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Effets des changements climatiques sur la biodiversité

Céline Bellard

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Céline Bellard. Effets des changements climatiques sur la biodiversité. Sciences agricoles. Université Paris Sud - Paris XI, 2013. Français. NNT : 2013PA112269 . tel-01079440

HAL Id: tel-01079440

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UNIVERSITE PARIS-SUD

ÉCOLE DOCTORALE : SCIENCES DU VÉGÉTAL
Laboratoire d'Ecologie Systématique et Evolution

DISCIPLINE : BIOLOGIE

THÈSE DE DOCTORAT

Soutenance prévue le 19/11/2013

par

Céline BELLARD

**Effets des changements climatiques sur la
biodiversité**

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Remerciements

Ma thèse a été l'aventure la plus enrichissante de ma vie, aussi bien scientifiquement qu'humainement et l'occasion de nombreuses rencontres, d'échanges et de collaborations. Je tiens donc à remercier toutes les personnes qui ont contribué à cette thèse, de près ou de loin. Merci à chacun d'entre vous pour votre contribution, sans vous cette thèse ne serait pas ce qu'elle est et ce travail aurait été tellement moins intéressant.

La première personne que je tiens à remercier est mon cher directeur de thèse. Je tiens tout particulièrement à te remercier de m'avoir fait confiance dès le début et de m'avoir tant appris. Grâce à toi j'ai appris à faire de la recherche, et à comprendre le monde de la recherche. Tu m'as également appris à argumenter, il fallait au moins ça pour te convaincre. Merci également d'avoir toujours été enthousiaste à mes idées, et de m'en avoir apporté de nouvelles chaque semaine ! Je te remercie sincèrement de m'avoir ouvert toutes ces portes. Je n'aurais pas pu imaginer avoir autant de liberté et de confiance pour une thèse et j'ai conscience de la chance que j'ai eu de t'avoir comme directeur de thèse. Je souhaite également remercier le CNRS d'avoir financé cette thèse.

Je tiens aussi à remercier Wilfried de s'être autant impliqué dans mes projets de recherche, d'avoir toujours été disponible lorsque j'avais des questions et pour la pertinence de ses commentaires qui m'ont toujours aidé à avancer et à améliorer mon travail, et enfin merci pour l'accueil à Grenoble.

Je tiens également à remercier mon jury de thèse d'avoir accepté de lire toutes ces pages. Etant l'auteur principal de cette thèse, j'ai conscience du nombre important de pages et du travail que représente une lecture de manuscrit de thèse. Merci à vous de prendre le temps de me donner votre avis sur ce manuscrit. Je voudrais remercier Antoine, de m'avoir chaleureusement accueilli à Lausanne et d'avoir accepté d'être mon rapporteur malgré un emploi du temps déjà bien chargé. Je tiens également à remercier Paul de m'avoir impliqué dans de nombreux projets intéressants, et d'avoir accepté d'être dans mon jury de thèse. Merci également à Ana pour la pertinence de tes commentaires lors de ces réunions improvisées et d'avoir accepté d'être dans ce jury. Enfin je tiens également à remercier François Sarrazin d'avoir accepté d'être rapporteur de ma thèse.

Un grand merci à mes deux principaux piliers, « room mates » et désormais amies. Merci de m'avoir accompagné durant ces quatre merveilleuses années et de m'avoir autant fait rire ! Si vous ne vous êtes pas encore reconnues, merci à vous les filles Elsa et Gloria! Merci à Elsa d'avoir toujours été de bon conseil, d'avoir toujours été enthousiaste, optimiste, disponible et travailleuse, de m'avoir appris à relativiser et de ne jamais abandonner. Et merci également d'avoir eu le courage de lire cette thèse en entier ! Tu feras probablement partie du top 10 !

Un *gran* merci à toi G.M. de Cordoba, pour ta gentillesse, ces discussions passionnées, et cette magnifique personne que j'ai découverte. Merci d'avoir toujours été là pour discuter « *travail* », de m'avoir aidé à rédiger ces mails un peu délicats qui demandent un certain temps de réflexion, d'avoir toujours relu avec enthousiasme mes articles, de m'avoir appris à être rigoureuse. Je n'atteindrai jamais ton niveau de rigueur mais pour chaque projet dans lequel je me lancerai j'essaierai d'atteindre au moins 1/10^{ème} de la rigueur selon Gloria. Merci encore de ces heures de discussions sur la recherche qui m'ont permis de trouver les réponses que je cherchais.

Merci à vous les filles d'avoir vraiment été de vrais piliers pendant cette thèse et de m'avoir aidé pour chacun des aspects qu'une thèse peut comporter ! Je ne suis pas encore partie mais j'espère déjà revenir et en pleine forme pour la 13^{ème} édition du tri-relais !

Un grand merci également à mes deux binômes de thèse à qui je souhaite décerner une mention spéciale. Cette thèse n'aurait été qu'une pâle version de ce qu'elle est sans l'aide exceptionnelle de Camille et de Boris. Honneur à la gente féminine d'abord donc merci à toi Camille. Merci d'avoir été ma première étudiante et une excellente étudiante pendant près de deux années ! Merci d'avoir toujours été aussi organisée, efficace, disponible et enthousiaste. C'était pour moi une immense chance de pouvoir travailler avec toi pendant tout ce temps et extrêmement stimulant de le faire. Un grand merci également à Boris ! Merci Boris, je n'aurai jamais pu penser que ce seul petit mail pourrait avoir autant de conséquences sur ma thèse, et pourtant ... Tu t'es toujours impliqué à 200% dans mes projets et tu m'as toujours poussé à aller plus loin. J'espère que ces deux binômes de thèse perdureront au delà de la thèse. C'était particulièrement enrichissant de travailler et de discuter sciences et de nos projets pendant ces dernières années.

Je voudrais également remercier l'ensemble des co-auteurs des différents articles qui se sont toujours impliqués et ont toujours répondu présent lorsque j'en avais besoin.

J'étais particulièrement contente de venir au laboratoire chaque matin malgré d'interminables

trajets en RER et de vous voir chaque jour pendant ces quatre dernières années. Merci à toi Amélie pour ces pauses rafraichissantes, tes nombreuses questions souvent un peu farfelues. Merci également à Laetitia d'être à l'origine de mes premières pauses dans le labo fournis. Merci également à toutes ces personnes géniales que j'ai rencontré au laboratoire Constance, Pauline, Alok, Nicolas, Yuya, Stephen et Emmanuelle. Je n'oublierai pas non plus de citer Carmen, Cléo, Jean-michel, Marc, Florence, Sophie, Nadia, Nathalie, Lydie, Sandrine, Sébastien, qui ont fait parti de mon quotidien pendant ces trois années de thèse. Je tiens également à remercier toutes les personnes qui sont au laboratoire ESE et en particulier à l'équipe EPC et à tous ceux qui ont contribué d'une façon ou d'une autre à la réalisation de ce travail. Merci à vous !

Un merci tout particulier à Julien d'avoir relu cette thèse et d'être mon ami depuis toutes ces années.

Un immense merci à mes parents pour leur soutien et la confiance illimitée qu'ils m'ont toujours porté et d'avoir fait de moi celle que je suis.

Et merci à toi JF pour ton aide, ton écoute, tes conseils et ton soutien sans faille ces dernières années qui m'ont permis de terminer cette thèse dans les meilleures conditions

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ANNEXE 2 : **Bellard, C.**, Leclerc, C. & Courchamp, F. Impact of sea level rise on the french islands worldwide. Publié dans la revue *Nature conservation*.

ANNEXE 3 : Cornille, A., Giraud, T., **Bellard, C.**, Tellier, A., Le Cam, B., Smulders, M. J. M., Kleinschmit, J., Roldan-Ruiz, I. and Gladieux, P. (2013), Postglacial recolonization history of the European crabapple (*Malus sylvestris* Mill.), a wild contributor to the domesticated apple. *Molecular Ecology*.

ANNEXE 4: F. Courchamp, B. D. Hoffmann, J. Russell, C. Leclerc and **C. Bellard** Climate change and conservation: keeping island biodiversity afloat. Soumis dans la section *Forum Policy* de la revue *Trends in Ecology and Evolution*.

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1. INTRODUCTION GENERALE

1.1.LA BIODIVERSITE, ESSENTIELLE POUR L'HUMANITE

1.1.1. DEFINITION DE LA BIODIVERSITE

La définition de la biodiversité a été établie au sommet de la Terre de Rio en 1992: « *La diversité biologique est la variabilité des organismes vivants de toute origine y compris, entre autres, les écosystèmes terrestres, marins, et autres écosystèmes aquatiques et les complexes écologiques dont ils font partie ; cela comprend la diversité au sein des espèces et entre espèces ainsi que celles des écosystèmes* ». La biodiversité résulte de la diversité des formes et des modes de vie sur Terre. Afin de mieux appréhender ce que le terme « biodiversité » signifie, on le définit à trois niveaux hiérarchiques différents: la diversité génétique, la diversité spécifique et la diversité des écosystèmes. L'ensemble de ces trois niveaux est nécessaire au maintien de la diversité biologique.

La diversité génétique correspond à la diversité des allèles au sein des individus d'une même espèce. Les marqueurs moléculaires sont les indicateurs de la variabilité génétique les plus fréquemment utilisés. Certaines espèces sont génétiquement très variables comme le riz asiatique (*Oryza sativa*) et ses 50 000 gènes alors que la drosophile ne compte par exemple que 13 600 gènes. Par ailleurs, une faible diversité allélique peut conduire à une mauvaise qualité de sperme et à un faible taux de reproduction, comme pour le guépard. Au contraire, une importante variabilité génétique permet aux espèces de s'adapter plus facilement aux pressions environnementales. Les cultures sont ainsi plus résistantes aux maladies lorsque la diversité génétique est importante (Zhu *et al.*, 2000). La diversité spécifique incarne le second niveau de la biodiversité, qui est généralement le plus utilisé et étudié en écologie. Ce niveau se caractérise par le nombre d'espèces différentes que contient un écosystème donné. Selon les estimations, entre 3,6 millions et 117,7 millions d'espèces sont comptées sur Terre (May, 2010; Scheffers *et al.*, 2012). On admet généralement que la diversité spécifique est plus importante aux tropiques : ainsi en Sibérie on trouve environ une espèce d'arbre par hectare (Taiga), contre plus de 450 arbres par hectare en Equateur (forêt tropicale de plaine). La diversité spécifique est importante, par exemple elle permet une augmentation de la production de biomasse des plantes avec la diversité spécifique (Cardinale *et al.*, 2007). Enfin, la diversité des écosystèmes inclut l'ensemble des organismes vivants qui forment une unité fonctionnelle par leurs interactions. Les écosystèmes se caractérisent par une association de différentes communautés, leurs relations structurelles et fonctionnelles avec leur

environnement et entre elles. Il existe de nombreux types d'écosystèmes allant du désert aux forêts tropicales.

Un autre aspect important de la biodiversité est son perpétuel dynamisme : la diversité biologique évolue et change en permanence. Certains changements se produisent périodiquement au sein même des espèces comme la migration saisonnière chez les oiseaux. De même, le saumon de l'Atlantique fraie dans les rivières d'eau douce, migre en mer afin d'atteindre la maturité sexuelle et enfin retourne en eau douce pour se reproduire, au cours de l'année. Cette périodicité existe également au sein des écosystèmes, où les interactions entre différents organismes sont parfois régies par des changements annuels ou saisonniers. Les écosystèmes changent alors en taille et en structure au cours du temps. Les incendies réguliers dans le sud-est des Etats-Unis représentent un bon exemple d'un écosystème adapté aux feux périodiques. Lorsque les feux sont artificiellement supprimés le sous-étage de la forêt devient dense, la diversité spécifique diminue ainsi que la productivité. Au contraire, les feux occasionnels permettent l'entretien d'une mosaïque de communautés de plantes à différents stades de colonisation, ce qui induit une augmentation de la richesse spécifique et de la résilience aux perturbations environnementales (Fuhlendorf *et al.*, 2008).

Dans cette thèse, je me suis principalement intéressée à un seul niveau de la biodiversité : la biodiversité spécifique. Il s'agit du niveau le plus intuitif et le plus facile à étudier à l'échelle mondiale, et il permet également de mettre en avant les tendances pour un grand nombre d'espèces.

1.1.2. LA BIODIVERSITE, LE PILIER DE LA VIE

L'humanité dépend de l'ensemble des trois niveaux de la biodiversité pour de nombreux aspects, tels que la nourriture, les médicaments et les ressources énergétiques, et pourtant ce n'est qu'en 1992, au sommet de la terre de Rio de Janeiro qu'il a été décidé de faire une priorité de la protection et de la restauration de la diversité du vivant. La quantité de découvertes et d'usages issus de l'étude de la biodiversité est considérable: l'aspirine extraite à partir du saule blanc, le bois, la laine, le caoutchouc et les aliments sont de parfaits exemples. La biodiversité a également une valeur à usage indirect, de nombreuses espèces ont par exemple un rôle de dispersion, de même, la pollinisation permet la reproduction de la plupart des plantes. En effet, plus de 80% de la production des espèces végétales en Europe dépend directement de la pollinisation. A l'échelle mondiale, les insectes pollinisateurs représentent un apport de près de 9,5% de la valeur de la production alimentaire mondiale

(Gallai *et al.*, 2009). C'est également grâce à la biodiversité que l'air est purifié ou encore que les sols sont protégés de l'érosion (Cardinale *et al.*, 2012). La biodiversité a un rôle essentiel au sein de la biosphère, car elle permet l'existence même des conditions favorables à la vie sur Terre. Chaque espèce interagit avec d'autres espèces et a une fonction précise dans l'écosystème. En outre, plus un écosystème contient un nombre d'espèces important, plus il est capable de faire face aux perturbations (Cardinale *et al.*, 2012), notamment en raison de la diversité des réponses fonctionnelles des espèces et à la redondance écologique à l'intérieur même des écosystèmes.

Pour autant, la biodiversité n'a pas qu'une valeur instrumentale pour l'homme. Elle a également une valeur identitaire et culturelle, comme la chasse au lion qui est un élément fondamental du passage de témoin entre les générations en Somalie : c'est ce que l'on définit comme la valeur patrimoniale de la biodiversité (Cormier Salem *et al.*, 2002). On peut également définir la valeur intrinsèque de la biodiversité comme une estimation de la valeur de la biodiversité pour elle-même.

Ainsi, la biodiversité a un rôle primordial et fondamental pour de nombreux aspects, c'est pourquoi des directives afin de la protéger ont été mises en place ces dernières années. Les directives énoncées à la conférence sur la biodiversité de Johannesburg en 2002 ont fixé comme objectif l'arrêt de l'érosion de la biodiversité pour 2010. Cependant, le rassemblement des nations unies en 2012 (Rio +20) n'a pu que constater non seulement l'échec de l'arrêt de l'érosion de la biodiversité mondiale mais également l'accélération de cette érosion.

1.1.3. UNE BIODIVERSITE FRAGILE

L'état actuel de la biodiversité ne correspond qu'à une étape de son histoire. De nos jours, 99% des espèces ayant existé sur Terre au cours des 3,5 derniers milliards d'années se sont éteintes (Novacek, 2001). L'extinction d'espèces est donc un phénomène naturel et les espèces actuelles ne représentent qu'un petit échantillonnage des espèces ayant déjà vécu sur Terre. D'une manière générale, la Terre a déjà connu cinq grandes crises d'extinction massive depuis le Cambrien. Il est aujourd'hui démontré que la Terre subit sa 6^{ème} grande crise d'extinction et qu'elle est imputable à l'espèce humaine. Cette période a ainsi été nommée l'anthropocène (Caro *et al.*, 2012). La principale particularité de la crise d'extinction d'espèces que l'on observe aujourd'hui est que le taux d'extinction est 100 à 1000 fois plus élevé que le taux d'extinction moyen qu'a connu la Terre auparavant (Pimm & Raven, 2000).

La première phase de cette crise d'extinction a eu lieu il y a entre 50 000 et 100 000 ans. Elle coïncide avec la première étape de colonisation de nouvelles régions par les premiers hommes. La deuxième phase a débuté avec l'augmentation de la population humaine conduisant à l'apparition de l'agriculture et donc à la destruction de l'habitat. Ainsi 95% de la mégafaune de l'Amérique du Nord a disparu il y a déjà 11 000 ans. Enfin, la révolution industrielle qui a débuté au 19^{ème} siècle représente la troisième phase d'extinction (Awise *et al.*, 2008).

La proportion d'espèces considérées comme « éteintes » par l'Union Internationale pour la Conservation de la Nature (IUCN) est de 0.8% des espèces de plantes et 1.5% des espèces d'animaux. En outre, près de 22% des animaux et 60% des plantes (Figure 1) sont considérées comme « menacées » (ayant un statut d'espèces en danger critique d'extinction, en danger d'extinction ou vulnérable) selon les critères établis par l'UICN. De plus, 23% à 36% des mammifères, oiseaux et amphibiens utilisés pour la nourriture ou la médecine sont actuellement menacés d'extinction. Si l'on se concentre uniquement sur les races d'animaux domestiques, 21% d'entre elles sont menacées d'extinction (Butchart *et al.*, 2010). Il faut cependant noter que seule une petite fraction de la biodiversité est en réalité étudiée et la plupart des groupes d'invertébrés sont à ce jour encore sous-étudiés, avec seulement 4.13% d'espèces évaluées pour le risque d'extinction par l'UICN en 2013 comparé aux 1.7 millions espèces décrites (IUCN, 2013). Par conséquent, nous commençons seulement à identifier les menaces qui pèsent sur ces groupes (Cardoso *et al.*, 2011; Collen *et al.*, 2012). Globalement, selon l'UICN, les scientifiques ont à ce jour évalué l'état des populations de seulement 10% des espèces décrites.

L'autre particularité de cette crise d'extinction est que l'homme est directement ou indirectement lié à l'ensemble des causes de la perte de la biodiversité : la perte d'habitat, les invasions biologiques, la pollution, les changements climatiques et la surexploitation (Sala *et al.*, 2000). L'ensemble de ces facteurs de perte de biodiversité est lié au besoin croissant des populations humaines en ressources et en énergie. Bien que l'on estime que la première cause actuelle de perte de biodiversité est liée à la destruction d'habitat, suivi de près par les invasions biologiques, le changement climatique risque de devenir la plus importante cause de perte de biodiversité dans les années à venir (Pereira *et al.*, 2010).

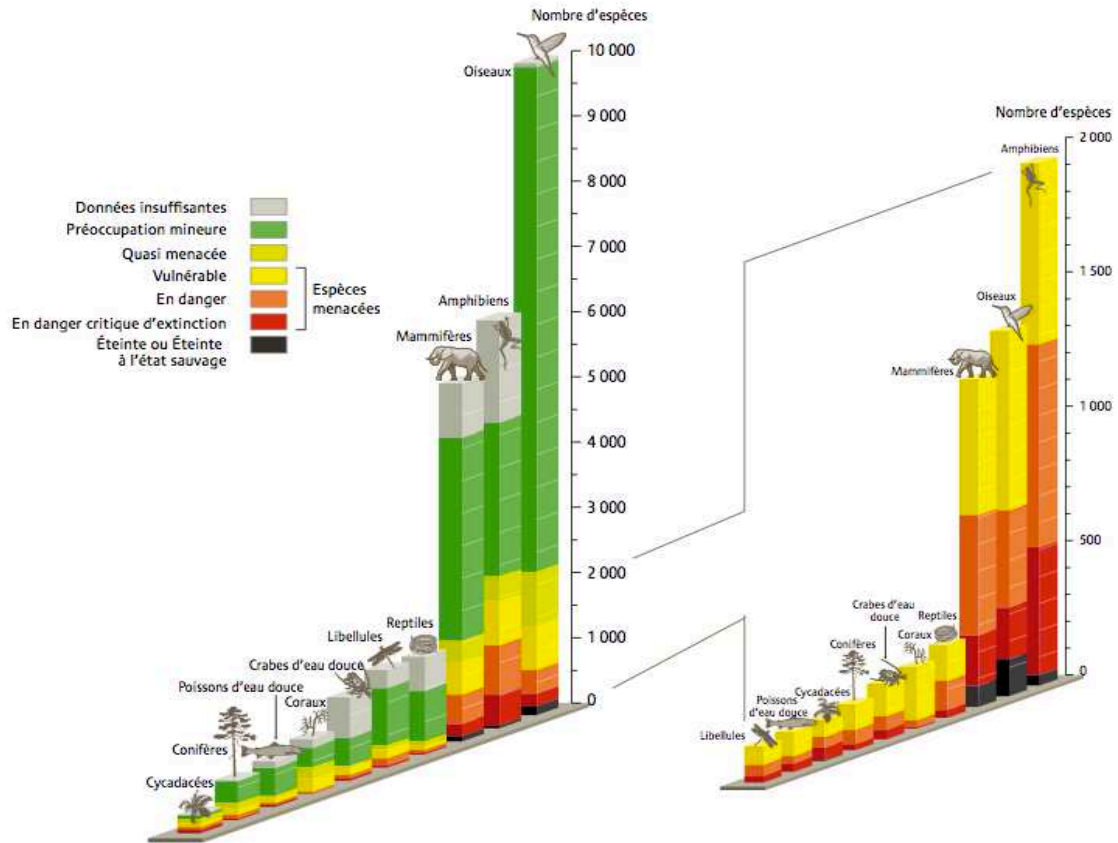


Figure 1 : Nombre et proportion pour chaque catégorie de menace, d'espèces issues de groupe taxonomiques qui ont été largement évalués ou dont le statut a été estimé à partir d'un échantillon aléatoire de 1500 espèces (libellules et reptiles). Source IUCN

1.2. LES CHANGEMENTS CLIMATIQUES

1.2.1. LES CHANGEMENTS CLIMATIQUES: DEFINITIONS ET SPECIFICITÉS.

Selon l'IPCC (Intergovernmental Panel of Climate Change), le changement climatique est défini comme: *“une variation de l'état du climat que l'on peut déceler par des modifications de la moyenne et/ou de la variabilité de ses propriétés et qui persiste pendant une longue période (généralement pendant des décennies ou plus)”* (IPCC et al., 2007). Depuis ces dernières années, le changement climatique est devenu l'un des sujets les plus étudiés. Près de 100 000 études scientifiques ont discuté des changements climatiques ces dix dernières années.

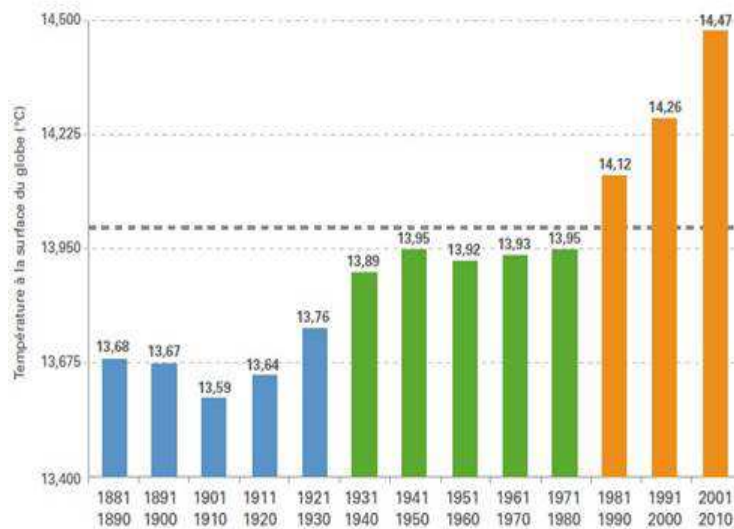


Figure 2 Moyenne décennale des températures à la surface du globe (°C) issus du rapport de l'organisation météorologique mondiale.

Parmi les conséquences de ces changements climatiques, la première est que les températures ont en moyenne augmenté dans le monde d'environ $+0.74^{\circ}\text{C}$ [$0.56\text{-}0.92^{\circ}\text{C}$] depuis 1979. Le changement du climat est sans équivoque (IPCC *et al.*, 2007), l'ensemble des continents (sauf l'Antarctique) ont subi un réchauffement important ces 50 dernières années. Par ailleurs, la première décennie du 21^{ème} siècle est à la fois la plus chaude et la plus arrosée depuis 1881 (Figure 2) ("Organisation Mondiale de la Météorologie," 2013). Le climat est un phénomène dynamique, que ce soit à l'échelle journalière ou celle des temps géologiques, il a toujours fluctué et continuera à le faire dans le futur. D'importants changements de climat qui ont déjà eu lieu dans le passé ont été à l'origine de bouleversements écologiques majeurs comme la crise de la fin du crétacé qui a entraîné la disparition de 76% des espèces présentes (Barnosky *et al.*, 2011). Mais ce qui rend ce récent changement climatique si particulier est la vitesse à laquelle il a lieu. On estime que la vitesse du changement de climat est 100 fois supérieure à celle produite au cours des temps géologiques (Pimm & Raven, 2000). De plus, la seconde particularité de ce changement climatique est l'origine de ce dernier. Selon l'IPCC, les rejets de gaz à effet de serre dus à l'activité humaine sont à l'origine des changements climatiques avec un degré de confiance très élevé (90%). On estime que ces rejets (dioxyde de carbone, méthane et oxyde nitreux), qui remplissent l'atmosphère depuis des milliards d'années, ont fortement augmenté depuis 1750. En particulier, la concentration du CO_2 a augmenté de 80% entre 1970 et 2004 (IPCC *et al.*, 2007). De plus en 2005, les concentrations en CO_2 et CH_4 ont largement excédé l'intervalle de la variation naturelle observé durant les

650 000 dernières années (IPCC *et al.*, 2007). Les principales causes de la libération de ces gaz dans l'atmosphère sont l'utilisation de combustibles fossiles et l'agriculture.

1.2.2. LES DIFFERENTES COMPOSANTES DES CHANGEMENTS CLIMATIQUES

Bien que le changement climatique soit souvent associé à une hausse globale de la température, il englobe en réalité un plus grand nombre de phénomènes. Un tel réchauffement entraîne par exemple une augmentation moyenne du niveau des mers. Depuis 1961, le niveau moyen de la mer a ainsi augmenté de 1.8 mm/an (IPCC *et al.*, 2007) et s'est accéléré avec 3.1 mm/an d'augmentation depuis 1993 (IPCC *et al.*, 2007), soit le double de celui constaté en moyenne sur tout le 20^{ème} siècle (>1.6 mm par an) ("Organisation Mondiale de la Météorologie," 2013). Cette augmentation est principalement due à la dilation thermique des océans pour 57% et à la fonte des glaciers pour 28% (Cazenave & Llovel, 2007; IPCC *et al.* 2007). Globalement, la fonte des glaciers et le déclin de la couverture neigeuse s'est accéléré dans les deux hémisphères. L'étendue annuelle moyenne des glaces a diminué de 2,7% par décennie dans l'océan Arctique, et un recul encore plus important a été observé durant la période d'été (7,4%). Par ailleurs, le régime des précipitations change également. On a ainsi observé une augmentation significative des précipitations dans le nord de l'Europe, dans l'est de l'Amérique du Nord et du Sud et dans le centre de l'Asie, alors qu'elles ont diminué au Sahel, en Méditerranée, en Afrique austral et dans une partie de l'Asie du Sud entre 1900 et 2005. De plus, les nombreuses observations depuis 1970 mettent en évidence une augmentation progressive de l'activité cyclonique dans l'Atlantique Nord (IPCC *et al.*, 2007). Enfin, l'augmentation de la concentration en CO₂ dans l'atmosphère a accentué l'acidité du milieu marin, avec un pH océanique ayant diminué d'environ 0.1 unité depuis 1750 (IPCC *et al.*, 2007). Le changement climatique en cours, risque ainsi de s'accroître si aucune mesure n'est mise en œuvre pour stopper les émissions de CO₂. C'est pour cette raison que de nombreuses études ont cherché à prévoir l'évolution des changements climatiques futurs selon différents scénarios de développements économiques et technologiques.

1.2.3. PROJECTIONS FUTURES DES CHANGEMENTS CLIMATIQUES

En faisant l'hypothèse que les émissions mondiales de gaz à effet de serre augmenteront dans les prochaines décennies, il est possible d'inférer une augmentation moyenne de la température et de simuler l'évolution du système climatique au cours du temps. Il existe

plusieurs prédictions de température et de précipitations qui sont disponibles pour différents scénarios d'émission de CO₂ et pour une vingtaine de modèles climatiques de circulation générale (Figure 3). J'ai utilisé trois modèles climatiques différents, les plus classiquement utilisés dans la littérature durant cette thèse : HADCM3 : *Hadley Centre for Climate Prediction and Research, Met Office (UKMO), UK* ; BCM2 : *Bjerknes Centre for Climate Research (BCCR), Univ. Of Bergen, Norway* et CSIRO2 : *The centre for Australian weasther and climate research, CSIRO and the bureau of meteorology*. Par ailleurs, j'ai aussi utilisé deux scénarios d'émissions de CO₂ contrastés. Le scénario A1B qui correspond à un monde futur où la croissance économique sera très rapide, la population mondiale atteindra un maximum au milieu du siècle pour décliner ensuite et de nouvelles technologies plus efficaces seront introduites rapidement, on prévoit également un équilibre entre les combustibles fossiles et les sources d'énergie autres que fossiles, la technologie n'étant pas excessivement dépendante d'une source d'énergie particulière. J'ai également utilisé le scénario B2A, il correspond à un monde où l'accent est placé sur des solutions locales de viabilité économique, sociale et environnementale. Il s'agit d'un niveau intermédiaire de développement économique et d'évolution technologique qui est moins rapide que dans le scénario A1B. D'après ces scénarios, la température moyenne pourrait augmenter de 1,1°C à 4,4°C à la fin du siècle par rapport aux années 1990. Il est également hautement probable que l'on observe une hausse des précipitations aux latitudes élevées et, au contraire, une diminution sur les zones subtropicales. Les modèles de prédiction des évènements climatiques extrêmes montrent que l'intensité des ouragans, tornades, sécheresses ou inondations, pourraient augmenter durant les prochaines décennies. Au contraire, le nombre de cyclones tropicaux pourraient diminuer sur l'ensemble de la planète (IPCC *et al.*, 2007). Par ailleurs, le dernier rapport de l'IPCC concernant l'augmentation du niveau de la mer faisait état d'une hausse probable de 18 à 59 cm pour la période comprise entre 2090-2099 (IPCC *et al.*, 2007). Désormais, il est largement accepté que la hausse moyenne du niveau de la mer risque d'être plus importante, entre 0,5 et 2,3 mètres à la fin de ce siècle (Rahmstorf, 2007; Pfeffer *et al.*, 2008; Grinsted *et al.*, 2009; Nicholls & Cazenave, 2010; Traill *et al.*, 2011). Globalement, il reste difficile de prévoir l'ensemble des conséquences du réchauffement climatique, notamment en raison de nombreuses interactions et d'effets en cascades qui peuvent avoir lieu en conséquence d'une simple hausse de la température.

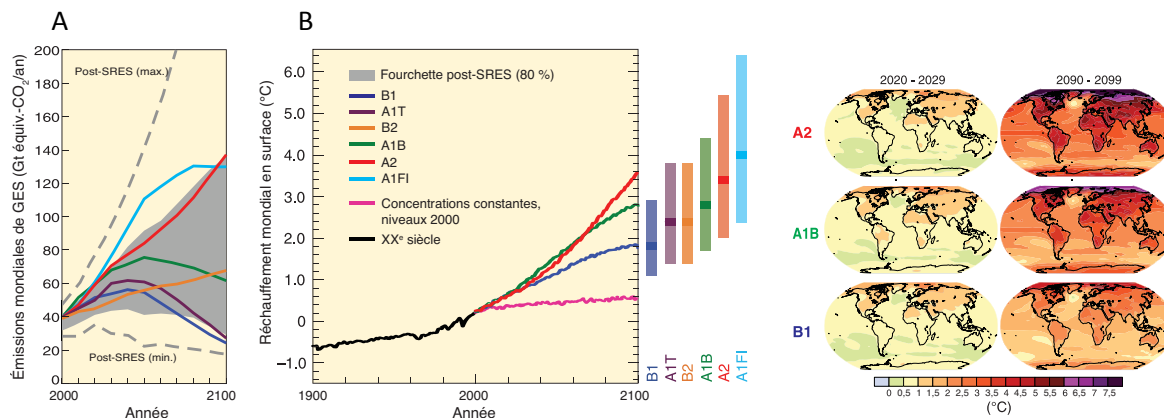


Figure 3 A Scénarios d'émissions de gaz à effets de serre pour la période de 2000 à 2100 B projections relatives aux températures en surface. Tiré de l'IPCC 2007

1.3. EFFETS DES CHANGEMENTS CLIMATIQUES SUR LA BIODIVERSITE

1.3.1. EFFETS ACTUELS DES CHANGEMENTS CLIMATIQUES SUR LA BIODIVERSITE

Les multiples composantes des changements climatiques peuvent affecter l'ensemble des niveaux de la biodiversité. Ce sujet a surtout été développé dans le Chapitre 1 et dans l'étude de Parmesan et al. (2006) mais nous allons brièvement décrire comment les changements climatiques peuvent affecter ces différents niveaux. Tout d'abord, en raison des changements climatiques la diversité génétique peut diminuer, ce qui peut également affecter le fonctionnement des écosystèmes et leur résilience aux pressions environnementales (Botkin *et al.*, 2007). Par ailleurs, les changements climatiques peuvent également avoir des conséquences au niveau des individus et des populations. C'est par exemple le cas pour de nombreuses espèces introduites, pour lesquelles la sélection naturelle a été à l'origine de changements phénotypiques qui a permis l'augmentation de leur capacité d'adaptation (Lavergne *et al.*, 2010). Au-delà des effets au niveau de la diversité génétique ou spécifique, les changements climatiques peuvent modifier l'ensemble des relations interspécifiques qui régissent les communautés comme les relations de compétition, de proie/prédateurs (Gilman *et al.*, 2010) et ainsi modifier les communautés d'espèces et les écosystèmes (Walther, 2010). L'une des principales causes de ces changements interspécifiques est le changement dans la phénologie des espèces. De nombreuses études ont révélé un changement dans la phénologie en Europe et en Amérique du nord qui est probablement lié aux changements climatiques

(Walther et al., 2002). Les événements de printemps, comme la date de floraison, ont lieu 2,3 jours plus tôt par décennie par rapport à ce qu'ils étaient auparavant (Parmesan & Yohe, 2003). Une étude sur une période de 40 ans en Russie a montré que les événements de phénologie année après année chez les plantes, les reptiles et les insectes ont varié, mais que ces espèces ont conservé un fort degré de synchronie (Ovaskainen *et al.*, 2013). Parmesan et al. (2003) a également mis en évidence que le déplacement d'aires de distribution pour 279 espèces était d'environ 6,1 km par décennie vers les pôles. En général, les adaptations des espèces aux changements climatiques peuvent être spatiales (déplacement d'aires de distribution), temporelles (changement de phénologie) ou encore à l'échelle même de l'organisme (modification des taux hormonaux) (voir Figure 2, Chapitre 2). Les deux premiers types d'adaptation sont particulièrement bien documentés et étudiés alors que les changements physiologiques ne sont que très peu étudiés. De manière générale, il reste difficile de mettre en évidence des relations directes entre le changement climatique et les récents changements aux différents niveaux de la biodiversité ou même à la seule échelle de l'espèce, d'autant que les données biologiques à très long terme sont encore rares.

Il est également important de mentionner que la majorité des études qui s'intéressent aux conséquences actuelles des changements climatiques sur la biodiversité se penchent majoritairement sur les aspects négatifs. Or il a été mis en évidence que des températures plus clémentes et une augmentation du CO₂ pourraient être bénéfiques pour de nombreuses plantes (Mainka and Howard, 2010).

1.3.2. PREDICTIONS DES PERTES DE BIODIVERSITE SUITE AUX CHANGEMENTS CLIMATIQUES.

Dans la partie précédente, nous avons montré que les espèces peuvent répondre de multiples façons aux changements climatiques. Actuellement, de nombreuses études visent à prédire les conséquences de ces futurs changements climatiques sur la biodiversité. L'ensemble de ces études utilise des approches de modélisation corrélative (voir section 1.5.2.1). Elles prédisent une perte importante de la biodiversité mais également une forte variabilité dans leurs estimations allant par exemple de 0,3% à 30% pour les oiseaux (Jetz *et al.*, 2007) ou de 2 à 84% de perte d'espèces de plantes par pixel en Europe (Thuiller *et al.*, 2005, voir Figure 4 du Chapitre 2). En se focalisant sur les 25 hotspots de biodiversité, il a également été montré que 39 à 43% des espèces endémiques de ces hotspots pourraient disparaître dans le pire des scénarios (Malcolm *et al.*, 2006). En ce qui concerne les

écosystèmes aquatiques, la perte de richesse spécifique des poissons pourrait atteindre 75% dans certaines rivières (Xenopoulos *et al.*, 2005). Finalement, en fonction des taxons ou des régions étudiés, les estimations de perte de biodiversité sont très variables (Bellard *et al.*, 2012). Pour autant, ces estimations sont supérieures aux taux d'extinction actuels mais également aux taux d'extinction estimés par les données fossiles (Pereira *et al.*, 2010). Par ailleurs, une étude menée par l'UICN utilisant 9856 oiseaux, 6222 amphibiens, et 799 récifs coralliens, estiment que 35% des oiseaux, 52% des amphibiens et 71% des espèces des récifs coralliens ont des caractéristiques qui les rendent particulièrement vulnérables aux changements climatiques (Foden *et al.*, 2008).

Finalement, seule une faible proportion d'études testent expérimentalement les conséquences de ces changements à l'échelle d'une seule population ou même d'une communauté simplifiée. De plus, la majorité des études se concentrent sur des taxons qui ne représentent qu'une faible partie de la biodiversité : les plantes, les mammifères, les reptiles et les poissons.

1.3.3. INTERACTIONS POSSIBLES AVEC D'AUTRES MENACES

De nombreuses études ont suggéré que les changements climatiques et les autres menaces qui pèsent sur la biodiversité comme le changement d'utilisation des sols, les invasions biologiques, la pollution ou la surexploitation pourraient interagir pour conduire à des conséquences encore plus importantes (Sala *et al.*, 2000; Brook *et al.*, 2008; Walther *et al.*, 2009). Par exemple, la fragmentation de l'habitat et la surexploitation ont conduit à une diminution 50 fois plus rapide des populations de rotifères (Mora *et al.*, 2007). De plus, la plupart des extinctions qui se sont déjà produites ont impliqué différents facteurs d'extinctions. L'un des exemples les plus célèbres de synergie entre différents facteurs d'extinctions est le cas des amphibiens des forêts tropicales du Costa Rica. Dans cet exemple, il a été montré que 67% des 110 amphibiens endémiques ont disparu entre 1980 et 1990 à cause d'une espèce invasive, un agent parasitaire et en raison du réchauffement climatique (Pounds *et al.*, 2006). Dès 2000, Sala *et al.* (2000) ont mis en avant que la fragmentation de l'habitat, la pollution, la surexploitation ou les invasions biologiques pourraient interagir avec les changements climatiques et conduire à des effets encore plus importants sur la biodiversité. Pourtant, très peu d'études ont aujourd'hui explicitement étudié les effets synergiques possibles entre les différents facteurs d'extinction (*e.g.*, Jetz *et al.*, 2007; Ficetola *et al.*, 2007; Murray *et al.*, 2012; Leroy *et al.*, 2013). On peut quand même citer quelques

études qui ont discuté théoriquement des effets potentiels des changements climatiques sur les invasions biologiques (Hellmann *et al.*, 2008; Bradley *et al.*, 2009; Walther *et al.*, 2009; Diez *et al.*, 2012) ou qui ont modélisé à l'échelle d'une espèce (Leroy *et al.*, 2013) ou d'un seul groupe taxonomique (Peterson *et al.*, 2008) cette interaction explicitement. C'est pourquoi, je me suis intéressée dans le cadre de mon projet de thèse à l'effet conjugué des changements climatiques et des changements d'utilisation des sols sur les invasions biologiques.

1.4. LES ESPECES INVASIVES UNE MENACE À PART ENTIERE.

1.4.1. CARACTERISATION DES INVASIONS BIOLOGIQUES

DEFINITION

Une invasion biologique est le résultat d'une introduction délibérée ou accidentelle d'une population d'espèce dans un milieu qui n'est pas son milieu d'origine. Avant d'être qualifiée d'espèce invasive, une population de cette espèce doit franchir différentes étapes (Blackburn *et al.*, 2011) (Figure 4). Une fois introduite dans un nouveau milieu l'espèce doit s'adapter aux nouvelles conditions biotiques et abiotiques afin de survivre et de se reproduire, l'espèce est alors dite naturalisée (Richardson *et al.*, 2000). Un des principaux facteurs de succès dans ce cas est la pression de propagule (le nombre d'individus introduits) (Lockwood *et al.*, 2005). Plus le nombre d'individus introduits est important, plus la population est en mesure de s'adapter aux nouvelles conditions (car en moyenne la diversité génétique augmente avec le nombre d'individu) ce qui permet de faire face à d'éventuelles pressions de sélection (Lockwood *et al.*, 2005). La dernière étape de l'invasion se caractérise par une expansion spatiale de la population. Cette étape dépend largement des capacités de dispersion de l'espèce mais également de la structure spatiale du paysage (With, 2002). Il faut noter que toutes les espèces qui sont introduites dans de nouveaux écosystèmes ne deviennent pas nécessairement invasives. On considère, d'une façon très générale, que sur 10% des espèces introduites qui se retrouvent dans le milieu, seules 10% sont capables de survivre et de se reproduire et que parmi cette faible proportion seulement 10% vont générer un impact néfaste sur les communautés natives. En Europe par exemple sur 10 000 populations non natives seules 11% ont un impact écologique (Vilà *et al.*, 2010). Cependant cette proportion d'espèces invasives varie grandement en fonction de l'écosystème d'accueil et de la pression de propagule qu'il reçoit. De plus, il reste difficile de démontrer l'impact des espèces invasives sur les communautés naturelles, c'est pourquoi l'ensemble de la communauté

scientifique n'est toujours pas d'accord sur l'ajout systématique de la notion d'impact dans la définition d'une espèce invasive. J'ai délibérément choisi d'utiliser le terme espèce invasive et non envahissante tout au long de ce manuscrit de thèse. J'ai notamment fait ce choix pour deux principales raisons. Tout d'abord le terme invasive est de plus en plus utilisé dans la langue française, ensuite il me semble que le terme envahissant ne traduit pas suffisamment de la notion d'impact.

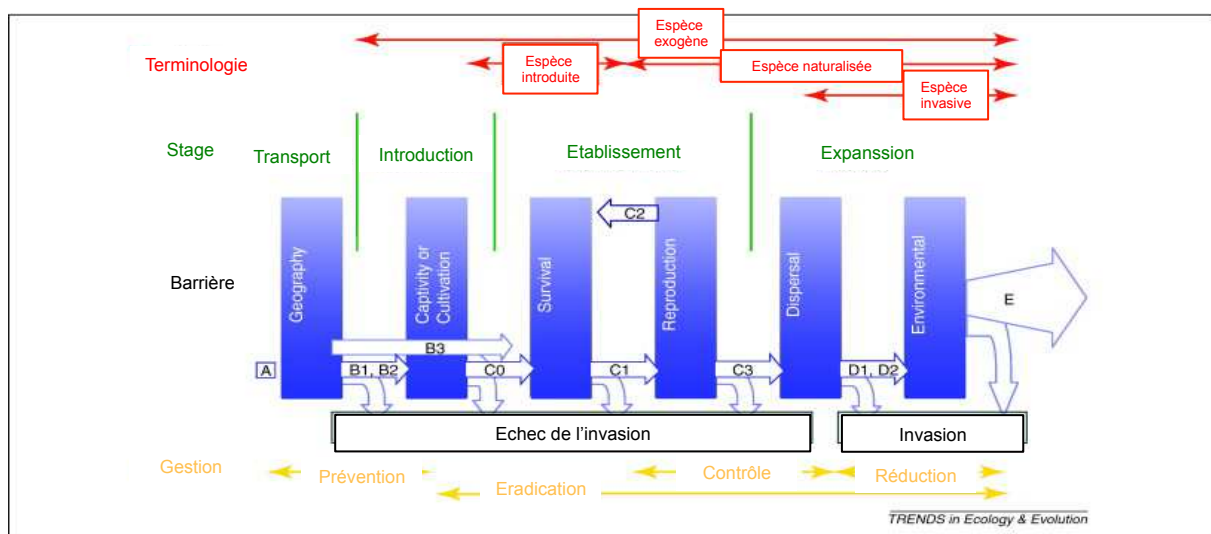


Figure 4 Les différentes étapes d'invasion, figure de Blackburn et al. 2011.

Par ailleurs, l'origine géographique de l'espèce peut également amener à certains désaccords (Valéry *et al.*, 2009, 2013). Dajoz (2008) définit par exemple les espèces invasives comme « celles qui, par leur prolifération dans les milieux naturels ou semi-naturels, y produisent des changements significatifs de composition, de structure et/ou de fonctionnement des écosystèmes » (Dajoz, 2008). Willanson (1996) parle d'invasion biologique quand un organisme, accroît durablement son aire de répartition, quelque soit sa région d'origine ou son impact. Il me semble qu'intégrer la notion d'impact dans la définition d'une espèce invasive est indispensable. En effet, la menace exercée par les espèces invasives est encore mal connue du grand public et le message risque alors d'être plus confus si nous incluons parmi les espèces invasives, des espèces dont on a pu montrer qu'elles n'ont aucun impact. C'est pourquoi dans cette thèse je définis une espèce invasive comme une espèce introduite dans des aires se situant hors de son aire native, où elle est capable de s'établir, de se propager, et de générer un impact négatif sur l'écosystème envahi. Il est également important de préciser qu'une espèce définie comme exogène dans un écosystème peut devenir invasive après un

certain temps de latence (« time lag »), la plupart des invasions n'étant pas immédiatement des succès (Crooks & Soule, 1999). Par exemple, les fourmis de feux ont été importées aux Etats-Unis en 1918, et ce n'est que 20 ans plus tard que les populations ont commencé à envahir la plupart des états (Callcott & Collins, 1996).

STATUT ET TENDANCES

L'homme a transporté des espèces invasives pendant des millénaires mais deux étapes importantes ont influencé l'évolution du nombre d'espèces invasives : la fin du Moyen âge et le début de la révolution industrielle (Hulme, 2009). En effet, la fin du Moyen âge correspond au début des explorations, à la naissance du colonialisme et à un changement radical de l'agriculture, du commerce et de la démographie humaine. Ensuite, la révolution industrielle coïncide avec une augmentation du commerce internationale, la construction de canaux, de routes et de voies ferroviaires. Par ailleurs, l'augmentation importante durant les dernières décennies des échanges commerciaux et humains, notamment via le tourisme, a considérablement multiplié les opportunités d'introductions d'espèces. De nombreuses espèces sont désormais capables de franchir des frontières géographiques (océans, chaînes de montagne), qui étaient autrefois infranchissables. En Europe le nombre d'espèces invasives a ainsi augmenté de 76% entre 1976 et 2007 (Butchart et al., 2010). La pression qu'exercent les espèces invasives sur la biodiversité a également augmenté en Asie (Xu *et al.*, 2012), en Amérique du nord (Levine & D'Antonio, 2003; Aukema *et al.*, 2010) et en Europe (Waage *et al.*, 2008). Cette augmentation exponentielle du nombre d'espèces introduites conduit indéniablement à une augmentation du nombre d'invasions biologiques. Elle conduit également à une homogénéisation des espèces au fil du temps. Par exemple, la totalité de la faune actuelle de mammifères non volants présent en Corse, s'est uniquement constituée avec des espèces introduites au fil des 7500 dernières années.

1.4.2. CONSEQUENCES DES INVASIONS BIOLOGIQUES

Les espèces invasives représentent actuellement la seconde plus importante menace qui pèse sur la biodiversité (Corvalan *et al.*, 2005) et ont été la première cause d'extinction d'espèce au cours des 500 dernières années (Donlan & Wilcox, 2008). De nombreux cas d'extinction d'espèces en raison de la présence d'espèces invasives ont été mis en évidence. Par exemple les mammifères terrestres sont à l'origine de l'extinction d'espèces d'amphibiens, d'oiseaux, de poissons (Courchamp *et al.*, 2003). L'UICN a également démontré que les espèces invasives étaient responsables à elles seules de 11% des menaces

qui pèsent sur les amphibiens et 8% des menaces qui pèsent sur les mammifères (IUCN, 2013). Par ailleurs, les îles sont particulièrement touchées avec 67% des oiseaux considérés comme menacés par les espèces invasives contre 8% pour les oiseaux dits « continentaux » (IUCN, 2013; Blackburn et al., 2004; Duncan & Blackburn, 2007). De plus, le risque d'extinction des oiseaux, des mammifères et des amphibiens a largement augmenté ces dernières années en raison des espèces invasives (Figure 5). Les espèces invasives sont d'ailleurs le facteur le plus important expliquant l'aggravation du statut UICN des amphibiens (McGeoch *et al.*, 2010). De nombreuses études ont également montré que la présence d'herbivores, de décomposeurs ou de prédateurs invasifs peut conduire à une transformation de la composition des communautés ou modifier les propriétés même d'un écosystème (Deutsch *et al.*, 2008).

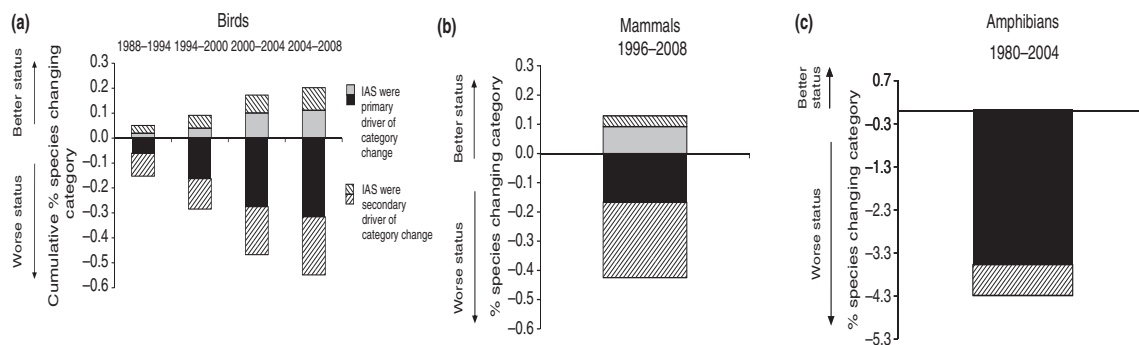


Figure 5 Nombre d'oiseaux (a), de mammifères (b) et d'amphibiens (c) subissant un changement de statut UICN en raison de l'effet des espèces invasives, issu de McGeoch *et al.*, (2010).

Les conséquences des espèces invasives pour la société sont également nombreuses, elles touchent à la fois l'écologie, l'économie mais également la santé. Les dommages des invasions coûtent chaque année plus de 1,4 milliards de dollars, soit 5% de l'économie mondiale (Nature conservancy, 2013), elles sont également responsables de la transmission de nombreuses maladies, et peuvent perturber d'importants services éco-systémiques tels que la sécurité alimentaire et l'accès à l'eau (Vilà *et al.*, 2010).

1.4.3. INTERACTIONS ENTRE LES CHANGEMENTS CLIMATIQUES ET LES INVASIONS

Les caractéristiques même des espèces invasives, comme leurs capacités à survivre dans des environnements changeants ou à se reproduire, pourraient conduire à de meilleures chances de survie face aux espèces natives pendant une période de changements climatiques. En fait, les changements climatiques peuvent d'altérer l'ensemble des étapes d'une invasion (la pression de propagule, la colonisation, la probabilité d'établissement et l'expansion) mais également la gestion des espèces invasives (Hellmann et al., 2008; Pyke et al., 2008 ;Diez et al., 2012) (Figure 6). Les changements climatiques peuvent par exemple offrir de nouvelles opportunités afin de franchir des barrières géographiques qui étaient auparavant insurmontables. Ils peuvent également fournir de nouvelles routes d'invasions. La diminution de la couverture neigeuse de l'arctique a déjà permis l'arrivée d'une nouvelle espèce de diatomée (Reid *et al.*, 2007). De plus, les événements climatiques tels que les tsunamis, dont la fréquence risque d'augmenter dans le futur peuvent jouer un rôle primordial pour amener de nouvelles espèces à des milliers de kilomètres de distance (Diez *et al.*, 2012). Le tsunami de mars 2011 qui a frappé le Japon est responsable de l'arrivée de 30 à 50 nouvelles espèces de plantes et d'animaux y compris des espèces invasives, sur les côtes américaines (Chapman, 2013). L'ouragan Katrina en 2006 a également permis le déplacement de millions de tonnes de bois infestés par les termites (Mainka & Howard, 2010). Les changements climatiques risquent donc d'affecter à la fois la fréquence des invasions et les voies d'invasions. Ils peuvent également agir indirectement sur les espèces invasives en diminuant la capacité de survie des espèces natives là où les espèces invasives ont de plus grandes capacités d'adaptation.

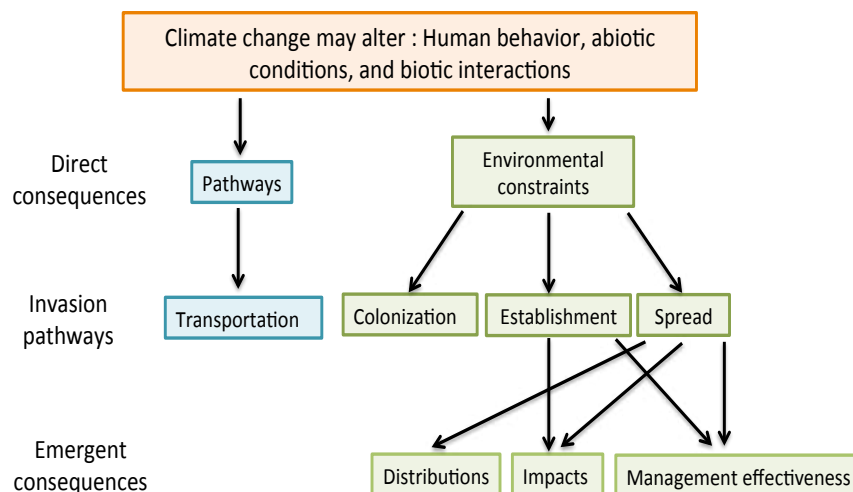


Figure 6 Les conséquences des changements climatiques sur les invasions biologiques (d'après Hellman et al. 2008)

Une étude menée à Harvard a d'ailleurs montré que les espèces invasives ont déjà été largement favorisées par les récents changements climatiques (Willis & Bhagwat, 2009). En effet, depuis 1850, seules les espèces capables d'ajuster le « timing » de leur physiologie ont profité de la hausse des températures pour s'étendre, alors que les espèces moins flexibles ont décliné parfois jusqu'à l'extinction locale (Willis & Bhagwat, 2009). De plus, les changements climatiques peuvent augmenter les possibilités d'invasion en créant des perturbations dans les écosystèmes. Des espèces introduites qui étaient limitées par des périodes de croissance trop courtes, et n'étant donc pas capables de donner des fruits ou de concurrencer les espèces résidentes, pourraient être favorisées par les changements climatiques (e.g., *Prunus laurocerasus*, dans les zones tempérées d'Europe centrale). L'augmentation des niveaux de CO₂ pourrait également favoriser les taux de croissance de la plupart des plantes invasives (Mainka and Howard, 2010).

En outre, les changements climatiques vont directement influencer les contraintes environnementales qui limitent l'aire de répartition de ces espèces. De nombreuses études ont ainsi tenté d'évaluer le changement d'aire de répartition des espèces invasives en raison des changements climatiques, mais aucune étude n'a analysée un large échantillon d'espèces invasives issu de différents groupes taxonomiques. Peterson et al. (2008) a étudié les changements d'aires potentielles de 2 362 espèces de plantes européennes montrant globalement un déclin de 2,4 à 3,1%. Cette étude est la première à avoir mis en évidence, sur un grand nombre d'espèces, qu'elles ne répondent pas uniformément aux changements climatiques. Certaines espèces de plantes de l'hémisphère sud tendent à augmenter leur potentiel d'invasion, là où les espèces de l'hémisphère nord diminuent plutôt leur potentiel invasif (Peterson *et al.*, 2008). Pour autant il faut savoir qu'en général les espèces invasives n'envahissent que la moitié de leur aire potentielle et qu'il faut environ 150 ans pour qu'une néophyte atteigne son pic d'expansion (Gassó *et al.*, 2012). Il faut également noter que la plupart des recherches qui étudient les effets des changements climatiques sur la biodiversité sont restreintes au groupe des plantes; ce sujet reste donc encore largement inexploré pour les autres groupes taxonomiques. Finalement, les changements climatiques vont influencer à la fois la répartition des espèces invasives, mais également leur impact sur les communautés natives.

1.5. PROBLEMATIQUE ET PLAN DE THESE

1.5.1. PROBLEMATIQUE

Comme le soulignent les éléments précédents, le changement climatique est probablement un des défis majeurs des prochaines décennies pour la biodiversité. De nombreuses études révèlent déjà des conséquences importantes du réchauffement climatique sur la biodiversité. Ces études démontrent également qu'un bouleversement du cortège des espèces et de nombreux risques d'extinction pourraient se produire à l'avenir. À l'heure actuelle, en raison de la multiplication des études et des approches employées, il est difficile d'avoir une vision synthétique des conséquences potentielles des changements climatiques sur la biodiversité.

L'objectif principal de ce travail de thèse a été d'améliorer la caractérisation et la quantification des différents impacts des changements climatiques sur la biodiversité à l'échelle mondiale par des approches de modélisations et de méta-analyses. Pour commencer ce travail de thèse, nous avons passé en revue la littérature sur les effets des changements climatiques sur la biodiversité. Nous avons également discuté des approches utilisées, afin de mettre en lumière les lacunes et limites de ce type d'approches. Le premier Chapitre de ma thèse porte donc sur une synthèse de 122 articles qui discutent des effets potentiels des changements climatiques sur la biodiversité (à ces trois différents niveaux). Suite à cette revue, nous avons mis en évidence des pistes de recherche qui ont été jusqu'à présent peu étudiées, et qui pourraient aider à une meilleure compréhension et évaluation des conséquences des changements climatiques. Nous avons notamment identifié trois défis majeurs :

- (1) De considérer les conséquences potentielles de la hausse du niveau des mers, une des composantes des changements climatiques qui est actuellement peu étudiée;
- (2) D'étudier les synergies possibles entre différents facteurs de changements globaux : étudier les effets conjugués des changements climatiques et des changements d'utilisation des sols sur les invasions biologiques et
- (3) D'inscrire les études des changements climatiques dans une perspective de conservation en se focalisant sur les hotspots de biodiversité.

Dans le cadre de ces recherches, nous nous sommes focalisés sur deux modèles d'études : les hotspots de biodiversité et la liste des 100 cas d'espèces invasives parmi les

pires au monde. De plus, nous nous sommes concentrés sur deux approches complémentaires : les modèles de distribution d'espèce et l'analyse des climats analogues.

1.5.2. LES APPROCHES ET MODELES D'ETUDE

Lors de ma thèse je me suis attachée à décrire et comprendre les effets des changements climatiques sur la biodiversité et sur la distribution des espèces invasives à de grandes échelles spatiales (les hotspots de biodiversité ou le monde) et temporelles (2050 ou 2100). Jusqu'à présent peu d'études ont analysé les différentes conséquences des changements climatiques en tenant compte de la hausse du niveau des mers. De plus, aucune étude à ma connaissance n'a examiné les effets conjugués des changements climatiques et des changements d'utilisation des sols sur différents groupes taxonomiques d'espèces invasives. En effet, la majorité des études se concentre sur une seule espèce, ou un seul groupe taxonomique (*e.g.*, les plantes). Afin de mener à bien cette thèse, j'ai notamment utilisé les modèles de distribution d'espèces pour d'étudier les conséquences des changements climatiques et des changements d'utilisation des sols sur la distribution des « 100 espèces invasives parmi les pires au monde ». De plus, j'ai utilisé des analyses de climats analogues afin de déterminer l'exposition et la vulnérabilité des hotspots de biodiversité aux changements climatiques.

1.5.2.1. MODELES DE DISTRIBUTION D'ESPECES

Ces dernières années ont vu un intérêt grandissant pour les modèles de distribution d'espèces. Ces modèles empiriques sont basés sur des observations de distribution d'espèces analysant la relation statistique (ou corrélation) entre la distribution d'une espèce et les valeurs des variables abiotiques (climatiques, types d'habitats) ou biotiques (interactions avec d'autres espèces) où l'espèce est présente. Ils sont basés sur l'hypothèse que les variables incorporées dans les modèles sont les principaux facteurs qui influencent la distribution d'une espèce. Les variables incorporées dans le modèle peuvent être théoriquement biotique ou abiotique. En réalité, on choisit des variables qui peuvent avoir un effet direct ou indirect sur la distribution des espèces et qui sont disponibles. Ainsi, des variables biotiques importantes sont souvent absentes de ce type de modèle. Pourtant il est par exemple important de considérer la distribution de l'espèce étudiée mais également des espèces qui sont en interaction avec cette dernière (Barbet-Massin & Jiguet, 2011). De plus, l'utilisation des

modèles de distribution d'espèces suppose que l'espèce modélisée est en équilibre avec son environnement, ce qui n'est pas toujours le cas, en particulier pour les espèces invasives (Broennimann *et al.*, 2007; Gallien *et al.*, 2012). En dépit de ces limitations, ces modèles offrent une méthode robuste pour prédire la distribution d'une espèce et ont de nombreuses applications (Jeschke & Strayer, 2008). Ces modèles ont notamment été utilisés pour évaluer les conséquences des changements climatiques sur des espèces menacées d'extinction (Leroy *et al.*, 2013), pour prévenir les invasions en définissant les zones favorables aux espèces invasives (Ficetola *et al.*, 2007) ou encore pour reconstruire les distributions passées d'espèces (voir annexe 3 : Cornille *et al.* 2013). La première étape consiste à calibrer les modèles avec les données de distribution de l'espèce et des variables environnementales actuelles. De nombreux types de modèles statistiques peuvent être utilisés pour prédire la distribution d'une espèce, telles que les méthodes de régression (GLM, GAM et MARS), les méthodes de classification (CTA) ainsi que les méthodes d'apprentissage (MaxEnt, ANN, RF et GBM). En utilisant les mêmes données de répartition d'espèces et de pseudo absences (absences générées aléatoirement où l'espèce n'est pas présente), les résultats des modèles statistiques peuvent être variables. Il a donc été conseillé de réaliser des distributions consensus (*i.e.*, moyenner les résultats de répartition potentielle d'espèces obtenues à partir de plusieurs de ces modèles statistiques) (Araújo & New, 2007). Ainsi, on peut prédire l'ensemble de la distribution potentielle d'une espèce à une échelle spatiale ou temporelle définie (Figure 7). Il existe plusieurs façons d'évaluer les performances des modèles, en prenant en compte les pourcentages de présences et d'absences correctement prédites (AUC, indice de Boyce et le TSS), (voir le Chapitre 6 pour les détails méthodologiques).

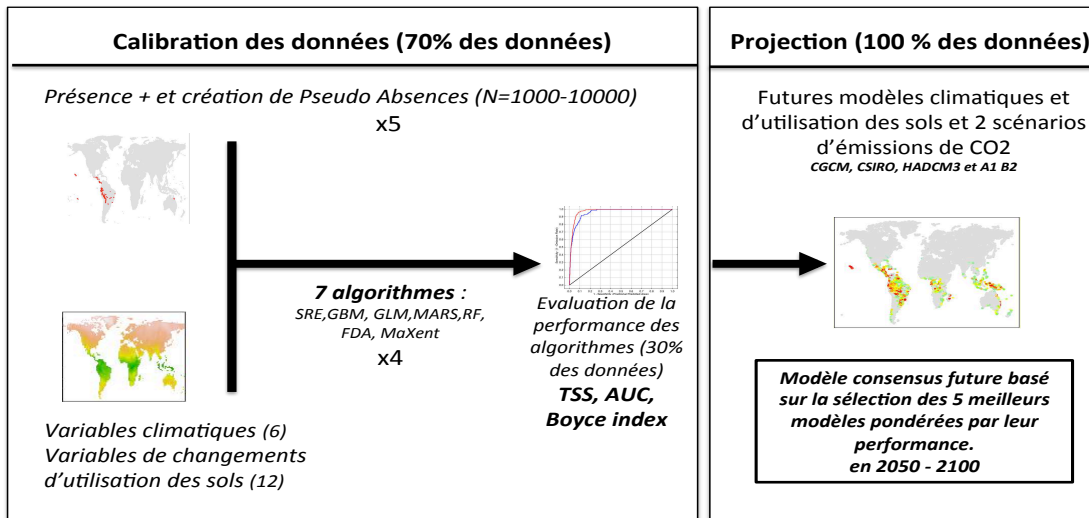


Figure 7 Étapes de la modélisation des distributions d'espèces. Les données de présence pour chacune des espèces sont collectées. Nous créons également des pseudo-absences pour chacune des espèces, car il n'est pas possible à l'échelle mondiale d'obtenir de réelles données d'absence. Nous avons également sélectionné les variables climatiques et de changements d'utilisation des sols qui ne sont pas corrélées entre elles (Pearson >0.75). Ensuite, à partir de 7 algorithmes, des modèles statistiques ont été calibrés sur 70% des données. Nous avons testé ces modèles statistiques indépendamment sur 30% des données et évalué la proportion de présences effectivement prédites comme présences et la spécificité qui est la proportion de pseudo-absences effectivement prédites comme pseudo-absences. Enfin, nous avons sélectionné les 5 meilleurs modèles en fonction de leur évaluation afin de projeter les effets des changements climatiques et les changements d'utilisation des sols sur les distributions futures des espèces d'intérêt.

1.5.2.2. LES ANALYSES DE CLIMAT ANALOGUE

Les analyses de climat analogue représentent une approche complémentaire pour évaluer le risque de changement climatique, sans inférer aucune préférence climatique aux espèces. Il est ainsi possible d'évaluer dans quelle mesure le climat futur va être différent du climat actuel. Contrairement aux modèles de distribution d'espèces, cette approche n'est pas espèce-centrée, mais région-centrée. Cette méthode consiste à calculer la dissimilarité entre les climats actuels et futurs dans une zone définie. Le « climat » est défini comme un ensemble multiple de variables de température et de précipitations. On peut alors calculer un seuil à partir duquel on va considérer que le climat est significativement différent de la zone géographique initiale dans l'espace et dans le temps. Les climats analogues sont donc définis comme des conditions climatiques qui sont semblables alors que les climats non analogues représentent des conditions climatiques qui sont significativement différentes. Cette méthode permet d'identifier les aires de fort changement climatique et notamment de localiser les zones où le climat actuel risque de disparaître (Williams *et al.*, 2007; Veloz *et al.*, 2011). Actuellement, les articles étudiant l'effet du climat sur la biodiversité utilisent surtout des modèles de distribution d'espèces, et très peu d'approches de climat analogue. Pourtant cette

approche a de nombreux avantages car elle permet de travailler à l'échelle de la région plutôt que d'être centrée sur une espèce cible et ne se base sur aucune hypothèse concernant les préférences thermiques d'une espèce ou sur ses capacités d'adaptation (Veloz *et al.*, 2011). En outre, c'est une approche complémentaire aux modèles de distribution d'espèces qui permet de déterminer les régions qui vont subir à la fois une perte de climat analogue et l'apparition de nouveaux climats. Cette méthode a été utilisée dans les Chapitre 7 et 8.

1.5.2.3. LES 35 HOTSPOTS DE BIODIVERSITE

Nous sommes actuellement dans une des plus grandes crises d'extinction que la Terre n'ait jamais connu. Les budgets alloués à la conservation à l'échelle du globe sont insuffisants au regard du nombre d'espèces menacées d'extinction. Identifier des priorités de conservation est donc crucial. C'est dans ce contexte que Norman Myers a défini en 1988, 10 forêts tropicales étant à la fois riches en termes de biodiversité et très menacées. En 1990, Myers ajouta 8 nouveaux « hotspots » de biodiversité à protéger en priorité. En 2000, cette liste a été réactualisée à 25 hotspots de biodiversité (Myers *et al.*, 2000) puis à 34 depuis 2004 (Mittermeier *et al.*, 2004) et finalement 35 depuis 2012 (Mittermeier *et al.*, 2012) (Figure 8). Ces hotspots répondent désormais à deux critères précis: ils doivent contenir au moins 1 500 espèces de plantes endémiques vasculaires et ils doivent avoir perdu au moins 70% de leur habitat original. Alors que les hotspots ne représentent que 2,3% de la surface terrestre, ils contiennent un nombre d'espèces endémiques extrêmement élevé. Environ 50% des plantes mondiales et 42% des espèces de vertébrés terrestres sont endémiques aux hotspots. Par ailleurs, 22 939 espèces de vertébrés terrestres sont présent dans les hotspots, soit 77% des espèces de vertébrés terrestres mondiaux (Schmitt, 2012). Les hotspots de biodiversité représentent donc à la fois les régions les plus riches en termes d'espèces endémiques et les régions les plus menacées à l'échelle mondiale. Cette liste a rencontré un large succès car plus de 750 millions de dollars ont été investis dans la sauvegarde et de protection des hotspots et plus de 9000 études scientifiques ont cité l'article de Myers. Cependant, l'ajout d'un nouvel hotspot de biodiversité à cette liste, laisse à penser que les efforts pour conserver la biodiversité sont actuellement insuffisants et que l'évaluation de la biodiversité doit constamment être menée afin de mettre en œuvre les hiérarchisations nécessaires au maintien de cette biodiversité. Par ailleurs, aucune étude n'a encore été menée pour mettre en avant le succès écologique de la mise en place des hotspots.

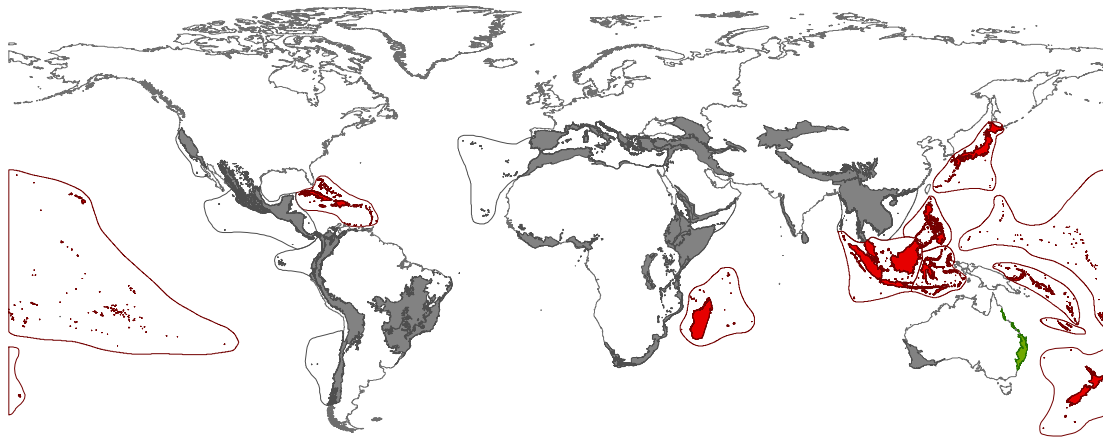


Figure 8 35 Hotspots de biodiversité, en rouge les dix hotspots insulaires et en gris les 24 hotspots terrestres et en vert le 35^{ème} hotspot : Forests of East Australia

1.5.2.4. LES 100 ESPECES INVASIVES PARMIS LES PIRES DANS LE MONDE

Dans les Chapitres 4, 5 et 6 nous avons utilisé la liste des 100 espèces invasives parmi les pires espèces invasives au monde. Cette liste a été établie par un groupe d'experts : « Invasive Species Specialist Group », (ISSG) au sein de l'UICN. Cette liste a été publiée en 2000 par plus de 1 000 biologistes des invasions du monde entier. L'un des objectifs principaux de cette liste était d'arriver à mieux communiquer sur les espèces invasives. A la différence des autres menaces qui pèsent sur la biodiversité, les invasions biologiques sont particulièrement hétérogènes en termes : d'origine (elles sont causées par différentes espèces), d'impacts économiques, écologiques et sanitaires. En outre, la gestion des invasions biologiques est dans certains cas compliquée voire inenvisageable selon le stade de l'invasion et le milieu envahi. Par ailleurs, éradiquer des espèces invasives d'un milieu pose également des problèmes d'éthique auprès du public (Lodge & Shrader-Frechette, 2003). Les habitants et usagers des différents milieux et écosystèmes sont en général peu informés sur cette menace, alors même que l'humain est la première source de diffusion de ces espèces. C'est dans cet objectif que la liste des 100 espèces invasives parmi les pires a été mise en place. Cent espèces ont ainsi été sélectionnées selon deux critères principaux : (1) d'importantes conséquences sur la biodiversité et/ou les activités humaines et (2) une illustration des défis importants associés aux invasions biologiques. Cette liste est donc particulièrement intéressante pour ce type d'étude. En effet, ces espèces représentent les espèces invasives qui sont parmi les plus dangereuses au monde, elles touchent les quatre principaux continents, et

menacent à la fois des écosystèmes marins et des écosystèmes terrestres (Figure 9A). Seuls le désert du Sahara, le Groenland, le nord de la Russie et l'Antarctique sont exempts de la présence de ces espèces. Par ailleurs, cette liste inclue 11 groupes taxonomiques différents. Les 100 espèces regroupent ainsi trois micro-organismes, cinq champignons, quatre plantes aquatiques, 30 plantes terrestres, neuf invertébrés aquatiques, 17 invertébrés terrestres, trois amphibiens, huit poissons, trois oiseaux, deux reptiles et 14 mammifères (Figure 9B). Cette liste illustre bien la diversité des groupes taxonomiques d'espèces invasives qui menacent actuellement la biodiversité. Récemment, une des cent espèces a été éradiquée, le Rinderpest virus qui est à l'origine de la peste bovine, il a alors été décidé d'ajouter une nouvelle espèce invasive à la liste des 100 (voir Chapitre 3) afin de continuer à communiquer sur ces espèces invasives et leurs impacts. De plus, ces espèces ont d'importantes conséquences économiques et/ou écologiques. Il est donc important d'identifier les régions qui pourraient être favorables à ces espèces invasives dans le futur, afin de mieux contrôler et gérer l'établissement des invasions biologiques. Par exemple, *Miconia calvescens* qui a été introduit à Tahiti en 1937 a réussi à envahir plus de la moitié de l'île de Tahiti (Meyer & Florence, 1996). En plus de menacer entre 70-100 espèces de plantes natives en étouffant la végétation, *Miconia calvescens* est aussi capable d'engendrer une modification physique de l'habitat (Meyer & Florence, 1996). Cette espèce est aussi connue pour favoriser les glissements de terrain et augmenter le potentiel d'érosion (Meyer & Florence, 1996). De plus, son coût économique est important, pour la seule île de Oahu, le coût de la gestion de *Miconia calvescens* est d'environ cinq millions de dollars par an (Burnett *et al.*, 2007).

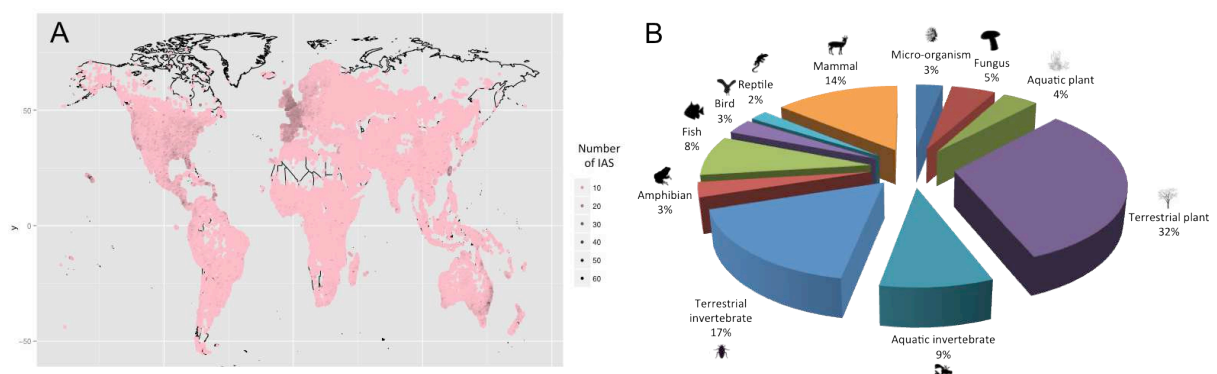


Figure 9 Distribution spatiale des taxons parmi la liste des 100 espèces invasives (A) et répartition des différents groupes taxonomiques (B).

1.5.3. PLAN DE LA THÈSE

Cette thèse a été construite en trois parties distinctes dont les objectifs étaient respectivement :

- (1) De considérer certaines conséquences potentielles de la hausse du niveau des mers;
- (2) D'étudier les effets conjugués des changements climatiques et des changements d'utilisation des sols sur les invasions biologiques et
- (3) D'inscrire les études des changements climatiques dans une perspective de conservation en se focalisant sur les hotspots de biodiversité.

Dans la Partie 1, Chapitre 1, nous nous sommes attachés à faire une synthèse de l'ensemble de la littérature qui discute des effets actuels des changements climatiques sur la biodiversité à ces trois niveaux. Nous avons également étudié les effets potentiels de ces changements climatiques sur la biodiversité future et fait un état des lieux des méthodologies utilisées pour prédire la perte de biodiversité suite aux changements climatiques en discutant des différentes lacunes associées à ce type de méthodes. Finalement, cette synthèse a permis de montrer qu'un nombre important de défis demeure pour que la recherche actuelle puisse être capable d'évaluer précisément l'effet des changements climatiques sur la biodiversité. Dans cette thèse j'ai essayé de répondre à certains de ces défis. Par exemple, j'ai pris en compte les conséquences de la hausse du niveau des mers, une des composantes importantes des changements climatiques. Ainsi, dans la Partie 2, Chapitre 2, nous avons étudié les conséquences de la hausse moyenne du niveau des mers sur les dix hotspots insulaires. Dans ce Chapitre nous avons modélisé une hausse du niveau de la mer de 1 m, 2 m, 3 m et 6 m sur les 4 447 îles des dix hotspots insulaires à travers le monde. Nous avons d'abord exploré les conséquences d'une telle hausse pour l'habitat insulaire, c'est à dire le pourcentage de la superficie qui pourrait être submergée, mais également le nombre d'îles et la localisation des îles qui risquent d'être les plus vulnérables à une augmentation du niveau de la mer. Enfin nous avons utilisé une relation théorique classiquement utilisée en écologie, la relation endémique aire-espèce, afin de quantifier le nombre d'espèces endémiques qui seraient potentiellement affectées en fonction des différents scénarios. Par ailleurs, nous nous sommes focalisés sur un cas d'étude, la Nouvelle-Calédonie, ce qui nous a permis de comparer les résultats de pertes d'espèces endémiques en utilisant (i) la relation endémique aire-espèces mais également (ii) de réelles données d'aires de répartition d'espèces endémiques. Nous avons aussi étudié l'effet de l'élévation du niveau de la mer sur les îles françaises (résultats en

annexe 2). Dans cette annexe, nous avons considéré à la fois l'augmentation homogène et hétérogène du niveau de la mer. Une augmentation homogène correspond à une hausse moyenne du niveau de la mer qui se produit partout à la même vitesse. En effet, la hausse moyenne du niveau des mers est en réalité hétérogène en raison de l'expansion océanique thermique. Certaines régions devraient subir une augmentation du niveau de la mer alors que d'autres régions au contraire devraient connaître une baisse du niveau de la mer. Le manuscrit issu de ce projet a été publié dans la revue « *Nature conservation* » et est présenté en Annexe 2.

Un des autres résultats marquant du Chapitre 1 est qu'en général la majorité des études se concentre sur l'effet seul des changements climatiques (Bellard *et al.*, 2012). En effet, ces études n'analysent pas les effets conjugués des différentes menaces qui pèsent sur la biodiversité. Or de nombreuses études ont discuté des interactions possibles entre les différentes menaces qui pèsent sur la biodiversité (Brook, Sodhi, & Bradshaw, 2008; Sala *et al.*, 2000). En particulier, de nombreuses études théoriques ont émis le postulat que les changements climatiques peuvent altérer la dynamique des invasions biologiques (Hellmann *et al.*, 2008; Walther *et al.*, 2009), mais finalement seules quelques études ont étudié cette interaction pour un grand nombre d'espèces (Peterson *et al.*, 2008). De même, les changements d'utilisation des sols ont probablement une grande influence sur la distribution des espèces invasives (Roura-Pascual *et al.*, 2011), mais l'interaction entre ces trois menaces n'a pas encore été étudiée à grande échelle. Dans la partie 3, nous avons donc étudié les conséquences des changements climatiques et des changements d'utilisation des sols sur les invasions biologiques. Dans cet objectif, nous avons utilisé la liste des 100 cas d'espèces invasives parmi les pires au monde. Le Chapitre 3 a donc eu pour but de présenter la liste des 100 et l'ajout d'une nouvelle espèce à cette liste. Ce Chapitre servira d'avant propos pour le Chapitre 4 et 5. D'autres facteurs liés à la présence de l'homme peuvent également influencer la distribution des espèces invasives (voir (Roura-Pascual *et al.*, 2011; Gallardo & Aldridge, 2013). Dans le Chapitre 4, nous avons analysé l'importance relative des facteurs climatiques (*e.g.*, température moyenne annuelle, précipitation), d'habitats (*i.e.*, l'hétérogénéité d'habitat, la gamme d'altitude, richesse spécifique), humains (*i.e.*, distance aux aéroports, densité humaine) et d'utilisation des sols (*e.g.*, couverture herbacée) sur la distribution actuelle de ces 100 espèces invasives. Ce chapitre a également permis d'identifier les régions les plus favorables à la présence de ces espèces invasives à travers le monde. Ensuite dans le Chapitre 5, nous avons modélisé l'effet à la fois des changements climatiques et des changements futurs d'utilisation des sols sur la distribution de ces 100 espèces invasives. Nous avons

utilisé différents modèles de distribution d'espèces, différents modèles climatiques et différents scénarios de changement d'utilisation des sols afin de construire un modèle « ensemble forecast » pour l'ensemble de ces 100 espèces aux horizons 2050 et 2100. A partir de ces modèles de distribution, nous avons pu construire une carte mettant en évidence les régions qui pourraient devenir favorables ou défavorables pour un nombre important d'espèces invasives dans le futur. Ce Chapitre a également permis d'étudier l'évolution quantitative des aires de répartition de ces espèces et ainsi, de mettre en évidence la façon dont les espèces répondent aux changements climatiques et aux changements d'utilisation des terres. Enfin, dans la partie 4 (Chapitre 6 et 7), nous avons étudié les conséquences des changements globaux sur les hotspots de biodiversité. Cette analyse a été menée dans un contexte de conservation à l'échelle des 34 hotspots, et à l'échelle du dernier hotspot de biodiversité décrit : « Forests of East Australia ». Dans le Chapitre 6, nous avons évalué l'exposition des 34 hotspots de biodiversité aux changements climatiques, aux changements d'utilisation des sols et aux 100 espèces invasives en utilisant deux approches différentes: une analyse de climat analogue; et des modèles de distribution d'espèces. L'étude de ces différentes menaces a permis d'établir des priorités de conservation relatives pour les 34 hotspots de biodiversité. Enfin, dans le Chapitre 7 nous avons étudié les effets directs (changement de température et de précipitation) et indirects (l'élévation du niveau des mers) des changements climatiques au sein du 35^{ème} hotspot. Dans ce chapitre, nous avons également établi des priorités de conservation au sein même du hotspot selon la valeur de biodiversité des différentes régions, leur niveau de protection actuel, et l'exposition aux changements climatiques.

PLAN DE THESE

Partie 1 Etat des lieux de l'impact des changements climatiques sur la biodiversité

Chapitre 1 Review Impacts of climate changes on the future of biodiversity
Publié dans la revue *Ecology letters* (2012)

Partie 2 Effet de l'élévation du niveau des mers sur les habitats insulaires

Chapitre 2 Impacts of sea level rise on the ten insular hotspot
Publié dans la revue *Global Ecology and Biogeography* (2013)

Partie 3 Interactions entre les invasions biologiques, les changements climatiques et les changements d'utilisation des sols.

Avant propos : Chapitre 3 The 100th of the world's worst invasive alien species ?
In press *Biological Invasion* (2013)
La version courte de cet article a été publiée dans la section Correspondance de Nature (2013)
(Annexe 1)

Chapitre 4 Current main factors that drive the most dangerous invasive alien species
En préparation

Chapitre 5 Future invasions by the "100 of the world's worst invasive species"
Publié dans la revue *Global Change Biology* (2013)

Partie 4 Menaces sur les hotspots de biodiversité et hiérarchisation

Chapitre 6 :Biodiversity hotspot vulnerability to global change
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Chapitre 7 Direct and indirect effects of climate change within the world's 35th biodiversity hotspot: Forests of East Australia En préparation

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Bellard, C., Leclerc, C. & Courchamp, F. Impact of sea level rise on the french islands worldwide. Publié dans la revue *Nature conservation*.

Annexe 3

Cornille, A., Giraud, T., **Bellard, C.**, Tellier, A., Le Cam, B., Smulders, M. J. M., Kleinschmit, J., Roldan-Ruiz, I. and Gladieux, P. (2013), Postglacial recolonization history of the European crabapple (*Malus sylvestris* Mill.), a wild contributor to the domesticated apple. Publié dans la revue *Molecular Ecology*.

Annexe 4

F. Courchamp, B. D. Hoffmann, J. Russell, C. Leclerc and **C. Bellard** Climate change and conservation: keeping island biodiversity afloat. Soumis dans la section *Forum Policy* de la revue *Trends in Ecology and Evolution*.

Annexe 5 Matériel supplémentaire du chapitre 1

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Chapitre 1

Impacts of climate change on the future of biodiversity

Résumé

Ces dernières années de très nombreuses études se sont intéressées à l'effet des changements climatiques sur la biodiversité. Le premier travail de cette thèse a par conséquent, été de rédiger une synthèse de la majorité de ces études. Dans cette synthèse, nous avons tout d'abord étudié les conséquences des changements climatiques à l'échelle de l'individu, des communautés, des écosystèmes et des biomes. Cela a permis de mettre en évidence trois axes non exclusifs de réponse des espèces aux changements climatiques: un axe temporel (changements de phénologie), un axe spatial (changement de l'aire de distribution) et enfin un axe propre à l'individu (changement de physiologie). Dans cette synthèse, nous avons également discuté des principales caractéristiques et limites des approches utilisées traditionnellement pour quantifier les conséquences des changements climatiques sur la biodiversité. Ce travail a aussi permis de synthétiser les prédictions de perte de biodiversité de l'ensemble de ces études et également de mettre en évidence la variabilité des différentes estimations de perte de biodiversité selon la méthode utilisée, le groupe taxonomique étudié, la métrique de biodiversité utilisée, ou encore selon l'échelle spatiale et temporelle considérées. Pourtant, un des résultats importants est qu'absolument toutes les prédictions s'accordent à dire que les pertes potentielles de biodiversité en raison des changements climatiques risquent d'être extrêmement importantes dans le futur, menant potentiellement à la 6^{ème} extinction de masse. Finalement dans une dernière partie, nous avons révisé les différents défis qui restent à surmonter dans ce domaine.

Cette partie correspond à l'article publié suivant:

C. Bellard, C. Bertlesmeier, P. Leadley, W. Thuiller & F. Courchamp (2012) Impacts of climate change on the future of biodiversity. In Ecology letters, 15, 365-377.

REVIEW AND SYNTHESSES

Impacts of climate change on the future of biodiversity

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Abstract

Many studies in recent years have investigated the effects of climate change on the future of biodiversity. In this review, we first examine the different possible effects of climate change that can operate at individual, population, species, community, ecosystem and biome scales, notably showing that species can respond to climate change challenges by shifting their climatic niche along three non-exclusive axes: time (e.g. phenology), space (e.g. range) and self (e.g. physiology). Then, we present the principal specificities and caveats of the most common approaches used to estimate future biodiversity at global and sub-continental scales and we synthesise their results. Finally, we highlight several challenges for future research both in theoretical and applied realms. Overall, our review shows that current estimates are very variable, depending on the method, taxonomic group, biodiversity loss metrics, spatial scales and time periods considered. Yet, the majority of models indicate alarming consequences for biodiversity, with the worst-case scenarios leading to extinction rates that would qualify as the sixth mass extinction in the history of the earth.

Keywords

Biodiversity, climate change, species extinctions.

Ecology Letters (2012) 15: 365–377

INTRODUCTION

Predicting the response of biodiversity to climate change has become an extremely active field of research (e.g. Dillon *et al.* 2010; Gilman *et al.* 2010; Pereira *et al.* 2010; Salamin *et al.* 2010; Beaumont *et al.* 2011; Dawson *et al.* 2011; McMahon *et al.* 2011). Predictions play an important role in alerting scientists and decision makers to potential future risks, provide a means to bolster attribution of biological changes to climate change and can support the development of proactive strategies to reduce climate change impacts on biodiversity (Pereira *et al.* 2010; Parmesan *et al.* 2011). Although there is relatively limited evidence of current extinctions caused by climate change, studies suggest that climate change could surpass habitat destruction as the greatest global threat to biodiversity over the next few decades (Leadley *et al.* 2010). However, the multiplicity of approaches and the resulting variability in projections make it difficult to get a clear picture of the future of biodiversity under different scenarios of global climatic change (Pereira *et al.* 2010). Hence, there is an urgent need to review our current understanding of the effects of climate change on biodiversity and our capacity to project future impacts using models. To this end, we have reviewed both the ranges of possible impacts of climate change that operate at individual, population, species, community, ecosystem and biome scales and the different responses that could occur at individual, population or species levels. We then present the principal specificities and caveats of the most common approaches used to model future biodiversity at global and sub-continental scales and we synthesise their results focusing on how model combinations are used to project the impacts of climate change on species loss. Finally, we highlight several challenges for future research, from theoretical (e.g. emerging models) and applied (e.g. population conservation and exploitation) realms.

BIODIVERSITY AND CLIMATE CHANGE: EFFECTS AND RESPONSES

Climate change effects on biodiversity

The multiple components of climate change are anticipated to affect all the levels of biodiversity, from organism to biome levels (Fig. 1, and reviewed in detail in, e.g. Parmesan 2006). They primarily concern various strengths and forms of fitness decrease, which are expressed at different levels, and have effects on individuals, populations, species, ecological networks and ecosystems. At the most basic level of biodiversity, climate change is able to decrease genetic diversity of populations due to directional selection and rapid migration, which could in turn affect ecosystem functioning and resilience (Botkin *et al.* 2007 but, see Meyers & Bull 2002). However, most studies are centred on impacts at higher organisational levels, and genetic effects of climate change have been explored only for a very small number of species.

Beyond this, the various effects on populations are likely to modify the 'web of interactions' at the community level (Gilman *et al.* 2010; Walther 2010). In essence, the response of some species to climate change may constitute an indirect impact on the species that depend on them. A study of 9650 interspecific systems, including pollinators and parasites, suggested that around 6300 species could disappear following the extinction of their associated species (Koh *et al.* 2004). In addition, for many species, the primary impact of climate change may be mediated through effects on synchrony with species' food and habitat requirements (see below). Climate change has led to phenological shifts in flowering plants and insect pollinators, causing mismatches between plant and pollinator populations that lead to the extinctions of both the plant and the pollinator with expected consequences on the structure of plant–pollinator networks (Kiers *et al.* 2010; Rafferty & Ives 2010). Other modifications of interspecific relationships (with competitors, prey/predators, host/parasites or

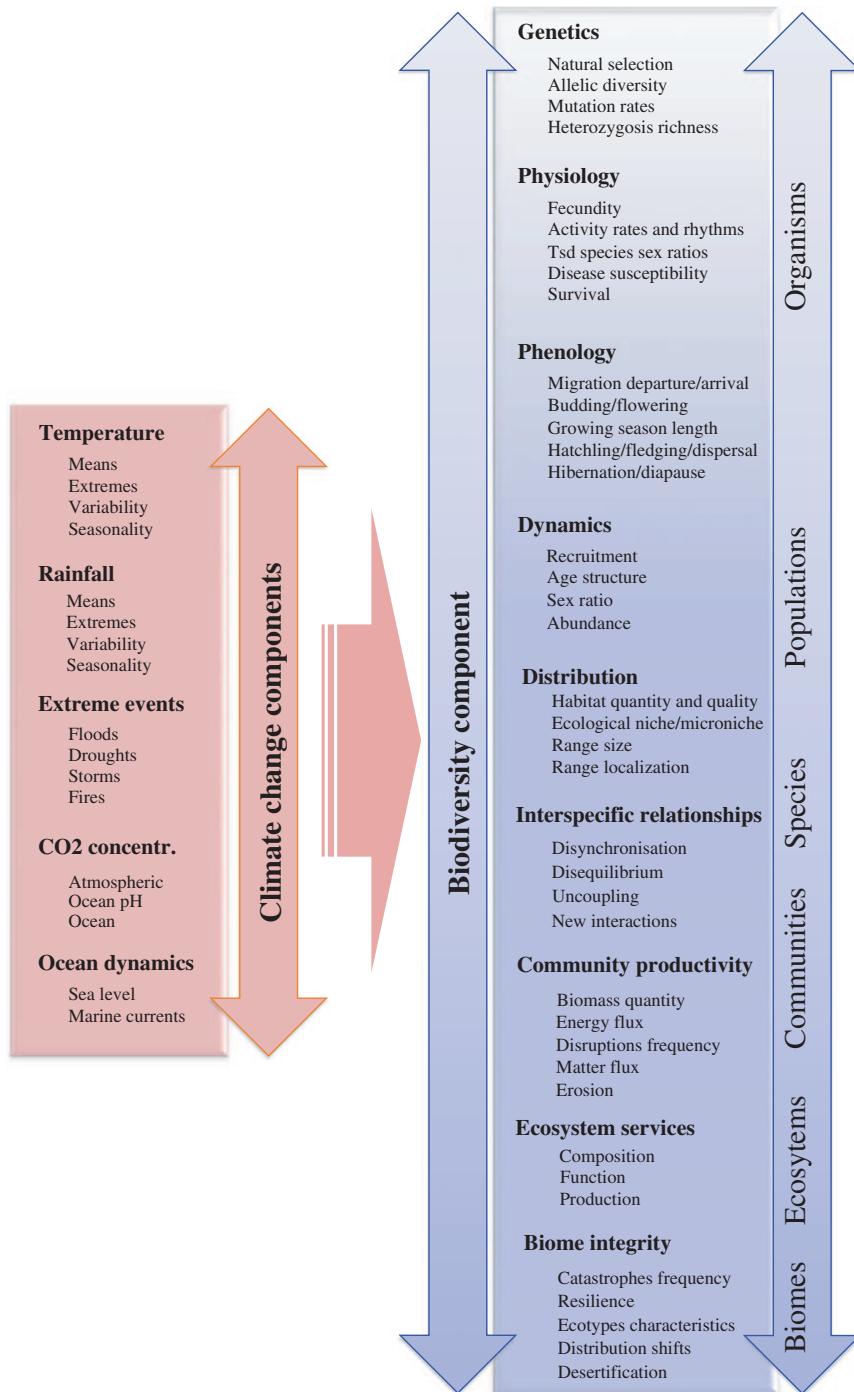


Figure 1 Summary of some of the predicted aspects of climate change and some examples of their likely effects on different levels of biodiversity.

mutualists) also modify community structure and ecosystem functions (Lafferty 2009; Walther 2010; Yang & Rudolf 2010).

At a higher level of biodiversity, climate can induce changes in vegetation communities that are predicted to be large enough to affect biome integrity. The Millennium Ecosystem Assessment forecasts shifts for 5–20% of Earth's terrestrial ecosystems, in particular cool conifer forests, tundra, scrubland, savannahs and boreal forest (Sala *et al.* 2005). Of particular concern are 'tipping points' where ecosystem thresholds can lead to irreversible shifts in biomes (Leadley *et al.* 2010).

A recent analysis of potential future biome distributions in tropical South America suggests that large portions of Amazonian rainforest could be replaced by tropical savannahs (Lapola *et al.* 2009). At higher

altitudes and latitudes, alpine and boreal forests are expected to expand northwards and shift their tree lines upwards at the expense of low stature tundra and alpine communities (Alo & Wang 2008). Increased temperature and decreased rainfall mean that some lakes, especially in Africa, might dry out (Campbell *et al.* 2009). Oceans are predicted to warm and become more acid, resulting in widespread degradation of tropical coral reefs (Hoegh-Guldberg *et al.* 2007). The implications of climate change for genetic and specific diversity have potentially strong implications for ecosystem services. The most extreme and irreversible form of fitness decrease is obviously species extinction. To avoid or mitigate these effects, biodiversity can respond in several ways, through several types of mechanisms.

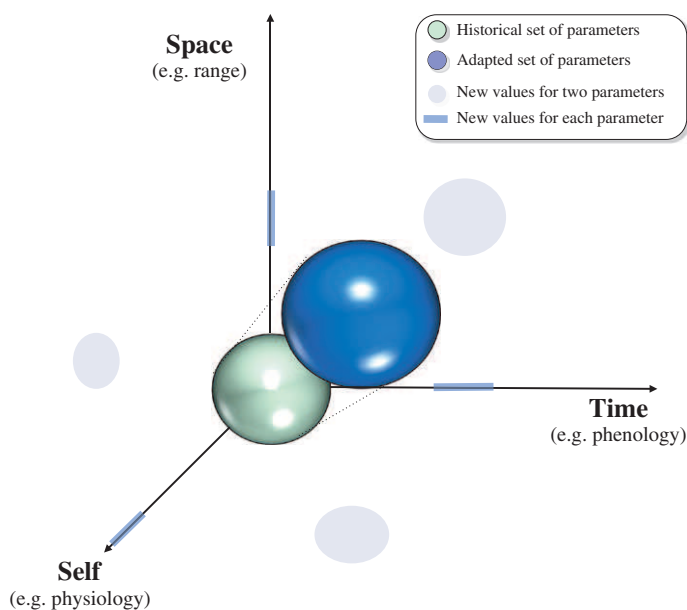


Figure 2 The three directions of responses to climate change through phenotypic plasticity or evolutionary responses: moving in space (dispersing to areas with suitable habitat or changing location on a microhabitat scale), shifting life history traits in time (adjusting life cycle events to match the new climatic conditions, including phenology and diurnal rhythms), or changing life history traits in its physiology to cope with new climatic conditions. Species can cope with climate change by shifting along one or several of these three axes.

Biodiversity responses to climate change

Because of climate changes, species may no longer be adapted to the set of environmental conditions in a given region and could therefore fall outside its climatic niche. As other components of the ecological niche of species are not supposed to change directly, we will hereafter refer only to climatic niches of species (i.e. the climatic components of the *n*-dimensional hypervolume *sensu* Hutchinson). To persist, individuals, populations or species must produce adaptive responses, which can be of several types, and are provided by two categories of mechanisms.

Response mechanisms: plastic vs. genetic

One of the crucial questions in the debate on ecological effects of climate change is whether or not species will be able to adapt fast enough to keep up with the rapid pace of changing climate (Lavergne *et al.* 2010; Salamin *et al.* 2010). Whatever the type of adaptive responses, underlying mechanisms are either due to micro-evolution (i.e. species can genetically adapt to new conditions through mutations or selection of existing genotypes Salamin *et al.* 2010) or plasticity, which provides a means of very short-term response (within individual's lifetimes, Charmantier *et al.* 2008). It may involve intraspecific variation in morphological, physiological or behavioural traits, which can occur on different time scales within the populations' spatial range (Bortkin *et al.* 2007; Chevin *et al.* 2010). Empirical evidence suggests that plastic contribution is often more important than genetic contribution, as observed in birds and marmots (Hoffman & Sgro 2011). On the other hand, there is increasing empirical evidence that evolution can be very rapid (Lavergne *et al.*

2010). This is the case for many introduced species, for which selection-driven phenotypic changes have enhanced the invasive potential (e.g. Phillips 2009). Recent experiments on evolutionary rescue also confirm that rapid evolution through mutation and selection could allow species with rapid life cycles to adapt very severe and rapid environmental changes (Bell & Gonzalez 2009).

Responses: along three axes

Whatever the mechanisms involved in response to climate change, species can in theory change, and changes have already been observed, along three distinct but non-exclusive axes (Fig. 2): spatial, temporal or self. The first two axes correspond to easily observable and well documented responses to global warming (Parmesan 2006). 'Self' corresponds to less visible physiological and behavioural changes that allow species to adapt to the new climatic conditions in the same spatial and temporal frame.

Spatial. First, species can track appropriate conditions in space and follow them. This is typically done through dispersion, but spatial changes are not limited to this: shifts to a different habitat at the local or micro-habitat levels are also relevant. One of the best-documented responses – from both palaeontological records and recent observations – is a spatial shift of species tracking suitable climatic conditions at the regional scale. Latitudinal and altitudinal range shifts have already been observed in more than 1000 species – especially those with high dispersal capacities like birds, insects and marine invertebrates (Parmesan 2006), leading to a reduction in range size particularly in polar and mountaintop species (Forero-Medina *et al.* 2010). However, individuals shift their distribution to stay in quasi-equilibrium with the climatic conditions they are adapted to, but they may not be adapted to other abiotic variables such as photoperiod or novel biotic interactions (Visser 2008). In these cases, micro-evolution may be needed for them to persist (Visser 2008).

Temporal. To keep up with changing abiotic factors that show cyclic variation over time, such as temperature on a daily or yearly period, individuals can also respond to climate change through a shift in time (on a daily to seasonal basis). Phenology, i.e. the timing of life cycle events such as flowering, fruiting and seasonal migrations, is one of the most ubiquitous responses to 20th century climate warming. It has already been documented in many species (Parmesan 2006; Charmantier *et al.* 2008). In a meta-analysis of a wide range of species including animals and plants, the mean response across all species responding to climate change was a shift in key phenological events of 5.1 days earlier per decade over the last 50 years (Root *et al.* 2003). Flowering has advanced by more than 10 days per decade in some species (Parmesan 2006). These phenological changes can help species keep synchrony with cyclical abiotic factors. Yet, they can also be disruptive, by increasing asynchrony in predator-prey and insect-plant systems (Parmesan 2006), which may lead to species extinction. Temporal shifts may also occur at a small temporal scale, e.g. with behaviours or activity patterns adjusted in daily activity rhythms to match the energetic costs of a different climatic condition.

Self. Last, species can cope with changing climatic conditions by adapting themselves to the new conditions in their local range, rather than by tracking their current optimal conditions in space or time. For lack of a better term, we refer to these *in situ* changes that are not related to spatial or temporal changes, as changes in 'self'. Species can move along this third, 'self' axis by physiological alterations that allow tolerance to warmer or drier conditions or by behavioural

modifications of their diet, activity and energy budget, for example. Although they are often less obvious than changes in time or space, some physiological responses have already been reported (Johansen & Jones 2011) during the 20th century climate change, especially from many ectotherms, as their locomotion, growth, reproduction and sex determination are temperature sensitive (Tewksbury *et al.* 2008). However, for many traits, plastic phenotypic responses should reach a physiological limit and 'saturate' in extreme environments. For example, body size or metabolic rate cannot increase or decrease indefinitely under sustained environmental change (Chevin *et al.* 2010). In this case, strong selection is needed to cope with climate change. As they remain in the same spatial and temporal frame, thereby limiting alterations of interspecific relationships, changes in self also have different consequences for ecosystem responses than do changes in time and space.

Failing to adapt along one or several of these three axes, population or species will go extinct locally or globally. There is thus a multitude of possible responses for species to cope with climate change, and in fact relatively few taxa went extinct following climate change during the Quaternary period (Botkin *et al.* 2007). This should help temper catastrophist predictions regarding the global effects of the current climate change on biodiversity. However, the responses of many populations are likely to be inadequate to counter the speed and magnitude of the current climate change. In addition, unlike in past periods of climate change, species have now to cope with additional threats, some of which may act in synergy with climate change (Botkin *et al.* 2007). As we are already facing an irrefutable biodiversity crisis, the number of species that may go extinct following climate change has become a major concern over the last few years.

ASSESSING THE FUTURE OF GLOBAL BIODIVERSITY

Our understanding of the effects of global climate change on biodiversity and its different levels of response is still insufficiently well developed. Yet, it is enough to raise serious concern for the future of biodiversity. The most pressing issue is to quantitatively assess the prospects for biological diversity in the face of global climate change. Although several methods exist to draw inferences, starting with existing palaeontological or recent data, experiments, observations and meta-analyses (e.g. Lepetz *et al.* 2009), ecological modelling is the most commonly used tool for predictive studies. Progress in this field is characterised by both an extremely high pace and a plurality of approaches. In particular, there are three main approaches to projecting species loss, concentrating either on future changes in species range or species extinction or changes in species abundance. However, all three modelling approaches have so far largely focused on one axis of response (change in space), largely overlooking the importance of the other aspects. In addition, they seldom account for the mechanisms of these responses (plasticity and evolution). We briefly discuss herein the basic principles and the weakness of the models that are the most widely used at global or at large regional scales in this context, focusing on representative examples of recent work. Table 1 summarises the specific advantages and limitation of each model type.

Biodiversity range models components

Studies modelling species' range shifts are generally based on the assumption that species niches are defined by a small set of

environmental variables, i.e. the species' 'climate niche', defines the suitable climatic habitat for that particular species. These Bioclimatic Envelope Models relate current species ranges to multiple climatic variables and thereby define the climatic niche (envelope) for each species. It is then possible to project this niche for different future climate scenarios to determine the potential redistribution of the suitable climate space of the species. The extinction risks can then be calculated in different ways using species–area relationships (Thomas *et al.* 2004) or IUCN status (Thuiller *et al.* 2005). Despite a number of limitations (lack of biological process as well as methodological and theoretical issues, Soberon & Nakamura 2009), species distribution models still constitute the bulk of studies in this domain (Sinclair *et al.* 2010).

Shifts in distinct vegetation types, often referred to as biome or habitat shifts are often simulated with Dynamic Vegetation Models (DVM). These models forecast shifts in vegetation and associated biogeochemical and hydrological cycles in response to climate change. DVMs use time series of climate data (e.g. temperature, precipitation, humidity, sunshine days) and take into account constraints of topography and soil characteristics to simulate monthly or daily dynamics of ecosystem processes. Plant species are represented as groups with similar physiological and structural properties, termed Plant Functional Types (PFTs), which are designed to represent all major types of plants (Sitch *et al.* 2008). PFT distributions can then be used to estimate changes in biome or habitat ranges. Currently, DVMs are of limited use for projecting responses in biodiversity directly (i.e. the absence of animals and the limitation to *c.* 10 PFTs exclude direct utilisation). However, coupled with extinction models, they allow extinction risk for species to be estimated at the regional or global scale (e.g. van Vuuren *et al.* 2006).

Species loss models components

The simplest method for calculating extinction risk is to assume that species go extinct when they no longer have any suitable habitat (Jetz *et al.* 2007). This may underestimate extinctions because species often enter an 'extinction vortex' well before they lose their entire habitat. Yet, it could also substantially overestimate extinctions because many species have weak habitat specificity (Malcolm *et al.* 2006; Willis & Bhagwat 2009).

The species–area relationship (SAR), an empirical relationship between the number of species and the land area of a region, is often used to estimate extinction risk (Thomas *et al.* 2004). Species extinctions are calculated as a direct function of habitat loss or climate-induced range contraction based on the observation that extinction risk increases with decreasing range and population size. SAR methods may over- or underestimate species extinction risk depending on the capacity of species to persist in small populations or adapt to novel environments, and they also fail to provide a time frame in which extinctions are likely to occur (Chevin *et al.* 2010) because the extinction debt is not accounted for (Pereira *et al.* 2010). The relevance of using this relationship to project biodiversity loss is still hotly debated (He & Hubbell 2011).

The IUCN has developed criteria to assess species extinction risk for their Red List of the conservation status of plant and animal species (Baillie *et al.* 2004). These include 90 biological traits identified as enhancing species' vulnerability (e.g. habitat specialisation, narrow environmental tolerance, dependence on specific environmental triggers, dependence on interspecific interactions or poor ability to

Table 1 Advantages and disadvantages of the two components of major modelling approaches used to estimate loss of biodiversity due to climate change. See Fig. 3 for illustrations of how the two components can be combined to estimate biodiversity loss

	Advantages	Disadvantages	Key references
Biodiversity range model components			
Bioclimatic envelope models (BEM)	Can be applied to a large number of species and a variety of taxonomic groups Implicitly capture many ecological processes in the relationship between occurrence data and spatial information Require few data	Do not explicitly account for mechanisms that mediate species range May handle novel climates poorly Lack temporal dynamics Assume that the current distribution of a species is a good indicator of suitable climate	Alo & Wang (2008), Araujo <i>et al.</i> (2011), Baillie <i>et al.</i> (2004), Beaumont <i>et al.</i> (2008, 2011), Botkin <i>et al.</i> (2007), Bradley <i>et al.</i> (2010), Brook <i>et al.</i> (2008)
Dynamic vegetation models (DVMs)	Include the dynamics of plant growth, competition and, in a few cases, migration Allow the identification of future trends in ecosystem function and structure Can be used to explore feedbacks between biosphere and atmospheric processes	Require detailed physiological data Do not include plant interactions with other taxonomic groups Limit biodiversity to a very small number of plant functional types Do not take into account fine scale spatial heterogeneity Are not adapted for predicting species extinctions at local scales	Akçakaya <i>et al.</i> (2006), Anderson <i>et al.</i> (2009), Bakkenes <i>et al.</i> (2002), Brook <i>et al.</i> (2008, 2009), Campbell <i>et al.</i> (2009)
Species loss model component			
Species–area relationships (SAR)	Are easy to couple with distribution models because they are based on range or habitat loss Can be applied to a variety of taxonomic groups Require few data	Use values of key parameters that are not well constrained Lack empirical evidence concerning applicability of SAR for climate change or at species range level Lack temporal dynamics Don't account for processes influencing extinction rates (e.g. population dynamics, adaptive responses)	Alo & Wang (2008), Campbell <i>et al.</i> (2009), Carnaval <i>et al.</i> (2009), Charmantier <i>et al.</i> (2008)
IUCN status methods	Use a widely accepted measure of threat Are simple to couple with distribution models because partly based on criteria of range or habitat loss	Depend on thresholds that are somewhat arbitrary Rely on sole criteria of declining range size in most studies Often don't respect time frame for declines (i.e. 10 years or three generations in most cases)	Alo & Wang (2008), Araujo <i>et al.</i> (2011), Chevin <i>et al.</i> (2010)
Dose–response relationships	Are anchored in measured responses of biodiversity to global change drivers Can assess the impact of a wide range of global change factors alone or their cumulative effects Can include time lags	'Undisturbed' ecosystems used as baseline are difficult to define Inadequately account for interactions between global change drivers Lack validation at large regional or global scales Use metrics that are difficult to relate to common biodiversity indices	Bakkenes <i>et al.</i> (2002), Barnosky <i>et al.</i> (2011)

disperse to or colonise a new range, Foden *et al.* 2008). Recent attempts at projecting climate change impacts on biodiversity have used the IUCN status metric to obtain estimates of extinction rates based on projected range shifts (Thuiller *et al.* 2005), although the use of IUCN status for this purpose has also been questioned (Akçakaya *et al.* 2006).

In dose–response relationship (DRR) models, observational data and experiments can be employed to generate empirical relationships between the relative importance of global drivers (dose) and changes in species loss (response).

Most models focus on species extinctions, which are only the last step of a decline in abundance and are a less immediate (although dramatic) impact of climate change. This fact has led to the development of new models that attempt to quantify the impact of human activities on species abundance (i.e. an equivalent of DRR for species abundance). Impacts on biodiversity are estimated using biodiversity indicators including mean species abundance (MSA, Alkemade *et al.* 2009) and Biodiversity Intactness Index (Biggs *et al.* 2008). For example, the GLOBIO model uses a matrix of changes in mean local species abundances following conversion between

two land use or land cover categories, derived from empirical studies (Leadley *et al.* 2010). These types of models use species abundances in pristine ecosystems as a baseline, and thereby provide a measure of the distance from 'naturalness' of plant and animal communities following human disturbance. Species abundance models based on plant traits and abiotic characteristics can also provide evidence of changes in ecosystem services (Lavorel *et al.* 2011).

There are, however, several major limitations to these models, especially concerning the indices of biodiversity derived from DRR applied to species abundance. They depend largely on the quality of the input data (of which much more is needed than in most other models), uncertainty cannot be taken into account, and they are difficult to relate to commonly used biodiversity indices (Alkemade *et al.* 2009).

Model combinations

Current modelling techniques usually incorporate a succession of one (or several) future socio-economic scenario(s), one (or several)

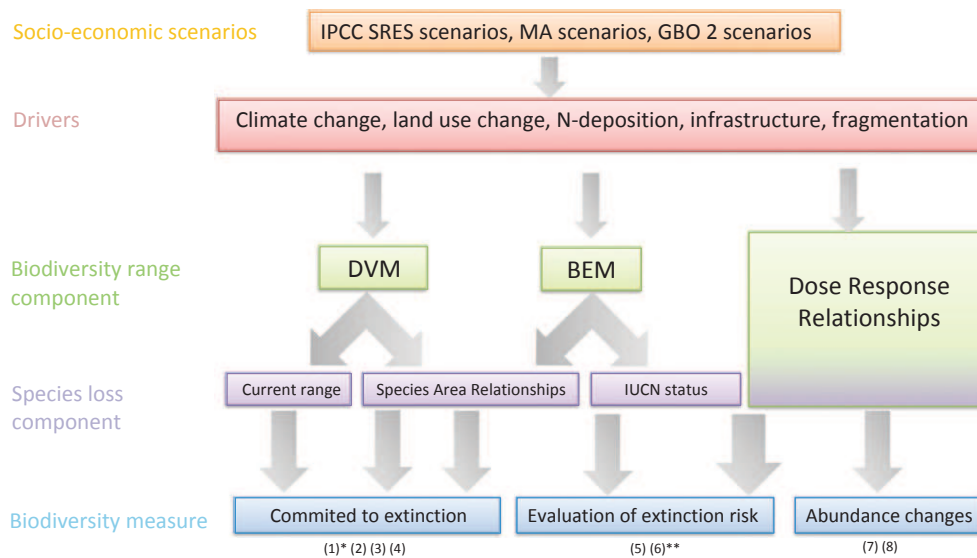


Figure 3 Examples on successive combinations of socioeconomic scenarios, projections of extinction drivers, biodiversity range or species loss models and biodiversity metrics, leading to projections of biodiversity losses following climate change. Numbers correspond to references (see Appendix S2 for details and reference list).

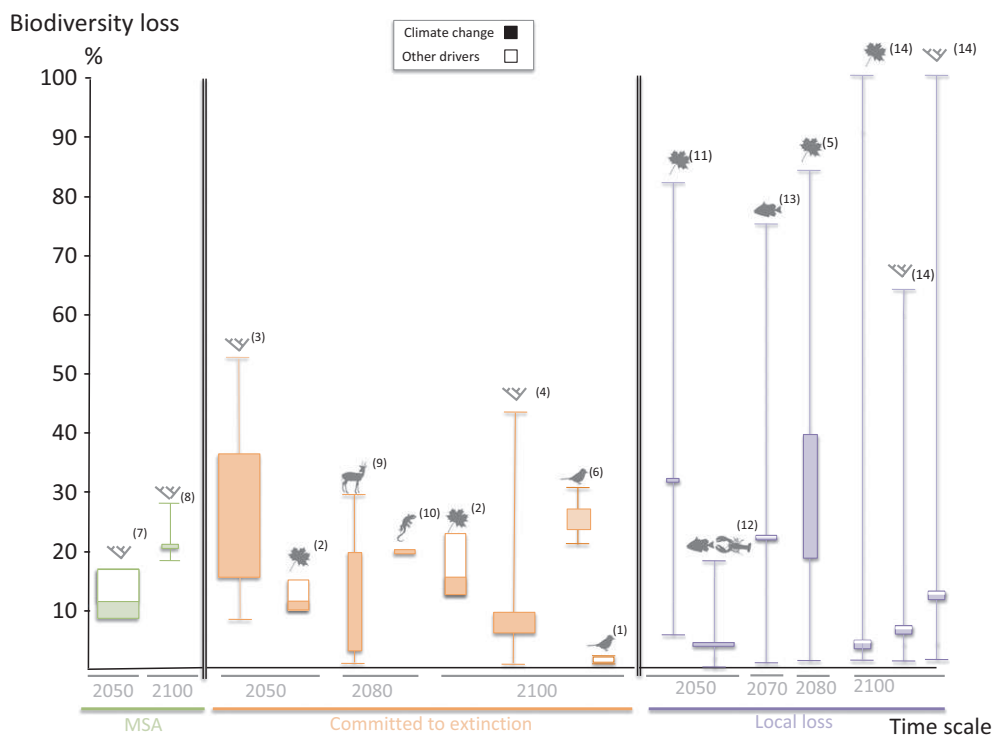


Figure 4 Projections of loss of biodiversity due to climate change, for different taxonomic, temporal and spatial scales. The width of the box illustrates three levels of generality: global scale and several taxonomic groups (∞), global scale and only one taxonomic group, continental scale and only one taxonomic group. The box is delimited by the upper and lower boundaries of the intermediate scenario, while maximum and minimum values of the whiskers indicate the highest and lowest biodiversity losses across all projections. This figure illustrates that the different studies (i) generally predict significant biodiversity loss and (ii) use a combination of different biodiversity metrics, taxonomic groups and spatial scale and time horizon, making generalisations difficult. Numbers correspond to references (see Appendix S2 for details and references).

extinction driver(s), one biodiversity range or species loss models (Fig. 3). They then express their projections in terms of various extinction metrics. This has generated a variety of ‘model combinations’ leading to a wide range of projections that are not straightforward to compare, as the underlying assumptions differ greatly. We

have synthesised in Fig. 4 the results of all such projections made at a global scale either geographically or taxonomically. Despite important differences and some bias (e.g. marine biodiversity is still poorly represented), these models generally indicate that many species can be expected to decline rapidly at a global scale.

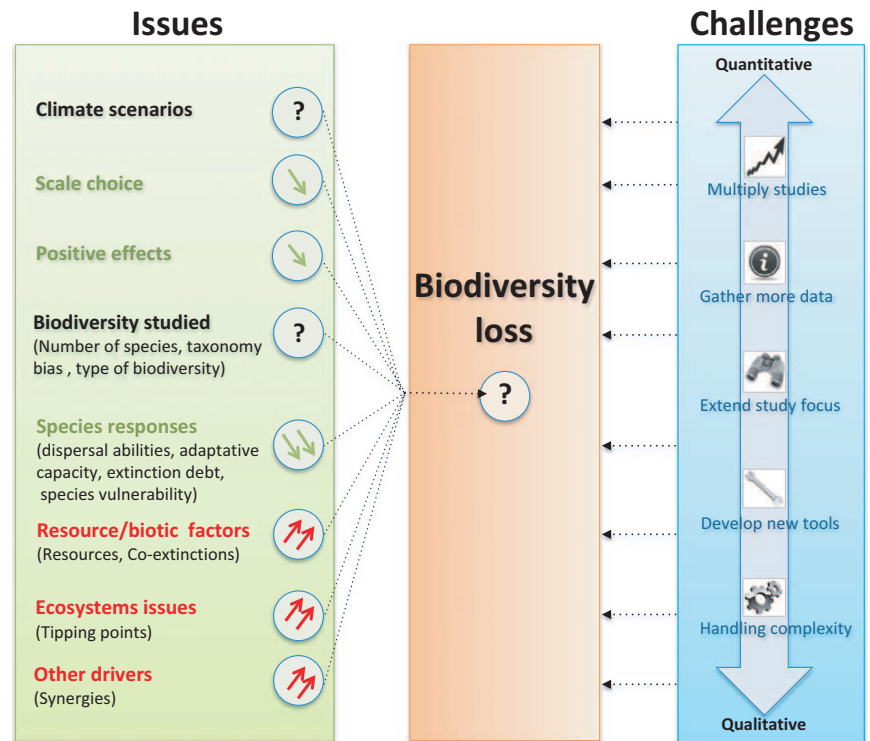


Figure 5 Issues and challenges for climate change driven biodiversity loss. Examples of each are presented and discussed in the main text. The issues are in the first box, which represents the main factors of uncertainty and the direction of the likely current bias (green factors and arrow down is a likely overestimation, while red factors and arrow up is a likely underestimation; both can occur simultaneously, according to the approach taken in different studies; black factors and question marks are for unknown direction of misestimation; double arrow means very large expected effect). Challenge types range from quantitative (such as increasing the number of studies and the quantity of available data, or extend the focus of studies to include more factors) to more qualitative ones (developing new tools and progressing in resolving complexity).

Projections of species loss

The field of climate change biology has thus followed several distinct and independent lines of model development (Fig. 3). This is potentially advantageous, as the convergent predictions can be regarded as an indication of robustness. In essence, the results show that local species extinctions cover an extremely large range, with some areas experiencing virtually no losses and others facing nearly complete loss of current species. High local losses can concern relatively large areas; for example, Bakkenes *et al.* (Bakkenes *et al.* 2002) estimated that more than 16% of European landmass would have local species losses exceeding 50% by 2050. This must be distinguished from projections of species extinctions at the global level, which are unsurprisingly lower than at the local level, since local extinctions do not necessarily lead to global extinctions. Nevertheless, even these global estimates suggest major losses of biodiversity due to global climate change that are generally higher than current rates of loss and far higher than rates of species extinctions documented in the fossil record (Pereira *et al.* 2010; Barnosky *et al.* 2011). For example, one of the earliest global studies estimated that by 2050 15–37% of species are committed to extinction under intermediate climate warming (Thomas *et al.* 2004). Birds are projected to be particularly sensitive to climate change. Two studies have calculated losses by 2100 due to climate change: these range from less than 0.3% of the world's 8750 species of land birds would be committed to extinction (Jetz *et al.* 2007) and up to 30% of the 8400 land bird species in the Western Hemisphere could go extinct (Sekercioglu *et al.* 2008). Regarding the vulnerability of 25 major biodiversity hotspots, Malcolm and colleagues suggested that the extinctions of endemic species could reach 39–43% under in worst-case scenarios, representing the potential loss of 56 000 endemic plant species and 3700 endemic vertebrate species (Malcolm *et al.* 2006).

Studies based on changes in species abundance generally predict an erosion of biodiversity in the same order of magnitude as species extinction models do, i.e. losses of 11–17% of MSA by the end of the century (Alkemade *et al.* 2009). Using data from 9856 birds, 6222 amphibians and 799 coral reefs, the IUCN forecasted that *c.* 35% of the world's birds, 52% of amphibians and 71% of warm water reef-building corals are particularly susceptible to climate change (Foden *et al.* 2008). Variability in local extinctions is significantly higher than in global extinctions projections. Indeed, in some regions the species composition will not change at all and in others almost all species will be lost following climate change. Estimated losses of riverine fish richness at a local scale vary considerably between 0 and 75% according to the river considered (Xenopoulos *et al.* 2005). Similarly, estimated local losses of plant diversity in Europe range from 2 to 84% of species lost per pixel (Thuiller *et al.* 2005).

Overall, the diversity of taxonomic groups studied, of biodiversity loss metrics, of spatial scales and time periods render complex and uncertain comparisons between these studies. In addition, the large array of modelling techniques further complicates the comparisons. Moreover, several studies assess the combined effects on future biodiversity of both climate change and land use, making it difficult to distinguish the effect of each. Finally, there is growing concern that the underlying assumptions of all of these models could lead to large over- or underestimations of potential species losses (Pereira *et al.* 2010; Dawson *et al.* 2011). These are summarised in Fig. 5. As an example, a recent study suggests that the realised effects of climate change might far exceed the current predictions (Maclean & Wilson 2011). Based on a global multi-taxa meta-analysis of recorded ecological responses, they estimated that the mean observed extinction risk by 2100 is systematically higher than the mean predicted extinction risk across the theoretical studies considered in the meta-analysis: 12.6% in plants (vs. 4% predicted), 9.4% in inverte-

brates (vs. 7.2% predicted) and 17.7% in vertebrates (vs. 12.4% predicted). Overall, these estimates of biodiversity loss are obviously a major concern.

WHAT FURTHER IMPROVEMENTS ARE NEEDED?

Climate change ecology is still in its infancy, and tremendous improvements are made rapidly in virtually all aspects of this emerging field. Critical requirements to be able to predict future trends include the need to study a much larger part of biodiversity, to overcome several major model limitations, to account for co-extinctions and other major drivers of biodiversity loss and to validate models by comparing projections with observations. These limitations are detailed below. Figure 5 provides a summary of the directions in which each of these weaknesses is likely to affect the current projections on biodiversity loss, as well as the major types of challenges that have to be faced to overcome these uncertainties.

Climate scenarios

Climate scenarios depend on a wide range of socio-economic storylines for greenhouse gas emissions in the future, including the Special Report on Emissions Scenarios Millennium Assessment and Global Biodiversity Outlook scenarios (Pereira *et al.* 2010), and on a broad suite of General Circulation Models used to calculate climate change for given trajectories of greenhouse gas emissions. This means that the projections of species loss can yield highly contrasting results depending on the choice of combinations of emissions scenarios and climate models, independently of the model of biodiversity response that is used (Beaumont *et al.* 2008). In addition, internal climate model variability could result in greater differences in projected species' distributions than variability between climate models (Beaumont *et al.* 2007). In addition, 4–39% of the world's landmass will experience combinations of climate variables that do not currently have equivalent values anywhere on the globe (so called no-analogue climates, Williams *et al.* 2007). One key challenge is to provide robust and credible uncertainty intervals for all model outcomes and, if possible, to reduce them.

Scale choice

The choice of the spatial resolution scale is probably one of the most important factors generating variability. For example, a coarse, European-scale model (with 10' × 10' grid cells) predicted a loss of all suitable habitats during the 21st century, whereas a model using local-scale data (25 × 25 m grid cells) predicted persistence of suitable habitats in up to 100% of plant species (Randin *et al.* 2009). These differences are probably explained by the failure of coarser spatial scale models to capture both local topographic diversity and habitat heterogeneity (Luoto & Heikkinen 2008; Randin *et al.* 2009). On one hand, global models can be used for a large number of species but focus on one type of species' response and therefore lack biological realism. On the other hand, population or species models provide insight into a very limited range of species, typically at regional scales (i.e. adaptation phenology, dynamic population) but cannot provide global scale trends. This is a classical trade-off between precise small-scale models and coarse large-scale models that lack biological realism (Thuiller 2003).

Positive effects

Climatic changes could also have positive effects on biodiversity. For instance, more clement temperatures and increased CO₂ are likely to be beneficial to many plants, resulting in an acceleration of biomass production. Milder winters might increase survival of many currently threatened species in temperate regions. Increased precipitation may also benefit some plant communities and species depending on them. Moreover, several studies reported detrimental effects of climate change on biological invasions (e.g. Peterson *et al.* 2008). Although few studies report beneficial effects of global changes on biodiversity, they certainly exist and add to the difficulty of getting a clear overview of the effects of climate changes on the biodiversity of our planet.

Biodiversity measures

Even in the most ambitious studies, the range of species studied always represents a small percentage of known biodiversity. All studies are taxonomically biased, as they generally concentrate on a few conspicuous taxonomic groups such as plants, mammals and birds (Thuiller *et al.* 2011), with a particularly strong bias towards terrestrial vs. marine biodiversity. However, it is generally recognised that the vast majority of biodiversity in terms of species richness, evolutionary divergence, biomass and even ecosystem functioning is represented by 'cryptic biodiversity', especially micro-organisms and insects (Esteban & Finlay 2010). Similarly, there are important biases in data collection both across regions and ecosystems (McMahon *et al.* 2011). Furthermore, most studies focus on species richness, because it is thought to influence the resilience and resistance of ecosystems to environmental change. However, a few studies have explored the impact of climate change on functional (Thuiller *et al.* 2006) and phylogenetic diversity (Thuiller *et al.* 2011), and the effects on genetic diversity are only beginning to be explored. Moreover, it is likely that different levels of diversity are affected differently by climate change, so these should be evaluated in parallel to provide a broad picture of biodiversity response to climate change (Devictor *et al.* 2010).

In addition, there are different indicators of biodiversity change, such as the number of species 'committed' to extinction (Thomas *et al.* 2004; Pereira *et al.* 2010), extinction risk (Thuiller *et al.* 2005), or change in abundances (Alkemade *et al.* 2009; Leadley *et al.* 2010). The number of species 'committed' to extinction is probably not the most appropriate metric to forecast the future of biodiversity because the extinction debt could vary from decades to centuries (Kuussaari *et al.* 2009). A complementary metric of biodiversity can be changes in MSA, which is an index defined as the mean abundance of original species relative to their abundance in undisturbed ecosystems. As extinction is only the last step in the process of species decline, the MSA can provide a metric to evaluate ecosystem degradation. In addition, we need new approaches to predict the impacts of climate change at the community level (i.e. Mokany & Ferrier 2011). Currently, neither the estimates of species losses nor of the qualitative impacts on ecosystem functioning and services are satisfactory to give a global overview of the impacts of climate change (Dale *et al.* 2010).

Limitations of predictive tools

Each of the modelling approaches reviewed has methodological, spatial and temporal limitations that constrain their predictive power

(e.g. McMahon *et al.* 2011). In general, models do not take into account the multiple responses of species to climate change, but rather focus mainly on one axis, spatial shifts of potential habitat (Fig. 2). The temporal and the physiological responses are generally overlooked, as are the genetic and plastic capacity of species (Lavergne *et al.* 2010; Salamin *et al.* 2010). In addition, species are commonly considered as static and independent entities, although their dynamics and their role in ecological networks are both known to be essential. However, a new generation of models is emerging that focuses on more realistic biological hypotheses and meets some of the challenges posed by each limitation (e.g. Thuiller *et al.* 2008; Brook *et al.* 2009; Gallien *et al.* 2010).

Species responses

Current global extinction models make very coarse assumptions about species responses. For example, the dispersal capability is a major issue for projections of future biodiversity. Until recently, models often addressed dispersal issues by using two extreme assumptions of either unlimited or no species dispersal (Thomas *et al.* 2004). This is clearly convenient for practical purposes, but most species are between these extremes. In addition, exceptional occurrences of long-distance dispersal are thought to have helped past species surmount prehistoric climate changes (Dawson *et al.* 2011 and references therein). Although rare, these events are of crucial significance in the current context, as they could in many cases make the difference between species survival and extinction, especially as human-mediated long-distance dispersion is now common for many organisms.

Inherent differences in vulnerability are not always taken into account when making large-scale correlative predictions of the future of biodiversity. Indeed, most models work under the very strong hypotheses that species currently live in an optimal climatic niche and that they cannot survive if there is a change in the climatic conditions that contribute to define this niche. Such a hypothesis amounts to overlook the potential of adaptability of species. Numerous studies have shown that species are capable of fast responses through phenotypic plasticity or microevolution (Lavergne *et al.* 2010). Before being able to forecast species trajectories with some credibility, we therefore need to assess properly the vulnerability of species (including exposure, sensitivity, adaptive capacity and migration potential), habitats and regions to different components of climate change (Dawson *et al.* 2011; McMahon *et al.* 2011). Despite growing evidence for rapid adaptive evolution in response to climate change, the consequences of such evolution on species persistence remain to be explored (Lavergne *et al.* 2010). Currently, more flexible models of micro-evolutionary processes combine population-based information with phylogenetic comparative methods to provide an estimation of the evolutionary potential (Salamin *et al.* 2010). Moreover, populations can be locally adapted to specific climatic conditions and therefore, models treating a species as a single homogeneous unit might be flawed. Consequently, studying under which circumstances losses in genetic and species diversity at local to regional scales occurred in the past could improve models outputs (Dawson *et al.* 2011; McMahon *et al.* 2011).

Population and metapopulation dynamics

An inherent property of current global extinction models is that they do not take into account population or metapopulation dynamics that

determine species distributions, population structure and extinction risk at a local scale. Models are often based on habitat reduction and do not offer a mechanism by which the species' fitness is reduced and ultimately led to extinction. Recently, new mechanistic niche models have endeavoured to estimate key fitness components such as survival, growth, development and reproduction as a function of species attributes (i.e. physiology, phenology, behaviour) that vary with climatic conditions (Kearney *et al.* 2010).

Currently the probability of extinction is based on a projection of suitable habitats entirely lost (species will be committed to extinction) or partially lost (species will increase their extinction risk), although it is possible to combine niche models and abundance data (Iverson & Prasad 1998). In fact, on one side some species are more likely to go extinct because they consist of small and disconnected populations and on the other side, some species have shown compensatory changes in demographic rates following climate change (Doak & Morris 2010). The approach of population viability analysis (PVA) in this context could provide a good alternative. It is used to estimate the likelihood of a population's extinction within a given number of years through the species' demographic characteristics and environmental variability, instead of species range shifts. Only a few studies have used PVA to predict the effects of climate change on extinction risks (Keith *et al.* 2008; Anderson *et al.* 2009), in part because this approach requires data on population dynamics that are not available for most species.

In addition, physio-demo genetic models could provide the most realistic method to forecast the future of key species, as they consider simultaneously demographic (e.g. growth, rate of survival and reproduction, migration processes, environmental stochasticity), physiological (e.g. metabolic rate) and genetics parameters (heritability and norm of reaction). However, studies using physio-demo genetic models to evaluate the impacts of climate changes remain scarce (Kramer *et al.* 2010).

Co-extinctions

Whether centred on a single species or taking into account large taxonomic groups, most studies and all models have disregarded interspecific relationships such as competition, facilitation or mutualism. Beyond single-species extinctions, both direct and indirect processes can lead to cascading and catastrophic co-extinctions, also called 'chains of extinction' (Brook *et al.* 2008). Despite the importance of interspecific interactions, these relationships are exceptionally difficult to model; this is especially cogent in the context of lack of data on population dynamics and trophic webs (McMahon *et al.* 2011). As each species comes with its cortege of specific parasites and symbionts, as well as many trophic relationships, the consequences of global change on biodiversity might be substantially underestimated when focusing on species-specific extinction rates (Koh *et al.* 2004; Yang & Rudolf 2010). There is an urgent need not only to go beyond the single-species approach, but also to get past the species richness approach and to consider interspecific interactions, trophic webs and ecological networks (Bascompte 2009).

Synergies between extrinsic drivers of extinction

Research on future species extinctions has so far mostly considered a limited set of the predicted changes. For example, sea level rise has seldom been considered, although the most recent scenarios

projecting up to 2 m of rise by 2100 are raising new concerns for coastal and insular biodiversity (Grinstead *et al.* 2009). In addition, studies have mainly focused on the sole impact of climate change, sometimes considering a single additional driver (e.g. land-use change). These limitations may often lead to overly optimistic estimates. Indeed, other components of global change, such as habitat fragmentation, pollution, overexploitation and biological invasions have all been documented as major, additional threats for the future of biodiversity, with possible synergies, or reinforcing feedbacks between them (Sala *et al.* 2000). For instance climate-induced facilitation of invasions can occur at all stages of the invasion process (Walther *et al.* 2009; Bradley *et al.* 2010). In an experimental context, habitat fragmentation and overfishing combined with global warming have led to a decline in rotifer populations of up to 50 times faster than when either threat acts alone (Mora *et al.* 2007). In this case, dose-response relationship models could offer a powerful approach because they could simulate the impacts of many drivers of species extinctions.

Overall, despite important uncertainties and much conflicting imprecision, both under- and overestimating species loss, the very large underestimations due to co-extinctions, synergies and tipping points are extremely worrisome for the future of biodiversity (Fig. 5). Given the attractiveness of quantitative projections from mathematical models, it is tempting to underestimate their limitations. To minimise this risk, it is crucial to use a variety of complementary approaches, ranging from observational studies (palaeontological data, phenological responses, adaptive capacity) to field and laboratory experiments (on genetic, species and ecosystem levels) (Dawson *et al.* 2011).

BIODIVERSITY MANAGEMENT

The large variation of responses of different species necessitates the use and integration of multiple approaches to further our understanding of the impacts climate change can have on biodiversity (Dawson *et al.* 2011). Similarly, our responses in terms of biodiversity management ought to transcend disciplines. Beyond this, global climate change prompts several methodological issues and the implications for conservation and management of biodiversity and ecosystem services.

Conservation of species and ecosystems

The large projected impacts of climate change on biodiversity at all levels mean that ecologists must quickly rise to the challenge of providing scientific guidance for the development of conservation strategies (Pressey *et al.* 2007; Araújo *et al.* 2011; Dawson *et al.* 2011). A major role of conservation planning is to design reserve networks that protect biodiversity *in situ*. Currently few studies have attempted to use modelling for conservation purposes (Araújo *et al.* 2011). It is increasingly important to protect the heterogeneity of habitats as well as genetic diversity within a species to sustain the capacity of a species to adapt. Also, the characteristics of protected areas, where planning has to be done decades in advance (Hansen *et al.* 2010), need to be reviewed under climate change. Climate modelling can help to re-evaluate the current set of protected areas, their places, size, layout and design (Araújo *et al.* 2011). In particular, protection should be prioritised for places that minimise the effects of climate change – like forests, which contribute strongly to local climatic conditions – as well as for climate refuges for biodiversity (Carnaval *et al.* 2009).

Finally, model predictions of where, when and how future risks may affect species, biomes or ecosystems could assist in identifying the most appropriate conservation measures. For instance, species or ecosystem projected to be primarily affected by climate change may require adapted measures compared to species negatively affected by land-use change that could persist through protection of their remaining natural habitat (Hannah *et al.* 2007). In many cases there may no longer be any overlap between a species' current range and its possible future range. As this situation will lead to extinction, climate change has been a major argument for the proponents of human-assisted colonisation (Loss *et al.* 2011). In this increasingly hot debate, case-by-case decisions have been advocated, based on the balance between threatened status of a species and threat of that species for the recipient ecosystem, as well as the socioeconomic context in which conservation is taking place (Richardson *et al.* 2009; Dawson *et al.* 2011). A widespread view is that an important strategy is to enhance landscape connectivity to enable species to move through a matrix of interconnected habitats to favour escapes from unsuitable climatic conditions (Hannah *et al.* 2007).

It is also essential to shift from a species centred focus to a holistic view encompassing species interaction networks, and other aspects of biodiversity such as functional and phylogenetic diversities (Devictor *et al.* 2010). Beyond these various strategies, there is a growing call to go past the predictive focus and start aiming for an integrated and unified framework to identify species vulnerability and adapt biodiversity management interventions (Dawson *et al.* 2011). In this regard, preventive actions are of foremost importance. For example, it should be remembered that the proportion of species extinction is a power function of the expected global warming (Hansen *et al.* 2010). Minimising global warming could therefore have nonlinear effects in the preservation of species from extinction, with each tenth of degree avoided saving an increasing number of species (Hansen *et al.* 2010). Acting to reduce global warming itself, and not only its effect on biodiversity, should remain *a priority* in conservation sciences. In addition, reducing other global change drivers could increase overall resilience of biodiversity in the face of climate change (Hughes *et al.* 2003).

Ecosystem services

Other aspects of biodiversity management will be affected by global change and will need adapting, including wildlife exploitation [e.g. forestry (Dale *et al.* 2010) or fisheries (Stram & Evans 2009)], agronomy (Howden *et al.* 2007), pest and invasive species control (Ziska *et al.* 2011) or human and wildlife disease management (Harvell *et al.* 2002). For example, major challenges in agronomy include the need to shift to species or varieties better adapted to particular components of climate change or to rethink strategies to control invasive and pest outbreaks, finding solutions in the increasing competition for water between the natural and the agricultural ecosystems, improving infrastructures and adapting cropping systems to meet future demands of a growing population living on poorer biodiversity resources (Howden *et al.* 2007).

Given the tremendous ecological impact of alien invasive species, and the expected exacerbation of invasion due to climate change (Walther *et al.* 2009), it is urgent to increase predictive power in this field. It is also crucial to move beyond predictions (Dawson *et al.* 2011) and to strengthen risk assessment, protocols of screening and of early detection, vector control and integrated management in area

and/or of invasive species that will become at higher risk following climate change. Similar efforts are imperative for other drivers of biodiversity loss, such as overexploitation or habitat destruction.

CONCLUSION

Ecologists are developing a better understanding of the mechanisms by which species and ecosystems can be impacted by climate change. The timing of species' life cycle events is expected to be further altered, species distributions will change radically, trophic networks will be affected and ecosystem functioning may be severely impaired, leading in the worst cases to countless species extinctions. Over the past decades, some of this understanding has been effectively translated into mathematical models that can be used to forecast climate change impacts on species distributions, abundance and extinctions. These models are characterised by their high diversity of underlying structures and assumptions, with predictions differing greatly depending on the models used and species studied. Most of these models indicate alarming consequences for biodiversity with worst-case scenarios leading to extinction rates that would qualify as the sixth mass extinction in the history of the earth (Barnosky *et al.* 2011). However, all current approaches have serious weaknesses. An evaluation of known mechanisms of climate impacts on biodiversity suggests that the lack of several key mechanisms in models may lead to either very large underestimations or overestimations of risks for biodiversity. Improvements in existing models and, in particular, a new generation of models must address the shortcomings of current models to reduce uncertainties. It is also crucial to improve our understanding of the vulnerability of biodiversity to climate change, to develop other predictive approaches and to go beyond predictions.

Crucially, the diversity of approaches, methods, scales and underlying hypotheses used has led to an ensemble of global quantitative predictions that can seldom be compared. Consequently, we are left with a mosaic of information that cannot provide a quantitative, coherent picture of future biodiversity loss. Yet, standardisation of future studies (of taxonomic groups, methods, time horizon, scale, etc...), which might help decrease uncertainty, would do so at the expense of the breadth of knowledge and of a much needed innovation in this field. In this regard, a solution may come from a collective effort in conducting large meta-studies that would encompass many components of variability (biodiversity, time and space scale, models,) to both infer similarities and assess sources of inconsistency. Given its scale, such an ambitious endeavour needs an enduring cooperative effort from coordinated research groups. The long awaited Intergovernmental Platform on Biodiversity and Ecosystem Services (Perrings *et al.* 2011) could provide the impetus for building such national and international efforts. A major near-term target to substantially improve our understanding, predictive capacity and reactive potential will be to contribute to this new IPCC-like assessment for biodiversity and ecosystem services.

ACKNOWLEDGEMENT

All authors wrote the review and are grateful for the very constructive comments of five referees. The review was written while the authors were supported by various grants: CéB from the CNRS, CIB from the Région Ile-de-France (03-2010/GV-DIM ASTREA), WT and PL from the French "Agence Nationale de la Recherche" (ANR) with the project SCION (ANR-08-PEXT-03), WT from ANR with the project

DIVERSITALP (ANR-07-BDIV-014) and from the European Commission's FP6 ECOCHANGE project (GOCE-CT-2007-036866) and FC from ANR with the project RARE (2009 PEXT 010 01).

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Editor, Hector Arita

Manuscript received 23 May 2011

First decision made 27 June 2011

Second decision 2 Nov 2011

Manuscript accepted 17 December 2011

Conclusion

Les conclusions de cette étude ont permis de montrer que l'étude des changements climatiques en écologie en est encore à ses débuts, et que de nombreuses améliorations doivent encore être réalisées. Les projections actuelles des conséquences de ces changements climatiques révèlent des chiffres alarmants de perte de biodiversité pour la fin de ce siècle. Cependant, la diversité des approches, des méthodes, des échelles et des hypothèses sous-jacentes rend les prédictions difficilement comparables. Ainsi, l'ensemble des approches utilisées a des lacunes qui nécessitent une attention particulière et des améliorations dans les années à venir.

Par exemple, les mécanismes clefs tels que l'adaptation des espèces devront être intégrés aux prédictions futures. De plus, la biodiversité est actuellement mal représentée dans ce type d'études. En effet, la grande majorité des études ne considère que les mammifères, oiseaux et plantes, et peu d'études se concentrent sur les invertébrés (voir néanmoins Leroy *et al.* 2013), alors que ce seul groupe représente 80% des espèces d'animaux ou de plantes présentes sur Terre. Une autre caractéristique de la majorité des études est qu'elles modélisent uniquement l'effet des changements climatiques, sans étudier les synergies entre les changements climatiques et les autres menaces telles que les changements d'utilisation des sols ou les invasions biologiques. De plus, ces études se limitent aux changements de températures et de précipitations et ne considèrent pas les autres composantes climatiques telle que l'élévation du niveau des mers.

La connaissance de ces lacunes a permis de définir un cadre à cette thèse et à guider les questions scientifiques qu'on y a développées. En particulier dans le second chapitre de ma thèse et l'annexe 2, j'ai donc étudié les conséquences de la hausse du niveau des mers sur la biodiversité insulaire tandis que dans le Chapitre 5 j'ai cherché à étudier l'effet combiné des changements climatiques et des invasions biologiques ce qui a permis de montrer des évaluations plus complexes que celles traditionnellement prédites.

Chapitre 2

Impact of sea level rise on the ten insular biodiversity hotspots

Résumé

Comme on l'a montré dans le premier chapitre, malgré une augmentation croissante des études portant sur les conséquences des changements climatiques, aucune évaluation des effets de la hausse du niveau des mers sur les écosystèmes insulaires n'avaient été réalisée jusqu'à aujourd'hui. Pourtant, les 180 000 îles présentes à travers le monde contiennent près de 20 % de la biodiversité mondiale. Parmi ces habitats insulaires, de nombreuses îles risquent d'être menacées par une hausse du niveau des mers. Nous avons donc étudié, dans ce chapitre, les conséquences d'une hausse du niveau des mers sur les 10 hotspots de biodiversité insulaires (4 447 îles) et les espèces endémiques qu'on y trouve. En particulier, nous avons modélisé les conséquences de l'élévation du niveau des mers de 1, 2, 3 et 6 mètres sur ces hotspots. Pour chacun de ces scénarios nous avons calculé le nombre d'îles totalement submergées ainsi que la perte d'habitat partielle de chacune de ces îles. Ensuite, en utilisant la relation endémique aire-espèce, nous avons estimé le nombre d'espèces de plantes, d'amphibiens, d'oiseaux, de reptiles, de mammifères et de poissons qui risquaient d'être affectées par cette menace dans le futur. Globalement, nous avons montré qu'entre 6 et 19% des 4 447 îles risquaient d'être totalement inondées. De plus, nous avons montré que tous les hotspots ne sont pas menacés de façon homogène par la hausse du niveau des mers. En effet, d'après nos résultats, les îles caribéennes, les philippines et le Sondaland sont les plus vulnérables. En conclusion, ce travail a permis de montrer qu'il est indispensable de considérer la hausse du niveau des mers comme une menace majeure pesant sur le futur de la biodiversité insulaire.

Cette partie correspond à l'article publié suivant:

C. Bellard, C. Leclerc, & F. Courchamp (2013) Impacts of sea level rise on the ten insular biodiversity hotspots. In *Global Ecology and Biodiversity*, in press.

RESEARCH
PAPER



Impact of sea level rise on the 10 insular biodiversity hotspots

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ABSTRACT

Aim Despite considerable attention to climate change, no global assessment of the consequences of sea level rise is available for insular ecosystems. Yet, over 180,000 islands world-wide contain 20% of the world's biodiversity. We investigated the consequences of sea level rise for the 10 insular biodiversity hotspots world-wide and their endemic species. This assessment is crucial to identify areas with the highest risk of inundation and the number of endemic species at risk of potential extinction.

Location Ten insular biodiversity hotspots including the Caribbean islands, the Japanese islands, the Philippines, the East Melanesian islands, Polynesia-Micronesia, Sundaland, Wallacea, New Caledonia, New Zealand and Madagascar and the Indian Ocean islands (i.e. 4447 islands).

Methods We investigated four scenarios of projected sea level rise (1, 2, 3 and 6 m) on these islands. For each scenario, we assessed the number of islands that would be entirely and partially submerged by overlying precise digital elevation model and island data. We estimated the number of endemic species for each taxon (i.e. plants, birds, reptiles, mammals, amphibians and fishes) potentially affected by insular habitat submersion using the endemic–area relationship.

Results Between 6 and 19% of the 4447 islands would be entirely submerged under considered scenarios (1–6 m of sea level rise). Three hotspots displayed the most significant loss of insular habitat: the Caribbean islands, the Philippines and Sundaland, representing a potential threat for 300 endemic species.

Main conclusions With the current estimates of global sea level rise of at least 1 m by 2100, large parts of ecosystems of low-lying islands are at high risk of becoming submerged, leading to significant habitat loss world-wide. Therefore, the threat posed by sea level rise requires specific policies that prioritize insular biota on islands at risk as a result of near future sea level rise.

Keywords

Biodiversity hotspots, climate change, endemic–area relationship, endemic species, islands, sea level rise.

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INTRODUCTION

Global rise in sea levels is one of the most certain consequences of global warming (Nicholls & Cazenave, 2010), yet it remains one of the least studied topics in ecology. Sea level change is of considerable interest because of its potential impact on human populations living in coastal areas (50% of the world population will live within 100 km of the coast by 2030 (Small & Nicholls,

2003; Bindoff *et al.*, 2007), and because of the potential associated economic losses (9% of global gross domestic product; Hanson, 2010). In addition, sea level rise is of major importance for ecosystems and human populations surrounded by seas, as it will directly reduce habitat availability, sometimes drastically for the smallest islands. The 180,000 islands world-wide harbour over 20% of the world's biodiversity (Kier *et al.*, 2009), and a direct reduction of their habitat therefore will have major

consequences. Such reduction, and the subsequent decrease of biodiversity, will be the most direct and inevitable outcome of sea level rise. Ongoing research suggests that the conclusions of the last Intergovernmental Panel on Climate Change (IPCC) report concerning the future increase of global mean sea level rise ((18–59 cm between present day, assuming a 1980–1999 baseline and 2090–2099; IPCC *et al.*, 2007) may be too conservative, because they do not account for the melting and sliding of land ice in Greenland and the Antarctic. Several more recent studies strongly suggest that sea level rise could be substantially greater, i.e. an increase of 0.5 to 2.3 m by the end of this century (Rahmstorf, 2007; Pfeffer *et al.*, 2008; Grinsted *et al.*, 2009; Nicholls & Cazenave, 2010; Traill *et al.*, 2011). Worst case scenarios of ice sheet melting and sliding lead to estimates of sea level rise of 4 to 6 m in the next centuries (Overpeck *et al.*, 2006). Such increases could lead to the immersion of very large portions of many low-elevation islands, and in many cases to their total submersion, obviously threatening the most dramatic consequences for local biodiversity.

Already, studies on specific archipelagos, large oceanic regions or continental regions show that sea level rise will have important consequences and should be more deeply studied (Hanson, 2010; Hinkel *et al.*, 2010; Menon *et al.*, 2010; Webb & Kench, 2010; Traill *et al.*, 2011; Wetzel *et al.*, 2012). So far, no studies have focused on the consequences of sea level rise for insular biota on a global scale. Estimates of the number of islands that are globally at risk for complete or significant submergence due to sea level rise are required in order to evaluate the consequences for insular biodiversity. These results are of major importance to identify and prioritize conservation actions on islands that are particularly vulnerable to sea level rise. Islands are generally considered centres of biodiversity, due to very high rates of endemism (9.5 and 8.1 times higher than continents for vascular plants and vertebrates, respectively) (Kier *et al.*, 2009). Overall, about 70,000 vascular plant species are endemic to islands (Kier *et al.*, 2009). Biodiversity hotspots have been defined as the 34 regions where biodiversity is both the richest and the most threatened (Mittermeier *et al.*, 2004). Recently, one hotspot has been added to this list (the forest of the north-east part of Australia) (Mittermeier *et al.*, 2012). Together, these hotspots harbour an exceptionally high number of vascular plant species, notably over 164,200 endemic species (Mittermeier *et al.*, 2004). Within these regions, 10 are constituted only or mainly by islands (insular hotspots). We expect considerable loss of insular biodiversity consisting exclusively or mainly of islands under the currently admitted sea level rise scenarios through the permanent inundation of low-lying regions. We define inundation as due to shoreline retreat when low-lying areas are gradually submerged by ocean waters. This assessment is crucial to identify areas at the highest risk of inundation and the potential number of endemic species at risk of extinction.

Here, we assess the impacts of sea level rise on the 4447 islands included in the 10 insular biodiversity hotspots. This sample includes islands of various sizes, geological types and elevations, and covers virtually all latitudes in the Pacific, Indian and Atlantic oceans. We investigated four scenarios of projected sea level

rise on these islands and provide estimations of entire and partial island loss and its associated endemic biodiversity. We used the endemic–area relationship (EAR) to obtain an estimate of the number of endemic species for each taxon considered to be potentially affected by submersion of insular habitat (Harte & Kinzig, 1997). Since sea level rise based on the IPCC scenarios (0.35 m) is now considered too conservative (Nicholls & Cazenave, 2010), we considered four different homogeneous projections including a rise of 1, 2, 3 and 6 m (Overpeck *et al.*, 2006; Rahmstorf, 2007; Grinsted *et al.*, 2009). Yet our estimates of insular habitat loss are conservative since we did not consider horizontal erosion loss and extreme events (e.g. storms, tsunamis, hurricanes, centennial tides). Digital elevation models constructed by overlying precise elevation data with sea level projections enables the assessment of the number of islands entirely and partially submerged under different sea level rise scenarios. This illustrates the extent to which coastal areas are susceptible to permanent inundation. We also highlight the case study of New Caledonia to compare potential loss of endemic species predicted both by the EAR and the use of precise endemic species distribution data for New Caledonia. More precisely, we intend to explore these three questions:

1. What is the effect of four sea level rise scenarios (1, 2, 3 and 6 m) on the distribution and magnitude of insular habitat loss (i.e. partial and complete losses of islands) for the 4447 islands of the insular biodiversity hotspots?
2. Which insular hotspots are the most threatened by an increase in sea level in terms of partial loss and/or entirely inundated islands as a consequence of the different scenarios of sea level rise?
3. How many endemic plant, mammal, reptile, bird, fish and amphibian species may be at risk of global extinction due to sea level rise in both insular hotspots and globally?

MATERIALS AND METHODS

Data

Study islands

To qualify as a hotspot of biodiversity a region had to contain at least 1500 vascular plants as endemics (> 0.5% of the world's total) and to have 30% or less of its original vegetation remaining (Myers *et al.*, 2000). Ten insular biodiversity hotspots fall into this definition. In order to be exhaustive, we considered both islands and islets as 'islands'. First, we included 5792 islands in the 10 insular biodiversity hotspots that are composed mainly of islands or groups of islands (Fig. 1) from 'The Biodiversity Hotspots – Conservation International' (2012; http://www.conservation.org/where/priority_areas/hotspots/pages/hotspots_main.aspx). Island size ranges are from less than 22 ha (Surprise Island) to 725,000 km² (Borneo) and they encompass all latitudes and geological types of island ecosystems (Fig. 1). All the islands studied are located in the Atlantic, Indian or Pacific oceans. Island polygon delineations were derived from 'The Biodiversity Hotspots – Conservation International' (2012; <http://>

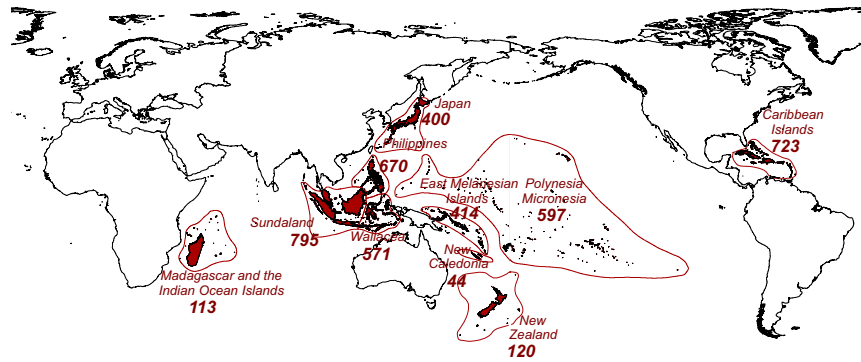


Figure 1 Maps representing the 4447 islands selected across selected 10 biodiversity hotspots.

www.conservation.org/where/priority_areas/hotspots/pages/hotspots_main.aspx). The polygons were used as a mask to extract the elevation data.

Elevation data

Our island elevation dataset is based on the digital elevation model (DEM) from NASA's Shuttle Radar Topography Mission (SRTM). We used the extract function from the raster package (R version 2.15) for all the 5792 islands included in the insular hotspots. We excluded from the analysis 1345 islands for which elevation data were not available (e.g. small islands). These small islands are of minor relevance for the study because they host almost no endemic species. Our study finally included 4447 islands, covering 82% of the total area of the 10 insular hotspots (see Table S1 in Supporting Information for the precise number of islands per hotspot).

Biodiversity data

The 10 insular hotspots contain more than 50,000 endemic plant species and more than 670 endemic mammals. To estimate the biodiversity that is threatened by sea level rise at the hotspot scale, we focused on endemic species (and did not consider total biodiversity in the hotspots). We used the number of endemic species for different taxa present in each hotspot from Mittermeier *et al.* (2004). For each hotspot, we extracted the number of endemic plants, mammals, birds, reptiles, amphibians and freshwater fishes (see Table S2). Because these estimates are at the hotspot level, we also evaluated the number of endemic species for each taxonomic group per island. Knowing the number of endemic species for each hotspot, we calculated the number of endemic species for each island according to island size (see below).

Assessing impacts of sea level rise on islands

Sea level rise scenarios

We considered four different sea level rise scenarios, ranging from very optimistic to extreme, yet all remaining realistic for the next centuries. We calculated the area of land loss due to inundation by island and by insular hotspot. First, we consid-

ered a global sea level rise of 1 m by 2100, which is slightly below the average of six recent projections of sea level rise for 2100 (Overpeck *et al.*, 2006; Rahmstorf, 2007; Pfeffer *et al.*, 2008; Grinsted *et al.*, 2009; Nicholls & Cazenave, 2010). We also explored a realistic upper bound of a 2 m sea level rise (Nicholls & Cazenave, 2010) and a 3 m sea level rise (Hansen, 2007). Finally, we also considered the more extreme scenarios of ice sheet melting that lead to estimates of sea level rise of up to 6 m (Overpeck *et al.*, 2006; Menon *et al.*, 2010; Wetzel *et al.*, 2012). This last scenario represents an extreme limit of sea level rise for the next centuries, but it is unlikely for 2100. More precise sea level rise scenarios are currently unavailable, because data on geomorphology for all these islands are lacking. Even if future sea level rise is likely to be heterogeneous and lunar effects or isostatic rebound could both lead to a fall or rise of sea level at a local scale, the regional variation in sea level rise is hard to predict. Therefore we did not extrapolate heterogeneity, due to these high uncertainties (Nicholls & Cazenave, 2010). It is commonly accepted that homogeneous rise is an acceptable approximation (Wetzel *et al.*, 2012). Further, static drowning conditions of coastal areas are assumed, whereas it is recognized that in reality the coastal response to sea level rise may be more complex, especially in for clastic coast lines (Nicholls *et al.*, 2007). We also did not consider connectivity of cells, and assumed that all areas below sea level will be permanently inundated. We used the DEM for the 4447 islands using R version 2.15 to calculate the sum of the number of pixels under the four sea level rise projections for the 10 insular hotspots, as well as for the 4447 islands individually.

Endemic species at risk of submersion

A precise number of endemic species for each of the 4447 islands individually was not available, thus we used the number of endemics per hotspot. However, the number of endemic species per hotspot provides a robust dataset of endemic species for these islands, contrary to many global datasets. The EAR provides a first approximation to estimate the proportion of endemic species vulnerable on each island per insular hotspot. Ecologists and biogeographers have long recognized that species richness (S) increases with area (A) at a decreasing rate and thus eventually levels off (Rosenzweig, 1995). The EAR performs

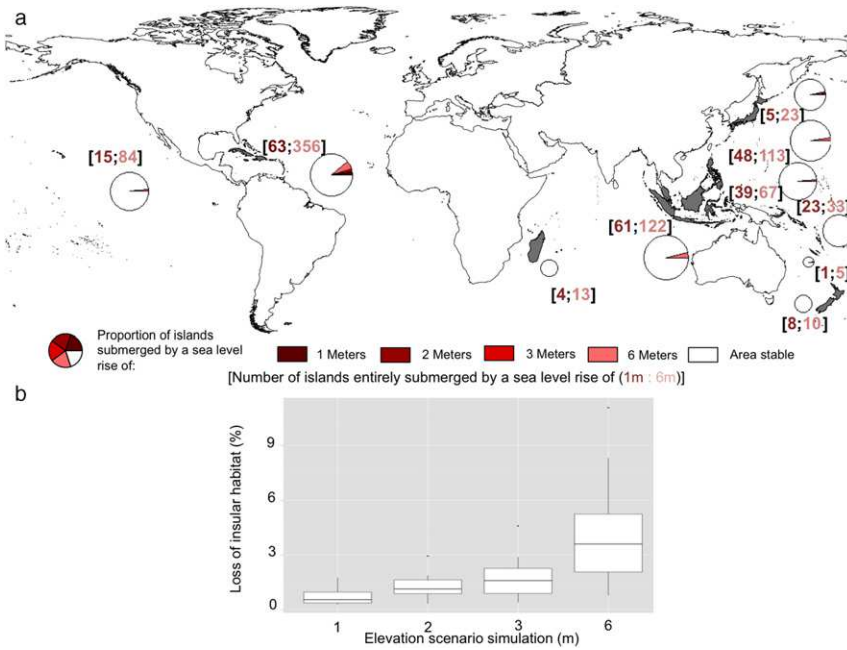


Figure 2 Potential loss of insular habitat for each of the hotspots (a) according to the sea level stand above mean sea level (1, 2, 3 and 6 m). The size of the pie chart is relative to the number of islands in the hotspot. The first number in the brackets corresponds to the number of islands entirely submerged under a scenario of sea level rise of 1 m, and the second number represents the number of islands entirely submerged under a scenario of sea level rise by 6 m (b) and for all the 10 insular hotspots.

better than the species–area relationship (SAR) in predicting the potential number of extinctions due to habitat decrease (Kinzig & Harte, 2000) and is currently preferred over the classic SAR approaches (Harte & Kinzig, 1997). To derive a more realistic relationship under this possibility, the EAR takes into account the number of species expected to be confined to smaller patches within the total area of habitat loss:

$$f_{\text{lost-EAR}} = \Phi_A z'$$

where Φ_A is the ratio of future to present area ($A_{\text{future}}/A_{\text{current}}$) and z' is a constant [$z' = -\ln(1 - 1/2^z)/\ln(2)$]. A_{future} represents the calculated loss of terrestrial area as a result of an increase in sea level by 1, 2, 3 or 6 m and A_{current} represents the current area of each island.

Following Kier *et al.* (2005), we chose a z value adapted for each hotspot, according to its biome type. We attributed a different z value for tropical and subtropical moist broadleaf forests in Asia ($z = 0.26$), Central America ($z = 0.33$), South America ($z = 0.32$), Australia and Africa ($z = 0.24$), and tropical and subtropical dry broadleaf forests ($z = 0.21$).

First, we calculated the fraction of endemic species threatened at the hotspot level. We calculated A_{future} and A_{current} as the fraction of original habitat lost by insular hotspot. Second, we calculated the fraction of endemic species threatened by sea level rise for each island. Using the fraction of original habitat lost by insular hotspot, we calculated the number of endemic species threatened in each hotspot for six taxa (i.e. plants, freshwater fishes, amphibians, reptiles, birds and mammals) by each sea level rise scenario. We then calculated the number of species threatened of each of these taxa by island, using the EAR fraction calculated at island level. The number of species of each of the six taxonomic groups affected both within each hotspot and

island was then inferred from the degree of habitat reduction following an increase in sea level.

Case study: New Caledonia

We decided to validate our model using the New Caledonian hotspot as a case study for which there was the rare availability of precise data for endemic species distribution. We obtained endemic species–area distribution polygons provided by the International Union for Conservation of Nature (IUCN) database (IUCN, 2012). We used polygons of species distributions for 6 mammals, 61 reptiles, 24 birds and 64 plants. Then, we assumed that the species distributions within the hotspot changed proportionally to the degree of marine intrusion in the hotspot and we calculated proportional range losses for each species. The results of this case study analysis were used to help qualify the utility of our EAR methods for predicting potential number of species at risk of extinction.

RESULTS

Potential consequences of sea level rise on insular habitats

Our results indicated that increase in sea level led to a significant impact on insular habitat. On average almost 1% of land area of the hotspot would be permanently inundated under an increase of sea level by 1 m, a figure that rises to 4.1%, for a 6 m rise in sea level (Fig. 2a). This represents roughly 25,200 km² at risk of inundation for a 1 m rise in sea level and more than 167,000 km² at risk of inundation for a 6 m rise in sea level, which is equivalent to the total area of Uruguay. We identified

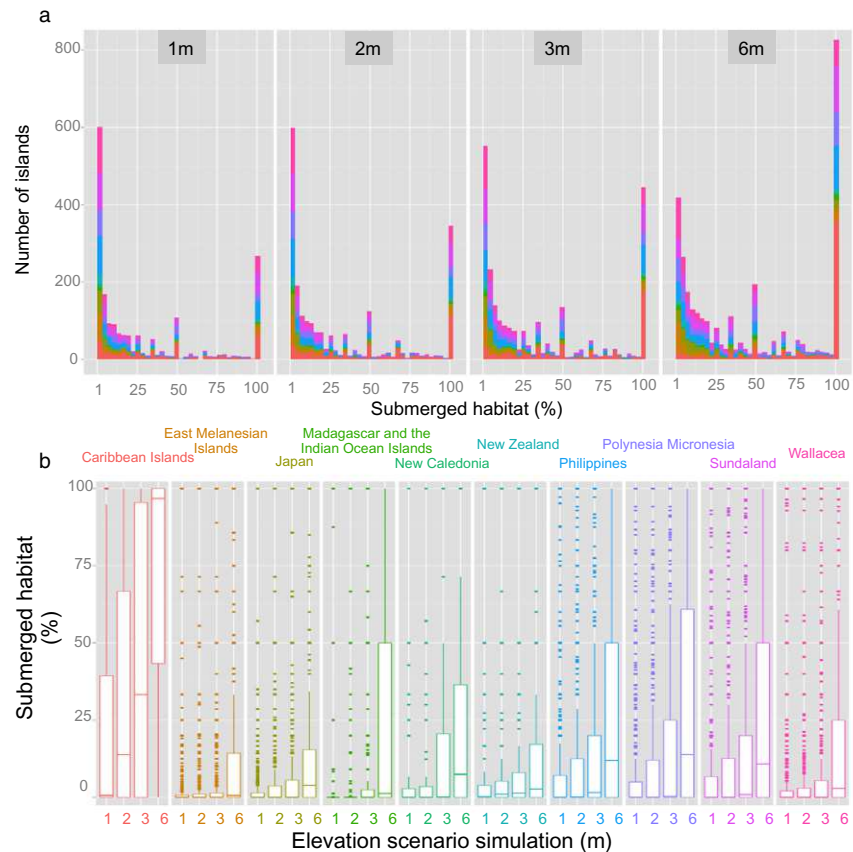


Figure 3 (a) Number of islands that suffer from 1 to 100 % of submerged insular habitat according to the four projections of rising sea levels (1, 2, 3 and 6 m) for the 10 insular hotspots. The colours of the histogram correspond to the name of the hotspots in panel (b). (b) Boxplot of percentage of habitat submerged for the 10 insular hotspots and the four different sea level rise scenarios. The line in the box indicates the median value of the data.

different patterns of potential insular loss among the hotspots of biodiversity (Fig. 2b). Three hotspots appeared to be particularly threatened: the Caribbean islands, Sundaland and Japan, which, for a 6 m rise in sea level may have 11.1, 5.6 and 4.1%, respectively, of their area inundated (Table S3).

We also calculated the loss of habitat per island, starting with the number of islands that may be totally submerged following sea level rise (i.e. number of islands lost). Under the 1-m rise scenario, at least 6% of the islands could be totally and permanently submerged, while the figure rises to 18.6% under the 6-m scenario (Fig. 2). Overall, 267 to 826 islands could be permanently inundated in the future (Table S4). The Caribbean islands hotspot was the most threatened, with 8.7% of its islands entirely submerged with only a 1-m increase (i.e. 63 islands lost). Sundaland and the Philippines were also particularly affected, with a potential loss of 61 (7.7%) and 48 (7.2%) islands, respectively, following the lowest estimate of a 1-m increase in sea level. Under the most extreme scenario for sea level rise (6 m), we predicted the total submersion of up to 356 (49.2%), 122 (15.3%) and 113 (16.9%) islands for the Caribbean islands, Sundaland and the Philippines, respectively. On the contrary, the Japanese hotspot should be the least affected with only 1.2% (i.e. five islands) of the islands predicted to be entirely submerged with a sea level rise of 1 m, and 5.7% (i.e. 23) lost under the highest rise scenario (6 m).

In addition, many islands were predicted to suffer from loss of a very large portion of their habitat: 11.4% (1 m) to 32.1% (6 m) of all islands may have a size reduction of at least 50% in the

future. Here again, the Caribbean islands hotspot was the most threatened with 23% (i.e. 165) to 73% (i.e. 533) of its islands half-submerged. Polynesia-Micronesia and Sundaland were also significantly threatened by major submersion, with 10% (i.e. 59 half-submerged islands) to 36% (i.e. 215) of islands half-submerged for Polynesia-Micronesia and with 12% (i.e. 99) to 26% (i.e. 210) of islands half-submerged for Sundaland. Only 58% (1 m scenario) to 29% (6 m scenario) of islands will be spared from partial immersion (no loss) in the future. Japan, the East Melanesian islands and New Zealand were predicted to be the least affected by sea level rise, with fewer than 60 islands combined that are threatened by having 50% of their area inundated in the future. Figure 3(a) gives the distribution of lost area by island for the 10 hotspots predicted under the four scenarios, while Fig. 3(b) gives the median area loss per island for the 10 hotspots predicted under the four scenarios (see also Table S4).

Potential consequences of sea level rise for endemic species

Using the EAR at the hotspot scale, we estimated that from 1 (1 m) to 55 (6 m) endemic species may be at high risk of extinction due to rising seas. The distribution among the six taxonomic groups was very uneven: most of the species predicted to be lost were plants, while almost no amphibians, mammals or fishes were predicted to be lost. This is due to the large number of endemic plants, and relatively (to plants) low numbers of endemic amphibians, mammals and fishes in these islands. In

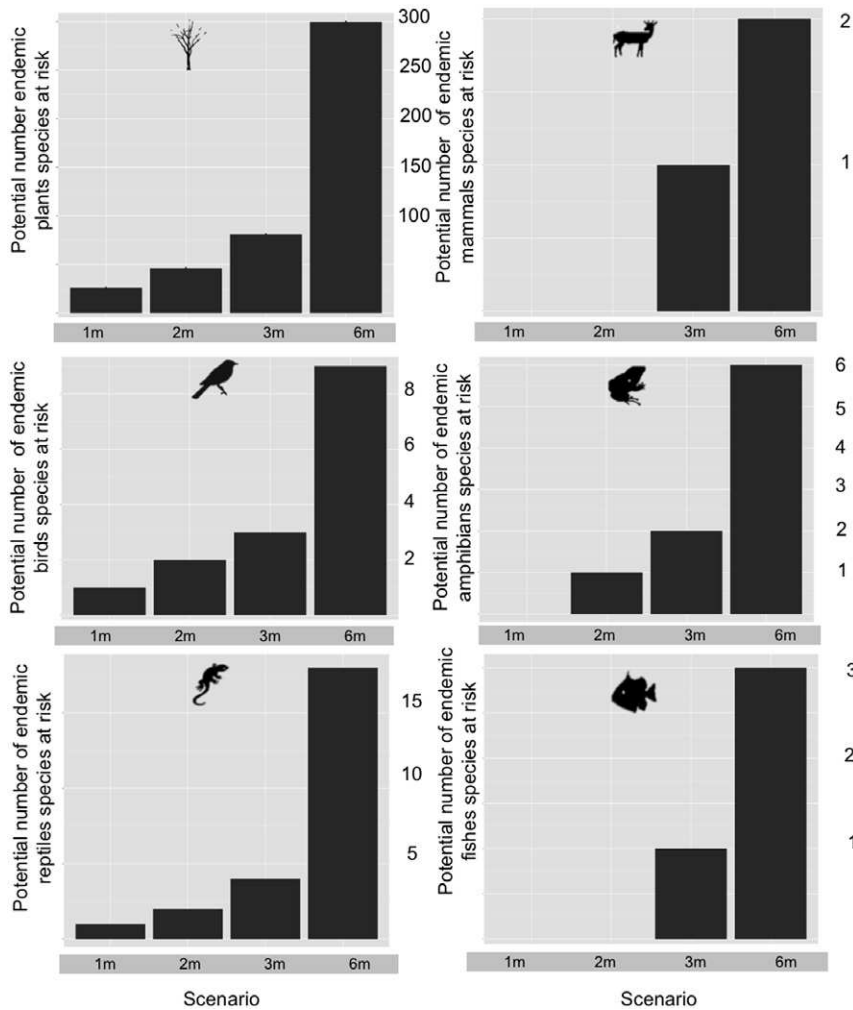


Figure 4 Number of endemic plants, birds, reptiles, mammals, amphibians and fishes at risk of extinction by sea level rise, for the 10 insular hotspots under the four different sea level rise scenarios.

In addition, insular hotspots are not composed of a single large territory, but are divided into many isolated islands, and assessments at hotspot level lead to over-estimations. Figure 4 shows the number of endemic plants, birds, reptiles, mammals, amphibians and fishes likely to be lost following sea level rise in the 10 insular biodiversity hotspots. The EAR also provided an estimate of the number of endemic species – for each taxonomic group – that were threatened at the island level. This estimate was used to deduce the potential number of species at risk of extinction per taxonomic group when individual islands are partially or entirely submerged. For the 1 m rise scenario, the sum of endemic species threatened across all the islands was predicted to be 26 plants, one bird and one reptile, while for the worst scenario (6 m) the loss was predicted to be of six endemic amphibians, two mammals, eight birds, three fishes, 18 reptiles and 300 plants. Overall, a small number of endemic species might be affected by sea level rise, given our estimations. However, our method for estimating the number of endemic species potentially affected is simple and must be considered with caution.

Finally, using New Caledonia as a case study, we showed that the percentage of submerged species–area distribution is likely

to be low among the taxa (Table 1). None of the species were predicted to lose their entire species–area distributions, which is consistent with the results from the EAR. However, endemic plants were predicted to be the most vulnerable to sea level rise, 1.25 to 7.65% of submerged areas were predicted, under an increase in sea level of 1 and 6 m, respectively (Table 1). In addition, eight endemic plants that are already classified as critically endangered by the IUCN are likely to be significantly affected by sea level rise in the future (see Table 1).

DISCUSSION

Studying 4447 islands world-wide in 10 different insular hotspots over three oceans, we showed that predicted rises in sea level should lead to the total loss of hundreds of these islands and to a very large reduction in their habitat for hundreds of others. The number of endemic species potentially affected by habitat reduction as a result of sea level rise determined by this study is relatively low compared with other climate change threats (Bellard *et al.*, 2012). Yet it is highly probable that inclusion of non-endemics as well as endemics living on islands beyond these hotspots would increase the number of species

Table 1 The percentage of species–area distribution submerged under four different scenarios of sea level rise for mammals, reptiles, birds and plants endemic to the New Caledonia hotspot. Among the different taxa, we selected the species that were predicted to have at least 10% of their species–area distribution submerged under an increase of sea level by 6 m.

Taxa	Species	IUCN status	Percentage of submerged species–area distribution (%)			
			Sea level rise by 1 m	Sea level rise by 2 m	Sea level rise by 3 m	Sea level rise by 6 m
Mammals	<i>n</i> = 6		0.27	0.55	0.95	2.07
Birds	<i>n</i> = 24		0.27	0.56	0.94	2.2
Reptiles	<i>n</i> = 61		0.3	0.58	0.96	2.21
	<i>Nannoscincus hanchisteus</i>	CR	1.41	2.11	3.52	12.68
	<i>Caledoniscincus auratus</i>	EN	0.94	2.82	5.63	11.86
	<i>Bavayia exsuccida</i>	EN	1.14	2.64	5.04	10.66
Plants	All (<i>n</i> = 64)		1.25	2.58	3.98	7.65
	<i>Eugenia lepredourii</i>	CR	5.75	10.6	14.72	23.32
	<i>Pittosporum taniaum</i>	CR	5.17	9.21	13.58	19.14
	<i>Randia pancheriana</i>	VU	3.41	6.5	9.14	16.23
	<i>Eugenia dagostini</i>	EN	1.83	4.65	8.19	15.79
	<i>Eugenia metzdorfi</i>	EN	1.51	3.68	5.94	13.48
	<i>Ochrosia inventorum</i>	CR	3.09	5.68	7.61	13.36
	<i>Tinadendron noumeanum</i>	CR	2.72	5.16	6.76	13.24
	<i>Diospyros veillonii</i>	CR	2.55	4.84	6.34	11.58
	<i>Canavalia favieri</i>	CR	2.63	4.83	6.5	11.4
	<i>Syzygium pendulinum</i>	EN	2.74	5.14	7.02	11.3
	<i>Trigonostemon cherrieri</i>	CR	1.27	3.04	4.99	11.24
	<i>Callerya neocaledonica</i>	CR	2.56	4.7	6.28	11.16
	<i>Eugenia daenikeri</i>	EN	2.25	4.24	5.62	10.49
	<i>Psychotria deverdiana</i>	VU	1.45	3.22	5.36	10.33
	<i>Atractocarpus platyxydon</i>	VU	1.6	3.25	4.96	10.22

IUCN, International Union for Conservation of Nature; CR, critically endangered, EN, endangered, VU, vulnerable.

threatened. In addition to the number of endemic species, insular hotspots harbour a number of non-endemic species; and additional 95,000 plant, 1200 mammal, 2100 reptile and 900 amphibian species inhabit these 10 hotspots alone (Myers *et al.*, 2000).

Our approach has already been used successfully in similar studies. For example, Menon *et al.* (2010) used similar methods to analyse the effects of sea level rise world-wide on marine intrusion in terrestrial ecoregions. Wetzel *et al.* (2012) also used this approach to study the effect of sea level rise on the extinction risk for 54 mammals of the Indo-Malaysian islands. In both cases, results were of the same order of magnitude regarding the percentage area loss predicted for 1 and 6 m of sea level rise, with the highest area losses concentrated in the same geographic regions (i.e. Southeast Asia and associated islands and north-eastern South America). Regarding the potential number of endemic species at risk, our results were also on the same order of magnitude as those of Menon *et al.* (2010). The vertical resolution of our global DEM was limited to a vertical resolution of 1 m; a higher-resolution DEM would yield more precise predictions of area change. Also we did not consider connectivity of cells, and assumed that all areas under sea level would be permanently inundated, which is not necessarily the case. Some areas may be completely surrounded by higher-elevation areas

and thereby protected from marine intrusions, and other areas with elevations below the scenario of sea level rise are already inland water bodies, which therefore should not be included in calculations of newly inundated areas. However, in this last case, species that are salt-intolerant may be at risk of extinction. Using current endemic species distribution data for New Caledonia, we showed that our results from EAR approaches were likely to be consistent regarding the number of species that are at risk of extinction. Because the EAR assumed an exponential relationship between area and the number of endemic species, the estimation of the number of endemic species threatened on small islands is likely to be low. In addition, we removed from our study all islands below 22 ha (because elevation data are lacking for these islands). Therefore, because sea level rise will disproportionately affect small and low-lying islands like atolls, our predictions underestimate the loss of these insular habitats, and any endemic species that may inhabit them. However, endemic species on even very small islands are not unheard of [e.g. one endemic bird species on Surprise Island, New Caledonia (area 0.22 km²), which became extinct in 2000 because of invasive rats; Caut *et al.*, 2008]. Conversely, the SAR overestimates biodiversity, resulting in exaggerated values of potential biodiversity losses (He & Hubbell, 2011). Despite inherent limitations, we believe that our range estimates for both islands and species

loss are realistic. In fact, many of our assumptions may lead to underestimations of insular habitat loss. In particular, we assumed no lateral erosion, no tidal range, no centennial tides or floods, nor associated increased salinity on new shorelines. The nonlinear response of clastic coastlines to sea level rise may influence a larger inland area compared with a reconstructed study based on the drowning of static coastlines (Nicholls *et al.*, 2007). Indeed, although a small increase in sea level can be balanced by sediment supply and morphological adjustments, especially for reef islands (see Webb & Kench, 2010), exceeding a critical sea level threshold can lead to an irreversible process of drowning. In addition, an acceleration in sea level rise will widely exacerbate beach erosion around the globe (Brown & McLachlan, 2002). Wetzel *et al.* (2012) considered such erosion that could potentially affect zones for at least 20 m above mean sea level vertically and 100 km horizontally. In addition, the vulnerability of an island to morphological change varies according to differences in island topography and geomorphological characteristics, such as reef elevation (Webb & Kench, 2010). Due to the complexity of these phenomena, we did not infer potential morphological adjustment or resilience of islands in our study. We also did not consider the indirect loss of habitat that will result from the displacement of human populations from submerged areas, nor the potentially devastating ecological consequences of urban and intensive agricultural areas being relocated from coastal zones to the hinterlands. This impact has, however, recently been shown to be of a similar magnitude, and sometimes greater, than the losses directly due to sea level rise (Wetzel *et al.*, 2012). Because insular hotspots are densely populated islands (about 2.08 billion people, 31.8% of all humanity, in just 15.9% of earth's land area), they might be more threatened by these secondary effects than the primary effects. In addition, we did not consider the consequences of sea level rise on local populations of insular biota that may lead to higher risk of extinction for some vulnerable non-endemic species. We also did not consider the effects of fragmentation or secondary extinctions due to the loss of important species (e.g. resources, pollinators, dispersers, etc.). Finally, we omitted additional, and sometimes synergistic, effects of other aspects of climate change, and other drivers of global change (such as biological invasions), which are now known to be major threats for biodiversity in hotspots in general and on islands in particular (Courchamp *et al.*, 2003; Malcolm *et al.*, 2006).

To conclude, from 6 to 19% of the 4447 islands of insular hotspots considered could be entirely submerged following an increase in sea level by 1 to 6 m, respectively. In addition, more than 10% of all islands will lose at least 50% of their area in the future. The relative effect of sea level rise on habitat differs substantially among geographic regions. We identified three hotspots that were predicted to suffer the most important potential loss of insular habitat: the Caribbean islands, Sundaland and the Philippines. In contrast, the East Melanesian islands hotspot was predicted to be the least affected by sea level rise. The resulting loss of biodiversity is expected to be significant, with the potential for loss of dozens of endemic species within these islands under the most conservative estimates, this

loss rising up to hundreds of species depending on the scenario used. When we summed the potential number of species at risk of extinction for each island, endemic plants were the most affected, with 26 to 300 at risk of submersion compared with the other groups. Given the enormous potential impact on vulnerable and unique endemic species, it is striking that studies assessing the effects of future sea level rise are relatively rare. It is therefore crucial to investigate the predicted effects of sea level rise globally in order to anticipate adequate conservation programmes. We have predicted that sea level rise is likely to lead to the loss of large portions of insular habitat that harbour several unique subspecies. New prioritization programmes for islands have to be established in order to mitigate the impacts of sea level rise. For example, in order to anticipate threats and prepare adequate conservation actions (e.g. local protection, identification of refuges or translocation programs), conservation managers have to prioritize specific islands that are threatened by permanent inundation and those that harbour vulnerable endemic biodiversity. The Caribbean islands, Sundaland and the Philippines have to be monitored and protected in this regard. For example, collecting seeds of endemic plant species from these islands could be considered a priority in the next decades. Moreover, in the context of species translocation, regions that are less vulnerable to sea level rise, such as the East Melanesian islands, could be selected. Given the logistic, human and economic efforts allocated to island restoration programmes, also in the context of alien invasive species, prioritization of islands should take into account their vulnerability to sea level rise. It may not be optimal to invest first in islands that will be destroyed by inundation within merely a few decades.

To conclude, with accepted projections of sea level rise now far exceeding 1 m (Overpeck *et al.*, 2006; Rahmstorf, 2007; Pfeffer *et al.*, 2008; Grinsted *et al.*, 2009; Nicholls & Cazenave, 2010), the improvement of estimates of the associated loss of insular habitat and biodiversity becomes essential, and its negative effects must be added to the increasing list of factors threatening biodiversity in the future.

ACKNOWLEDGEMENTS

This work was funded by the Centre National de la Recherche Scientifique (CNRS) and Agence Nationale de la Recherche (ANR). We are grateful to Gloria Luque and Jessica Abbate for corrections on the manuscript. We are thankful to the editor in chief, David Currie, editor Jeremy Kerr and one anonymous referee for comments. We are also grateful to R. Kenneth for valuable comments on the manuscript. We thank E. Bonnaud, S. Gregory, Y. Watary, P. Leadley and A.P. Moller for comments and discussions about previous versions of the manuscript. None of the co-authors have any conflict of interest to declare.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Table S1 Table indicating for the 10 insular hotspots: their original extent (km²), the number of islands contained in each of them, the number of islands with elevation data and the percentage of area that studied islands covered in the hotspot.

Table S2 Number of endemic species of six different groups (i.e. plants, mammals, birds, reptiles, amphibians and fishes) in the 10 hotspots obtained from Mittermeier *et al.* (2004).

Table S3 Number of cells (one pixel = 0.22 km²) and endemic species that are potentially threatened by sea level rise among the hotspots.

Table S4 Partial losses of insular habitat in the 10 different hotspots. We classed the number of islands according to their potential percentage area inundated per island. We divided them into six different classes: islands that may be completely inundated (i.e. 100%), islands whose area may be inundated between 75 and 100%, between 75 and 50%, between 50 and 25%, between 25 and 0%, and islands that are safe from any inundation.

BIOSKETCH

Céline Bellard works on the effects of global change (e.g. climate change, invasive alien species) on the future of biodiversity at a global scale. This paper formed part of her PhD research at the University of Paris-Sud. **Camille Leclerc** has a Master of Science in ecology from the University of Paris-Sud. She is a student at the ESE lab, working on the analysis of climate change and biodiversity with a statistical approach. She is interested in various scientific ideas on amphibian taxa, climate change and conservation subjects. **Franck Courchamp** is a senior researcher for the CNRS at the University of Paris-Sud. He leads a research team examining various aspects of biodiversity dynamics, including invasive alien species, Allee effects, overexploitation of rare species and global environmental changes. F.C. and C.B. conceived the ideas. C.B. and C.L. analysed the data. C.B. and F.C. wrote the paper and all authors commented on the manuscript.

Editor: Jeremy Kerr

Conclusion

Les objectifs de ce chapitre étaient de traiter des conséquences de la hausse du niveau des mers sur les hotspots insulaires et de leurs 4 447 îles réparties à travers le monde et d'évaluer l'effet potentiel de cette menace sur la biodiversité endémique vivant dans ces hotspots.

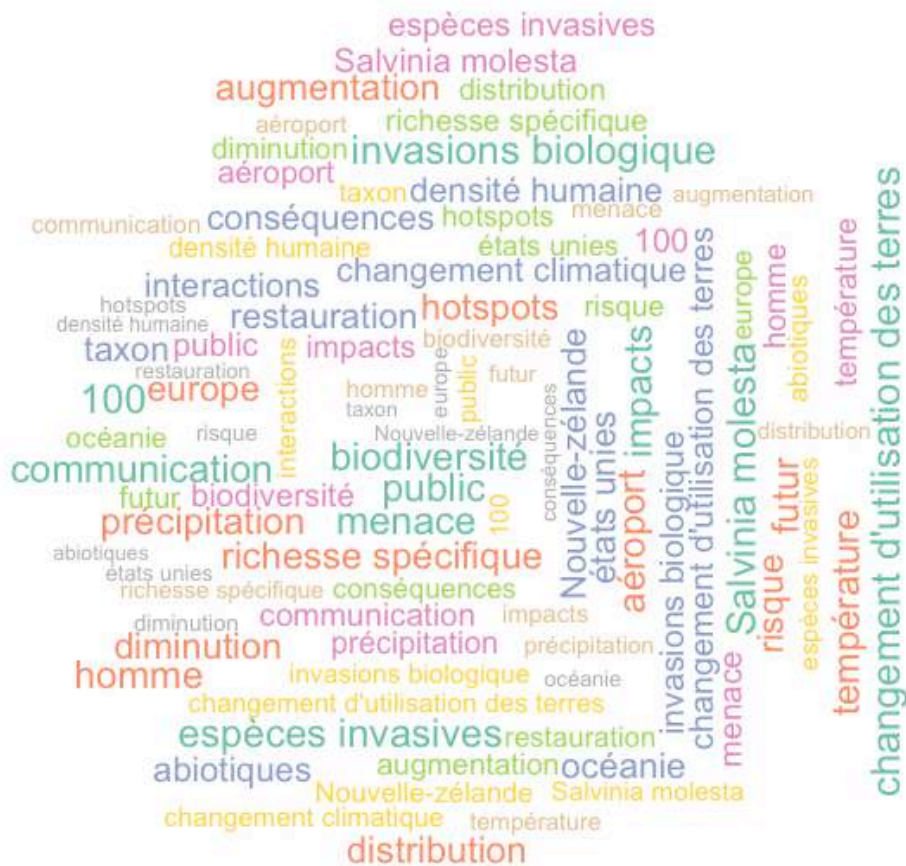
Nos résultats démontrent qu'entre 6% et 18.6% des îles situées dans les hotspots (soit entre 267 à 826 îles) risquent d'être entièrement submergées dans le futur. Nous avons identifié les îles caribéennes comme les plus vulnérables à une hausse du niveau des mers avec une perte totale de plus de 63 à 356 îles de l'archipel. Malgré les incertitudes associées à ce type d'analyse (e.g., la connectivité des cellules), cette étude a permis de mettre en avant que certains hotspots qui sont considérés comme des zones à protéger en priorité risquent d'être fortement affectés par cette menace dans les années à venir.

Par ailleurs, l'article présenté en Annexe 2 analyse les conséquences de la hausse du niveau des mers sur les 1 269 îles françaises. Bien que ce travail n'ait visé qu'à évaluer le nombre d'îles qui risquaient d'être totalement submergées, il a permis de mettre en avant deux résultats importants. Premièrement, nos résultats indiquent que 5% des îles françaises risquent d'être totalement inondées dans le cas d'une hausse du niveau de la mer de 1 m. La France représentant le 2nd domaine maritime mondiale, ce résultat a des implications importantes pour le pays. Par ailleurs, en prenant l'exemple de la Nouvelle Calédonie, nous avons montré que les plantes endémiques qui présentent déjà un risque d'extinction élevé (statut UICN : « Critically endangered ») sont les plus vulnérables à une hausse du niveau des mers. En effet, ces plantes sont principalement localisées sur le littoral.

Ces deux études ont permis d'identifier les régions mondiales les plus vulnérables à une hausse du niveau des mers. Ces régions doivent être particulièrement surveillées dans le cadre des changements climatiques. En outre, ces deux études montrent des résultats similaires avec près de 5 à 6% des îles potentiellement inondées avec une hausse du niveau de la mer d'un mètre. Les résultats ont également révélé qu'il manquait cruellement de données d'élévation des habitats insulaires avec une résolution suffisamment fine pour évaluer l'impact de l'élévation du niveau des mers sur les petites îles de faibles altitudes. Il est donc primordial d'améliorer les données dans ce domaine afin d'évaluer plus précisément l'effet potentiel de la hausse du niveau des mers.

Partie 3

4. Interactions changements climatiques, changements d'utilisation des sols et invasions biologiques



Avant propos : Chapitre 3

The 100th of the world's worst invasive alien species

Résumé

Les invasions biologiques font partie des principaux facteurs menaçant la biodiversité. Une liste des 100 parmi les pires espèces invasives a été établie par l'ISSG (Invasive Species Specialist Group, UICN) il y a une dizaine d'années afin de communiquer sur les espèces invasives. Récemment le virus de la peste bovine a été retiré de cette liste en raison du succès de son éradication. Cet article a été dédié à l'ajout d'une espèce à la liste des 100 espèces parmi les pires au monde. Pour ce faire, une liste de 10 000 espèces invasives a été établie à partir de leur fréquence d'occurrence dans les 16 bases de données nationales et internationales sur les espèces invasives. Ensuite, en tenant compte à la fois du nombre de continents envahis, de l'impact écologique, économique ou sociétal, dix espèces ont été sélectionnées. Finalement, la mise en place d'un site web a permis d'élire la 100^{ème} espèce (*Salvinia molesta*) auprès de 652 experts issus de 63 pays. Nous espérons que ce nouvel ajout à la liste va permettre d'attirer l'attention du public sur les conséquences des espèces invasives et va amener à une prise de conscience de la gravité que pose cette menace pour la biodiversité.

Cette partie correspond à l'article suivant:

G. M. Luque, C. Bellard, C. Bertelsmeier, E. Bonnaud, P. Genovesi, D. Simberloff & F. Courchamp, The 100th of the world's worst invasive alien species In Biological invasions, *in press*.

The 100th of the world's worst invasive alien species

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Received: 14 May 2013 / Accepted: 18 September 2013
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Abstract Biological invasions are among the greatest threats to global biodiversity, but in contrast to most other global threats, they suffer from specific communication issues. Our paper presents the first new addition to the widely cited IUCN list of “100 of the world’s worst invasive species”, a list created a decade ago in response to these communication issues. We briefly present this list, the recent removal of one species from that list, and the rationale to include a novel, 100th species to replace it. The new species of this list, giant salvinia (*Salvinia molesta*), was chosen by the community of invasion biologists (over 650 experts from over 60 countries). This new addition to the list will draw public attention to the damage caused by invasive alien species and it will help stimulate the necessary discussion of this critical issue in science and policy circles.

Keywords *Salvinia molesta* · Biological invasions · ISSG

Introduction

Although invasive alien species (IAS) are regarded as the second largest threat to biodiversity worldwide (after habitat loss; Clavero and Garcia-Berthou 2005; Simberloff et al. 2013), and their economic cost probably exceeds US\$300 billion per year worldwide (Pimentel et al. 2000; Genovesi 2011), the increased adoption of specific legislation by many nations has had limited effect on the rate of new introductions (McGeoch et al. 2010). In Europe for example, over twelve thousand alien species have been documented (Hulme et al. 2009), with an increase of over 76 % in alien species over the last 40 years (Butchart et al. 2010). Despite the progress of a large, dedicated community of researchers and managers worldwide, management successes against invasive alien species are still outnumbered by new introductions. Obviously, our improved knowledge about the harm they can cause, better management procedures to prevent new introductions, and more efficient eradication protocols remain insufficient (Genovesi 2011). New introductions in fact parallel the increase in intercontinental transportation of goods and people, which allows species to overcome long distances and geographical barriers. In addition, owing to the frequent time lags between introduction and observed impact,

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the full extent of current invasions will not be recognized for several decades (Essl et al. 2011). Biological invasions might also increase further in the future because of global environmental changes, in particular climate and land use changes (Walther et al. 2009; Bellard et al. 2013).

Need to communicate about IAS

Although the current biodiversity crisis has generated concern both among the general public and with decision makers, IAS have proven difficult to deal with. In particular, awareness of the threat represented by biological invasions is impeded by the lack of a clear, identifiable target, owing to the tremendously high number of IAS and the even higher number of species that have the potential to become invasive. Consequently, not only are the programs aiming to limit the impacts of IAS still insufficient, but also the very awareness of the threats caused by IAS remains diffuse. Given these difficulties, invasion biologists have recognized that the need to communicate more efficiently and authoritatively is a key to success. Yet, among so many species of microorganisms, plants, invertebrates, and vertebrates, marine, freshwater, and terrestrial alike, communication efforts are often diluted, whereas specific targets are better at eliciting attention from the public and decision makers. In 1999, the International Union for the Conservation of Nature (IUCN), through its Invasive Species Specialist Group (ISSG) of the Species Survival Commission, set up a remarkable communication tool to address this issue: a list of 100 high-profile invasive species, all known to be tremendously harmful and prompting a dire need for conservation action. Subsequently, the list of “100 of the world’s worst invasive alien species” has boosted global awareness.

100 of the world’s worst invasive species

This list of 100 species was derived according to two criteria: their serious impact on biodiversity and/or on human activities, and their potential to illustrate important issues surrounding biological invasions (Lowe et al. 2004). To ensure the inclusion of a wide variety of examples, only one species from each genus was selected. As a result, the 100 species belong to

many taxonomic groups, from microorganisms to plants and vertebrates (Fig. 1). They come from all continents and have impacts on local biodiversity and ecosystem functioning, and on agriculture, forestry, or aquaculture; they affect landscape or real estate values and constitute health hazards, as allergens or as disease vectors. Two points were relentlessly emphasized as this list was promoted. First, absence from the list does not imply that a species poses a lesser threat. Second, these are not the 100 worst invaders, but 100 among the worst. Evidently, it would be very hard to rank diverse species with such varied impacts. The aim of this list was to highlight the importance of invasive alien species, by emphasizing those that belong to the list, but avoiding at all cost downplaying the importance of the thousands of species not on this list.

This list has been a tremendous success in terms of communication, with over 1,000 citations in the scientific literature and a number of similar lists promulgated for different regions or environments (e.g., Strefataris and Zenetos 2006; Vilà et al. 2009). Among the achievements is the successful global eradication of the rinderpest virus, a mere decade after the list was constructed, which reduced it to 99 species (World Organisation for Animal Health 2011). Subsequently, it was decided to replace the eliminated species, to keep the list at 100, rather than working to reduce it progressively. This course of action has the double advantage of highlighting yet another major invader and insisting on the fact that species that are not on the IUCN 100 list can nonetheless be among the worst invaders worldwide. On the contrary, constantly reducing the list would have given the misleading impression that IAS were getting gradually fewer.

The selection of the 100th species

To this effect, it was decided to enlist the community of invasion biologists in selecting the new, 100th IAS for the list. As it would be difficult to get a meaningful consensus from a pool of tens of thousands of IAS species, we first selected a reasonable number of candidates among which the community was invited to choose. Following the same thinking behind the development of the original list, this approach was not meant to be an accurate and objective selection of the worst invaders, but rather a rational selection of some

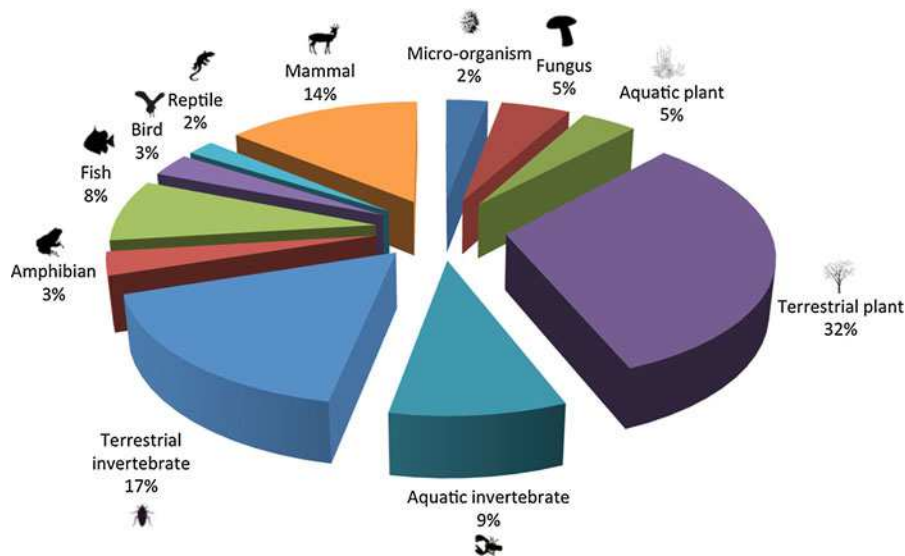


Fig. 1 Taxonomic representation of 100 of the world's worst alien invasive species

of the worst, as it is difficult to classify objectively and quantitatively one species as worse than another. We thus amassed invasive alien species inventories/checklists from 16 global and national databases, including the ISSG Global Invasive Species Database (GISD), CABI Invasive Species Compendium (ISC) and DAISIE (Delivering Alien Invasive Species Inventories for Europe), and selected over 10,000 IAS that we ranked based on the number of times they were listed. We then accounted for emerging threats, i.e., species that are not yet widespread but that are known to have major impacts and/or a high spread rate, so that they would rise in the ranking. We selected the first 50 species and assigned to each of them a score of (1) spread: the number of continents already invaded and (2) impact: ecological, economic and/or health. We finally eliminated the species in genera that were already represented in the 100-list, as well as those that had a strong positive value (cultural or economic). We then selected the 10 species with the highest sum of scores. These 10 species were six aquatic and four terrestrial organisms, five plants and five animals. They came from South and North America, Asia, Europe and Oceania and had strong ecological, economic and/or health impacts. They included organisms that are invasive throughout the world, such as the American waterweed *Elodea canadensis*, but also still localized but very fast spreading organisms, such as the lionfish *Pterois volitans*, or species with very high local impact, such

as the Burmese python *Python molurus bivittatus*. The address of a dedicated web site (Courchamp 2013) was distributed via various networks to the invasion biology community throughout a period of 3 months. The site included a description of the selection protocol, a short presentation of the 10 candidates and an explanation on how to vote online for the latest and 100th representative of the IUCN “100 of the worst” list. We used the Condorcet Vote, a procedure that selects the candidate (here a species) that would win by majority rule in all pairings against the other candidates (Courchamp 2013). It requires only one round of voting.

A total of 652 experts from 63 countries voted, and they selected giant salvinia, *Salvinia molesta*, as the 100th species to join the IUCN list of “100 of the world's worst invasive alien species”. It is a free-floating aquatic fern (Fig. 2) native to southeastern Brazil, first observed outside its native range in 1939. It has since spread widely throughout the tropics and subtropics across the world and is currently found in 31 countries on 4 continents (Fig. 2). This plant is moved in part by the trade in ornamental plants for fish tanks and ponds. The presence of giant salvinia is prominent in slow-moving, quiet freshwater systems. Its fast growth rate, under optimal conditions, enables this plant to double its abundance in only a few days. It forms 10–20 cm thick floating mats (Fig. 2) that prevent light penetration of the water column, reducing oxygen content and degrading water quality for



Fig. 2 **a** Close up of *S. molesta*, **b** free-floating aquatic group of salvinia, **c** floating mats of salvinia in Australia, **d** records of salvinia worldwide collected from a variety of databases including GBIF (<http://data.gbif.org>), CABI (www.cabi.org/isc), and IOBIS (<http://www.iobis.org>)

aquatic organisms, drastically damaging these ecosystems over large areas (Fig. 2). In addition, dense mats of salvinia can impede water-based transport,

reduce water quality, impair aesthetic values, clog irrigation and power generation intakes, and harm local fisheries (Julien et al. 2002). Maintaining giant salvinia at low levels is generally attempted by the use of herbicides, which are notoriously costly. Biological control programs can achieve local successes but have not controlled salvinia in other areas, nor prevented its spread (Room et al. 1984; Julien et al. 2002).

Although salvinia definitely deserves its place in the list, other species among the 10 candidates, and beyond, could have been selected instead. The new status of salvinia does not make it suddenly more invasive, more damaging or more rapidly spreading. Nor has the need to remove it from invaded areas, or to prevent new introductions, suddenly become more critical. However, a listing in this very special catalogue will surely grant this species some extra attention, which will help impede its establishment and spread from now on. Invasion biologists also expect and hope that this new addition to the list will draw public attention to the damage caused by IAS in general. The IUCN list of “100 of the world’s worst invasive alien species” is a potent communication tool. One of the expectations of the invasion biology community when building this list was, oddly, that it would help them to remove species from it, as often as possible. Control of alien invasive species, even eradication when possible, is crucial to preserve biodiversity and lower costs for human societies. However, although reactive programs are required, they remain far more expensive than proactive programs (Kaiser and Burnett 2010). Prevention, early detection, and rapid response are the three pillars of success, and this rest on effective communication.

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Conclusion

Dans ce chapitre nous avons présenté la démarche qui a permis d'ajouter *Salvinia molesta* à la liste des « 100 of the world's worst invasive alien species ». Cette liste a été créée en 1999 pour porter à l'attention du plus grand nombre la menace que pose actuellement les invasions biologiques. A la différence des autres menaces qui pèsent sur la biodiversité, la communication sur les espèces invasives se fait principalement à l'échelle d'une espèce. Le public connaît le problème posé par *Caulerpa taxifolia* ou *Vespa velutina* mais le concept d'espèce invasive est quant à lui méconnu et l'étendue des impacts de cette menace sont largement sous-estimés par le public. Pour autant, il faut rappeler que la première source d'invasion est l'homme de par sa capacité à se déplacer rapidement sur de grandes distances. C'est pourquoi il est important d'alerter la société de ce fléau pour la biodiversité. L'ajout d'une nouvelle espèce à la liste des 100 permet aussi de garder le même niveau de mise en garde contre les espèces invasives et la menace qu'elles représentent. Ce chapitre a fait l'objet de deux publications, une publication courte (Annexe 1) dans *Nature* qui a principalement servi de moyen de communication pour alerter les médias et le public sur ce projet et une publication plus longue dans *Biological invasions* qui a permis d'expliquer plus en détails le travail qui a été effectué pour aboutir à l'ajout de cette espèce.

Cette liste des « 100 of the world's worst invasive alien species » a été utilisée dans les chapitres 4, 5 et 6. Les espèces présentes dans cette liste font parties des espèces invasives qui sont parmi les plus dangereuses au monde et menacent à la fois des écosystèmes marins et des écosystèmes terrestres. Il est donc important d'identifier les régions qui sont favorables à ces espèces invasives, et déterminer quels sont les facteurs qui influencent la distribution de ces espèces, cette question a fait l'objet d'un manuscrit dans le Chapitre 4.

Chapitre 4

Current main factors that drive the most dangerous invasive alien species

Résumé

Les politiques de gestion des espèces invasives sont en augmentation constante, mais elles sont à la fois insuffisantes et inefficaces pour faire face à cette menace. Dans cette étude, nous avons analysé le rôle que jouent les facteurs climatiques (*e.g.*, température et précipitation), humains (*e.g.*, distance aux aéroports, densité humaine), d'habitats (*e.g.*, richesse spécifique, NDVI) et d'utilisation des sols (*e.g.*, couverture herbacée) sur la distribution actuelle des « 100 espèces invasives parmi les pires au monde ». Dans ce but, nous avons utilisé une procédure de calcul des importances relatives des variables et des modèles de distribution d'espèces afin d'identifier les principaux facteurs influençant la distribution de ces espèces invasives, mais également afin de déterminer les régions qui présentent des conditions favorables à la présence de ces espèces invasives. Nos résultats révèlent que les variables climatiques, suivie par la distance aux aéroports, sont celles qui permettent le mieux d'expliquer la distribution de ces espèces. Nous avons également identifié: l'ouest de l'Europe, les Etats-Unis, le sud-est de l'Australie, la Nouvelle-Zélande, les îles indonésiennes et le Japon, comme les régions qui présentent les conditions les plus favorables à la présence de ces espèces. La compréhension des facteurs qui influencent la distribution des espèces invasives est essentielle pour améliorer les prédictions, mais également pour mettre en place des stratégies de contrôle efficaces.

Cette partie correspond à l'article en préparation suivant :

C. Bellard, B. Leroy, W. Thuiller, M. Bakkenes, & F. Courchamp, Current main factors that drive the most dangerous invasive alien species

Current drivers of the invasion risk by the “100 of the world’s worst invasive species”

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Introduction:

Increasing trade and tourism associated with globalization and expansion of the human population have facilitated intentional and unintentional movement of species across their natural boundaries. Consequently, many of these alien species have become invasive (Hulme, 2009). Invasive alien species cause serious impacts not only for native biodiversity but also to economy and human health, and therefore can have important consequences for society (Simberloff *et al.*, 2012; Vilà *et al.*, 2010). Recently, the number of invasive alien species has drastically increased around the world, particularly in Europe (Butchart *et al.*, 2010; Waage *et al.*, 2008; Hulme, 2009), in China (Xu *et al.*, 2012) and in North America (Levine & D'Antonio, 2003; Aukema *et al.*, 2010), despite a significant increase of the number of national and international invasive alien species policy plans (Butchart *et al.*, 2010). For these reasons, better mitigating invasive alien species and their effects has increasingly become a major focus in both basic and applied ecology.

The invasion process consists of a series of steps, including transportation, establishment and spread (Hellmann *et al.*, 2008). Once invasive alien species have been established they are difficult to eradicate (Rejmánek *et al.*, 2005); hence, prevention is by far the most cost-effective management (Simberloff *et al.*, 2012). Consequently, in order to develop effective strategies for the management of invasive alien species, we need both to understand the basic requirements of invasive alien species to survive, establish and spread and to use this information to establish maps of invasion risks.

Climate similarity between native and other regions is considered as an essential requirement for successful invasions (Ficetola *et al.*, 2007), but other abiotic factors could also play an important role. Indeed, economic and demographic factors determine the outcome of invasion through the propagule pressure, pathways of introduction or the intensity of anthropogenic disturbance (Pysek *et al.*, 2010; Hulme, 2009; Spear *et al.*, 2013). Overall, these current studies have shown an important influence of climate factor, human factor (*i.e.*, demography and wealth) and habitat factor (*i.e.*, biotic resistance by native taxa) in explaining the distribution of a few selected invasive alien species. Moreover, the effect of land use and climate factors as drivers of invasive alien species is also increasingly accepted (Mattingly & Orrock, 2013; Chytrý *et al.*, 2012a). There is, however, no consensus regarding their relative importance (Pysek *et al.*, 2010). Yet, understanding and disentangling which factors between climate, land use, habitat and human factors contribute the most to successful invasions needs to be explored, in particular at a global scale.

To date, a large number of studies have investigated potential suitable areas on invasive species using species distributions models (DeVaney et al., 2009; Taylor et al., 2012; Pyšek et al., 2012; Beaumont et al., 2009). However, they mainly focused on single species, when the identification of situations associated with high risks of invasion requires the analysis of a large number of invasive alien species simultaneously (Cadotte *et al.*, 2006). In addition, most of the few studies that explore the role of environmental and human factors on biological invasion focus on one species only (e.g., Argentine ants, *Linepithema humile*: Roura-Pascual et al., 2011) or a few taxonomic group on a small region (e.g., Europe: Pyšek et al., 2010 or Great Britain: Gallardo & Aldridge, 2013).

In this paper, we investigated the main drivers explaining the current distributions of a large number of invasive alien species. Then, we predict the areas of current invasion risks worldwide, based on their suitability for invasive alien species on the basis of these main drivers. To this aim, we used the list of the “*100 of the worst’s world invasive species*”, which includes invasive species of a large variety of taxa, and with contrasted ecological profiles (Lowe et al., 2000). Using species distribution models, this paper aims to explore (i) the relative roles of climate, human, habitat and land use factors in determining the successful invasions across different taxonomic group and (ii) the regions that are at higher risk of vulnerability regarding these invasive alien species worldwide.

Materials and Methods

Data

Invasive alien species data

The International Union for the Conservation of Nature list of “*100 of the world’s worst invasive alien species*” has been developed in 2000 by the Invasive Species Specialist Group, a global network of invasion biology experts, with inputs from a wider community of practitioners and scientists (Lowe et al., 2000). This list includes three micro-organisms, five macro-fungi, four aquatic plants, 30 terrestrial plants, nine aquatic invertebrates, 17 terrestrial invertebrates, three amphibians, eight fishes, three birds, two reptiles and 14 mammals (Lowe et al., 2000). We made an extensive search for records from both the native and invaded ranges as recommended by Gallien et al. (2010) of all the 100 species (see Bellard et al., 2013 for details). Rinderpest virus was removed from the list of the 100 because it is now eradicated and replaced by a new species the Giant salvinia (Luque *et al.*, 2013). Four other species were excluded from the analyses because of insufficient number of records (*i.e.*, *Asterias amurensis*, *Corbula amurensis*, *Eleutherodactylus coqui* and *Morella faya*).

Explanatory variables

Four major types of explanatory factors were considered: climatic, land use, habitat and human related variables, totalling 23 variables.

Climate variables

To characterize present-day climate, we used climatic data (averaged from 1950-2000) from the Worldclim database (Hijmans *et al.*, 2005) at a 0.5 degree resolution. We selected six climatic variables (*i.e.* (1) mean diurnal range, (2) maximum temperature of the warmest month, (3) minimum temperature of the coldest month, (4) annual precipitation, (5) precipitation of the wettest month, (6) precipitation of the driest month. These variables provide a combination of means, extremes and seasonality that are known to influence species distribution (Root *et al.*, 2003) and were not inter-correlated (pair-wise $r_{\text{Pearson}} < 0.75$) (Braunisch *et al.*, 2013).

Land use variable

Land use and land cover variables were simulated by the Globio3 land model at a 0.5 degree resolution (Alkemade *et al.*, 2009; Millennium Ecosystem Assessment *et al.*, 2005). We re-classified them into 11 land cover type variables by grouping some of them together (see (Bellard *C et al.*, 2013)). These land use variables consisted of the proportion of the grid cell covered by (7) tree cover, (8) tree cover regularly flooded, (9) habitat mosaic, (10) tree cover burnt, (11) shrub cover, (12) herbaceous cover, (13) cultivated and managed areas, (14) bare areas, (15) water areas (16) snow and ice and (17) artificial surfaces and associated areas.

Habitat variable

We calculated (18) the species richness per grid cell, which was derived from the IUCN database for mammals, amphibians and reptiles and from Birdlife International and NatureServe (2012). This variable could be translated as the resilience of habitats to invasive alien species. We also calculated the available energy on the basis of the (19) Normalized Difference Vegetation Index (NDVI), as a surrogate of plant productivity. We measured habitat heterogeneity with two different surrogates: (20) a Shannon coefficient that represents the diversity of habitat using the land use database in each grid cell and (21) the elevational variation coefficient for each grid cell.

Human related variables

Nowadays, several factors have been used in the literature as surrogates of propagule pressure, such as economic development and human population density (Pysek *et al.*, 2010; Gallardo & Aldridge, 2013; Roura-Pascual *et al.*, 2011). Here, we used two human variables that are likely to represent propagule pressure (22) human population density per km² and (23) distance to the nearest airport. We used minimum distance to an airport as there is increasing evidence that aviation is a more significant pest entry than might be expected based solely on cargo volumes (Hulme, 2009).

Species Distribution Model projections

Modeling process

We modeled the global potential distribution of the 95 retained invasive species combining available occurrences with the climatic, land use, habitat and human variables set that we assumed to be important for invasive species. We used seven different species distributions models, within the Biomod v.2.0 platform (Thuiller *et al.*, 2009). These models were: Generalized Linear Model, Generalized Boosting Trees, Multivariate Adaptive Regression Splines, Random Forest, Flexible Discriminant Analysis, Classification Tree Analyses (see Thuiller *et al.*, (2009) for details about these six modeling techniques) and Maximum entropy (see Elith *et al.*, (2011) for Maximum entropy details). Three sets of Pseudo Absences (PAs) were generated by selecting from 1000 to 10,000 random points across the world, according to the number of presences: N (if $N \leq 1000$ then 1000 PAs were selected, else 10,000 PAs were selected) (as recommended by Barbet-Massin *et al.*, (2012)) and equal weightings were given to presences and PAs.

Evaluating model performance

We evaluated the predictive performance of each model using a repeated split sampling approach in which models were calibrated over 70% of the data and evaluated over the remaining 30%. This procedure was repeated four times. We used two different statistical metrics: the True Skill Statistics (Allouche *et al.*, 2006) and Area Under the receiver operating characteristic Curve (AUC) (Fielding & Bell, 1997). The True Skill Statistics (TSS) accounts for both sensitivity (*i.e.*, correctly predicted presences / (correctly predicted presences + predicted absences)) and specificity (*i.e.*, correctly predicted absences / (correctly predicted absences + predicted presences)). TSS ranges from -1 to +1, where +1 indicates perfect agreement, and values of zero or less represent a performance no better than random (Allouche *et al.*, 2006). AUC values must range from 0.5 to 1 (for models with perfect

predictive ability), and AUC above 0.8 are considered to have “good” discrimination abilities (Swets, 1988). All calibrated models performed very well here, with an average AUC value of 0.98 and an average TSS value of 0.87 (Supplementary Fig. S1). This makes the interpretation of our results consistent over all species.

Relative importance of the variables to predict the distribution range

Because our modeling protocol is based on different modeling techniques with different criteria, the predictive power of each variable is difficult to assess and compare among models. Therefore, we applied a method that allows assessing the importance of each variable independently of the modeling technique, this method is implemented in BIOMOD as the “variable importance” procedure (Thuiller *et al.*, 2009). This procedure includes different steps. First, the model is calibrated with all the variables. Second, a standard prediction is made on the basis of all the variables. Third, the assessed variable is randomized, and a new prediction is made with the randomized variable. Finally, the correlation between the standard prediction and the prediction with the randomized variable is calculated. If the correlation is high, then the considered variable poorly contributes to the prediction; and the predictive power of the variable is low. Conversely, if the correlation is low, then the predictive power of the variable is high. For each of the 23 variables, this randomization procedure was computed 10 times per calibrated model, resulting in 150 randomization tests per variable and per model (10 randomization tests \times 5 evaluation runs \times 3 pseudo-absence runs). This procedure provided the average predictive importance per variable and per model for each species.

Ensemble modeling approach

The final calibration of every model for making invasion scenarios used 100% of available data. We used an ensemble forecast approach to account for the variability among the seven species distribution models to get the central tendency (Araújo & New, 2007) only keeping the projections for which the model’s evaluation estimated by TSS that were higher than 0.6 (e.g. Gallien *et al.* 2012). Because of the potential problems raised by Lobo *et al.* (2008) on the use of AUC as a measure of model performance, we used TSS for the final consensus distributions. The final current consensus distributions were obtained by calculating the weighted mean proportional to their TSS evaluation of the distribution for each species (Marmion *et al.*, 2009). Then, we transformed the probability maps obtained from the ensemble projections into binary suitable/non suitable maps using the threshold maximising the TSS, as proposed by Allouche *et al.* (2006). This should ensure the most

accurate predictions since it is based on both sensitivity and specificity (Jiménez-Valverde & Lobo, 2007). We obtained one current binary distribution map per species.

Results :

Drivers of invasive alien species distribution

Overall, climate variables were the most important predictors, followed by human variables and habitat variables (Figure 2). In contrast, land use variables were the least important predictors. Nevertheless, we observed a high variability of variable importance among species. The *minimum temperature of the coldest month* (average 0.29) was the most important predictor for all the taxonomic groups, followed by *distance to airport* (except for micro-organisms for which *human population density* was the second most important variable). In particular, *distance to airports* was highly important for birds (0.30) compared to the other taxonomic group (average 0.15). Then, the current distribution of our species was best explained by: *temperature of the warmest month* (0.09), *precipitation of the wettest month* (0.08), *species richness* (0.07), *human population density* (0.07) and *precipitation of the driest month* (0.07). In particular, species richness was highly important for reptiles (0.12), mammals (0.07), fishes (0.10), terrestrial plants (0.09) and terrestrial invertebrates (0.05) (Figure S2). Similarly, *human population density* was a good explanatory variable for aquatic plants (0.16), aquatic invertebrates (0.10) and terrestrial invertebrates (0.12). *Shannon habitat index* was only slightly important for these invasive species. The most influential land use variables (<0.02) were *tree cover*, *cultivated areas*, *artificial surfaces* and *habitat mosaic*. Also note that *habitat mosaic* (0.03) and *artificial areas* (0.03) were important land use variables for reptiles.

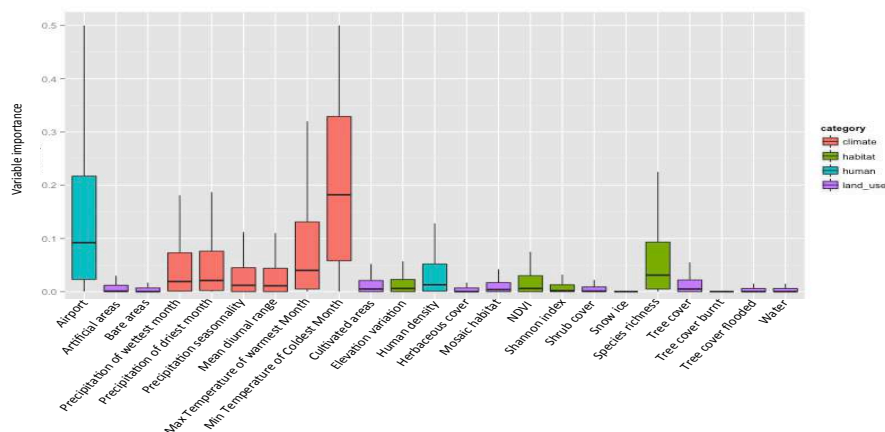


Figure 1: Boxplot of the variable importance for the climate, habitat, human and land use variables for the species of the “100 of the world’s worst invasive alien species”.
Taxa suitability response to environmental variables

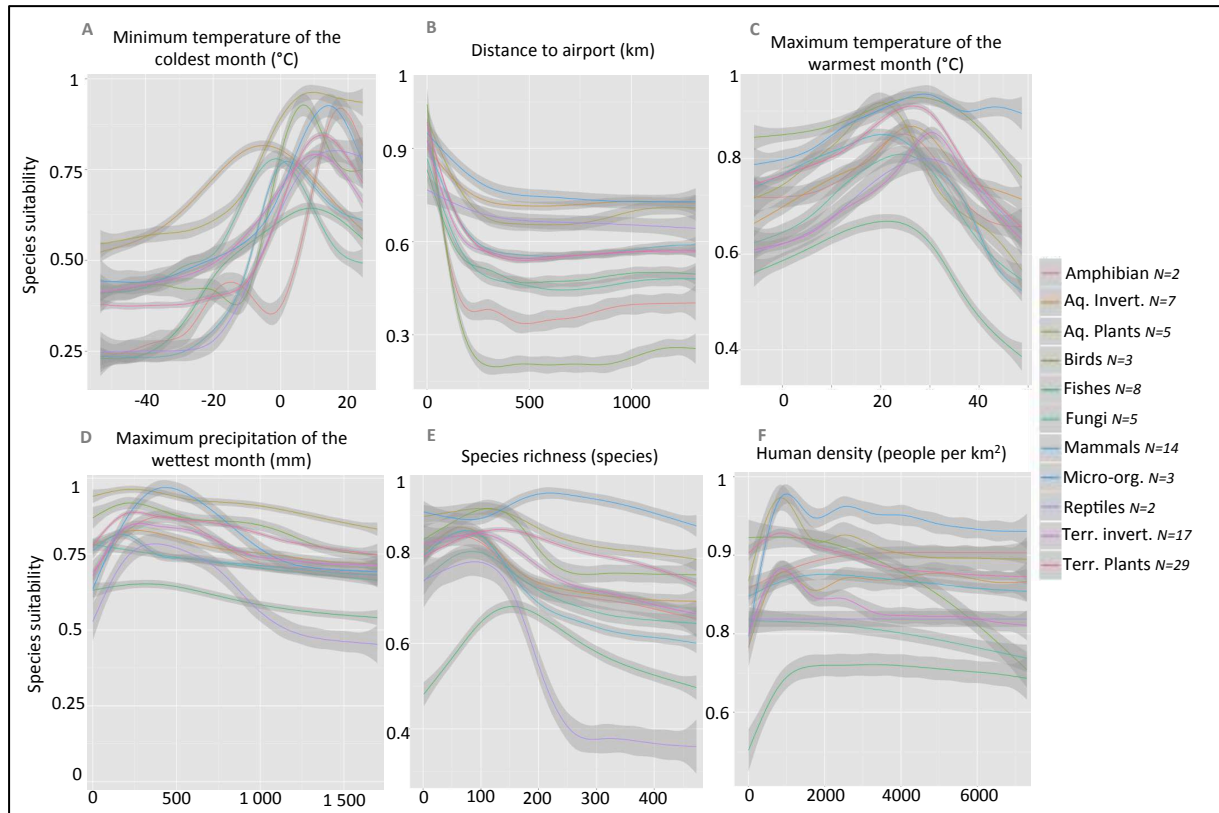


Figure 2: Predicted responses of the invasive alien taxa to the six best environmental predictor variables. Solid lines: fitted GAM function based on all response curves from the three PAs runs and six modeling techniques. Grey areas represent 95% confidence intervals.

The fitted response curves showed a strong response of the invasive taxa to the six best environmental predictor variables (Figure 2). Most of the taxa showed a uni-model response to precipitation or temperature-related variables (Figure 2ACD). A strong response was predicted to the distance to airports, with a dramatic decrease a short distance away (300km), especially for birds (Figure 2B), while reptiles, aquatic invertebrates and aquatic plants showed a slower decrease. The different patterns per taxa for *species richness* and *human population density* were more complex. Indeed, environmental suitability was predicted to be high at low *species richness* (except for fishes) and with a decrease above 100 species per pixel for reptile, mammal, fungi, aquatic invertebrates and birds (Figure 2E), while there was a linear response for micro-organisms and aquatic plants. In contrast, environmental suitability increased with *human population density* for fish, terrestrial invertebrates, micro-organisms and aquatic plants from 0 to 1,000 individuals per km², with no further effect above. However, we observed a linear response to *human population density* for the other taxa.

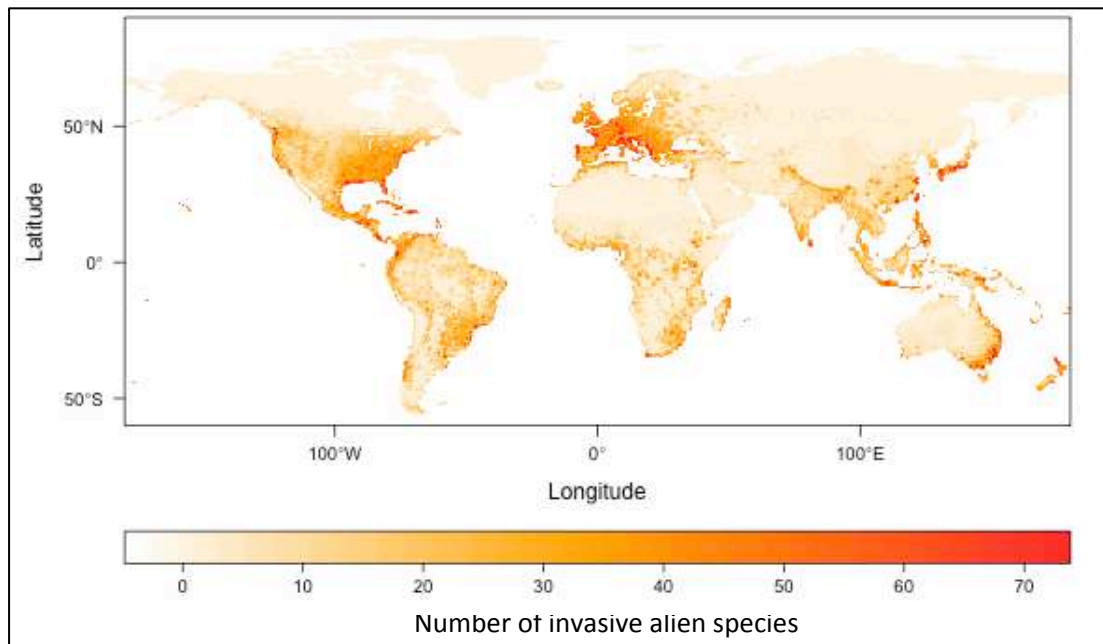


Figure 3: Map of the current number of invasive alien species among the list of the “100 of the world’s worst invasive species” that could find suitable conditions.

Suitable conditions for invasive alien species

Overall, several large regions were predicted to be currently suitable for a high number of invasive alien species (*i.e.*, between 40 and 70 invasive alien species): Western and Central Europe, North America, eastern Australia and New Zealand, some of the Indonesian islands and Japan). Our results also showed that Central and South America, especially Caribbean islands, South Africa and Indonesia were also suitable for an important number of invasive alien species (*i.e.*, between 20 and 40 invasive alien species; Figure 3). In contrast, large regions such as Russia and most of Asia, North Africa and Middle East as well as most of Australia were not predicted to be suitable to these invasive alien species. Moreover, the spatial distribution of suitable conditions varied between taxa: while mammals were predicted to find suitable conditions almost everywhere over the world, terrestrial plants were mainly predicted to find suitable conditions over Central America, the pacific islands and Europe (Figure S4).

Finally, we quantified the number of pixel per region and observed a high percentage of invasive alien species in Oriental (16.6 invasive alien species), Neotropical (13 invasive alien species) and Australasia (10.7 invasive alien species) regions (Figure 4 and S3). On the contrary, the number of invasive alien species was lower in Palearctic and Nearctic regions.

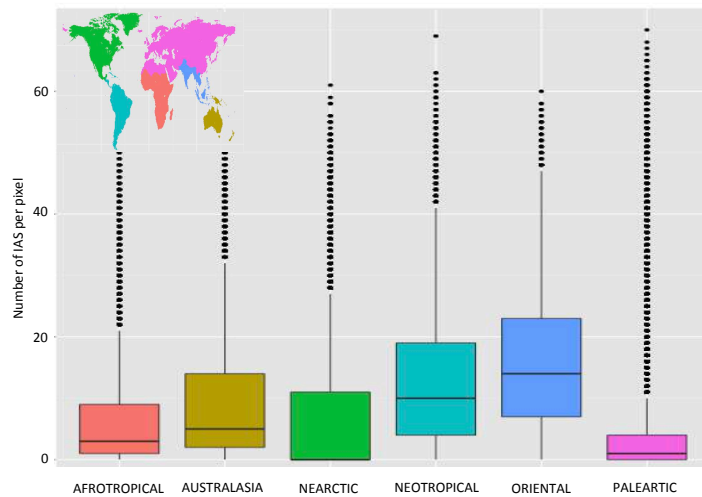


Figure 4 Percentage of the number of invasive alien species for the different region.

Discussion:

Climate variables and the propagule pressure (through *distance to airport* and *human population density*) were predicted to be primarily responsible for the distribution of the global invaders studied here. Despite the inclusion of potential surrogates of disturbed habitat, the most important predictors were mainly related to temperature and precipitation. This supports the fact that climate matching between native and invaded regions is an undeniable requirement for successful invasions (Ficetola *et al.*, 2007). This result also confirms the consistency to use mainly climate variables in species distributions models to identify the risk of invasions following climate change.

Nevertheless, we also demonstrated the importance of socio-economic factors, in particular closeness to airports and human population density, both identified as important predictors of invasive alien species distributions. The importance of these factors can be explained by their relationship with the introduction pathways. Indeed, increases in the rates of biological invasion have been linked to the continued expansion of the worldwide airline transportation network (Tatem & Hay, 2007; Tatem, 2009). For example, among others, plant pathogens are often found in air cargo (McCullough *et al.*, 2006). Regarding aquatic species, the importance of seaports have also been demonstrated as an important contributor to their distribution (Gallardo & Aldridge, 2013). Overall, increases in the number and spread of alien species has been strongly associated with substantial increases in the extent and volume of trade and transport, particularly over the last 25 years (Levine & D'Antonio, 2003; Hulme *et al.*, 2009).

Contrarily to expectations, the influence of biotic resistance (i.e., *species richness*), known as a crucial driver of invasions (see for example Roura-Pascual et al., 2011) and our metric of *Shannon habitat index*, were only slightly related to the global distribution pattern. Moreover, the relationship between *species richness* and invasive alien species suitability was particularly complex revealing that biotic resistance through a high number of native species is not systematically related to a lower rate of establishment of invasive alien species. This last result will need further research to understand fully the complexity of the relationship between species richness and invasiveness.

Similarly and despite the often cited importance of land use variables (e.g., Roura-Pascual et al., 2011; Chytrý et al., 2012b;), these variables were mainly lowest-ranked variables, only 4 out of 11 (*tree cover*, *cultivated area*, *artificial surfaces* and *mosaic habitat*) emerging as moderately important predictors for some particular species. This result could be partially explained by these variables being mostly important at a local level while the resolution used in this study is not adapted to capture local factors.

Furthermore, our map risk analyses provide additional insights into risk evaluation at the world scale. We demonstrated that Western and Central Europe, North America, eastern Australia and New Zealand, some of the Indonesian islands and Japan were predicted to be particularly at risk for these invasive alien species. As these regions represent some of the most important trade areas around the world, these regions could be highly threatened by invasive species.

Furthermore, species distribution models have some limitations, in particular when there is a need to take into account for other drivers of invasions such as biotic interactions or local climate conditions (Araújo & Luoto, 2007; Kharouba *et al.*, 2013). For these reasons, species distributions models provide potential suitable areas but these areas will not necessarily be fully occupied by invasive species. In addition, we assumed that some human activities such as distance to airport associated with increasing population density, and land-use classes were not completely independent, an approximation that may slightly influence our results. However, our study provides useful information about the suitable areas for these invasive alien species. Besides, we provide crucial information about the current drivers of invasion by these 100 species.

Implications for adaptive management of invasive alien species

Our results have two main implications for future management strategies of invasive species. First, we identified potential “at-risk” regions with respect to these global invaders using species richness of invasive species, which have been shown to be a valuable indicator of biological invasions (Catford *et al.*, 2012). The highlighted geographic patterns implicated that the risk for biological invasion by these invasive alien species differed across regions. In particular, our results highlighted that climate similarity and highly connected regions are particularly vulnerable to invasive alien species. As the “at-risk” regions are prone to be under a high propagule pressure, they should be priority for prevention of invasive alien species. Besides, as fast economic development has been also demonstrated to accelerate biological invasions (Lin *et al.*, 2007), the developing countries highlighted in our at-risk maps should also be closely monitored.

Second, our results confirmed that invasive alien species are highly dependent on the climatic suitability, but also on the propagule pressure. Yet, propagule pressure had not been explicitly integrated into species distribution models, leading to increase difficulty to inform upon geographically targeted policies to prevent and manage biological invasions (but see Chiron *et al.*, 2009; Gallardo & Aldridge, 2013). Therefore, taking into account the socio-economical drivers in future research will provide insight into the pathways of biological invasion and therefore facilitate the prioritization and identification to prevent introduction and establishment of invasive alien species. Actually, despite a significant literature on biological invasions (reviewed in Lowry *et al.*, 2012), this study is, to our knowledge, the first to provide a global map of potential suitable areas for such a large sample of some of the most invasive species, with an evaluation of the drivers that explain the current distribution of these invasive species.

To conclude, high probabilities of a successful invasion will result from a closer climate match between the current distribution of these species and the areas to be invaded, associated with a high propagule pressure. Finally, this study provides strong evidence of the importance to consider socio-economic factors for management of biological invasions.

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Conclusion

Les objectifs de ce chapitre étaient de quantifier l'importance relative des variables climatiques, humaines, d'habitats et d'occupations des sols pour expliquer la distribution actuelle des 100 espèces invasives. Ce chapitre visait également à construire une carte représentant les régions à risque concernant ces espèces invasives.

Nos résultats ont démontré que les variables climatiques sont les variables les plus importantes qui permettent d'expliquer la distribution de ces espèces. L'utilisation de variables climatiques dans des modèles de distribution d'espèces est donc pertinente. Plus surprenant, la distance aux aéroports et la densité humaine sont également des facteurs clés qui influencent la distribution de ces espèces. Ces facteurs doivent donc être considérés dans les modèles de distribution d'espèces invasives. Néanmoins, il n'est pas possible d'intégrer ces facteurs lors de l'évaluation des distributions futures de ces espèces invasives car ces variables ne sont pas disponibles à cette échelle de temps. Ce chapitre a également révélé que si nous voulons combattre efficacement les invasions biologiques, il sera nécessaire de limiter l'influence de ces facteurs. Par exemple, en mettant en place une surveillance intense dans les aéroports se situant dans les zones favorables aux espèces invasives révélées par l'analyse. Plus généralement, cette étude a également permis de mettre en évidence l'importance de tenir compte des facteurs socio-économiques lors de la gestion des espèces invasives.

Néanmoins, ce chapitre a uniquement permis d'évaluer les régions qui sont aujourd'hui potentiellement favorables à ces espèces invasives. Si nous voulons mettre en place des stratégies de gestion adaptée, nous devons également étudier les conséquences des changements climatiques sur les aires potentielles de répartition de ces espèces dans le futur. Ainsi le chapitre 5 a pour but d'évaluer les conséquences des changements climatiques et des changements d'utilisation des sols sur la distribution de ces espèces invasives dans le futur.

Chapitre 5

Will climate change promote future invasions ?

Résumé

La perte d'habitat et les invasions biologiques sont reconnues comme les deux plus grandes menaces qui pèsent sur la biodiversité. Le changement climatique pourrait exacerber ces menaces et ainsi conduire à une perte encore plus importante de la biodiversité dans le futur. En utilisant les modèles de distribution d'espèces, nous avons modélisé les régions favorables aux « *100 of the world's worst invasive species around the world* » d'ici à 2100. Nous avons montré que les changements climatiques et les changements d'utilisation des sols peuvent conduire à des modifications importantes des répartitions spatiales de ces espèces. En particulier, nous avons identifié trois régions qui présentent un risque élevé d'invasions: l'Europe, le nord ouest américain et l'Océanie. Nous avons également montré que certaines régions pourraient être moins favorables à la présence de ces espèces invasives dans le futur. En outre, selon les taxons étudiés, les aires de répartition peuvent augmenter ou diminuer. Etant donné les conséquences économiques, sanitaires et écologiques de ces espèces invasives, les changements d'aires de répartition dans le futur pourraient avoir des conséquences importantes pour la société.

Cette partie correspond à l'article soumis suivant:

**C. Bellard, W. Thuiller, B. Leroy, P. Genovesi, M. Bakkenes & F. Courchamp (2013)
Will climate change promote future invasions ? *Global Change Biology*, in press.**

Will climate change promote future invasions?

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Abstract

Biological invasion is increasingly recognized as one of the greatest threats to biodiversity. Using ensemble forecasts from species distribution models to project future suitable areas of the 100 of the world's worst invasive species defined by the International Union for the Conservation of Nature, we show that both climate and land use changes will likely cause drastic species range shifts. Looking at potential spatial aggregation of invasive species, we identify three future hotspots of invasion in Europe, northeastern North America, and Oceania. We also emphasize that some regions could lose a significant number of invasive alien species, creating opportunities for ecosystem restoration. From the list of 100, scenarios of potential range distributions show a consistent shrinking for invasive amphibians and birds, while for aquatic and terrestrial invertebrates distributions are projected to substantially increase in most cases. Given the harmful impacts these invasive species currently have on ecosystems, these species will likely dramatically influence the future of biodiversity.

Keywords: Climate change, invasive species, land use change, species distribution models

Received 24 May 2013 and accepted 17 July 2013

Introduction

Climate changes, including extreme climatic events (i.e., flood, fires), can enhance invasion processes, from initial introduction through establishment and spread (Walther *et al.*, 2009; Diez *et al.*, 2012), and consequently have a profound influence on the environment. In addition, human activities such as transcontinental transportation, land degradation and agricultural systems, lead to the spread of many non-indigenous species (Foley *et al.*, 2005). Thus, the concurrent effects of climate and land use changes can further increase the already dramatic rates of biological invasions. For example, in Europe the number of invasive alien species increased by 76% in the last 30 years (Butchart *et al.*, 2010). Invasive alien species are likely causing an array of ecological, economic and health impacts for invaded countries (Simberloff *et al.*, 2012), that may become visible only long after introduction (Essl *et al.*, 2011). However, our limited knowledge of the impacts of climate and land use changes on biological invasions hinders our ability to measure, predict, and mitigate the growing effects of these two factors on invasive alien species. Therefore, the question of how the inter-

play between climate and land use change will influence the global process of invasions is thus becoming of prime relevance for natural resource management. Moreover, anticipating future distributions of invasive alien species is essential to facilitate pre-emptive and effective management actions such as prevention of introductions and opportunities for eradication. Risk maps summarizing land suitability for invaders can be useful tools for anticipating species' invasions and controlling their spread (Jiménez-Valverde *et al.*, 2011). Identification of areas where policies could benefit from synergies between climate, land use change and invasive species management is also of prime relevance.

Attempts to predict future ecologically suitable areas for the establishment of invasive alien species have been made on single species (O'Donnell *et al.*, 2012; Ficetola *et al.*, 2007; Larson & Olden, 2012). While many authors have warned about the potential synergistic feedbacks between climate and land use changes on species distributions (Brook *et al.*, 2008; Hellmann *et al.*, 2008; Walther *et al.*, 2009), few studies have examined these interactions explicitly (Murray *et al.*, 2012; Jetz *et al.*, 2007; Butchart *et al.*, 2012; Leroy *et al.*, 2013) and none have done so specifically for any invasive alien species. To address this gap, we report here a comprehensive evaluation of the dual effects of climate and land use changes on the 100 of the world's worst invasive

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species from the International Union for the Conservation of Nature list of the Invasive Species Specialist Group. This list regroups species with some of the largest impacts on biodiversity and/or human activity and represents a range of ecological strategies over 10 different taxonomic groups.

In this study, we used ensemble forecast projections extracted from multiple species distribution models (SDMs), several global climate models, and land cover change scenarios to predict future suitability for each of the 100 invasive alien species. Second, using these ensemble projections, we mapped the potential level of invasion at different time-slices (current, 2050 and 2100). Third, using projected species range changes for the different taxonomic groups of the 100 invasive alien species, we assessed the future vulnerability of various biome types to these invasive alien species.

Materials and methods

Data

Climate data. To characterize present-day climate, we used climatic data (averaged from 1950–2000) from the Worldclim database (Hijmans *et al.*, 2005) at a 0.5° resolution. We selected six climatic variables: (i) mean diurnal range, (ii) maximum temperature of warmest month, (iii) minimum temperature of coldest month, (iv) annual precipitation, (v) precipitation of wettest month, and (vi) precipitation of driest month (Table S1 for references details). These variables provide a combination of means, extremes and seasonality that are known to influence species distribution (Root *et al.*, 2003) and we selected only variables that were not collinear (pair-wise $r_{\text{Pearson}} < 0.75$). In the case of freshwater species, many studies have revealed strong correlations between spatial patterns and climatic variables (Jocque *et al.*, 2010), mostly temperature and the availability of water, and have used species distributions models to successfully predict the distribution of fishes (McNyset, 2005) and mussels (Drake & Bossenbroek, 2004). Future climate data were extracted from the Global Climate Model data portal (http://www.ccafs-climate.org/spatial_downscaling/). These models were statistically downscaled from the original Global Change Model outputs with the Delta method (Ramirez-Villegas & Jarvis, 2010). Due to large effects of different atmosphere ocean global circulation models (AOGCMs) on species range projections, simulations of future climate were based on three different AOGCMs (HADCM3, CSIRO2 and CGCM2) averaged from 2040 to 2069 ('2050') and 2070 to 2099 ('2080'). We used two different scenarios (A1B, B2A) that reflect different assumptions about demographic, socioeconomic and technological development on greenhouse gas emission (Solomon *et al.*, 2007). A1B scenario represents a maximum energy requirement, emissions balanced across fossil and non-fossil sources and B2A represents a lower energy requirement and thus lower emissions scenario than A1B (Solomon *et al.*, 2007).

Land use data. Current and future global land use and land cover variables were simulated by the Globio3 land model at a 0.5° resolution for two different emission scenarios A1B and B2A (Millennium Ecosystem Assessment *et al.*, 2005; Alkemada *et al.*, 2009). These data together with climate were used to model the potential distribution of the species in the 100 world's worst invasive species list (see below). For the two selected emission scenarios, we re-classified the 30 different land cover types from the Globio3 data (Bartholomé & Bellard, 2005) into 12 land cover type variables by grouping some of them together. These land use variables consisted of the proportion of the grid cell covered by (i) tree cover, (ii) tree cover regularly flooded, (iii) mosaic habitat, (iv) tree cover burnt, (v) shrub cover, (vi) herbaceous cover, (vii) cultivated and managed areas, (viii) bare areas, (ix) water bodies, (x) snow and ice, (xi) artificial surfaces and associated areas and (xii) pasture. We calculated for each pixel the proportion of each land cover type in 1970–2000 ('current'), '2050' and '2100'.

Biome data. We used 14 different type of biomes: (i) boreal forest, (ii) cool coniferous forest, (iii) grassland and steppe, (iv) hot desert, (v) ice, (vi) savanna, (vii) scrubland, (viii) temperate deciduous forest, (ix) temperate mixed forest, (x) tropical forest, (xi) tropical woodland, (xii) tundra, (xiii) warm mixed forest, and (xiv) wooded tundra, that we extracted from the IMAGE 2.4 model for each 0.5° cell (Leemans & Born, 1994; Prentice *et al.*, 1992). The biome data were used to compare the future potential number of invasive alien species per biome.

Invasive alien species data. We collected current distribution data for the species on the list 100 of the world's worst invasive alien species, compiled by the International Union for the Conservation of Nature (IUCN, Lowe *et al.*, 2000). Developed in 2000 by the ISSG global network of over 1000 invasion biology experts, this synthesis included input from the wider community of practitioners and scientists with expertise on all taxonomic groups and environments. The list provides the most geographically and taxonomically representative set of the most dangerous invasive alien species around the world, causing significant impacts on biodiversity and/or human activity in all ecosystems.

We chose these 100 species in an attempt to objectively explore patterns of change (i.e., range expansion versus retractions) and geographic patterns (i.e., into some regions and biomes but not others) for different taxonomic groups. They share the following specifications: (i) large impact on biodiversity and/or human activity, (ii) threaten a variety of taxonomic groups, ecosystems, types of impacts; (iii) illustration of important issues surrounding biological invasions. This list includes three micro-organisms, five macro-fungi, four aquatic plants, 30 terrestrial plants, nine aquatic invertebrates, 17 terrestrial invertebrates, three amphibians, eight fishes, three birds, two reptiles and 14 mammals (Lowe *et al.*, 2000). Rinderpest virus was removed from the list of the 100 because it is now eradicated. We made an extensive search for records from both the native and invaded ranges as recommended by

Gallien *et al.* (2010) for all the 99 species. Data were collected from a variety of online databases, references and personal communications (Table S2 for details).

We collected on average 3850 records per species with a minimum of 46 records for the least documented species. We found records of the 99 species from all over the world (except in Sahara region, northeastern Russia, northern Canada and Greenland).

Species distribution model projections

Modeling process. We modeled the potential distribution of the 99 invasive species by combining available occurrences with a set of six climatic variables and 12 land use variables that we assumed to be important for invasive species. Analysis of the climate and land use preferences of a species can therefore be used to predict areas where the species could occur at global scales. Although other factors such as soil properties or micro-climate also determine the presence or absence of a species at the local scale, we assumed that climate and land use were the most important explanatory variables of species distribution at the global scale. We used six different SDMs, within the biomod v.2.0 platform (Thuiller *et al.*, 2009) carried out on the R platform. These models were: Generalized Linear Model, Generalized Boosting Trees, Multivariate Adaptive Regression Splines, Random Forest, Flexible Discriminant Analysis and Maximum Entropy. More details about the first five modeling techniques can be found in Thuiller *et al.*, (2009) and in Elith *et al.* (2011) for Maximum Entropy. All models required presence and pseudo-absences (PAs or background). Five sets of PAs were generated by selecting from 1000 to 10 000 random points across the globe, according to the number of presences N (if $N \leq 1000$ then 1000 PAs were selected, else 10,000 PAs were selected) [as recommended by Barbet-Massin *et al.* (2012)]. Equal weightings were given to presences and PAs.

Evaluating model performance. We evaluated the predictive performance of each model using a repeated split sampling approach in which models were calibrated over 70% of the data and evaluated over the remaining 30%. This procedure was repeated four times. We used two different statistical metrics: the true skill statistics (TSS) (Allouche *et al.*, 2006) and Area Under the ROC Curve (AUC) (Fielding & Bell, 1997). The TSS accounts for both omission and commission errors, and ranges from -1 to $+1$, where $+1$ indicates perfect agreement and 0 represents a random fit (Allouche *et al.*, 2006). AUC values range from 0 to 1 , and according to Swets (1988), an AUC above 0.8 is considered to have 'good' discrimination abilities. All calibrated models performed very well with an average AUC value of 0.983 ± 0.002 and an average TSS value of 0.911 ± 0.007 (Fig. S1). We also used the Boyce index to assess model performance (Boyce *et al.*, 2002; Petitpierre *et al.*, 2012). The Boyce index only requires presence data, where AUC and TSS require both presence and absence data. Boyce index measures how much model predictions differ from random distribution of the observed presences across the prediction gradients. Values of Boyce index vary between -1 and

$+1$. Positive values indicate a model with present predictions that are consistent with the distribution of presences in the evaluation dataset; values close to zero mean that the model is not different from a random model. We calculated the Boyce index for each of the 60 models (GLM, MARS and MaXent) per species. On average, MARS (0.819 ± 0.322) and MaXent (0.817 ± 0.225) gave a very good evaluation measure, whereas GLM (0.367 ± 0.286) was less robust, but still gave fair predictions based on the Boyce index. This makes the interpretation of our results consistent over all species.

Ensemble modeling approach. The final calibration of every model for generating invasion scenarios used 100% of available data. We used an ensemble forecast approach to account for the variability among the six species distribution models and the three general circulation models to get the central tendency (Araújo & New, 2007). To make sure no spurious models were used in the ensemble projections, we only kept the projections for which the model's evaluation estimated by AUC and TSS were higher than 0.8 and 0.6 , respectively (e.g., Gallien *et al.*, 2012), and a weight proportional to their TSS evaluation was associated with each model. Because of the potential problems raised by Lobo *et al.* (2008) on the use of AUC as a measure of model performance, we decided to use TSS for the final consensus distributions. The final current and future consensus distributions were obtained by calculating the weighted mean of the distribution for each scenario (Marmion *et al.*, 2009). This resulted in one current probability distribution map and three future probability distribution maps (because we used three global circulation models) for each emission scenario (A1B and B2A) and each species. Future probability maps were therefore averaged for each scenario. Then, we transformed the probability maps obtained from the ensemble projections into binary suitable/non-suitable maps using the threshold maximising the True Skill Statistics, as proposed by Allouche *et al.* (2006). This was done to ensure the most accurate predictions since it is based on both sensitivity and specificity (Jiménez-Valverde & Lobo, 2007). We obtained one current binary distribution map and three future binary distribution maps per emission scenario and per species. Consensus binary maps were obtained attributing presence when the majority of GCMs (i.e., two of three) predicted presence, otherwise predicting absence. Since projections were not based on an equal-area projection system, cell sizes decrease pole-ward. Therefore, we calculated the area of each cell and weighted the cells of the world map by their area.

Results

Future hotspots of invasion (i.e., >60 invasive alien species) were projected to mostly occur in eastern United States, northeastern Europe, southwest Australia and New Zealand. Indonesian and Pacific islands region, central Africa, and southern Brazil could be affected at a lower rate (i.e., $20\text{--}40$ invasive alien species), regardless of the time-slice or climate scenario used (Fig. 1a).

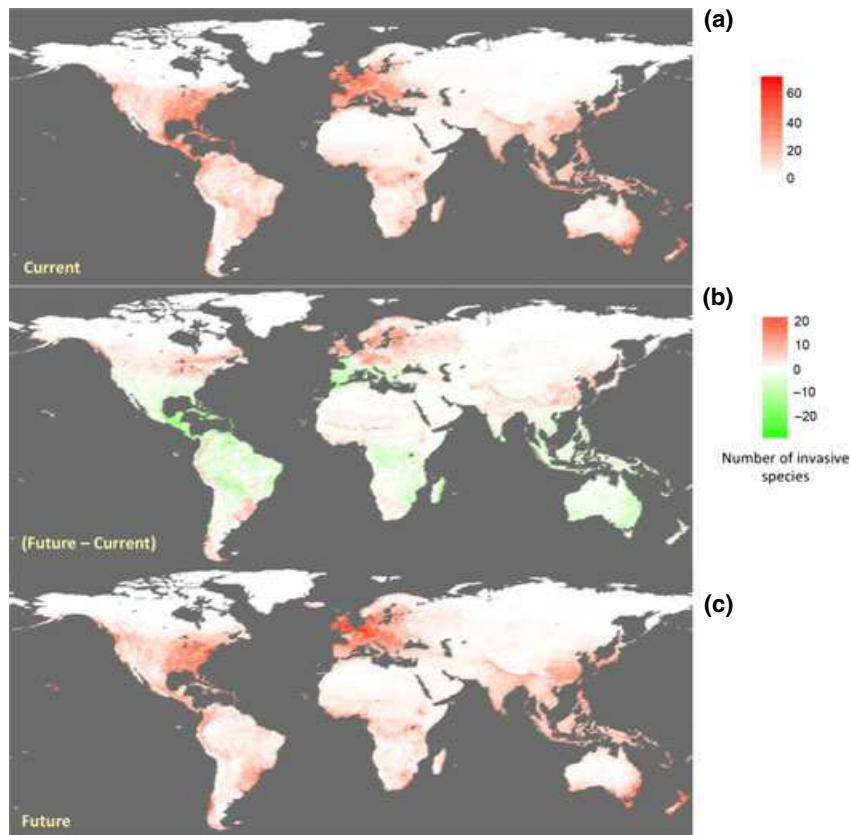


Fig. 1 Global distribution of invasive species under current and future scenarios. (a) Projected richness in invasive species by 2000, (b) Relative change in invasive species richness between 2000 and 2100 and (c) Projected richness in invasive species by 2100.

Changes of future number of invasive alien species showed important geographic variation, allowing for the detection of areas more vulnerable to invasions and those that might actually lose invasive alien species. Under all scenarios, an increase in the number of invasive alien species was projected for northwestern Europe and northeastern United States, India and eastern China (Fig. 1b). On the contrary, a decrease in the number of invasive alien species was projected for Central and South America, southwestern Europe, central Africa, and Indonesian and Pacific islands regions, eastern Australia. Globally, most areas projected to increase in the number of invasive alien species are located in continental and temperate climatic zones, especially in the northern hemisphere, while the potential number of invasive alien species largely decreased in the tropical regions at low latitudes. Climate and land use changes could create opportunities for many temperate species to spread at higher latitudes but could also lead to a significant loss of tropical invasive alien species. For example, several invasive alien species were projected to expand their ranges into more temperate regions in northern Europe (Fig. 1b). Globally, the number of

invasive alien species susceptible to invade new regions in the future tended both to be higher in the northern hemisphere compared to the southern, and to decrease at lower latitudes (Fig. 1a).

More precisely, our analyses revealed that biomes harboring extreme climatic conditions such as ice, hot desert, tundra and wooded tundra were not predicted to be suitable for invasive alien species by 2100 (Fig. 2 and Table S3). Other biomes tended to have suitable environmental conditions for a high number of invasive alien species in the future, especially temperate deciduous forests (27, average number of invasive alien species per pixel), warm mixed forest (22), temperate mixed forest (16) and tropical forest and woodland (12) (Table S3). The highest increase of invasive alien species, among the 14 types of terrestrial biomes, was projected to occur in temperate mixed forests (+4.5%, i.e., average invasive alien species per pixel), followed by cool coniferous forests (+3.4%), whereas tropical forests (-4%) and tropical woodlands (-4.4%) might become suitable for a lower number of invasive alien species in the future. In other words, biomes expected to shift into future extreme climatic zones (e.g., tropical forest) were

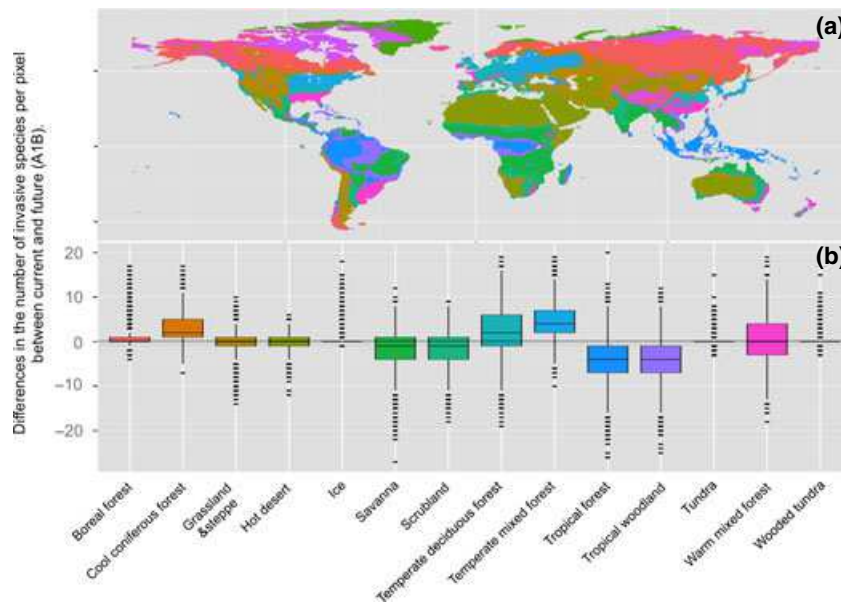


Fig. 2 Effect of climate and land use changes on the number of invasive species per pixel in each biome. (a) Map representing the biomes and (b) the associated boxplots representing the net potential changes of invasive species number between 2000 and 2100, under the A1B emission scenarios.

predicted to lose invasive alien species, whereas biomes (e.g., temperate mixed forest) that occurred at higher latitudes, where the climate will be less extreme, were predicted to gain some invasive alien species.

Among the 100 invasive alien species, range size expanded on average from 2 to 6% for both CO₂ emission scenarios (Table S4). However, this slight increase masked high variation across taxonomic groups: amphibians (−65%), birds (−24%), and fungi (−11%) could experience strong range size shrinkage under future projections (Fig. 3). Range size distribution of fishes (−1%), mammals (−4%) and reptiles (−4%) were predicted to remain stable, while aquatic invertebrates (+59%), aquatic plants (+12%), micro-organisms (+17%), and terrestrial invertebrates (+18%) were predicted to largely expand their potential range distributions. While our results predicted convergent patterns of range size change within amphibians and micro-organisms (i.e., either shrink or expand), divergent patterns were observed within the majority of the other groups, particularly within terrestrial invertebrates, plants, and fungi (Fig. 4).

Discussion

Using state-of-the-art of species distribution models, our findings identify three future hotspots of invasion: Europe, northwestern North America, and South Australia and New Zealand, whatever the climate scenario used. Globally, the number of invasive alien species in

the future tended to be higher in the northern hemisphere compared to the southern and to decrease at lower latitudes. Many studies suggest that global change will, on average, increase the risk of invasion (Walther *et al.*, 2009; Bradley *et al.*, 2012). Surprisingly, we did not find a global increase in invasive species distributions following climate and land use changes. We found contrasting projected changes in species distributions among regions and taxa. For example, Central America, northern South America, Western Europe (e.g., Portugal, Spain and France), central Africa, eastern Australia, and Indonesia all showed a decrease in the expected number of future invasive alien species. We also showed consistent expected distribution shrinkage for invasive amphibians and birds, and a substantial distribution increases for most aquatic and terrestrial invertebrates. The range sizes for fishes, mammals, and reptiles are expected to remain stable on average, although we observed some local shifts in species area distributions.

Although our approach has merits, we also faced limitations that call for further refinements. First, our results should be interpreted with respect to these invasive alien species only, as they are not a representative sample of all global invasive alien species (i.e., they are mostly invasive in temperate areas). Despite this sample bias, these 100 invasive alien species include some of the most harmful and widespread invasive alien species in the world, and they have already demonstrated their ability to establish and spread into new

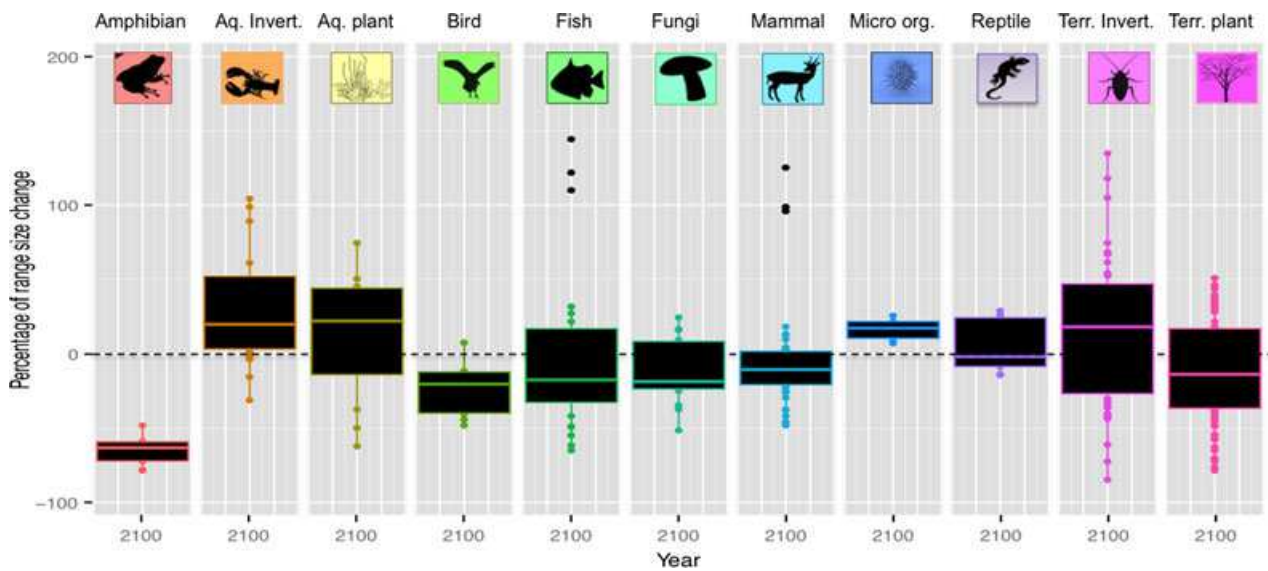


Fig. 3 Range size change for the different taxonomic groups of the 100 invasive species. Boxplot of the effect of climate and land use changes on invasive alien species range size (estimated by counting the number of suitable pixels) under A1B scenario for each species sorted by taxonomic group.

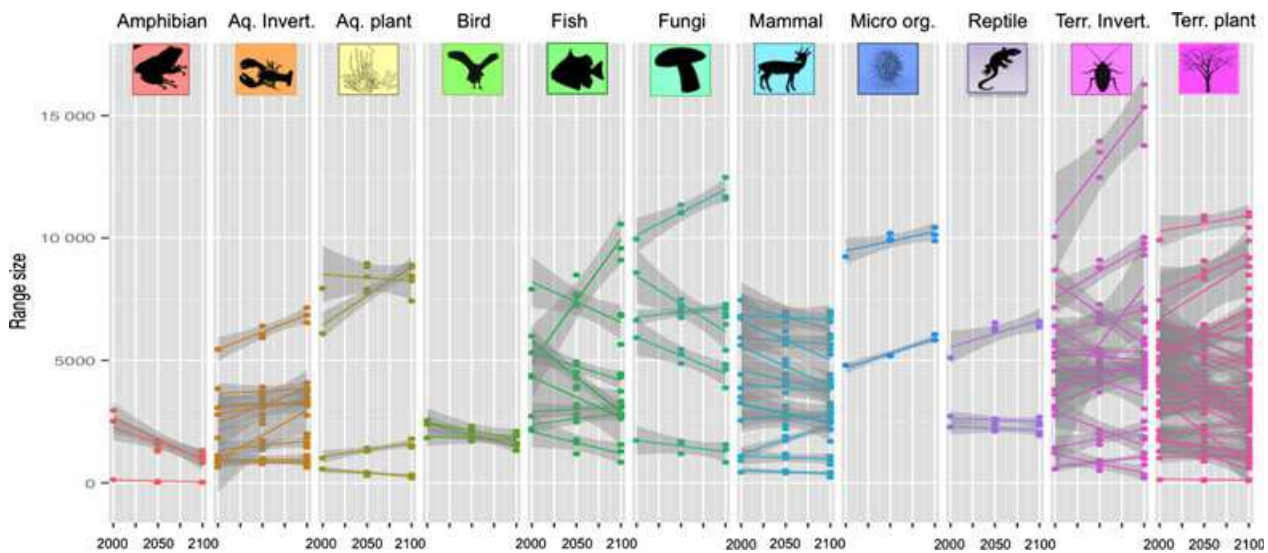


Fig. 4 Temporal range size change for the 100 invasive alien species among the different taxonomic groups. Effect of climate and land use changes on range size (estimated by counting the number of suitable pixels) under A1B scenario for each species along the different time-slices. Smoothing was performed for each species using linear regression.

ecosystems. Therefore, the expansion of these invasive alien species will result in new ecological interactions with consequences that are often hard to predict, but are likely to be negative for native ecosystems, economies and human health (Simberloff *et al.*, 2012). In addition, new invasive alien species are also expected to emerge as a consequence of the ongoing climate and land use changes (Hellmann *et al.*, 2008). However, the

range contractions we have predicted for some of these dangerous invasive alien species should provide some good news for those concerned with their management and eradication. In fact, reduced climatic suitability on currently invaded areas may make invasive species less competitive, therefore potentially leading to retreat (Pyke *et al.*, 2008; Bradley *et al.*, 2009).

We are aware that the methodology of projecting species distributions into the future is known to be limited by the amount of information able to be incorporated in the models (Schwartz, 2012). Likewise, in our study, climate and land use are assumed to be the only drivers of change for these invasive alien species distributions. We only considered abiotic variables, our analyses disregarded dispersal capacities, biotic interactions, and opportunity of invasive alien species introduction (Gaston & Fuller, 2009). Recent studies provided strong evidence that biotic and abiotic factors are determinants in the pattern of invasive alien species (Roura-Pascual *et al.*, 2011; Gallardo & Aldridge, 2013). The potential presence of suitable environmental conditions for a 'new' species does not automatically lead to successful establishment, meaning SDMs may often overestimate the full extent of predicted invasions. Species must travel across major geographic barriers to their new location, and they must survive and tolerate environmental and biotic conditions at the arrival site. However, these cannot presently be incorporated into our analyses. Results of SDMs are also potentially limited in their ability to predict species occurrences in novel environmental space, because we could not forecast if species will or will not occupy the new conditions that were not available to them before. Finally, we assume that invasive alien species are in equilibrium with their environment, which is not necessary the case as many invasive alien species have recently been introduced into new ecosystems.

A careful investigation of some methodological uncertainties in our studies confirms the consistency of our findings (see Methods). The results from the three different global circulation models at the two different periods (i.e., 2050 and 2100) are consistent, supporting our main conclusions.

Here, we show for the first time that the magnitude and the pattern of invasion around the world is projected to change in the 21st century for a large sample of invasive alien species, following expected changes in climate and land use. Our projections show that the number of invasive alien species should increase in northeastern Europe and northeastern United States more than elsewhere. These resulting maps indicating future hotspots of invasion help point to global zones in which emphasis should be placed on prevention and early detection, for the protection of future biodiversity in these areas. We also clearly showed that some regions (i.e., at lower latitudes) will lose invasive alien species. The potential absence of suitable conditions for an invasive alien species is one of the stronger findings since it is based on real presence in the current distribution. This result could be explained both because these regions will suffer from extreme climate conditions for

invasive alien species (Beaumont *et al.*, 2010; Neelin *et al.*, 2006) and future important local climate changes have been shown to occur at low latitudes, including the Caribbean/Central America region and equatorial South America (Williams *et al.*, 2007). Habitat degradation through deforestation was also projected to increase in tropical regions (Laurance *et al.*, 2012). Additionally, it has been shown that tropical regions might become extremely sensitive to climate change because the increase in absolute temperatures relative to the past variability is relatively large compared to temperate regions (Beaumont *et al.*, 2010). These results are of primary importance as it suggests that some invasive alien species could suffer from climate and land use changes. These potential local extinctions could create restoration opportunities for some regions such as Central America or southeast of Australia because management of invasive alien species could be easier for species that are currently at the limit of their abiotic tolerance. Globally, our results suggest strongly that biological communities will see important reorganizations in the future owing to shifting area distribution of many invasive alien species. SDMs are cost effective, giving the opportunity to prioritize and focalize actions including financial investments for certain regions. Our results provide valuable insights of plausible and possible future hotspots of invasions. They also highlight the need to account for both climate and land use change when focusing on biotic exchanges. Overall, the general picture painted here is that the question of whether climate and land use changes will favor invasive alien species is not likely to have a simple universal answer.

To conclude, we provide a new picture of future invasions, highlighting that responses of invasive alien species to global change will depend both on the region considered and on the taxa considered. These results are of major importance for Europe, northeast United States, Central America and Africa, Indonesian and Pacific islands regions because suitability of these regions to invasive alien species could be strongly modified. The impacts of these invasive alien species on these regions might become even more important in the future. We suggest that prompt responses to the introduction of invasive alien species and control of invasions should be a key component of the global efforts to mitigate the effects of climate change. Governments should also regulate the importation of species through black-listing, and activate early warning and rapid response frameworks, since such actions are decisive in preventing invasions and ecologically less risky than postponed interventions (Simberloff *et al.*, 2012). Finally, our models predict that restoration opportunities resulting from climate change will exist in the future. Eradication and control programs should

be continued for invasive alien species that will suffer from global changes, but also encouraged by our findings.

Acknowledgements

The article was written while the authors were supported by various grants, CB from the CNRS (PhD contract), FC and WT from the French 'Agence Nationale de la Recherche' (ANR) with the RARE (2009 PEXT01001) and SCION (ANR-08-PEXT-03) projects. It has also been supported by an European program BI-ODIVERSA: FFII. WT received also funding from the European Research Council under the European Community's Seven Framework Programme FP7/2007-2013 Grant Agreement no. 281422 (TEEMBIO). We thank Gloria Luque and Elsa Bonnaud for constructive criticism and discussions on an earlier version of the manuscript. We also thank Josh Donlan and Jessica Albate for English corrections on the manuscript. We gratefully acknowledge useful comments from the anonymous referees that improved the different version of the manuscript. We are also grateful to the many colleagues who provided species occurrences data (see Table S2 for details). All co-authors have no conflict of interest to declare.

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Supporting Information

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

Figure S1. Boxplots of TSS and an average Area Under the operating characteristic Curve in a ROC analysis values for all the calibrated models.

Table S1. Environmental variables list.

Table S2. List of the 100 cases of the world's worst invasive species with data sources and number of occurrences.

Table S3. Percentage of net change of the number of IAS for the 14 types of biomes under the A1B and B2 scenarios.

Table S4. Percentage of net change between current and future scenarios (A1B and B2) of the range size for the different taxa.

Conclusion

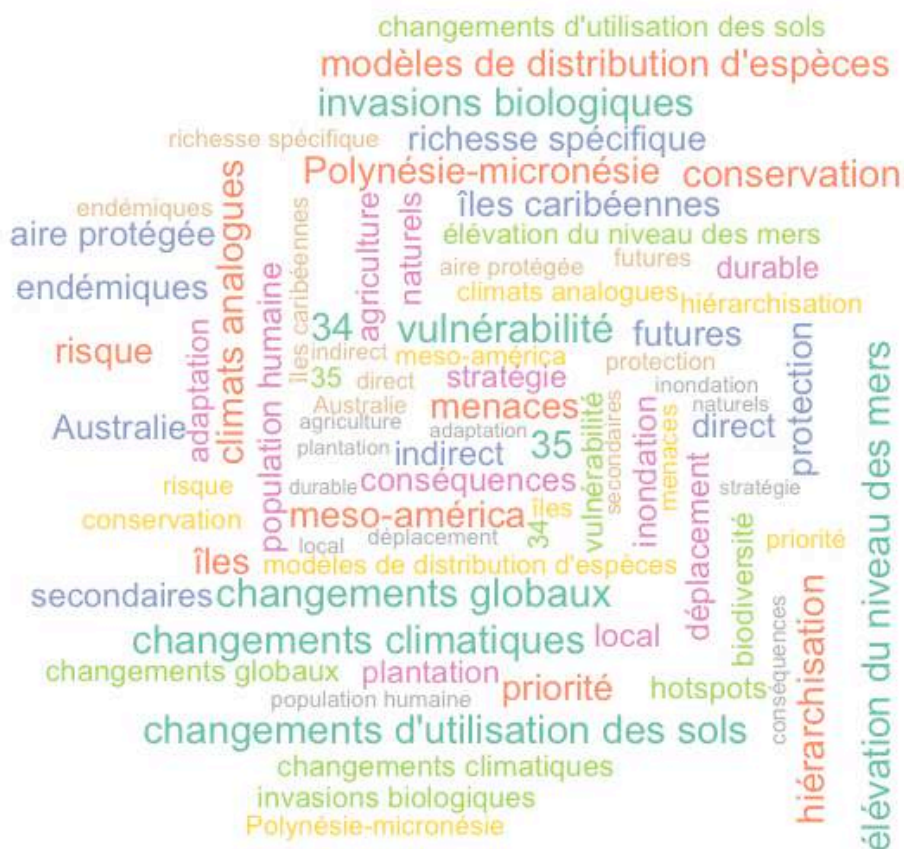
Cet article a permis de mettre en évidence que, selon la région, le taxon ou même l'espèce considérée, les changements climatiques et d'utilisation des sols ne vont pas avoir les mêmes conséquences sur les espèces invasives. Globalement, nos résultats révèlent que le nombre d'espèces invasives deviendra plus important dans l'hémisphère nord par rapport à l'hémisphère sud. Ainsi, l'Europe du Nord, l'est de l'Amérique du Nord, la Nouvelle Zélande et l'Australie seront favorables à un grand nombre d'espèces invasives d'après nos résultats. Dans un contexte de prévention des espèces invasives, ces régions sont à surveiller en priorité afin de limiter l'arrivée d'espèces non-natives. Au contraire, l'Amérique centrale, l'ouest de l'Europe, l'Afrique centrale, l'est de l'Australie et l'Indonésie montreront une diminution potentielle du nombre d'espèces invasives dans le futur. Ce résultat implique notamment que des stratégies de contrôle des espèces invasives et de restauration des écosystèmes pourront être mises en œuvre dans ces régions.

Enfin, de nombreuses études théoriques avaient discuté des conséquences négatives des changements climatiques sur les invasions biologiques, en particulier chez les plantes alors que notre étude révèle des résultats plus contrastés. De plus, cette étude est la première à considérer un nombre aussi important d'espèces invasives issus de différents groupes taxonomiques dans le cadre des changements climatiques et des changements d'utilisation des sols. Il faut également rappeler que les résultats issus de ces modèles sont uniquement basés sur des variables abiotiques et que d'autres facteurs, tels que la densité humaine peuvent aussi jouer un rôle sur la distribution de ces espèces (voir Chapitre 4) et devront être pris en compte dans des analyses futures. Cette étude a notamment fait l'objet d'un *Research highlights* dans la revue *Nature climate change*.

Finalement, dans le Chapitre 6, nous nous sommes intéressés aux conséquences de ces menaces sur les 35 hotspots de biodiversité. Le Chapitre 6 a donc pour objectif d'évaluer la vulnérabilité des hotspots aux invasions biologiques, mais également aux changements climatiques et aux changements d'utilisation des terres.

Partie 4

5. Menaces sur les hotspots de biodiversité et hiérarchisation



Chapitre 6

Biodiversity hotspot vulnerability to global change

Résumé

Les changements globaux risquent d'avoir des conséquences importantes sur la biodiversité dans le siècle à venir. Les 34 hotspots de biodiversité sont devenus des priorités de conservation internationales avec d'importants efforts alloués à leur conservation. Cependant, peu d'études se sont intéressées aux effets des changements globaux sur ces hotspots. Nous avons donc évalué l'exposition des hotspots aux changements climatiques en utilisant des analyses de climat analogue. Nous avons également quantifié l'évolution des changements d'utilisation des sols dans ces hotspots. Enfin, nous nous sommes intéressés à la présence de conditions favorables aux espèces invasives en utilisant des modèles de distribution d'espèces sur les « *100 of the world's worst invasive alien species* ». Nos résultats ont montré qu'en moyenne 31% des climats présents dans les hotspots pourraient disparaître à l'avenir. Par ailleurs, la Polynésie Micronésie, le Méso-Amérique et les îles de l'est mélanésien pourraient être les régions les plus affectées par la perte de climat. En outre, les hotspots qui sont majoritairement composés d'îles se sont révélés être les plus favorables à la présence de ces espèces invasives. En conclusion, ces résultats ont démontré qu'il est important de considérer les menaces futures dans le cadre de la mise en place de priorité de conservation, en particulier car les hotspots ne sont pas égaux face aux menaces que représentent ces changements globaux.

Cette partie correspond à l'article soumis suivant:

**C. Bellard, C. Leclerc, B. Leroy, M. Bakkenes, S. Veloz, W. Thuiller, & F. Courchamp
Biodiversity hotspot vulnerability to global change, *major revision* in *Global Ecology and Biogeography***

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Biodiversity hotspot vulnerability to global change

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Key word: biodiversity hotspots, climate changes, land use changes, biological invasions.

31 **Aim** By the end of the 21st century, global changes are predicted to have large consequences
32 on biodiversity. The 34 biodiversity hotspots have become international priorities for
33 conservation, with important efforts allocated for their study and preservation. However, the
34 potential effects of global changes on hotspots have received relatively little attention so far.
35 For the first time, we quantified the exposure of biodiversity hotspots to the combined effects
36 of human-induced climate, land-use change and biological invasions.

37 **Location** 34 biodiversity hotspots worldwide

38 **Methods** Using dissimilarity climate analyses, we quantify (i) the exposure of biodiversity
39 hotspots to climate change, by estimating the novelty of future climates and disappearance of
40 extant climates (ii) the hotspot vulnerability to land modification and degradation by
41 quantifying changes in land cover variables over the entire habitat and (iii) the future
42 suitability of 100 IAS in the 34 biodiversity hotspots by characterising the combined effects
43 of climate and land use changes on the future range distribution of the “*100 of the world’s*
44 *worst alien invasive species*”.

45 **Results** Our findings showed that on average hotspot may experience 31% of loss in analogue
46 climate, with some hotspots more affected than others (*i.e.* Polynesia-Micronesia,
47 Mesoamerica and East-Melanesian Islands). The greatest climate change was projected in
48 low-latitude hotspots. In addition, the 34 hotspots were on average suitable to 17% of invasive
49 species considered. Hotspots that are mainly islands or group of islands were
50 disproportionately suitable for a high number of invasive species in the future. Finally,
51 combining the three potential threats, we identified four hotspots as especially vulnerable to
52 global changes in the future: Caribbean islands, Western Ghats Sri Lanka, Polynesia
53 Micronesia and Mesoamerica.

54 **Main conclusions** These results highlight the pressing need to consider different drivers of
55 global change in conservation planning.

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65 **Introduction**

66 The current biodiversity extinction crisis is a major challenge facing humanity today (Araújo
67 & Rahbek, 2006). The unprecedented rapid global change that is currently occurring is
68 commonly believed to have the potential to exacerbate both the pace and the amplitude of this
69 crisis. In particular, rates of climate change are projected to increase (Solomon *et al.*, 2007)
70 and novel combinations of climatic conditions are expected in wide regions in the coming
71 decades (Williams *et al.*, 2007; Beaumont *et al.*, 2010). Extensive evidences from the fossil
72 record (Lorenzen *et al.*, 2011), recently observed trends (Parmesan, 2006) and predictive
73 studies (Bellard *et al.*, 2012) all suggest that climate change is likely to have a large impact on
74 biodiversity, from organisms to biomes. Similarly, habitat change (loss, fragmentation and
75 degradation), mostly due to agriculture expansion, urbanization and grazing is considered the
76 first contemporary threat to terrestrial species worldwide (Sala *et al.*, 2000). In addition,
77 through ever-increasing public and global trade, invasive alien species (IAS) have been
78 introduced into most ecosystems throughout the planet, severely affecting ecological
79 networks, biodiversity and ecosystem functioning. The extent of the impacts of the thousands
80 of IAS worldwide is such that biological invasions are cited as the second largest cause of
81 biodiversity loss worldwide (Simberloff *et al.*, 2013).

82 In this context, it is especially striking that relatively few studies have aimed at
83 assessing the vulnerability of the biodiversity hotspots to climate, land use changes, and
84 invasive alien species. Intuitively, we want to conserve the most threatened areas first, but we
85 also want to get the greatest efficiency for conservation resources (Mittermeier *et al.*, 2004;
86 Murdoch *et al.*, 2007). This paradox can be resolved by identifying areas that hold species
87 found nowhere else and in which species are highly threatened, 34 mega diverse regions have
88 been defined as places of biodiversity vulnerability and irreplaceability (Mittermeier *et al.*,
89 2004). These hotspots harbour exceptional concentrations of endemic species (i.e., a
90 minimum of 1500 endemic species of vascular plants) and have experienced exceptional
91 habitat loss or degradation (i.e., a loss of over 70% of their original natural vegetation).
92 Collectively, the 34 hotspots shelter over 150,000 single-hotspot endemic plant species (no
93 less than 50% of the world's total) and nearly 13,000 endemic terrestrial vertebrates (42% of
94 the world's total) on a remaining habitat concentrated within a mere 2.3% of the earth's
95 surface (Mittermeier *et al.*, 2004). Moreover, over two-thirds of globally threatened species
96 are single-hotspot endemics (Mittermeier *et al.*, 2004) and it is highly probable that a large
97 proportion of threatened species are endemic to combinations of hotspots (Mittermeier *et al.*,
98 2012). These regions have become international priorities for conservation, with important

99 efforts and resources allocated for their study and preservation, possibly already in excess of
100 US\$1 billion in conservation funding (Schmitt, 2012). Yet, the future effects of different
101 components of global change on the biodiversity hotspots have received remarkably little
102 attention (but see Beaumont et al., (2010) that focused on the most exceptional eco-regions
103 and Malcolm et al., (2006) that focused on the sole effect of global warming on the 25
104 biodiversity hotspots). Standard conservation practices may prove insufficient to maintain the
105 biodiversity of many of these hotspots if only current threats are taken into account. We
106 therefore aim at providing rigorous estimates of future impacts of global change (climate
107 changes, land use changes and biological invasions), which are essential for the future
108 conservation efforts underway in these hotspots.

109 We examine the effects of projected future global change on 34 biodiversity hotspots
110 for 3 complementary aspects. We quantify (i) the exposure of biodiversity hotspots to climate
111 change; (ii) the hotspot vulnerability to land modification and degradation and (iii) the future
112 suitability of 100 IAS in the 34 biodiversity hotspots. Exposure to climate change is assessed
113 by estimating the novelty of future climates and disappearance of extant climates and the
114 associated number of endemic species potentially affected; vulnerability to land use change is
115 assessed by quantifying changes in land cover variables over the entire habitat; sensitivity to
116 IAS is estimated by characterising the combined effects of climate and land use changes on
117 the future range distribution of the “*100 of the world’s worst alien invasive species*”.

118

119 **Material & Method**

120 **Data**

121 *Climate data*

122 Current climatic data were obtained from the Worldclim database (Hijmans *et al.*, 2005) at
123 10’ resolution. We selected 6 different climate variables linked to temperature and
124 precipitation (see Table S1). These variables were selected as they provide a combination of
125 means, extremes and seasonality that are known to influence the distribution of species (Root
126 *et al.*, 2003) and they were not collinear (pair-wise $r_{\text{Pearson}} < 0.75$). Future climate data were
127 extracted from the Global Climate Model data portal ([http://www.ccafs-
128 climate.org/spatial_downscaling/](http://www.ccafs-climate.org/spatial_downscaling/)) at the same 10’ resolution. These data were statistically
129 downscaled from global circulation models with the Delta method (Ramirez-Villegas &
130 Jarvis, 2010). Simulations of future climate were based on three general circulation models
131 (HADCM3, CSIRO2 and CGCM2) averaged from 2070 to 2099 (“2080”). We used two
132 different scenarios (A1B, B2A) that reflect different assumptions about demographic, socio-

133 economic and technological development on greenhouse gas emission (Solomon *et al.*, 2007).
134 A1B represents maximum energy requirements, emissions balanced across fossil and non-
135 fossil sources and B2A represents lower energy requirements and thus lower emissions than
136 A1B (IPCC *et al.*, 2007)

137

138 *Land use data*

139 Current and future global land use and land cover were simulated by the Globio3
140 model at 0.5° resolution (Millennium Ecosystem Assessment, 2005; Alkemade *et al.*, 2009).
141 For the two selected emission scenarios A1B and B2A, 30 different land cover types from the
142 Globio3 data (Bartholomé & Belward, 2005), were re-classified into 12 land cover type
143 variables by grouping some of them (see Table S1). We calculated for each pixel the
144 proportion of each land cover type in 1970-2000 (“current”) and 2080. These data together
145 with climate were used to model the potential distribution of the list of the “*100 of the world’s*
146 *worst invasive species*” (see below).

147

148 *Invasive species data*

149 The Invasive Species Specialist Group (ISSG) of the International Union for the
150 Conservation of Nature (IUCN) has created a list of the “*100 of the world’s worst invasive*
151 *species*”, including taxonomically varied species with major spread and impact worldwide
152 (Lowe S., Browne M. & M., 2000) to highlight the impacts to biodiversity that these invaders
153 can cause. In their invaded range, each of these 100 IAS threatens a large number of native
154 species, either directly or indirectly (Lowe S., Browne M. & M., 2000). Occurrence records
155 from both the native and invaded ranges as advised by Gallien *et al.* (2010) of all species were
156 collected from a variety of online databases, references and personal communications (see
157 Table S3 for detailed). Because many records of IAS have been collected between 1950 and
158 2000, we used current climate data period between 1950-2000. We collected on average 3,850
159 records per species with a minimum of 46 records for the least documented species.
160 Rinderpest virus was removed from the list of the 100 because it is now eradicated.

161

162 **Climate analysis**

163 *Analysis of (non) analogous climates*

164 The boundaries of hotspots were originally determined by “biological commonalities”
165 (Myers *et al.*, 2000). Each of the areas features a separate biota or community of species that
166 fits together as a biogeographic unit. We therefore made the assumption that hotspots have

167 specific climates, which explain the biodiversity found in these regions. Other factors,
168 however, like historical processes, contemporary ecological factors, inherent biological
169 properties of taxa, topography, soil types and their combinations also contribute to the high
170 rate of endemism in these regions (Cowling & Samways, 1995; Jetz et al., 2004).

171 We used the methodology developed by Williams et al., (2007) to quantify climate
172 dissimilarities between current and future climate. To quantify climate dissimilarities between
173 the 20th and 21st century within hotspots, we calculated the Standardized Euclidean Distances
174 (SED) as follows:

$$SED_{ij} = \sqrt{\sum_{k=1}^6 \frac{(a_{kj} - b_{ki})^2}{S_{kj}^2}}$$

175 where a_{kj} and b_{ki} are the 1950–2000 (“current”) and 2070–2099 (“future”) means for
176 climate variable k at grid points i and j , and s_{kj} is the standardization value for 1950–2000.
177 The standardization values were temperature seasonality variable for temperature variables
178 and precipitation seasonality variable for precipitation variables. Standardizing each variable
179 places all climate variables on a common scale (Veloz *et al.*, 2012). High SED values
180 correspond to high climate dissimilarities between two periods and may potentially indicate
181 novel or disappearing climates. For more details about the method see (Williams et al., 2007;
182 Veloz et al., 2012).

183 We then calculated a SED threshold (SED_t) for each hotspot to discriminate the limit
184 above which the climate was no longer considered as analogue to the current conditions (i.e.,
185 climate loss). SED_t was determined comparing the distribution of SED values between the
186 hotspot and the rest of the world for 20th-century climate. We used the Receiver Operating
187 Characteristic (ROC) to determine the SED_t value that provides the optimal separation within-
188 and between-surface histograms (Oswald *et al.*, 2003) (see Figure S1 for method). Therefore,
189 each SED_t is associated to an evaluation of the threshold (i.e., Area Under the Curve). Four
190 biodiversity hotspots were excluded from analysis because the low value of their AUC (i.e.,
191 less than 0.6) indicated that the critical threshold cannot discriminate between analogue and
192 no-analogue climates (Guinean forests of West Africa, Mountains of Southwest China, New
193 Caledonia and Cerrado). For 4 very large hotspots (Horn of Africa, Indo-Burma,
194 Mediterranean Basin, Sundaland), the threshold was averaged on the basis of 10 random
195 samplings of 10 000 values of each SED. All the threshold values are presented in Table S4.

196 Using these SED_t , we calculated two indices of climatic risk for each hotspot, based
197 on an identical metric of multivariate dissimilarity. First, we calculated (*i*) the climatic

198 distance between the end-21st-century simulation for each hotspot grid point and its closest
199 analogue from the global pool of 20th-century climates (*i.e.*, an index of the novelty of future
200 climates), and (*ii*) the climatic distance between the 20th-century realization for each hotspot
201 grid point and its closest 21st-century climatic analogue (*i.e.*, an index of disappearance of
202 extant climates). The first metric identifies novel climates, climate conditions with no
203 contemporary analogue globally, whereas the second metric identifies disappearing climates,
204 contemporary climate conditions within the hotspot that have no future analogue globally.

205

206 *Assessing climate change impacts on endemic species*

207 We used the number of endemic species present in each hotspot from Mittermeier
208 (2004) to estimate the potential number of endemic species that are directly threatened by
209 climate change (Table S2). We performed the climate analysis within the hotspot, assuming
210 these define limits of climate suitability for the species that live therein. Yet, species may be
211 forced, and able, to move outside these limits to find suitable climate conditions in the future.
212 In those cases (assuming such migration to follow climate is unhindered), the number of
213 endemic species threatened by climate changes would have been overestimated (except for
214 insular hotspot, for which such migration is prevented by the geographical barriers of the
215 oceans). Therefore, we extended this analysis of climatic risk to a radius of 500 km (except
216 for insular hotspot) around each hotspot, to produce conservative identifications of novel and
217 disappearing climates (Williams et al., 2007). The value of 500 km was chosen
218 conservatively, as it largely exceeds the highest known rates of plant migration during the last
219 glaciation (Ritchie *et al.*, 1986). As a proxy for the distance a species might need to travel to
220 maintain an equilibrium with its currently occupied climate space, we calculated the
221 geographical distance between the current analogue climate and its closest analogue for the
222 present, and compared it to the geographical distance between the current analogue climate
223 and its closest analogue in the future. This value will give an indication of geographical
224 distance between closest analogues currently and in the future, although suitable conditions
225 could be found closer.

226 We evaluated the number of endemic species that are potentially threatened by climate
227 change by measuring extent of the loss of analogue climate. Ecologists and bio-geographers
228 have long recognized that species richness (S) increases with area size (A) at a decreasing rate
229 and thus eventually levels off (Rosenzweig, 1995). The curve that correctly describes the rate
230 of extinction as habitat area decreases is called the Endemics Area Relationship (EAR) (Harte
231 & A P Kinzig, 1997). Here, we assumed that analogue climate area loss within a hotspot is a

232 proxy of potential habitat loss in that hotspot. We thus used the EAR to quantify the potential
233 number of endemic species sensitive to climate change. The EAR was chosen over Species-
234 Area Relationships (SAR) because predictions from SAR in some cases overestimate the
235 number of extinctions (A.P. Kinzig & Harte, 2000). To derive a more realistic relationship
236 under this possibility, EAR takes into account the number of species expected to be confined
237 to smaller patches within the total area of habitat loss.

$$f_{lost-EAR} = (\Phi_A)^{z'}$$

238 where Φ_A is the fraction of original analogue climate loss ($A_{future}/A_{current}$), with $A_{current}$ the
239 current area of hotspot, A_{future} the remaining area with SED values less than the critical
240 threshold and z' a constant ($z' = -\ln(1-1/2^z)/\ln(2)$). We used 3 different values of z : the typical
241 value of fragmented habitats (e.g. $z=0.25$, (T.M. Brooks *et al.*, 2002); a conservative value
242 more typical of continental situations (e.g. $z=0.15$, (Malcolm *et al.*, 2006); and an
243 intermediate value (e.g. $z=0.2$ (Bergl *et al.*, 2007)).

244

245 **Land use analysis**

246 For the two scenarios, we intersected our gridded projections of land use with the boundaries
247 of the 34 hotspots. We then calculated the average proportion of each land use class in each of
248 the pixel per hotspot for the current and future periods. We calculated for each of the 34
249 hotspots, the percentage of changes according to the different land cover class between
250 “2000” and “2080” for the two emission scenarios.

251

252 **Invasive species distribution modelling**

253 We modeled the potential distribution of the invasive species in the 34 hotspots by combining
254 available occurrences with a set of climatic and land use variables that we assume to explain
255 these species distributions (see Supplementary Information 1 for details). We used 6 different
256 SDMs implemented within the BioMod v.2.0 platform (Wilfried Thuiller *et al.*, 2009). We
257 evaluated the predictive performance of each model using a 4-fold repeating split sampling
258 approach in which models were calibrated over 70% of the data and evaluated over the
259 remaining 30% records. The models were evaluated with both the True Skill Statistics
260 (Allouche *et al.*, 2006) and Area Under the ROC Curve (Fielding & Bell, 1997). The final
261 calibration of predicted models used 100% of available data and was obtained by calculating
262 the weighted mean of the distribution for each scenario. To make sure no spurious models
263 were used in the ensemble projections, we only kept the projections for which the model's

264 evaluation estimated by AUC and TSS were higher than 0.8 and 0.6 respectively (e.g.(Gallien
265 *et al.*, 2012)), and a weight proportional to the TSS evaluation was associated to each model.
266 Because of the potential problems raised by (Lobo *et al.*, 2008) on the use of AUC as a
267 measure of model performance, we decided to use TSS for the final consensus distributions.
268 TSS consider both omission and commission errors. Then, we transformed the probability
269 maps obtained from the ensemble projections into binary suitable/non-suitable maps using the
270 threshold maximizing the TSS for each species. All data processing and statistical analyses
271 were performed using R version 2.15 (R Development Core Team, 2012).

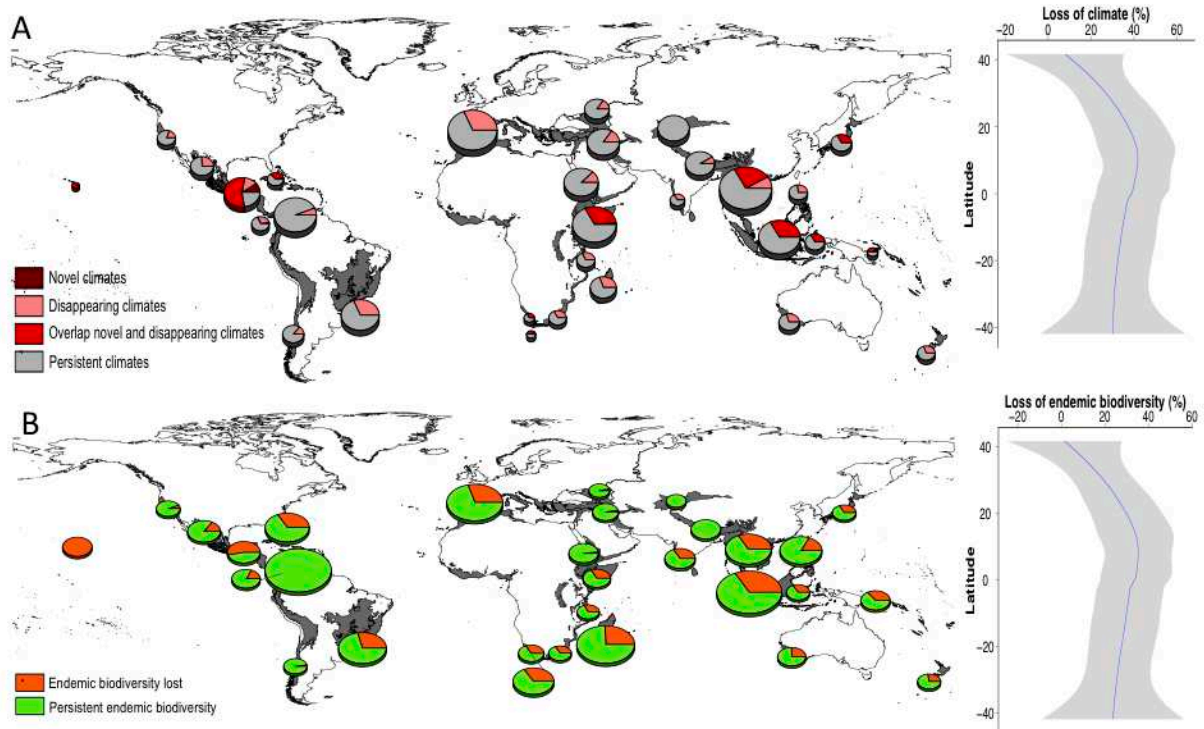
272

273

274 **Results**

275 **Climate change within biodiversity hotspots**

276 Our analysis suggest that, overall, 68 to 93% of the existing climate within hotspots
277 should remain stable in the future. Globally, the average fraction of land area per hotspot with
278 novel climate was about 16%. The distribution of these novel climates was strongly
279 concentrated in three hotspots: Polynesia Micronesia (98%), Mesoamerica (65%) and East
280 Melanesian Islands (43.4%). The same three hotspots concentrated the largest proportion of
281 disappearing climate with 99%, 68% and 41% respectively. On average, hotspots may
282 experience 31% of loss in analogue climate in the future. The distribution of novel and
283 disappearing climate were principally concentrated at low latitudes, and decreased pole ward
284 (Figure 1A). Using areas with a loss of analogue climate as a proxy for habitat loss, we
285 calculated that climate changes might negatively influence on average 25% of endemic
286 species (with $z=0.2$, Figure 1B) for each of the hotspots. Numbers of endemic species
287 potentially affected by climate change were only slightly affected by the z value (see
288 Kolmogorov-Smirnov test, $P>0.05$ for all paired tests in Table S6). The absolute numbers of
289 endemic species vulnerable to climate change were 5,362 species in Sundaland, 3,540 species
290 in Mediterranean Basin, 3,309 species in Polynesia-Micronesia and 3,215 species in
291 Madagascar. The closest analogue climate for any point in any continental hotspot was
292 predicted to become three times farther than it is currently (Figure S2). The Mediterranean
293 Basin may be the most impacted hotspot in this regard, with distances reaching up to 1,145
294 km further than currently.



295

296 **Figure 1:** (A) Map showing analogue climate loss in 2080 for the A1B emissions scenario. The size of the pie
 297 represents the area of each hotspot (note the smaller pie for Polynesia-Micronesia). (B) Map showing the proportion
 298 of endemic species threatened by loss of analogue climate under A1B scenario, in 2080. The size of the pie represents
 299 the number of species endemic to each hotspot. The right-hand graphs show the slight effect of latitude on climate
 300 change and on biodiversity loss, the smooth curve had been performed with a "loess" method and the confidence
 301 interval represents the standard error.

302

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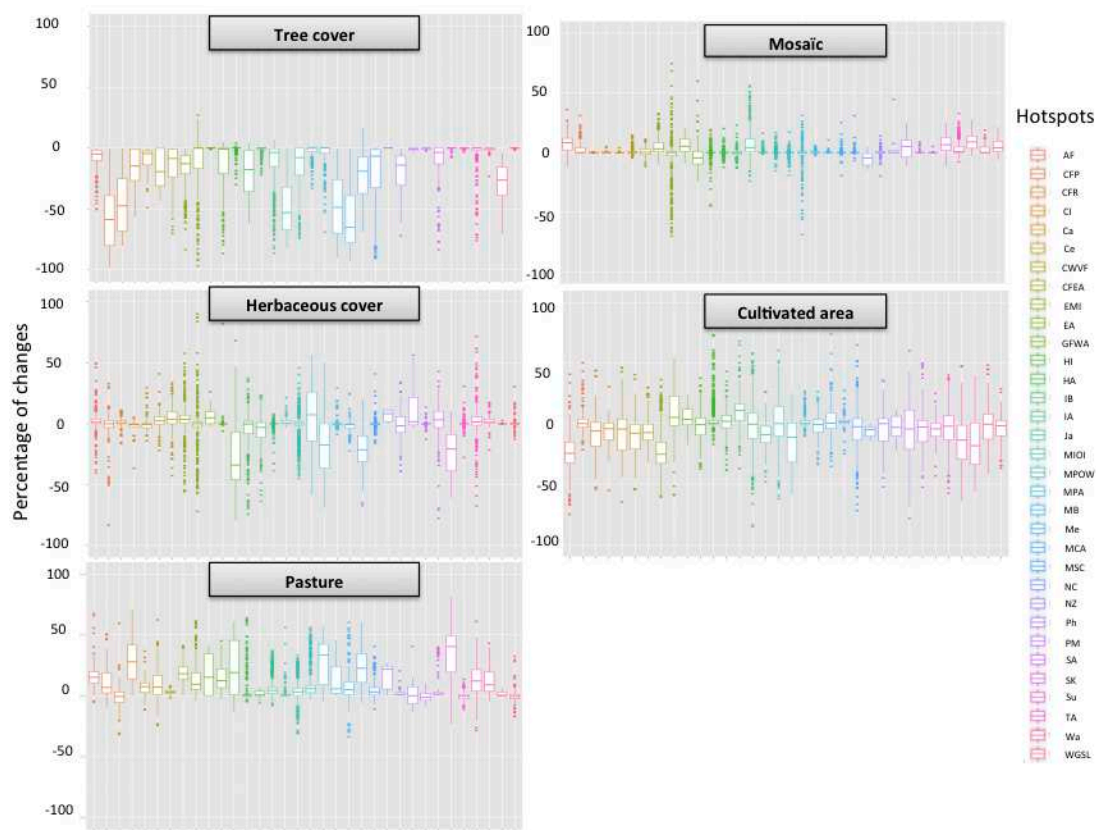
304

305 **Land use changes in the hotspots**

306

307 Globally, among the 12 different land use classes, only 5 classes showed major changes
 308 between current and future periods (Figure 2). Over the next decades, tree cover, herbaceous
 309 cover and cultivated area might decrease with -12.9% of their current cover, -2.32% and -
 310 5.06% respectively. On the opposite mosaic cover and pasture area might increase in the next
 311 decades with +2.16% and +9.77% respectively. Among them, California Floristic Region,
 312 Japan and Mesoamerica might lose at least 50% of their tree cover, New Caledonia 25% of its
 313 shrub cover and Himalaya 25% of its herbaceous cover. In addition, some hotspots showed an
 314 important increase (>25%) of their pasture cover (i.e. Caribbean islands, Maputaland-
 315 Pondoland-Albany and Succulent Karoo).

316



317

318 **Figure 2** Percentage of changes for six different classes of land use between the current and future (2080) period
 319 in term of tree cover, mosaic, shrub cover, herbaceous cover, cultivated area and pasture. Results here are for the A1B
 320 emission scenarios. Results for the B2A emissions scenario are given in Appendix Figure S3. Abbreviations are
 321 explained in Appendix section.

322

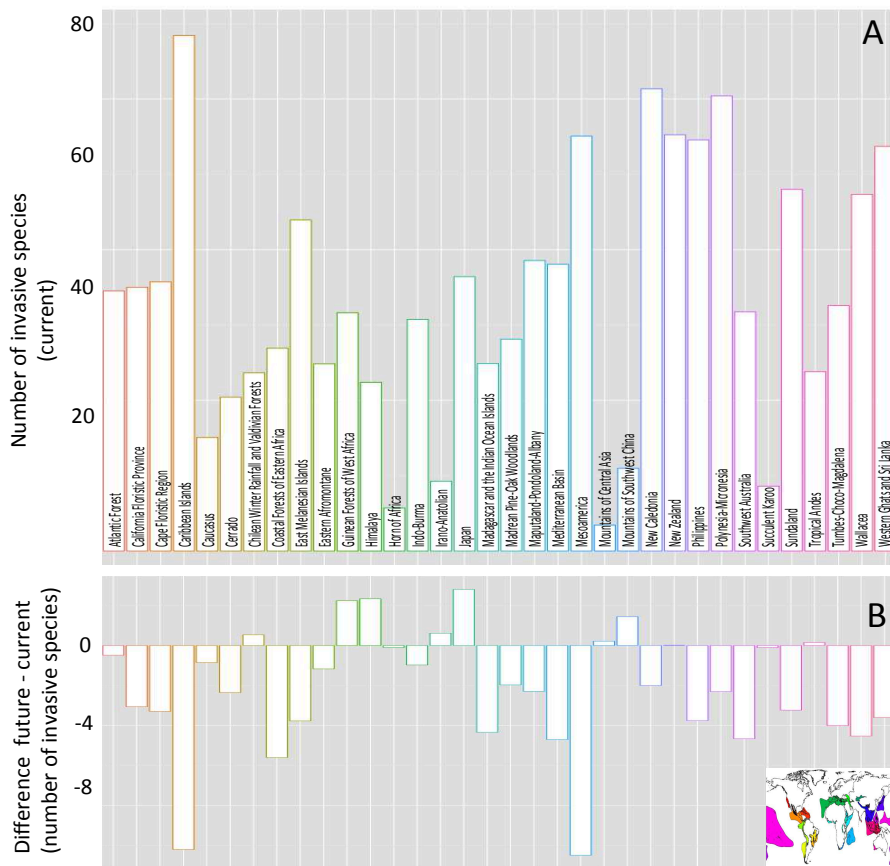
323

324 **Biological invasions in the hotspots**

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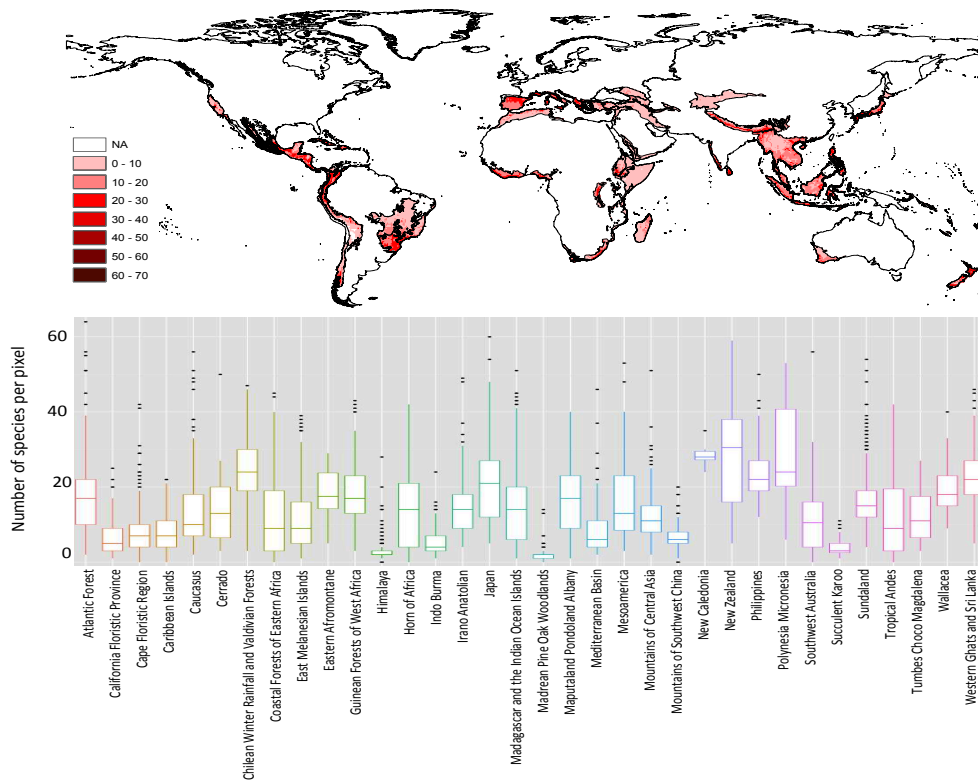
327 Results showed that all 34 hotspots are currently suitable for on average 16.8 ± 8.5 IAS (i.e.,
 328 invasion of at least one pixel of the hotspot) (Figure 3A) and these results are robust regarding
 329 AUC and TSS values (Figure S4). In particular, three hotspots were predicted to be
 330 potentially favourable to more than 30 IAS in the future: Caribbean islands, New Caledonia
 331 and Polynesia Micronesia (Figure 3AB). In the future, most of the hotspots will be suitable
 332 for fewer IAS, although the absolute number will remain very high (Figure 3B).



333

334 **Figure 3** (A) Average of the number of invasive species that have suitable climatic and land use conditions for the
 335 current period per hotspot. (B) Difference between the current and future (2080) periods in term of number of
 336 invasive species per hotspots. Results here are for the A1B emission scenarios.
 337

338 Surprisingly, Mesoamerica, Caribbean islands, Coastal Forests of Eastern Africa and
 339 Mediterranean Basin will probably be less threatened by 5 to 10 less IAS than they are
 340 currently. Both among and within hotspots, we found interesting spatial variations in areas
 341 potentially suitable to IAS, especially regarding the number of species finding suitable
 342 conditions (Figure 4A). Globally, the average number of IAS per pixel could vary from 2 (e.g.
 343 Mountains of central Asia) to 34 (e.g. Caribbean Islands). Although all hotspots were suitable
 344 for IAS, five hotspots were high even suitable: New Caledonia, Polynesia Micronesia, New
 345 Zealand, Caribbean islands, and Philippines in the future. Interestingly, those five hotspots
 346 were mainly islands or group of islands. However, the spatial variability within hotspots
 347 revealed important differences regarding the temporal trend in invasion risk. Much of Central
 348 America and South of Atlantic forest was likely to be increasingly at risk, as it was the case
 349 for the northern part of the Mediterranean basin, Southeast Asia and New Zealand. On the
 350 opposite, Mesoamerica was projected to be relatively less vulnerable in the future.
 351



352

353 **Figure 4** (A) Map representing the number of invasive species per pixel in the 34 hotspots by 2080. (B) Number
 354 of invasive species per pixel for the 34 different hotspots.

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357 **Discussion**

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Focusing on the regions of the planet of highest importance for biodiversity, our study revisited three major threats of global change (climate, land use change and biological invasions) to 34 biodiversity hotspots. Our study adopted an original global approach, with the analysis of (non)-analogous climates, of the changes in land use and in the vulnerability to the “100 of the worst invasive species in the world” IUCN list. Moreover, we considered three main drivers of biodiversity: climate changes, land use changes and biological invasions on the richest biodiversity region around the world. Our findings showed that climate change, land use change and biological invasions are likely to have all significant effects on biodiversity hotspots. Malcolm et al. (2006) already highlighted that global warming will significantly affect the 25 biodiversity hotspots, however they did not consider other main drivers of biodiversity. Specifically, we showed that climate dissimilarities will be more important in hotspots than in the rest of the world (Williams et al., 2007), hotspots will suffer from important land use changes and be suitable for at least twice as many IAS per pixel than the rest of the world, both currently and in the future.

373 One possible explanation for the high vulnerability of hotspots to IAS is that hotspots
374 are already highly disturbed, with only 30% of remaining primary vegetation and in the future
375 this trend will likely increase. Therefore IAS thriving in disturbed habitat may be particularly
376 favoured in biodiversity hotspots compared to other parts of the world less disturbed. In
377 addition, IAS have already been shown to have a devastating impact on island hotspots
378 (Steadman, 1995). On average, 16.8 ± 8.5 IAS were predicted to be able to invade at least one
379 part of any hotspot. Because some of these IAS are already present in many of the hotspots,
380 the decrease in the environmental suitability for IAS could offer new opportunities to manage
381 or eradicate some IAS in these places (Bradley *et al.*, 2009).

382 Besides, hotspots may experience significant loss in analogue climate in the future
383 (31%), this loss may be particularly important at low latitudes. In order to find the closest
384 suitable climatic conditions, species unable to adapt to the new conditions will have to
385 migrate further than 1000 km. Because some hotspots are coastal some species will be limited
386 by water and the loss of climate will have dramatic consequences if species are not able to
387 adapt rapidly. In addition, results showed that land use changes could particularly affect three
388 hotspots (*i.e.* California Floristic Region, Japan and Mesoamerica) that might lose at least
389 50% of their tree cover area. Our results were consistent for IAS and land use analyses
390 regarding the two CO₂ emission scenarios, whereas we observed some differences for
391 analogue climate analyses (see Supporting information).

392 The vulnerability of the 34 hotspots to the three main drivers of global change was
393 heterogeneous, with some hotspots clearly more at risk than others. Averaging the rank of
394 three different threats Caribbean islands, Western Ghats Sri Lanka, Polynesia Micronesia and
395 Mesoamerica were the most threatened hotspot (Table S8). During the past several thousand
396 years, the Pacific has already experienced more species extinction than any other region on
397 Earth (Steadman, 1995). Our results indicate that this region should be prioritized for
398 monitoring efforts and for future conservation actions. By including the number of endemic
399 species and the proportion of protected areas, we also provided an updated value of each
400 hotspot vulnerability with respect to their original definition: high levels of both biodiversity
401 and high level of threat (Mittermeier *et al.*, 2004). We highlighted that among the current
402 definition of biodiversity hotspots some should receive higher attention in the future. Based
403 on our results, Sundaland, Indo-Burma, Caribbean islands and Mesoamerica were the most
404 vulnerable hotspots taking into account both the number of endemic species harboured by the
405 hotspot and the proportion of protected areas (see Table S8). Indeed, these four hotspots were
406 the most exposed to climate changes, land use changes and biological invasion (averaging the

407 three different threats) and also the most vulnerable with the highest number of endemic
408 species and the lowest level of protection compared to the other hotspots. Of particular
409 interest in this regard is a comparison of our results with those from Malcolm et al. (2006)
410 studies (25 hotspots). Where Malcolm et al. (2006) highlighted Cape Floristic Region,
411 Caribbean islands, Mediterranean basin and Tropical Andes that were the most threatened
412 hotspots by global warming, we highlighted supplementary hotspots that were not identified
413 previously. Consequently, we provide strong evidences to the need to incorporate different
414 drivers of biodiversity and not only climate changes.

415 Although we tried to minimize the inherent uncertainties associated with our analysis,
416 not all possible uncertainties were accounted for. First, our study made the assumption that
417 the extent of analogous modern climate exerted strong influences on endemism and may lead
418 to an increase of the hotspot vulnerability regarding endemic species when such climates
419 change. However, the lack of current analogues for future climates limits our ability to
420 validate ecological model predictions (Williams et al., 2007), and the used endemic area
421 relationship remains coarse estimation of species that are susceptible to be affected in the
422 future. Particularly, because z values are known to vary across taxonomic groups (Horner-
423 Devine *et al.*, 2004), but we did not consider that into our analyses. Moreover, climate change
424 has occurred historically with glacial and interglacial cycles and all endemic species have had
425 to contend with this in the past. Therefore, some endemic species may be able to adapt to the
426 new conditions (Lavergne *et al.*, 2010).

427 In addition, our analysis of IAS potential distribution was based on correlative species
428 distribution models, thereby focusing on the climatic and land use suitable areas, and
429 overlooking propagule pressure, species introduction and biotic interactions associated with
430 their subsequent establishment. Therefore, we probably overestimated invasion that is likely
431 to occur (regarding these 99 IAS), especially because many of these invasive species may
432 never be introduced in some suitable areas. However, it is clear from both the high number of
433 IAS that may find suitable conditions and the high proportions of invaded area that such
434 impacts would lead to significant effects. Although species distribution models are classically
435 used for such studies, there are many caveats that limit the value of their quantitative
436 predictions (Gallien *et al.*, 2010; Araújo & Peterson, 2012) but see also (Warren, 2012). The
437 availability of presence data is a key constraint when using species distribution models. To
438 maximize the quality of predictions, we encompassed the entire range of each species,
439 comparing the distribution from many global databases and we included both the native and
440 invaded ranges of species (Gallien *et al.*, 2010). Although some spatial bias appeared in the

441 data collected (i.e. almost no IAS occurrences in north of Russia, North of Canada and west
442 of Sahara), globally the entire world was covered by the sampling effort (see Figure S7) and
443 all the hotspots were well covered by sampling effort, therefore results from these regions are
444 robust in this regard. Besides, we applied a modelling protocol that was robust (e.g. Araújo &
445 New, 2007; Thuiller et al., 2009) to limit the inevitable uncertainties associated with presence
446 only data and niche modelling techniques (Wiens *et al.*, 2009; Veloz *et al.*, 2012). Given the
447 extent of the study regions, simplifications were inevitable, and it was not possible to consider
448 other factors such as environmental factors (e.g. soil properties, pH), or human trade for IAS
449 (e.g. trade roads) at these spatial and time scales. The most important limitation with respect
450 to modelling IAS is that the models assume that species are in equilibrium with their
451 environment, which is not necessarily the case here. In addition, we only focused on the
452 suitability of hotspots to these IAS, but we did not consider the potential ecological impact of
453 these species. Yet, ecological impacts of IAS have been extensively studied and shown to be
454 in many cases important (e.g., Simberloff et al., 2012). There is no *a priori* reason to believe
455 that the impacts of these 99 species (which are among the worst of the world in terms of
456 impact) would be of less ecological magnitude for the hotspots than for ecosystems where
457 they have been assessed.

458 Despite these uncertainties, our assessments have profound consequences for
459 conservation among the biodiversity hotspots. Our analyses highlighted the urgent need to
460 explicitly incorporate global change (climate, land use changes and biological invasions) into
461 future conservation in the hotspots (Pressey *et al.*, 2007). More precisely, a paradigm shift to
462 first target the regions of greatest threat under global change and then to take into account
463 both biodiversity harboured by these regions and level of protection seems particularly
464 necessary. The three drivers of global change we studied here imply very different strategies
465 for conservation (Dawson *et al.*, 2011). Climate change is now inevitable and its effects on
466 biodiversity ought to be minimized, in part by facilitating native species movements to more
467 climatically suitable areas (Hodgson *et al.*, 2009). Establishing protected areas that remain
468 resilient to climate and land use change is a further challenge. Species movement may be
469 impossible in heavily fragmented habitat (especially on islands) and the rate and magnitude of
470 climatic changes is such that many endemic species may be unable to disperse quickly
471 enough. For the species concerned, translocate species to other locations where the climate is
472 suitable is maybe the latest solution (Thomas 2011). In addition, land use changes may both
473 complicate species movement through increasing fragmentation and facilitate establishment
474 of IAS through increasing disturbing habitats. In contrast, biological invasions are still

475 avoidable and the most efficient conservation actions have been shown to be introduction
476 prevention and rapid response (Simberloff et al., 2013).

477 To conclude, the threats posed by global change are clearly a concern for all 34
478 hotspots, with some of them highly vulnerable to global changes. We provide strong
479 evidences that the three drivers of global changes: climate changes, land use changes and
480 biological invasions will influence the future of the biodiversity hotspots. Because these
481 hotspots are already under dire threat of pollution, overexploitation and other causes of
482 biodiversity loss, our results must be considered holistically, as additional threat to these
483 fragile concentrations of biodiversity.

484

485

486 **Acknowledgments**

487

488 The article was written while the authors were supported by various grants, CB from the
489 CNRS (PhD contract), FC from the French “Agence Nationale de la Recherche” (ANR) with
490 the project RARE (2009 PEXT01001). WT received funding from the European Research
491 Council under the European Community's Seven Framework Programme FP7/2007-2013
492 Grant Agreement no. 281422 (TEEMBIO). BL was funded by the "Service du Patrimoine
493 Naturel" (SPN, MNHN, Paris). We thank Gloria Luque for constructive criticism on an earlier
494 version of the manuscript. We would acknowledge all the people that sent us useful
495 information and precise data for the “*100 of the world's worst invasive species*”, all the names
496 are reported in Table S3. All co-authors have no conflict of interest to declare.

497

498 **Biosketch**

499 Céline Bellard works on the effects of global change (e.g. climate change, invasive alien
500 species) on the future of biodiversity at a global scale. This paper formed part of her PhD
501 research at the University of Paris Sud.

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Conclusion

Dans ce chapitre nous avons analysé l'exposition des hotspots aux changements climatiques, aux changements d'utilisation des sols et aux 100 espèces invasives. Nos résultats ont permis de mettre en évidence que ces trois menaces pourraient avoir des conséquences importantes sur les hotspots de biodiversité, mais de façon hétérogène. Par exemple, la Polynésie-Micronésie est le hotspot le plus exposé à une perte de climat analogue, alors que la Nouvelle-Calédonie présente des conditions favorables à un nombre important d'espèces invasives dans le futur. Ces résultats ont également permis d'établir que le Sondaland, l'Indo Burma, les îles caribéennes et la Méso-Amérique sont les hotspots qui sont les plus exposés à ces menaces, mais également les plus riches en terme de biodiversité endémique et les moins protégés. En conclusion, ces hotspots doivent être des priorités de recherche et de conservation dans le contexte des changements climatiques.

Cependant, cette analyse a uniquement permis de mettre en lumière des hotspots qui risquent d'être exposés à des menaces supplémentaires à l'avenir. En général, la conservation s'opère à une échelle locale. Il est donc nécessaire d'évaluer les effets des changements climatiques à une échelle plus fine afin de proposer des recommandations de stratégies de conservation pertinentes et efficaces.

Chapitre 7

Direct and indirect effects of climate change on the 35th hotspot : Forest of East Australia

Résumé

Le changement climatique dont la hausse du niveau des mers représente une menace directe pour la biodiversité. De plus, les conséquences secondaires des changements climatiques et de la hausse du niveau des mers tels que les déplacements humains vont également avoir des conséquences importantes pour la biodiversité. Ainsi, déterminer les conséquences directes et indirectes des changements climatiques sur des régions extrêmement riches en biodiversité est essentiel pour mettre en œuvre des stratégies de conservation efficaces. Dans ce chapitre, nous avons évalué la part d'habitats inondés en raison de la hausse du niveau des mers dans le 35^{ème} hotspot de biodiversité, qui vient d'être défini (*i.e.*, Les forêts de l'est Australien). Nous avons également évalué les conséquences des changements climatiques dans ce hotspot en utilisant des analyses de climats analogues. Finalement, nous avons quantifié la superficie des classes d'occupation des sols et la taille de la population humaine qui sont susceptibles d'être affectées dans le futur par ces changements climatiques. Ainsi, nos résultats ont révélé que le changement de climat local affecterait près de 100 000 km² de la superficie du hotspot et que près de 58 000 personnes pourraient être contraintes à la migration en raison d'une hausse du niveau des mers d'un mètre. Finalement, nous avons proposé des stratégies complémentaires de conservation qui pourraient être mis en place afin de limiter les conséquences des changements climatiques sur la biodiversité mais aussi sur l'agriculture.

Cette partie correspond à l'article en préparation suivant:

C. Bellard, C. Leclerc, B. Hoffman & F. Courchamp Direct and indirect effects of climate change on the 35th hotspot : Forests of East Australia.

Effects of climate change on the 35th biodiversity hotspot

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Key word: biodiversity hotspots, climate changes, sea-level rise, land use, human displacement

Abstract

Aim Climate change including sea-level rise is likely to become the most important direct threat for biodiversity. Secondary consequences of climate change to agro-ecosystems and displacement of people will also affect the future of biodiversity. As such, understanding the consequences of climate change within rich biodiversity regions should be a high priority for researchers and managers alike. Here, we provide for the first time a comprehensive evaluation of the potential effect of climate change including the secondary consequences on environmental systems.

Location The 35th biodiversity hotspot: The forests of East Australia

Methods We assessed the area submerged using precise digital elevation model under two scenarios of projected sea-level rise (1 and 2m). We also quantified standardized Euclidian Distances between current and future climates to determine future climate change throughout the hotspot. We subsequently quantified the secondary consequences of climate change on land use classes and the human population.

Results Local climate change was found to have the greatest influence occurring over almost 100 000 km². Sea-level rise affected only 860 km², but displacing about 60,000 people. Local climate change and sea-level rise mainly affected the *Conservation and natural environment land use* and *Production from dryland agriculture and plantation* classes. Overall, half of the hotspot area had high species richness and low protection.

Main conclusion Given the extent of projected climate change, considerable pro-active and adaptive conservation strategies are required to minimise negative conservation implications. In particular, research and conservation strategies should focus on the north and south of the hotspot, as these areas will be particularly exposed to climate change. Finally, as climate change inevitably progresses, the balance between the needs of society and environment will need to be refined regionally to ensure sustainability.

Introduction

Global changes, from habitat loss and biological invasions to climate change, have initiated the sixth great mass extinction event in Earth's history (Barnosky et al., 2011). Among these, climate change, which involves changes in temperature, precipitation, ocean acidification and sea-level rise, is likely to become the most important direct threat for biodiversity (Pereira et al. 2010; Bellard et al. 2012). Indirectly, climate change may also affect biodiversity by altering existing threats, such as by modifying the distribution and abundance of invasive alien species (Hellmann et al., 2008; Walther et al., 2009; Bellard et al., 2013a). All biomes will be influenced by climate change (Williams et al., 2007), and although many species will be able to adapt to climate change effects, many others are likely to go extinct (Bellard et al. 2012), resulting in biodiversity impoverishment. Secondary consequences of climate change will also affect regional biodiversity, notably from changes to agro-ecosystems (Fischer et al., 2005; Hannah et al., 2013), and displacement of people (Wetzel et al., 2012). Such changes place added pressure on conservation and underdeveloped areas by shifts in exploitation and subsequent additional environmental degradation.

Part of the adaptation process of biota to climate change is the ability to disperse to new locations if the local environment becomes unfavourable. Unfortunately most of the world's conservation zones are highly fragmented. This is a consequence of historical conservation areas being based solely on the protection of remnant habitats or particular species (Williams et al., 2011). Only more recently has the concept of connectivity between conservation zones become a focus to allow movement of species among regions. Moreover, connectivity is particularly salient in response to climate change (Hodgson et al., 2009). However our understanding of the consequences of climate change, and therefore the conservation needs in the future remain highly rudimentary, leaving high levels of uncertainty for making conservation planning and management decisions.

Coastal dunes and insular regions are predicted to be among the first environments affected by climate change (Feagin et al., 2005). Some biodiversity hotspots appear to be also highly vulnerable to climate change, especially to sea-level rise (Malcolm et al., 2006; Bellard et al., 2013a, 2013b). Biodiversity hotspots harbour an exceptionally high number of endemic vascular plant species (over 164,200 endemic species) and they are already extremely threatened (Mittermeier et al., 2004). As such, understanding the consequences of climate change within these regions should be a high priority for researchers and managers alike

(Schmitt, 2011). Yet, we are unaware of any study that has simultaneously assessed the potential direct and indirect effects of climate change including the secondary consequences on any environmental system.

One such region that both could be highly susceptible to climate change but has great capacity for effective conservation management is the newly identified 35th biodiversity hotspot “Forests of East Australia”. This entity occurs along a discontinuous coastal stretch of Australia’s east coast and also incorporates eight islands (Figure 1A, S1). Only 23% of its natural habitat remains, but a wide range of environments still harbour many endemic species, including at least 2,144 plants, 28 birds, 70 reptiles, 10 freshwater fish, 38 amphibians and 6 mammals (Williams et al., 2011). The human population has a rapidly increasing influence within the hotspot, with a population of over nine million in 2006, and an average population density of 36 people per km², mainly concentrated along the coast. The predominantly coastal and fragmented nature of this hotspot, combined with a growing population, suggests a potentially high vulnerability to the effects of climate change.

Here, we provide for the first time a comprehensive evaluation of the potential effects of climate change, using the new 35th biodiversity hotspot as a case study. Specifically, we quantify (i) the hotspot vulnerability to sea-level rise; (ii) the exposure of the hotspot to “local climate change”, defined here as predicted climate change within each study unit (pixel) and (iii) the secondary consequences of climate change on land use classes and subsequent human population displacement. Because most conservation planning and actions are established without considering future climate changes, we further aimed to establish priorities throughout the hotspot under climate change threat. In particular, we identify areas of greatest biodiversity value that have low protection levels, and are highly vulnerable to future threats.

Materials & Methods

Forests of East Australia

Approximately 58,900 km² (23%) of the hotspot comprises primary vegetation. A total of 165,400 km² (65%) is under some form of production land use (see Table S1 for the land use classifications and sources). This includes 13,700 km² (8.3%) of *Intensive* land use, 70,400 km² (42.6%) of *Production from dryland agriculture and plantations* land use, 5,700 km² (3.4%) of *Production from irrigated agriculture and plantations* land use and finally 75,600 km² (45.7%) of *Production from relatively natural environments* land use (Williams et al., 2011). A combined total of about 46,600 km² (18.41%) of the land area is protected within IUCN protected area categories I-VI: about 15,800 km² (6.24%) within category I (*i.e.*, Strict

Nature Reserve), 2,200 km² (9.96%) within category II (*i.e.*, National park), about 200 km² (0.09%) within category III (*i.e.*, Natural Monument), about 100 km² (0.04%) within category IV (*i.e.*, Habitat/species Management Area), about 100 km² (0.04%) within category V (*i.e.*, Protected Landscape) and about 5,200 km² (2.04%) within category VI (*i.e.*, Managed Resource Protected Area).

Sea-level rise

We quantified the hotspot's vulnerability to 1m and 2m sea-level rise by determining the land area (including standing fresh water such as rivers, lakes, wetlands and associated habitat) that will be submerged by sea water. The scenarios of 1m and 2m are concordant with recent projections of future sea-level rise (Overpeck et al. 2006; Rahmstorf 2007; Pfeffer et al. 2008; Grinsted et al. 2009; Nicholls & Cazenave 2010). Hotspot elevation data were obtained from the digital elevation model from NASA's shuttle radar topography mission (Jarvis et al., 2008). We calculated the area of land loss due to inundation using the same methodology that had been used in (Bellard et al., 2013b). In brief, we used the extract function from the raster package for the hotspot and his eight associated islands in order to assess the vulnerability of each pixel to the sea level rise. Some areas with elevations below the projected sea-level rise are already inland water bodies and therefore should not be included in the calculations of newly inundated areas. To overcome this shortcoming, we first considered only cells below a projected sea-level rise that are initially flooded. Then we only considered flooded cells that connected to the ocean.

Climate change

Data

To determine areas that would experience climate change, we compared current climates with simulations of future climates. Current climatic data, being data averaged from 1950-2000, were obtained from the Worldclim database (Hijmans et al., 2005) at 10' resolution. We used six different climate variables linked to temperature and precipitation that we assumed to provide a combination of means, extremes and seasonality of climate following the methodology of Bellard et al., (2013b). The climate variables were annual mean temperature, maximum temperature of warmest month, minimum temperature of coldest month, annual precipitation, precipitation of wettest month and precipitation of driest month. Future climate data were extracted from the Global Climate Model data portal (Global Climate Model, 2013) at the same 10' resolution (Ramirez-Villegas & Jarvis, 2010). Simulations of future climate

were based on three general circulation models (HADCM3, CSIRO2 and CGCM2), with data averaged from 2070 to 2099. We used two CO₂ emission scenarios (B2A, A1B), being a low and a high emission scenario respectively, to capture the range of potential climatic outcomes. These scenarios reflect different assumptions about demographic, socio-economic and technological development on greenhouse gas emissions (Solomon et al. 2007).

Climate analog analysis

We used the methodology developed by Williams et al., (2007) to quantify climate dissimilarities (*i.e.*, Standardized Euclidean Distances, SED) between current and future climates within the hotspot, as follows:

$$SED_{ij} = \sqrt{\sum_{k=1}^6 \frac{(a_{kj} - b_{ki})^2}{s_{kj}^2}}$$

where a_{kj} and b_{ki} are the current and future means for climate variable k at grid points i and j , and s_{kj} is the standardized current climate value. The standardization values were temperature seasonality for temperature variables and precipitation seasonality for precipitation variables. Standardizing each variable places all climate variables on a common scale (Veloz et al., 2012). High SED values correspond to high climate dissimilarities between two periods and potentially indicate novel or disappearing climates. For more details about the method see (Williams et al., 2007; Veloz & Williams, 2011).

We calculated a SED threshold (SED_t) for the hotspot to discriminate the limit above which the climate was no longer considered analogous to current conditions (*i.e.*, climate loss). SED_t was determined by comparing the distribution of SED values between the hotspot and the rest of the world for the current period. We used the Receiver Operating Characteristic to determine the SED_t value that provides the optimal separation within- and between-surface histograms (Oswald et al., 2003). Therefore, the SED_t is associated with an evaluation of the threshold (*i.e.*, Area Under the Curve, AUC). We obtained an AUC value of 0.714, which represents a good evaluation measure.

Using the SED_t , we calculated three indices of climatic change. First, we calculated the SED between the current and future climate data for each grid point (an index of the intensity of local climate change). Then we calculated the SED between the future for each hotspot grid point and its closest analogue from the global pool of current climates (an index of the novelty of future climates, with no contemporary analogue globally), and we calculated the SED between the current climate for each hotspot grid point and its closest future climate analogue

(an index of disappearance of extant climate, being contemporary climate conditions that have no future analogue globally).

Secondary consequences of climate change and sea level rise

We quantified the secondary consequences of climate change due to inundation or loss of analogous climate on land use classes (and their sub-classes) and human population displacement. Spatial analysis of percentage of land use and land cover classes affected by climate change and sea-level rise was based on the Australian catchment-scale land use map, which is the latest national-scale land use map of Australia (ALUM, 2010). We used the classification based on the Australian Land Use and Management Version 7 at 50m resolutions (ALUM, 2010). For each affected area, we calculated the proportion of each land use class and subclass, including protected areas. Human population density data was sourced from the gridded population of the world version 3 (CIESIN, 2013).

Species richness and protection analysis

We explored the relationship between type of protected area and species richness using a bivariate plot at 0.5° resolution. Species occurrence data recorded between 1990 and 2010 were sourced from the Atlas of Living Australia database for 18,414 species from 7 different taxa: amphibians, N=119; arthropods, N=5531; fish, N=1098; mammals, N=218; molluscs, N=923; plants, N=10,267 and reptiles, N=258 (Atlas of Living Australia, 2013). Species richness ranges from 0 to 943 species per pixel in the hotspot, all taxa combined, with a median species richness at 53 species. In the few instances where pixels contained no data on species, we retained such data because removing them could lead to overestimation of the species richness affected by climate change. We classified “low species richness” as ≤ 53 species and “high species richness” when there were > 53 species. “Low protected area” was defined as unprotected area, other minimal use and IUCN protected area categories V and VI, while “high protected area” was defined as IUCN categories I, II, III and IV.

Results

Sea-level rise

In total, almost 890 km² (0.26%) of the hotspot’s land area would be permanently inundated with a 1 m sea-level rise, increasing to 1,980 km² (0.59%) with a 2 m sea-level rise, with water intrusion reaching up to 35 km inland (Figure 1C). Consequently, around 58,000

(0.69%) to 62,000 (0.74%) people would be displaced, especially around Grafton, Port Macquarie and Taree (Figure S2 and Table S2). All of the eight islands would have no more than 4% of area inundated per island.

Climate change

In total, 98.35 and 100% of the existing climates throughout the hotspot were predicted to persist in the future under the A1B and B2A scenarios respectively. The fraction of land area with a novel climate (previously not occurring anywhere within the hotspot) was only 1.65%. However, persistence of climates did not necessarily mean that such climates were predicted to remain in the same areas. Indeed, significant change of climates was predicted to occur, with local climate change forecast over 40.61% and 10.27% under the A1B and B2A scenarios respectively. Local climate change was strongly concentrated in southern New South Wales and north Queensland under the A1B emission scenario (Figure 1B); the same was so for the local loss of climate for both scenarios (Figure S3).

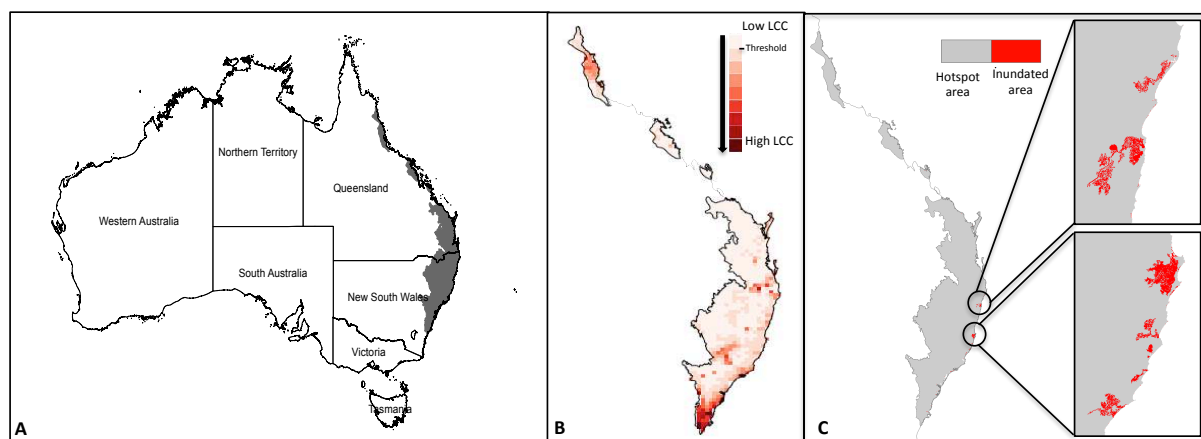


Figure 1 The hotspot and its exposure to climate change. (A) Localization of the Forests of East Australia hotspot (black area). (B) Indices of local climate change (LCC) for the A1B scenario, represented by the standard Euclidian distance between the current and future climate predictions for each grid point (see main text for details). The threshold represents the value at which the climate is significantly different from the current climate found in the hotspot (i.e., non analogous climate). (C) Areas predicted to be permanently under water with 2m sea-level rise.

For any point in the hotspot, the mean geographic distance to the closest analogue climate was predicted to become twice as far than it is currently, from 145 km to 322 km under the A1B scenario by 2100 (Figure S4). Overall, 1 to 5 million people (15 and 59% of the hotspot population) will be affected by significant climate change according to the emission scenarios (Table S2).

Secondary consequences of climate change and sea level rise

Considerable areas of the land use class *Production from dryland agriculture and plantation* 233 km² (36.47%) and 652 km² (45.37%) were projected to become inundated following 1 and 2 m sea-level rise respectively, similarly so for *Water*, with 293 km² (45.89%) and 524 km² (36.47%) respectively (Figure 2). The most affected sub-classes of *Production dryland agriculture and plantation* were mainly *Native and exotic pasture mosaic* and *Cropping*, and those for *Water* were *River and Marsh and wetland* (see Table S3). About 81 km² (12.68%) and 149 km² (10.40%) of the *Conservation and natural environments* land use class was projected to be submerged under the 1 and 2m scenarios respectively. In contrast, only 27 km² (4.3%) and 72 km² (5.03%) of the inundated areas were of the *Urban or agricultural* land use class under the two scenarios respectively.

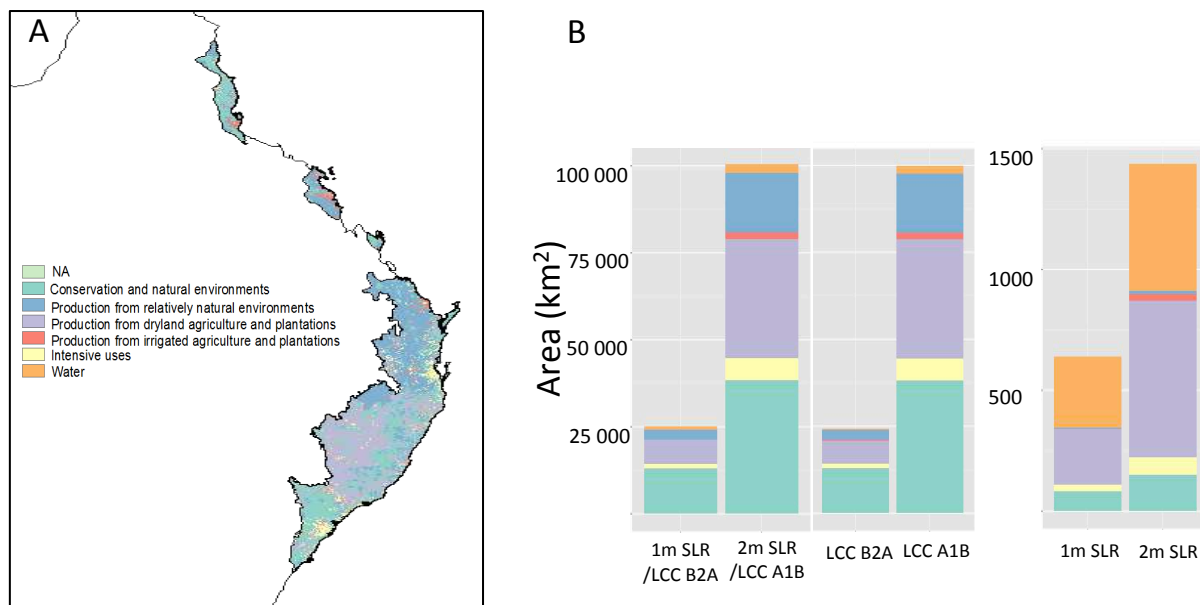


Figure 2 (A) Map of the hotspot with the six different land use classes: Conservation and natural environments, Production from relatively natural environments, Production from dryland agriculture and plantations, Production from irrigated agriculture and plantations, Intensive uses and Water. (B) Land area (km²) of the land use and cover classes predicted to be affected by local climate change and sea-level rise under two scenarios A1B (2m sea-level rise) and B2A (1m sea-level rise).

The land use class of *Conservation and natural environment* was projected to experience greatest local climate change, with 13,003 km² (53.26%) and 38,222 km² (38.32%) affected under the B2A and A1B emission scenarios respectively, predominantly within the sub-classes of *National park* and *Residual native cover* (Table S3). The next most affected land use class was *Production from dryland agriculture and plantations*, with 6,670 km² (27.32%) and 34,150 km² (34.24%) respectively, predominantly in the *Native and exotic pasture mosaic* (Table S3). Significant local climate change was also predicted to affect 2,942 km²

(12.05%) and 16,941 km² (16.98%) respectively of the land use class *Production from relatively natural environments* (Table S3).

Overall, combining local climate change and sea-level rise, *Conservation and natural environment* was the most affected land class (13,080 km² (52.41%) and 38,319 km² (38.15%)) under the combined 1m/B2A and 2m/A1B scenarios respectively (Figure S5, Table S4). The next most affected land use class was *Production from dryland agriculture and plantations* (6,841 km² (27.41%) and 34,365 km² (34.22%) respectively), followed by *Production from relatively natural environments* (2,946 km² (11.8%) and 16,956 km² (16.88%) respectively) (Table S4).

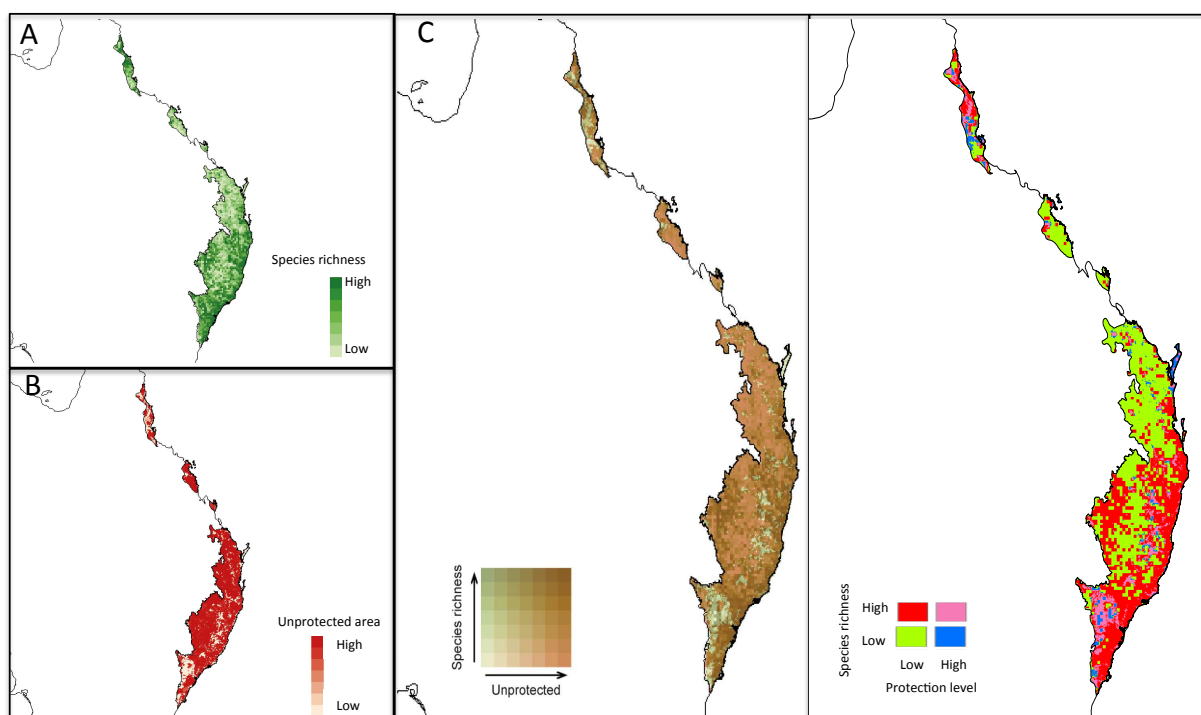


Figure 3 Species richness and protection levels in the hotspot. (A) Species richness. (B) Protection levels. (C) Bivariate plot of species richness and protection levels. (D) Map showing areas according to their species richness and protection levels. Areas in red are those with a low protection level and high species richness.

Species richness and protection analysis

Over the entire hotspot, we observed a high regional variation of species richness (Figure 3A). The level of protection was relatively low, with 87% of the area unprotected (i.e., IUCN categories V and VI, Strict unprotected area and other minimal uses). Regions with the lowest protection level and low species richness were mainly concentrated in inland Queensland and New South Wales (Figure 3C,D). The regions containing the highest species richness and having the lowest protection were north Queensland, southern New South Wales and coastal

New South Wales (Figure 3C,D). The two former of these regions were also among the most affected by local climate change.

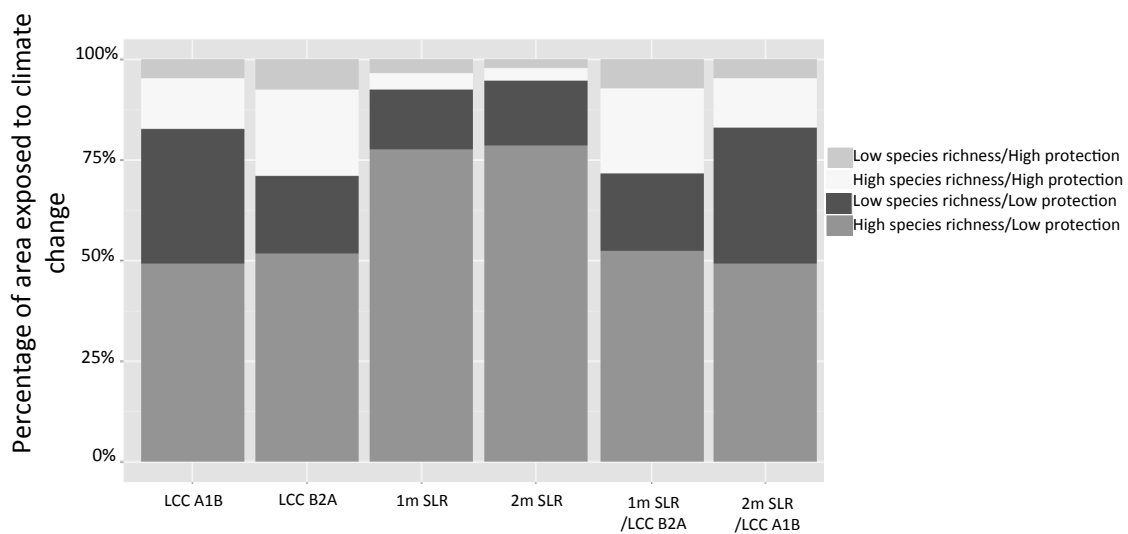


Figure 4 Percentage of area exposed to local climate change (LCC, under A1B or B2A scenarios) or sea-level rise (SLR, under 1m or 2m sea-level rise) for combinations of protection level and species richness.

More than 75% of the area affected by sea-level rise was in regions with high species richness and low protection. Local climate change also affected mainly high species richness and low protection area: 49% and 52% affected under the A1B and B2A scenarios respectively. Local climate change also affected 12% and 22% of areas with high species richness and high protection in the A1B and B2A scenarios respectively.

Considering all components of climate change simultaneously, areas with low protection and high species richness comprised 50% or more of the total affected area in all scenarios, followed by areas with low protection and low species richness, which ranged between 19 and 34% of the total affected area (see Figure 4-Table S5).

Discussion

The Forests of East Australia hotspot has been recently identified based on historic perturbations such as land clearing (Williams et al., 2011). This study has clearly shown that future issues such as climate change are also likely to have significant consequences for this hotspot.

Three key points of climate change effects on the hotspot can be drawn from the results. First, local climate change was predicted to be widespread, occurring over a combined area of approximately 100 000 km², predominantly in the far north and south. Unlike other hotspots,

which are predicted to be subject to significant levels of inundation from sea-level rise (Bellard et al., 2013a), this hotspot will only lose 890 km² to sea-water intrusion under the 1m scenario, concentrated in the coastal southeast. So from a biodiversity management perspective, conservation action requirements will be greatest for local climate changes rather than habitat inundation.

Second, the great extent of local climate change will mainly in natural areas (e.g., National park), of which about 50% currently has low protection. Most likely, some species will be able to adapt into these new climate conditions through spatial or physiological changes (Lavergne et al., 2010), as is already being recorded (Peñuelas et al., 2013), but many other will not (Bellard et al., 2012a). Furthermore, the effect of climate change will also occur on primary production land areas. This finding would merely involve a change in both productivity and production type throughout the existing production areas. For example, current research confirms that crops would respond positively to elevated CO₂ in the absence of climate change (e.g. Ainsworth & Long, 2005), but the associated impacts of high temperature, changes in precipitation, and possibly increased frequency of extreme climatic events, will probably depress yields and increase production risks (Fischer et al., 2005). Besides, land use conversion could result in greater loss of remnant habitat as some land use areas will need be moved to other areas. Habitat loss due to agricultural conversion and activities is already the greatest threat affecting species in the eastern of Australia (Evans et al., 2011), and climate change impacts are likely to exacerbate this issue.

Third, despite the relatively small area anticipated to be inundated by sea-level rise, this change will displace at least 58,000 people (at current population figures). Inundated area will occur predominantly (about 75%) from land with high species richness and low protection. The consequences here are twofold. First, although nothing can be stated about where these people would translocate to, ultimately the translocation process would place at least some additional conservation pressure throughout the remaining hotspot area, including additional remnant habitat loss. Second, there are likely to be numerous species whose distributions are entirely or predominantly within the projected inundation zones.

There are important caveats to our approach that need to be addressed. First, the direct and indirect impacts of climate change were found to be dependent upon CO₂ emission scenario, showing the high importance to consider different emission scenarios. When assessing the impact of climate change on land use patterns, we also assumed that in the future years, they would remain spatially the same as currently, which is not necessarily the case. We also expected that land area below sea-level rise will be inundated, although a low increase in sea-

level can be balanced by sediment supply and morphological adjustments (Webb & Kench, 2010). However, an increase of sea-level by one meter should not be compensated by these physical responses. Moreover, species richness may not provide the best illustration of global biodiversity to assess the effects of direct and indirect effects of climate change in general as we did not consider directly genetic, functional or ecosystem diversities. However, species richness is useful to compare between different sites and conservation schemes and allows us to establish some prioritizations. Although areas with low species richness may still have high importance for biodiversity, because they can harbour highly threatened species, endemic species, or highly ecosystem value.

Overall, we identified specific regions of the hotspot that were predicted to be highly affected by climate change, this provide a strong basis to focus research directions and management actions to minimise potential negative consequences of climate change for biodiversity and agriculture (Howden et al., 2007; Mawdsley et al., 2009; Gillson et al., 2013). From the main findings here, we recommend three priority conservation actions for the hotspot.

First, greatest conservation benefits would be obtained by increasing the conservation status of areas in the northern and southern extremities of the hotspot. These regions contained the highest species richness, but had the lowest protection and were among the areas most affected by local climate change. However, established protected area may not be sufficient to save species from climate change, we can also expect a high need for species to move. Ultimately, greater conservation outcomes will be achieved by increasing the area of conservation zones, particularly for currently low protection areas with high species richness, or containing species of conservation concern.

Second, to accommodate the great number of species range shifts likely to occur throughout the hotspot, there will need to be greater connectivity of conservation zones (Hodgson et al., 2009), particularly north-south. However some species disperse slowly and many are not able to cross natural and human-created barriers (Broennimann et al. 2006), and intervention like assisted translocation may be required (Thomas, 2011). Determining which species will and will not require intervention, and if such intervention is possible or feasible will increasingly need to become a proactive management action. The science and risk management of species translocations and conservation introductions is rapidly maturing, and guidelines exist to inform the process (IUCN, 2012; Harris et al., 2013).

Third, greater preparedness for change will reduce long-term climate change issues. For example, major threat for this hotspot also include invasive alien species and habitat

fragmentation as almost two thirds of Australia's threatened species are impacted by introduced plants or animals (Evans et al., 2011) and invasive alien species will also be affected by climate change (Hellmann et al., 2008). However it remains unclear if these species will be promoted or disadvantaged (Bellard et al., 2013c), thus such research should also be a priority. Furthermore, this work has clearly shown that some specific land uses within the hotspot will experience change within a relatively short time, so planning for changed climate conditions should be a management priority. Proactively, this would involve incorporating suitable future land usage in current land management and infrastructure development, especially for agriculture, and making such planning at broad regional levels, not just locally. Such a governance reform away from short-term and sectoral management to long-term regional management is in-line with Australia's major environmental strategy (Natural Resource Management Ministerial Council, 2010).

To conclude, our study provides further evidence that sea-level rise and local climate change will have major consequences for biodiversity, agriculture and human migration. As climate change inevitably progresses, the balance between the needs of society and environment will need to be refined regionally to ensure sustainability. Moreover, our results suggest that vulnerable area to direct and indirect effects of climate change are mainly insufficiently protected. If we are to prevent massive species loss, the need for suitable conservation and sustainable development is also essential in the biodiversity hotspots. Finally, because conservation planning under future threat has mostly escaped the attention of previous evaluation, there is an urgent need to include direct and indirect effects of climate change on biodiversity, agriculture and society in future conservation planning.

Acknowledgments

The article was written while the authors were supported by various grants, CB from the CNRS (PhD contract), FC from the Biodiversa EraNet FFII project.

Contribution

C.B., C.L. and FC conceived the ideas. C.L. and C.B. analysed the data. C.B. wrote the first draft of the manuscript and C.L., B.H. and F.C. wrote and commented on the manuscript.

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Conclusion :

Dans ce chapitre, nous avons étudié l'effet direct et indirect du changement climatique sur les forêts de l'est australien que représente le 35^{ème} hotspot de biodiversité. Tout d'abord, nous avons montré que le changement de climat local affecterait une part importante de la superficie de ce hotspot, au contraire de l'élévation du niveau des mers. Pour autant, les conséquences secondaires de la hausse du niveau des mers pourraient être particulièrement importantes pour les populations humaines, avec près de 58 000 personnes potentiellement à déplacer. En outre, les zones d'habitat naturel et les zones d'agriculture seront les classes d'occupation des sols les plus affectées par le changement climatique. Au sein de ce hotspot, nous avons identifié que les extrémités nord et sud du hotspot seraient particulièrement exposées et vulnérables au changement climatique car ces régions ne sont actuellement que peu protégées. Des mesures de protection et d'adaptation aux changements climatiques devront donc être mises en places dans ces régions. Ainsi, nous avons proposé trois stratégies complémentaires de conservation qui pourraient être mises en place afin de limiter les conséquences des changements climatiques sur la biodiversité, mais aussi sur l'agriculture. Ces stratégies comprennent l'augmentation des aires protégées au sein de ce hotspot mais également la mise en place de corridors biologiques afin d'améliorer la connectivité au sein du hotspot. En outre, si la biodiversité n'est pas capable de s'adapter et de migrer vers des régions plus favorables, des mesures de translocation pourront être envisagées.

Cet article a deux implications importantes. Premièrement, il a permis d'illustrer que les conséquences secondaires du changement climatique et notamment de la hausse du niveau des mers pourraient être plus importantes que les effets directs de cette menace. Ensuite, cet article a permis d'illustrer que ce type d'approche est utile pour mettre en avant les régions qui méritent une attention particulière dans le cadre des changements climatiques.

6. Synthèse, limites, implications et perspectives

6.1.SYNTHESE GÉNÉRALE

La biodiversité mondiale est aujourd'hui extrêmement menacée en raison de la perte d'habitat, de la pollution, de la surexploitation, des invasions biologiques ou encore de la synergie de ces différents facteurs. En effet, sur les 65 518 espèces évaluées par l'UICN, plus d'un millier sont considérées comme déjà éteintes ou probablement éteintes et pas moins de 20 219 sont considérées comme menacées (IUCN, 2013). En plus des menaces précédemment citées, certaines études récentes ont montré que l'ensemble des niveaux de la biodiversité pourrait être concerné par les changements climatiques (Pereira *et al.*, 2010; Maclean & Wilson, 2011; Bellard *et al.*, 2012;Peñuelas *et al.*, 2013). Bien qu'aujourd'hui les extinctions d'espèces attribuées exclusivement aux changements climatiques soient rares (voir l'exemple des amphibiens du Costa Rica, Pounds et al., 2006), il apparaît évident que les effets des changements climatiques sur la biodiversité seront considérables dans un futur proche. C'est pourquoi il est important de quantifier dès aujourd'hui, les effets potentiels de cette menace, afin de pouvoir prévenir ses effets et de mettre en place des mesures de gestion et de conservation nécessaires. Les études sur l'effet des changements climatiques n'en sont qu'à leurs débuts et de nombreuses questions restent posées (voir partie 1). C'est dans ce cadre que s'inscrit ce travail de thèse. En effet, comme mentionné dans l'introduction, **l'objectif principal de ce travail a été d'améliorer la caractérisation et la quantification des différents impacts des changements climatiques sur la biodiversité à l'échelle mondiale par des approches de modélisation et de méta-analyses.**

Afin de répondre à cet objectif, cette thèse a été construite en trois parties dont les objectifs étaient respectivement :

- (1) De considérer certaines conséquences potentielles de la hausse du niveau des mers;
- (2) D'étudier les effets conjugués des changements climatiques et des changements d'utilisation des sols sur les invasions biologiques et
- (3) D'inscrire les études des changements climatiques dans une perspective de conservation en se focalisant sur les hotspots de biodiversité. Dans la suite, je vais synthétiser les principaux résultats de ces trois parties puis je vais discuter des avancées et limites des différentes méthodologies utilisées dans cette thèse, et enfin dans une dernière partie je discuterai des implications des résultats et des perspectives de ce travail de thèse.

6.1.1. LES EFFETS DE LA HAUSSE DU NIVEAU DES MERS

Dans la seconde partie de cette thèse, nous avons étudié l'effet de l'élévation du niveau des mers dans les habitats insulaires. Les études actuelles ont estimé que la hausse du niveau des mers devrait atteindre au minimum un mètre d'ici la fin du siècle (Rahmstorf, 2007; Pfeffer *et al.*, 2008; Grinsted *et al.*, 2009). Plusieurs études à l'échelle mondiale (Menon *et al.*, 2010; Hinkel *et al.*, 2010) se sont intéressées à l'influence de l'élévation du niveau des mers sur les continents. D'autres études à une échelle régionale (Wetzel *et al.*, 2012, 2013) se sont penchés sur les conséquences d'une telle hausse sur les habitats insulaires, mais aucune de ces études n'a analysé l'effet sur les habitats insulaires à l'échelle mondiale. Dans le Chapitre 2, nous avons montré que sur **les 4 447 îles des hotspots insulaires, entre 6 et 19% risquaient d'être entièrement submergées**. Des résultats comparables ont été trouvés pour les îles françaises (voir Annexe 2). Nos résultats montrent que (1) **trois hotspots ont un risque élevé d'inondation dans le futur: les îles caribéennes, les Philippines et le Sondaland** ; (2) **plus de 300 espèces endémiques sont menacées par l'élévation du niveau des mers** ; et (3) **parmi les plantes qui sont déjà classées comme menacées d'extinction selon les statuts UICN, la majorité sont également vulnérables à l'élévation du niveau des mers**. Nos résultats sur les pertes d'habitats insulaires sont du même ordre de grandeur que les prédictions de Wetzel *et al.*, (2012) et Menon *et al.*, (2010). Dans le Chapitre 7, l'étude du 35^{ème} hotspot a permis de montrer qu'un **pourcentage important d'habitats dits « naturels » risquait d'être menacé** par l'élévation du niveau des mers. Dans ce même chapitre, nous avons montré que **les effets secondaires des changements climatiques risquaient d'être très importants aussi bien en terme sociétal qu'économique**. En effet en Australie, on a estimé que plus de 60 000 personnes habitant dans les régions côtières seraient exposées à la hausse du niveau des mers et pourraient être contraintes au déplacement vers l'intérieur des terres. Toujours en Australie, **les plantations de production de bois et les pâturages destinés aux élevages représentent l'une des principales classes d'occupation des terres touchées par les inondations**, avec près de 700 km² vulnérables aux inondations. Vraisemblablement, nous pouvons nous attendre à un déplacement de ces terres vers l'intérieur de l'Australie. Dans une moindre mesure, la couverture aquatique (rivières, lacs, estuaires) pourrait être également affectée par les inondations avec 293 km² et 524 km² potentiellement inondés par une hausse du niveau de la mer de 1 et 2 m.

Ces résultats sont en accord avec l'étude de Wetzel et al. (2012) qui avait mis en évidence l'importance de considérer les effets secondaires dus à l'élévation du niveau des mers. Néanmoins nos prédictions sont moins alarmantes que celles de Wetzel et al. (2012) probablement car cette étude a également considéré le phénomène d'érosion horizontale (l'érosion peut affecter des régions jusqu'à 20 m au-dessus du niveau de la mer et 100 km horizontalement), ce qui augmente considérablement les pertes d'habitats prédites. Ainsi, même s'il est important de tenir compte de l'effet de l'érosion, les méthodes utilisées actuellement pour évaluer les conséquences de ce phénomène ne sont pas suffisamment précises pour être considérées à une échelle globale.

Finalement, cette partie a permis de mettre en évidence que les conséquences de la hausse du niveau des mers sur les habitats insulaires, sont importantes et multiples, et vont porter à la fois sur la biodiversité, et la société. Dans la partie suivante, je vais synthétiser les principaux résultats mettant en évidence l'importance de considérer simultanément différentes menaces qui pèsent sur la biodiversité.

6.1.2. INTERACTIONS ENTRE LES CHANGEMENTS CLIMATIQUES, LES ESPECES INVASIVES ET LE CHANGEMENT D'OCCUPATION DES SOLS.

De nos jours, la gestion des espèces invasives est principalement conduite à travers le contrôle et l'éradication de ces dernières (Simberloff *et al.*, 2012), ce qui est particulièrement coûteux et ne signifie pas nécessairement une garantie de succès à long terme. La prévention au contraire est un moyen moins coûteux et plus efficace pour limiter les invasions (Simberloff *et al.*, 2012), néanmoins elle reste difficile à mettre en œuvre (Peterson & Vieglais, 2001). C'est dans le contexte d'amélioration de cette prévention que nous avons développé des modèles de distribution d'espèces invasives (Chapitre 4, 5 et 6). Nous avons d'abord cherché à comprendre comment les changements climatiques et le changement d'occupation des sols pouvaient influencer la distribution spatiale des espèces invasives dans le futur. Pour cela nous avons choisi de nous concentrer sur l'étude des 100 espèces invasives parmi les pires au monde (Lowe *et al.*, 2000). Nous avons ensuite utilisé nos résultats de prédictions de la répartition future de ces 100 espèces afin d'évaluer la vulnérabilité des hotspots de biodiversité aux invasions biologiques (Chapitre 6). Tout d'abord nous avons montré que **le nombre d'espèces invasives qui pourraient avoir des conditions environnementales favorables dans le futur pourrait être plus important dans l'hémisphère nord, mais diminuerait en Amérique du Sud, en Australie et en Afrique**

centrale. Ces résultats n'excluent pas des augmentations locales de certaines espèces invasives, mais montrent qu'en moyenne une partie des 100 espèces ne bénéficieront plus de conditions de développement favorables dans ces régions dans le futur. Ces résultats sont particulièrement surprenants et intéressants car les effets des changements climatiques et des changements d'occupations des sols sur la distribution des espèces invasives montrent des résultats très contrastés entre les différents continents. Ces résultats peuvent être mis en parallèle avec ceux de Peterson, qui a mis en évidence un résultat identique chez les plantes natives du continent européen (Peterson *et al.*, 2008). Il faut par ailleurs noter que l'étude de Peterson ne concernait qu'un seul groupe taxonomique présent en Europe dont les espèces ne sont pas nécessairement invasives. A ma connaissance, ce travail représente la première tentative de prendre en compte simultanément l'effet des changements climatiques et des changements d'utilisation des sols sur différents taxons d'espèces invasives. Habituellement, les études théoriques suggèrent que les changements climatiques vont favoriser les espèces invasives (Walther *et al.*, 2009; Bradley *et al.*, 2012; Diez *et al.*, 2012). Cependant, ce chapitre a permis d'illustrer que **la réponse des espèces invasives aux changements climatiques et aux changements d'occupations des sols est très variable.** Ainsi, nos résultats montrent **que l'aire potentielle de distribution peut évoluer de façon très différente suivant le groupe taxonomique et l'espèce considérée** (voir aussi à ce propos: Ficetola, Thuiller, & Miaud, 2007; Larson & Olden, 2012; O'Donnell *et al.*, 2012). Ces résultats peuvent être utilisés pour identifier les régions à surveiller et à contrôler avec attention dans les années à venir en raison de l'augmentation des conditions favorables aux espèces invasives, mais également pour identifier les opportunités de restauration des écosystèmes pour les régions qui deviendront moins favorables aux espèces invasives. Il est possible d'expliquer en partie ces résultats car la majorité des espèces de cette liste sont présentes dans des régions tempérées; ainsi un réchauffement climatique ne permettra pas à ces espèces d'envahir les zones tropicales, mais tendra plutôt à les faire se déplacer vers des régions plus au nord. Par ailleurs, la diminution du nombre potentiel d'espèces invasives aux faibles latitudes peut également s'expliquer en partie par l'apparition de nouveaux climats dans ces régions (Williams & Jackson, 2007).

Dans la suite de ce travail, nous avons choisi d'étudier l'évolution du nombre d'espèces invasives et de leur aire de répartition des 34 hotspots de biodiversité. Les résultats ont montré un faible renouvellement à l'échelle des hotspots, c'est à dire qu'en moyenne les espèces qui possédaient des conditions favorables dans le présent se retrouvaient dans le futur. Nos résultats ont également montré que les hotspots de biodiversité ont des conditions

environnementales plus propices à la présence d'espèces invasives que le reste du monde. Ces résultats peuvent en partie s'expliquer du fait que ces hotspots contiennent 21% de la population humaine mondiale sur seulement 13% de la surface habitable terrestre (Williams et al., 2011). De plus, la densité humaine s'est avérée être un des facteurs clefs expliquant la présence d'espèces invasives (Gallardo & Aldridge, 2013 et voir aussi le Chapitre 4). En particulier, nos résultats ont permis de montrer qu'actuellement **quatre hotspots sont prédits pour être particulièrement favorables aux espèces invasives : les îles caribéennes, la Nouvelle Calédonie, la Polynésie-Micronésie et la Nouvelle Zélande**. Dans le futur, les îles caribéennes montreront des conditions moins favorables à un certain nombre d'espèces invasives. Les conditions futures considérées comme propices aux espèces invasives montrent une évolution entre les hotspots mais aussi au sein même des hotspots. Globalement, **les hotspots majoritairement composés d'îles (îles caribéennes, Polynésie-Micronésie, Nouvelle Zélande, Nouvelle Calédonie, Philippines et les Ghats Occidentaux-Sri Lanka) présenteront des conditions particulièrement favorables aux espèces invasives dans le futur**, d'après notre étude.

Les résultats combinés aux effets directs des changements climatiques et des changements d'occupation des sols nous ont permis d'établir des priorités de conservation entre les différents hotspots (Chapitre 6 et 7).

6.1.3. MENACES SUR LES HOTSPOTS DE BIODIVERSITE ET HIÉRARCHISATION

Dans la 4^{ème} partie de cette thèse, nous avons cherché à déterminer et à quantifier la vulnérabilité des hotspots de biodiversité à la perte de climat analogue, mais également à l'évolution des classes d'occupations des sols et à la présence potentielle d'espèces invasives, dans le futur (Chapitre 6). Jusqu'à aujourd'hui il n'existait pas aucune étude visant à étudier la vulnérabilité des hotspots de biodiversité faces aux menaces futures. L'objectif de cette partie était de tenir compte de ces menaces afin d'établir des priorités de conservation à l'échelle des hotspots et au sein même d'un hotspot. Le Chapitre 6 a montré qu'en moyenne **31% des climats présents dans les hotspots pourraient disparaître à l'avenir**. Par conséquent, le fort taux d'endémisme de plantes vasculaires, la vulnérabilité et le caractère unique des hotspots est corrélé avec une robustesse de ces régions face au changement climatique dans le futur (voir aussi (Iwamura *et al.*, 2013). Cependant, **la Polynésie Micronésie, Méso-**

Amérique et les îles de l'est mélanésien se sont révélés être les régions les plus affectées par la perte de climat analogue (Figure 10). Nos résultats ont montré également que **la concentration de perte de climat analogue serait principalement localisée à proximité de l'équateur** et diminuerait en allant vers les pôles. Ces mêmes hotspots pourraient également subir l'apparition de nouveaux climats. En effet, ces régions étant les plus chaudes de la planète, ce sont les premières à sortir des climats actuellement présents sur terre et les nouveaux climats y apparaîtront en priorité. Le changement de précipitations apparaît également important aux faibles latitudes mais reste toutefois secondaire. Ces résultats sont concordants avec l'étude de Williams et al., (2007). En outre, nos résultats révèlent que **la forêt atlantique, les îles caribéennes et les Philippines sont les hotspots les plus affectés par la perte d'habitat naturel.**

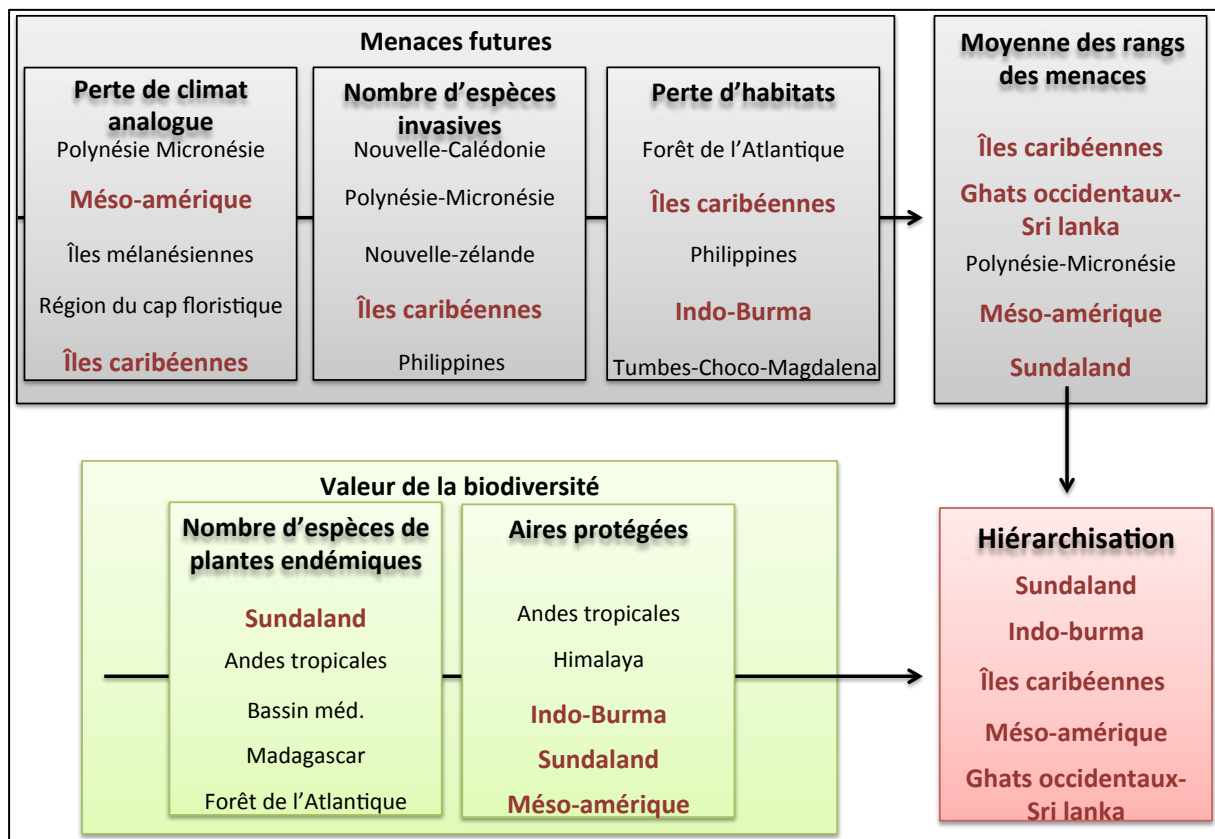


Figure 10 Classement des cinq premiers hotspots soumis à une perte de climat analogue, à un nombre important d'espèces invasives, et à une perte d'habitat dits « naturels » dans le futur., Classement des 5 hotspots comportant le plus important nombre d'espèces de plantes endémiques vasculaires et la plus faible proportion d'aires protégées.

En ce qui concerne la vulnérabilité aux espèces invasives, nos résultats démontrent que certains hotspots sont plus favorables à ces espèces invasives que d'autres (voir section 5.1.2). **En tenant compte à la fois des changements climatiques, des changements**

d'occupation des sols et des espèces invasives, nous avons montré que les hotspots n'étaient pas vulnérables aux changements globaux de façon homogène. Alors que la Polynésie-Micronésie est particulièrement exposée à la perte de climat analogue et aux espèces invasives, la forêt de l'atlantique représente le hotspot qui risque le plus de perdre des habitats naturels dans le futur. Nous avons établi que les îles caribéennes, les Ghats occidentaux-Sri Lanka, la Polynésie-Micronésie ainsi que le Méso-Amérique étaient les hotspots qui sont les plus menacées par les trois changements globaux là où Malcolm et al., (2006) avait uniquement mis en évidence la région floristique du cap, les îles caribéennes, le bassin méditerranéen, et les Andes tropicales, comme les hotspots vulnérables aux seuls changement climatiques. **Ce chapitre a donc permis de mettre en évidence l'importance de considérer différents facteurs de changements de biodiversité afin d'identifier les hotspots les plus menacés aux changements futurs. Nous avons également illustré qu'il est possible d'établir des priorités de conservation entre les hotspots selon les menaces futures, la biodiversité présente et le niveau de protection du hotspot.** Par exemple, en considérant à la fois le pourcentage d'aire protégée et le nombre d'espèces endémiques présent dans les hotspots, le Sondaland, l'Indo-Burma, les îles caribéennes et le Méso-Amérique sont les hotspots qui sont les plus vulnérables aux changements globaux mais également ceux qui sont les moins protégés et les plus riches en terme de biodiversité (voir Chapitre 6).

Par ailleurs, dans le Chapitre 7, nous avons analysé à la fois les effets directs et indirects (effets de la hausse du niveau des mers) du changement climatique au sein du 35^{ème} hotspot de biodiversité: les forêts de l'est australien. Dans ce hotspot, **la superficie potentiellement affectée par le changement climatique local (près de 100 000 km²) est plus importante que la superficie affectée par la hausse du niveau des mers.** Nous avons également démontré que les conséquences secondaires (déplacement humain ou classes d'occupation des sols menacées) peuvent aussi être très importantes. **Les habitats naturels et les terres issus de l'agriculture ou des plantations seraient les premières classes d'occupation des sols à être exposées.** En outre, nos résultats ont montré que **plus de 50% de l'habitat exposé aux menaces est actuellement insuffisamment protégé malgré la présence d'une biodiversité riche.** Par exemple, au sein même de ce hotspot, l'extrême nord de l'état du Queensland ainsi que l'extrême sud du New South Wales, qui renferment une richesse spécifique très importante, sont les états qui sont les plus exposés aux changements climatiques et les moins protégés actuellement.

6.2. AVANCÉES ET LIMITES METHODOLOGIQUES

6.2.1. ANALYSE DES EFFETS DE LA HAUSSE DU NIVEAU DES MERS

UTILISATION DES « DIGITAL ELEVATION MODELS »

Différents modèles d'élévation des îles mondiales présentant des résolutions spatiales variables sont actuellement disponibles dans le domaine de la recherche. Néanmoins, les modèles d'élévation couramment utilisés jusqu'à présent présentent des résolutions assez grossières (e.g. Menon et al., 2010 ou Li et al. 2009). Par exemple, Wetzel a calculé que sur les 12 000 îles du Pacifique et du sud-est asiatique seules 2 700 îles sont couvertes par le GTOPO30 modèle (Wetzel *et al.*, 2013). Ces modèles induisent donc à une sous-estimation des résultats de pertes d'habitat insulaire. C'est pourquoi, dans les Chapitres 2 et 7, nous avons choisi d'utiliser des « Digital Elevation Model » (DEM), qui présentent une meilleure résolution spatiale (90m). Cette fine résolution permet de bien représenter les contours côtiers, de prendre en compte des pertes partielles d'habitats insulaires, et d'inclure les îles de petites superficies (Voir par exemple la comparaison entre le modèle GTOPO30 et DEM en Figure 11).

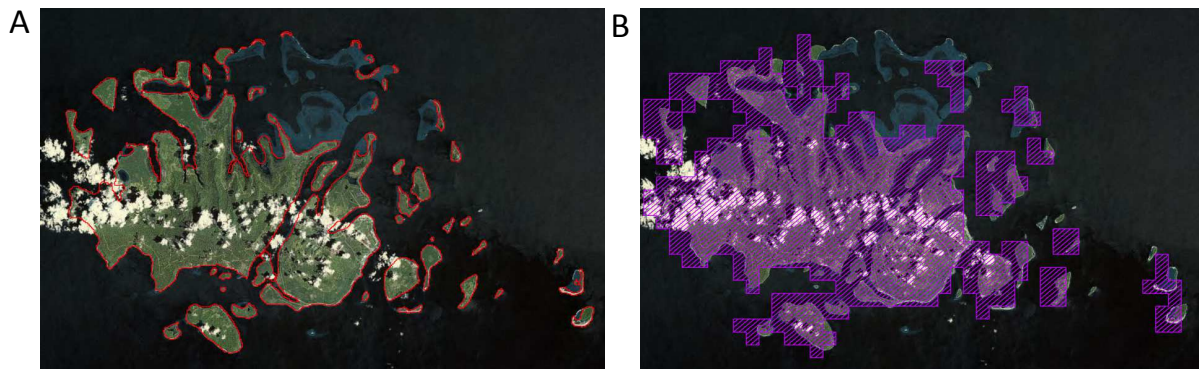


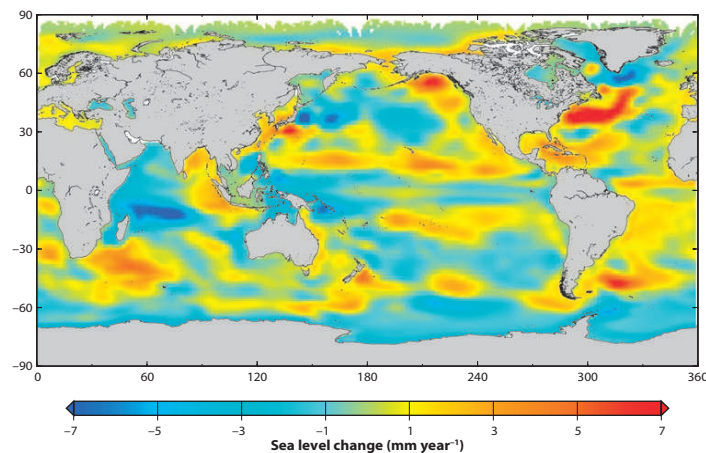
Figure 11 Comparaison entre le DEM SRTM (90m), utilisé lors de cette thèse (A) ; versus GTOPO30 (1km de résolution spatiale) (B) en ce qui concerne la côte, la forme et le nombre d'îles pour les îles du sud est asiatique. Il faut noter que les petites îles ne sont pas présentes avec le modèle GTOPO30 à cause de la résolution grossière et que la perte d'habitat insulaire est plus grossière dans ce cas. Figure de Wetzel et al. 2013.

Cependant, même si le modèle DEM est plus précis, certaines petites îles qui sont prédites pour être submergées dans l'Annexe 2 sont tout de mêmes absentes de ce modèle. Par exemple, en utilisant le DEM dans le Chapitre 2, les résultats montrent qu'aucune des îles de la Nouvelle Calédonie ne risque d'être totalement inondée par la hausse du niveau des mers ce qui contredit l'Annexe 2 où nous mettons en évidence que des dizaines d'îles de la Nouvelle Calédonie risquent d'être submergées. Pour obtenir ces résultats, nous avons utilisé

dans l'Annexe 2 une base de données encore plus précise provenant de l'Institut Géographique National (IGN), qui nous informe de l'élévation maximale pour chacune des îles, même pour les îles de très faible superficie. **Les résultats de pertes potentielles d'îles en raison de l'élévation du niveau des mers dans le Chapitre 2 (en comparaison avec l'annexe 2) sont donc sous-estimés.** Pour autant, l'utilisation des DEMs présente également des avantages puisqu'ils permettent de tenir compte des pertes partielles d'habitats insulaires, ce qui n'est pas possible avec l'approche basée sur les données IGN.

Une des autres limitations de cette approche est que l'ensemble des études qui quantifient l'effet de l'élévation du niveau des mers modélise une hausse moyenne à la résolution d'un mètre, ce qui peut potentiellement surestimer les prédictions de perte d'habitats insulaires. Malheureusement, nous avons également dû utiliser une telle résolution car **les DEMs tels que celui que nous avons utilisés à l'échelle globale ou régionale ne sont pas suffisamment précis pour pouvoir considérer des scénarios de moins d'un mètre.** Il faut noter que ce point est délicat car les prédictions de hausse du niveau des mers pour la fin de ce siècle sont comprises entre environ 0,5 à 2,3 m (Rahmstorf, 2007; Pfeffer *et al.*, 2008; Grinsted *et al.*, 2009). Notre scénario d'élévation minimal du niveau de la mer étant d'un mètre, il n'a pas été possible de tester la fourchette basse de cette estimation et nous avons donc potentiellement surestimé les pertes d'habitats insulaires.

En outre, une des autres limites de notre étude est que nous avons pris en compte qu'une hausse homogène du niveau des mers car aucun modèle de hausse hétérogène pour différents scénarios climatiques n'est actuellement disponible. En outre, les prédictions de hausse du niveau des mers issus de ces modèles hétérogènes restent très incertains en raison des incertitudes liés à la fonte des glaces (Cazenave & Llovel, 2010).



Cependant, nous avons qualitativement montré dans l'annexe 2 que **les prédictions d'îles entièrement submergées pour les scénarios hétérogènes et homogènes apparaissent comme similaires**. Ainsi bien que nous ayons considéré uniquement un scénario homogène de hausse du niveau des mers dans le chapitre 2, on peut espérer que nos résultats restent pertinents à cet égard.

DYNAMIQUE DE REPONSE GEOMORPHOLOGIQUE DU LITTORAL

A l'heure actuelle, les approches que nous utilisons sont extrêmement simplifiées. **Nous ne tenons pas compte des phénomènes d'érosion, ce qui peut conduire à une sous-estimation des résultats** (Wetzel *et al.*, 2012). Wetzel (2012) suggère que l'érosion peut affecter des régions jusqu'à 20 m au-dessus du niveau de la mer et 100 km horizontalement. Bien que cette étude considère, à juste titre, les conséquences potentielles de l'érosion, il s'agit d'une estimation encore relativement grossière qui surestime probablement les résultats et rajoute de l'incertitude aux estimations de perte d'habitats, l'érosion étant un phénomène complexe à quantifier.

De plus, **nous n'avons pas considéré la réponse géomorphologiques des côtes**. Il a par exemple été montré que seules 14% des îles étudiées dans le centre du Pacifique ont vu leur superficie diminuer ces dernières années, malgré une hausse moyenne du niveau de la mer 2 mm/an (Webb & Kench, 2010). Ces auteurs ont montré que la dynamique de réponse des atolls dépendait principalement des conditions locales, de la morphologie mais également de facteurs anthropogéniques telles que la présence d'infrastructures côtières (Webb & Kench, 2010). Une faible hausse du niveau de la mer peut ainsi être compensée par un apport en sédiment et des ajustements morphologiques, mais lorsque le seuil critique est dépassé, les conséquences d'inondations peuvent être considérables et irrémédiables. Par ailleurs, les mécanismes de formation des îles pourraient probablement permettre aux atolls de perdurer malgré une hausse du niveau de la mer de 0,5 m (Kench *et al.*, 2009). Cependant, on peut soulever deux principales critiques à propos de cet argument. D'une part la vitesse d'augmentation du niveau des mers risque d'être significativement plus rapide que celle qu'on pu subir ces îles dans le passé. Par exemple, la vitesse d'élévation du niveau des mers était de 2.8mm/an entre 1992 et 2001 (Church *et al.*, 2006) et les plus récentes estimations font part d'une augmentation potentielle de 10 mm/an en 2050 et 2100 (Grinsted *et al.*, 2009). Il faut comparer cette vitesse à celle qu'à connu la Terre depuis 3000 ans, c'est à dire 0,1 à 0,2 mm/an. D'autre part, l'acidification des océans risque également de limiter la capacité de calcification des récifs coralliens, ce qui pourrait par conséquent altérer la réponse

morphologique des îles. Ainsi, **la morphologie des îles, leur capacité à répondre aux phénomènes d'érosion et l'accrétion s'avèrent être des phénomènes clefs pour déterminer l'impact potentiel de l'élévation du niveau des mers sur les habitats insulaires** et ils devront être étudiées en détail pour pouvoir déterminer leurs effets exactes. En conclusion, **l'absence de prise en compte des réponses géomorphologiques du littoral conduit nécessairement à ajouter de l'incertitude à nos prédictions.**

CONNECTIVITE DES PIXELS

Une des autres limitations importantes de ce Chapitre 2, est que **nous n'avons pas tenu compte de la connectivité des pixels** en raison des limites techniques et informatiques, **ce qui peut évidemment mener à des surestimations de la perte d'habitat.** Par exemple, les surfaces qui sont entourées de régions plus élevées en altitude seront protégées des intrusions marines ne devraient pas être considérées dans les calculs d'aires inondées. Pour déterminer l'importance de la surestimation, nous avons tenu compte à l'échelle d'un seul hotspot, de la connectivité des cellules dans le Chapitre 7. Nous avons alors estimé que lorsque l'on considère la connectivité des cellules, **la perte d'habitat au sein du hotspot « Forest of East Australia » était de 0.26% et 0.59% pour le scénarios 1m et 2m, alors que les pertes estimées étaient de 0.59% à 0.95% lorsque l'on ne tenait pas compte de la connectivité.** Cela montre que nous surestimons probablement les pertes partielles d'habitats insulaires dans nos résultats du Chapitre 2. C'est pourquoi l'analyse à l'échelle des îles entièrement submergées du Chapitre 2 est plus précise et conservatrice que l'analyse sur les pertes partielles d'habitats insulaires en ce qui concerne ce chapitre.

LIMITES DES PREDICTIONS DES EFFETS SUR LA BIODIVERSITE

Peu d'études écologiques ont aujourd'hui analysé les conséquences de la hausse du niveau des mers sur la biodiversité, à l'échelle d'une population ou d'un écosystème. Par ailleurs, l'ensemble des études qui se sont intéressés à cette question ont fait la même simplification : un habitat inondé est un habitat potentiellement perdu. Ainsi, Menon et al. (2010) ont utilisé la relation « aire-espèce » afin d'estimer la part de la biodiversité qui est potentiellement en danger. Quant à Wetzel et al. (2012), ils ont utilisé les aires de distribution d'espèces afin de quantifier la proportion de ces aires de distributions qui est vulnérable à la submersion. Dans le Chapitre 2, nous avons utilisé ces deux types d'approches, en dépit des limites expliquées au début de ce paragraphe. Dans un premier temps, la relation endémique aire-espèce a permis d'estimer globalement le nombre d'espèces endémiques qui risquait d'être exposée à

une hausse du niveau de la mer. Cette relation a également été utilisée dans le Chapitre 7 pour estimer le nombre d'espèces endémiques qui risquent de souffrir de la perte de climat analogue. Cette approche permet d'estimer à grande échelle la part de la biodiversité qui risque d'être menacée et évite les surestimations liées à l'utilisation de la relation aire-espèces (voir He & Hubbell, 2011). Il faut cependant noter que cette relation peut varier en fonction du groupe taxonomique (Storch *et al.*, 2012), mais qu'il n'a pas été possible d'en tenir compte sauf pour les plantes. Nous avons donc choisi d'utiliser les différentes valeurs de z en fonction des régions d'intérêt.

Par la suite, nous avons utilisé les données d'aires de distribution des plantes endémiques de la Nouvelle Calédonie, ce qui a permis de comparer les résultats issus des deux méthodes. Nous avons mis en évidence que dans le cas de la Nouvelle Calédonie **les résultats des deux méthodes étaient similaires au regard de la part de la biodiversité vulnérable à une hausse du niveau des mers**. Cette seconde méthode a également permis d'identifier les espèces qui risquaient d'être vulnérables à la montée des eaux. De plus, il a été possible de déterminer à l'échelle spécifique les espèces en danger d'extinction là où l'utilisation de la relation endémique-aire espèces permet uniquement d'évaluer la part de la richesse spécifique qui risque d'être en danger.

INTERACTIONS AVEC D'AUTRES COMPOSANTES DES CHANGEMENTS

CLIMATIQUES

Dans le Chapitre 2 par exemple, nous avons uniquement considéré les effets indirects du changement climatique tels que la hausse du niveau des mers. Néanmoins, la hausse du niveau des mers n'est qu'une conséquence des changements climatique. Par exemple, cette élévation du niveau des mers est lié principalement à la hausse des températures (Cazenave & Llovel, 2010). C'est pourquoi dans le Chapitre 7, nous avons modélisé à la fois les changements de températures, les changements de précipitations (effets directs) et de la hausse du niveau des mers (effets indirects) sur le 35^{ème} hotspot de biodiversité. Cette approche nous a permis de mettre en évidence **l'importance de considérer les effets directs et indirects des changements climatiques simultanément**. En particulier, nos résultats ont montré que les régions risquant de souffrir des effets directs et indirects du changement climatique n'étaient pas forcément les mêmes. Par exemple, la partie sud-est de l'état du Queensland est principalement exposée à une hausse du niveau des mers, alors que l'extrême nord du Queensland et sud du New South Wales sont particulièrement vulnérables à un changement de climat local. Pour autant, il n'a pas été possible de tenir compte des

nombreuses autres composantes des changements climatiques comme de l'augmentation des événements climatiques extrêmes (ouragans, tsunamis, tempêtes) notamment en raison d'une grande incertitude liée à la prédictibilité de ce type d'évènement. D'autre part, d'autres facteurs de perte de biodiversité comme la perte d'habitat, les espèces invasives, la surexploitation, la pollution peuvent interagir avec les changements climatiques (Sala *et al.*, 2000), et il importe d'en tenir compte. Par exemple, les invasions biologiques qui représentent une des principales causes d'extinction dans les îles (Donlan & Wilcox, 2008) devraient être incluses dans ce type de modèle afin de mieux rendre compte des risques d'extinction d'espèces pour les habitats insulaires. **Nos estimations concernant la part de la biodiversité présentant un risque d'extinction en raison des changements climatiques devront donc être affinées dans de futures analyses.**

6.2.2. ANALYSE DES INTERACTIONS ENTRE LES CHANGEMENTS CLIMATIQUES, LES ESPECES INVASIVES ET LE CHANGEMENT D'OCCUPATION DES SOLS.

Dans la partie 3 de cette thèse, nous avons utilisé des modèles de distribution d'espèces qui sont des approches complexes nécessitant de faire des choix méthodologiques (tels que le nombre d'occurrence minimal d'une espèce) pouvant influencer les résultats. Les choix méthodologiques qui ont été faits avec cette approche ont été majoritairement guidés par la littérature (e.g., Araújo & New, 2007; Barbet-Massin, Jiguet, Albert, & Thuiller, 2012; Ferrier *et al.*, 2006; Guisan & Zimmermann, 2009; Marmion, Parviainen, Luoto, Heikkinen, & Thuiller, 2009). Je vais exposer ici les principales incertitudes liées à l'utilisation de ce type d'approche dans un contexte d'invasion biologique. Cette partie ne vise pas à faire une liste exhaustive des limites associées à l'utilisation de ce type de modèle, même s'il est évident que chaque approche de modélisation a des contraintes méthodologiques temporelles et spatiales qui limitent leur pouvoir prédictif (McMahon *et al.*, 2011; Leroy B., 2012).

DONNEES D'OCCURRENCES

Les résultats des projections des modèles sont largement dépendants des données d'occurrences d'espèces intégrées dans les modèles. Idéalement, les données de présence doivent représenter un échantillonnage homogène sans biais spatial (Araújo & Guisan, 2006) afin de développer des politiques efficaces de gestion (Jetz *et al.*, 2012). Cependant de tels jeux de données sont très rarement disponibles, en particulier à grande échelle.

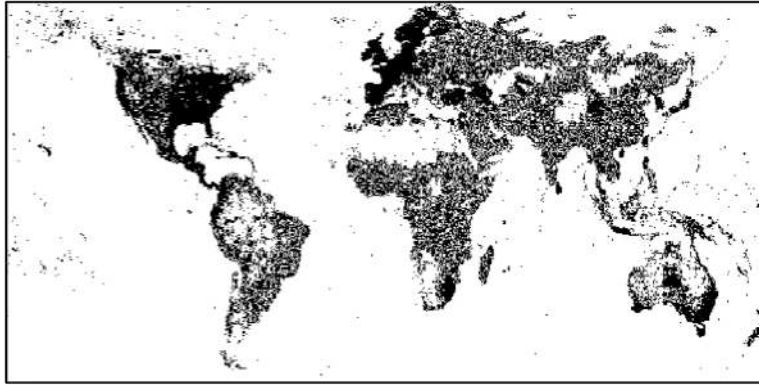


Figure 12 Distribution spatiale des points d'occurrences collectées de la liste des 100 parmi les pires espèces invasives au monde

De plus, le biais d'échantillonnage peut être lié aux biais de détection des espèces mais également aux biais d'effort d'échantillonnage (voir discussion Leroy B., 2012). Il existe par exemple de nombreux programmes de détection des espèces invasives en Europe et en Australie, ce qui permet d'avoir des données d'occurrences abondantes sur les espèces invasives. Au contraire, sur le continent africain, il est beaucoup plus difficile d'obtenir des données d'occurrences (Figure 12). De plus, même si ces données existent localement, elles ne sont pas nécessairement mises à disposition sur des bases de données accessibles. La collecte de données réalisée lors de cette thèse a nécessité plusieurs mois de travail, et de nombreuses vérifications ont été effectuées tout au long de ce travail. Cependant, des manques d'information sur l'occurrence des espèces peuvent apparaître si les données sur le terrain ne sont pas récoltées ou que la présence de l'espèce dans certaines régions n'est pas encore connue, il n'est évidemment pas possible de considérer de telles données.

Tout d'abord afin de collecter le maximum d'informations sur les occurrences, nous avons compilé les données d'occurrences à partir de différentes bases de données disponibles en ligne tels que (GBIF, CABI, OBIS, LIFEMAPPER, IUCN, Aquamap) avec parfois des redondances entre les différentes bases de données. Nous avons vérifié pour chacun des points d'occurrence s'il correspondait bien à une région ou un pays envahi selon la base de données ISSG et CABI. Lorsqu'un pays était indiqué dans les bases de données de l'ISSG ou CABI comme envahi mais qu'aucun point de présence n'existait dans les différentes bases de données, nous avons cherché dans les références associées aux pays indiqués, des points de présence. Nous avons alors ajouté de nouvelles coordonnées lorsqu'elles étaient disponibles et contacté les experts de l'ISSG pour ces espèces afin d'obtenir des données supplémentaires (points GPS, rapport, communication personnelle, références de la littérature). Nous avons également contacté les experts associés à certaines espèces dans le cas d'une ambiguïté concernant la taxonomie de l'espèce afin de récolter des informations supplémentaires. Par

ailleurs, si une espèce était présente dans une région, mais que cette région n'était pas listée comme « envahie » nous avons également mené des recherches supplémentaires afin de vérifier la présence ou non de l'espèce dans cette région. Finalement, nous avons collecté en moyenne 3 850 occurrences par espèce, ce qui est plus de 100 fois la limite minimale utilisée par les études utilisant des modèles de distribution d'espèces (e.g., Parker-allie, Musil, & Thuiller, 2009; Peterson, Stewart, Mohamed, & Arau, 2008). Afin de diminuer le biais d'autocorrélation spatiale des données, nous avons agrégé les données d'occurrence dans des cellules de 0.5° de résolution (voir Chapitre 4).

CHOIX DES VARIABLES ENVIRONNEMENTALES UTILISEES

Dans le cadre des modèles de distribution d'espèces, il est nécessaire de sélectionner des variables environnementales supposées influencer significativement la répartition des espèces que l'on veut considérer. Cependant, toutes les variables ne sont pas disponibles à grandes échelles temporelles ou spatiales. Comme dans la plupart des cas, il n'existe aucun a priori sur les préférences environnementales des espèces et si l'étude se fait pour différents groupes taxonomiques, on utilise généralement l'ensemble des variables non corrélées entre elles ($r_{\text{pearson}} < 0.75$). Ainsi, même si ces variables n'influencent pas directement la répartition des espèces, elles remplacent en général les variables plus proximales (Austin 2007). D'autre part, même si la sélection de variables devrait principalement se faire grâce à une bonne connaissance écophysiologie des espèces, cela n'a pas été possible dans notre cas en raison de la grande échelle de notre étude et de la diversité des groupes taxonomiques considérés. **Nous avons donc sélectionné des variables climatiques liées à la température et aux précipitations pouvant potentiellement influencer la distribution de ces espèces.** En ce qui concerne les espèces marines, différentes études ont montré de fortes corrélations entre les distributions spatiales des espèces et les variables climatiques (Jocque *et al.* 2010) telles que la température et la disponibilité en eau. Ces variables ont d'ailleurs été utilisées avec succès pour prédire la distribution d'espèces de poissons ou de moules (Drake & Bossenbroek 2004; McNyset 2005). L'étude présente dans le Chapitre 5 a également montré que les variables climatiques sont les principaux prédicteurs de la distribution des espèces invasives marines à la résolution de 0.5°. En outre, les espèces invasives sont influencées par le niveau d'anthropisation des habitats (Pysek *et al.* 2010; Roura-Pascual *et al.* 2011), nous avons donc ajouté des données d'occupation des sols à notre analyse. **L'ajout de ces données pour prédire la distribution des espèces invasives est un point innovant de cette analyse car**

peu d'études avaient jusqu'à présent intégré ce type de variables afin de prédire l'aire de distribution future favorable aux espèces invasives.

DONNEES CLIMATIQUES ET D'OCCUPATION DES SOLS

Pour les Chapitres 5 et 6, nous avons utilisé différents modèles climatiques (HADCM3, CSIRO2 et CGCM2) et différents scénarios climatiques. Ces modèles climatiques sont basés sur des scénarios socio-économiques d'émissions de gaz à effet de serre pour le futur et sur différents modèles de circulation générale. Les résultats de projections issus de ces modèles peuvent être très contrastés car ils utilisent des scénarios de CO₂ différents mais aussi des modèles de circulation générales ayant des caractéristiques très différentes (Beaumont *et al.* 2008). C'est pourquoi, il importe d'utiliser plusieurs **modèles climatiques différents afin de capturer la gamme des changements futurs possibles, et de réduire l'incertitude sur les hypothèses « sous-jacentes » des modèles et scénarios climatiques** (Buisson, Thuiller, Casajus, Lek, & Grenouillet, 2010). Ainsi, il aurait été bénéfique d'intégrer un plus grand nombre de modèles climatiques dans le cadre de cette thèse, cependant, lorsque le travail de modélisation a commencé, il n'existait que trois modèles climatiques mis à disposition qui modélisaient les deux scénarios d'émissions de CO₂. Ces deux scénarios sont: le scénario A1B : besoins énergétiques maximum, émissions équilibrées entre sources fossiles et non-fossiles ; B2A besoins énergétiques inférieurs, émission inférieures (IPCC *et al.* 2007). Quant aux variables d'occupation des sols, nous avons utilisé les données issues du modèle Globio3 (Alkemade *et al.* 2009). L'avantage principal de ces données est qu'elles peuvent être utilisées en complément des données climatiques, car elles ont été générées à partir des mêmes scénarios d'émissions de CO₂. Mais la principale limite est qu'elles ajoutent nécessairement de l'incertitude aux prédictions car ces données sont obtenues à partir d'un certain nombre d'hypothèses comme, par exemple, l'évolution de la couverture végétal en fonction du climat (Alkemade *et al.* 2009). Par ailleurs, dans le Chapitre 7, nous avons utilisé des données de d'occupation des sols issus du modèle Australien (ALUM, 2010) pour étudier le 35^{ème} hotspot. Cette classification nous a permis d'obtenir des informations sur l'occupation des sols à une résolution fine de 50 m. Cependant, ces données ne sont disponibles que pour la période actuelle, et il n'existe pas de classification à une résolution aussi précise pour le futur. Nous avons donc été contraints de faire l'hypothèse que les classes d'occupation des sols qui risquaient d'être affectées dans le future seraient les mêmes que celles que l'on trouve actuellement dans le 35^{ème} hotspot.

RESOLUTION SPATIALE ET TEMPORELLE DES MODELES

Le choix de la résolution spatiale est probablement un des facteurs induisant le plus de variabilité dans les prédictions des modèles. Une étude sur les Alpes a par exemple mis en évidence qu'avec une résolution grossière (10' x 10') la perte d'habitat favorable était totale dans certains pixels alors qu'en considérant une résolution plus fine (25m x 25m), les conditions restaient favorables pour la plupart des espèces de plantes (Randin *et al.* 2009). En fait, les conditions microclimatiques, la diversité topographique locale et l'hétérogénéité de l'habitat non prise en compte à basse résolution sont à l'origine d'une telle différence (Luoto & Heikkinen, 2008; Randin *et al.*, 2009). Dans le cadre de cette thèse, les chapitres 4, 5 et 6 se basent sur des résolutions spatiales grossières (0.5°) car les données d'occupation des sols n'étaient pas disponibles à une plus fine résolution. Ainsi, l'absence d'influence de la richesse spécifique en espèce native, de la diversité d'habitat ou des variables associées aux changements d'occupation des sols, dans le Chapitre 5, est peut être liée à une résolution trop grossière qui ne permet pas de capturer les effets de ces variables. Nous avons choisi dans le cadre de cette thèse d'utiliser la meilleure résolution disponible pour l'ensemble des variables climatiques et d'occupation des sols. De plus, pour des raisons de temps de calcul il n'aurait pas été de toute façon possible de choisir une résolution plus fine pour modéliser les 100 espèces invasives. Il a donc fallût faire un compromis adéquat entre des modèles précis à petite échelle et les modèles à plus large échelle qui manquent nécessairement de réalisme biologique (voir à ce sujet Thuiller 2003).

La dimension temporelle est également particulièrement importante dans le contexte des invasions biologiques. Nous avons collecté les données d'occurrences pour la même période que les données climatiques et d'occupations des sols (c'est-à-dire 1950-2000), mais nous avons également utilisé des données d'occurrence entre 2000-2010. Il est ainsi possible qu'en tenant compte de ces points d'occurrences, certaines espèces invasives se soient installées dans des régions alors que les conditions climatiques ou d'occupation des sols n'étaient pas encore favorables dans nos modèles. Par conséquent, il est possible que nous ayons introduit de l'incertitude dans les modèles si les données d'occurrence entre 2000 et 2010 correspondent à des climats très différents de la moyenne 1950-2000 (voir Leroy B., 2012 sur le biais temporel).

PROTOCOLE DE MODELISATION ET INDICES D'EVALUATION DES MODELES

De nombreuses études visent à améliorer les protocoles de modélisation de distribution d'espèces (Dormann *et al.* 2007; Beaumont *et al.* 2009; Marmion *et al.* 2009;

Barbet-Massin *et al.* 2012; Araújo & Peterson 2012). Nous avons essayé d'appliquer le protocole de modélisation le plus robuste en décrivant chacune des étapes qui avaient été appliquées. Nous avons également justifié les choix méthodologiques en suivant les recommandations de la littérature dans les différents manuscrits. Les valeurs d'évaluation de performance des modèles étant très élevées, ceci témoigne en partie de la pertinence des choix qui ont été faits.

Afin d'évaluer la performance des modèles, nous avons utilisé trois mesures d'évaluation différentes comme l'AUC, le TSS et l'indice de Boyce (Fielding & Bell 1997; Boyce *et al.* 2002; Allouche *et al.* 2006). L'AUC et le TSS considèrent à la fois la sensibilité (la proportion de présence observée correctement prédite) et la spécificité (la proportion de pseudo-absence « observée » incorrectement prédite). Les évaluations issues de l'AUC et du TSS indiquent que nos modèles sont robustes (voir Chapitre 4 et 5). Néanmoins, **ces évaluations étant basées sur des données de présences et de pseudo-absences et non sur de réelles données d'absences nous avons également choisit d'utiliser l'indice de Boyce.** L'indice de Boyce estime dans quelle mesure les prédictions de présence des modèles diffèrent d'une distribution aléatoire de présences observées. L'avantage de l'indice de Boyce est qu'il est basé uniquement sur des données de présence. **Les évaluations calculées pour l'indice de Boyce indiquent également que les résultats sont robustes de ce point de vue, ce qui renforce la pertinence de nos résultats** (voir Chapitre 5).

IMPLICATIONS DE L'APPARITION DE NOUVEAUX CLIMATS POUR LES MODELES DE DISTRIBUTION D'ESPECES

Dans le chapitre 6, nous avons montré que certaines régions du monde allaient perdre une part importante de leur climat d'origine et parfois être affectées par de nouveaux climats. Cette tendance est particulièrement claire à proximité de l'équateur au sein des hotspots (voir aussi Williams *et al.* (2007)). Il est important de noter que, comme montré dans le chapitre 6, l'apparition de nouveaux climats au sein d'un hotspot ne signifie pas nécessairement que ce climat n'est pas présent sur Terre mais plutôt que ce climat n'a jamais été présent au sein de ce hotspot. La présence de ces nouveaux climats représente un défi important pour les modèles de distribution d'espèces. En effet, bien qu'il soit admis que les modèles de distribution d'espèces n'englobent pas l'ensemble de la niche fondamentale en raison de l'absence des facteurs biotiques et des capacités de dispersion, elle peut également être incomplètement représentée si ces modèles ne sont pas entièrement circonscrits par les climats actuels (Williams & Jackson, 2007). De plus, la distribution actuelle des espèces ne

fournit aucune information sur la réponse potentielle d'une espèce confrontée à de nouveaux climats. **Ainsi, l'incertitude des prédictions issues des modèles de distribution d'espèces est plus importante dans les régions susceptibles de voir apparaître de nouveaux climats.** En général, nos résultats ont montré que la perte d'espèces invasives n'était pas associée à l'apparition de nouveaux climats. Néanmoins, certaines régions où on observe un recul potentiel du nombre d'espèces invasives, sont tout de même affectées par ces nouveaux climats (e.g., le Méso-Amérique (65% de nouveaux climats) ou pour les îles caribéennes (34% de nouveaux climats)).

LISTE DES 100 CAS D'ESPECES INVASIVES PARMIS LES PIRES AU MONDE

Il est important de souligner que la liste des 100 parmi les pires espèces invasives dans le monde, ne représente pas un classement des pires espèces invasives. De plus, cette liste n'est pas une liste représentative des espèces invasives d'un point de vue taxonomique, biogéographique, des impacts écologiques, économiques ou sociétaux. Par exemple, il existe un biais au niveau des espèces sélectionnées : peu d'espèces présentes dans cette liste sont problématiques pour le continent africain. Les espèces présentes dans cette liste posent principalement problème pour l'Europe, les îles indonésiennes, l'Amérique du nord, l'Australie et la Nouvelle-Zélande. En dépit de ces restrictions, ces espèces font parti des espèces les plus dangereuses et les plus problématiques au monde et ont déjà démontré leur importante capacité à s'établir, s'étendre et à menacer de nombreux écosystèmes (Lowe et al., 2000). Il était donc pertinent et nécessaire d'évaluer les effets combinés des changements climatiques et des changements d'utilisation des sols sur ces espèces invasives pour la recherche fondamentale (e.g., compréhension des facteurs influençant la distribution actuelle de ces espèces) et la recherche appliquée (e.g., la gestion de ces espèces invasives).

UTILISATION DES MODELES DE DISTRIBUTION D'ESPECES DANS UN CONTEXTE D'INVASION

Les modèles de distribution d'espèces sont des outils intéressants et utiles dans le cadre de la prévention des invasions biologiques (Jiménez-Valverde *et al.*, 2011). En effet, la combinaison des conditions climatiques et des autres variables environnementales permet d'expliquer le succès ou non des invasions. Cependant, **dans certains cas les espèces invasives occupent des niches climatiques distinctes entre les régions natives et les régions envahies** (Broennimann *et al.*, 2007; Gallagher *et al.*, 2010), même si le déplacement

de « niche » semble rare chez certains groupes taxonomiques tels que les plantes terrestres invasives (Petitpierre *et al.*, 2012). L'analyse des climats analogues entre les « niches natives » versus « niches envahies » permettra à l'avenir de mieux comprendre l'évolution de préférendum des espèces, et de déterminer si le changement de niche a eu lieu en bordure de niche ou s'il s'agit plutôt d'une toute nouvelle enveloppe climatique. Il est donc possible que **certaines régions n'aient pas encore été envahies** (par exemple on a observé qu'il faut environ 150 ans avant qu'une néophyte n'atteigne son pic d'expansion en Europe (Gassó *et al.*, 2010)), ainsi **la « niche » capturée par les modèles de niches est potentiellement incomplète.**

De plus, **toutes les espèces qui sont introduites grâce à des conditions favorables ne vont pas nécessairement se propager et avoir des conséquences néfastes sur l'habitat hôte, les conditions biotiques peuvent également jouer un rôle important.** Cependant, les espèces de la liste des « 100 parmi les pires espèces invasives au monde », possèdent des caractéristiques qui font que si la pression de propagule est suffisamment importante alors l'espèce sera *a priori* capable de survivre, de se reproduire, de se propager et d'avoir des effets négatifs sur la biodiversité.

En outre, comme nous l'avons illustré dans le Chapitre 4, **la pression de propagule (e.g., distance aux aéroports et la densité humaine) joue un rôle essentiel pour expliquer la distribution de ces espèces invasives.** Par conséquent, il est probable que l'utilisation des modèles de distribution d'espèces a tendance à surestimer les futures aires de répartition dans le cas d'une augmentation future de l'aire de répartition favorable car la pression de propagule n'est pas prise en compte. Comme le déplacement humains et le commerce augmente continuellement (Hulme *et al.*, 2009), il est fort à parier que cela favorisera les opportunités d'invasions des espèces, par exemple, en les aidant à franchir des barrières géographiques auparavant infranchissables. Il faut également rappeler que les facteurs climatiques peuvent également être à l'origine des invasions, récemment, l'ouragan Katrina a permis d'étendre les invasions de termites avec plusieurs millions de tonnes de bois infestées qui ont été déplacées sur plusieurs centaines de kilomètres (Mainka & Howard, 2010).

Finalement dans les Chapitres 5 et 6 nous avons uniquement considéré l'effet des changements climatiques et des changements d'utilisation des sols sur la distribution des espèces invasives mais les conséquences de ces deux facteurs sur la pression de propagule ou sur les impacts de ces espèces invasives n'ont pas été considéré, bien que l'effet potentiel de ces changements sur les voix d'invasions et leurs impacts a été discuté dans la littérature (voir Hellmann *et al.*, 2008; Walther *et al.*, 2009).

6.2.3. LIMITES DE L'ANALYSE SUR LES HOTSPOTS DE BIODIVERSITE ET LEUR PRIORITISATION.

LES ANALYSES DE CLIMAT ANALOGUE

Dans les Chapitres 6 et 7, nous avons utilisé les analyses de climat analogue afin d'évaluer l'exposition des hotspots de biodiversité aux changements climatiques. Cependant, l'utilisation de cette analyse implique la formulation de nombreuses hypothèses. En particulier, nos analyses de climat analogue ne considèrent que des variables climatiques et n'incluent pas des variables édaphiques telles que **la composition du sol et la teneur en éléments nutritifs**. Pourtant, ces variables **pourraient grandement influencer la future distribution des espèces, en particulier pour le groupe des plantes**. Dans cette thèse, nous avons choisi trois variables générales liées à la température et trois liées aux précipitations. Le choix des variables aurait pu être différent si le but de l'analyse était, par exemple, d'étudier les contraintes environnementales directes d'une espèce de plante donnée. De plus, la standardisation et le poids donnés aux variables sont également des éléments critiques de ce type d'analyse. Dans cette thèse, nous avons choisi de standardiser les données par la variabilité interannuelle de la température et des précipitations de chacun des pixels (voir aussi Williams *et al.*, 2007; Veloz & Williams, 2011). Cette approche de standardisation permet de donner le même poids à toutes les variables et donc d'éviter une sur-représentation des variables liées aux précipitations.

Finalement, un des autres éléments qui peut fortement influencer ce type d'analyse est le calcul du seuil qui permet de discriminer entre le climat analogue versus le climat non analogue. Il existe différentes approches qui peuvent permettre de discriminer les climats analogues et non analogues. Par exemple, Williams *et al.* (2007), ont choisit de calculer ce seuil en discriminant les différents biomes terrestres et en prenant la moyenne des différents seuils. Dans le cadre de cette thèse nous avons calculé pour chacun des 34 hotspots, ce seuil en séparant les climats au sein d'un hotspot par rapport à ceux du reste du monde. Ce qui signifie, que si un climat était par exemple présent à 600 km de la frontière du hotspot et qu'on le retrouve dans le hotspot, il sera tout de même considéré comme non analogue (même si en réalité ce climat aura un analogue à l'échelle de la planète). Cela implique que les **résultats de perte de climat analogue sont propres à chaque hotspot et n'implique pas une perte de climat à l'échelle de la planète**. Finalement, il faut noter que ce sont les mêmes régions géographiques qui ont présenté de nouveaux climats en utilisant notre méthode et

celle de Williams. Cependant, d'autres analyses seraient nécessaires afin de mieux déterminer les implications de l'utilisation de différents seuils.

Finalement, il faut savoir que les analyses de climat analogue ont déjà été utilisées avec succès pour identifier les futurs points chauds de changement de climat (Diffenbaugh *et al.*, 2008) ou encore afin de localiser les aires qui sont exposées à une perte et/ou apparition de nouveaux climats (Williams & Jackson, 2007). De plus, comme nous l'avons vu dans le Chapitre 4 les variables climatiques sont les principaux facteurs influençant la distribution des espèces. **Il était donc raisonnable de penser que l'analyse des changements de climat peut nous informer sur les conséquences à venir pour la biodiversité** bien qu'il ne faut pas oublier que de nombreuses espèces sont potentiellement capables de s'adapter aux conditions climatiques changeantes (Lavergne *et al.*, 2010).

CUMUL DES MENACES QUI PESENT SUR LES HOTSPOTS

Dans le but de proposer une hiérarchisation des hotspots de biodiversité, nous avons évalué l'effet cumulé des changements climatiques, des changements d'occupation des sols et des invasions biologiques sur les hotspots de biodiversité. Pour cela, nous avons notamment classé les hotspots en fonction de leur vulnérabilité aux différentes menaces. Néanmoins nous n'avons pas tenu compte du recouvrement des menaces. En conséquence, dans notre analyse, les zones affectées par les trois menaces sur trois aires distinctes du hotspot auront des valeurs de vulnérabilité plus fortes que celles pour lesquelles les trois menaces se recouvrent sur la même aire. Cette limite fera l'objet d'un travail plus approfondi de synthèse des différentes menaces (élévation du niveau des mers, changements climatiques locaux, changements d'utilisation des sols et invasions biologiques) qui pèsent sur les 35 hotspots de biodiversité (voir la partie implication).

LA BIODIVERSITÉ ETUDIÉE

Notre analyse de hiérarchisation dans le Chapitre 6 a également permis de prendre en compte le nombre d'espèces endémiques de plantes présentes dans chacun des hotspots. Cependant, lorsque nous faisons la même analyse en considérant d'autres groupes taxonomiques, tels que les mammifères, poissons, amphibiens, oiseaux et reptiles, les résultats que nous obtenons sont différents. En effet, les hotspots qui comportent le plus grand nombre d'espèces de plantes vasculaires endémiques ne sont pas les mêmes pour tous les autres groupes (voir Figure 13). Dans ce chapitre, il était justifié d'utiliser les plantes car les hotspots de biodiversité ont été sélectionnés selon le nombre d'espèces de plantes vasculaires endémiques qu'ils comportent (Myers *et al.*, 2000). En outre, la richesse spécifique n'est pas

corrélée aux nombres d'espèces endémiques au sein des hotspots (Orme *et al.*, 2005), ce qui signifie que **la hiérarchisation réalisée dans le Chapitre 6 est uniquement basée sur le nombre d'espèces endémiques de plantes et n'est pas valable si l'on s'intéresse à d'autres groupes taxonomiques ou à un autre niveau de la biodiversité.** Ainsi une importante richesse spécifique peut être trouvée dans un hotspot qui n'abrite pourtant qu'un faible nombre d'espèces endémiques.

Au contraire, dans le Chapitre 7 la hiérarchisation a été établie en utilisant des données de richesse spécifique ce qui nous a permis de tenir compte d'un grand nombre de groupes taxonomiques (e.g., plantes, mammifères, amphibiens et oiseaux). Cependant, **il faut noter que même dans les études les plus ambitieuses, la part de la biodiversité étudiée ne représente qu'une faible proportion de la biodiversité existante.** De plus, la diversité phylogénétique (Thuiller *et al.*, 2011) ou la diversité fonctionnelle (Thuiller *et al.*, 2006) représentent également des composantes importantes de la biodiversité, mais elles n'ont pas pu être prises en compte ici (Devictor *et al.*, 2010).

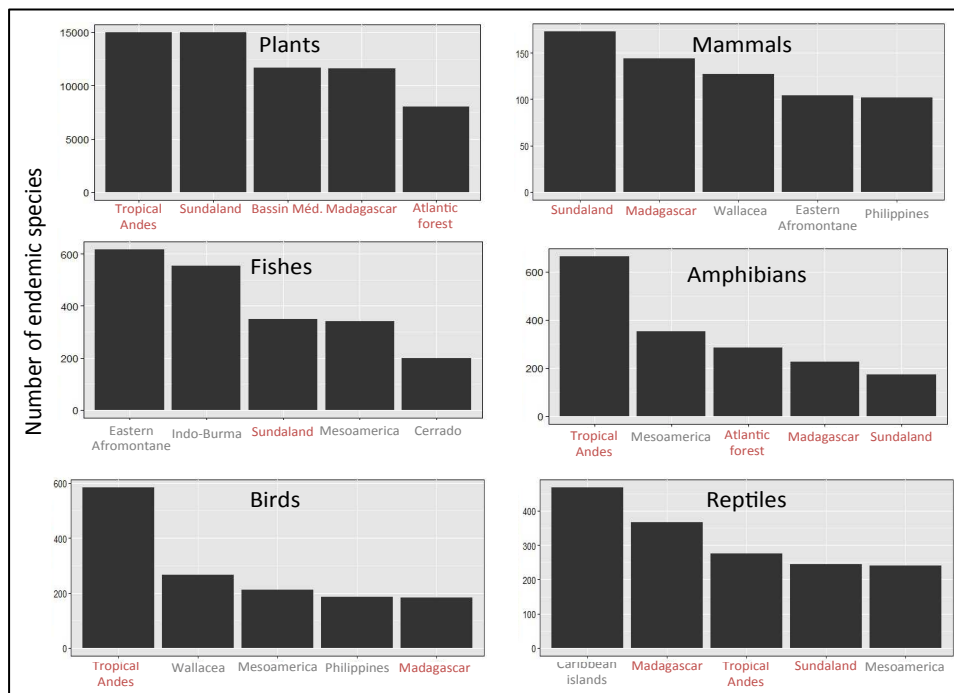


Figure 13 Nombre d'espèces endémiques maximal incluse dans les hotspots selon différents groupes taxonomiques. En rouge, le nom des cinq hotspots qui contiennent le plus grand nombre de plantes endémiques vasculaires.

6.3.PERSPECTIVES ET IMPLICATIONS

6.3.1. LES EFFETS DE LA HAUSSE DU NIVEAU DES MERS

PERSPECTIVES DE RECHERCHE

Lorsque ce travail de thèse a débuté, aucune étude n'avait analysé les conséquences de la hausse du niveau des mers sur les habitats insulaires à l'échelle planétaire. De plus, actuellement moins d'une dizaine d'études ont analysé ces conséquences sur la biodiversité à une échelle régionale ou locale (voir Fish et al., 2005; Mendoza-González, Martínez, Rojas-Soto, Vázquez, & Gallego-Fernández, 2013; Menon et al., 2010; Wetzel et al., 2013, 2012). On estime avec un degré de confiance élevé que l'érosion du littoral, les inondations et d'autres phénomènes s'accroîtront en raison de la montée du niveau des mers (Solomon *et al.* 2007b). L'étude de l'effet de la hausse du niveau des mers en est seulement à ses débuts et gagnera à être poursuivie et complétée avec l'amélioration des outils de modélisation et de la résolution spatiale des données. De plus, l'ensemble de ces études fait l'hypothèse simpliste qu'un habitat dont l'élévation est inférieure à la hausse prédite du niveau de la mer est un habitat « perdu ». L'étude de Webb & Kench (2010a) a notamment montré qu'une hausse du niveau des mers ne se traduit pas nécessairement par une perte de superficie. Il est donc recommandé d'étudier en détail la morphologie locale et la relation érosion et accrétion lorsque les données sont disponibles, afin de mieux estimer les impacts futurs de l'élévation du niveau des mers (Webb & Kench, 2010).

Il existe également une grande incertitude concernant l'ampleur de la hausse future du niveau des mers. Le rapport de l'IPCC de 2007 faisait état d'une hausse probable allant jusqu'à 59 cm d'ici à 2100 (IPCC et al., 2007), or les études actuelles prédisent une hausse qui devrait, en moyenne, plutôt atteindre le mètre (Rahmstorf, 2007; Pfeffer *et al.*, 2008; Grinsted *et al.*, 2009). Cette incertitude est principalement liée au manque de connaissance concernant la vitesse de fonte des glaciers (Hansen, 2007). Pour faire face à cette incertitude, la plupart des études utilisent différentes projections de hausse du niveau des mers allant d'un mètre à plusieurs mètres. Cependant, si nous voulons prédire de façon plus précise les futures pertes d'habitats, nous avons besoin de prédictions plus robustes.

De plus, l'amélioration des prédictions est également largement dépendante des données d'élévation utilisées. Il a par exemple été montré que pour des modèles plus complexes avec des données plus précises, un changement dans l'élévation de l'ordre de quelques centimètres peut avoir des conséquences importantes (Gesch, 2009). Il est donc

indispensable d'améliorer à la fois les connaissances sur les prédictions des futures hausses du niveau des mers et sur les modèles d'élévation à l'échelle planétaire.

Il est également nécessaire d'étudier les effets secondaires d'une hausse du niveau des mers tels que les déplacements de population humaine ou de terres exploitées, qui risquent d'avoir des conséquences importantes pour les habitats concernés (Hoozemans *et al.* 1993; Nicholls & Lowe 2004; Wetzel *et al.* 2012). L'utilisation d'approches combinées pour étudier à la fois les effets directs du changement climatique et les effets indirects (Chapitre 7) est indispensable. Car même si les implications et les réponses à apporter sont différentes, l'ensemble des effets se produira simultanément.

IMPLICATIONS POUR LA SOCIÉTÉ

Dans le Chapitre 2 et 7, les résultats ont montré qu'une hausse du niveau de la mer d'à peine un mètre, pourrait avoir de graves conséquences pour la société humaine. En effet, environ 23% de la population mondiale habite à moins de 100 km des côtes et d'ici 2030, ce chiffre atteindra près de 50% de la population mondiale (Small & Nicholls, 2003; Bindoff *et al.*, 2007). En outre, la densité des populations du littoral est environ trois fois plus élevée que la densité moyenne (Small & Nicholls, 2003).

En outre, l'ensemble des hotspots insulaires étant des régions très peuplées (31.8% de la population humaine mondiale), les déplacements de population dû à l'élévation du niveau des mers risquent d'avoir de graves conséquences pour ces régions (voir Mittermeier *et al.*, 2012 et le Chapitre 7). En ce qui concerne l'Europe, entre 200 000 et 780 000 personnes risquent d'être affectées par les inondations d'ici à 2100 (Hinkel *et al.*, 2010).

En ce qui concerne l'économie, la zone littorale présente la plus grande concentration d'activités économiques (Nicholls & Tol, 2006). Le coût des inondations dans les 136 grandes villes côtières en 2005 était de 6 milliards de dollar par an, il pourrait atteindre 52 milliards en 2050 (Hallegatte *et al.*, 2013). Une autre étude en Europe a montré que le coût total des inondations, de l'intrusion saline et de l'érosion des terres pourrait ainsi atteindre près de 17 milliards de dollars à la fin de ce siècle en Europe (Hinkel *et al.*, 2010). Dans la thèse nous avons également mis en évidence qu'une part non négligeable de la surface du 35^{ème} hotspot utilisée pour l'agriculture ou l'exploitation risquait d'être submergées, entraînant des implications économiques particulièrement importantes (Fankhauser, 1995; Tol, 2007).

Finalement, même si l'adoption de mesures d'atténuation pourrait significativement réduire les effets d'une hausse du niveau des mers, les pays européens commencent à peine à tenir compte de ces problèmes (Tol *et al.*, 2008).

IMPLICATIONS POUR LA BIODIVERSITE

Dans le Chapitre 2, nous avons vu que les implications de la hausse du niveau des mers pourraient être très importantes. Cependant, notre évaluation de la part de la biodiversité affectée s'est limitée à dénombrer le nombre d'espèce dont l'habitat pourrait être touché. Quelques études ont évalué l'impact d'une hausse du niveau des mers à l'échelle d'une seule espèce (Fish *et al.* 2005; Linhoss *et al.* 2013; Mendoza-González *et al.* 2013) mais les conséquences à l'échelle des communautés, ou des écosystèmes sont encore inconnues. Pour autant, certaines communautés des zones d'estuaires qui sont biologiquement très riches, risquent d'être les premières communautés à être inondées. De plus, les effets physiologiques d'une inondation à l'échelle des organismes sont également absents de la littérature.

Pourtant, il est indispensable d'étudier les réponses des espèces à la hausse du niveau des mers. Si le taux d'augmentation du niveau des mers est suffisamment lent, la végétation sera potentiellement capable de migrer et la perte de biodiversité sera ainsi réduite. Cependant, si la vitesse d'augmentation est trop importante alors les espèces ne seront pas capables de s'adapter suffisamment rapidement et les pertes de biodiversité seront ainsi plus importantes. Dans ce dernier scénario, il sera indispensable de maintenir et de développer les corridors écologiques qui permettront aux espèces de migrer (Pearson & Dawson, 2003). Les implications pour la conservation seront donc potentiellement très importants (McLeod *et al.*, 2010), en particulier pour les populations présentes sur des îles complètement submergées qui sans intervention humaine sont vouées à disparaître.

IMPLICATIONS POUR LA CONSERVATION

Dans ce qui suit, je me suis concentrée sur les implications pour la conservation de la hausse du niveau des mers dans les écosystèmes insulaires. Cette question a fait l'objet d'un court manuscrit actuellement soumis dans la section *Policy forum* de TREE (voir Annexe 4). De nombreux programmes de recherches ont mis en œuvre des priorités d'éradications dans les îles ces dernières années (Armstrong & Seddon, 2008; Keitt *et al.*, 2011). Les principaux critères qui ont été pris en compte dans ces programmes sont : la biodiversité menacée, la faisabilité de l'éradication, le coût économique et la possibilité de nouvelles invasions (Brooke *et al.*, 2007; Donlan & Wilcoxon, 2009; Ratcliffe *et al.*, 2009; Capizzi *et al.*, 2010; Harris *et al.*, 2012). Cependant, ces modèles de hiérarchisation ne prennent pas en compte les menaces potentielles de la hausse du niveau des mers ou de l'exposition aux changements climatiques (néanmoins voir Linhoss *et al.*, 2013; McLeod *et al.*, 2010). Dans ce manuscrit nous avons notamment mis en évidence que sur les 604 éradications insulaires de vertébrés

qui ont eu lieu pendant les dernières décennies, 26 îles seraient complètement submergées en raison d'une hausse du niveau de la mer d'un mètre. Par conséquent, dans certaines îles les efforts de restauration menés afin de sauver les espèces endémiques à long terme pourraient être vains.

Ainsi, le dernier recours pour ces espèces serait alors des actions de translocation (Thomas, (2011) mais voir aussi Webber *et al.*, (2011). Trois scénarios généraux de conservation peuvent être proposés dans le cas des espèces insulaires menacées. Tout d'abord, l'espèce peut être déplacée dans une île proche où des informations paléo-écologiques montrent que l'espèce a déjà été présente sur cette île et qu'elle sera capable d'y survivre à long terme et ne deviendra pas invasive. Cette approche est déjà utilisée dans des programmes de réintroductions, en outre, elle est particulièrement adaptée dans le cas des oiseaux tropicaux du Pacifique où les données historiques sont abondantes (Steadman & Martin, 2003; Steadman, 2006). La seconde option implique quant à elle de déplacer l'espèce vers un habitat favorable sans justification historique de la présence de l'espèce sur cette île. Dans ce cas, l'utilisation de modèles de distribution d'espèces permettra d'aider à identifier des régions qui sont actuellement favorables ou qui le deviendront dans le future (Chauvenet *et al.*, 2013). Enfin, la dernière option serait de déplacer temporairement l'espèce vers des sanctuaires *ex situ*, jusqu'à ce qu'un habitat favorable à long terme soit découvert ou restauré. Par exemple, le rétablissement des Kakapos (*Strigops habroptilus*) en Nouvelle-zélande a été possible grâce à une translocation initiale sur des îles exemptes de prédateurs. En parallèle, deux grandes îles font l'objet de travaux de restauration écologique afin de préparer un habitat approprié pour le Kakapo, qui permettrait sa survie à long terme sans intervention humaine (Edge *et al.*, 2011).

Pour conclure, nos résultats suggèrent qu'il est nécessaire de développer des programmes de recherche qui tiennent compte des effets directs et indirects de l'élévation du niveau des mers, afin d'identifier et de protéger les habitats mais aussi les espèces vulnérables et ainsi maximiser « le retour sur investissement » des programmes de conservation mis en œuvre.

6.3.2. INTERACTIONS ENTRE LES CHANGEMENTS CLIMATIQUES, LES CHANGEMENTS D'OCCUPATION DES SOLS ET LES INVASIONS BIOLOGIQUES

PERSPECTIVES DE RECHERCHE

La menace que pose actuellement les espèces invasives continue d'augmenter et cela malgré des progrès significatifs de gestion des espèces invasives et de l'adoption de politiques de lutte contre la propagation de ces espèces. De façon générale, les changements climatiques, le changement d'utilisation des sols et la poursuite du développement du commerce mondial risquent d'augmenter les opportunités d'introduction d'espèces non-natives. En outre, les changements climatiques et d'utilisation des sols peuvent affecter directement le succès des invasions en augmentant la survie, la reproduction et l'aire de distribution favorable, mais également indirectement en créant des perturbations dans les habitats ce qui diminuera la résistance des communautés naturelles aux invasions. Dans le cadre de cette thèse, je me suis donc intéressée à comprendre comment le changement climatique futur et le changement d'utilisation des sols pourraient affecter l'aire de distribution potentielle des espèces invasives. Pour cela, je me suis uniquement penchée sur les facteurs abiotiques extrinsèques. Or, de nombreux facteurs intrinsèques aux espèces, en particulier chez les plantes, expliquent le succès invasif de ces espèces, tels qu'un taux de reproduction élevé ou encore la présence d'organes clonaux (Cadotte *et al.*, 2006; Pysek & Richardson, 2007). Une des pistes qui me semble donc prometteuse serait d'analyser les facteurs intrinsèques aux espèces qui les prédisposent à envahir un nouvel habitat et à le modifier significativement. L'usage de modèles hybrides qui utilisent des modèles de distribution d'espèces pour contraindre les paramètres de modèles mécanistiques (survie ou taux de dispersion) n'en est qu'à ses débuts et devra être développé. En effet, ces méthodes semblent très prometteuses pour prédire la répartition potentielle des futures espèces invasives et leur dynamique de populations (Gallien *et al.*, 2010). L'étude des traits biologiques permettrait également d'identifier les espèces non-natives ayant un potentiel invasif important (voir à ce sujet Pysek & Richardson, 2007) et permettrait également de prédire leurs impacts (Pyšek *et al.*, 2012).

D'autres facteurs extrinsèques, tels que les caractéristiques de l'habitat à envahir sont également déterminants dans le succès des invasions et devront être pris en compte. Par exemple, les habitats présentant une haute diversité en espèces offrent une meilleure résistance aux « envahisseurs », alors que les habitats avec peu d'espèces facilitent leur implantation (Roura-Pascual *et al.*, 2011 et Chapitre 4). L'influence des activités humaines

peut également être particulièrement importante à la fois car ces activités contribuent aux transports des espèces invasives mais également car elles contribuent à la dégradation des habitats (Chytrý *et al.*, 2012). Par conséquent, le succès futur d'une invasion dépend à la fois de ces traits biologiques qui permettront à l'espèce de s'adapter ou non au nouvel environnement, de se reproduire, de se disperser et d'être capable d'entrer en compétition avec les espèces des communautés locales, mais ce succès est également fortement dépendant de l'habitat et du climat de la nouvelle région envahie et de l'invasibilité de la communauté locale. Afin d'avoir une vision globale de l'effet des changements climatiques et d'utilisation des terres sur les espèces invasives, il est important de considérer l'ensemble des facteurs intrinsèques et extrinsèques qui influencent le processus d'invasion.

IMPLICATION POUR LE FUTUR DE LA BIODIVERSITE

Nous avons vu dans le Chapitre 5 que les changements climatiques et les changements d'utilisation des sols pourraient augmenter le nombre d'espèces invasives qui trouveraient des conditions favorables dans certaines régions dans le futur. L'établissement de nouvelles espèces invasives pourrait avoir un impact direct au niveau des communautés, par exemple, en réduisant la richesse spécifique des plantes ou leur diversité (Hejda *et al.*, 2009; Richardson & Gaertner, 2013). Au contraire, l'arrivée d'un nombre important d'espèces non natives dans les îles pourrait conduire à des naturalisations (Sax & Gaines, 2008), et ainsi augmenter la richesse spécifique de ces dernières, si ces apports sont supérieurs aux pertes d'espèces natives dues aux invasions. En outre, les nombreux déplacements d'aire de répartition des espèces invasives ou non natives (Peterson *et al.*, 2008 et Chapitre 5) pourraient induire d'importantes réorganisations des communautés biologiques dans les prochaines décennies. La présence d'espèces invasives peut également altérer les structures des écosystèmes et parfois même dégrader des services éco-systémiques (e.g., (Bergstrom *et al.*, 2009; Vilà *et al.*, 2010; Pyšek & Richardson, 2010). Cependant, il est actuellement très difficile de démontrer les impacts des invasions biologiques sur la biodiversité, par conséquent évaluer leurs conséquences sur la biodiversité dans le futur reste un défi majeur pour les décennies à venir. De même, nous avons démontré que les changements climatiques et les changements d'utilisation des sols pourraient diminuer les conditions environnementales favorables de certaines espèces invasives, et il serait ainsi possible de restaurer des populations natives, si les conditions restent favorables pour ces espèces (Bradley *et al.*, 2009) et qu'une gestion active de ces espèces invasives est mis en œuvre dans ces régions.

IMPLICATION POUR LA GESTION DES ESPECES INVASIVES

Le changement climatique peut altérer l'ensemble des étapes du processus d'invasion mais également le coût et la faisabilité des actions de gestion (Hellmann *et al.*, 2008). Nous avons vu dans le Chapitre 5 que les changements climatiques et les changements d'utilisation des sols pourraient augmenter le nombre d'espèces invasives qui trouveraient des conditions favorables dans le futur mais également diminuer ce nombre dans certaines régions. La richesse en espèces invasives est considérée comme un bon indicateur du risque d'invasions (Catford *et al.*, 2012). Pour autant l'utilisation de ce type d'indicateurs n'est pas encore répandu bien qu'il pourrait permettre d'établir des priorités pour les régions vulnérables. La prévention reste le moyen le plus efficace et le moins coûteux pour gérer les espèces invasives (Pluess *et al.*, 2012; Simberloff *et al.*, 2012). Des systèmes d'évaluation du risque pour les plantes ont été mis en place en Australie avec succès (>90% des invasives ont été correctement identifiés (Gordon *et al.* 2008)), mais également en Nouvelle Zélande, aux Etats Unis (Gordon *et al.*, 2008) et au Japon (Nishida *et al.*, 2008). L'utilisation de modèles de distributions d'espèces permet même d'évaluer les plantes qui sont les plus susceptibles de poser problème sur le plan national en Australie (NTA, 2007). L'Europe est également en train de travailler sur une législation permettant la mise en place d'une prévention efficace contre les espèces invasives. La mise en place de listes noires intégrant les futures espèces potentiellement envahissantes dans les grands sites d'échanges commerciaux et humains (aéroports et ports) pourrait permettre d'identifier les espèces et de limiter leur arrivée. Cependant les moyens actuellement mis en place d'un point de vue législatifs (Butchart *et al.*, 2010) ou logistiques sont encore très insuffisants. Par ailleurs, la mise en place de législation prenant en compte l'évolution des processus d'invasion dus aux changements climatiques est actuellement manquante (Mainka & Howard, 2010).

En outre, la diminution des conditions environnementales propices pour certaines espèces invasives localement pourrait créer des conditions favorables au contrôle de ces dernières, en particulier dans les îles. De plus, de nombreuses améliorations ont été mises au point et appliquées ces dernières années pour contrôler ou éradiquer les espèces invasives (Pluess *et al.*, 2012). Sur 784 programmes d'éradications de vertébrés invasifs conduits dans les îles seuls 88 ont échoués (Pluess *et al.*, 2012). Il est possible que les changements climatiques et d'utilisation des sols apportent des conditions environnementales moins favorables et donc rendent certaines espèces invasives moins compétitives et diminuent leur

aire de répartition (Bradley *et al.*, 2009), facilitant ainsi les programmes de gestion des espèces invasives.

Il est important de noter qu'à la fois la surestimation et la sous-estimation de la présence d'espèces invasives peuvent avoir d'importantes implications dans le cadre de la gestion de ces dernières. La sous-estimation peut conduire à l'apparition et à la propagation d'une espèce invasive dans des régions où des mesures de confinement ou de surveillance n'ont pas été mises en œuvres. Au contraire, une surestimation de la présence d'espèces invasives peut conduire à une perte de temps et d'effort de gestion dans certaines régions (Baxter & Possingham, 2011).

IMPLICATION POUR LA DÉFINITION DES ESPÈCES INVASIVES

Finalement, les changements climatiques vont également avoir d'importantes implications pour la définition même de ces espèces invasives. Généralement, une espèce invasive est définie comme une espèce exotique (non-native) qui a été introduite délibérément ou non par l'homme. Une espèce est dite invasive si elle est capable de se reproduire et de s'étendre dans l'écosystème d'accueil (Richardson *et al.*, 2000), mais aussi si cette espèce a des conséquences écologiques ou économiques néfastes (Lodge *et al.*, 2006). Seuls certains scientifiques ne tiennent pas compte de la notion d'impact pour définir une espèce invasive car il est en réalité compliqué de démontrer l'impact des espèces invasives, notamment en raison du temps de latence entre l'arrivée d'une espèce, son expansion et ses conséquences sur la biodiversité.

Il est vrai que dans un contexte de changements climatiques, une re-définition des espèces invasives semble nécessaire (Hellmann *et al.*, 2008; Walther *et al.*, 2009). En effet, de nouvelles espèces pourraient devenir invasives, d'autres espèces actuellement invasives pourraient diminuer leur aire de distribution mais également leur impact et de nombreuses espèces natives pourraient déplacer leur aire de distribution dans de nouvelles régions où elles étaient absentes (Hellmann *et al.*, 2008). Ainsi, une petite partie de la communauté scientifique prône l'abandon de la distinction entre les espèces natives versus non-natives et les espèces transportées par l'homme versus par d'autres vecteurs (Davis, 2009; Valéry *et al.*, 2009, 2013). Une nouvelle définition basée sur l'implication de l'homme à au moins une étape du processus d'invasion a finalement été proposée (Engel *et al.*, 2011), dans ce cas les espèces amenées par des événements climatiques extrêmes (dont l'augmentation est indirectement due à l'homme) seraient incluses dans cette définition. Il faut noter que le débat

reste ouvert et qu'aucun consensus n'a encore été adoptée dans la communauté scientifique à propos des implications des changements climatiques sur cette définition.

6.3.3. MENACES SUR LES HOTSPOTS DE BIODIVERSITE ET HIERARCHISATION FACE AUX CHANGEMENTS GLOBAUX.

PERSPECTIVES DE RECHERCHE

Dans cette partie nous nous sommes intéressé à l'effet des menaces futures sur les hotspots de biodiversité. Les hotspots ont été définis par Myers comme des régions qui sont à la fois irremplaçables du point de vue de la biodiversité, mais également extrêmement menacées. Le recensement de telles zones a permis d'identifier 35 régions dans le monde présentant des caractéristiques exceptionnelles en terme de biodiversité mais ayant également des environnements très dégradés. Ces hotspots de biodiversité ont un taux d'endémisme remarquable avec près de 1 500 espèces de plantes vasculaires endémiques, et près de 22 939 espèces de vertébrés terrestres soit 77% des vertébrés de la planète. En outre, les hotspots de biodiversité possèdent un taux élevé de diversité taxonomique (Williams *et al.*, 2011). L'habitat initial de ces hotspots a été particulièrement dégradé avec près de 85% de l'habitat initial aujourd'hui détruit. Cependant, le recensement de ces régions débuté dans les années 2000, a permis d'en faire des priorités en terme de conservation. En effet, cela a permis de mobiliser des fonds significatifs pour la conservation dans ces régions (Myers *et al.*, 2000). Par exemple, entre 2000 et 2010, huit hotspots ont permis de soulever plus de 400 subventions pour un total de 110 millions de dollars. Cependant, les stratégies de conservation des hotspots n'ont jusqu'à aujourd'hui pas tenu compte des menaces futures qui pourraient peser sur ces régions. Nous avons donc cherché à déterminer l'importance de la prise en compte de ces menaces dans ces régions et à proposer des recommandations de conservation, notamment en terme de priorité, pour ces différents hotspots.

Ce travail a permis de définir certains hotspots comme prioritaires dans le cadre des changements globaux. Cette hiérarchisation a été établie en fonction du nombre de plantes endémiques présent dans ces hotspots. Cependant, l'approche utilisée dans cette partie a ses limites. En particulier, il serait intéressant de hiérarchiser les hotspots de biodiversité en fonction de la richesse des autres groupes taxonomiques, ou de la biodiversité fonctionnelle ou phylogénétique. Cette analyse permettrait de comparer les différentes hiérarchisations et d'identifier les composantes de la biodiversité qui seraient sous-représentées. Par exemple,

alors que la diversité fonctionnelle est actuellement sous-représentée dans les aires protégées en France, la diversité taxonomique est quant à elle surreprésentée (Devictor *et al.*, 2010).

En outre, comme mentionné dans la section limite 6.3.2, nous avons tenu compte des menaces en moyennant les différents rangs de ces menaces par hotspot. Cependant, il est possible qu'il existe un recouvrement des différentes menaces. Il est donc important de pouvoir distinguer les recouvrements de menaces, et ainsi de déterminer les régions soumises à une combinaison de menaces. Par ailleurs, notre étude se restreint aux effets des changements globaux à la fin de ce siècle. Or les différentes menaces qui pèsent sur ces régions risquent d'évoluer au cours du temps. Par exemple, une étude récente a montré que les conséquences initiales des invasions peuvent être très importantes mais qu'une stabilisation des impacts peut se produire après plusieurs années chez les plantes (Dostál *et al.*, 2013). Par conséquent, les recommandations de conservation peuvent également évoluer au cours du temps et doivent être révisés en permanence. Il serait donc pertinent d'étudier l'évolution dans le temps du recouvrement de ces menaces et ainsi établir des stratégies de conservation qui ne soient pas figées dans le temps. C'est pourquoi nous avons prévu de tenir compte de ces recouvrements et de la dimension temporelle de l'ensemble des différentes menaces (hausse du niveau des mers, analyse de changements climatiques, risque d'invasion) sur les 35 hotspots de biodiversité dans de futures études, en se basant sur les travaux précédents dans ce domaine comme Evans *et al.*, (2011) et Coll *et al.*, (2012).

IMPLICATION DE LA VULNERABILITÉ AUX CHANGEMENTS GLOBAUX POUR LA BIODIVERSITÉ DES HOTSPOTS

Les implications des changements climatiques et des changements d'utilisations des sols pour la biodiversité sont difficiles à déterminer. Cependant, il a été démontré que le développement de nouvelles communautés de plantes non analogue durant la dernière ère glaciaire était associé à la présence de nouveaux climats (Williams & Jackson, 2007). Ainsi, il est possible que de nouvelles communautés de plantes se forment dans les hotspots dans lesquels de nouveaux climats vont apparaître dans le futur. En outre, les déplacements d'aires de distribution des espèces peuvent également aboutir à des modifications des assemblages d'espèces (Devictor *et al.*, 2008). Au cours du siècle dernier, des changements de composition des communautés en raison des changements climatiques ont déjà été mis en évidence (Moritz, 2008). Finalement, de nouvelles interactions spécifiques pourront se développer au sein des futurs assemblages non analogues aux assemblages d'espèces actuels, ce qui pourra entraîner le déclin d'autres espèces. De plus, dans le Chapitre 7, nous avons montré que les

habitats naturels tels que les parcs nationaux pourraient être particulièrement exposés aux changements de climats locaux, et qu'ils sont aujourd'hui insuffisamment protégés. De même, les résultats du chapitre 6 ont démontré que les habitats naturels vont diminuer dans certains hotspots, menaçant ainsi les espèces qu'ils abritent. Par conséquent, de nombreuses espèces présentes dans ces hotspots pourraient être vouées à disparaître si elles ne sont pas capables de s'adapter (Lavergne *et al.*, 2010; Peñuelas *et al.*, 2013). Par ailleurs, une large proportion des terres issues de l'agriculture ou de la production pourrait être exposée aux changements climatiques, ce qui pourrait entraîner une accélération de la perte d'habitats naturels à cause du déplacement de ces dernières.

IMPLICATION POUR LA CONSERVATION DES HOTSPOTS DE BIODIVERSITÉ

Dans les chapitres 6 et 7 de cette thèse, nous avons tenté d'établir des priorités de conservation pour les différents hotspots de biodiversité. Un résultat important mis en évidence, est qu'il est essentiel de tenir compte des menaces futures qui pèsent sur les hotspots de biodiversité. Jusqu'à présent ces hotspots ont été sélectionnés sur des menaces passées, et les stratégies de conservation ont majoritairement été établies sur ces critères. Cette thèse a permis de révéler qu'ils seront impactés par les changements globaux dans le futur et qu'il est possible de mettre en place des moyens de conservation pour limiter les effets de ces menaces. Par ailleurs, identifier les régions clefs qui méritent une attention particulière est un premier pas essentiel pour développer des stratégies de conservation à l'échelle régionale comme souligné par Maiorano *et al.*, (2012).

De manière générale, les stratégies de conservation peuvent s'appliquer au niveau des habitats au sein même des hotspots. Ils peuvent impliquer (i) Le maintien des aires protégées actuelles. Beale *et al.* (2013) a par exemple montré que le maintien des aires protégées est une stratégie de conservation efficace qui a jusqu'à présent permis de maintenir les 139 populations d'oiseaux de la savane tanzanienne en dépit des changements climatiques et environnementaux entre 1960-2006. En outre, le maintien des aires protégées actuelles a un coût relativement faible (Mittermeier *et al.*, 2003) en comparaison avec la création de nouvelles zones de conservation. De plus, (ii) L'établissement de nouvelles aires protégées et l'augmentation des statuts de conservation de ces dernières le long de gradient latitudinaux et altitudinaux est également une stratégie de conservation applicable au sein des hotspots. En effet, en raison du réchauffement climatique, les espèces vont avoir tendance à se déplacer vers les latitudes et altitudes plus élevées (Hickling *et al.*, 2006). Ces déplacements d'aires de répartition pourraient conduire les espèces en dehors des zones protégées, comme le

suggèrent de nombreuses études (Hannah *et al.*, 2005; Hole *et al.*, 2009). (iii) Une augmentation de la connectivité entre les aires protégées par la création de corridors permettront également à la biodiversité de se déplacer afin d'atteindre l'habitat favorable (Hodgson *et al.*, 2009). Actuellement, la superficie des hotspots qui est protégée est de 12% (Williams *et al.* 2011). Un des objectifs établis lors de la dernière conférence de la convention pour la conservation de la biodiversité est d'atteindre les 17% d'aires protégées d'ici à 2020. Ainsi, tenir compte des futures menaces qui pèsent sur ces régions afin d'atteindre les 17% semblent être une stratégie pertinente. Même si en pratique, le renforcement des stratégies de conservation dépend également largement des populations locales dont il est indispensable de tenir compte lors de l'établissement de nouvelles zones de conservation.

Par ailleurs, la conservation au sein des hotspots devra également (iv) directement impliquer une gestion active à l'échelle des espèces. Par exemple, en privilégiant la translocation de populations qui sont très menacées et dont l'intérêt écologique est important (Thomas, 2011). Enfin, (v) il est également possible de réduire les pressions des autres menaces qui pèsent sur ces espèces vulnérables. Par exemple, la présence d'espèces invasives en raison d'une forte pression de propagule, peut être limitée en créant des zones tampons et en augmentant la surveillance aux abords des aires protégées (Spear *et al.*, 2013). Le contrôle et la prévention de l'arrivée de nouvelles espèces sont des moyens de gestion indispensables pour ne pas augmenter la pression sur la biodiversité. En particulier, car la population humaine augmente rapidement dans ces régions (Williams, 2011) et qu'elle est un facteur majeur expliquant la distribution de ces espèces invasives. Enfin, une étude récente a montré qu'il était possible d'établir différentes stratégies de conservation permettant d'augmenter la capacité adaptative des écosystèmes, selon la qualité des habitats des écorégions et la stabilité climatique future à laquelle ils seront soumis (Watson *et al.*, 2013). Il serait donc intéressant d'étudier comment appliquer de telles stratégies de conservation pour les hotspots de biodiversité.

6.4. CONCLUSION GÉNÉRALE

L'objectif général de ce travail de thèse était d'améliorer la connaissance sur la caractérisation et la quantification des impacts des changements climatiques sur la biodiversité, à l'échelle mondiale, par des approches de modélisations et de méta-analyses. Le message le plus important de cette thèse est que **les effets des changements climatiques risquent d'augmenter la pression qui pèse sur la biodiversité dans le futur**. Par exemple, nos résultats ont montré que près de 6% des îles des hotspots insulaires pourraient être submergées, conduisant à une augmentation du risque d'extinction pour près de 300 espèces endémiques. De plus, nos résultats ont révélé que les hotspots seraient particulièrement vulnérables aux changements climatiques avec une perte moyenne de 31% de leur climat actuel. **En outre, les conséquences des changements climatiques sur la biodiversité peuvent être renforcées en raison de l'interaction avec d'autres menaces**. Par exemple, dans le Chapitre 5 nous avons notamment montré que les changements climatiques et les changements d'utilisation des sols pourraient altérer les invasions biologiques. De plus, le Chapitre 6 a révélé que la majorité des hotspots sont menacés par différents changements globaux. **Finalement, les conséquences de ces menaces vont directement et indirectement affecter les espèces, les habitats, mais également les populations humaines**. En effet, le Chapitre 7 a illustré comment les changements climatiques et la hausse du niveau des mers vont affecter à la fois les parcs nationaux, la population humaine et l'agriculture.

Nous sommes actuellement dans la 6^{ème} crise d'extinction d'espèce et la perte de la biodiversité s'intensifie chaque année, malgré des efforts notables de la communauté scientifique pour alerter le grand public. Néanmoins, à l'avenir si nous voulons mettre en œuvre des stratégies de conservation efficaces, il est indispensable de développer des collaborations étroites avec les acteurs locaux tels que les gestionnaires des parcs nationaux. En effet, la mise en œuvre de plans de gestion de sauvegarde d'habitats ou d'espèces ne peut se faire qu'en intensifiant les collaborations avec l'ensemble des acteurs impliqués. En outre, il est de la responsabilité du monde scientifique de diffuser les connaissances accumulées afin d'informer le grand public et les grandes instances gouvernementales sur les risques encourus. En effet, bien que le monde scientifique continue à intensifier ses recherches sur cette thématique et que des progrès majeurs aient été réalisés dans ce domaine, il reste un décalage important entre le monde de la recherche et la prise de conscience de cette menace par le public. En outre, sans le soutien du public, la mise en œuvre de stratégies d'atténuations et d'adaptations efficaces dans les politiques actuelles ne pourra pas avoir lieu.

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Annexe 1 :
**Monster fern makes IUCN
invader list**

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Monster fern makes IUCN invader list

The list of 100 of the world's worst invasive alien species, compiled by the International Union for Conservation of Nature (IUCN), aims to help biodiversity conservation efforts worldwide (see go.nature.com/qa9z1g). After a position on the list fell vacant as a result of the global eradication of the rinderpest virus (see, for example, *Nature* **474**, 10–11; 2011), we coordinated the community of invasion biologists in a unique initiative to vote for a replacement.

We assessed more than 10,000 invasive species from the world's largest databases for their capacity to spread and for their potential ecological or economic impact.

More than 650 experts from 63 countries then voted on the ten candidate species we shortlisted, and selected the giant salvinia (*Salvinia molesta*), an aquatic fern.

Native to Brazil, this fern has spread throughout the tropics and subtropics. It doubles in abundance within days, forming thick, floating mats that block light from expanses of water, reduce its oxygen content and degrade water quality. They also impede water-based transport, clog irrigation and power-generation systems, and harm local fisheries.

Now in the global spotlight, this new entrant to the IUCN list is set to increase public awareness of the harm caused by invasive species and to stimulate more discussion in science and policy circles.

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Avoid more organ transplant scandals

Our institution is launching an international transdisciplinary initiative to improve the lamentable state of solid-organ

transplantation in Germany and to help fulfil society's obligations towards millions of organ donors and recipients worldwide (see go.nature.com/z5b7uo).

The mortality rate following liver transplantation has risen alarmingly across the country over the past few years. The survival rate after one year is only 72% in Germany, which is 20% lower than in the United States and the United Kingdom, even though Germany has more transplant centres and fewer organ donors per capita (see go.nature.com/pgmrpn; in German). Such scandals are leading to a steady decline in altruistic organ donations, with an 18% drop in the first quarter of this year compared with the same period in 2012.

The situation largely reflects the weak regulation of organ transplantation in Germany, especially by comparison with other countries such as the Netherlands and Denmark (C. Metz and N. Hoppe *Eur. J. Health Law* **20**, 113–116; 2013). Proposals to rectify this include setting up an independent institute of transplantation medicine that has regulative and standard-setting powers (see go.nature.com/yzl4km; in German).

A lack of good prognostic models compounds the likelihood of transplantation failure. Such models would allow clinical urgency to be weighed against transplantation outcome. We are therefore planning systematic multicentre trials to evaluate the prognostic value of liver-allocation scores.

Our initiative also aims to address the dearth of quality-management systems that are properly founded on comprehensive, evidence-based data and on precise methodology that considers patients' needs and expectations.

The early results are promising. We intend to publish regular updates to provide essential information to the transplantation community and

to ensure openness to the public.

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Satellites: make data freely accessible

The cost of accessing satellite data is hampering the widespread application of satellite monitoring, a vital tool for controlling deforestation (Jim Lynch *et al. Nature* **496**, 293–294; 2013) and for biodiversity assessments. We urge government agencies that produce taxpayer-funded satellite images to make these available free of charge and in user-friendly formats.

Lynch and colleagues' call for daily satellite observations of forests worldwide would mean aggregating information from numerous satellites that are operated by many countries. Assembling the large data sets needed for global monitoring would be prohibitively expensive, however, because national governments do not have a free-access policy for their satellite images.

One solution would be to combine data from the US Landsat satellites with those from the European Space Agency's planned Sentinel-2 satellites, which could deliver optical imagery with global coverage every 3–5 days. The distribution of Landsat imagery has increased by two orders of magnitude since 2008, when the US Geological Survey made all the data free to access online. Data from NASA's MODIS and all of their Earth-observation imagery are also available for free, as are data from the China–Brazil Earth Resources Satellite programme.

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Satellites: ambition for forest initiative

We disagree strongly with the suggestion by Jim Lynch and colleagues that the outputs of the Global Observation of Forest and Land Cover Dynamics panel and the Global Forest Observations Initiative “lack ambition and an understanding of the potential of satellites” (*Nature* **496**, 293–294; 2013).

As participants in these programmes and in the United Nations Programme on Reducing Emissions from Deforestation and Forest Degradation (UN-REDD), we aim to show how remote sensing can help systematic global monitoring to make REDD+ a reality in the context of wider societal engagement. (REDD+ is a climate-mitigation initiative under the UN Framework Convention on Climate Change (UNFCCC).)

We also question the feasibility of Lynch and colleagues' call for rapid-response satellite monitoring of deforestation to be enshrined in international law under the UNFCCC, given national sovereignty concerns and the fact that we are not yet in a position to mitigate the problems of cloud cover. Although radar can penetrate cloud, the technology cannot yet capture changes in forest ecosystems in a systematic and repeatable way.

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CONTRIBUTIONS

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**Supplementary information to:
Monster fern makes IUCN invader list**

Full list of co-signatories to a Correspondence published in *Nature* **498**, 37 (2013);
<http://dx.doi.org/10.1038/498037a>.

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Citation :

Luque G. M., Bellard C., Bertelsmeier C., Bonnaud E., Genovesi P., Simberloff D. and Courchamp F. 2013. Monster fern makes IUCN invader list. *Nature*, 498 : 37

Annexe 2 :

**Impact of sea level rise on
the french islands worldwide.**

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Potential impact of sea level rise on French islands worldwide

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Academic editor: *Klaus Henle* | Received 16 May 2013 | Accepted 21 August 2013 | Published 2013

Citation: Bellard C, Leclerc C, Courchamp F (2013) Potential impact of sea level rise on French islands worldwide. *Nature Conservation* 13(1): 1-10. doi: 10.3897/natureconservation.v13i1.5533

Abstract

Although sea level rise is one of the most certain consequences of global warming, yet it remains one of the least studied. Several studies strongly suggested that sea level rise will accelerate in the future with a potentially rise from 0.5 to 2 m at the end of the century. However, currently island conservation programs do not take into account the potential effects of sea level rise. Therefore, we investigated the potential consequences of sea level rise for 1,269 French islands worldwide, by assessing the total number of island that will be totally submerged for three different scenarios (1, 2 and 3 m). Under the worst scenario, up to 12% of all islands could be entirely submerged. Two regions displayed the most significant loss of island: New Caledonia and French Polynesia. Focusing on New Caledonia, we highlighted that endemic plant species that are already classified as critically endangered by the IUCN will be the most vulnerable to sea level rise. Losses of insular habitats will thus be important in the next decades for the French islands. Given that French islands covers all latitudes in the Pacific, Indian and Atlantic oceans and in the Mediterranean, our results suggested that the implications for the 180 000 islands around the world should be considerable. Therefore, decision makers are required to define island conservation priorities that will suffer of the future sea level rise.

Keywords

French islands, sea level rise, insular biodiversity, climate change

Introduction

Despite considerable attention to global change effects, few studies focused on the consequences of sea level rise (Menon et al. 2010; Wetzel et al. 2012; Schmidt et al. 2012). Many studies showed that global warming will be one of the biggest threat to future biodiversity, and predictions could play an important role in alerting scientists and decision makers to support the development of proactive strategies to reduce climate change impacts on biodiversity (Bellard et al. 2012). Potential effects of sea level rise are of considerable interest because of its potential impact on biodiversity and society. By 2030, 50% of the world population will live within 100 km of the coast (Small and Nicholls 2003; Bindoff et al. 2007). The two major causes of global sea level rise are thermal expansion of the oceans (water expands as it warms) and the loss of land-based ice due to increased melting. During recent years, for which the observing system is much better, thermal expansion and melting of land ice each account for about half of the observed sea level rise (Solomon et al. 2007). Several recent studies strongly suggest that sea level rise will increase by 0.5 to 2.3 m at the end of the century (Rahmstorf 2007; Pfeffer et al. 2008; Grinsted et al. 2009; Jevrejeva et al. 2010; Nicholls and Cazenave 2010; Traill et al. 2011). Most dramatic scenarios of ice sheet melting and sliding lead to potential sea level rise of 4 to 6 m (Overpeck et al. 2006). Sea level increases could lead to the total immersion of many low-lying islands, associated with potential important consequences for biodiversity. Surprisingly, few studies have focused on consequences of sea level rise on islands and their biodiversity, only specific archipelagos that represent very limited subsets of existing islands (Baker et al. 2006; Webb and Kench 2010; Wetzel et al. 2012; Bellard et al. 2013), or on continental coastlines (Menon et al. 2010; Hinkel et al. 2010; Traill et al. 2011) have been studied. Yet, islands are generally considered as important hotspots of biodiversity due to very high endemism richness, about 70,000 vascular plant species are endemic to islands (Kier et al. 2009). In particular, among French territories, four of them are present in biodiversity hotspots. Although French islands only represent 0.08% of Earth land surface, they contain 1.4% of the plants, 3% of the molluscs, 2% of fishes, 1% of reptiles and 0.6% of birds of the world. Therefore, one could expect significant loss of insular biodiversity due to sea level rise. For example, the endangered Lower Keys Marsh rabbit (*Sylvilagus palustris hefneri*) already lost 64% of its habitat, the majority due to sea level rise (>48%) (Schmidt et al. 2012). While actions to mitigate climate change and its consequences in islands are being debated, few studies regard the potential impact of an increase of sea level on insular habitats.

Here, we assessed impacts of sea level rise on islands ($n= 1269$) under French jurisdiction. This sample includes islands of various sizes, geological types and elevations, and covers all latitudes in the Pacific, Indian and Atlantic oceans and in the Mediterranean. We investigated three scenarios of projected sea level rise on these islands, to provide estimations of loss of entire islands. First, we considered a global sea level rise by 1 m that is slightly below the average of six recent projections of sea level rise for 2100 (Overpeck et al. 2006; Rahmstorf 2007; Pfeffer et al. 2008; Grinsted et al. 2009; Jevrejeva et al. 2010; Nicholls and Cazenave 2010). We also explored another

realistic upper bound of 2 m sea level rise (Nicholls and Cazenave 2010) and an extreme scenarios of 3 m (Hansen 2007). In addition, we studied sea level rise of two different types: a uniform increase over the globe or a recent projection that considers the regional variability of sea level rise based on a synthesis of 16 sea level rise models (see Figure 2B for details). The latter projection is more realistic because heterogeneous ocean warming will lead to non-uniform thermal expansion (Cazenave and Llovel 2010) and leads to average rises of 1.05, 2.10 and 3.15 m, hereafter termed ~ 1 m, ~ 2 m and ~ 3 m in order to compare with homogeneous rises.

For each scenario, we assessed the number of islands that would be entirely submerged, which was estimated by overlying maximal island elevation with local sea level projections. These must be considered very conservative estimates of biodiversity impacts of sea level rise on islands because we only consider losses on islands that are totally submerged. Finally, we also highlighted a case study of New Caledonia taking into account partial habitat losses of islands and potential loss of endemic plant species area distribution due to sea level rise.

Materials and methods

French islands

In order to be exhaustive, we defined both islands and islets as “islands”, the only difference being the size (islet have a smaller area). The majority of islands represent single landmasses, but in some cases, mostly for atolls like Tuamotu, islands may consist of numerous islets sharing a common geological origin. France possesses around 2,000 islands across the world, but many are located in rivers or lakes. Among oceanic islands, topographic data are available for 1,269 islands that encompass all latitudes and geologic types of island ecosystems. Moreover, French islands are present in 4 of the 25 hotspots of global biodiversity including the Caribbean islands, Indian Ocean islands, Polynesia Micronesia islands, and New Caledonia islands (Myers et al. 2000). Furthermore, the French maritime domain encompasses 10% of the coral reefs and 20% of the atolls of the planet.

Elevation data

Island coordinates were derived mostly from the Geonames database (<http://www.geonames.org/>) and inspection of satellite imagery on Google earth. To obtain data on maximal elevation (*i.e.*, the difference in meters between sea level and the highest point) of each island, we used two different databases: IGN map (National Institute of Geographic information) where maximum elevation is provided for most of the studied islands (<http://www.geoportail.fr/>) and elevation data from Google Earth for the few remaining islands. For those few islands, Google Earth was used to check that at least one point in elevation was higher than the considered sea level rise.

Assessing impacts of sea level rise on islands

Sea level rise scenarios

Islands are identified as submerged if their highest elevation is below the considered sea level rise projection. We used two different scenarios of sea level rise. First, we used a homogeneous scenario, where sea level rise is equal at all latitudes and longitudes. Then, we used a heterogeneous projection of sea level, where we considered spatial variability of the rates of sea level rise, which is mostly due to non-uniform changes in temperature and salinity, and related to changes in the ocean circulation. For the homogeneous scenario, we used an uniform increase of sea level by 1, 2 and 3 meters over the globe. For the heterogeneous scenario, we used the IPCC map that represents an ensemble mean of 16 Atmosphere-Ocean General Circulation Models, under the scenario A1B, which considered regional variability. Using ArcGIS, we determined the location of each island and we attributed the sea level value of increase by 2100 that varied from 0.05 m to 0.65 m for each island according to the projected local sea level rise. Because it is impossible to obtain island elevation data in decimeter units, we rounded off to the full next meter, always making a conservative estimate when doing so (e.g., 1.8 m to 2.7 m was considered as 2 m, see Fig. 2B for details). As mean sea level rise based on the IPCC scenarios (0.35 m) is now considered too conservative (Nicholls and Cazenave 2010), we have considered three different heterogeneous projections : a mean rise of 1.05 m, 2.10 m 3.15 m to match with the homogeneous scenarios of 1, 2 and 3 m. In the main text, these are notated as ~1 m, ~2 m and ~3 m, respectively. We assumed that all Mediterranean islands will be subject to an increase in sea level from 0.35 to 0.45 m (like the Atlantic zone) because data produced for 2021-50 mean projected an increase of sea level that ranges between +7 and +12 cm (Gualdi et al. 2013).

Number of island submerged

We used total island submersion as a metric because accurate digital elevation models (DEM) are not publicly available for all these islands, especially low-lying islands that are expected to be the most vulnerable to sea level rise. Additionally, assessing sea level rise impacts on low-lying islands is impossible without high resolution because most of the current satellite-based DEMs contain biases that greatly exceed the precision required for a study of low lying island submersion (Hinkel et al. 2010).

Case study of New Caledonia

Elevation data

In order to consider partial habitat losses, we used the Digital Elevation Model (DEM) from NASA's Shuttle Radar Topography Mission (SRTM) (Jarvis et al. 2008), we did not consider connectivity of cells or lateral erosion. We also calculated the sum of the number of pixels under the 3 different sea level rise projections by island and for the entire region using R.15 version.

Endemic plant species

We obtained endemic species area distribution polygons provided by the IUCN database for each of the 64 plants (IUCN 2012). Then, we calculated the species area distribution that will be submerged under an increase of sea level by 1, 2 and 3 meters for each endemic plant species within New Caledonia according to their spatial distribution.

Results

Potential island losses

We calculated the number of islands entirely submerged under three different scenarios of sea level rise (~ 1 , ~ 2 and ~ 3 m) and two projections homogeneous and heterogeneous. Our results indicated that about 5% of islands would be entirely submerged with a globally uniform sea level rise of 1 m (Figure 1). This corresponds potentially to 64 French islands that will be vulnerable to an increase of sea level by 1 meter. The uniform increase of sea level by 3 m increased this estimate to about 11% (*i.e.*, 145 islands). Using a spatially heterogeneous sea level rise scenario, we showed greater losses ranging from 6% to 12% of submerged islands for scenarios of ~ 1 and ~ 3 m, respectively (see Figure 1 and Material and methods). This last result corresponds potentially to 83 and 156 islands that will be at risk of submersion in the future. Globally, the number of islands potentially vulnerable to sea level rise was slightly more important for heterogeneous scenarios, whereas results using homogeneous scenarios were lower. However, for all projections considered, the regions with the most important number of islands potentially threatened were New Caledonia (>30% of the total islands entirely submerged were located in New Caledonia), French Polynesia (>30%) and the Mediterranean (10%), although many islands will also be submerged in other regions such as Caribbean islands, Madagascar and Guyana (Figure 2A and Figure 3).

Consequently, rising sea would potentially threaten a considerable part of French insular biodiversity, especially in New Caledonian region. Considering that at least 5% of the number of islands will be entirely submerged under an increase of sea level by 1 meter, many plants will be endangered by an increase of sea level as well as other species located in these islands. In addition, other islands that are not under French jurisdiction but that are located in these regions could be highly vulnerable to sea level rise, and the potential losses of insular habitat could be very similar at the world scale.

New Caledonia case study

Because our results showed that New Caledonia region is particularly sensitive to sea level rise, we decided to study the potential partial losses in this region. Overall, our results showed that between 1.7 and 2% of New Caledonian area will be permanently

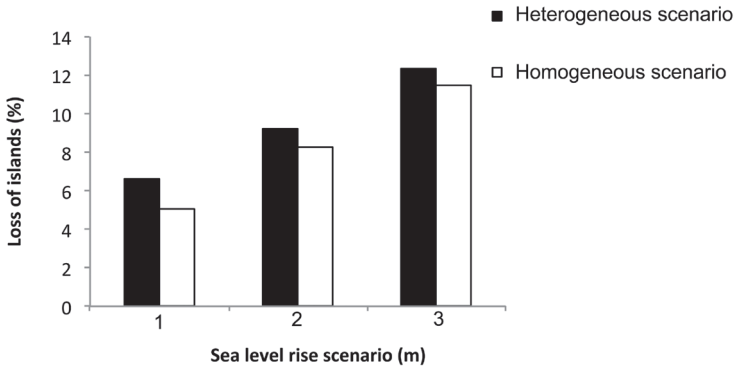


Figure 1. Percentage of islands entirely submerged under three scenarios (lower ≈1 m, middle ≈2 m and upper ≈3 meters) and two projections (homogeneous rise and heterogeneous rise).

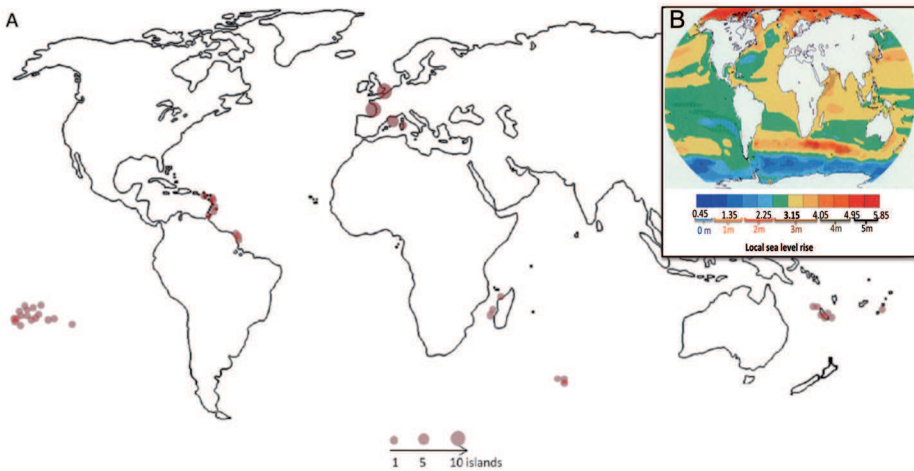


Figure 2. A Spatial distribution of submerged French islands following the pessimistic scenario (-3 m rise) **B** Local sea level change (m) due to ocean density and circulation change relative to the global average during the 21st century under SRES A1B scenario.

submerged under an increase of sea level rise by 1 to 3 meters, respectively (Figure 4AB). Taking into account partial losses of New Caledonian islands, we estimated that between 2.3% and 6.8% of islands will have more than half of their area entirely submerged. With an increase of sea level by 1 meter, 29.5% of New-Caledonian islands will have between 1 and 25% of their area inundated. Based on our results, more than 50% of islands will be safe from permanent inundation because of their high elevation profile (Figure 4C) although we recognized that indirect effects of sea level rise such as lateral erosion could lead to significant effects for these islands.

Using the endemic plant species distribution, we estimated the species area distribution that will be submerged under an increase of sea level by 1, 2 and 3 meters. We then calcu-

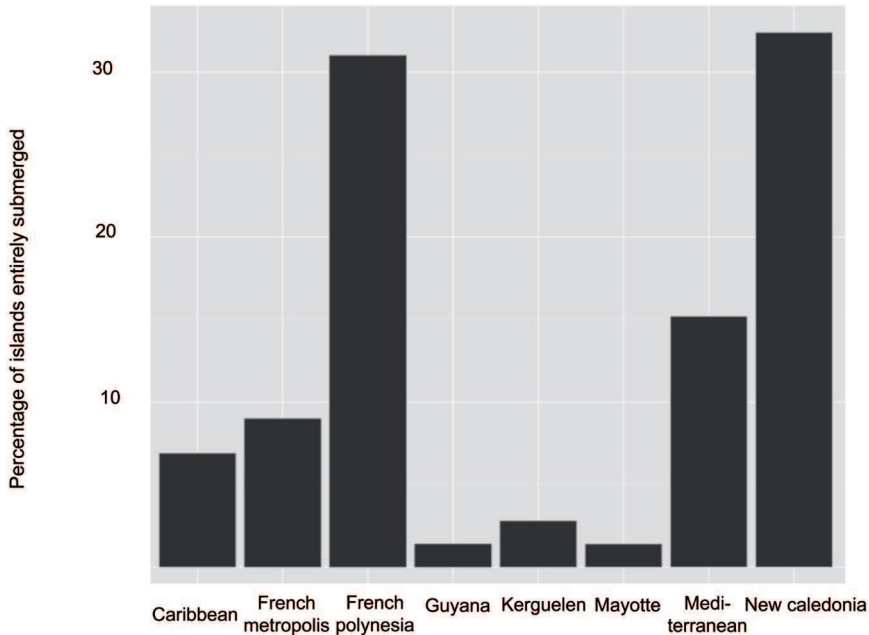


Figure 3. Spatial distribution of the entirely submerged islands for the different French regions under an increase of sea level by 3 meters.

lated the potential area losses for each endemic plant species under the different scenario of sea level rise and we averaged according to the IUCN status. Overall, our results showed that endemic plant species will lose between 1.25% and 3.98% of their area distribution under an increase of sea level by 1 and 3 meters, respectively (Figure 5). With an increase of sea level of 3 meters, the habitat loss of the species that are classified as “least concern” by the IUCN was 1.16%, while it reached 6.88% for the “critically endangered” plant species. These results highlighted that the vast majority of endemic plant species vulnerable to an increase of sea level, are already at a high risk of extinction. Consequently, species that already are at higher risk of extinction will lose the largest habitat following sea level rise.

Discussion

Over the next 60 years, sea level rise and higher storm frequency, together with natural and human-induced subsidence, population growth and urbanization, will cost roughly 9% of global GDP (Hanson et al. 2010). However, little attention has been paid to island vulnerability directly caused by sea level rise (Menon et al. 2010; Wetzel et al. 2012). It is clear that sea level rise will be the largest driver of habitat loss for insular habitats (Wetzel et al. 2012). Sea level rise is a particularly critical consideration for preserving coastal biodiversity, yet many approaches for prioritizing conservation networks do not take this into account (Runting et al. 2013). Our results predicted that impacts of sea level rise on insular French

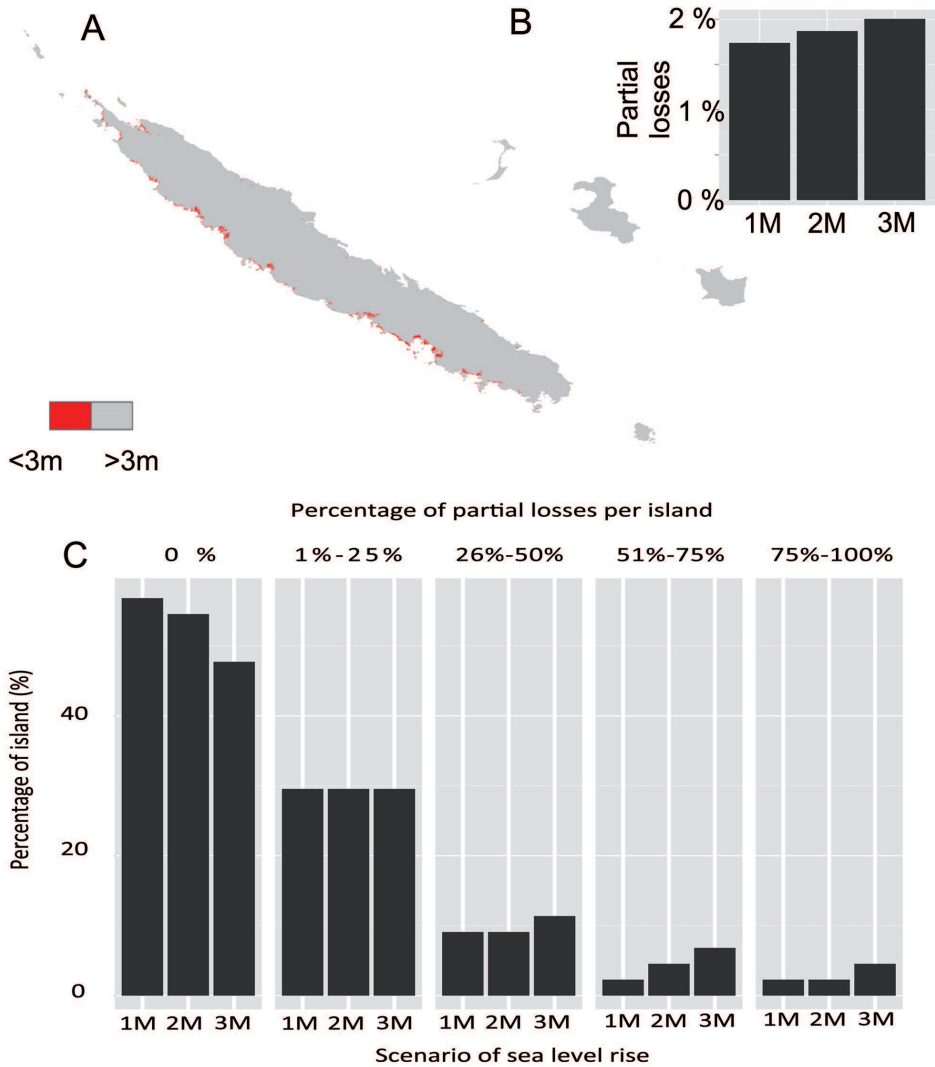


Figure 4. **A** Map representing the partial habitat losses of New Caledonia region with an increase of sea level by 3 meters **B** Percentage of areas partially submerged in New Caledonia region under an increase of sea level by 3 meters **C** Percentage of island that are partially submerged for different classes of submersion.

habitats are likely to be important, especially for two regions: New Caledonia and French Polynesia. Under an increase of sea level by 1 m, at least 5% of islands will be potentially entirely submerged. Our pessimistic scenario projected a loss of up to 11% of French islands. Globally, we did not observe important differences between homogeneous and heterogeneous projections results. Other studies that attempted to study the potential impacts of sea level rise in terrestrial eco-regions (Menon et al. 2010) and on Indo-Malaysian islands (Wetzel et al. 2012) showed results of the same order of magnitude. We do regret our in-

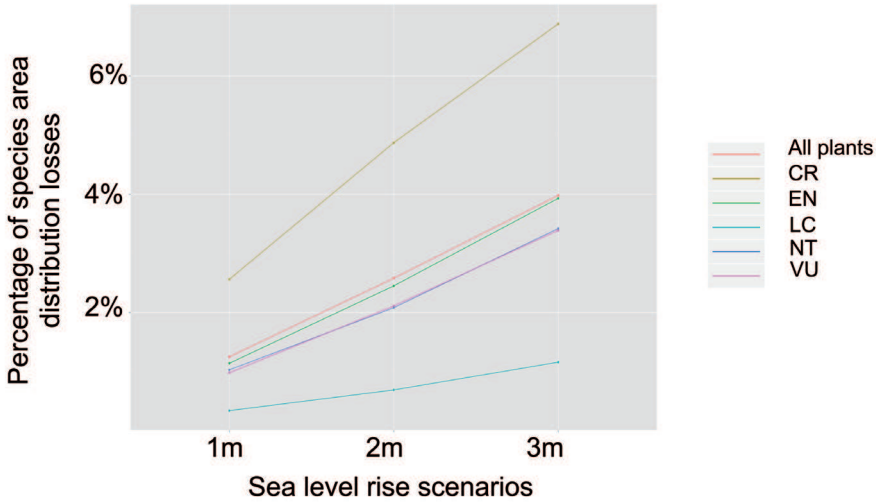


Figure 5. Percentage of species area distribution submerged under 3 different scenario of sea level rise for 64 endemic plants. We grouped the different species according to their IUCN status. CR : Critically endangered, EN : endangered, VU : vulnerable, NT : Near threatened and LC : least concern.

ability to work with a greater precision of elevation data and to take into account partial habitat losses due to marine intrusion for all the French islands. However taking into account partial losses of New Caledonia, we showed that this region will also suffer from significant partial losses of insular habitat. Therefore, neglecting partial loss of islands means that the impact of sea level rise will cause probably more dramatic land losses than projected by the study for the other regions. Actually, several factors may underestimate habitat loss estimations, especially: lateral erosion, tidal range, centennial tides or floods and increased salinity on new shorelines. For instance, beach erosion along the United States East Coast due to sea level rise was about two orders of magnitude greater than the rate of sea level rise (Zhang et al. 2004). This means that, for example, a 1 meter rise of sea level would create habitat loss of about 100 meters inland along the coasts due to lateral erosion. Therefore, results are conservative and they give evidence that sea level rise represents an important threat on insular biodiversity over the next decades. We did not either consider the indirect habitat losses following displacement of human population from inundated areas and the potential important ecological consequences if urban and intensive agricultural areas in the coastal zones of islands are relocated to the hinterland (Wetzel et al. 2012), though these effects have been shown to be sometimes greater than the losses directly due to sea level rise.

Then, regarding endemic species distributions over New Caledonia, we showed that species that are already at risk of extinction were the most vulnerable to sea level rise. This result is particularly important, because it means that endemic plants that are at risk of extinction are mainly located on the coastal areas. Although we focused on endemic plant species, rising seas will also flood other populations of different taxonomic groups including invertebrates and vertebrates. In addition, the two most important regions that are susceptible to be threatened by sea level rise are part of

biodiversity hotspots. For instance, French Polynesia contains 85 of the 425 atolls of the world that shelter nearly 19,000 vascular plant species including 3,450 endemic species. These species may also have to face many threats such as salinity intrusion, submersion, soil erosion and climate changes.

We attempt a first approximation of the potential impact of sea level rise on French biodiversity following marine intrusion. In our study, most of islands that showed important vulnerability to sea level rise were atolls. Their remoteness from mainland, flat topography and great susceptibility to natural disturbances (e.g., hurricanes) might lead to a low biodiversity present in these islands. Thus, the biodiversity on small islands and other low-lying coastal regions appeared to be highly vulnerable to sea level rise, but it is unclear how many species could be lost under existing sea level rise projections. To conclude, some patterns emerging from this study provided useful information for conservation planning. As our climate continues to change at a faster rate than previous century, sea level rise will create further challenges for the conservation of insular ecosystem in French territories, and in low lying areas worldwide. Given that French islands covers all latitudes in the Pacific, Indian and Atlantic oceans and in the Mediterranean, with the French maritime domain being ranked as the second largest in the world, our results suggested that the implications for the 180 000 world islands around the world should be considerable. Assuming that French islands are representative of worldwide islands, roughly 10,800 islands could be entirely lost with the 1 meter scenario. Consequently, new prioritizations programs for islands have to be established in order to mitigate the impacts of sea level rise. For example, in order to anticipate threats and prepare adequate conservation actions (e.g., local protection, identification of refuges or translocation programs), conservation managers have to target specific islands that have high risk of being permanently inundated within the next decades. Our results suggested that the effects of sea level rise will be particularly dangerous for New Caledonia, and French Polynesia. Considering their important contribution to global biodiversity and the threat of sea level rise for future biodiversity of some of these islands, there is an urgent need that islands feature prominently in global and regional conservation prioritization schemes. In addition, with accepted projections of sea level rise now exceeding one meter, the improvement of estimates of the associated loss of insular habitat and biodiversity becomes essential. In addition, it would be advantageous for decision makers to have more certainty about future sea level rise, the nonlinearity of ice-sheet melt makes accurately predicting the change in sea level at a particular date unattainable at present (Hansen 2007). We hope that this study will provide a first valuable attempt for new research efforts in this direction.

Acknowledgements

This work was funded by Centre National de la Recherche Scientifique (CNRS) and Agence Nationale de la Recherche (ANR). The authors are thankful to D. Harris and L. Bull who built the French island database and to H. Kreft for his valuable comments and interest on the manuscript in 2010. We also thank E. Bonnaud, S. Gregory, G.

Luque, Y. Watary, P. Leadley, and A.P. Møller for their helpful comments on the manuscript. We are also greatly thankful to the referees of Peerage of science who provided constructive criticisms on an early version of this manuscript and to B. Brook for his valuable comments.

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Annexe 3 :

**Postglacial recolonization
history of the European
crabapple (*Malus sylvestris*
Mill.) a wild contributor to
the domesticated apple.**

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Postglacial recolonization history of the European crabapple (*Malus sylvestris* Mill.), a wild contributor to the domesticated apple

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Abstract

Understanding the way in which the climatic oscillations of the Quaternary Period have shaped the distribution and genetic structure of extant tree species provides insight into the processes driving species diversification, distribution and survival. Deciphering the genetic consequences of past climatic change is also critical for the conservation and sustainable management of forest and tree genetic resources, a timely endeavour as the Earth heads into a period of fast climate change. We used a combination of genetic data and ecological niche models to investigate the historical patterns of biogeographic range expansion of a wild fruit tree, the European crabapple (*Malus sylvestris*), a wild contributor to the domesticated apple. Both climatic predictions for the last glacial maximum and analyses of microsatellite variation indicated that *M. sylvestris* experienced range contraction and fragmentation. Bayesian clustering analyses revealed a clear pattern of genetic structure, with one genetic cluster spanning a large area in Western Europe and two other genetic clusters with a more limited distribution range in Eastern Europe, one around the Carpathian Mountains and the other restricted to the Balkan Peninsula. Approximate Bayesian computation appeared to be a powerful technique for inferring the history of these clusters, supporting a scenario of simultaneous differentiation of three separate glacial refugia. Admixture between these three populations was found in their suture zones. A weak isolation by distance pattern was detected within each population, indicating a high extent of historical gene flow for the European crabapple.

Keywords: approximate Bayesian computation, ecological niche modelling, fruit tree, intraspecies diversification, microsatellite

Received 4 July 2012; revision received 11 December 2012; accepted 13 December 2012

Introduction

The climatic oscillations of the Quaternary Period clearly affected the distribution and genetic structure of many

species (Hewitt 2004; Lascoux *et al.* 2004). In Europe, many temperate species faced with the expansion of ice sheets over the northern part of the continent survived periods of glaciation in small ice-free spots in Southern and south-eastern Europe (called glacial refugia), in which conditions were more favourable (Hewitt 2004; Schmitt 2007). These range contractions were followed

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by range expansions during the interglacial periods, with populations at the northern boundaries of refugia expanding into the large territories further north, which became increasingly hospitable as the climate rapidly warmed. Such shifts in distribution following rapid climate change are excellent models for understanding the mechanisms by which intra- and interspecific genetic differentiation arises and is maintained (Hewitt 1990, 1996, 2004; Petit *et al.* 2004; Schmitt 2007; Excoffier *et al.* 2009; Petit & Excoffier 2009). Identification of the geographical area that served as refugia that existed during the last glacial maximum (LGM) can also help set priorities for the conservation and management of genetic resources (Hampe & Petit 2005). Furthermore, understanding past population dynamics is also important to make predictions of the effects of current climate change on species distribution and survival (Petit *et al.* 2004, 2008; Nogués-Bravo *et al.* 2008; Provan & Bennett 2008).

Trees are fascinating models for investigating the impact of climatic fluctuations on species colonization, adaptation, speciation and extinction (Petit & Hampe 2006; Savolainen & Pyhäjärvi 2007). Retrospective analyses based on paleoecological and genetic data have greatly increased our understanding of tree phylogeography (Hewitt 2000; Davis & Shaw 2001; Lascoux *et al.* 2004; Petit *et al.* 2004; Stewart *et al.* 2010). A combination of population genetic studies and explicit species distributions determined from fossil pollen and macrofossil evidence has revealed that trees recolonized higher latitudes during the Holocene, following expansion from southern glacial refugia (Brewer *et al.* 2002; Cheddadi *et al.* 2006; Magri *et al.* 2006), but also from small populations that persisted in more northern 'cryptic' refugia (Anderson *et al.* 2006; Parducci *et al.* 2012). However, additional studies of other species are required for more general conclusions to be drawn regarding the impact of historical contingencies and differences in climatic niches (from southern temperate to southern boreal) and mechanisms of gene dispersal on interspecific differences in postglacial histories. In particular, the postglacial evolutionary histories of wind-dispersed tree species growing in high-density populations have been extensively documented (*e.g.* Petit *et al.* 2002; Heuertz *et al.* 2006), but fewer studies have focused on low-density, animal-dispersed fruit trees (Palmé & Vendramin 2002; Oddou-Muratorio *et al.* 2004; Jolivet & Degen 2011). Animal-dispersed species would be expected to have stronger genetic structures and weaker dispersal capacities than wind-dispersed species, whereas low-density species would be expected to have higher dispersal capacities than high-density species (Vekemans & Hardy 2004; Hardy *et al.* 2006). It remains unclear how the balance between these two life

history traits characteristics of fruit trees—animal mediated dispersal and a low density—as well as the importance of outcrossing shapes the genetic diversity and genetic structure of populations during post-LGM recolonization.

Most previous studies investigating the phylogeography of European tree species were based on chloroplast DNA sequences. An advantage is that maternally inherited markers often display stronger differentiation between populations than biparental markers, due to their smaller effective size and lack of recombination. However, it has repeatedly been argued that this lack of recombination together with selective pressures and interspecific organelle introgressions can bias biogeographic inferences (Ballard & Whitlock 2004). Conversely, microsatellites have proved powerful for the elucidation of species history and recent hybridization (Lu *et al.* 2001; Randi & Lucchini 2002). Although DNA sequence information can be more useful for dating ancient demographic events, studies using microsatellites should help to unravel recent demographic processes, which have received little attention to date, such as gene flow between recolonization wave fronts.

Postglacial recolonization routes have been inferred from patterns of population structure (Taberlet *et al.* 1998; Lascoux *et al.* 2004; Schmitt 2007). However, until recently, the lack of suitable and tractable statistical methods for distinguishing between different demographic scenarios and estimating demographic and population parameters (effective population size, divergence time between populations and the amount of gene flow between populations) (Richards *et al.* 2007) hindered the accurate and precise inference of complex scenarios. Approximate Bayesian computation (ABC) provides a robust framework, allowing powerful inferences of a species' past demography (Beaumont *et al.* 2002; Bertorelle *et al.* 2010; Csilléry *et al.* 2010). In particular, it enables probabilistic comparisons of alternative demographic scenarios (Bertorelle *et al.* 2010). A new framework has recently been developed, called ecological niche models (ENM), which may further improve inferences of the postglacial history of species by a complementary approach to genetic inference (Carstens & Richards 2007; Richards *et al.* 2007; Waltari *et al.* 2007; Brown & Knowles 2012).

The European crabapple (*Malus sylvestris*), a woody fruit species occurring across Western and Central Europe (Larsen *et al.* 2006), is a tree of the Rosaceae family, mainly pollinated by bees and flies, that grows in low-density populations in natural habitats. A great diversity of wild animals feeds on apple fruits but their efficiencies as seed dispersal vectors are unknown (Larsen *et al.* 2006). *Malus sylvestris* has been identified as a major contributor to the genome of the cultivated

apple *Malus domestica* (Cornille *et al.* 2012) and is considered to be endangered (Jacques *et al.* 2009). Efforts to decipher the genetic structure and demographic history of this tree species are thus timely (i) to mitigate the effects of climate change and prevent negative effects of habitat fragmentation on this endangered species and (ii) to increase the genetic resources available for apple breeding programs, through the identification of genes conferring resistance to pathogens or tolerance of diverse abiotic stress conditions. The genetic structure of the European crabapple has been studied only in limited areas (Coart *et al.* 2003; Larsen *et al.* 2006) and appears to be weak at fine scale, suggesting a high dispersal capacity. No study has yet investigated the phylogeography of this emblematic wild European species across its entire distribution range. We therefore used population genetic analyses and ENM to investigate the glacial refugia and postglacial recolonization history of *M. sylvestris*. For genetic analyses, we used a comprehensive set of *M. sylvestris* individuals sampled throughout Europe and 26 microsatellite markers. We addressed the following questions: (i) Did wild apples survive the last glacial period in a single refuge area in Europe or at multiple areas? Did all relict populations contribute equally to the postglacial recolonization of Europe by wild apples? (ii) Can we detect the genetic consequences of successive founder events during postglacial colonization, that is, does genetic diversity decline with increasing distance from refugia? (iii) Can we detect genetic patterns of isolation-by-distance (IBD) and obtain information about dispersal capacities? (iv) Did admixture occur between recolonizing populations during expansion of the postglacial range of this species? (v) Can we reconstruct habitats that were suitable for the European crabapple in the past by ENM methods?

Materials and methods

Sampling

We have previously demonstrated the existence of gene flow from the cultivated apple *M. domestica* to the European wild apple (Cornille *et al.* 2012). We therefore initially carried out a STRUCTURE 2.3.3 (Pritchard *et al.* 2000) analysis, including 40 reference *M. domestica* cultivars previously identified as displaying no introgression from the European crabapple (i.e. with membership coefficients >0.9 to the *M. domestica* gene pool), and the entire *Malus sylvestris* data set comprising 837 individuals. We retained only the 381 individuals assigned with a value of >0.9 to the *M. sylvestris* gene pool for further analyses. Leaf material was collected at 37 sites (including 25 sites with at least four individuals) across Europe (Table S1 and Fig. S1, Supporting information), covering

most of the geographical distribution of the European crabapple except Spain and Sweden (see Euforgen map of the European crabapple http://www.euforgen.org/fileadmin/www.euforgen.org/Documents/Maps/PDF/Malus_sylvestris.pdf). As the European crabapple is a scattered species (i.e. 1 individual/ha), we defined site as a group of close individuals (<20 km); the geographical coordinates for each site were defined as the average of geographical coordinates over all individuals from that site.

DNA extraction and microsatellite genotyping

DNA was extracted with the NucleoSpin[®] plant DNA extraction kit II (Macherey & Nagel, Düren, Germany). PCR amplification was performed with the Multiplex PCR kit (Qiagen). We used 26 microsatellites, distributed over the 17 chromosomes, typed in 10 different multiplex reactions as previously described (Patocchi *et al.* 2009; Cornille *et al.* 2012). We retained only multilocus genotypes with fewer than 25% missing data. We checked the suitability of the markers for population genetic analysis with ARLEQUIN (Excoffier & Lischer 2010). None of the 26 microsatellite markers deviated significantly from the neutral equilibrium model, as shown by the nonsignificant *P*-values obtained in Ewens–Watterson tests, and no pair of markers was in significant linkage disequilibrium (Raymond & Rousset 1995; Rousset 2008). The markers used may therefore be considered to be unlinked and to be evolving in a quasi-neutral manner.

Descriptive statistics

We tested for the occurrence of null alleles with MICROCHECKER 2.2.3 (Van Oosterhout *et al.* 2004). Allelic richness and private allele richness were calculated with ADZE (Szpiech *et al.* 2008), for sites (i.e. geographical locations) and populations (i.e. clusters inferred by TESS analyses including hybrids up to 0.55 membership coefficient in the given cluster), using sample sizes of $N = 12$ (six individuals \times two chromosomes) and $N = 200$ (100 individuals \times two chromosomes), corresponding to the smallest number of observations for sites and populations, respectively. Heterozygosity, Weir and Cockerham *F*-statistics and Hardy–Weinberg equilibrium were assessed with GENEPOP 4.0 (Raymond & Rousset 1995; Rousset 2008). Only sampling sites with at least four successfully genotyped specimens were included in site-specific computations (25 sites in total comprising $N = 344$ individuals) except for ADZE analysis in which 22 sites were included (i.e. geographical locations with at least four individuals and within which at least two individuals were successfully genotyped for each marker). The population-specific

computations excluded five individuals that were not clearly assigned to any population, leaving a sampling size of $N = 376$ individuals.

Population subdivision, genetic variability and isolation by distance

We used the individual-based Bayesian clustering methods implemented in STRUCTURE 2.3.3 (Pritchard *et al.* 2000) and TESS 2.3.1 (Chen *et al.* 2007) to investigate population subdivision. These methods are based on the use of Markov chain Monte Carlo (MCMC) simulations to infer the assignment of genotypes into K distinct clusters. The underlying algorithms attempt to minimize deviations from Hardy–Weinberg and linkage disequilibria within each cluster. The clustering procedure of TESS also includes a spatial component, such that genotypes from geographically closer locations are considered more likely to belong to the same cluster. In TESS analyses, we used the conditional autoregressive (CAR) Gaussian model of admixture with a linear trend surface, setting the spatial interaction parameter (ρ) at 0.6. These parameters (ρ and trend) affect the weighting assigned to spatial proximity when clustering genotypes.

For both methods, ten independent analyses were carried out for each number of clusters K ($2 \leq K \leq 6$ for TESS and $1 \leq K \leq 6$ for STRUCTURE), with 500 000 MCMC iterations after a burn-in of 50 000 steps. Outputs were processed with CLUMPP 1.1.2 (Jakobsson & Rosenberg 2007), for the identification of potentially distinct modes (i.e. clustering solutions) in replicated runs for each K . A G' -statistic >80% was used to assign replicates to a common TESS mode. We determined the amount of additional information explained by increasing K using the ΔK statistic (Evanno *et al.* 2005) for STRUCTURE analyses and the rate of change of the deviation index criterion (DIC) when increasing K for TESS analyses.

We checked for IBD patterns as previously described (Loiselle *et al.* 1995). A Mantel test with 10 000 random permutations was performed between the individual coefficient of relatedness F_{ij} and the matrix of the natural logarithm of geographical distance. These analyses were performed with SPAGED1 1.3 (Hardy & Vekemans 2002). Spatial patterns of genetic variability were visualized by mapping variation in allelic richness for 22 sites in total (i.e. geographical locations with at least four individuals and within which at least two individuals were successfully genotyped for each marker) across space with the interpolation kriging function in ARCGIS (ESRI, Redlands, CA, USA), using a spherical semivariogram model.

Approximate Bayesian inference

We found weak genetic differentiation in the European crabapple between the north-eastern and south-eastern populations identified with TESS. We therefore investigated whether the observed pattern of genetic diversity resulted from (1) the simultaneous expansion of three independent populations (i.e. western, south-eastern and north-eastern; referred to as W, SE and NE) or (2) simultaneous expansions of the W and SE populations, followed by the divergence and expansion of the NE population derived from the SE population (i.e. resulting from a more recent colonization wave front). We used ABCtoolbox (Wegmann *et al.* 2010) to compare these two scenarios, with and without the occurrence of gene flow (Fig. 1). The juvenile period of *M. domestica* lasts 5–10 years and no data for this parameter are available for *M. sylvestris*. We therefore assumed a generation time of 7.5 years. We estimated the effective size of each population (N_W , N_{NE} , N_{SE}), the rate of migration between populations for each generation (m_{x-y} : migration rate from population x to y per generation), the exponential growth rate of each population (G_W , G_{NE} , G_{SE}) and the divergence times (T_{EXP} and T_{NE-SE}). The boundaries of the uniform (or log-uniform) prior distributions (Table S2, Supporting information) were chosen based on preliminary analyses run with very large priors (not shown). The ‘populations’ used in these analyses are the main clusters identified by Bayesian clustering methods.

For all models, identical microsatellite data sets were simulated for 14 of our loci (Ch01h01, Ch01h10, Ch02c06, Ch02d08, Ch05f06, Ch01f02, Hi02c07, Ch02c09, Ch03d07, Ch04c07, Ch02b03b, MS06g03, Ch04e03 and Ch02g01) that had been reported to carry perfect repeats (Gianfranceschi *et al.* 1998; Liebhard *et al.* 2002; Silfverberg-Dilworth *et al.* 2006), increasing confidence in the simulated mutation model. We checked that TESS yielded the same pattern of population structure with these 14 markers as observed with the 26 markers. Using CLUMPP (Jakobsson & Rosenberg 2007), we showed that both sets of markers [14 vs. 26 single sequence repeat (SSR)] gave similar clustering patterns (data not shown, similarity index $G' = 96\%$ for $K = 3$). We generated 2×10^6 genetic data sets from coalescent simulations, using model parameters drawn from prior distributions (Table S2, Supporting information) under the four previously specified scenarios. For each simulation, we calculated two summary statistics per population: H , the mean heterozygosity across loci and K , the mean number of alleles across loci. We also calculated pairwise F_{ST} (Weir & Cockerham 1984) and genetic distances ($\delta\mu^2$) (Goldstein *et al.* 1995) between pairs of populations. We

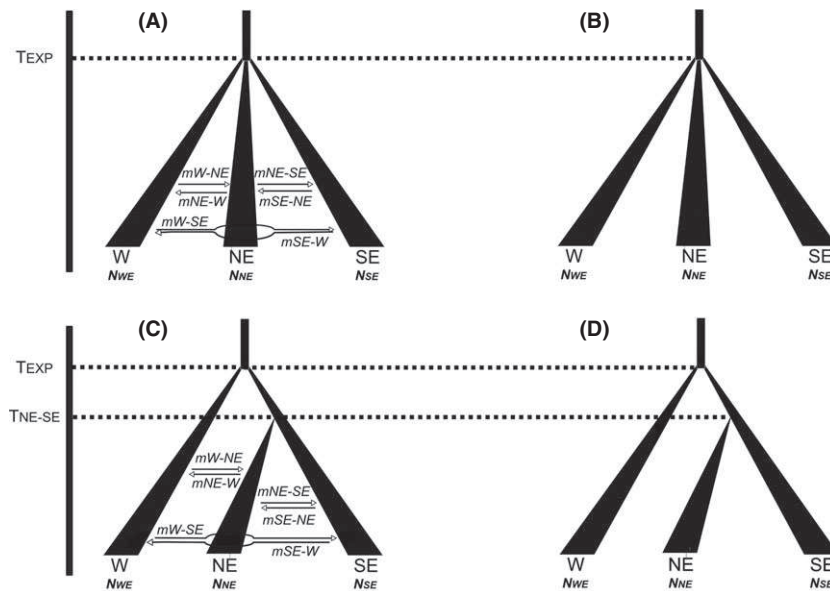


Fig. 1 Demographic models compared in approximate Bayesian computations. Model *a* assumes that three populations [western (W), south-eastern (SE), north-eastern (NE)] diverged and underwent simultaneous exponential growth; bidirectional gene flow was assumed between all pairs of populations. Model *b* is identical to model *a* but without gene flow. Model *c* assumes that the W and SE populations expanded simultaneously and that the NE population subsequently diverged from the SE population, with all populations undergoing exponential growth; bidirectional gene flow was assumed between all population pairs. Model *d* is identical to model *c* but without gene flow. N_x : effective population size of population x , m_{x-y} : gene flow per generation from population x to population y , T_{EXP} : divergence time at the beginning of the Holocene, T_{NE-SE} : time at which the NE population split from the SE population.

conducted a preliminary principal component analysis (PCA) with R software (MASS package, function `prcomp`), based on 3000 simulated data sets for *M. sylvestris*, for the four models, to reveal visual correlations between the main model parameters and the summary statistics (Tellier *et al.* 2011).

We assumed a generalized stepwise model of microsatellite evolution (Estoup *et al.* 2002). The mutation rate was allowed to vary across loci, with locus-specific mutation rates being drawn from a gamma distribution (α , α/μ) in which μ is the mutation rate per generation and α is a shape parameter. We assumed a log-uniform prior distribution for μ [0.00001, 0.02] and a uniform distribution for α [1, 30].

We compared the four models by calculating their Bayes factors (Wegmann *et al.* 2010) and estimating their relative posterior probabilities, based on the 1% of simulated data sets most closely matching the observed data (i.e. 2000 simulated data sets). Once the best model had been chosen, we estimated demographic parameters under this scenario, using a general linear model (ABC-GLM) postsampling regression adjustment for the 2000 retained simulations (Leuenberger & Wegmann 2010; Wegmann *et al.* 2010). We report the mode and 95% highest posterior density (HPD) interval for each model parameter estimate.

The performance of the method for discriminating between competing historical models was assessed by analysing test data sets (called pseudo-observed data sets) simulated with the same number of loci and individuals as for the observed data sets. We simulated 2000 such data sets for each competing model, using parameter values drawn from the same prior distributions as for the original analyses. We determined the relative posterior probabilities of competing models for each pseudo-observed data set, using the model choice procedure, as described above (Wegmann *et al.* 2010). Confidence in model choice was then estimated from the percentage of times that a given scenario did not have the highest posterior probability of the competing scenarios when it was actually the true scenario (type I error) and the percentage of times that a given scenario had the highest posterior probability when it was not the true scenario (type II error).

Projections of Malus sylvestris distribution during LGM

We modelled the climatic niche of *M. sylvestris* from the current species distribution with the BIOMOD package (v 1.1-7.00, 2011-08.03; Thuiller *et al.* 2009) downloaded from WORLDCLIM data set v1.4 (<http://www.worldclim.org/>;

Hijmans *et al.* 2005) and records of the presence of *M. sylvestris* obtained for sampled individuals ($N = 381$). We estimated the pairwise correlation of values for the 19 bioclimatic variables by calculating Pearson's correlation coefficients and retained only the variables that were not strongly correlated (i.e. with Pearson's correlation coefficients < 0.75). We tested both sets of bioclimatic variables because we had no primer assumptions about species' preferences, and we wanted to compare the respective LGM projections when taking into account autocorrelation and the overfitting of the data. We removed duplicated coordinate data points, resulting in 73 presences in total (Dataset S1, Supporting information) to evaluate the distribution at the LGM. These models make the assumptions that climate is one of the main factors driving species distribution and that the climatic niche of this species has remained largely unchanged in recent centuries (Text S1, Supporting information).

Results

Population structure

Summary statistics for genetic variability are shown in Tables S3 and S4 (Supporting information). For the 25 sites with at least four samples, the mean number of genotypes was 13.8 ± 8.4 (average \pm standard deviation), allelic richness was 3.7 ± 0.4 (range: 2.6–4.4) and genetic diversity was 0.84 ± 0.14 (range: 0.55–0.89), on average, across markers. Heterozygote deficit, estimated over the whole data set, was highly significant ($P < 0.001$), but low ($F_{IS} = 0.03$, with a mean of 0.03 ± 0.07 per site and per marker). The mean F_{ST} s across loci were small ($F_{ST} = 0.10$, range: 0.008–0.280) but significant, for all pairs of sites ($P < 0.02$, Table S5, Supporting information).

The results of TESS analyses are shown in Figs 2 and 3. For $K = 2$, the analyses revealed a clear west/east partitioning. The simulations for $K = 3$ split the eastern cluster into NE and SE clusters. A similar pattern was obtained for $K = 4$, whereas for $K = 5$, a fourth cluster was identified in Bosnia-Herzegovina. STRUCTURE analyses generated congruent clustering patterns (Figs S2 and S3, Supporting information).

In TESS analyses, DIC values decreased monotonically from $K = 2$ to $K = 6$. Thus, increasing the number of clusters continually improved the fit of the model to the data. However, DIC seemed to decrease more slowly after $K = 3$ (Fig. S4, Supporting information), suggesting that further increases in K provided little information. In STRUCTURE analyses, the mode of the ΔK statistic was observed at $K = 2$ ($\Delta K = 1670$, $Pr \ln L = 2683$, Fig. S5, Supporting information), but ΔK was

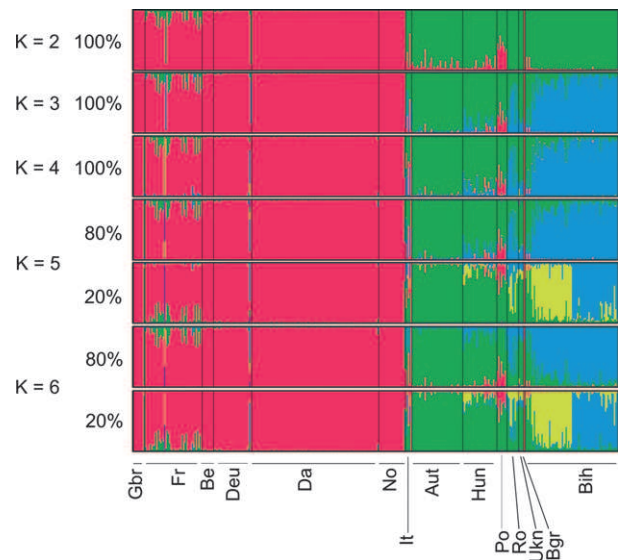


Fig. 2 Population structure in the European crabapple *Malus sylvestris* ($N = 381$, 37 sites across Europe), inferred with the Bayesian clustering algorithm implemented in TESS. Each individual is represented by a vertical bar, partitioned into K segments representing the proportions of ancestry of its genome in K clusters. When several clustering solutions ('modes') were represented within replicate runs, the proportion of simulations represented by each mode is shown. For a better visualization, the 37 sites were grouped by country. Gbr, Great Britain; Fr, France; Be, Belgium; Deu, Germany; Da, Denmark; No, Norway; It, Italy; Aut, Austria; Hun, Hungary; Po, Poland; Ro, Romania; Ukn, Ukraine; Bgr, Bulgaria; Bih, Bosnia-Herzegovina.

still high at $K = 3$ ($\Delta K = 480$, $Pr \ln L = 838$), suggesting further improvement in the fit of the model. Based on the narrow geographical distribution of the clusters inferred at $K > 3$, and the ΔK and DIC values obtained, $K = 3$ was considered the most biologically relevant clustering solution for subsequent historical inference.

We used the TESS membership coefficient inferred at $K = 3$ to define the three populations used in subsequent analyses. Genotypes were assigned to a given population if their membership coefficient for that population exceeded 0.55. Five genotypes could not be assigned to any population and were not included in subsequent analyses; $N = 376$ individuals were thus retained for population-specific computations. The three populations are hereafter referred to as the 'western' (W, red, $N = 213$), the 'north-eastern' (NE, green, $N = 90$) and 'south-eastern' (SE, blue, $N = 73$) populations. The W population was relatively homogeneous, with 91% of genotypes having membership coefficients > 0.9 for that population (Figs 2 and 3). The NE and SE populations presented higher levels of admixture, with 31% ($N = 28$) and 26% ($N = 19$) of genotypes, respectively, having membership coefficients < 0.9

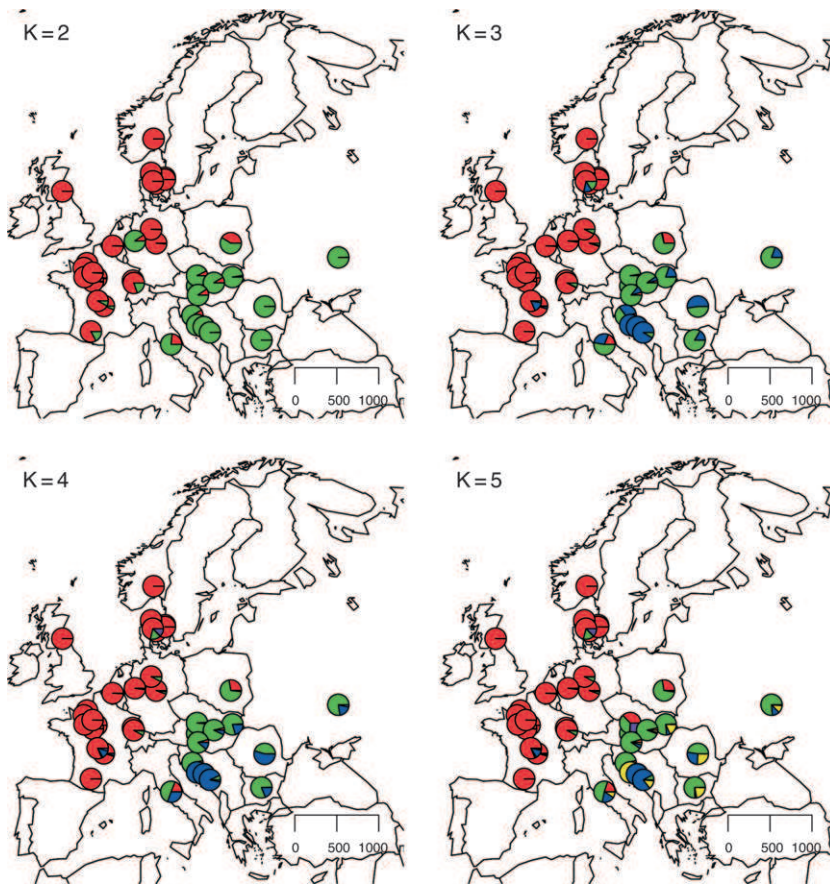


Fig. 3 Maps representing the mean membership proportions for K clusters, for samples of *Malus sylvestris* collected from the same site ($N = 381$, 37 sites across Europe). Scale is in kilometres. Membership proportions were inferred with the Bayesian clustering algorithm implemented in TESS. At $K = 5$ the results presented are those of the minor clustering solution ('mode'), showing the geographical location of the fourth previously identified cluster (yellow, Fig. 2).

(Figs 2 and 3). Admixed genotypes in the NE population were assigned to both the W ($N = 7$) and SE ($N = 14$) populations, whereas admixture in the W and SE populations occurred only with the NE population (Figs 2 and 3).

Population-specific polymorphism summary statistics are shown in Table 1. Genetic differentiation was weakest between the NE and SE populations ($F_{ST} = 0.04$, $P < 0.001$), and higher between the W and NE ($F_{ST} = 0.09$, $P < 0.001$) or W and SE ($F_{ST} = 0.12$, $P < 0.001$) populations. The W population had a significantly lower genetic variability than the NE and SE populations, in terms of both genetic diversity (H_E) [Wilcoxon signed rank (WSR) tests: $V = 271$, $P = 0.007$ and $V = 229$, $P = 0.008$ respectively] and allelic richness (A_r) (WSR: $V = 351$, $P < 0.0001$ and $V = 345$, $P < 0.0001$, respectively). The W population contained a similar number of private alleles to the NE population (WSR: $V = 262$, $P = 0.08$), but significantly lower than that of the SE population (WSR: $V = 341$, $P < 0.0001$). The NE and SE populations displayed similar levels of H_E (WSR: $V = 338$, $P = 0.7$), but the SE population had a higher allelic richness (WSR: $V = 320$, $P < 0.0001$) and a larger number of private alleles (WSR: $V = 338$, $P < 0.0001$) (Table 1).

The map of interpolated allelic richness (Fig. 4) showed that genetic diversity decreased with increasing latitude. Within each of the three populations, genetic differentiation and geographical distance were significantly correlated (Table 1), consistent with an IBD model. The spatial Sp statistic can be used to quantify spatial structure; lower Sp values are associated with greater dispersal capacities and/or effective population sizes. Sp values were very low both overall and within each population (Table 1), lying close to 0 ($Sp = 0.04$, $P < 0.0001$). This suggests that each population had a high dispersal capacity and/or a large effective population size.

Models of population expansion and estimation of demographic parameters

We used ABC to determine statistically which of the following scenarios provided the most likely explanation for the existence of the three genetically differentiated populations of *Malus sylvestris* in Europe: (i) the simultaneous expansion of three independent populations (W, SE and NE) that had differentiated during the last period of glaciations, with (model *a*) or without

Table 1 Genetic polymorphism and spatial pattern of differentiation within each population in *Malus sylvestris*. Five genotypes could not be assigned to any population, and thus, analyses were conducted on a total of $N = 376$ individuals

	Population		
	W (red)	NE (green)	SE (blue)
Microsatellite polymorphism			
N	213	90	73
H_O	0.69	0.77	0.80
H_E	0.74	0.85	0.88
F_{IS}	0.07***	0.10***	0.09***
A_r	11.5	15.3	17.3
A_p	1.3	2.1	4.4
Spatial pattern (logarithm)			
Sp	0.005	0.004	-0.003
Mean[Ln(<i>dist</i>)]	1.3	1.3	0.8
b	-0.006***	-0.004***	-0.001***
$F_{(1)}$	0.03	0.01	0.02
r^2	0.008	0.008	0.009

N : sample size of each population; H_O and H_E : observed and expected heterozygosities; F_{IS} : inbreeding coefficient; A_r : mean allelic richness for loci, corrected by the rarefaction method, estimated for a sample size of 100; A_p : number of private alleles, corrected by the rarefaction method, estimated for a sample size of 100; Sp: Sp parameter; mean[Ln(*dist*)]: mean of the logarithm of the geographical distance between genotypes; b regression slope between F_{ij} and the logarithm of geographical distance; $F_{(1)}$: mean F_{ij} between individuals from the first distance class; r^2 : squared correlation coefficient between the logarithm of geographical distance and F_{ij} .

*** $P < 0.001$.

(model *b*) gene flow, (ii) divergence and expansion of the W and SE populations, followed by the divergence and expansion of the NE population derived from the SE population (i.e. resulting from a more recent colonization wave front), with (model *c*) or without (model *d*) gene flow (Fig. 1). The correlations between model parameters and summary statistics are presented in Fig. S6 (Supporting information). The relative posterior probabilities calculated for each model provided the strongest statistical support for model *a*, suggesting that the three populations (W, SE and NE) diverged simultaneously, with all populations growing exponentially and bidirectional gene flow occurring between each pair of populations during expansion (Table 2; Bayes factor for model *a* = 4.37). The models with the NE population diverging from the SE population (models *c* and *d*) had the lowest relative posterior probabilities (Table 2). The migration rates per generation were estimated at $m_{W-SE} = 0.01$ [95% HPD: 0–0.21], $m_{W-NE} = 0.03$ [0–0.21], $m_{SE-NE} = 0.01$ [0–0.22], $m_{SE-W} = 1.01 \times 10^{-15}$ [0–0.17], $m_{NE-SE} = 1.01 \times 10^{-15}$ [0–0.21] and $m_{NE-W} = 0.05$ [0–0.27]. We obtained estimates of effective population sizes of 40 883 [524–828 327] for N_W , 20 691 [505–565 916] for N_{NE} and 40 882 [524–828 327] for N_{SE} . Using a generation time of 7.5 years, we estimated the population split to have occurred 303 016 years ago [120 963–545 649] (Fig. S7, Supporting information).

We also checked that the power of the analysis was sufficiently high to discriminate between the competing models: for model *a* against all three other models, the type I error rate and the mean type II error rate were 0. Overall, ABC analyses provided clear strong support

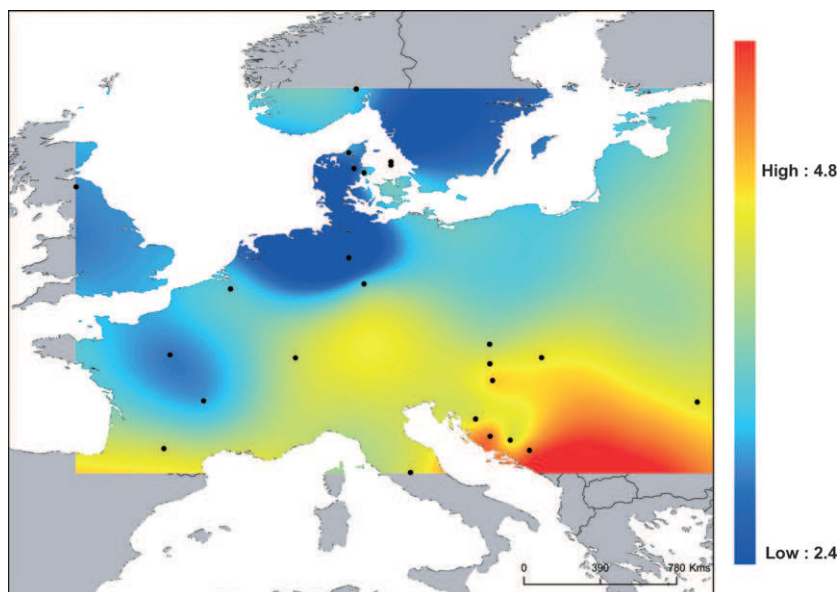


Fig. 4 Map of overall allelic richness (22 sites).

Table 2 Relative posterior probabilities (p) and Bayes factor (BF) for the four historical models compared by approximate Bayesian computations. The models are described in Fig. 1

Model	p	BF
<i>a</i>	0.81	4.37
<i>b</i>	0.19	0.23
<i>c</i>	$2.3e^{-12}$	$2.3e^{-12}$
<i>d</i>	$1.0297e^{-56}$	$1.03e^{-56}$

for gene flow between recolonizing refugia and for the simultaneous divergence of the three populations.

Ecological niche modelling

Model performance, as assessed from the AUC (Area Under the receiver operating characteristic Curve), was high for all six algorithms (Table S6, Supporting information; $AUC = 0.98 \pm 0.01$), indicating that all six algorithms fit the data well (Monserud & Leemans 1992; Fieldings & Bell 1997; Allouche *et al.* 2006). With thresholds maximizing the True Skill Statistic (TSS), *M. sylvestris* had a good TSS value of 0.79 ± 0.04 . We ran ENM with both sets of past climate data, CCSM2 and MIROC, but only MIROC gave consistent results across Europe. We therefore present projections based on MIROC data (Figs 5b and S8b, Supporting information). The projection onto current climate layers identified a putative suitable climate area essentially located in Western Europe for *M. sylvestris* (Figs 5a and S8a, Supporting information). The MIROC model predicted that the areas suitable for this species during the LGM were limited to lower latitudes than those considered suitable today and were more fragmented, with in particular low probability of contact between Eastern and Western Europe, in agreement with the genetic data (Figs 5 and S8, Supporting information). The climatic model suggested that populations of the European crabapple may have been maintained in areas further north than the typical glacial refugia (Hewitt 2004), with possible continuity between the populations from Western Europe, Italy and the Balkans. The predicted distribution, however, does not show a refugial distribution in isolated places as expected if the species survived in nunataks in northern latitudes.

Discussion

Paleodistribution modelling and genetic data allowed inferences on the phylogeography of the European crabapple, an endangered species and valued genetic resource for apple breeding. The distribution predicted based on climatic data was overall consistent

with population genetic analyses, altogether suggesting population and range contractions of *Malus sylvestris* during the last glaciation with a fragmentation between Eastern and Western Europe followed by postglacial recolonization of Europe.

Glacial refugia for *Malus sylvestris*

Malus sylvestris displayed a clear geographical pattern of population structure, with three differentiated populations in Europe: (i) a western population (W) spanning a huge area from France to Norway, and an eastern group subdivided into (ii) a north-eastern (NE) population around the Carpathian Mountains and (iii) a south-eastern (SE) population located at the north-east edge of the Balkan Peninsula. The strong differentiation between the three populations and the decreasing allelic richness at increasing latitudes suggest that the European crabapple contracted its range to southern glacial refugia, one of which probably was in the Iberian Peninsula or in the south of France, and another one in the Balkans.

The NE population growing around the Carpathian Mountains displayed a low level of genetic differentiation from the SE population, but had a high level of allelic richness. There were two possible origins for this population: a refugium from north-eastern Europe that came into secondary contact with the SE population and a wave front from the Balkan refugium during the recolonization of Europe. ABC analyses evaluating the fit of various demographic models to microsatellite data showed that the most strongly supported scenario was the simultaneous divergence of the three populations, with gene flow between all population pairs. The NE population, therefore, probably originated from a glacial refugium rather than during the postglacial recolonization of Europe.

The geographical pattern of population structure uncovered in *M. sylvestris* is consistent with those found in other animal, plant and fungal taxa (Hewitt 2004; Lascoux *et al.* 2004; Schmitt 2007; Vercken *et al.* 2010) and, in particular, with the patterns commonly found in temperate forest trees (Petit *et al.* 2002; Heuertz *et al.* 2004, 2006; Magri *et al.* 2006). Indeed, the existence of a large western European population and differentiated eastern populations in the Balkans Peninsula has been reported in *Quercus* sp., *Abies alba* and *Fraxinus excelsior*. In some other tree species, such as *Alnus glutinosa* (King & Feris 1998) and the common beech *Fagus sylvatica* (Magri *et al.* 2006), the existence of additional refugia in the eastern part of Europe, particularly in the Carpathian Mountains, has been suggested on the basis of the high level of genetic diversity in cpDNA and pollen fossil records (Magri *et al.* 2006). Our microsatellite

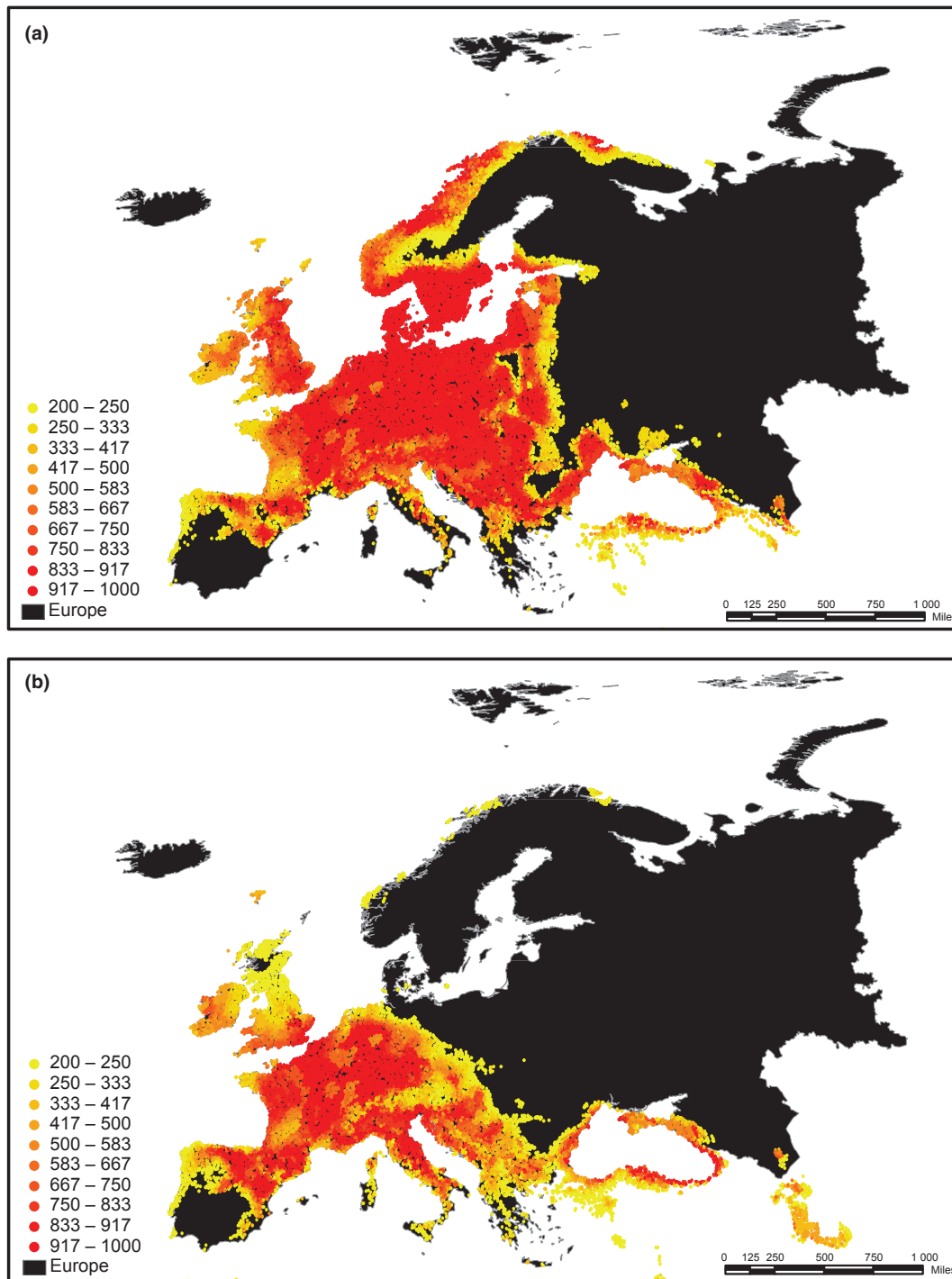


Fig. 5 Ensemble forecasting of the six different algorithms predicting the current (a) and last glacial maximum (LGM) (b) suitable climate area distribution for *Malus sylvestris*. The probabilities ($\times 1000$) of a suitable habitat are given in the legend.

markers clearly identified a distinct genetic cluster around the Carpathian Mountains in the European crabapple. A similar situation has been suggested for the common ash *Fraxinus excelsior* (Heuertz *et al.* 2004), but no clear origin of the Carpathian population could

be established due to a lack of samples in this area. Our ABC analyses indicated that the NE population originated at the same time as the other recolonizing populations, thus suggesting that the Carpathian Mountains may have acted as a glacial refugium for temperate

forest tree species, as for other temperate species, including mammals, reptiles and amphibians (Provan & Bennett 2008; Stewart *et al.* 2009). The existence of such a 'northern' glacial refugium is consistent with the results of ENM, suggesting that *M. sylvestris* may have survived at high latitudes. In some tree species, such as *Fagus sylvatica*, it has been suggested that such a northern refugium may have served as the main source population for the recolonization of Eastern Europe after the LGM, whereas a south-eastern population spread over a much more limited area during postglacial recolonization (Hu *et al.* 2008).

For ash, silver fir, oaks and beech, Italy has been identified as a possible additional glacial refugium, isolated from other lineages by the Alpine barrier (Taberlet *et al.* 1998). We detected no footprint of an Italian refugium in *M. sylvestris*. This may be due to the lack of pure *M. sylvestris* from this region. Our samples from Italy indeed were all introgressed by the cultivated apple *M. domestica*, which may be linked to the introduction of the cultivated apple in Europe by the Romans in Italy, probably 3000 years ago (Mabberley *et al.* 2001). For the W population, which probably expanded from an Iberian refugium, the level of allelic richness was high, but significantly lower than that in the eastern populations. These differences in genetic variability may be due to much more severe climatic episodes (i.e. arid and cold) during the Quaternary Period in this region than in other parts of Europe (Petit *et al.* 2003). Tree populations that survived successive ice ages in the Iberian Peninsula were restricted to a few small suitable areas and were thus smaller than those in other parts of Europe.

Suture zones and recolonization fronts for the European crabapple

There were two main waves of recolonization by *M. sylvestris* from the glacial refugia in Europe: Western Europe, right into the north, was probably recolonized by populations from the Iberian Peninsula or the south of France, whereas the population from the Carpathian Mountains spread, albeit to a lesser extent, northwards in Eastern Europe. The population from the Balkan refugium does not seem to have recolonized large areas.

Our microsatellite markers indicate some admixture in the three populations. The W population contained the smallest number of admixed individuals and displayed the highest level of genetic differentiation from the other populations. This pattern suggests higher levels of recent genetic exchange between the SE and NE populations. The lack of samples from Central Europe may have resulted in an underestimation of the number

of individuals with admixed ancestry in the western and eastern populations, but ABC analyses provided a high level of confidence for the choice of the model assuming gene flow between populations.

The biogeographic scenario uncovered in our study, with two main recolonization fronts in Western and Eastern Europe, has been demonstrated for many other temperate tree species (Heuertz *et al.* 2004; Lascoux *et al.* 2004). Suture zones in Central Europe, as detected for the European crabapple, are also typical of other temperate tree species (Petit *et al.* 2002; Heuertz *et al.* 2004, 2006; Magri *et al.* 2006; Liepelt *et al.* 2009). However, a clear suture between SE and NE populations and evidence for admixture have not been reported before. These findings demonstrate the utility of nuclear microsatellite markers for retracing the ancient demographic history of populations and the extent of admixture in phylogeographic studies.

Historical gene flow and dispersal capacity in the European crabapple

The European crabapple is dispersed by animals, but the weak spatial genetic structure within each population at the European scale, weak IBD patterns and low *Sp* values suggest that this species may be dispersed over large distances. These results are consistent with those previously reported for scattered temperate tree species (Oddou-Muratorio *et al.* 2004; Oddou-Muratorio & Klein 2008). The high dispersal capacity of the European crabapple and its current wide distributional range extending into the northern-most parts of Europe characterize this species as a rapid colonizer (Svenning & Skov 2007), consistent with its high pioneering capacity (Larsen *et al.* 2006).

Ecological niche models

Ecological niche models projections onto current climate layers resulted in a current suitable habitat for the European crabapple covering most of Europe, except southern Spain and Italy, consistent with the Euforgen map of actual distribution (http://www.euforgen.org/fileadmin/www.euforgen.org/Documents/Maps/PDF/Malus_sylvestris.pdf), although this extends further east than the region studied in this study. Predictions showed that the distribution of the European crabapple, like those of many other European tree species (Svenning *et al.* 2008), was affected by climate changes during the Quaternary Period, with a contraction and fragmentation of populations. The modelling results suggested possible refugia in the European crabapple in the north-east, southeast and west, concordant with the distribution of the three genetic clusters and ABC results.

Despite the overall concordance between ENM and genetic data, the predicted past distribution extends northwards up within the extent of the glaciers. This raises questions about the accuracy of ENM for paleoreconstructions and their interpretation, including limitations concerning the available predictor variables (Araújo & Guisan 2006). Indeed, in these models, the species niche is defined in terms of temperature and precipitation data only. Although climate is one of the main factors underlying species distribution, other factors will need to be taken into account in the future (Pearson & Dawson 2003), including dispersal processes (using hybrid approaches), biotic interactions (*e.g.* competitors and pollinators) and stages of succession in forests. One of the main issues of niche modelling is the assumption of niche conservatism. If the species niche shifts over time, the species may not respond to climate change in a predictable way (Jezkova *et al.* 2011). In addition, calibrating the climatic niche of species under current conditions and projecting them to non analogous conditions in the past would lead to spurious response curves and therefore to naïve projection (Thuiller *et al.* 2004).

From population structure to conservation strategies

Our inferences suggest high rates of historical gene flow between European crabapple populations, but current migration rates may be different, especially due to forest fragmentation. As a wild relative and contributor to the cultivated apple (Cornille *et al.* 2012), the European crabapple is a target for conservation and sustainable management programs for genetic resources. Knowledge of the existence and location of differentiated populations and of admixture zones is essential to guide conservation programs (Pautasso 2009). We report here the south of France, the Balkans and the Carpathian Mountains as hotspots of genetic diversity. In addition the admixture zones correspond to 'melting pots' of genetic diversity (Petit *et al.* 2003; Liepelt *et al.* 2009; Jay *et al.* 2012) that may include recombinant genotypes well suited to new environmental conditions and capable of facing up to global warming. The genetic uniqueness of southern 'rear-edge' populations, such as the populations from the South of France, is thus also of key importance for long-term conservation purposes (Petit & Hampe 2006).

Acknowledgements

We thank the *Région Ile de France* (PICRI), IDEEV and SBF (*Société Botanique de France*) for funding, *Plateforme de Génotypage GENTYANE* INRA UMR 1095 and Pauline Lasserre for assistance with genotyping. We

thank all those who helped with sampling (Table S1, Supporting information). We thank Xavier Vekemans, Bruno Fady and three anonymous referees for very useful suggestions.

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-
- G.T. and G.P. conceived and designed the experiments. G.T., C.A. and G.P. obtained funding. C.A. performed the experiments. C.A. analysed the data. B.C., G.P. and T.A. contributed analysis tools. C.A., G.T., L.C.B., K.J. and R.R.I. provided samples. C.A., G.T., B.C., T.A., S.M.J.M., R.R.I. and G.P. wrote the paper.
-

Data accessibility

Microsatellites data are published on the DRYAD repository with sampling locations, the ecological niche models data and the TESS input used for analyses and ABCtoolbox inputs, doi: 10.5061/dryad.sn1 m7.

Supporting information

Additional supporting information may be found in the online version of this article.

Dataset S1 X/Y coordinates of presences of *Malus sylvestris* in Europe used for ENM.

Text S1 ENM methodology used to project paleodistribution of *Malus sylvestris*.

Fig. S1 Sampling of the different *Malus sylvestris* sites through Europe.

Fig. S2 Bayesian clustering results of *Malus sylvestris* in Europe ($N = 381$) using the program STRUCTURE from $K = 2$ to $K = 6$.

Fig. S3 Maps of mean membership probabilities per site from the STRUCTURE analysis for *Malus sylvestris* assuming 2 to 5 clusters.

Fig. S4 Estimated number of populations in *Malus sylvestris* from TESS analyses using the DIC.

Fig. S5 Estimated number of populations in *Malus sylvestris* from STRUCTURE analyses using the ΔK .

Fig. S6 PCA on 3,000 simulations for *Malus sylvestris*.

Fig. S7 Marginal posterior distributions of demographic and historical parameters estimated by Simcoal2.

Fig. S8 Ensemble forecast using *Malus sylvestris* presence records and pseudo-absences projected onto the map of Europe and Western Russia using 19 bioclimatic variables.

Table S1 Description of the *Malus sylvestris* accessions analysed with their geographical origins and providers, and acknowledgement.

Table S2 Prior distributions used in approximate Bayesian computations.

Table S3 Summary statistics for each *Malus sylvestris* sampling site with at least four individuals.

Table S4 Summary statistics for the 26 microsatellite loci in *Malus sylvestris*.

Table S5 Pairwise genetic differentiation (F_{ST}) among the 25 sites.

Table S6 AUC Index for ENM ran with eight and 19 bioclimatic variables for each of the six models and each repetition.

Annexe 4 :

**Climate change and
conservation : keeping island
biodiversity afloat.**

**F. Courchamp, B. D. Hoffman, J. Russel, C.
Leclerc & C. Bellard.**

1 **Climate change and conservation: keeping island biodiversity afloat**

2

3

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19

20

21 **Key words:** Sea-level rise, Climate change, Climatic niche shift, Island conservation,

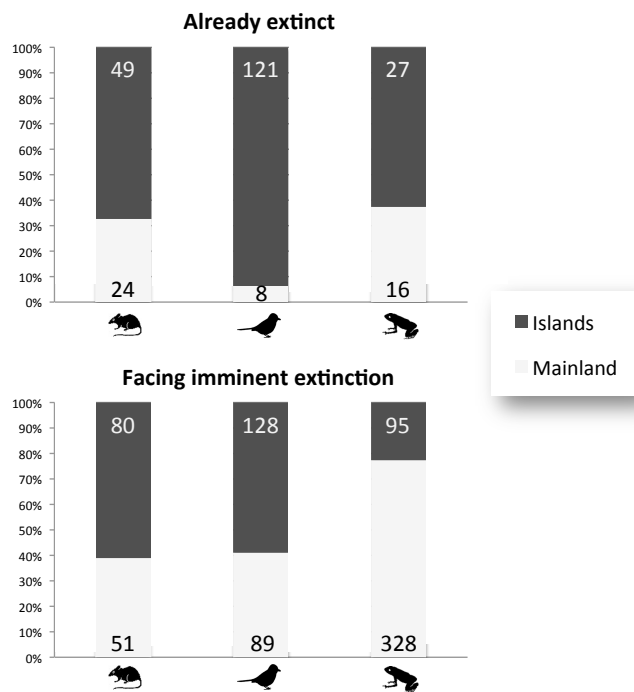
22 Prioritisation

23

24 **Island conservation on the longer term**

25 Island conservation programmes have been spectacularly successful over the past four decades,
26 yet they generally do not account for impacts from climate change. We argue that the full
27 spectrum of climate change, especially sea-level rise and loss of suitable climatic conditions,
28 should be rapidly integrated into island biodiversity research and management.

29
30 Conservation of biodiversity on islands is important globally because they are home to more than
31 20% of the world’s terrestrial plant and vertebrate species within less than five percent of global
32 terrestrial area. Endemism on islands is a magnitude higher than on continents [1]; 10 of the
33 world’s 35 biodiversity hotspots are entirely, or largely consist of, islands [2]. Yet this diversity
34 is highly threatened: over half of all recent extinctions have occurred on islands, which currently
35 harbour over a third of all terrestrial species facing imminent extinction [3] (Fig.1).



36

37 **FIGURE 1. Proportion of extinct and threatened on islands and on mainlands.** Numbers
38 are species and represent mammals (🐭), birds (🐦) and reptiles and amphibians (🐸), showing
39 terrestrial vertebrate biodiversity is generally more threatened on islands. Data are from [3].

40 In response to the biodiversity crisis, island conservation has been an active field of research and
41 action. Island conservation programmes have been spectacularly successful over the past four
42 decades. Hundreds of invasive species eradications and of endangered species translocations
43 have been successfully completed [4–7]. However, despite climate change being an increasing
44 research focus generally, climate change impacts have only just begun to be investigated on
45 island biodiversity. For example, invasive species eradications on islands have been prioritised
46 largely by native biodiversity threatened, eradication feasibility, economic cost and reinvasion
47 potential, but never by the threat of sea-level rise.

48

49 **The impact of sea-level rise on islands**

50 Recent research suggests impacts on islands from sea-level rise will be substantial [8–11].
51 Current scenarios for sea-level rise vary greatly, from low predictions of 0.5 to 2.3 m by 2100,
52 predominantly due to expansion of ocean surface water, to more dramatic predictions of 4 to 6 m
53 incorporating ice sheet melting and sliding (see [12] and [10] and references therein).
54 Increasingly, sea level rises between 1 and 2 meters on average within the next century are
55 considered very realistic. Despite clear and imminent risks, the consequences of sea-level rise for
56 island biodiversity remain one of the least studied of all climate change issues, both locally and
57 globally, which is surprising when one considers both the sheer number of islands concerned and
58 the potential impact. Even with the most optimistic scenario, many low-lying islands will simply
59 be entirely drowned, threatening some of the biodiversity benefits from recent conservation
60 actions. A recent analysis focusing on 4,500 islands in 10 biodiversity hotspots suggests that 6-
61 19% of these islands could be entirely submerged with 1-6 meter sea-level rise respectively,
62 threatening over 300 endemic extinction [10]. A similar study in the Pacific and Southeast Asia
63 predicts that 15-62% of 12,900 islands could be completely inundated [9]. More globally, a
64 recent study of over 1,200 islands from all oceans found comparable results, suggesting a

65 possibility of 6-12% of islands worldwide being entirely submerged by the end of this century
66 [11]. This would amount to the total loss of 10-20,000 of the 180,000 islands worldwide.
67 Additionally, many more islands will lose a significant portion of their area due to partial but
68 permanent inundation from sea-level rise [10,11].
69 Moreover, greater tidal ranges, and in particular centennial tides, will lead to periodic floods that
70 will destroy non-saline habitats. Increased frequency and amplitude of sea-water floods are also
71 expected to be more common with global climate change. Sea-level rise will also increase
72 coastal erosion (e.g., in the range of 50-200 times of sea-level rise) and saline water intrusion [8].
73 Furthermore, shoreline retreat will also lead to massive displacement of anthropogenic activities
74 from coasts [8].

75

76 **The loss of climates on islands**

77 Climatic shift is another issue that is particularly pertinent to island conservation. Following
78 climate change, the area of climatic parameters that is suitable for any given species is expected
79 to change spatially. This shift will occur predominantly upward (in altitude) and poleward (in
80 latitude, in the order of 150 km). On small islands this shift will likely project suitable climate
81 beyond island limits. Small islands will likely have a complete change of climatic parameters
82 over their entire surface and many species on those islands will potentially face only unsuitable
83 climatic conditions. Where continental species can avoid extinction by migrating to follow the
84 climate shift, many insular species will not. Being unable to disperse on their own off of the
85 island, they would thus have to adapt rapidly or will be committed to extinction.

86

87 Climate change should be integrated into research and management focused on island
88 biodiversity. Below are two approaches to do so, which will help identify solutions that will help
89 safeguard biodiversity and protect conservation investments against future global climate

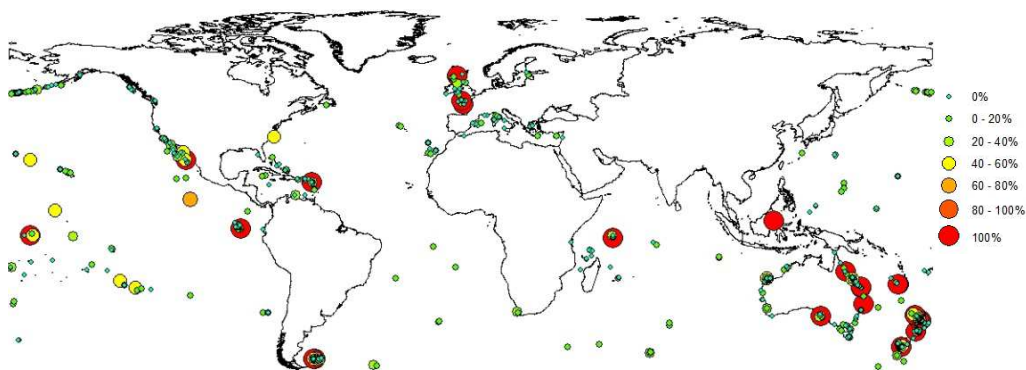
90 change.

91

92 **Integrate sea-level rise into prioritisation of islands restoration**

93 Over 900 successful non-native vertebrate eradications have been conducted on islands
94 worldwide [4]. In most cases, such as the Surprise Island project, restoration was conducted
95 without consideration of climate change (Box 1), resulting in some suboptimal choices for long-
96 term conservation benefits. Of 604 islands where invasive vertebrates have been eradicated [4]
97 and for which elevation data are available [10,11], 26 are predicted to be completely inundated
98 with only 1 metre of sea-level rise and many more will be impacted by partial habitat loss
99 (Fig.2). Researchers are increasingly developing prioritization frameworks to help guide
100 decision-making on which islands should be targeted for restoration via invasive species
101 removal. Sea-level rise and its impacts on islands should become a factor in prioritizing islands
102 for restoration. Data (e.g., elevation profiles) and a variety of inundation models at local,
103 regional, and global scales [13], are now increasingly readily available to do so.

104



105

106 **FIGURE 2. Predicted area submersion on islands with an invasive vertebrate**
107 **eradication.** The size and colour of points represent percentage of surface immersion. With a
108 1 metre sea level rise, 4% (26) of the 604 islands are estimated to be entirely under water and
109 many more will lose a large part of their habitat. Islands and their elevations come from the
110 Database of Island Invasive Species Eradications [4], which is combined with the island-sea-
111 level rise model from [10].

112

113 **Species translocations to save island species from climate-change**

114 In the face of climate change, many islands species may adapt or migrate to suitable habitat
115 within an island or to a nearby island. Many others, however, will not. This includes species that
116 conservation practitioners have already made substantial investments in protecting. For some of
117 these species, practitioners will eventually be faced with a decision of letting a species go extinct
118 by doing nothing or attempting to save it by actively moving it to suitable habitat. Managed
119 relocation would obviously be an action of last resort, but it has already been demonstrated as a
120 viable and successful strategy on islands, and includes one of conservation biology's most
121 celebrated success stories, the Chatham Island Robin (*Petroica traversi*) project. The science and
122 risk management of species translocations and conservation introductions is rapidly maturing,
123 and guidelines exist to inform the process [14].

124

125 **Conclusion: securing long-term conservation benefits**

126 Currently, the removal of invasive species from islands is one of society's most powerful tools
127 for preventing extinctions and restoring ecosystems. In order to safeguard the biodiversity
128 benefits secured through these restorations programmes and to maximise future benefits,
129 implications of climate change must become a priority for research and conservation agendas.
130 Research should focus on better understanding and predicting organismal and ecosystem-level
131 impacts on islands from sea-level rise and climatic shifts. Researchers and practitioners should
132 rapidly integrate these effects of climate change into the planning and prioritisations that are
133 currently taking place. They also should begin to assess island species that are most likely to be
134 at-risk from future climate change and the options for preventing their extinction, including
135 managed relocation.

136 **Box 1: The restoration of Surprise Island**

137 In the coming decades, thousands of low-lying coral atolls will be vulnerable to sea-level rise
138 around the world. Tropical atolls of some island nations are already experiencing inundation.
139 Importantly, sea-level rise is predicted to be heterogeneous: due to spatial heterogeneity of
140 surface temperatures, some oceanic areas will rise more than others. The persistence of atoll
141 islands will thus depend strongly on location, local conditions and geomorphology. On some
142 of these islands, the conservation benefits of important restoration efforts may therefore be
143 lost in the long term.



144
145 *Surprise Island (24 ha), 230 km north of New Caledonia.*

146
147 Surprise Island, located in the Entrecasteaux reef off New Caledonia, provides one example of
148 island conservation research and action that did not integrate climate change. Only a few
149 metres above sea level (see figure below), the small and remote island was the focus of a
150 research programme that ended in 2009 with the eradication of introduced rats (*Rattus rattus*),
151 mice (*Mus musculus*) and an invasive plant (*Cassytha filiformis*). The eradication of alien
152 invasive species from Surprise Island was a positive conservation action. It has undoubtedly
153 helped protect the local species for the coming decades, possibly preventing some of them
154 from local extinction. In addition, it provided us with a wealth of knowledge necessary for
155 island conservation that can be applied to other islands. Notably, research investigating
156 species interactions helped mitigate unexpected ecological chain reactions during

157 | eradications, which has been observed during other eradication programmes [15]. Research
158 | and conservation actions were a result of substantial investment in resources, lasting over a
159 | decade. Despite careful planning and long-term commitment, it did not occur to those of us
160 | involved in this programme that expected sea-level rise would threaten the benefits from our
161 | conservation actions.

162 | Many other alien species eradication programmes took place on islands that are doomed in the
163 | long term by sea-level rise. Of course, most of these eradication efforts occurred prior to our
164 | current understanding of climate change and ability to measure its impacts. Also, it is very
165 | likely that some of the eradications on doomed islands would still have commenced because a
166 | rapid response was required despite the long-term threat of climate change. Nonetheless,
167 | future conservation programme must now take this into account, by prioritising islands
168 | according to threats from sea-level rise and climate shifts and by considering translocation of
169 | island species doomed by climate change.

170 |

171 |

172 |

173 |

174 | **Acknowledgements**

175 | We thank Nick Holmes for access to the Island Invasive Species Eradications Database and C.

176 | Josh Donlan for discussions and input on the draft manuscript. FC was supported by the ANR.

177 | BDH and JR thank the Ecologie, Systématique & Evolution lab at the University of Paris Sud

178 | for hospitality. JR was supported by a sabbatical grant-in-aid from University of Auckland.

179 |

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- 215
- 216

Annexe 5 :
Matériel supplémentaire
chapitre 1

Supporting Information

Appendix S2 : Details of the legend of Figures 3 and 4.

Figure 3: Examples on successive combinations of socio-economic scenarios, projections of extinction drivers, habitat or species range models and extinction models and biodiversity metrics, leading to projections of biodiversity losses following climate change. Numbers correspond to references (see Appendix S2). * (1) also used species extinction model that corresponds to the extreme of the IUCN status approach where the number of species committed to extinction =100% habitat loss.** (6) also used both Dose Response Relationships between conservation status and the elevation limits and then estimated the effects of elevational limit shifts induced by climate change on the future conservation status.

Figure 4: Overview of projections of loss of biodiversity due to climate change, for different taxonomic, temporal and spatial scales. The width of the box illustrates the spatial and taxonomic scales: global scale and several taxonomic groups, global scale and only one taxonomic group, continental scale and only one taxonomic group (🌿 for plants, 🐟 for fish, 🐠 for aquatic invertebrates, 🦌 for mammals, 🦎 for lizards and 🐦 for birds, 🏞️ for several taxonomic groups). For each study, the box is delimited by the upper and lower boundaries of the intermediate scenario, while maximum and minimum values of the whiskers indicate the highest and lowest biodiversity losses across all projections. The numbers correspond to references (see Appendix S2). Note that biodiversity loss given by studies (11, 12, 13, 5) are local, therefore are respectively expressed per cell of 50 sq.km across Europe (10), per cell of 30' lat. by 30' long. grid of world ocean (12), per river (13) and per pixel of 10' grid (5). When there was no intermediate scenario (11), we defined the upper and lower limits of the box as the two middle values across all projections. In studies with more than one driver of species extinctions (*e.g.*, land-use changes (2), (6) and (1) or land-use changes, atmospheric nitrogen deposition and infrastructure development (7) and (8) or climate change and water withdrawal (12)), we calculated the mean proportion of losses due to climate change among the drivers, across all scenarios when it is possible (7),

(2) and (1). For these studies, the white fraction of the boxes indicates the proportion of species loss due to non-climate drivers for the intermediate scenarios and the coloured fraction indicates proportion of losses due to climate change. This figure illustrates that the different studies (i) generally predict significant biodiversity loss and (ii) use a combination of different biodiversity metrics, taxonomic groups and spatial scale and time horizon, making generalisations difficult.

Appendix S2 : References cited in Table 1, Figure 3 and Figure 4.

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Annexe 6 :
Matériel supplémentaire
chapitre 2

1
 2 **Table S1** Table indicating for the 10 insular hotspots: their original extent (km²), the number
 3 of islands contained in each of them, number of islands with elevation data and the percentage
 4 of area that studied islands covered in the hotspot.

5

Hotspot (Abbreviation)	Original extent (km ²)	Number of islands	Number of islands with elevation data	% of area estimated from the sampled islands
East Melanesian Islands (EMI)	99384	501	414	99.04
Philippines (Ph)	297179	754	670	100
Polynesia Micronesia (PM)	47239	1074	597	99.96
New Caledonia (NC)	18972	69	44	100
Japan (JA)	373490	462	400	100
New Zealand (NZ)	270197	161	120	100
Wallacea (Wa)	338494	728	571	100
Sundaland (Su)	1501063	983	795	100
Madagascar and the Indian Ocean Islands (MIOI)	600461	160	113	100
Caribbean Islands (CI)	229549	900	723	100

6

Table S2 Number of endemic species of 6 different groups (i.e., plants, mammals, birds, reptiles, amphibians and fishes) in the ten hotspots obtained from (Mittermeier et al., 2004).

Hotspot (Abbreviation)	Plants	Mammals	Birds	Reptiles	Amphibians	Fishes
Caribbean Islands (CI)	6550	41	167	468	164	65
East Melanesian Islands (EMI)	3000	39	154	54	38	3
Japan (JA)	1950	46	15	28	44	52
Madagascar and the Indian Ocean Islands (MIOI)	11600	144	183	367	226	97
New Caledonia (NC)	2432	6	23	62	0	9
New Zealand (NZ)	1865	2	89	37	4	25
Philippines (Ph)	6091	102	185	160	74	67
Polynesia Micronesia (PM)	3074	11	170	31	3	20
Sundaland (Su)	15000	173	146	244	172	350
Wallacea (Wa)	1500	127	265	99	32	50

Table S3 Number of cell (=pixel of 0.22 km²) and endemic species that are potentially threatened by sea level rise among the hotspot.

Hotspot	scenario 1M	scenario 2M	scenario 3M	scenario 6M
	Cell number	Cell number	Cell number	Cell number
CI	19720	32808	51183	123270
EMI	1345	1507	1787	3522
JA	30320	40806	52539	89421
MIOI	4576	7957	12938	37179
NC	374	755	1268	2717
NZ	4853	6604	9550	24282
Ph	7595	16643	23395	55069
PM	1740	2352	3276	7034
Su	39279	71978	123930	391174
Wa	5528	7991	11289	27247
	area km2	area km2	area km2	area km2
CI	4338.4	7217.76	11260.26	27119.4
EMI	295.9	331.54	393.14	774.84
JA	6670.4	8977.32	11558.58	19672.62
MIOI	1006.72	1750.54	2846.36	8179.38
NC	82.28	166.1	278.96	597.74
NZ	1067.66	1452.88	2101	5342.04
Ph	1670.9	3661.46	5146.9	12115.18
PM	382.8	517.44	720.72	1547.48
Su	8641.38	15835.16	27264.6	86058.28
Wa	1216.16	1758.02	2483.58	5994.34
	Nb species	Nb species	Nb species	Nb species
CI	1	2	6	46
EMI	0	0	0	0
JA	0	0	0	0
MIOI	0	0	0	0
NC	0	0	0	0
NZ	0	0	0	0
Ph	0	0	0	1
PM	0	0	0	0
Su	0	0	0	8
Wa	0	0	0	0

1 **Table S4** Partial losses of insular habitat in the 10 different hotspots. We classed the number
 2 of islands according to their potential percentage of area inundated per island. We divided in 6
 3 different classes: islands that may be completely inundated (i.e., 100%), islands whose area
 4 may be inundated between 75 and 100%, between 75 and 50%, between 50 and 25%, between
 5 25 and 0%, and islands that are safe from any inundation.

Hotspot	Scenario of SLR	Number of islands that may be at risk of submersion					0%
		100%	100-75%	75-50%	50-25%	25-0%	
CI	1M	63	32	70	69	143	346
	2M	113	47	96	58	143	266
	3M	175	60	83	95	114	196
	6M	356	90	87	52	68	70
EMI	1M	23	0	3	6	113	269
	2M	23	0	4	8	121	258
	3M	23	1	7	11	126	246
	6M	33	5	19	21	153	183
Ja	1M	5	0	7	9	115	264
	2M	8	0	13	15	134	230
	3M	10	2	12	21	151	204
	6M	23	5	17	29	178	148
MIOI	1M	4	1	1	1	13	93
	2M	6	0	4	5	18	80
	3M	6	1	8	3	23	72
	6M	13	2	16	10	24	48
NC	1M	1	0	1	4	13	25
	2M	1	0	2	4	13	24
	3M	2	0	3	5	13	21
	6M	5	0	5	6	16	12
NZ	1M	8	0	2	6	45	59
	2M	8	0	4	7	45	56
	3M	9	0	3	8	46	54
	6M	10	0	9	8	45	48
Ph	1M	48	8	19	28	194	373
	2M	56	12	31	27	211	333
	3M	71	17	34	39	218	291
	6M	113	27	55	62	225	188
PM	1M	15	8	36	35	137	366
	2M	24	8	41	47	149	328
	3M	33	13	52	56	156	287
	6M	84	41	90	46	169	167
Su	1M	61	6	32	21	217	458
	2M	64	12	34	32	240	413
	3M	72	12	43	56	244	368
	6M	122	24	64	94	237	254
Wa	1M	39	7	7	10	177	331
	2M	43	5	11	12	189	311
	3M	45	6	14	18	201	287
	6M	67	8	36	33	248	179

All hotspots	1M	267	62	178	189	1167	2584
	2M	346	84	240	215	1263	2299
3M	446	112	259	312	1292	2026	
6M	826	202	398	361	1363	1297	

Percentage of island

Hotspot		100%	100-75%	75-50%	50-25%	25-0%	0%
CI	1M	8.714	4.426	9.682	9.544	19.779	47.856
	2M	15.629	6.501	13.278	8.022	19.779	36.791
	3M	24.205	8.299	11.480	13.140	15.768	27.109
	6M	49.239	12.448	12.033	7.192	9.405	9.682
EMI	1M	5.556	0.000	0.725	1.449	27.295	64.976
	2M	5.556	0.000	0.966	1.932	29.227	62.319
	3M	5.556	0.242	1.691	2.657	30.435	59.420
	6M	7.971	1.208	4.589	5.072	36.957	44.203
Ja	1M	1.250	0.000	1.750	2.250	28.750	66.000
	2M	2.000	0.000	3.250	3.750	33.500	57.500
	3M	2.500	0.500	3.000	5.250	37.750	51.000
	6M	5.750	1.250	4.250	7.250	44.500	37.000
MIOI	1M	3.540	0.885	0.885	0.885	11.504	82.301
	2M	5.310	0.000	3.540	4.425	15.929	70.796
	3M	5.310	0.885	7.080	2.655	20.354	63.717
	6M	11.504	1.770	14.159	8.850	21.239	42.478
NC	1M	2.273	0.000	2.273	9.091	29.545	56.818
	2M	2.273	0.000	4.545	9.091	29.545	54.545
	3M	4.545	0.000	6.818	11.364	29.545	47.727
	6M	11.364	0.000	11.364	13.636	36.364	27.273
NZ	1M	6.667	0.000	1.667	5.000	37.500	49.167
	2M	6.667	0.000	3.333	5.833	37.500	46.667
	3M	7.500	0.000	2.500	6.667	38.333	45.000
	6M	8.333	0.000	7.500	6.667	37.500	40.000
Ph	1M	7.164	1.194	2.836	4.179	28.955	55.672
	2M	8.358	1.791	4.627	4.030	31.493	49.701
	3M	10.597	2.537	5.075	5.821	32.537	43.433
	6M	16.866	4.030	8.209	9.254	33.582	28.060
PM	1M	2.513	1.340	6.030	5.863	22.948	61.307
	2M	4.020	1.340	6.868	7.873	24.958	54.941
	3M	5.528	2.178	8.710	9.380	26.131	48.074
	6M	14.070	6.868	15.075	7.705	28.308	27.973
Su	1M	7.673	0.755	4.025	2.642	27.296	57.610
	2M	8.050	1.509	4.277	4.025	30.189	51.950
	3M	9.057	1.509	5.409	7.044	30.692	46.289
	6M	15.346	3.019	8.050	11.824	29.811	31.950
Wa	1M	6.830	1.226	1.226	1.751	30.998	57.968
	2M	7.531	0.876	1.926	2.102	33.100	54.466
	3M	7.881	1.051	2.452	3.152	35.201	50.263
	6M	11.734	1.401	6.305	5.779	43.433	31.349

All hotspots	1M	6.004	1.394	4.003	4.250	26.242	58.107
	2M	7.781	1.889	5.397	4.835	28.401	51.698
	3M	10.029	2.519	5.824	7.016	29.053	45.559
	6M	18.574	4.542	8.950	8.118	30.650	29.166

6

7

Annexe 7 :
Matériel supplémentaire
chapitre 4

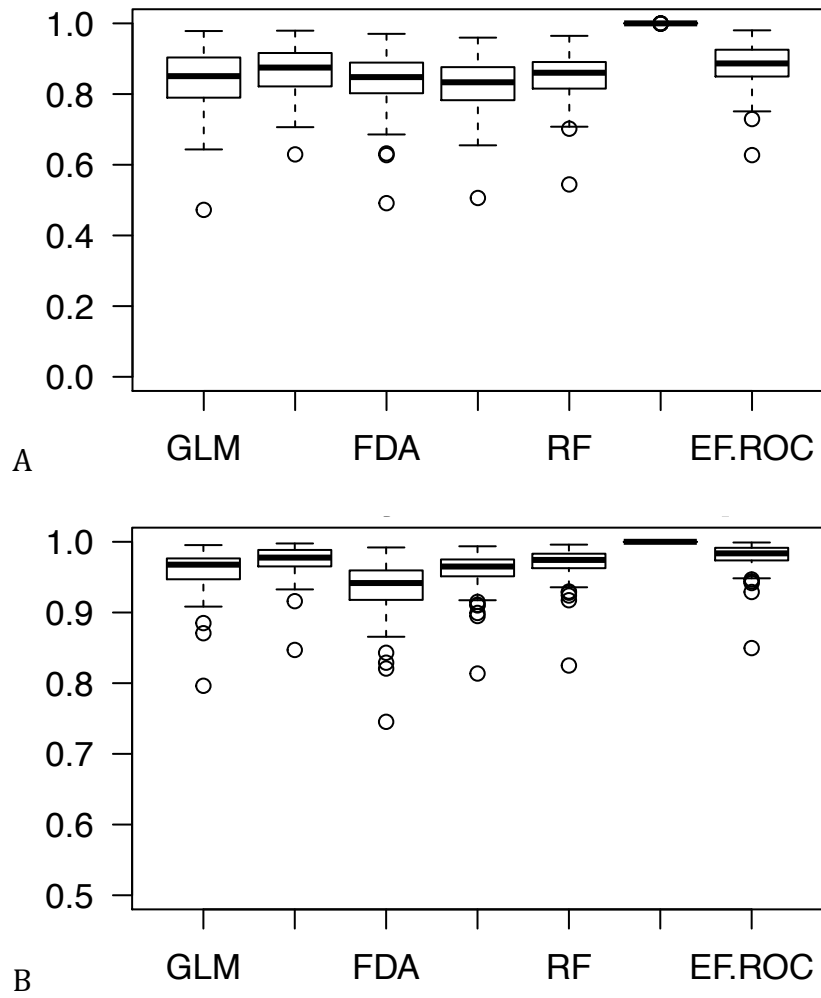


Figure S1: Evaluation performance of the different algorithms with TSS values (A) and AUC values (B)

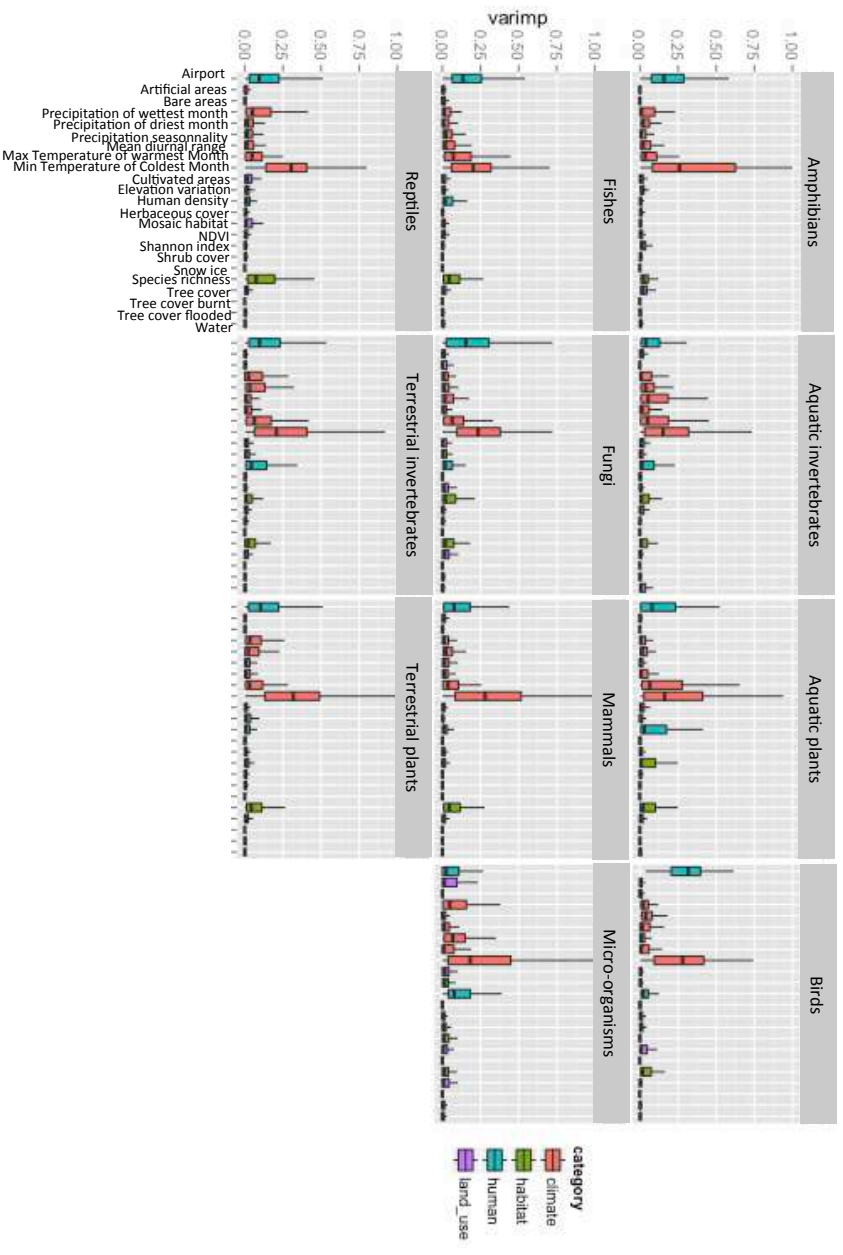


Figure S2 Boxplot of the variable importance for the different taxonomic group.

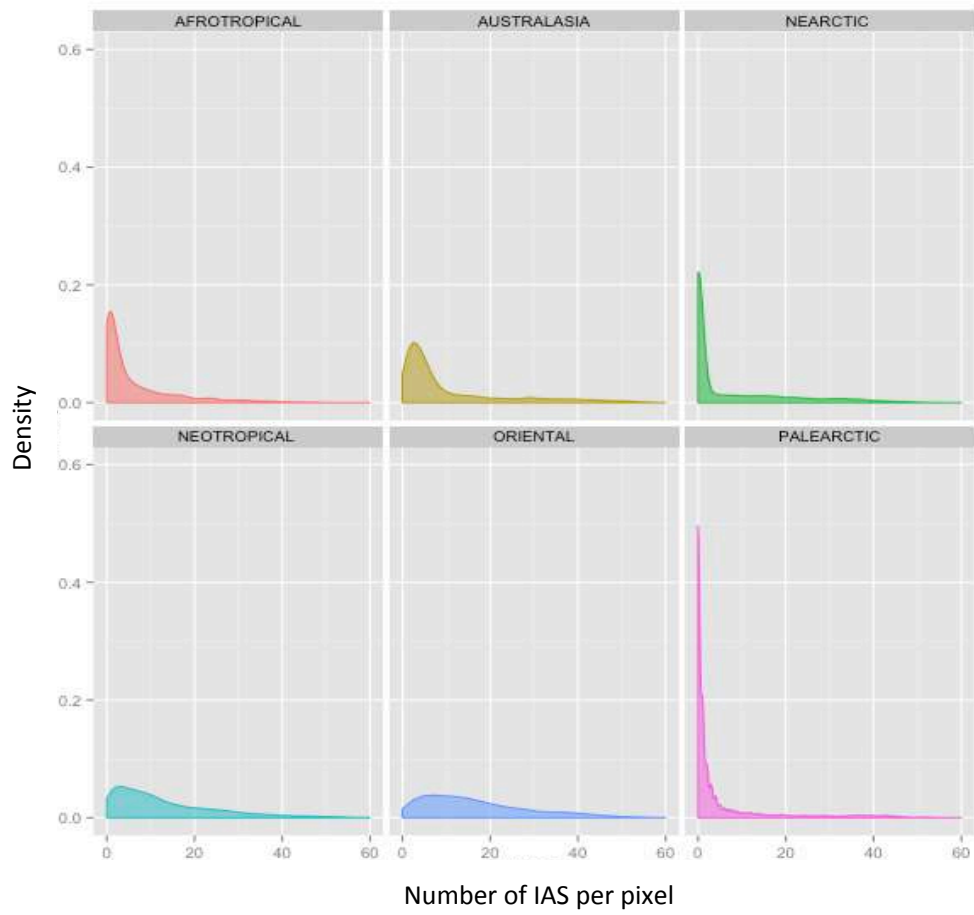


Figure S3 Distribution of the number of invasive species that was predicted to find suitable conditions in the different ecoregion.

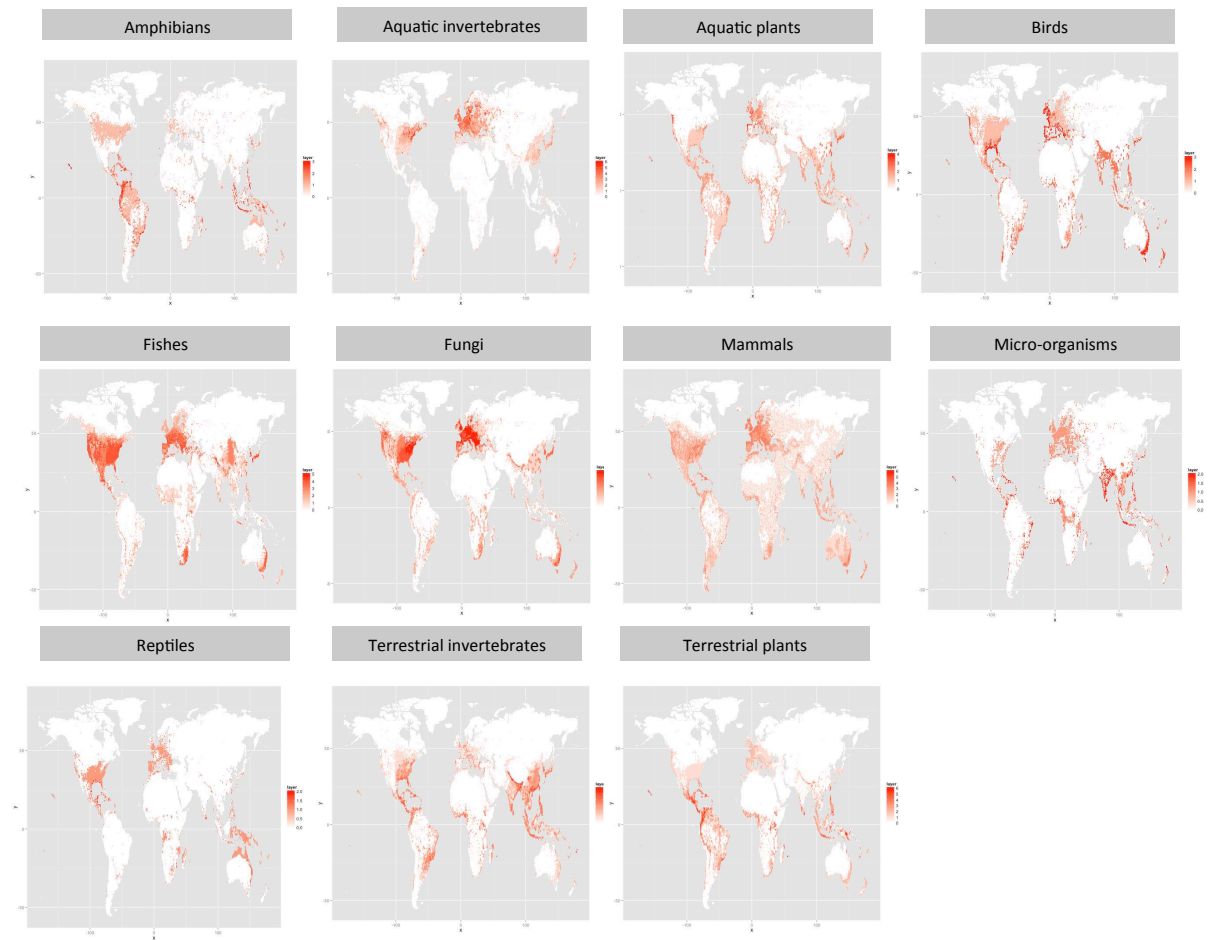


Figure S4 Predicted current spatial distribution over the world for the different taxonomic group.

Annexe 8 :
Matériel supplémentaire
chapitre 5

Supplementary figures and tables

Fig. S1: Boxplots of TSS and an average Area Under the operating characteristic Curve in a ROC analysis values for all the calibrated models.

First, we found performance differences regarding the different algorithms that we used for calibrated the models. FDA, MARS, SRE represent Factorial Discriminant Analysis, Multivariate Adaptive Regression Splines and Surface Range Envelops, respectively. We did not use SRE to the ensemble forecast model. Generalized Linear Models and Generalized Boosted Models performed less well in predicting the distribution of the 99 species compared to MaXent that was the most performed algorithm. EF.ROC represents the ensemble forecast model evaluation.

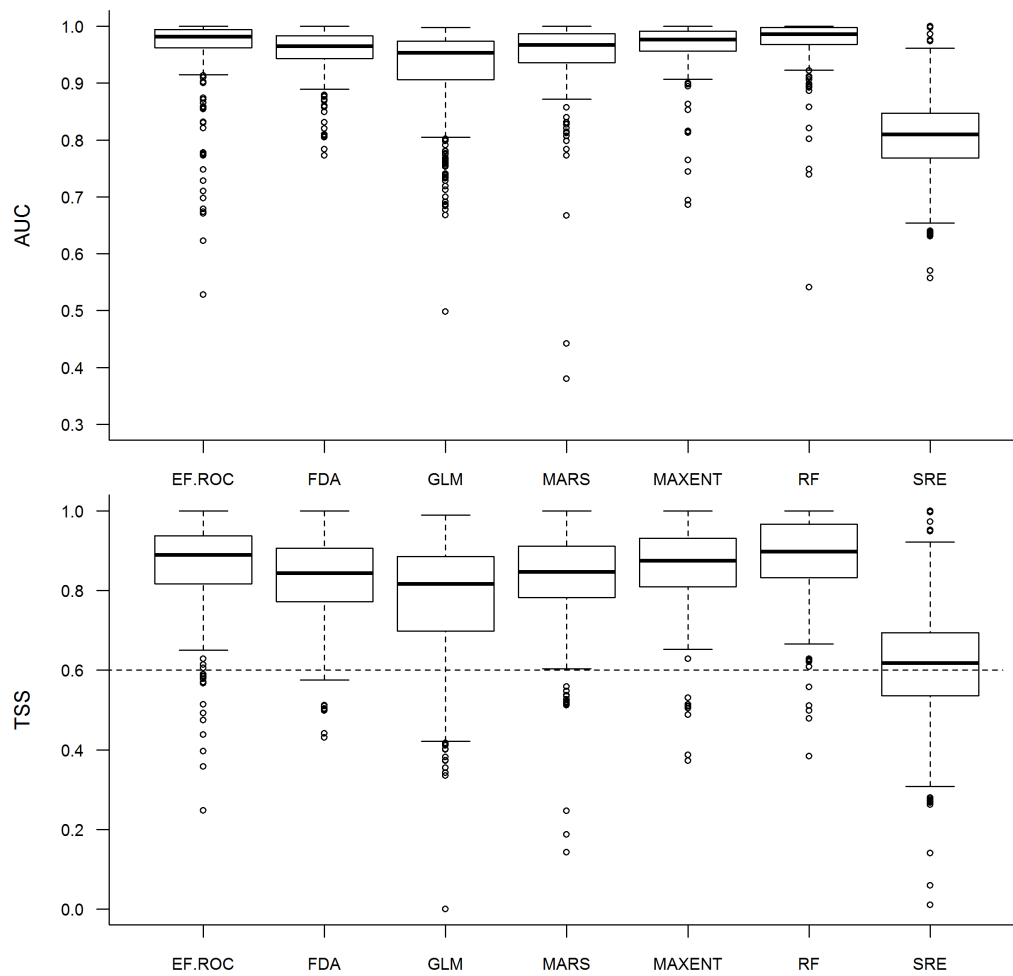


Table S1: Environmental variables list

We used 6 climate variables and 12 land use variables. These variables provide a combination of means, extremes and seasonality that are known to influence species distribution (Root et al., 2003) and we selected only variables that were not collinear (pair-wise $r_{\text{Pearson}} < 0.75$).

Type of variable	Variables	Sources
Climate	Annual mean temperature	Hijmans et al. 2005; http://ccafs-climate.org/
Climate	Maximum temperature of warmest month	Hijmans et al. 2005; http://ccafs-climate.org/
Climate	Maximum temperature of warmest month	Hijmans et al. 2005; http://ccafs-climate.org/
Climate	Maximum temperature of warmest month	Hijmans et al. 2005; http://ccafs-climate.org/
Climate	Maximum temperature of warmest month	Hijmans et al. 2005; http://ccafs-climate.org/
Climate	Precipitation of driest month	Hijmans et al. 2005; http://ccafs-climate.org/
Climate	Temperature seasonality	Hijmans et al. 2005; http://ccafs-climate.org/
Climate	Precipitation seasonality	Hijmans et al. 2005; http://ccafs-climate.org/
Climate	Mean Diurnal Range	Hijmans et al. 2005; http://ccafs-climate.org/
Land use	Tree cover	Alkemade et al. 2009
Land use	Tree cover, regularly flooded	Alkemade et al. 2009
Land use	Mosaic: Cropland / Tree cover / Shrub or Grass Cover / Other natural vegetation	Alkemade et al. 2009
Land use	Tree cover burnt	Alkemade et al. 2009
Land use	Shrub Cover closed-open	Alkemade et al. 2009
Land use	Herbaceous / Sparse herbaceous cover or sparse shrub cover	Alkemade et al. 2009
Land use	Cultivated and managed areas	Alkemade et al. 2009
Land use	Bare areas	Alkemade et al. 2009
Land use	Water Bodies	Alkemade et al. 2009
Land use	Snow and Ice	Alkemade et al. 2009
Land use	Artificial surfaces and associated areas	Alkemade et al. 2009
Land use	Pasture	Alkemade et al. 2009

Table S2. List of the 100 cases of the world's worst invasive species with data sources and number of occurrences.

All occurrence data were checked for each species. First we collected all the data from the online database (GBIF, CABI, OBIS, LIFEMAPPER, IUCN, Aquamap), with sometimes redundancies between online databases. For IUCN point, we performed a random selection of 30 000 points inside the range distribution of species (using R software). Then we checked whether the occurrence data corresponded to the invaded countries with ISSG and CABI information for each species. When necessary, we contacted experts to acquire additional data (GPS data points, information about the real distribution of species and taxonomy issues to avoid commission errors). We removed data points corresponding to building or greenhouse presence for each species. We gratefully acknowledge to the many colleagues who provided species occurrences data, information and references. We are also thankful to Shyama Pagad who helped us to contact expert and find species occurrences data.

Species	N	GBIF	ISSG	CABI	Other online database	refs	Pers. Comm.
<i>Acacia mearnsii</i>	1014	✓	✓				
<i>Achatina fulica</i>	279	✓	✓				
<i>Acridotheres tristis</i>	2690	✓	✓				
<i>Aedes albopictus</i>	263	✓	✓			(Moffett et al., 2009)	S. Pironon
<i>Anopheles quadrimaculatus</i>	61	✓	✓			(Moffett et al., 2009)	S. Pironon
<i>Anoplolepis gracilipes</i>	609	✓	✓		Ant distribution database		
<i>Anoplophora glabripennis</i>	188		✓	✓		(Lingafelter & Hoebeke, 2002)	F. Hérard,
<i>Aphanomyces astaci</i>	2535	✓	✓				
<i>Ardisia elliptica</i>	374	✓	✓	✓			
<i>Arundo donax</i>	1749	✓	✓				
<i>Asterias amurensis</i>	51	✓	✓	✓	OBIS		
<i>Banana bunchy top virus (BBTV)</i>	149					(Kumar et al., 2011)	R. Almeida ; M. Weight ; Cerruti Rr Hooks , J. Thomas
<i>Batrachochytrium dendrobatidis</i>	6558					(Aanensen et al., 2009 ; Aanensen & Spratt, 2007)	
<i>Bemisia tabaci</i>	759		✓	✓		(De Barro et al., 2011)	P.J. De Barro
<i>Boiga irregularis</i>	865	✓	✓	✓			
<i>Capra hircus</i>	704	✓	✓	✓	IUCN		
<i>Carcinus maenas</i>	5871	✓	✓	✓			
<i>Caulerpa taxifolia</i>	346		✓	✓	Lifemapper; DAISIE		
<i>Cecropia peltata</i>	466	✓	✓	✓			
<i>Cercopagis pengoi</i>	101	✓	✓	✓	INVADER		
<i>Cervus elaphus</i>	2140	✓			IUCN		
<i>Chromolaena odorata</i>	906	✓	✓	✓			
<i>Cinara cupressivora</i>	146		✓	✓			C. Montalva , V. El Mujtar, G. Watson ; A. Alvarado ; S. Murphy

<i>Cinchona pubescens</i>	289	✓	✓			
<i>Clarias batrachus</i>	190		✓	✓	Lifemapper; OBIS	
<i>Clidemia hirta</i>	741	✓	✓	✓		
<i>Coptotermes formosanus</i>	387	✓	✓	✓		(Vargo et al. 2003, 2006; Husseneder & Grace 2001; Li et al. 2010)
<i>Corbula amurensis</i>	125	✓	✓	✓	Lifemapper; OBIS	R.H. Scheffrahn, C. Husseneder, M. Jianchu, E. Vargo ; HF Li
<i>Cryphonectria parasitica</i>	77	✓	✓	✓		JK Thompson
<i>Cyprinus carpio</i>	5405	✓	✓	✓		
<i>Dreissena polymorpha</i>	5610	✓	✓	✓		
<i>Eichhornia crassipes</i>	1088	✓	✓	✓		
<i>Eleutherodactylus coqui</i>	624	✓	✓		IUCN	
<i>Eriocheir sinensis</i>	217			✓	OBIS	
<i>Euglandina rosea</i>	101		✓	✓	OBIS	
<i>Euphorbia esula</i>	4771	✓	✓	✓		
<i>Felis catus</i>	20128	✓	✓			
<i>Gambusia affinis</i>	4903	✓	✓	✓		E. Enatoli ; D. Macdonald ; B. Tershy
<i>Hedychium gardnerianum</i>	132	✓	✓		Lifemapper	
<i>Herpestes javanicus/auropunctatus</i>	141	✓	✓	✓	OBIS	S. Roy
<i>Hiptage benghalensis</i>	218	✓	✓	✓		J. Fujikawa, V. Florens ; S. Baret
<i>Imperata cylindrica</i>	4667	✓	✓	✓		
<i>Lantana camara</i>	1842	✓	✓	✓		
<i>Lates niloticus</i>	91	✓	✓	✓		
<i>Leucaena leucocephala</i>	1009	✓	✓	✓		
<i>Ligustrum robustum subsp. walkeri</i>	82		✓	✓		C. Lavergne
<i>Linepithema humile</i>	428	✓	✓	✓	Ant distribution database	
<i>Lithobates catesbeianus</i>	14734	✓			IUCN	
<i>Lymantria dispar</i>	486	✓	✓	✓		
<i>Lythrum salicaria</i>	41199	✓	✓	✓		
<i>Macaca fascicularis</i>	394	✓	✓	✓	IUCN	
<i>Melaleuca quinquenervia</i>	1324	✓	✓	✓		
<i>Miconia calvescens</i>	349	✓	✓			(Pouteau et al. 2010)
<i>Micropterus salmoides</i>	5712	✓	✓	✓		JY Meyer
<i>Mikania micrantha</i>	1058	✓	✓	✓		
<i>Mimosa pigra</i>	950	✓	✓	✓		
<i>Mnemiopsis leidyi</i>	271	✓	✓	✓	Aquamap	(Ghabooli et al. 2010)
<i>Morella faya</i>	25590	✓	✓	✓		T. Shiganov ; B. Gallardo
<i>mus musculus</i>	13828	✓	✓	✓		
<i>Mustela erminea</i>	6494	✓	✓	✓		
<i>Myocastor coypus</i>	1438	✓	✓	✓	IUCN	
<i>Mytilus</i>	307	✓	✓	✓		

<i>galloprovincialis</i>							
<i>Oncorhynchus mykiss</i>	4307	✓	✓	✓			
<i>Ophiostoma ulmi sensu lato</i>	123			✓			B. Clive
<i>Opuntia stricta</i>	500	✓	✓	✓			
<i>Oreochromis mossambicus</i>	760	✓	✓	✓			
<i>Oryctolagus cuniculus</i>	25596	✓	✓	✓	IUCN		
<i>Pheidole megacephala</i>	338	✓	✓	✓	Ant distribution database		
	731					(Commonwealth Mycological Institute 1942 ; Balci & Halmschlager 2003; Balci et al. 2007, 2009)	A. Cravador, E. Hansen, M. Wingfield ; B. Marçais ; B. Clive ; C. Robin
<i>Phytophthora cinnamomi</i>		✓	✓	✓			
<i>Pinus pinaster</i>	1936	✓	✓	✓			
<i>Plasmodium relictum</i>		✓	✓	✓	(Bensch et al. 2009)(Beadell et al. 2006)PM		R. Fleischer, S. Bensch, D. Lapointe, V. Palinauskas ; CT Atkinson ; RN Sehgal
	122					(Matsui et al., 2010; Ohbayashi et al., 2007)	
<i>Platydemus manokwari</i>	46	✓	✓	✓			
<i>Polygonum cuspidatum</i>	931	✓	✓	✓			
<i>Pomacea canaliculata</i>	97	✓	✓	✓	Lifemapper	(Hayes et al., 2008)	R. Cowie
<i>Prosopis glandulosa</i>	446	✓		✓			
<i>Psidium cattleianum</i>	120	✓	✓	✓			
<i>Pueraria montana var. lobata</i>	721	✓	✓	✓			
<i>Pycnonotus cafer</i>	2172	✓	✓	✓			
<i>Rattus rattus</i>	4769	✓	✓	✓		(Peacock, 2009)	
<i>Rhinella marina</i>	3237	✓	✓	✓	IUCN		
<i>Rubus ellipticus</i>	95	✓	✓	✓	IUCN		
<i>Salmo trutta</i>	21809	✓	✓	✓	IUCN		
<i>Schinus terebinthifolius</i>	153	✓	✓	✓	IUCN		
<i>Sciurus carolinensis</i>	14625	✓	✓	✓	IUCN		
<i>Solenopsis invicta</i>	947	✓	✓	✓	Ant distribution database		
<i>Spartina anglica</i>	1766	✓	✓	✓	IUCN		
<i>Spathodea campanulata</i>	222	✓	✓	✓	IUCN		
<i>Sphagneticola trilobata</i>	573	✓	✓	✓	IUCN		
<i>Sturnus vulgaris</i>	10466	✓	✓	✓	IUCN; Lifemapper		
<i>Sus scrofa</i>	40210	✓	✓	✓	IUCN	(Jaksic et al., 2002)	E. Baubet
<i>Tamarix ramosissima</i>	712	✓	✓	✓	IUCN		
<i>Trachemys scripta elegans</i>	597	✓	✓	✓	IUCN		
<i>Trichosurus vulpecula</i>	8818	✓	✓	✓	IUCN		
<i>Trogoderma</i>	282					(Banks, 1977;NASPI,	M. Shoaib Ahmed

<i>Ulex europaeus</i>	12548	✓	✓	✓	IUCN
<i>Undaria pinnatifida</i>	92	✓	✓	✓	IUCN;lifemapper
<i>Vespula vulgaris</i>	2454	✓	✓	✓	IUCN
<i>Vulpes vulpes</i>	21414	✓	✓	✓	IUCN
<i>Wasmannia auropunctata</i>	272	✓	✓	✓	Ant distribution database

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Table S3 Percentage of net change of the number of IAS for the 14 types of biomes under the A1B and B2 scenarios.

Biome	A1B					
	current	sd_current	2050	sd_2050	2080	sd_2080
Boreal forest	0.83	2.70	1.28	3.53	1.62	3.98
Cool coniferous forest	2.94	4.73	5.02	6.18	6.35	6.74
Grassland and steppe	4.69	5.85	4.80	5.61	4.71	5.29
Hot desert	1.93	2.44	1.82	2.16	1.76	1.97
Ice	0.07	0.51	0.22	1.25	0.33	1.85
Savanna	9.64	7.31	8.59	6.73	7.88	6.26
Scrubland	10.40	9.29	9.48	8.12	8.61	7.42
Temperate deciduous forest	24.95	12.59	27.38	13.30	27.32	13.55
Temperate mixed forest	11.96	10.52	15.14	11.72	16.46	12.11
Tropical forest	16.71	9.91	14.04	9.87	12.68	9.29
Tropical woodland	16.26	10.28	13.57	9.60	11.82	8.75
Tundra	0.21	0.99	0.27	1.28	0.29	1.41
Warm mixed forest	22.31	12.47	23.18	11.59	22.38	11.25
Wooded tundra	0.46	1.85	0.67	2.54	0.78	2.81
	B2A					
	current	sd_current	2050	sd_2050	2080	sd_2080
Boreal forest	0.83	2.70	1.05	3.20	1.28	3.49
Cool coniferous forest	2.94	4.73	3.78	5.44	4.72	5.82
Grassland and steppe	4.69	5.85	4.75	5.59	4.82	5.56
Hot desert	1.93	2.44	1.82	2.20	1.81	2.06
Ice	0.07	0.51	0.13	0.80	0.18	1.04
Savanna	9.64	7.31	9.52	7.22	8.94	6.92
Scrubland	10.40	9.29	9.84	8.39	9.49	8.04
Temperate deciduous forest	24.95	12.59	26.66	12.91	27.18	13.10
Temperate mixed forest	11.96	10.52	13.60	11.48	14.97	11.66
Tropical forest	16.71	9.91	15.66	10.26	14.63	10.00
Tropical woodland	16.26	10.28	15.61	10.31	14.53	9.98
Tundra	0.21	0.99	0.23	1.17	0.25	1.26
Warm mixed forest	22.31	12.47	23.24	11.73	22.82	11.45
Wooded tundra	0.46	1.85	0.56	2.28	0.65	2.48

Table S4: Percentage of net change between current and future scenarios (A1B and B2) of the range size for the different taxa.

Taxon	A1B		B2A	
	Net change Mean	Net change sd	Net change Mean	Net change sd
« 100 of the worst IAS »	2.18	55.48	6.09	46.41
Amphibian (N=3)	-64.67	9.80	-45.98	14.90
Aquatic invertebrates (N=9)	58.74	110.58	56.29	101.38
Aquatic plants (N=4)	12.37	43.74	13.49	32.21
Birds (N=3)	-24.11	18.89	-11.44	19.26
Fishes (N=8)	-1.16	56.27	-1.47	43.38
Fungi (N=4)	-10.66	22.81	-6.81	16.09
Mammal (N=14)	-4.05	35.03	-1.01	26.24
Micro organisms (N=3)	16.76	7.70	14.80	7.98
Reptile (N=2)	4.34	17.84	9.44	14.10
Terrestrial invertebrates (N=17)	17.57	56.60	16.64	42.84
Terrestrial plants (N=32)	-10.38	34.35	-2.41	26.86

Supplementary information 1: Packages used in this article

All the analyses of this article were performed with R platform version 2.15. We used mainly three different R packages: BioMod package to perform SDMs analyses, raster package to manage the data, ggplot2 to do the graphics.

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Annexe 9 :
Matériel supplémentaire
chapitre 6

Table S1: Environmental variables

For the climate analysis we used 6 climate variables (*i.e.* annual mean temperature, maximum temperature of warmest month, minimum temperature of coldest month, annual precipitation, precipitation of wettest month, precipitation of driest month) and we standardized by temperature and precipitation seasonality. For niche modeling analyses, we also used six climate variables (*i.e.* mean diurnal range, maximum temperature of warmest month, minimum temperature of coldest month, annual precipitation, precipitation of wettest month, precipitation of driest month) and 12 land use variables that are described below in the table.

Type of variable	Variables	Sources
Climate	Annual mean temperature	Hijmans et al. 2005; http://ccafs-climate.org/
Climate	Maximum temperature of warmest month	Hijmans et al. 2005; http://ccafs-climate.org/
Climate	Minimum temperature of coldest month	Hijmans et al. 2005; http://ccafs-climate.org/
Climate	Annual precipitation	Hijmans et al. 2005; http://ccafs-climate.org/
Climate	Precipitation of wettest month	Hijmans et al. 2005; http://ccafs-climate.org/
Climate	Precipitation of driest month	Hijmans et al. 2005; http://ccafs-climate.org/
Climate	Temperature seasonality	Hijmans et al. 2005; http://ccafs-climate.org/
Climate	Precipitation seasonality	Hijmans et al. 2005; http://ccafs-climate.org/
Climate	Mean Diurnal Range	Hijmans et al. 2005; http://ccafs-climate.org/
Land use	Tree cover (<i>i.e.</i> , broadleaved, evergreen broadleaved, deciduous closed broadleaved, deciduous open, needle-leaved, evergreen, needle-leaved, deciduous mixed leaf type).	Alkemade et al. 2009
Land use	Tree cover, regularly flooded (<i>i.e.</i> , fresh water, saline water,	Alkemade et al. 2009
Land use	Mosaic: Cropland (<i>i.e.</i> , Tree cover /other natural vegetation, cropland/Tree cover/Other natural vegetation, Shrub or Grass cover).	Alkemade et al. 2009
Land use	Tree cover burnt	Alkemade et al. 2009
Land use	Shrub Cover closed-open (<i>i.e.</i> , evergreen, deciduous).	Alkemade et al. 2009
Land use	Herbaceous / Sparse herbaceous cover or sparse shrub cover	Alkemade et al. 2009
Land use	Cultivated and managed areas	Alkemade et al. 2009
Land use	Bare areas	Alkemade et al. 2009
Land use	Water Bodies	Alkemade et al. 2009

Land use	Snow and Ice	Alkemade et al. 2009
Land use	Artificial surfaces and associated areas	Alkemade et al. 2009
Land use	Pasture	Alkemade et al. 2009

Table S2: Number of endemic species (i.e. plants, mammals, birds, reptiles, amphibians and freshwater fishes) from (Mittermeier et al., 2004).

Biodiversity hotspots	Number of endemic species
California Floristic Province (CFP)	2194
Caribbean Islands (CI)	7455
Madrean Pine-Oak Woodlands (MPOW)	4109
Mesoamerican (Me)	4153
Atlantic Forest (AF)	8732
Cerrado (Ce)	4689
Chilean Winter Rainfall-Valdivian Forests (CWRF)	2063
Tumbes-Chocó-Magdalena (TCM)	3114
Tropical Andes (TA)	16729
Caucasus (Ca)	1656
Irano-Anatolian (IA)	2557
Mediterranean Basin (MB)	11924
Mountains of Central Asia (MCA)	1516
Cape Floristic Region (CFR)	6272
Coastal Forests of Eastern Africa (CFEA)	1867
Eastern Afromontane (EA)	3359
Guinean Forests of West Africa (GFWA)	2220
Horn of Africa (HA)	2905
Madagascar and the Indian Ocean Islands (MIOI)	12617
Maputaland-Pondoland-Albany (MPA)	1973
Succulent Karoo (SK)	2458
East Melanesian Islands (EMI)	3288
Himalaya (HI)	3310
Indo-Burma (IB)	8042
Japan (Ja)	2135
Mountains of Southwest China (MSC)	3584
New Caledonia (NC)	2532
New Zealand (NZ)	2022
Philippines (Ph)	6679
Polynesia-Micronesia (PM)	3309
Southwest Australia (SA)	3026
Sundaland (Su)	16085
Wallacea (Wa)	2073
Western Ghats and Sri Lanka (WGSL)	3555

Table S3. List of the 100 cases of the world's worst invasive species with data sources and number of occurrences.

All occurrence data were checked for each species. First we collected all the data from the online database (GBIF, CABI, OBIS, LIFEMAPPER, IUCN, Aquamap), with sometimes redundancies between online databases. For IUCN point, we performed a random selection of 30 000 points inside the range distribution of species (using R software). Then we checked whether the occurrence data corresponded to the invaded countries with ISSG and CABI information for each species. When necessary, we contacted experts to acquire additional data (GPS data points, information about the real distribution of species and taxonomy issues to avoid commission errors). We removed data points corresponding to building or greenhouse presence for each species.

Species	N	GBIF	ISSG	CABI	Other online database	refs	Pers. communication
<i>Acacia mearnsii</i>	1014	✓	✓				
<i>Achatina fulica</i>	279	✓	✓				
<i>Acridotheres tristis</i>	2690	✓	✓				
<i>Aedes albopictus</i>	263	✓	✓			(Moffett et al., 2009)	S. Pironon
<i>Anopheles quadrimaculatus</i>	61	✓	✓			(Moffett et al., 2009)	S. Pironon
<i>Anoplolepis gracilipes</i>	609	✓	✓		Ant distribution database		
<i>Anoplophora glabripennis</i>	188		✓	✓		(Lingafelter & Hoebeke, 2002)	F. Hérard,
<i>Aphanomyces astaci</i>	2535	✓	✓				
<i>Ardisia elliptica</i>	374	✓	✓	✓			
<i>Arundo donax</i>	1749	✓	✓				
<i>Asterias amurensis</i>	51	✓	✓	✓	OBIS		
<i>Banana bunchy top virus (BBTV)</i>	149					(Kumar et al., 2011)	R. Almeida ; Cerruti Rr Hooks , J. Thomas
<i>Batrachochytrium dendrobatidis</i>	6558					Aanensen et al., 2009 ; Aanensen & Spratt, 2007)	
<i>Bemisia tabaci</i>	759		✓	✓		(De Barro et al., 2011)	P.J. De Barro
<i>Boiga irregularis</i>	865	✓	✓	✓			
<i>Capra hircus</i>	704	✓	✓	✓	IUCN		
<i>Carcinus maenas</i>	5871	✓	✓	✓			
<i>Caulerpa taxifolia</i>	346		✓	✓	Lifemapper; DAISIE		
<i>Cecropia peltata</i>	466	✓	✓	✓			
<i>Cercopagis pengoi</i>	101	✓	✓	✓	INVADER		
<i>Cervus elaphus</i>	2140	✓			IUCN		
<i>Chromolaena odorata</i>	906	✓	✓	✓			
<i>Cinara cupressivora</i>	146		✓	✓			C. Montalva , V. El Mujtar, G. Watson
<i>Cinchona pubescens</i>	289	✓	✓				
<i>Clarias batrachus</i>	190		✓	✓	Lifemapper; OBIS		
<i>Clidemia hirta</i>	741	✓	✓	✓			
<i>Coptotermes formosanus</i>	387	✓	✓	✓		(Vargo et al. 2003, 2006; Husseneder & Grace 2001; Li et al. 2010)	R.H. Scheffrahn, C. Husseneder, M. Jianchu, E. Vargo

<i>Corbula amurensis</i>	125	✓	✓	✓	Lifemapper; OBIS		
<i>Cryphonectria parasitica</i>	77	✓	✓	✓			
<i>Cyprinus carpio</i>	5405	✓	✓	✓			
<i>Dreissena polymorpha</i>	5610	✓	✓	✓			
<i>Eichhornia crassipes</i>	1088	✓	✓	✓			
<i>Eleutherodactylus coqui</i>	624	✓	✓		IUCN		
<i>Eriocheir sinensis</i>	217			✓	OBIS		
<i>Euglandina rosea</i>	101		✓	✓	OBIS		
<i>Euphorbia esula</i>	4771	✓	✓	✓			
<i>Felis catus</i>	20128	✓	✓				
<i>Gambusia affinis</i>	4903	✓	✓	✓			
<i>Hedychium gardnerianum</i>	132	✓	✓		Lifemapper		
<i>Herpestes javanicus/auropunctatus</i>	141	✓	✓	✓	OBIS		S. Roy
<i>Hiptage benghalensis</i>	218	✓	✓	✓			J. Fujikawa, V. Florens
<i>Imperata cylindrica</i>	4667	✓	✓	✓			
<i>Lantana camara</i>	1842	✓	✓	✓			
<i>Lates niloticus</i>	91	✓	✓	✓			
<i>Leucaena leucocephala</i>	1009	✓	✓	✓			
<i>Ligustrum robustum subsp. walkeri</i>	82		✓	✓			C. Lavergne
<i>Linepithema humile</i>	428	✓	✓	✓	Ant distribution database		
<i>Lithobates catesbeianus</i>	14734	✓			IUCN		
<i>Lymantria dispar</i>	486	✓	✓	✓			
<i>Lythrum salicaria</i>	41199	✓	✓	✓			
<i>Macaca fascicularis</i>	394	✓	✓	✓	IUCN		
<i>Melaleuca quinquenervia</i>	1324	✓	✓	✓			
<i>Miconia calvescens</i>	349	✓	✓			(Pouteau et al. 2010)	JY Meyer
<i>Micropterus salmoides</i>	5712	✓	✓	✓			
<i>Mikania micrantha</i>	1058	✓	✓	✓			
<i>Mimosa pigra</i>	950	✓	✓	✓			
<i>Mnemiopsis leidyi</i>	271	✓	✓	✓	Aquamap	(Ghabooli et al. 2010)	T. Shiganov
<i>Morella faya</i>	25590	✓	✓	✓			
<i>mus musculus</i>	13828	✓	✓	✓			
<i>Mustela erminea</i>	6494	✓	✓	✓			
<i>Myocastor coypus</i>	1438	✓	✓	✓	IUCN		
<i>Mytilus galloprovincialis</i>	307	✓	✓	✓			
<i>Oncorhynchus mykiss</i>	4307	✓	✓	✓			
<i>Ophiostoma ulmi sensu lato</i>	123			✓			
<i>Opuntia stricta</i>	500	✓	✓	✓			
<i>Oreochromis mossambicus</i>	760	✓	✓	✓			

<i>Oryctolagus cuniculus</i>	25596	✓	✓	✓	IUCN		
<i>Pheidole megacephala</i>	338	✓	✓	✓	Ant distribution database		
<i>Phytophthora cinnamomi</i>	731	✓	✓	✓		(Commonwealth Mycological Institute 1942 ; Balci & Halmschlager 2003; Balci et al. 2007, 2009)	A. Cravador, E. Hansen, M. Wingfield ; Benoit Marçais)
<i>Pinus pinaster</i>	1936	✓	✓	✓			
<i>Plasmodium relictum</i>	122	✓	✓	✓	(Bensch et al. 2009)(Beadell et al. 2006)PM		R. Fleischer, S. Bensch, D. Lapointe
<i>Platydemus manokwari</i>	46	✓	✓	✓		(Matsui et al., 2010; Ohbayashi et al., 2007)	
<i>Polygonum cuspidatum</i>	931	✓	✓	✓			
<i>Pomacea canaliculata</i>	97	✓	✓	✓	Lifemapper	(Hayes et al., 2008)	
<i>Prosopis glandulosa</i>	446	✓		✓			
<i>Psidium cattleianum</i>	120	✓	✓	✓			
<i>Pueraria montana var. lobata</i>	721	✓	✓	✓			
<i>Pycnonotus cafer</i>	2172	✓	✓	✓			
<i>Rattus rattus</i>	4769	✓	✓	✓		(Peacock, 2009)	
<i>Rhinella marina</i>	3237	✓	✓	✓	IUCN		
<i>Rubus ellipticus</i>	95	✓	✓	✓	IUCN		
<i>Salmo trutta</i>	21809	✓	✓	✓	IUCN		
<i>Schinus terebinthifolius</i>	153	✓	✓	✓	IUCN		
<i>Sciurus carolinensis</i>	14625	✓	✓	✓	IUCN		
<i>Solenopsis invicta</i>	947	✓	✓	✓	Ant distribution database		
<i>Spartina anglica</i>	1766	✓	✓	✓	IUCN		
<i>Spathodea campanulata</i>	222	✓	✓	✓	IUCN		
<i>Sphagneticola trilobata</i>	573	✓	✓	✓	IUCN		
<i>Sturnus vulgaris</i>	10466	✓	✓	✓	IUCN; Lifemapper		
<i>Sus scrofa</i>	40210	✓	✓	✓	IUCN	(Jaksic et al., 2002)	E. Baudet
<i>Tamarix ramosissima</i>	712	✓	✓	✓	IUCN		
<i>Trachemys scripta elegans</i>	597	✓	✓	✓	IUCN		
<i>Trichosurus vulpecula</i>	8818	✓	✓	✓	IUCN		
<i>Trogoderma granarium</i>	282					(Banks, 1977;NASPI, 2009)	M. Shoaib Ahmedani; P. Ponel, S. Pagad
<i>Ulex europaeus</i>	12548	✓	✓	✓	IUCN		
<i>Undaria pinnatifida</i>	92	✓	✓	✓	IUCN;lifemapper		
<i>Vespula vulgaris</i>	2454	✓	✓	✓	IUCN		
<i>Vulpes vulpes</i>	21414	✓	✓	✓	IUCN		
<i>Wasmannia auropunctata</i>	272	✓	✓	✓	Ant distribution database		

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Table S4. Standardized Euclidian Distance thresholds (SED_t) that distinguish analogue from non-analog climates for each hotspot. All the threshold have been calculated using the methodology detailed in Figure S1.

Biodiversity hotspot	Threshold
Atlantic Forest	10.94
Caucasus	12.568
Coastal Forests of Eastern Africa	3.808
California Floristic Province	4.922
Cape Floristic Region	0.402
Caribbean Islands	2.284
Chilean Winter Rainfall-Valdivian Forests	17.044
Eastern Afromontane	15.076
East Melanesian Islands	5.604
Horn of Africa	1.28
Himalaya	15.656
Irano-Anatolian	5.014
Indo-Burma	2.132
Japan	8.123
Mediterranean Basin	1.896
Mountains of Central Asia	63.488
Mesoamerican	0.338
Madagascar and the Indian Ocean Islands	4.904
Maputaland-Pondoland-Albany	4.347
Madrean Pine-Oak Woodlands	4.416
New Zealand	34.557
Philippines	28.806
Polynesia-Micronesia	0.581
Southwest Australia	3.975
Succulent Karoo	0.649
Sundaland	8.557
Tropical Andes	43.152
Tumbes-Chocó-Magdalena	5.156
Wallacea	5.542
Western Ghats and Sri Lanka	3.218
Mean distance threshold	10.6145

Table S5: Classification of land use classes in natural and/or artificial areas.

Land use class	Class
Tree cover	natural
Tree/shrub cover regularly flooded	natural
Mosaic : cropland / tree cover	natural & artificial
Tree cover burnt	natural
Shrub cover	natural
Herbaceous cover	natural
Cultivated and managed area	artificial
Bare areas	natural
Water bodies	natural & artificial
Snow and ice	natural & artificial
Artificial surfaces and associated areas	artificial
Pasture	natural & artificial

Table S6: Threatened endemic biodiversity due to climate change

We used 3 different values of z : the typical value of fragmented habitats (e.g. $z=0.25$, Brooks *et al.*, 2002); a conservative value more typical of continental situations (e.g. $z=0.15$, Malcolm *et al.*, 2006); and an intermediate value (e.g. $z=0.2$, Bergl *et al.*, 2007).

Biodiversity hotspots	Scenario A1					
	Percentage of species lost			number of endemic lost species		
	$z = 0.15$	$z = 0.20$	$z = 0.25$	$z = 0.15$	$z = 0.20$	$z = 0.25$
Atlantic Forest	28.216	28.77	29.204	2464	2512	2550
California Floristic Province	5.417	6.697	7.884	119	147	173
Cape Floristic Region	33.617	33.87	34.209	2108	2124	2146
Caribbean Islands	33.344	33.36	33.39	2486	2487	2489
Caucasus	2.626	3.533	4.439	43	59	74
Chilean Winter Rainfall-Valdivian Forests	1.903	2.659	3.4383	39	55	71
Coastal Forests of Eastern Africa	31.829	32.001	32.134	594	597	600
East Melanesian Islands	35.106	35.84	36.613	1154	1178	1204
Eastern Afromontane	1.097	1.634	2.22	37	55	75
Himalaya	0.344	0.587	0.885	11	19	29
Horn of Africa	33.333	33.333	33.333	968	968	968
Indo-Burma	33.333	33.333	33.333	2681	2681	2681
Irano-Anatolian	2.457	3.331	4.211	63	85	108
Japan	33.333	33.333	33.333	712	712	712
Madagascar and the Indian Ocean Islands	24.593	25.482	26.187	3103	3215	3304
Madrean Pine-Oak Woodlands	14.331	15.815	17.061	589	650	701
Maputaland-Pondoland-Albany	33.333	33.333	33.333	658	658	658
Mediterranean Basin	29.238	29.689	30.04	3486	3540	3582
Mesoamerican	50.553	53.499	56.105	2099	2222	2330
Mountains of Central Asia	0	0	0	0	0	0
New Zealand	26.364	27.096	27.673	533	548	560
Philippines	16.303	17.723	18.899	1089	1184	1262
Polynesia-Micronesia	100	100	100	3309	3309	3309
Southwest Australia	24.467	25.366	26.081	740	768	789
Succulent Karoo	33.333	33.333	33.333	819	819	819
Sundaland	33.333	33.333	33.334	5362	5362	5362
Tropical Andes	0.091	0.181	0.307	15	30	51
Tumbes-Chocó-Magdalena	16.845	18.264	19.457	525	569	606
Wallacea	33.333	33.333	33.333	691	691	691
Western Ghats and Sri Lanka	33.334	33.336	33.341	1185	1185	1185
MEAN	24.847	25.402	25.904	1256	1281	1303
TOTAL (Sum of all hotspots)	X	X	X	37682	38429	39089
Biodiversity hotspots	Scenario B2					
	Percentage of species lost			number of endemic lost species		
	$z = 0.15$	$z = 0.20$	$z = 0.25$	$z = 0.15$	$z = 0.20$	$z = 0.25$
Atlantic Forest	0	0	0	0	0	0
California Floristic Province	0	0	0	0	0	0
Cape Floristic Region	0.226	0.46	0.794	14	29	50
Caribbean Islands	0.001	0.003	0.008	0	0	1

Caucasus	0	0	0	0	0	0
Chilean Winter Rainfall-Valdivian Forests	9.118E-10	1.561E-08	1.387E-07	0	0	0
Coastal Forests of Eastern Africa	0	0	0	0	0	0
East Melanesian Islands	0.176	0.326	0.528	6	11	17
Eastern Afromontane	0	0	0	0	0	0
Himalaya	0	0	0	0	0	0
Horn of Africa	0	0	0	0	0	0
Indo-Burma	2.056E-07	1.928E-06	1.087E-05	0	0	0
Irano-Anatolian	0	0	0	0	0	0
Japan	4.655E-07	3.920E-06	2.031E-05	0	0	0
Madagascar and the Indian Ocean Islands	4.079E-10	7.669E-09	7.326E-08	0	0	0
Madrean Pine-Oak Woodlands	0	0	0	0	0	0
Maputaland-Pondoland-Albany	0	0	0	0	0	0
Mediterranean Basin	3.206E-10	6.952E-09	7.426E-08	0	0	0
Mesoamerican	11.386	14.577	17.648	473	605	733
Mountains of Central Asia	0	0	0	0	0	0
New Zealand	6.453E-07	5.378E-06	2.772E-05	0	0	0
Philippines	0	0	0	0	0	0
Polynesia-Micronesia	88.625	89.815	90.753	2933	2972	3003
Southwest Australia	0	0	0	0	0	0
Succulent Karoo	0	0	0	0	0	0
Sundaland	2.472E-06	1.692E-05	7.451E-05	0	0	0
Tropical Andes	0	0	0	0	0	0
Tumbes-Chocó-Magdalena	0.026	0.062	0.122	1	2	4
Wallacea	5.955E-06	3.971E-05	1.713E-04	0	0	0
Western Ghats and Sri Lanka	0.002	0.008	0.02	0	0	1
	3.348	3.508	3.662	114	121	127
	X	X	X	3427	3619	3809

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Statistical analyses

We performed a Kolmogorov–Smirnov two-sample test to compare distributions of number of endemic species affected by climate changes for three different z values. Factors were considered significant at $\alpha = 0.05$. Statistical analyses were conducted using R software. Numbers of endemic species affect by climate change were not affected significantly by the z value (Kolmogorov-Smirnov test, $P > 0.05$ for all paired tests).

Table S7: Kolmogorov-Smirnov test results – to compare the distributions of number of endemic species affected by climate changes for each z value.

	z=0.15 vs z=0.20	z=0.15 vs z=0.25	z=0.20 vs z=0.25
Scenario A1B	$D=0.100, P>0.05$	$D=0.133, P>0.05$	$D=0.100, P>0.05$
Scenario B2A	$D=0.033, P>0.05$	$D=0.067, P>0.05$	$D=0.067, P>0.05$

Table S8: Table of the rank for the 34 different hotspots according to number of endemic plant species for each hotspot, the proportion of area protected by IUCN classification (I to IV), the percentage of climate loss, the potential number of invasive alien species in the future, and the percentage of future artificial land under A1B emission scenario. We calculated the proportion of artificial land, by assigning the 12 land cover type variables to one of two categories: artificial and natural (see Table S5 for details), we excluded the artificial & nature categories from this analysis.

Hotspot	rank_ LCC	rank_ LU	rank_ IAS	rank_ end	rank_ PA	moy_threat	moy_priori
Atlantic_Forest	17	1	15	5	17	11.00	11.00
California_Floristic_Province	23	24	12	25	13	19.67	19.40
Cape_Floristic_Region	4	20	16	8	28	13.33	15.20
Caribbean_Islands	5	2	4	7	25	3.67	8.60
Causasus	24	11	30	32	12	21.67	21.80
Cerrado	30	30	26	10	14	28.67	22.00
Chilean_Winter_Rainfall- Valdivian_Forests	26	25	20	26	10	23.67	21.40
Coastal_Forests_of_Eastern_Afr ica	14	31	28	31	27	24.33	26.20
East_Melanesian_Islands	3	29	10	16	34	14.00	18.40
Eastern_Afromontane	27	16	24	24	7	22.33	19.60
Guinean_Forests_of_West_Afri ca	31	13	11	30	22	18.33	21.40
Himalaya	28	33	19	13	2	26.67	19.00
Horn_of_Africa	11	14	33	19	9	19.33	17.20
Indo-Burma	12	4	17	6	3	11.00	8.40
Irano-Anatolian	25	10	31	21	16	22.00	20.60
Japan	8	18	7	27	18	11.00	15.60
Madagascar_and_the_Indian_O cean_Islands	19	34	27	4	26	26.67	22.00
Madrean_Pine-Oak_Woodlands	22	21	23	11	29	22.00	21.20
Maputaland-Pondoland-Albany	13	26	14	28	20	17.67	20.20
Mediterranean_Basin	16	7	18	3	15	13.67	11.80
Mesoamerica	2	9	13	18	5	8.00	9.40
Mountains_of_Central_Asia	32	23	34	33	8	29.67	26.00
Mountains_of_Southwest_Chin a	33	32	29	12	30	31.33	27.20
New_Caledonia	34	28	1	23	33	21.00	23.80
New_Zealand	18	17	3	29	6	12.67	14.60
Philippines	21	3	5	9	24	9.67	12.40
Polynesia-Micronesia	1	19	2	14	31	7.33	13.40
Southwest_Australia	20	8	25	17	11	17.67	16.20
Succulent_Karoo	10	27	32	22	32	23.00	24.60
Sundaland	7	12	9	1	4	9.33	6.60
Tropical_Andes	29	15	22	1	1	22.00	13.60

Tumbes-Choco-Magdalena	15	5	21	20	23	13.67	16.80
Wallacea	9	22	8	34	21	13.00	18.80
Western_Ghats_and_Sri_Lanka	6	6	6	15	19	6.00	10.40

Supplementary information 1 :

We modelled the potential distribution of the 99 IS in the 34 hotspots by combining available occurrences with a set of 6 climatic variables and 12 land use variables that we assumed to be important for IS. Because many records of IAS have been collected before 1960 and after 1990, we decided to use current climate data period between 1950-2000. Since the land cover projections from Globio3 were at a lower resolution (0.5°) than the climatic ones, we aggregated the climatic variables at 0.5° resolution by averaging values within pixels. The niche modelling analyses were thus carried out at that 0.5° resolution. We used 6 different species distributions modelling techniques available within the BioMod (version 2.0) computational framework (Thuiller, Lafourcade, Engler, & Araújo, 2009). These models were: Generalized Linear Model, Generalized Boosting Trees, Multivariate Adaptive Regression Splines, Random Forest, Flexible Discriminant Analysis and Maximum entropy. More details about the first five modelling techniques can be found in (Thuiller et al., 2009) and (Elith et al., 2011) for Maxent only. All models required presence and pseudo-absences (PAs or background) data. 5 sets of PAs were generated by selecting from 1000 to 10,000 random points across the world, according to the number of presences N (if $N \leq 1000$ then 1000 PAs were selected, else 10,000 PAs were selected) (as recommended by (Barbet-Massin, Jiguet, Albert, & Thuiller, 2012)). Equal weightings were given to presences and PAs. We evaluated the predictive performance of each model using a split sampling approach in which models were calibrated over 70% of the data and evaluated over the remaining 30% of independent data. This whole procedure was repeated 4 times. The models were evaluated with the True Skill Statistics (Allouche, Tsoar, & Kadmon, 2006) and Area Under the ROC Curve (Fielding & Bell, 1997). The True Skill Statistics accounts for both omission and

commission errors, and ranges from -1 to +1, where +1 indicates perfect agreement and 0 represents a random fit (Allouche et al., 2006). AUC values range from 0.5 to 1 for models with perfect predictive ability, and according to Swets (1988), AUC above 0.8 are considered to have “good” discrimination abilities.

The final step of calibration of every model for making predictions used 100% of available data. We used an ensemble forecast approach to account for the variability among the six species distribution models and the three general circulation models to get the central tendency (Araújo & New, 2007). To make sure no spurious models were used in the ensemble projections, we only kept the projections for which the model’s evaluation estimated by AUC and TSS were higher than 0.8 and 0.6, respectively (e.g. (Gallien, Douzet, Pratte, Zimmermann, & Thuiller, 2012), and to each model was associated a weight proportional to their TSS evaluation. Because of the potential problems raised by (Lobo, Jiménez-Valverde, & Real, 2008) on the use of AUC as a measure of model performance, we decided to use TSS for the final consensus distributions. The final current and future consensus distributions were obtained by calculating the weighted mean of the distribution for each scenario (Marmion, Parviainen, Luoto, Heikkinen, & Thuiller, 2009). This resulted in one current probability distribution map and three probability distribution maps per scenario (because we used 3 GCM) per species. Future probability map were therefore averaged for each scenario. Then, we transformed the probability maps obtained from the ensemble projections into binary suitable/non suitable maps using the threshold maximising the True Skill Statistics, as proposed by (Allouche et al., 2006). This should ensure the most accurate predictions since it is based on both sensitivity and specificity (Jiménez-Valverde & Lobo, 2007). We obtained one current binary distribution map and three future binary distribution maps per scenario and per species. Consensus binary maps were obtained attributing presence when the majority of GCMs (i.e., 2 ou of 3) predicted presence, otherwise absence. Since projections were not

based on an equal-area projection system, pixel sizes decrease poleward. Therefore, we calculated the surface of each pixel and weighted the pixels of the world map by their area. To map the spatial distribution of IAS richness for the 99 IAS, we summed all species presence for each grid cell for current and future periods.

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Figure S1: Methodological choice of the threshold

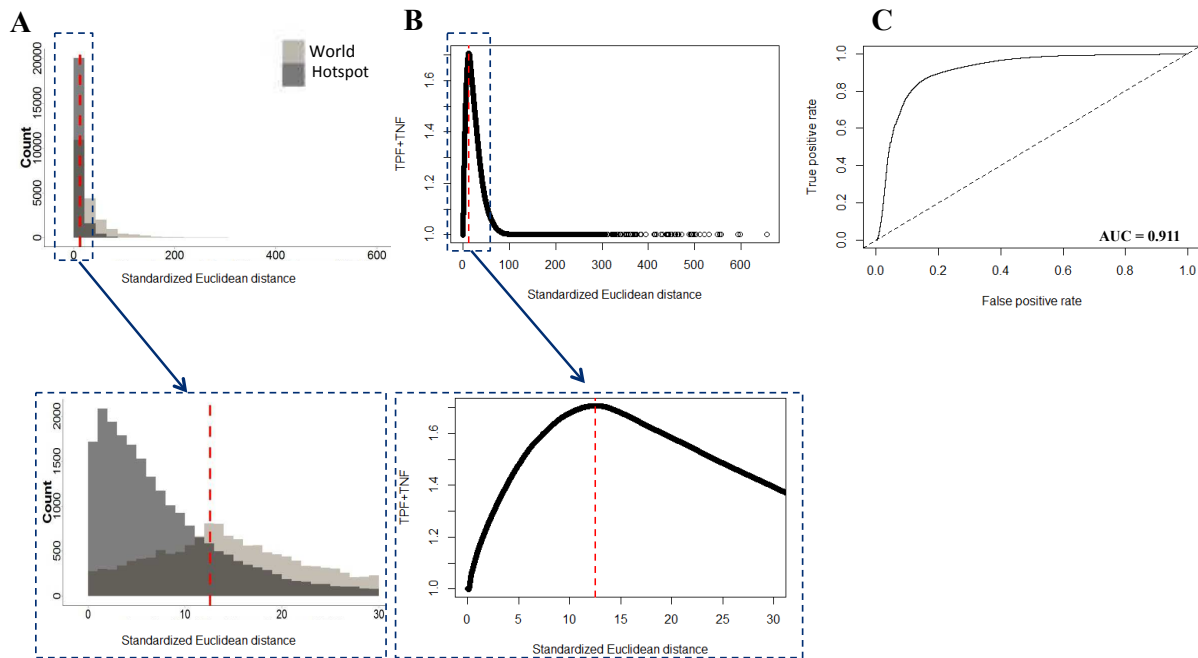


Diagram representing the successive steps to determine the SED threshold using the ROC methodology (Example with the Caucasus biodiversity hotspot)

A) Distributions of the SED values of a given biodiversity hotspot (dark grey) and the rest of the world (light grey).

B) The maximum sum of True Positive Fraction (TPF) and True Negative Fraction (TNF) value indicates the critical value for SED (Oswald et al. 2003) (red dashed line).

C) The corresponding ROC curve (package 'ROC') shows the relationship between False Positive Fraction (FPF) and TPF over the entire range of possible SED value. Specifically, each SED value has a corresponding TPF and TNF. TPF is the fraction of within surface comparisons that occurs below a given SED value, whereas TNF is the fraction of between surface comparisons that occurs above that value. TPF and TNF are inversely related to each other such that large SED values have high TPFs and low TNFs.

Figure S2: Geographical distance (km) to the closest analogous climate conditions between the current and future periods for the 21 continental hotspots. **A** Results are for the A1B emission scenarios; results for B2A scenario are given in **B** panel. See Table S2 for abbreviation details.

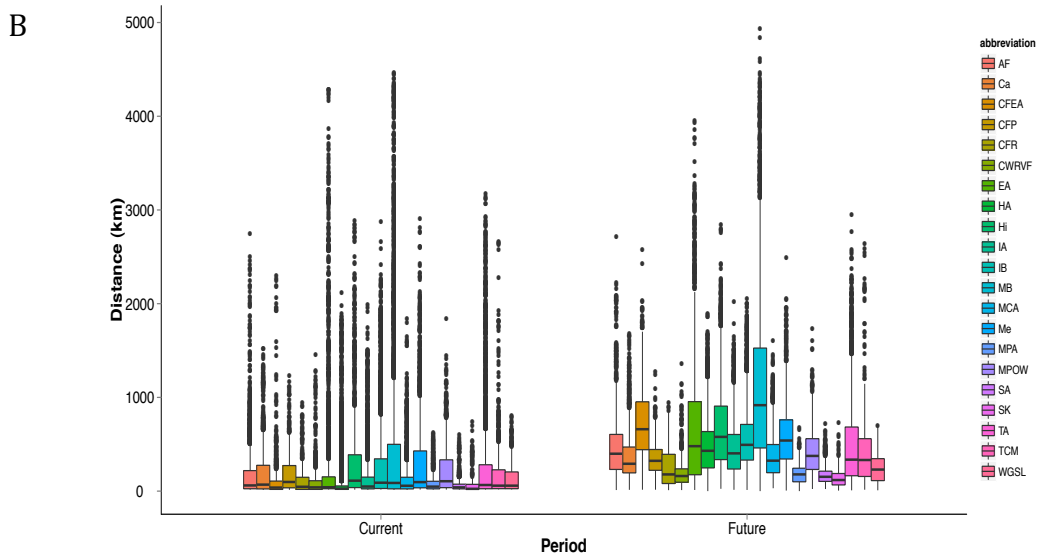
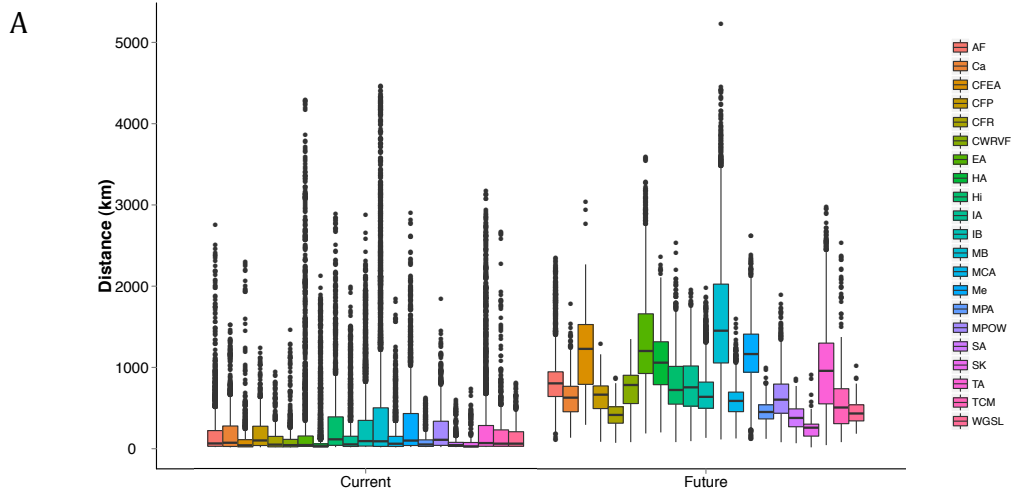


Figure S3: Percentage of changes for six different classes of land use between the current and future (2080) period in term of tree cover, mosaic, shrub cover, herbaceous cover, cultivated area and pasture. Results here are for the B2A emission scenarios.

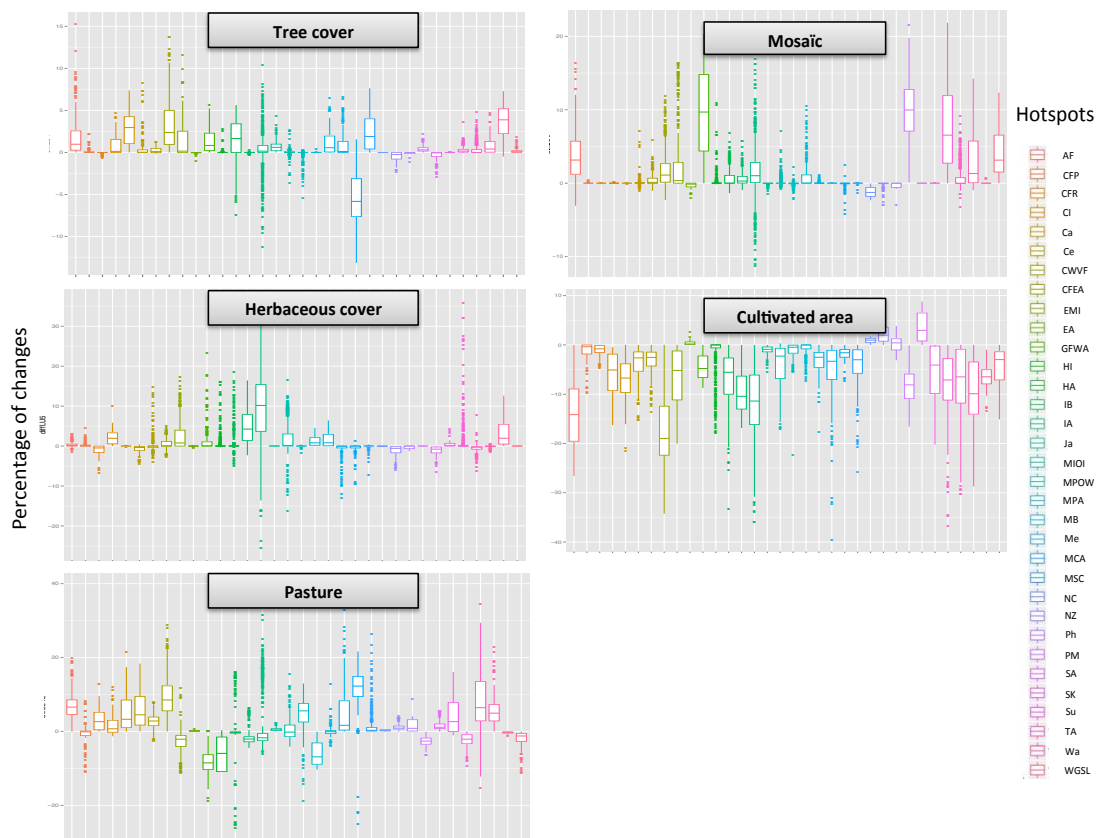


Figure S4: Boxplots of TSS and ROC values for the ensemble forecast projected model. All calibrated model performed very well (except for *Felis catus* and *Trogoderma granarium*). These results are not surprising because *Felis catus* is present almost everywhere on the Earth and its distribution is mainly explained by human presence. *Trogoderma granarium* has a low number of occurrences, therefore it is difficult to capture the range of environmental variables required for this species.

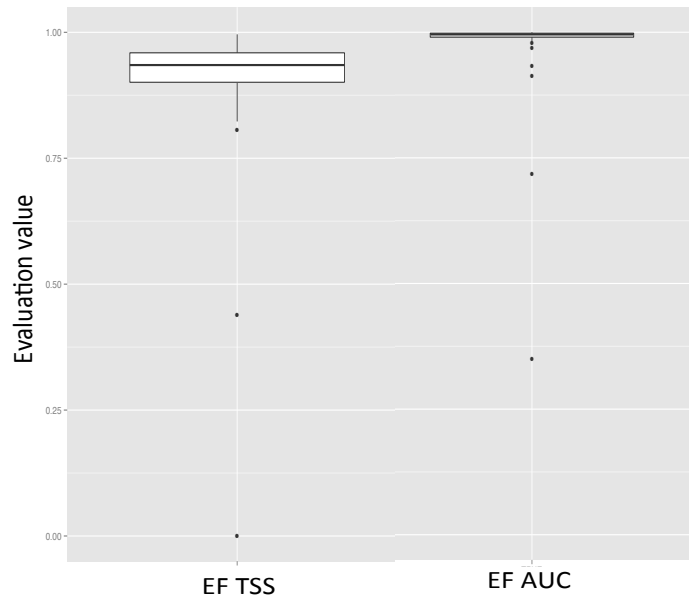


Figure S5: Number of invasive alien species per pixel in the 34 hotspots compared to the rest of the world, for both current and future periods (A) A1 scenario (B) B2 scenario. For both scenario, hotspots are most suitable to these 100 invasive species compared to the rest of the world for the current and future periods.

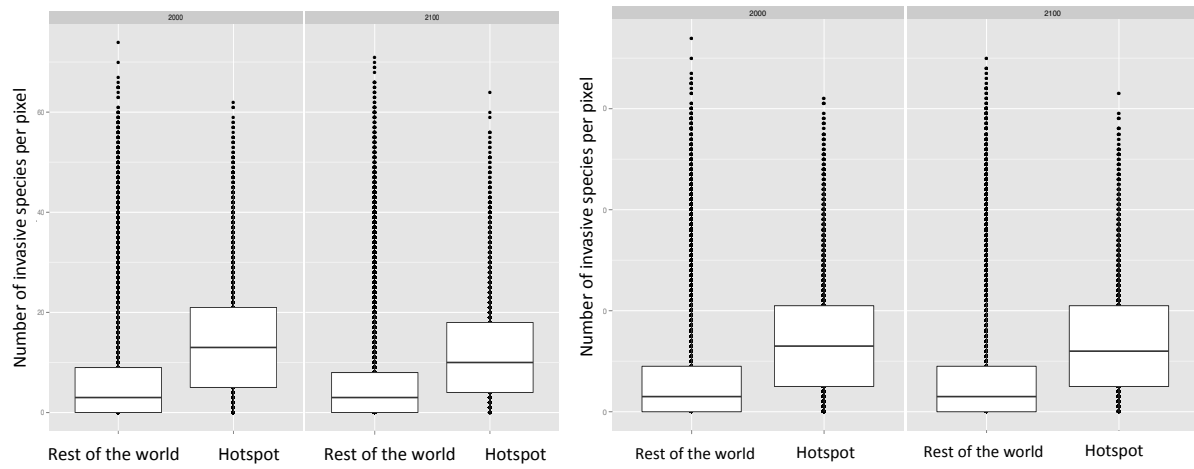


Figure S6: Map showing analog climate loss under B2 scenario in 2080. The size of the pie represents the area of each hotspot. (B) Map showing the proportion of endemic species threatened by loss of analog climate under B2 scenario. The size of the pie represents the number of species endemic to each hotspot. The right hand graph shows the slight effect of latitude on climate change related to biodiversity loss.

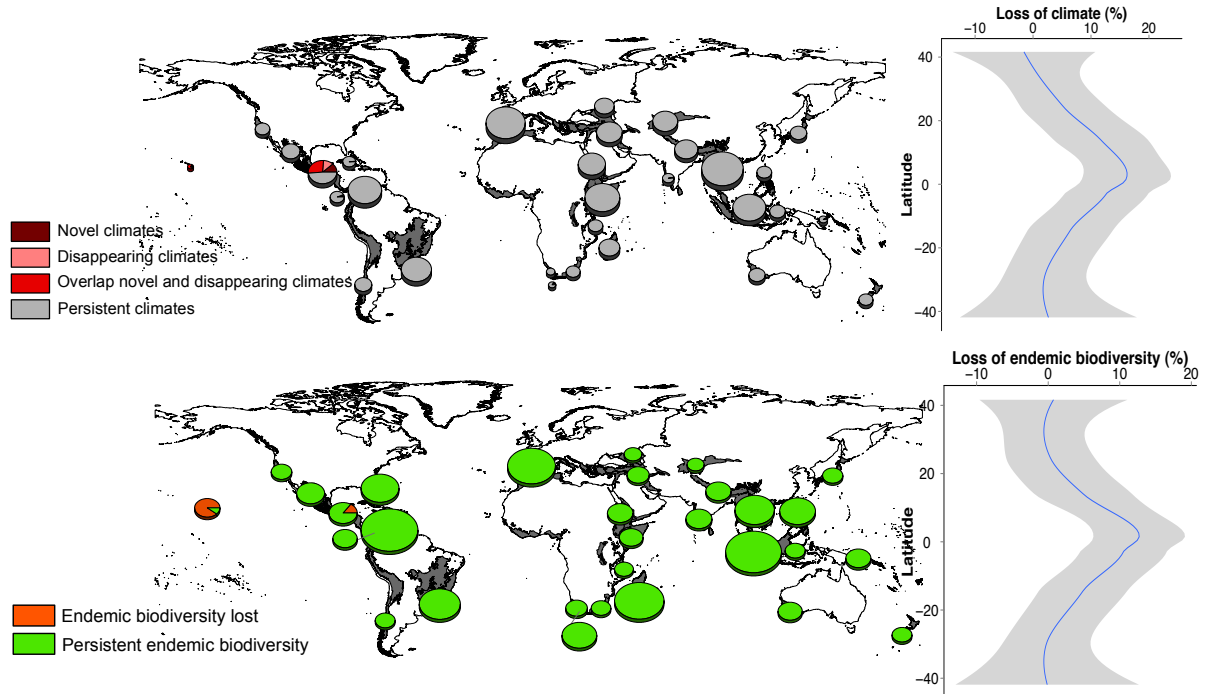
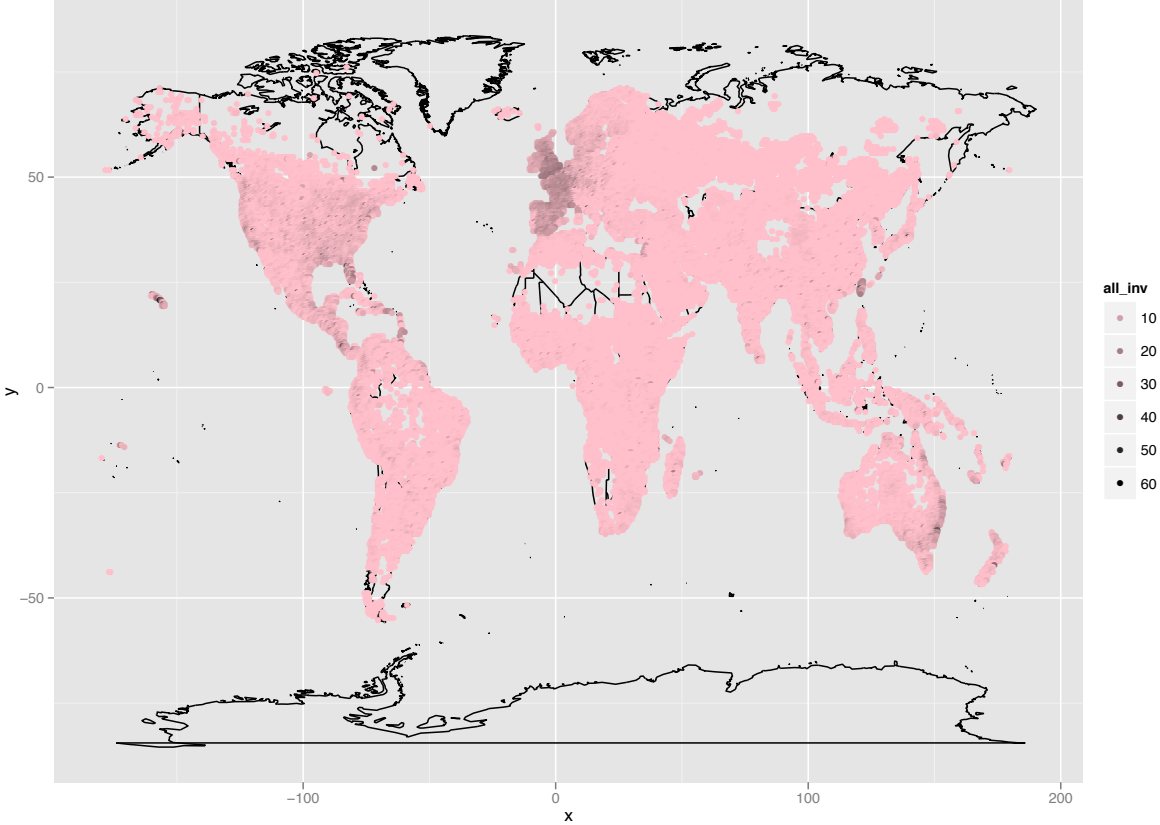


Figure S7: Collected occurrences of the 100 of the “world’s worst invasive species” over the world.



Annexe 10 :
Matériel supplémentaire
chapitre 7

Supplementary material

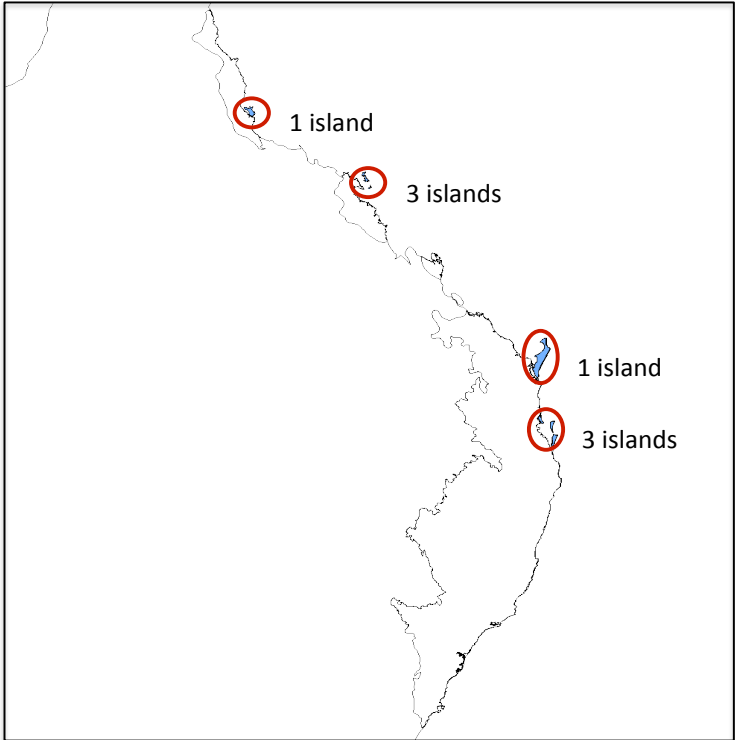


Figure S1 – Locations of the eight islands within the Forests of East Australia hotspot.

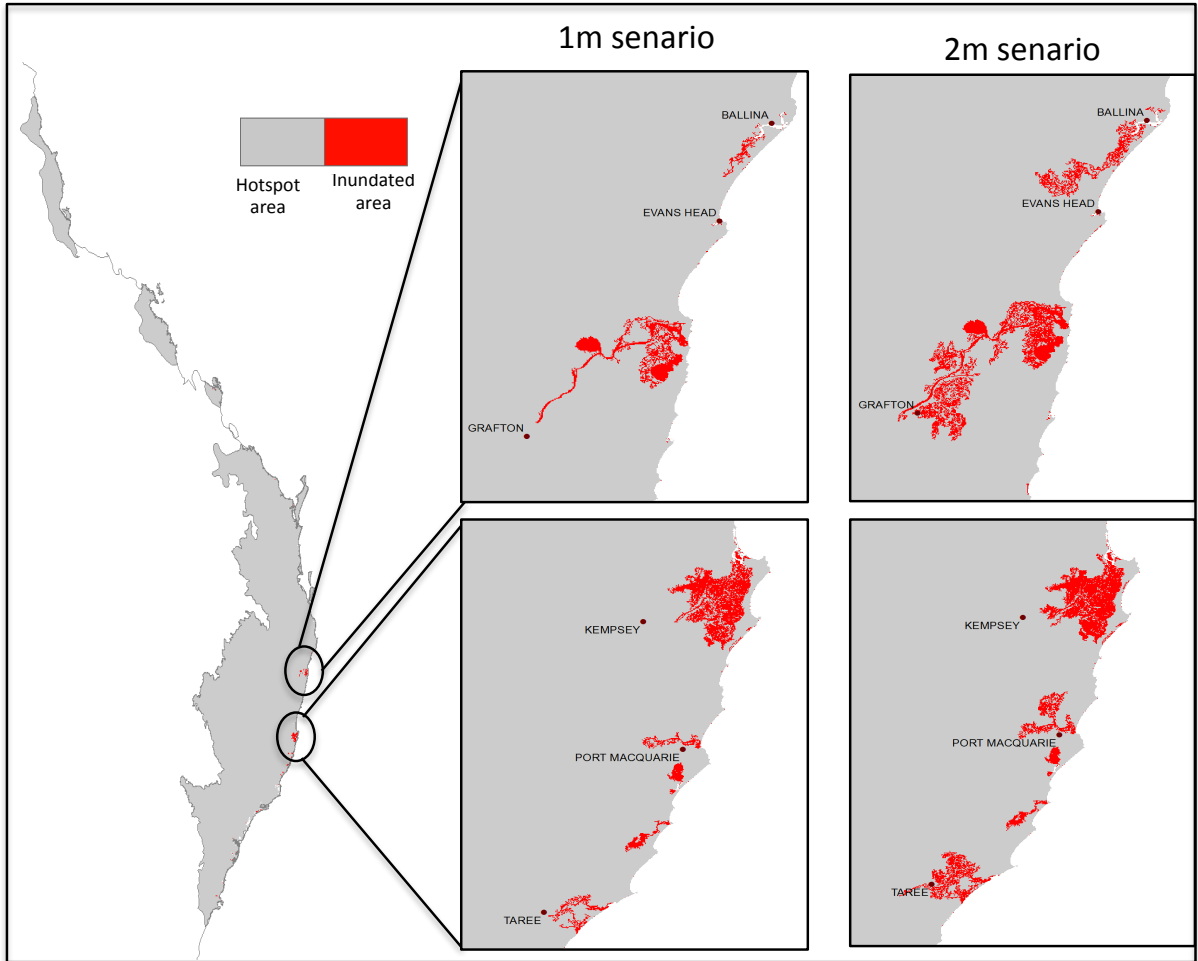


Figure S2 – Locations predicted to be inundated by sea-level rise under the 1 and 2m scenarios.

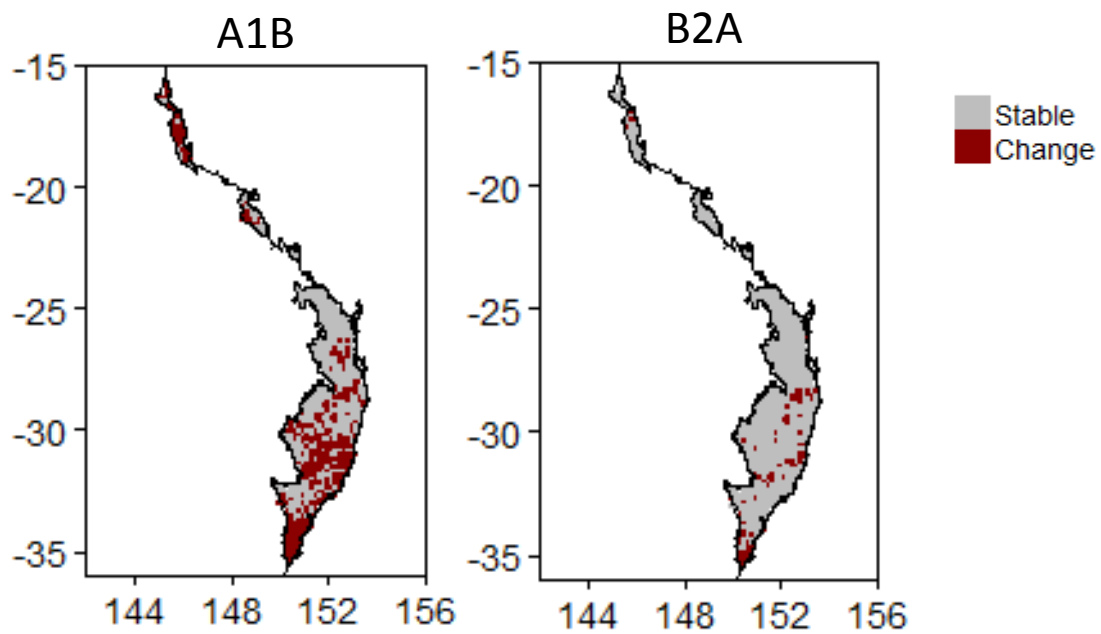


Figure S3 – Locations predicted to experience local climate change under the A1B and B2A emission scenarios.

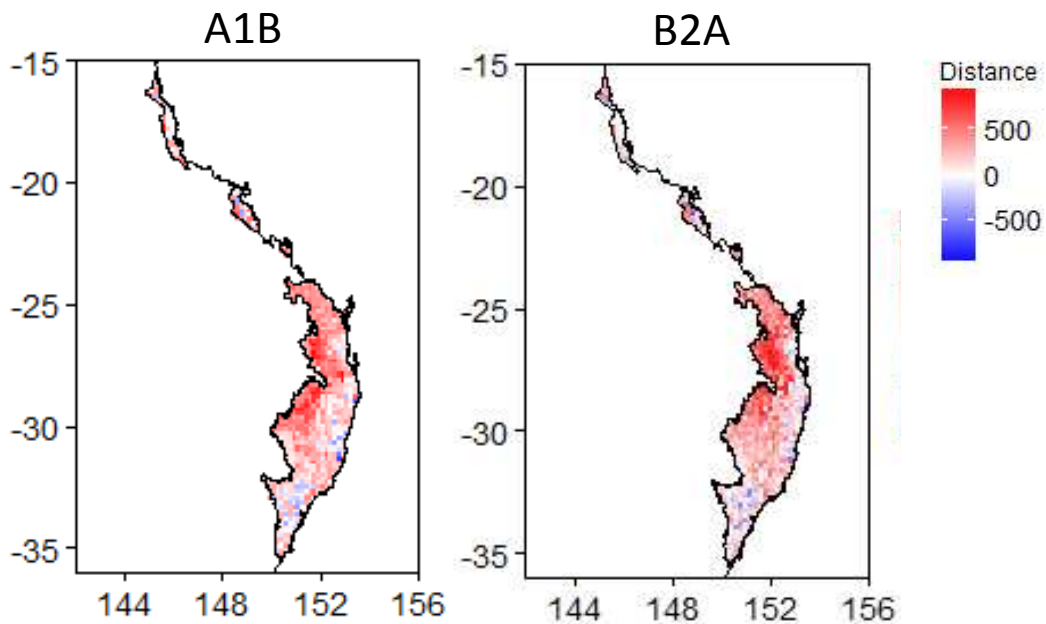


Figure S4 - Distance to the closest analog climate under the A1B and B2A emission scenarios.

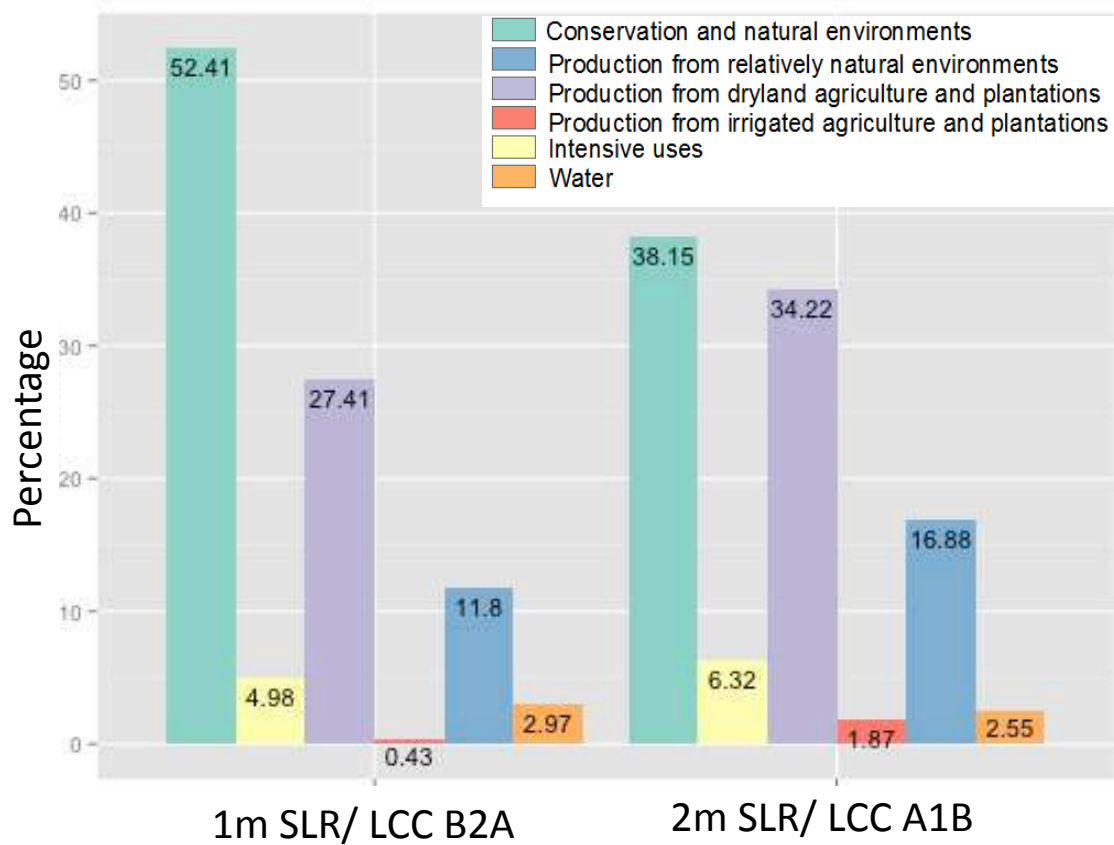


Figure S5 - Percentage of each land use class predicted to be affected by local climate changes and sea level rise.

Table S1 – Land use and cover classes and their associated sub classes based on the Australian catchment-scale land use map at 50m resolutions, which is the latest national-scale land use map of Australia (ALUM, 2010).

Land use and cover classes	sub classes
Conservation and natural environments	<i>National park</i>
	<i>Residual native cover</i>
	<i>Natural feature protection</i>
Production from dryland agriculture and plantations	<i>Native and exotic pasture mosaic</i>
	<i>Cropping</i>
	<i>Sugar</i>
Water	<i>River</i>
	<i>Marsh/wetland</i>
	<i>Marsh/wetland-conservation</i>
	<i>Estuary/coastal waters</i>
Production from relatively natural environments	<i>Production forestry</i>
	<i>Grazing native vegetation</i>
Intensive land use (urban and agricultural)	-
Production from irrigated agriculture and plantations	-

Table S2 - Number of people living within areas predicted to be subject to sea-level rise and local climate change.

Threat	Population	% population
Total	8,408,966	100
1m sea-level rise	58,034	0.69
2m sea-level rise	61,931	0.74
Local climate change (B2A scenario)	1,273,977	15.15
Local climate change (A1B scenario)	4,942,781	58.78

Table S3 - Percentage of land use and cover classes, and their associated sub classes affected by sea-level rise of 1 and 2 meters, and local climate change under the A1B and B2A emission scenarios. Data only provided for land use classes with > 5% contribution to total area affected

Land use and cover classes and sub classes	1m SLR	2m SLR	LCC B2A scenarios	LCC A1B scenarios
Conservation and natural environments	12.68	10.4	53.26	38.32
<i>National park</i>	81.92	74.8	59.84	43.88
<i>Residual native cover</i>	8.26	10.79	30.25	38.77
<i>Natural feature protection</i>	-	-	-	9.84
Production from dryland agriculture and plantations	36.47	45.37	27.32	34.24
<i>Native/exotic pasture mosaic</i>	82.28	73.66	94.62	90.19
<i>Cropping</i>	10.33	10.42	-	-
<i>Sugar</i>	-	12.62	-	-
Water	45.89	36.47	1.95	2.27
<i>River</i>	53.03	40.28	-	-
<i>Marsh/wetland</i>	27.63	36.33	-	-
<i>Marsh/wetland-conservation</i>	9.29	12.96	-	-
<i>Estuary/coastal waters</i>	6.75	6.99	-	-
Production from relatively natural environments	0.44	0.97	12.05	16.98
<i>Production forestry</i>	-	-	79.64	53.49
<i>Grazing native vegetation</i>	-	-	20.17	46.33
Intensive land use (urban and agricultural)	4.3	5.03	4.99	6.32
Production from irrigated agriculture and plantations	0.22	1.76	0.43	1.87

Table S4 - Percentage of land use classes affected by, local climate change and sea-level rise.

Land use and land cover classes	1m SLR/LCC B2A	SLR 2M-LCC A1B
Conservation and natural environments	52.41	38.15
<i>National park</i>	59.96	43.95
<i>Residual native cover</i>	30.13	38.7
<i>Natural feature protection</i>	-	9.82
Production from dryland agriculture and plantations	27.41	34.22
<i>Native/exotic pasture mosaic</i>	94.17	89.87
Production from relatively natural environments	11.8	16.88
<i>Production forestry</i>	79.53	53.53
<i>Grazing native vegetation</i>	20.28	46.29
Intensive land use (urban and agricultural)	4.98	6.32
Water	2.97	2.55
Production from irrigated agriculture and plantations	0.43	1.87

Table S5 - Percentage of areas with combinations of high or low protection and species richness, subject to 1 and 2 m sea-level rise (SLR), local climate change (LCC) under A1B and B2A scenarios, and paired combinations.

Protection level	Species richness	1m SLR	2m SLR	LCC B2A	LCC A1B	1m SLR /LCC B2A	2m SLR/LCC A1B
Low	High	77.52	78.56	51.94	49.26	52.48	49.37
Low	Low	15.09	16.26	19.15	33.60	19.09	33.56
High	High	4.06	3.01	21.53	12.34	21.14	12.28
High	Low	3.33	2.17	7.38	4.80	7.29	4.79

Abstract :

Global biodiversity is reducing at an unprecedented rate due to loss of habitat, biological invasions, pollution, and overexploitation. Furthermore, climate change and its synergy with other threats will probably become the main driver of biodiversity loss in this century. Nowadays, the multiplicity of approaches and the resulting variability in projections make it difficult to get a clear picture of the future of biodiversity due to climate change. Yet, the majority of models indicate alarming consequences for biodiversity, with the worst-case scenarios leading to increased extinction rates. The aim of this thesis was to improve the knowledge about different consequences of climate change on biodiversity worldwide. To achieve that I mainly used modelling and meta-analyses approaches. The first part of my work was to investigate the consequences of sea-level rise for the ten insular biodiversity hotspots and their endemic species, where I have found out that between 6 and 19% of the islands would be entirely submerged. Then, I studied the effects of climate and land use changes on biological invasions worldwide. The results showed that the responses of invasive species to climate and land use changes depend on region, taxa and species under focus. We identified three future hotspots of invasion in Europe, northeastern North America, and Oceania. We also emphasized that some regions could lose a significant number of invasive alien species. Furthermore, we found that hotspots that are mainly islands or groups of islands (*i.e.*, New-caledonia, Polynesia-Micronesia and New-zealand) are highly suitable for invasive species. Afterwards, I quantified the exposure of biodiversity hotspots to the combined effects of climate change, land use change and biological invasions. This work highlighted the pressing need to consider different drivers of global change in conservation planning, in particular for Sundaland and Indo burma hotspots that were predicted to be highly threatened to global changes with a high number of endemic species and low protection rate. Finally, implementation of effective conservation and adaptation strategies to protect habitats and species under global change can only be achieved through close collaboration with park managers and public support.

Key words:

Climate change, biodiversity hotspots, biological invasions, sea-level rise and conservation

Résumé :

Nous traversons actuellement une crise de perte de la biodiversité sans précédent. La dégradation des sols et la perte d'habitat, la pollution, la surexploitation et les invasions biologiques contribuent à cette perte mondiale de biodiversité. Par ailleurs, le changement climatique et ses interactions avec les autres menaces, sont probablement l'un des défis majeurs des prochaines décennies pour la biodiversité. À l'heure actuelle, en raison de la multiplication des études et des approches employées, il est difficile d'avoir une vision synthétique des conséquences potentielles de ces changements sur la biodiversité. L'objectif principal de ce travail de thèse a été d'améliorer la caractérisation et la quantification des différents impacts des changements climatiques sur la biodiversité, à l'échelle mondiale par des approches de modélisations et de méta-analyses. Une première partie de mes travaux a ainsi porté sur les conséquences potentielles de la hausse du niveau des mers sur les hotspots insulaires, au cours de laquelle j'ai mis en évidence les conséquences majeures d'une telle hausse pour certains de ces hotspots. Je me suis ensuite intéressée à l'étude des effets conjugués des changements climatiques et des changements d'utilisation des sols sur les invasions biologiques à l'échelle mondiale. Cette partie a permis de mettre en évidence que les conséquences des changements climatiques et des changements d'utilisation des sols sur les espèces invasives dépendent de la région, du taxon et de l'espèce considérée. Ainsi, j'ai mis en évidence que certaines régions pourraient être moins favorables à la présence d'espèce invasives dans le futur. En outre, cette partie a également mis en évidence que les hotspots majoritairement composés d'îles étaient particulièrement favorables à la présence de ces espèces invasives. Finalement, dans une dernière partie, j'ai étudié les conséquences des menaces futures pour les hotspots de biodiversité dans une perspective de conservation. Cette partie a notamment permis d'établir des priorités de recherche et de conservation entre les hotspots de biodiversité en tenant compte des futures menaces qui pèsent sur la biodiversité à l'échelle des hotspots, mais également au sein même des hotspots de biodiversité. Cependant, la mise en œuvre de plans de gestion de sauvegarde d'habitats ou d'espèces ne pourra se faire qu'en intensifiant les collaborations avec l'ensemble des acteurs impliqués. Plus généralement, la mise en œuvre de stratégies d'atténuation et d'adaptation efficaces aux changements climatiques ne pourra pas avoir lieu sans un soutien du grand public.

Mots clefs :

Changements climatiques, hotspots de biodiversité, invasions biologiques, conservation, hausse du niveau des mers.