distribution, showing that there are significant differences in environmental tolerances between species. These three indices (coherence, spatial species turnover and boundary clumping) were then compared against the values expected for purely random variations to assess their significance (see details of the null model below).

All the analyses were calculated using the Matlab "metacommunity" function developed by Presley et al. [5] (available from http://faculty.tarleton.edu/higgins/metacommunity-structure.html). The function can be used to test several null models. Here we used a null model where the species richness per site was fixed (equal to the observed richness), but the probability that a particular species occurred at that site varied according to the occurrence of that species (i.e.,

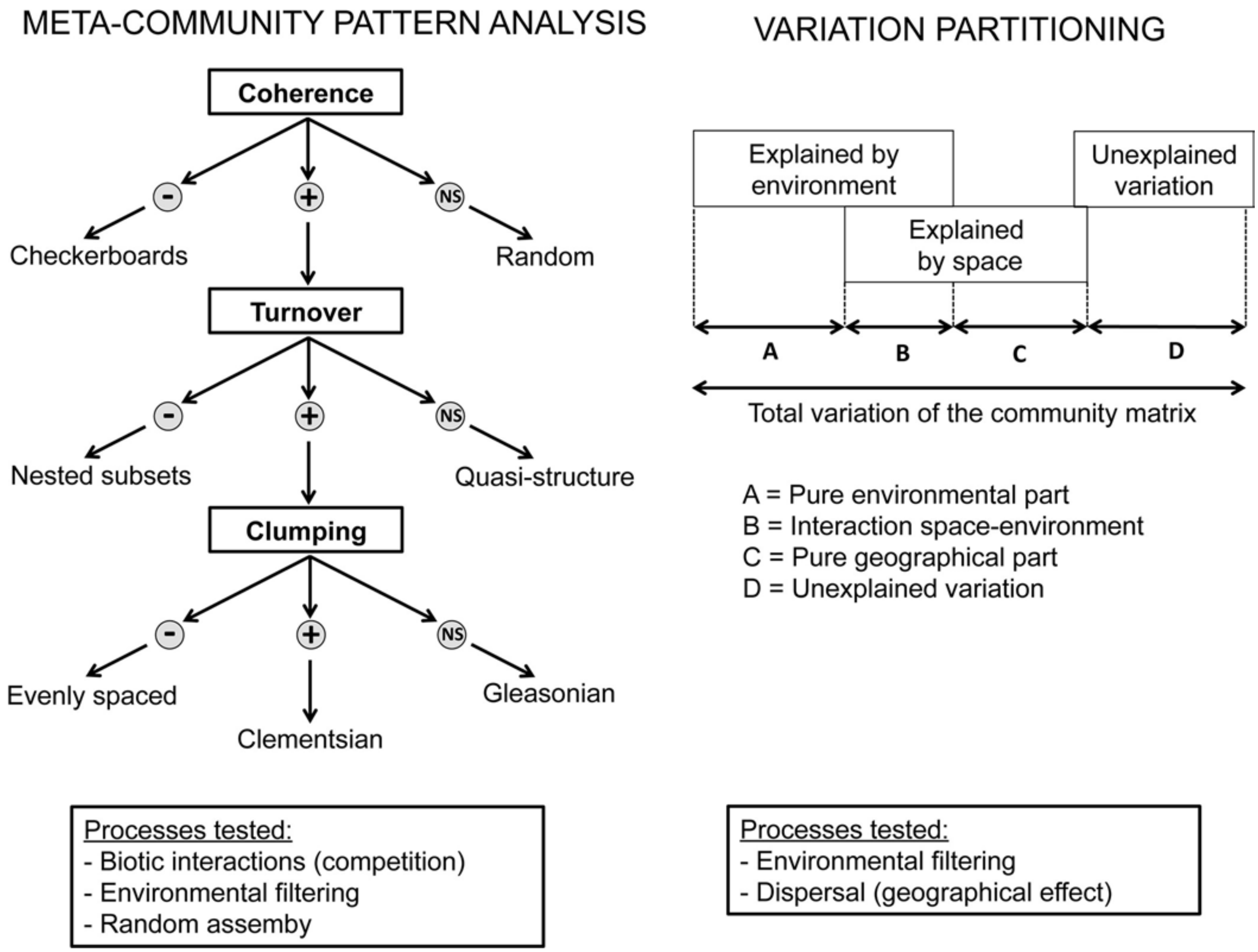

Fig 2. Description of methodology. Principles and comparison of the two methods: metacommunity pattern analysis characterizes the patterns generated by environmental factors, biotic interactions or random processes whereas variation partitioning can distinguish the effect of environment factors and dispersal on the community assembly.

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the most common species having a higher probability of occurrence). This model assumes that sites differ in suitability, and takes into account the commonness of each species (proportional occurrence). We performed 200 iterations (default parameter), see [32,33] for details.

For this first analysis, the data from each point count station (10 counts at each station) were pooled. The mean abundance of each species at each point count station was used as a proxy for their local abundance. Because land use varied between years, both the mean and the coefficient of variation of % composition for each environmental variable over the five year study period were analyzed in order to account for both the mean composition and the temporal variability of the landscape. Although the ordination is based only on species occurrences, the axes of the correspondence analysis are assumed to be related to a latent environmental gradient [34]. The correspondence with a real environmental gradient can be verified subsequently, by checking the correlation with measured environmental variables. Therefore we calculated the Pearson correlation between the first two axes of the reciprocal averaging and the various environmental variables (mean and coefficient of variation between the 5 years), measured at each site (i.e., the environmental gradient) and at each spatial scale (S4 Appendix) as well as the correlation with the species richness gradient (gradient of species richness between the different local communities).

Step 2: Variation partitioning. Variation partitioning [35,36] was used to decompose the total variation of community composition into the parts explained purely by environmental, spatial or temporal predictors as well as their interaction (Fig 2). This method allowed assessing the pure spatial structure that was not explained by environmental variables, the latter being attributed to spatial activities of individuals, such as dispersal [7,13,37]. Variation partitioning was based on multiple partial redundancy analyses (RDA), including environmental, geographical or temporal variables only or in combination. The fractions of the partitioning are then obtained by simple subtraction [37].

RDA is a constrained ordination method that can be used to analyze the community composition matrix with respect to explanatory matrices. It can be seen as an extension of multiple linear regressions for multivariate data. Abundance data were, first, Hellinger transformed. This transformation is recommended to reduce the asymmetry of community data containing many zeros prior to an ordination method such as RDA [35,38]. Geographical axes were obtained by Trend Surface Analysis (TSA) using a third degree polynomial of the geographic coordinates of the point counts (x and y coordinates), and nine different spatial functions were tested (x^3, y^3, xy^2, yx^2, x^2, y^2, xy, x, y; see [39]). This made it possible to model the spatial structure at different spatial scales by testing both linear and non-linear functions, but without considering excessively complex variations. Indeed, if too many functions are tested, there is a risk of interpreting random variations as a spatial effect, artificially increasing the spatial contribution; see [40]. In a preliminary analysis, we also compared this method with Principal Coordinates of Neighbour Matrices (PCNM), which revealed very similar qualitative results (S5 Appendix).

Both year and session were included as temporal predictors. Environmental and spatial variables were selected independently for each scale using a forward selection procedure to reduce the number of variables while keeping the variation explained by these variables to a maximum. This analysis used the "forward.sel" function of "packfor" R package (R.3.1.0, 2014) (available from R-forge: http://r-forge.r-project.org/R/?group_id=195), and the "varpart" function of the "vegan" package for the variation partitioning. This analysis was carried out for each environmental scale from 200 to 1400, in 200m intervals.

Step 3: Breaking down diversity patterns into landscape and species classes. In the above stages, the dataset was analyzed as if it were homogeneous. However, there were considerable differences in both landscapes and bird communities in the study area. For instance, landscapes ranged from highly intensive open fields without any trees, to mosaics of plots delimited by hedges. In the same way, the data set includes many species representing a wide panel of habitat preferences. To refine our findings, we explored whether results remained valid with habitat and species classes based upon major shared attributes. Environmental and spatial variables were selected independently for each habitat or species group and each spatial scales.

Species classes were based on co-occurrence patterns in the data set. To build the classes, the "dudi.coa" function of the "ade4" package (R.3.1.0, 2014) was used to perform a correspondence analysis (as described above). The species distribution (mean and standard deviation) was then ordinated along the first axis of the correspondence analysis which explained most of the variation (17.65%, see S1 Appendix), using the function "sco.distri" package (ade4, see S2 Appendix). The ordination values for the species along the first ordination axis were then transformed to Euclidean distances, and a dendrogram (hierarchical clustering) was built using these distances ("hclust" function, "stats" package, R.3.1.0, 2014; S2 Appendix). The dendrogram was used on the 40 bird species to define the three *a posteriori* classes. This partitioning aims to refine the analysis by controlling the main structuring gradient. This ordination axis could be interpreted as corresponding to a tree cover gradient, as we observed strong correlation with a wooded gradient (see result), so the first class was qualified as "open-land species" (7 species, N = 2327 observations), the second as "intermediate" (17 species, N = 1919 observations) and the third as "woodland species" (17 species, N = 1438 observations).

Due to the strong observed effect of the tree gradient on bird distributions, and because hedgerows are well known to shape bird communities in open landscapes, e.g. [41–43], the analyses were also refined by repeating each analysis for three classes of landscapes separately. The three classes of landscapes were defined from the density of tree cover. Hedgerows were assumed to have a similar effect to small patches of trees for farmland birds, so the two variables were combined (the linear shapefile of hedgerows was converted to polygon by allocating a width of 100m along all hedgerows). This was chosen based on tree avoidance distance for open-land species such as skylark *Alauda arvensis* [31], and to give more weight to linear components when pulling with surface areas. Finally, the area of tree cover (hedgerows and forest) around each point count station was calculated in a 200 m buffer zone around point counts. The three classes corresponded approximately to 0–35% (open landscapes, N = 756 observations), 35–70% (intermediate landscapes, N = 766 observations), 70–100% (wooded landscapes, N = 1068 observations) of tree cover, and had similar sample sizes (i.e. 76, 77 and 107 sites, respectively). Wooded landscapes comprised small fields, with a high proportion of perennial crops and a large number of hedges and forest fragments.

Results

Structuring processes at the metacommunity level

Our farmland bird community showed a clear Clementsian pattern along the first two axes of the reciprocal averaging (S3 Appendix): all species were distributed along the same environmental gradient (positive coherence), with a species replacement along this gradient (positive turnover), and apparent clusters of species sharing the same habitat preferences (positive boundary clumping). The environmental gradient structuring the reciprocal averaging axis corresponded to area of tree cover (Pearson correlation with the hedgerow/forest gradient, $r = 0.87$, $p<0.0001$, with hedgerow only $r = 0.74$, $p<0.0001$ and with forest only $r = 0.32$, $p<0.0001$), see S2 Appendix and S4 Appendix. Species richness at each point count station was also highly correlated ($r = 0.83$, $p<0.0001$) with this environmental gradient, indicating that more species were found in wooded landscapes (S2 Appendix). Bird communities also showed a Clementsian pattern along the second axis of the reciprocal averaging, which was correlated with urban land use ($r = 0.49$, $p<0.0001$) see S3 Appendix and S4 Appendix.

Variation partitioning made it possible to assess the relative importance of spatial, temporal and environmental factors in explaining bird community assembly (Fig 3). The total explained variation reached 17.4% (at 200 m), but decreased to 8.3% with increasing spatial grain (black curve, Fig 3). The relative contribution of each environmental variable was assessed using their F-ratio and represented as barplots below the curve. The environmental contribution was mainly explained by the presence of hedgerows (dark green bars in Fig 3A): hedgerows and forests represented 80% of the variation explained by environment at a 200m scale, and 63.3% at the 1400 m scale (Fig 3). In proportion of the total explained variation, the pure environmental (green curve), pure temporal (red curve) and pure geographical (blue curve) respectively represented 74.8%, 10.3% and 7.4% (Fig 3B). Therefore, most of the explained variation was accounted for by environmental variables.

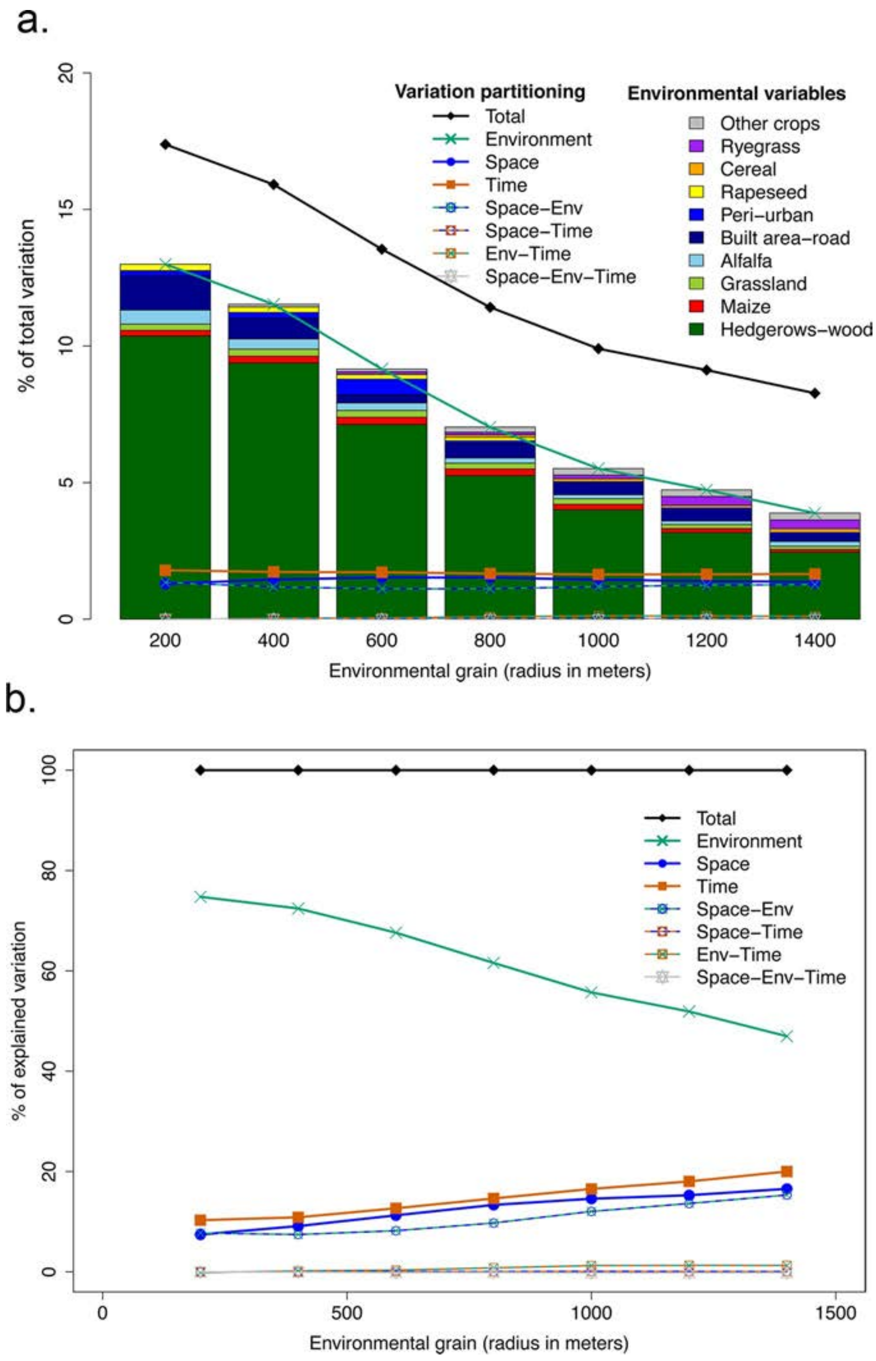

Fig 3. Global variation partitioning analysis (all species classes and all landscape classes). a. In percentage of the total variation b. In percentage of the explained variation. The variation explained by each variable (geographical = blue curve, environmental = green, temporal = red curve), and interaction are represented with respect to the total explained variation (black curve), at each environmental grain (x-axis). The barplot represents the relative effect of each environmental predictors based on the F-ratio.

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Spatial versus habitat effects using species class deconstruction

Species were grouped according to their habitat use based on the initial ordination axis (all species confounded), and therefore there was no a priori hypothesis on species traits or life history. However, a posteriori check reveals that these groups are ecologically relevant: the ordination axis was highly correlated with a tree cover gradient, so we defined these group as "open-land species", "intermediate" and "woodland species". Species within each group shared a combination of specific traits, see S7 Appendix. The open-land group is composed of ground nesting and migratory birds, with large body size for half of them, and all insectivorous species (adults or chicks, or both). By opposition group 3 ("woodland") contains species with smaller body size, mostly nesting on trees or cavities, and mostly sedentary. As expected, when the bird community was split into these three classes, the Clementsian pattern disappeared, with each class showing a random structure along the first axis (S3 Appendix), though a Clementsian structure was still observed along the second axis for intermediate and woodland species.

When partitioning per species, the models now only explain between 6% (wooded landscapes) and 9.5% (open landscapes) of the variance at 200m. The explanatory power then decreases when increasing grain size. While the environmental part still composes most of the explained variation for open-land species, the role of environment decreases from open-land to woodland species (S6 Appendix. and Fig 4B), explaining 5.5% of the variation for open-land species to only 2.6% for woodland species. Open land species respond more strongly to crop composition (especially grassland/alfalfa and rapeseed) than intermediate or woodland species, especially at smaller spatial grains (Fig 4B). Temporal variation appears constant across grain size and for each species group, while being proportionally more important for intermediate and woodland species, but remain overall quite low (around 2%). But if the deconstruction approach allows highlighting new structuring factors not visible in the global analysis (eg. crop composition for open-land species), our results globally show that when clustering by relevant species group, most of the variation seems now unexplained (result confirmed by both the meta-community pattern analysis and variation partitioning).

Spatial versus habitat effects using landscape deconstruction

When the same analyses were carried out separately for each class of landscape, the community structure still showed Clementsian patterns (see S3 Appendix) for open and wooded landscapes along the first axis, but was random for intermediate landscapes.

With this deconstruction, our models only allowed explaining from 6.5% (Intermediate landscapes at 1200m) to 12.2% (wooded landscape at 200m) of the variation, the spatial part representing around 2% of the total variation. Relative importance of environmental and geographical factors in explaining the variation in bird community also depended on landscape class (Fig 4A and S6 Appendix): in open landscapes (dominated by annual crops), the geographical component represented in average 2.3% of the total variation (so 30% of the explained variation) against 1.9% for the environment (24% of the explained variation), so the spatial component globally exceeded the environmental contribution except at the smallest spatial scale. In contrast, in wooded landscapes, the environmental factors were dominant for all spatial grains. In intermediate landscapes (mosaic of annual crops and hedgerows), the geographical factor was as important as environment only at large spatial grains.

The temporal factor remains relatively quite high in all landscapes, in comparison to other factors, but tends to slightly increase in absolute value from open landscapes to wooded landscapes. The deconstruction per landscape appears globally efficient to remove the dominant effect of wooded components, although this effect does not totally disappear, especially in the most wooded landscapes (wooded components still accounting for 45.9% of the variation explained by environmental variables at 200 m in wooded landscapes), see Fig 4A. Landscape deconstruction, therefore, revealed the effect of additional environmental factors that did not appear in the global metacommunity analysis, such as the importance of alfalfa/grassland and

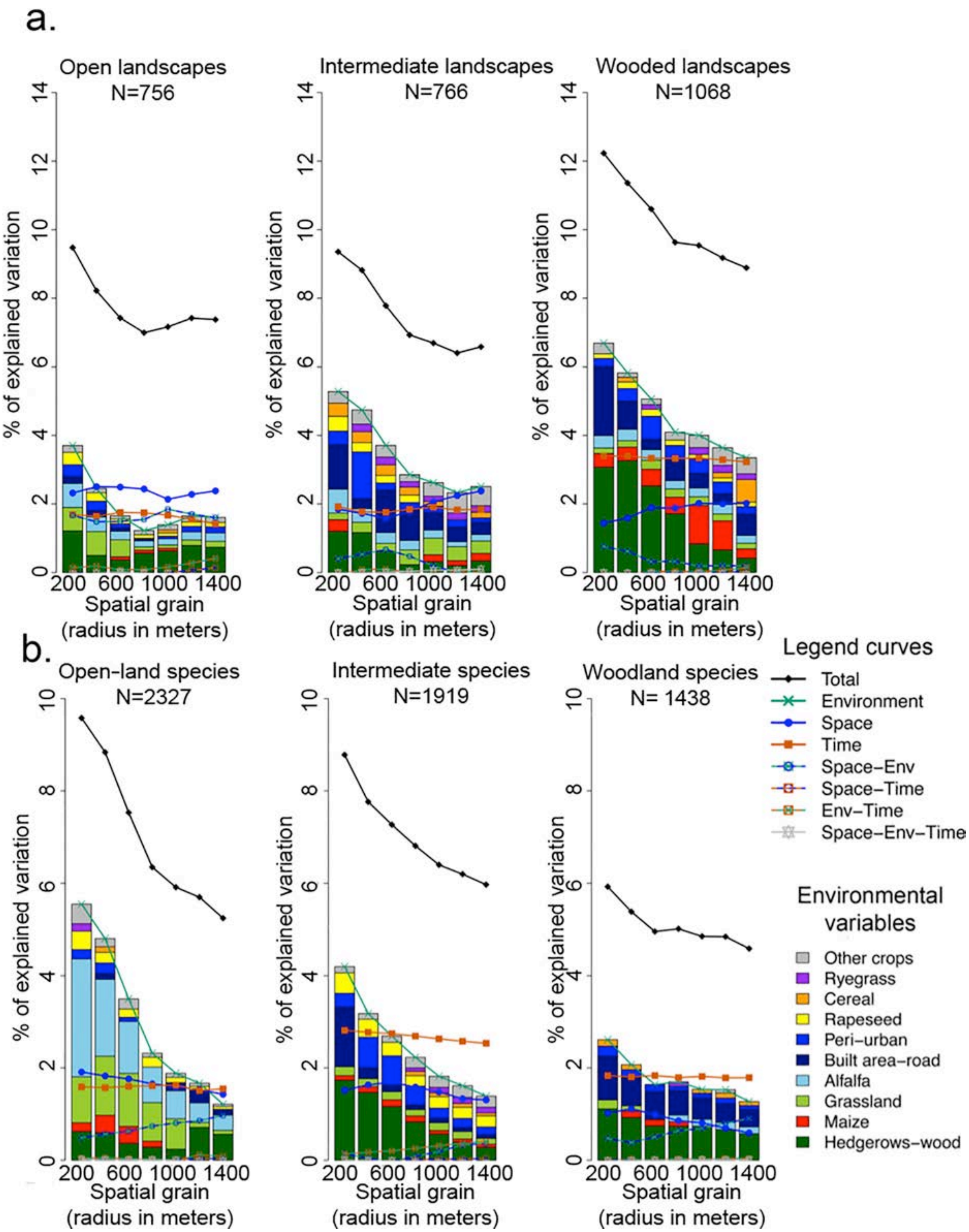

Fig 4. Variation partitioning per landscape and species class (% of explained variation). The curves represent the part of the explained variation by each variable: total (black), environmental (green), geographical (blue), temporal (red) and all interactions, at each environmental grain (x-axis). The barplot represents the relative effect of each of the environmental variables (based on the F-ratio). A. Partitioning per landscape B. Partitioning per species.

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rapeseed in open areas, and the proximity of urban area, alfalfa/grassland and other crops in wooded landscapes.

Discussion

Overall, our analyses show that the stochasticity have a prominent place in our system. Indeed, although the accuracy of environmental predictors and the deconstruction approach, a large amount of variation in community composition remains unexplained throughout all analyses, with as little as 6.5% and a maximum of 20% being explained by environment, spatial structure, seasonal or annual variation or by the interaction of these factors. This unexplained variation can be due either to nondeterministic fluctuations, to unmeasured variables (biotic or abiotic) or to spatial structures that are too complex to be described by our geographical functions [39].

The extent of our study area may also influence these results. Other studies have found that increasing the scale of analysis may change the total variance explained in community composition and / or diversity [19], the percent explained usually increasing at larger spatial scales. Here we varied the grain of the environmental predictors but, because of the nature of the study area, could not have varied too much the extent. But we still observed a decrease of explained variation from global analysis to the deconstruction per landscape type. The fact that the variance explained decreases when sites are grouped by landscape type confirms that landscape type was indeed a meaningful and powerful predictor in the first place. However, exploring what happens under the deconstruction approach allows investigating further whether or not there are other new predictors that appear as important once landscape type has been controlled for.

Among the deterministic processes involved, both variation partitioning and community pattern analysis showed that environment, especially as related to tree cover (hedgerows and forests), represent the main part of the explained variation of bird communities in agricultural landscapes and masked other variables at global scale. A dominant effect of environmental variables on bird community composition has been shown in numerous other studies at different spatial scales [20,21,44–46]. Here we also found a stronger effect of environmental variables at fine spatial grain (200m), a scale that matches better the bird territories in the breeding period, which usually range from 100 to 1000 m radius [47,48]. By contrast, the effect of the spatial component remained low and relatively constant at all spatial scales. The effect of tree cover on farmland birds has been clearly demonstrated [41,49], as trees and hedgerows provide key nesting habitats and song-posts for many bird species [50], while they may be avoided by other species, e.g., skylarks and yellow wagtails [31,51,52]. So the dominant effect of environmental variables and the low spatial component observed suggest that dispersal limitation is not a main driver of community assembly at global scale whatever the grain size, but that local habitat heterogeneity is key, especially as related to the existence of wooded areas.

Using the deconstruction approach, both variation partitioning and metacommunity pattern analysis leave a large proportion of variance unexplained, even more so than using a global analysis approach. This is probably due to the fact that our environmental correlates exhibit less variability when the landscape is deconstructed into categories, whereas our biological response variable does not. The dominant effect of environment at global scale and the increase of stochasiticity at local scale have also been shown for bird communities in another study on a coastal area, see [53]. In the deconstruction per species group, here again the ordination appear quite efficient to define species groups sharing similar habitat requirements. Meta-community pattern analysis seems a good method to reveal the dominant large scale ecological processes involved, and can constitute a useful step to allow a deconstruction at finer scales.

Indeed, the deconstruction approach revealed additional processes, both resulting from landscape types or species groups, a likely consequence of a strong species turnover of the community along forested gradients. The deconstruction per species show that woodland species respond more strongly to environmental predictors than open-land species. Despite of the deconstruction, the abundance of forest fragments and hedgerows remain the main predictor for woodland species. The quantity and quality of these semi-natural habitats may be so also an important criteria. By opposition the importance of crop composition appear now more clearly for open-land species.

But beyond only a preference in habitat type, these three groups tend also to associate species sharing specific traits. Many other studies have also highlighted the relevance of using species traits to explain community assembly patterns [54,55]. Most of the existing literature concern aquatic organisms and tend to show that ecological determinism, and especially the relative influence of environment compared to dispersal, increases with dispersal ability and body size of the organisms under study [56–59]. This could be explained by the fact that larger organisms are less plastic in their fundamental niche, or because more mobile species are able to track suitable environmental conditions better [57]. Our study suggests an opposite pattern (S7 Appendix), with a higher relative importance of spatial drivers for open-land species, a group that comprise only migratory or partially migratory species with, on average, larger body sizes, and comprising exclusively ground nesting species. The latter could make them more likely to disperse as compared to other groups (nesting in trees) since they need to cope with crop rotation. Therefore, this apparent contradiction with previous findings may just be explained by the fact that birds in our system are not restricted by dispersal limitation in itself (no limiting trait or physical barrier in environment) but are only constrained by tracking habitat changes.

The deconstruction per landscape type also reveal other processes. In wooded landscapes, environmental factors remained the main deterministic processes, whatever the spatial scale considered; in contrast in open landscapes, the spatial component exceeds the importance of environmental factors (except at the lowest spatial grain), explaining in average 2.3% of the total variation against 1.9% for the environment. Although we cannot totally exclude the possibility that the spatial effect results partly from the omission of some structuring environmental factors (such as agricultural practices) [60], this is unlikely to fully explain the observed patterns in our analyses. Indeed, the environmental data available here were highly detailed, and included land use for each single field, accurate mapping of hedgerows, wooded fragments and other semi-natural components, and changes through time for every year and land use type. Furthermore, the meta-community pattern analysis does not suggest a strong competition between species in our system (which would be characterized by a checkerboard pattern).

This pure spatial component that cannot be produced by the structuration of environmental variables may be attributed to spatial activities of individuals, such as adult dispersal and/or foraging activities [7,13,37]. Considering the high dispersal ability of birds, pure spatial structuration is expected to be low at local scale, as observed in other studies (eg. [20,53]). Here we suggest that this spatial effect may be explained by individual movements during the breeding season rather than by dispersal limitation *sensu stricto*. Theoretical and experimental studies suggest that dispersal is one of the possible strategies that can be selected in ecosystems characterized by a high spatiotemporal random environmental variation [61–63], a pattern expected with the crop rotations. Therefore, birds may need larger foraging habitats in less suitable areas, such as those represented by open habitats in agricultural fields. In addition, it has been shown that due to the low food availability in intensive farming areas, birds often travel further for foraging [64,65]. Supporting this idea, some long-term studies have indicated a dramatic decline of insects in Europe over the last decades [66,67], pattern that seems to be at least partly linked with farmland intensification.

If the high unexplained variation partly results from the loss of environmental heterogeneity with the partitioning per habitat, we still observed different patterns between wooded and open landscapes. In our study, the pattern observed in open landscapes suggests that bird community assembly in highly disturbed agricultural landscapes is more largely determined by stochasticity and spatial effects than in more perennial landscape. Similar conclusions seems to apply in urban areas [68]. In such highly unpredictable and changing landscapes, dispersal seems more important to deal with uncertainty, but can be not sufficient and result in ecological traps as suggested by some previous studies [69,70]. But, more generally, high stochasticity seems more the rule than the exception, a phenomena that also applies to more natural ecosystems [54,55]. This high unexplained variation may also partly result of imperfect detection. Although it has been shown in previous studies that 5 minutes point counts are usually sufficient to provide good estimates of species occurrences and community composition in open habitat like farmland, we are still unlikely to detect all individuals [29,30].

Conclusion

Our results highlight the critical need of conducting multi-scale studies and to consider several processes acting on the metacommunity at the same time. Using a combination of different methods and adopting a deconstruction approach can help improve our understanding of this complex set of community drivers.

Put in context, this study supports the idea that stochasticity and historicity are probably still very important components at the landscape scale. Part of the observed patterns are likely driven by unexpected fluctuations in population dynamics and space occupancy, while other sources of explanation might be found in the history of how individual bird territories came to be, such as colonization and extinction history, as well as lagged responses to major environmental changes [71].

Our results also emphasize the importance of wooded areas and landscape structure to explain community assembly of farmland birds. But they also highlight a higher role of dispersal in open habitats, which are more highly disturbed and unpredictable, and further suggest the importance of preserving source areas of biodiversity and maintaining landscape connectivity in these agricultural mosaics. Moreover, since open land species appear particularly sensitive to crop composition, and since there is a higher risk of potential mismatch between habitat preferences and breeding success in unpredictable landscapes, one may expect a positive effect of crop heterogeneity. Indeed a diversified landscape will more likely provide a suitable habitat and stable food resource at the territory scale [72,73]. However, our study only provided circumstantial evidence for this hypothesis, since results were based on spatial patterns. More direct tests of this hypothesis could be carried out by directly tracking animal movement in agricultural mosaics, and by further replicating spatially and temporally these analyses in other regions.

Supporting information

S1 Appendix. Species list (per class) and results of the redundancy analysis (RDA). We observe that the three species classes are ordinated along the first axis of the RDA, which is strongly correlated with a gradient of wooded component (see also S4 Appendix). This first axis explains 17.65% of the total variation, while the second axis explains 9.23%.
(DOCX)

S2 Appendix. Analysis of species co-occurrence by correspondence analysis. Species are distributed along a tree cover gradient (strong correlation with the first axis of the correspondence analysis). A dendrogram can be built by transforming the ordination value along this

axis into the Euclidean distance. Three species classes can be distinguished using the dendrogram, corresponding to openland, intermediate and woodland species.
(DOCX)

S3 Appendix. Results of the meta-community pattern analysis on the first two axis of the Redundancy Analysis (RDA). (see Presley, Higgins and Willig, 2010 and Leibold and Mikkelson, 2002)
The table present the value of the different indices, computed with the « meta-community function » in Matlab (see Leibold and Mikkelson, 2002):
Abs = the number of embedded absences in a given ordinated matrix
Apr = pvalue associated with embedded absences
MA = mean number of embedded absences base on null models
SA = standard deviation of number of embedded absences based on null models
Re = number of replacements (checkerboard)
Rpr = pvalue associated with replacements
MR = mean number of replacements base on null models
SR = standard deviation of number of replacements based on null models
M = Morisita Community index value
Mpr = pvalue associated with Morisita index
The resulting pattern is indicated for each analysis (global analysis, by landscape class, by species class or with both partitioning), for the first two axis of the redundancy analysis.
(DOCX)

S4 Appendix. Correlation between the RDA axis (first two axis) and the environmental variables at each environmental grain.
(DOCX)

S5 Appendix. Variation partitioning: comparison between two spatial models: Principal Coordinates of Neighbor Matrices (PCNM) and Trend Surface Analysis (TSA). Results are presented without the temporal component. In this analysis, all sessions and years have been pooled together. Because land use varied between years, both the mean (M) and the coefficient of variation (CV) of % composition for each environmental variable over the five year study period were analyzed in order to take account both the mean composition and the temporal variability of the landscape.
Although we observe similar patterns, PCNM give more importance to the geographical component and less to the environmental part.
(DOCX)

S6 Appendix. Variation partitioning for each class of landscapes (open, intermediate and wooded) (4a) and each class of species (open-land, intermediate and woodland species) (4b). The curves represent the variation explained by each variable: environmental (green), geographical (blue), temporal (red) and all interactions in relation to the part of explained variation (black), at each environmental grain (x-axis). This figure aims to compare the relative contribution of the deterministic processes, keeping the part of explained variation constant (100%). Unexplained variation does not appear on this figure.
A. Partitioning per landscape
The relative contribution of the spatial component decreases from open to wooded landscapes: the geographical part has a stronger effect than the environmental part in open landscapes whereas the environmental part dominates in wooded landscapes.
B. Partitioning per species
Spatial factors appear stronger in proportion for open-land species in comparison to woodland

species, but environmental effects remain dominant for each species classes.
(DOCX)

S7 Appendix. Table of species traits. The groups correspond to those defined by the correspondence analysis (see partitioning per species). The values of the traits correspond to a mean value per species, defined according to the literature. *Sources*:
1. Guide ornitho, *Lars Svensson*, *Peter J. Grant*, *Killian Mullarney*, *Dan Zetterström*, *edition 2011*
2. Website: *Oiseaux.net.*
(DOCX)

S8 Appendix. Database. The database contains all the data from the point counts and GIS data. This includes the ID of the point ("IdPoint"), the year and the session (2 sessions per year from 2009 to 2013). The abundance of each species is reported on the table. The first column ("Gradient_HedgerowsForest200m") corresponds to the gradient of wooded components used to do the partitioning per landscape. This variable was computed by summing the area of hedgerows (considering a buffer of 100m around this linear component) and woodland. The data base also included the areas of the 11 categories of land use: alfalfa, grassland, ryegrass, sunflower, spring crops of pea-flax-field beans, rapeseed, cereals, maize, other crops (e.g. mustard, sorghum, millet and tobacco, representing less than 2% of crops), urban, and forest and two linear components (roads and hedgerows). For each point count station, we recorded the area occupied by each land use category as well as the length of hedgerows and roads or paths within a buffer area from 200m to 1400m. Finally, the database contains the 9 spatial functions (third degree polynomial of the geographic coordinates of the point counts) used in the variation partitioning analysis ("Spatial1" to "Spatial9").
(XLS)

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References

1. Logue JB, Mouquet N, Peter H, Hillebrand H. Empirical approaches to metacommunities: a review and comparison with theory. Trends Ecol Evol. 2011 Sep; 26(9):482–91. https://doi.org/10.1016/j.tree.2011.04.009 PMID: 21641673

2. Leibold M a., Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF, et al. The metacommunity concept: a framework for multi-scale community ecology. Ecol Lett. 2004 Jun 4; 7(7):601–13.
3. Holyoak M, Leibold MA, Mouquet NM, Holt RD, Hoopes MF. Metacommunities: a framework for large-scale community ecology. In: Holyoak M, Leibold MA, Holt RD, editors. Metacommunities: spatial dynamics and ecological communities. University of Chicago Press, Chicago, USA; 2005. p. 1–31.
4. McIntire EJB, Fajardo A. Beyond description: the active and effective way to infer processes from spatial patterns. Ecology. 2009; 90(1):46–56. PMID: 19294912
5. Presley SJ, Higgins CL, Willig MR. A comprehensive framework for the evaluation of metacommunity structure. Oikos. 2010 Apr 16; 119(6):908–17.
6. Darmon G, Calenge C, Loison A, Jullien J-M, Maillard D, Lopez J-F. Spatial distribution and habitat selection in coexisting species of mountain ungulates. Ecography (Cop). 2012 Jan 3; 35(1):44–53.
7. Buschke FT, De Meester L, Brendonck L, Vanschoenwinkel B. Partitioning the variation in African vertebrate distributions into environmental and spatial components—exploring the link between ecology and biogeography. Ecography (Cop). 2014; 38(5):450–61.
8. Legendre P. Spatial Autocorrelation: Trouble or New Paradigm? Ecology. 1993 Sep; 74(6):1659–73.
9. Guichard F. Recent advances in metacommunities and meta-ecosystem theories. F1000Research. 2017 May 2; 6:610. https://doi.org/10.12688/f1000research.10758.1 PMID: 28529720
10. Mouquet N, Loreau M. Community Patterns in Source-Sink Metacommunities. Am Nat. 2003 Nov; 162 (5):544–57. https://doi.org/10.1086/378857 PMID: 14618534
11. Vellend M. Conceptual synthesis in community ecology. 2010; 85(2):183–206.
12. Brown BL, Sokol ER, Skelton J, Tornwall B. Making sense of metacommunities: dispelling the mythology of a metacommunity typology. Oecologia. 2017 Mar 22; 183(3):643–52. https://doi.org/10.1007/s00442-016-3792-1 PMID: 28008474
13. Cottenie K. Integrating environmental and spatial processes in ecological community dynamics. Ecol Lett. 2005 Nov; 8(11):1175–82. https://doi.org/10.1111/j.1461-0248.2005.00820.x PMID: 21352441
14. Soininen J. A quantitative analysis of species sorting across organisms and ecosystems. Ecology. 2014 Dec; 95(12):3284–92.
15. Hart SP, Usinowicz J, Levine JM. The spatial scales of species coexistence. Nat Ecol Evol. 2017 Aug 21; 1(8):1066–73. https://doi.org/10.1038/s41559-017-0230-7 PMID: 29046584
16. Huston MA. Biological Diversity. The Coexistence of Species on Changing Landscapes. Cambridge. New York; 1994. 681 p.
17. Azeria ET, Bouchard M, Pothier D, Fortin D, Hébert C. Using biodiversity deconstruction to disentangle assembly and diversity dynamics of understorey plants along post-fire succession in boreal forest. Glob Ecol Biogeogr. 2011 Jan 17; 20(1):119–33.
18. Marquet PA, Fernández M, Navarrete SA, Valdovinos C. Diversity emerging: towards a deconstruction of biodiversity patterns. In: Frontiers of Biogeography: New direction in the Geography nature. 2004. p. 191–209.
19. Meynard CN, Lavergne S, Boulangeat I, Garraud L, Van Es J, Mouquet N, et al. Disentangling the drivers of metacommunity structure across spatial scales. Gillman LN, editor. J Biogeogr. 2013 Aug; 40 (8):1560–71. https://doi.org/10.1111/jbi.12116 PMID: 24790288
20. Bonthoux S, Balent G. Bird metacommunity processes remain constant after 25 years of landscape changes. Ecol Complex. 2015 Mar; 21:39–43.
21. Divíšek J, Zelený D, Culek M, Šťastný K. Natural habitats matter: Determinants of spatial pattern in the composition of animal assemblages of the Czech Republic. Acta Oecologica. 2014 Aug; 59:7–17.
22. Storch D, Konvicka M, Benes J, Martinková J, Gaston KJ. Distribution patterns in butterflies and birds of the Czech Republic: separating effects of habitat and geographical position. J Biogeogr. 2003 Aug; 30 (8):1195–205.
23. Thuiller W, Araújo MB, Lavorel S. Do we need land-cover data to model species distributions in Europe? J Biogeogr. 2004 Mar; 31(3):353–61.
24. Poulsen JG, Sotherton NW, Aebischer NJ. Comparative nesting and feeding ecology of skylarks Alauda arvensis on arable farmland in southern England with special reference to set-aside. J Appl Ecol. 1998 Feb; 35(1):131–47.
25. Ponjoan A, Bota G, Mañosa S. Ranging behaviour of little bustard males, Tetrax tetrax, in the lekking grounds. Behav Processes. 2012 Sep; 91(1):35–40. https://doi.org/10.1016/j.beproc.2012.05.005 PMID: 22626823
26. Tagmann-Ioset A, Schaub M, Reichlin TS, Weisshaupt N, Arlettaz R. Bare ground as a crucial habitat feature for a rare terrestrially foraging farmland bird of Central Europe. Acta Oecologica. 2012 Feb; 39:25–32.

27. Leibold MA, Mikkelson GM. Coherence, species turnover, and boundary clumping: elements of meta-community structure. Oikos. 2002 May; 97(2):237–50.

28. Bretagnolle V, Berthet E, Gross N, Gauffre B, Plumejeaud C, Houte S, et al. Description of long-term monitoring of farmland biodiversity in a LTSER. Data Br. 2018 Aug; 19:1310–3.

29. Fuller RJ, Langslow DR. Estimating numbers of birds by point counts: how long should counts last? Bird Study. 1984 Nov; 31(3):195–202.

30. Bonthoux S, Balent G. Point count duration: five minutes are usually sufficient to model the distribution of bird species and to study the structure of communities for a French landscape. J Ornithol. 2011 Apr 13; 153(2):491–504.

31. Miguet P, Gaucherel C, Bretagnolle V. Breeding habitat selection of Skylarks varies with crop heterogeneity, time and spatial scale, and reveals spatial and temporal crop complementation. Ecol Modell. 2013 Sep; 266:10–8.

32. Leibold MA, Mikkelson GM. Coherence, species turnover, and boundary clumping: elements of meta-community structure. Oikos. 2002 May; 97(2):237–50.

33. Gotelli NJ. Null Model Analysis of Species Co-Occurrence Patterns. Ecology. 2000 Sep; 81(9):2606.

34. Gauch HG, Whittaker RH, Wentworth TR, Journal S, Mar N. A Comparative Study of Reciprocal Averaging and Other Ordination Techniques. J Ecol. 1977; 65(1):157–74.

35. Legendre P, Legendre L. Numerical Ecology, Third Edition. Elsevier, editor. Amsterdam; 2012. 1006 p.

36. Peres-Neto PR, Legendre P, Dray S, Borcard D. Variation partitioning of species data matrices: estimation and comparison of fractions. Ecology. 2006; 87(10):2614–25. PMID: 17089669

37. Legendre P, Borcard D, Peres-Neto PR. Analyzing or explaining beta diversity? comment. Ecology. 2008; 89(11):3238–44.

38. Legendre P, Gallagher E. Ecologically meaningful transformations for ordination of species data. Oecologia. 2001 Oct 1; 129(2):271–80. https://doi.org/10.1007/s004420100716 PMID: 28547606

39. Borcard D, Legendre P, Drapeau P. Partialling out the Spatial Component of Ecological Variation. Ecology. 1992; 73(3):1045–55.

40. Gilbert B, Bennett JR. Partitioning variation in ecological communities: do the numbers add up? J Appl Ecol. 2010 Oct 19; 47(5):1071–82.

41. O'Connor RJ. The importance of hedges to songbirds. In: Jenkins D, editor. Agriculture and the environments. Cambridge: Institute of Terrestrial Ecology; 1984. p. 117–23.

42. Balent G, Courtiade B. Modelling bird communities/landscape patterns relationships in a rural area of South-Western France. Landsc Ecol. 1992; 6(3):195–211.

43. Berg Å. Breeding birds in short-rotation coppices on farmland in central Sweden—the importance of Salix height and adjacent habitats. Agric Ecosyst Environ. 2002; 90(3):265–76.

44. Godinho C, Rabaça JE. Birds like it Corky: the influence of habitat features and management of 'montados' in breeding bird communities. Agrofor Syst. 2010 Aug 12; 82(2):183–95.

45. Reino L, Beja P, Araújo MB, Dray S, Segurado P. Does local habitat fragmentation affect large-scale distributions? The case of a specialist grassland bird. Divers Distrib. 2013; 19(4):423–32.

46. Moreira F, Beja P, Morgado R, Reino L, Gordinho L, Delgado A, et al. Effects of field management and landscape context on grassland wintering birds in Southern Portugal. Agric Ecosyst Environ. 2005 Aug; 109(1–2):59–74.

47. Soderstrom B, Part T. Influence of Landscape Scale on Farmland Birds Breeding in Semi-Natural Pastures. Conserv Biol. 2000 Apr; 14(2):522–33.

48. Pelosi C, Bonthoux S, Castellarini F, Goulard M, Ladet S, Balent G. Is there an optimum scale for predicting bird species ' distribution in agricultural landscapes? J Environ Manage. 2014; 136:54–61. https://doi.org/10.1016/j.jenvman.2014.01.022 PMID: 24561236

49. Fuller RJ, Trevelyan RJ, Hudson RW. Landscape composition models for breeding bird populations in lowland English farmland over a 20 year period. Ecography (Cop). 1997 Jun; 20(3):295–307.

50. Siriwardena GM, Cooke IR, Sutherland WJ. Landscape, cropping and field boundary influences on bird abundance. Ecography (Cop). 2012 Feb 3; 35(2):162–73.

51. Wilson JD, Evans J, Browne SJ, King JR. Territory Distribution and Breeding Success of Skylarks Alauda arvensis on Organic and Intensive Farmland in Southern England. J Appl Ecol. 1997 Dec; 34(6):1462.

52. Gilroy JJ, Anderson GQA, Grice P V., Vickery JA, Sutherland WJ. Mid-season shifts in the habitat associations of Yellow Wagtails Motacilla flava breeding in arable farmland. Ibis (Lond 1859). 2010 Jan 8; 152(1):90–104.

53. Gianuca AT, Bastazini VAG, Dias RA, Isabel M, Hernández M. Independent and shared effects of environmental features and space driving avian community beta diversity across a coastal gradient in southern Brazil. Austral Ecol. 2013; 38(8).

54. Van der Plas F, Janzen T, Ordonez A, Fokkema W, Reinders J, Etienne RS, et al. A new modeling approach estimates the relative importance of different community assembly processes. Ecology. 2015 Jun; 96(6):1502–15.

55. Janzen T, Alzate A, Muschick M, Maan ME, van der Plas F, Etienne RS. Community assembly in Lake Tanganyika cichlid fish: quantifying the contributions of both niche-based and neutral processes. Ecol Evol. 2017 Feb; 7(4):1057–67. https://doi.org/10.1002/ece3.2689 PMID: 28303177

56. Padial AA, Ceschin F, Declerck SAJ, De Meester L, Bonecker CC, Lansac-Tôha FA, et al. Dispersal Ability Determines the Role of Environmental, Spatial and Temporal Drivers of Metacommunity Structure. Guichard F, editor. PLoS One. 2014 Oct 23; 9(10):e111227. https://doi.org/10.1371/journal.pone.0111227 PMID: 25340577

57. Farjalla VF, Srivastava DS, Marino NAC, Azevedo FD, Dib V, Lopes PM, et al. Ecological determinism increases with organism size. Ecology. 2012 Jul; 93(7):1752–9. PMID: 22919920

58. Heino J. Does dispersal ability affect the relative importance of environmental control and spatial structuring of littoral macroinvertebrate communities? Oecologia. 2013 Apr 8; 171(4):971–80. https://doi.org/10.1007/s00442-012-2451-4 PMID: 22961400

59. De Bie T, Meester L, Brendonck L, Martens K, Goddeeris B, Ercken D, et al. Body size and dispersal mode as key traits determining metacommunity structure of aquatic organisms. Hillebrand H, editor. Ecol Lett. 2012 Jul; 15(7):740–7. https://doi.org/10.1111/j.1461-0248.2012.01794.x PMID: 22583795

60. Dray S, Pélissier R, Couteron P, Fortin M-J, Legendre P, Peres-Neto PR, et al. Community ecology in the age of multivariate multiscale spatial analysis. Ecol Monogr. 2012 Aug; 82(3):257–75.

61. Mathias A, Kisdi Èa, Olivieri I. Divergent evolution of dispersal in a heterogeneous landscape. Evolution (N Y). 2001 Feb; 55(2):246–59.

62. Achter J. D, Webb C. T. Mixed dispersal strategies and response to disturbance. Evol Ecol Res. 2006; (8):1377–92.

63. Friedenberg NA. Experimental evolution of dispersal in spatiotemporally variable microcosms. Ecol Lett. 2003 Oct; 6(10):953–9.

64. Britschgi A, Spaar R, Arlettaz R. Impact of grassland farming intensification on the breeding ecology of an indicator insectivorous passerine, the Whinchat Saxicola rubetra: Lessons for overall Alpine meadowland management. Biol Conserv. 2006 Jun; 130(2):193–205.

65. Schifferli L. Birds Breeding in a Changing Farmland. Acta Ornithol. 2001 Jul; 36(1):35–51.

66. Hallmann CA, Sorg M, Jongejans E, Siepel H, Hofland N, Schwan H, et al. More than 75 percent decline over 27 years in total flying insect biomass in protected areas. Lamb EG, editor. PLoS One. 2017 Oct 18; 12(10):e0185809. https://doi.org/10.1371/journal.pone.0185809 PMID: 29045418

67. Conrad KF, Woiwod IP, Parsons M, Fox R, Warren MS. Long-term population trends in widespread British moths. J Insect Conserv. 2004; 8(2/3):119–36.

68. Sattler T, Borcard D, Arlettaz R, Bontadina F, Legendre P, Obrist MK, et al. Spider, bee, and bird communities in cities are shaped by environmental control and high stochasticity. Ecology. 2010 Nov; 91 (11):3343–53. PMID: 21141195

69. Schlaepfer MA, Runge MC, Sherman PW. Ecological and evolutionary traps. Trends Ecol Evol. 2002 Oct; 17(10):474–80.

70. Santangeli A, Lehikoinen A, Bock A, Peltonen-Sainio P, Jauhiainen L, Girardello M, et al. Stronger response of farmland birds than farmers to climate change leads to the emergence of an ecological trap. Biol Conserv. 2018 Jan; 217:166–72.

71. Chamberlain DE, Fuller RJ, Bunce RGH, Duckworth JC, Shrubb M. Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. J Appl Ecol. 2000 Oct; 37(5):771–88.

72. Dunn JC, Hamer KC, Benton TG. Anthropogenically-Mediated Density Dependence in a Declining Farmland Bird. Moskát C, editor. PLoS One. 2015 Oct 2; 10(10):e0139492. https://doi.org/10.1371/journal.pone.0139492 PMID: 26431173

73. Fahrig L, Girard J, Duro D, Pasher J, Smith A, Javorek S, et al. Farmlands with smaller crop fields have higher within-field biodiversity. Agric Ecosyst Environ. 2015; 200:219–34.