Species distributions and climate change:current patterns and future scenarios for biodiversity

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Species distributions and climate change: current patterns and future scenarios for biodiversity

A dissertation submitted to the University of Copenhagen in accordance with the requirements of the degree of PhD at the Faculty of Science, Department of Biology, to be defended publicly before a panel of examiners
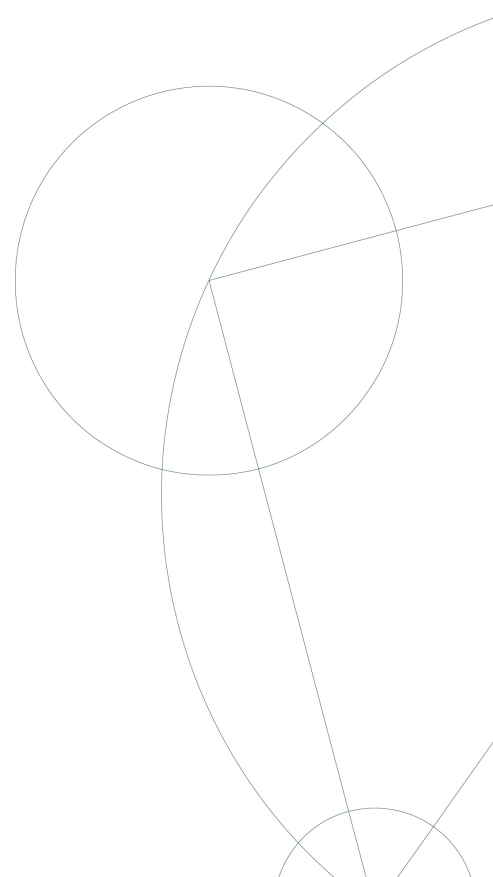
by

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February 2010

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Museo Nacional de Ciencias Naturales

Center for Macroecology, Evolution and Climate

"It is now clear that climate change is the major new threat that will confront biodiversity this century."

Lovejoy & Hannah 2005

Preface

This thesis is the result of a three-year PhD project which was jointly based at the Center for Macroecology, Evolution and Climate, Department of Biology, University of Copenhagen (Denmark) and the Biodiversity and Global Change Lab, Department of Biodiversity and Evolutionary Biology, National Museum of Natural Sciences (CSIC), Madrid (Spain). The project was jointly supervised by Prof. Dr. Carsten Rahbek (Copenhagen) and Prof. Dr. Miguel B. Araújo (Madrid).

The PhD project was temporally split into two equal parts performed at the two work places mentioned above. The project was funded by an internationalization stipend from the Danish Agency for Science, Technology and Innovation, administered by the University of Copenhagen.

The thesis consists of two parts. The first part is a synopsis which gives an overview of the background and the objectives of the thesis, summarizes and discusses the main findings, and outlines some perspectives for future research. The second part consists of five manuscripts, written as scientific papers, which comprise the core work of the PhD project. Finally, three supplementary chapters document some additional work on topics related to the objectives of the thesis.

Christian Hof

Copenhagen, February 2010

Contents

PART 2

APPENDIX

Summary

How does climate change affect biodiversity? – Answering this question is one of the most important tasks in current ecological research. Earth has been warming by 0.7°C during the last 100 years, and the consequences are already apparent in biotic systems. For example, species are responding by shifts of their distributional ranges, which affects the spatial patterns of species richness and turnover. Global temperatures are projected to rise by 1.8 - 4°C until the end of the century; hence climate change will most likely leave further imprints on species and ecosystems. This PhD thesis aims to contribute to a better understanding of the impacts of climate change on species distributions and spatial patterns of biodiversity.

Contemporary climate change is assumed to be one of the major future threats for biodiversity, due to its supposedly unprecedented velocity. On the contrary, recent studies suggest that climatic changes during and after the Pleistocene may have been much faster than commonly assumed. In one of the studies of this thesis I discuss the consequences of these findings for species and ecosystems. Since these rapid climate change events did not cause a broad-spectrum mass extinction, one might assume that most species may also be able to successfully cope with contemporary climate change. However, current ecosystems are heavily modified by humans. Among other factors, habitat destruction and fragmentation caused by anthropogenic land-use changes negatively affect species' strategies to cope with climate change. Therefore, although we need to rethink species' abilities to cope with rapid climate change, the interactions of different threats impose severe challenges for biodiversity. In a global assessment of future threats for amphibian diversity, I investigate the geography of climate change, land-use change and the fungal pathogen *Batrachochytrium dendrobatidis* (*Bd*). Results indicated that the regions with highest projected climate and land-use change impacts show a strong tendency of congruence, but show little overlap with regions of high *Bd* prevalence. Overall, two-thirds of the areas harboring the richest amphibian faunas may be heavily impacted by at least one of the major threats by 2080.

The stability of the climatic niche influences the need for a species to track climate change via dispersal, or its potential to adapt to novel climatic conditions. I therefore explore the phylogenetic signal in climatic niches of the world's amphibians, which serves as a surrogate quantification of niche stability. Results indicate an overall tendency of phylogenetic signal to be present in realised climatic niches, but signal strength varies across biogeographical regions and among amphibian orders.

The ability to successfully track climatic changes depends on dispersal, which is in turn influenced by ecological adaptations, such as the affiliation with a certain habitat type. A common hypothesis is that species adapted to less persistent habitats have evolved stronger dispersal abilities. Two studies of my thesis provide evidence for this hypothesis: (1) geographical distributions of dragonflies adapted to less persistent habitats show higher degrees of equilibrium with climatic conditions; (2) spatial patterns of European freshwater species richness and turnover differ strongly among habitats, indicating a faster post-glacial re-colonization of northern Europe by species adapted to habitats of lower persistence.

Resumé

Hvordan påvirkes biodiversiteten af klimaforandringerne? – At besvare dette spørgsmål er en af de vigtigste opgaver for økologisk forskning i dag. Jorden er blevet 0,7 °C varmere over de sidste 100 år, og konsekvenserne for biologiske systemer er allerede tydelige. For eksempel reagerer arter med forandringer i deres udbredelse, hvilket forandrer de rumlige mønstre i artsrigdom. Globale temperaturer forventes at stige med endnu 1,8 – 4 °C i løbet af dette århundrede; det er derfor sandsynligt at klimaforandringer vil påvirke arter og økosystemer yderligere. Denne ph.d.-afhandling sigter mod at bidrage til en bedre forståelse af klimaforandringernes indvirkning på arters udbredelse og på rumlige mønstre i artsrigdom.

De nuværende klimaforandringer formodes at blive en de største fremtidige trusler mod biodiversiteten, da man har ment at forandringen sker hurtigere end nogensinde før. Dog viser nyere studier at klimaforandringerne under og efter Pleistocæn muligvis er sket hurtigere end hidtil antaget. Da hurtige klimaforandringer ikke dengang udryddede mange arter, må man gå ud fra at de fleste arter også vil være i stand til at håndtere de nuværende klimaforandringer. Dog er nutidens økosystemer stærkt påvirkede af mennesker. Både habitat-ødelæggelse og landskabs-fragmentering, skabt af menneskers brug af jorden, har en negativ indvirkning på arters strategier til at håndtere klimaforandringer. Selv om vi er nødt til at gentænke arters evne til at klare hurtige klimaforandringer, udgør interaktionerne mellem forskellige trusler altså stadig en alvorlig udfordring for biodiversiteten. I en global undersøgelse af fremtidige trusler for diversiteten af padder undersøger jeg geografien af klimaforandringer, jordbrugsændringer og den patogene svamp *Batrachochytrium dendrobatidis* (*Bd*). Der var et stort sammenfald mellem de områder hvor påvirkningen fra klimaforandringer og jordbrugsændringer var størst, men kun et lille overlap med områder hvor *Bd* var almindelig. Alt i alt kan op mod to tredjedele af de områder i verden der har den rigeste padde-fauna blive stærkt berørt af en af de tre vigtige trusler inden 2080.

Stabiliteten af arters klimatiske niche afgør hvor nødvendigt det er for dem at følge klimaforandringer ved at sprede sig, og deres mulighed for at tilpasse sig nye klimatiske forhold. Jeg undersøger derfor det fylogenetiske signal i de klimatiske nicher for alle verdens padder, hvilket er en måde at kvantificere nichernes stabilitet. Resultaterne indikerer at der generelt er et fylogenetisk signal i arternes realiserede klimatiske nicher, men at styrken af signalet varierer på tværs af biogeografiske områder og mellem forskellige ordener af padder.

Evnen til at følge klimaet afhænger af spredningsevnen, som igen afhænger af økologiske tilpasninger såsom tilknytning til en bestemt habitattype. En udbredt hypotese er at arter der er knyttet til mindre varige habitater har udviklet en større evne til spredning. To studier i denne afhandling støtter denne hypotese: (1) den geografiske udbredelse af guldsmede som er knyttet til mindre varige habitater er i højere grad i ligevægt med de klimatiske forhold; (2) der er stor forskel på de rumlige mønstre i artsrigdom og turnover hos europæiske ferskvandsarter fra forskellige habitattyper, hvilket tyder på at arter der er tilpasset mindre varige habitater har genkoloniseret Europa hurtigere efter sidste istid.

Zusammenfassung

Welchen Einfluss hat der Klimawandel auf die biologische Vielfalt? – Die Beantwortung dieser Frage ist eine der wichtigsten Aufgaben aktueller ökologischer Forschung. Die Erde hat sich während der letzten 100 Jahre im globalen Durchschnitt um 0,7°C erwärmt, und die Folgen in biotischen Systemen sind bereits deutlich sichtbar. Arten reagieren etwa mit Verschiebungen ihrer Verbreitungsgebiete, was sich wiederum in den räumlichen Mustern der Artenvielfalt niederschlägt. Vorhersagen der globalen Temperaturerwärmung belaufen sich auf etwa 1,8 – 4°C bis zum Ende dieses Jahrhunderts; weitere gravierende Konsequenzen des Klimawandels für Arten und Ökosysteme sind zu erwarten. Ziel dieser Dissertation ist, einen Beitrag zu leisten zum besseren Verständnis der Auswirkungen des Klimawandels auf die geographische Verbreitung von Arten und auf die räumlichen Muster biologischer Vielfalt.

Insbesondere aufgrund seiner angeblich beispiellosen Geschwindigkeit wird der gegenwärtige Klimawandel als eine der größten Bedrohungen für die Biodiversität angesehen. Aktuelle Studien jedoch zeigen, dass die Klimaveränderungen während und nach dem Pleistozän deutlich schneller stattfanden als gemeinhin angenommen. Eines der Kapitel dieser Arbeit nimmt sich dieser Problematik an und diskutiert die Konsequenzen für biologische Systeme. Die Tatsache, dass ebendiese raschen Klimaveränderungen keine übergroße Zahl an Aussterbeereignissen mit sich brachten, mag den Schluss nahelegen, dass die meisten Arten auch dem gegenwärtigen Klimawandel gewachsen sein werden. Heutige Ökosysteme sehen sich jedoch mit dramatischen Eingriffen des Menschen konfrontiert. Vor allem die dem anthropogenen Landnutzungswandel geschuldete Zerstörung und Fragmentierung natürlicher Lebensräume hat negative Effekte auf die Strategien der Tier- und Pflanzenarten, erfolgreich auf den Klimawandel zu reagieren. Obwohl also unsere Sicht auf die Möglichkeiten der Organismen, mit schnellen Klimaveränderungen fertig zu werden, überdacht werden sollte, stellen die Interaktionen verschiedener negativer anthropogener Einflüsse eine gewaltige Herausforderung für Arten und Ökosysteme dar. Auch aufgrund der Bedeutung ebendieser Interaktionen befasst sich eines der Kapitel dieser Dissertation mit zukünftigen globalen Bedrohungsszenarien für die Biodiversität der Amphibien. Gegenstand der Studie sind insbesondere die räumliche Variation der Bedrohungsintensität von Klima- und Landnutzungswandel sowie des pathogenen Pilzes *Batrachochytrium dendrobatidis (Bd)*. Die Ergebnisse deuten darauf hin, dass die Regionen mit der voraussichtlich stärksten Intensität von Klima- und Landnutzungswandel eine hohe Kongruenz zeigen, während diese kaum mit den Gebieten einer hohen Vorkommenswahrscheinlichkeit von *Bd* überlappen. Bis zum Jahr 2080 könnten bis zu zwei Drittel der Regionen, die den höchsten Reichtum an Amphibienarten beherbergen, mindestens einer der angeführten drei wichtigsten Bedrohungen in hoher Intensität ausgesetzt sein.

Die Stabilität der klimatischen Nische einer Art beeinflusst einerseits die Notwendigkeit derselben, Veränderungen in den Klimabedingungen durch Ausbreitung zu folgen bzw. andererseits ihr Potential, neuen Klimabedingungen durch Anpassung zu begegnen. Aus diesem Grunde stellt die Untersuchung des phylogenetischen Signals in den klimatischen Nischen der Amphibien, welches als Surrogat für die Quantifizierung der Nischenstabilität herangezogen werden kann, einen weiteren Gegenstand dieser

Dissertation dar. Die Ergebnisse dieser Studie indizieren eine generelle Tendenz des Vorhandenseins eines solches phylogenetischen Signals, seine Stärke variiert jedoch zwischen biogeographischen Regionen und verschiedenen Amphibienordnungen.

Das Potential, erfolgreich auf Klimaveränderungen zu reagieren, hängt von der Ausbreitungsfähigkeit der Arten ab, welche wiederum von ökologischen Anpassungen, beispielsweise an einen bestimmten Habitattyp, beeinflusst wird. Dass Arten, welche an wenig stabile Lebensräume gebunden sind, eine bessere Ausbreitungsfähigkeit entwickelt haben, ist eine verbreitete Hypothese. Diese wird untermauert durch zwei Studien dieser Dissertation: Zum einen zeigen die geographischen Verbreitungen von an weniger stabile Habitate angepassten Libellen eine stärkere Tendenz zum Gleichgewicht mit klimatischen Bedingungen; zum anderen unterscheiden sich die Muster im Artenreichtum der europäischen Süßwasserfauna deutlich zwischen verschiedenen Habitattypen. Diese Unterschiede deuten auf eine schnellere nacheiszeitliche Wiederbesiedlung des nördlichen Europa durch Arten hin, die an Habitate von geringerer Stabilität gebunden sind.

PART 1

Synopsis

Species distributions and climate change: current patterns and future scenarios for biodiversity

- Synopsis -

1. Introduction

1.1 Species distributions and climate change

Species distributions are determined by a range of different factors, among which climate is one of the most important ones (von Humboldt 1808; Grinnell 1917; MacArthur 1972; Pearson & Dawson 2003). There is little doubt that climatic conditions influence the survival and reproduction of individuals and in turn the distributions of species, even though some controversy remains about the relative importance of climate as determinant of species distributions, e.g. compared to historical influences (Currie 1991; Rohde 1992; Jetz & Rahbek 2002; Hawkins *et al.* 2003; Currie *et al.* 2004; Rahbek *et al.* 2007). It is numerously documented that species have shifted their ranges in response to the climatic fluctuations during the Pleistocene (Zschokke 1908; Webb & Bartlein 1992; Hewitt 1999; Davis & Shaw 2001). During the last century, global average temperature has risen by approximately 0.7 °C, due to anthropogenic greenhouse gas emissions (IPCC 2007). Contemporary climate change has been shown to cause range shifts of species (e.g. Parmesan *et al.* 1999), as well as changes in phenology, physiology or morphology (Parmesan 2006). Global warming is projected to continue and increase during the next decades: depending on the climate change models and emission scenarios used, global average temperatures are projected to rise by 1.8 to 4.0 °C until 2100 (IPCC 2007; see also Serreze 2010 for a concise summary). Based on these climate change scenarios, dramatic consequences are anticipated for biodiversity (Williams *et al.* 2003; Thomas *et al.* 2004; Lovejoy & Hannah 2005; Thuiller *et al.* 2005; Colwell *et al.* 2008). Interactions between climate change and other threats, such as habitat destruction and the spread of infectious

diseases or invasive species, may further worsen the future perspectives for biodiversity (Sala *et al.* 2000; Harvell *et al.* 2002; Jetz *et al.* 2007; Brook *et al.* 2008).

1.2   The temporal stability of the climatic niche

The ecological niche of a species determines its responses to environmental conditions, and thus its distribution in space and time. Following Hutchinson (1957), the (fundamental) niche is the multi-dimensional environmental hyperspace in which a species can survive and maintain a positive rate of population growth. Thus, the climatic component of the fundamental niche hyperspace constitutes the climatic niche. The climatic niche of a species is influenced by its physiological, morphological and behavioural characteristics; it determines how the species responds to the climatic conditions of its environment.

Table 1 | Phylogenetic niche terminology

Term	Definition*
Phylogenetic niche signal	Tendency for related species to resemble each other's ecological characteristics more than species randomly drawn from a phylogeny (Blomberg & Garland 2002; Losos 2008).
Niche stability	Tendency for niche characteristics to remain unchanged over time (Nogués-Bravo 2009); indicated e.g. by strong phylogenetic signal of niche characteristics.
Niche lability	Tendency for niche characteristics to change over time; indicated e.g. by weak phylogenetic signal of niche characteristics.
Phylogenetic niche conservatism	Tendency of related species' niches to be even more similar than expected given their phylogeny (following Harvey & Pagel 1991; Losos 2008).

*Note that definitions remain partly controversial (see e.g. Wiens & Graham 2005; Losos 2008; Pearman *et al.* 2008). Definitions here are not intended to be authoritative, but are given for clarification.

When climatic conditions change, a species can respond by moving, adapting or going extinct (Holt 1990). In this context, the stability of the climatic niche (see Table 1 for terminological clarifications) is of fundamental importance: it influences the need for species to track climate change via dispersal, or its potential to adapt to novel climatic conditions (apart from phenotypic plasticity or population variability, see

chapter I). Since direct measurements of climatic niche stability are difficult to obtain (but see Vieites *et al.* 2009), surrogates are needed to quantify niche stability. The relationship between niche similarity and phylogenetic relatedness has been suggested as such a surrogate: understanding the extent to which there is a phylogenetic signal in ecological niches (Table 1) may help to understand the tendency of niches to evolve or to remain stable (Blomberg *et al.* 2003). This topic - the dynamics of the ecological niche in space and time - has gained increasing interest recently (Fig. 1; for recent reviews see Wiens & Graham 2005; Losos 2008; Pearman *et al.* 2008).
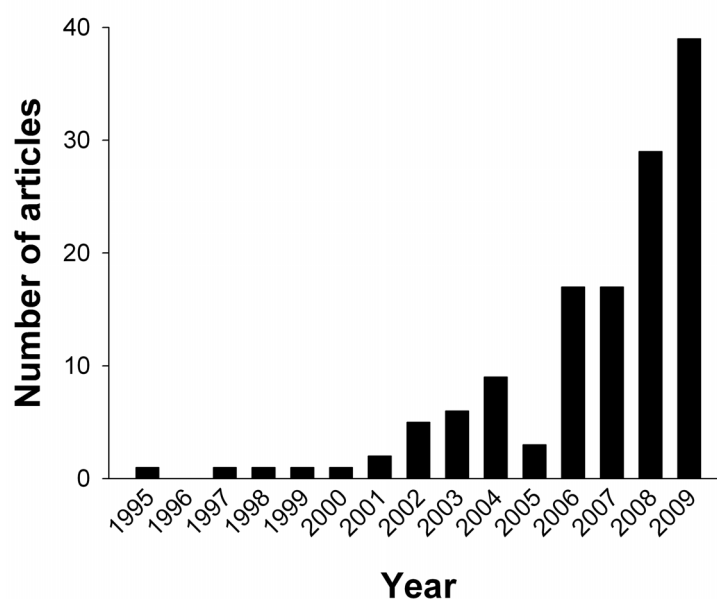
Figure 1 | Increase in studies investigating phylogenetic niche relatedness. Number of articles per year are obtained by a recent search (date: 27/01/2010) in the Web of Knowledge for studies (articles and reviews) investigating phylogenetic niche signal or phylogenetic niche conservatism (search phrase, TS = ((signal OR conservatism) AND niche AND phylogen*).

1.3   Dispersal and habitat stability

Dispersal is an important factor influencing species distributions, and therefore one of the key processes determining the spatial and temporal variation of biological diversity (Lomolino *et al.* 2006). It is generally defined as the movement of individuals away from their natal area or between two successive breeding areas (Clobert *et al.* 2001). Dispersal is affected by various biotic and abiotic factors. Geographical barriers impede dispersal processes, such as freshwater bodies for terrestrial, land masses for limnic biota, or mountain ranges and saline water bodies for both.

One of the ecological factors suggested to trigger dispersal is the stability of the habitat (Southwood 1962). Species adapted to habitats that are less persistent over time should have evolved stronger abilities to disperse than species adapted to habitats of higher persistence (Southwood 1962; Roff 1994; Zera & Denno 1997; Ribera & Vogler 2000). If they are stronger dispersers, species adapted to less persistent habitats may more successfully track fluctuations in climatic conditions (Heino *et al.* 2009).

1.4   Objectives of the thesis

The overall objective of my PhD thesis is to contribute to a better understanding of how climate change may impact biodiversity. The five chapters of the thesis aim to explore current patterns and future scenarios of species distributions and species richness in relation to climatic conditions, and to investigate the interplay of climate, dispersal and habitat adaptations. In particular, I

- explored the potential impacts of climate change and its interactions with other threats on biodiversity (chapters I and II);

- investigated the links between phylogenetic relationships and climatic niche similarity (chapter III);

- analysed the influence of habitat stability on dispersal ability – by exploring spatial diversity patterns and the equilibrium of species distributions with climatic conditions (chapters IV, V and supplementary chapter A).

2.   Summary and discussion of main findings

2.1   Potential impacts of climate change and its interactions with other threats on biodiversity

Contemporary climate change has been documented to cause biotic responses (for summaries, see Hughes 2000; McCarty 2001; Walther *et al.* 2002; Root *et al.* 2003; Parmesan & Yohe 2003; Parmesan 2006). Species are showing changes in timing of migration and breeding (Visser & Holleman 2001; Hassall *et al.* 2007; Tøttrup *et al.* 2008) and are shifting their distributions towards higher elevations and higher latitudes (Parmesan 1996; Parmesan *et al.* 1999; Hickling *et al.* 2005; Wilson *et al.* 2007; Kelly & Goulden 2008; Pöyry *et al.* 2009; Forister *et al.* 2010). Climate change projections have been extensively used to model future biodiversity scenarios. These are most

frequently based on potential changes of species distributions, and aim to predict changes in species richness and turnover, as well as species extinctions (Peterson *et al.* 2002; Thomas *et al.* 2004; Thuiller *et al.* 2005; Araújo *et al.* 2006; Levinsky *et al.* 2007; Pompe *et al.* 2008; Algar *et al.* 2009; Lawler *et al.* 2009; Lawler *et al.* 2010).

It is widely assumed that current and projected climate change is much more rapid than the climatic changes during and after the glacial-interglacial cycles of the Pleistocene. The most recent report of the Intergovernmental Panel of Climate Change (IPCC) states that "it is very likely that the global warming of 4°C to 7°C since the Last Glacial Maximum occurred at an average rate about ten times slower than the warming of the 20th century" (IPCC 2007, p. 435). However, evidence accumulates that the climatic changes during and after the Pleistocene may have been much faster than commonly assumed in studies assessing climate change impacts on biodiversity (Alley *et al.* 2003; Steffensen *et al.* 2008; see chapter I for a review of this evidence). Since these rapid climate change events did not cause a large number of extinctions (except for selected group, such as European trees or large mammals; Svenning 2003; Koch & Barnosky 2006), one might assume that species may also be able to cope successfully with current and future climate change.

However, conditions today are different from those of the past (chapter I): many current ecosystems are heavily used and modified by humans (Foley *et al.* 2005; Millennium Ecosystem Assessment 2005). Land-use changes and their consequences such as habitat destruction, degradation, and fragmentation impose severe pressures on species (Pimm & Raven 2000; Sala *et al.* 2000) and also limit the ability of species to cope with climate change, (Fig. 2, chapter I). Therefore, even though species' abilities to cope with rapid climate change may be greater than previously thought, the interactions of different anthropogenic threats, such as climate change and land-use change, impose severe challenges for species and ecosystems (Sala *et al.* 2000; Jetz *et al.* 2007; Brook *et al.* 2008; Forister *et al.* 2010).

For these reasons, thorough assessments of the interactions of different threats are urgently needed to project future scenarios of biodiversity. Amphibians appear to be the most severely threatened vertebrate taxon (Stuart *et al.* 2004; IUCN *et al.* 2008; Wake & Vredenburg 2008). They are particularly vulnerable to the impacts of climate and land-use change, due to their life cycle, physiology and limited dispersal abilities (Blaustein & Wake 1990; e.g. Alford & Richards 1999; Wells 2007). An additional threat for amphibian diversity is posed by the spread of chytridiomycosis, a disease

caused by the chytrid fungus *Batrachochytrium dendrobatidis (Bd);* outbreaks can cause dramatic population declines (Berger *et al.* 1998; Daszak *et al.* 1999; Lips *et al.* 2006) or even the extinction of entire species (Schloegel *et al.* 2006). Several studies have investigated the interactions of different threats for amphibians, such as the potential relationship of climate change and *Bd* infection (Pounds *et al.* 2006; Bosch *et al.* 2007; Lips *et al.* 2008). However, no study to date has assessed how the major threats for amphibians may spatially vary in the future on a global scale. Analyses of this kind are urgently needed to develop future scenarios of amphibian diversity and thus to enhance conservation efforts.
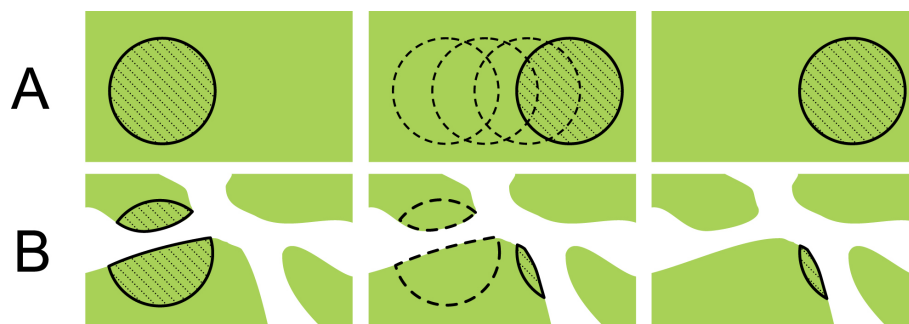

Figure 2 | The influence of habitat fragmentation on species' ability to track climate change via dispersal. (A) A species tracks climate change by gradually shifting its range through an undisturbed landscape, (B) the same situation in a fragmented landscape.

To help bridging this gap of knowledge, I assessed the potential impacts of future climate change on the distributions of the world's amphibian species and analysed the spatial variation of the three major threats climate change, land-use change and *Bd* for the year 2080 (chapter II). Results indicate that the regions with the most dramatic impacts of climate change on amphibian diversity are located in Africa, parts of northern South America, and the northern Andes (chapter II). Regions with highest projected climate change impacts overlap with regions of high projected land-use changes, but for frogs, e.g., there is almost no overlap between regions of high *Bd* occurrence and projected climate or land-use change impacts (Fig. 3, chapter II). Some regions, such as northern Central America or the northern Andes, that are particularly species-rich across taxa, are projected to be exposed to different threats (Fig. 3).

Overall, approximately two-thirds of the area harboring the richest amphibian faunas will likely be heavily impacted by at least one of the major threats by 2080. For amphibians, this tendency of spatial threat additivity may be particularly problematic, since their biology makes them vulnerable to a variety of threats (Wilbur 1980; Wells

2007; Wake & Vredenburg 2008). However, other factors such as chemical pollution and direct exploitation e.g. for food, medicine and the pet trade further worsen the perspectives for amphibians (Blaustein *et al.* 2003; Collins & Storfer 2003; Stuart *et al.* 2004). Thus, threats for the global diversity of amphibians may be far more severe than previous, mono-causal assessments have suggested, which imposes major challenges for sustainable amphibian conservation.
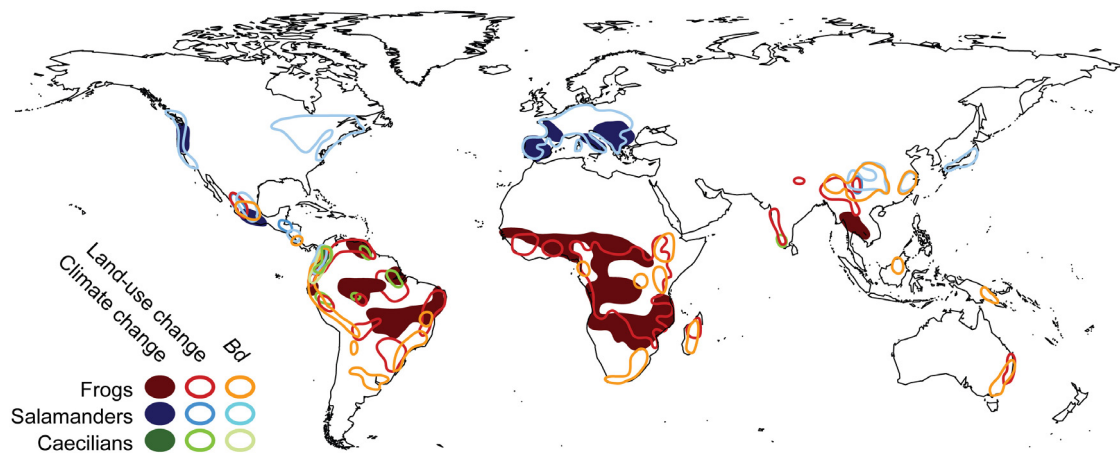

Figure 3 | Future threats for global amphibian diversity. Outlined areas indicate an overlap of high projected impact of the respective threat (see chapter II for details) with high species richness, separately for the different orders. Areas in dark red, for instance, are the areas with high frog species richness where a high proportion of the species are projected to "lose" climatic suitability by the year 2080.

2.2   Phylogenetic signal in climatic niche similarity

The question to which extent phylogenetically related species also share ecological requirements, has attracted increasing attention in recent years: a search within the Web of Knowledge revealed that almost two thirds of all articles and reviews on this topic were published from 2007 to 2009 (Fig. 1). Several reasons may have contributed to this popularity of the topic, all of which relate to the assumption that comprehending temporal niche dynamics contributes to a better understanding of dynamics of species distributions and species richness through space and time (Pearman *et al.* 2008). Firstly, the assumption of niche stability (see Table 1 for definitions of terms) may help to explain global biodiversity gradients, such as the difference in species richness between tropical and temperate regions (Wiens & Donoghue 2004; Hawkins *et al.* 2007). Secondly, niche stability obviously influences the ability of species to respond to environmental changes (see also sections 2.1 and 2.3, and chapter I), as well as e.g. the performance of invasive species in novel environments (Broennimann *et al.* 2007).

Thirdly, species distribution models (SDMs) rely on the assumption of niche stability. SDMs relate species occurrence data to environmental variables to project species distributions in space and time (Guisan & Zimmermann 2000; Guisan & Thuiller 2005); they have been shown to be powerful tools in various fields of ecological and conservation research. Confidence in their use would increase if a general trend in niche stability prevails over niche lability (Pearman *et al.* 2008).

The strength of the phylogenetic signal in ecological niche parameters has been suggested to serve as surrogate to quantify niche stability (Garland 1992; Blomberg *et al.* 2003; Rheindt *et al.* 2004; but see Revell *et al.* 2008; Ackerly 2009). Thus, understanding to which extent there is a phylogenetic signal in the climatic niche helps to comprehend climatic niche evolution in space and time. Although phylogenetically related species are often similar in their ecological requirements (Freckleton *et al.* 2002; Blomberg *et al.* 2003), the generality and the strength of a phylogenetic signal in ecological niches remains controversial (Pearman *et al.* 2008; Losos 2008). Furthermore, existence and strength of the phylogenetic signal vary depending on (1) spatial scale (e.g. local communities, isolated islands, or continents), (2) type of ecological trait under study (e.g. climatic or dietary characteristics), and (3) taxonomic (or phylogenetic) scale (e.g. intra-genus or inter-family comparisons) (see e.g. Peterson *et al.* 1999; Böhning-Gaese & Oberrath 1999; Prinzing *et al.* 2001; Brändle *et al.* 2002; Losos *et al.* 2003; Böhning-Gaese *et al.* 2003; Martinez-Meyer *et al.* 2004; Graham *et al.* 2004; Silvertown *et al.* 2006; Knouft *et al.* 2006; Entling *et al.* 2007; Evans *et al.* 2009).

To investigate whether species may be able to adapt to current and future climate change, the phylogenetic signal in the climatic niche is of particular interest. However, with few exceptions (e.g. Prinzing *et al.* 2001), comprehensive analyses on the strength of the phylogenetic signal in climatic niches remain scarce. In the first study of this kind on a global scale for an entire organism class, I explored the phylogenetic signal in climatic niches of the world's amphibians (chapter III). I first used a global family-level phylogeny to test for phylogenetic signal in species climate niches. Then I tested for the existence of phylogenetic signal and measured its strength separately for the three orders of amphibians (Anura, Caudata, and Gymnophiona) and for each of seven biogeographical regions. The results indicate that there is an overall phylogenetic signal in climatic niches, but that signal strength varies considerably among the three amphibian orders and across the different regions (Fig. 4). If the strength of the

phylogenetic signal is indeed an estimate of niche stability, these results lend support to the assumption that in some biogeographical regions (e.g. in Australasia or in the Afrotropics) there is a strong tendency for stability in climatic niches of amphibians (Fig. 4), which in turn may indicate that species in these regions will face increased challenges when confronted with severe climatic changes. However, as the analyses of this study are conducted with data of very coarse spatial and phylogenetic (i.e. taxonomic) resolution, I see them as a baseline for more detailed studies using data of finer geographical and phylogenetic resolution.
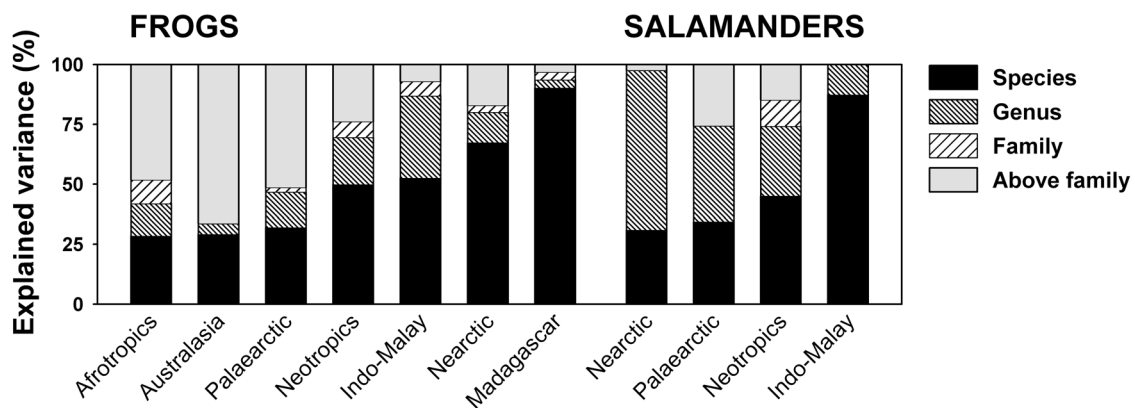

Figure 4 | Variation in the strength of the phylogenetic signal in climatic niches of frogs and salamanders. Bars show the proportions of variance in climatic niches that are explained at different taxonomic levels (see key). Bars are organised from lower (species) to higher (above-family) taxonomic levels. A black bar (e.g. Madagascan frogs or Indo-Malayan salamanders) would indicate that all variance lies at the species-level, and none is explained at higher taxonomic levels, thus indicating a weak phylogenetic signal. A high proportion of variance explained above the family level (e.g. Australasian or Palaearctic frogs) indicates a strong phylogenetic signal. Proportions of explained variance in niche positions are averaged across the two ordination axes which were used to quantify climatic niches (see chapter III for further details).

2.3   The influence of habitat stability on dispersal ability: Spatial patterns of freshwater diversity and the equilibrium of species distributions with contemporary climate

The habitat is a template for ecological strategies and life-history traits of species, such as the dispersal ability (Southwood 1977; 1988). Species adapted to habitats of lower persistence in space and time should have evolved stronger dispersal abilities than species adapted to habitats of higher stability (Southwood 1962); this constitutes the habitat-stability-dispersal hypothesis (HSDH; Fig. 5). Freshwater ecosystems provide an excellent opportunity to test the HSDH, since they can be roughly divided into less stable habitats of running water, such as creeks, rivers and streams (lotic habitats) and

more stable habitats of standing water, such as pools, ponds and lakes (lentic habitats; Bohle 1995; Dobson & Frid 1998; see also supplementary chapter A and references therein). Many freshwater animals have a distinct affiliation with one of the two habitat types (Illies 1966; 1978). According to the HSDH, species adapted to lentic habitats should have evolved stronger dispersal abilities than species adapted to lotic habitats (Ribera & Vogler 2000; Ribera 2008).
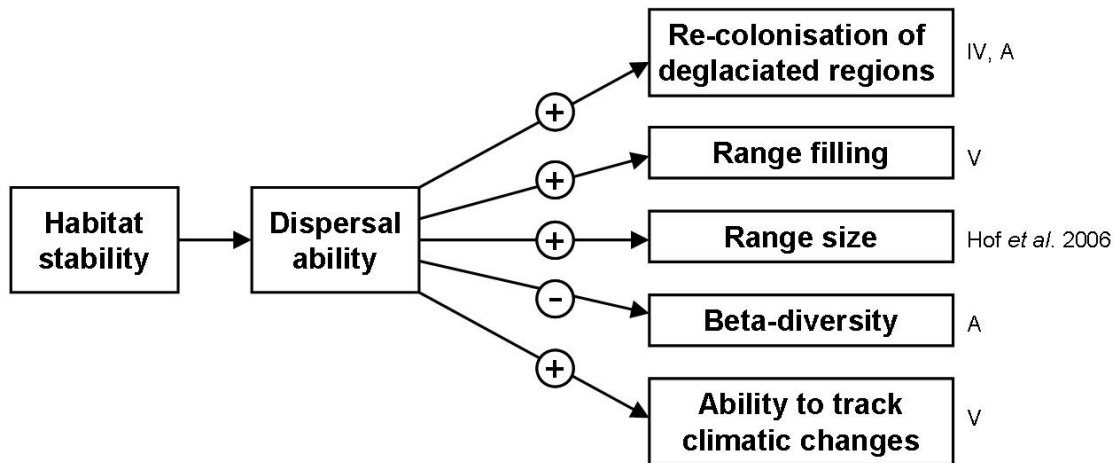

Figure 5 | The habitat-stability-dispersal hypothesis (HSDH). Habitat stability is assumed to influence dispersal ability. Lower habitat stability leads to stronger dispersal ability, which in turn leads to a faster re-colonisation of deglaciated regions, higher filling of potentially suitable ranges, larger range sizes, lower species turnover (beta-diversity), and a stronger ability to track climatic changes (but note that some of these consequences are not independent of each other). See the respective chapters and papers in the right column for details.

In a study exploring spatial diversity patterns in the European freshwater fauna, I showed that the latitudinal variation of species richness differed among groups of different habitat preference (supplementary chapter A): while lotic species showed a monotonic decrease of species richness with latitude, lentic species richness showed a hump-shaped relationship with latitude. Beta-diversity was generally lower in lentic than in lotic and groundwater species. I interpreted these results as a consequence of the different dispersal abilities of the respective groups, implying different abilities to re-colonise central and northern Europe after the last glaciation (supplementary chapter A; see also Hof *et al.* 2006). The availability of the respective habitats had only a weak effect on the differing spatial variation of species richness, especially for lotic habitats (chapter IV). These findings strengthen the support for the conclusions of supplementary chapter A.

Apart from biotic interactions (Hutchinson 1957), dispersal ability influences the extent to which a species occupies its potential range, which can be defined as the geographical area with suitable environmental conditions (Pulliam 2000; Gaston 2003; Soberón 2007). Range filling, a measure calculated as the ratio of the observed (or realised) and potential range (R/P ratio), has been suggested to indicate the extent of equilibrium of a species distribution with environmental conditions, and in turn to give an estimate of a species' dispersal ability (Svenning & Skov 2004; Munguía *et al.* 2008). If lentic species are indeed stronger dispersers than lotic species, R/P ratios of lentic species should be higher than those of lotic species. Further, lentic species should be able to more rapidly track changes in environmental conditions. I tested these predictions for 112 European dragonfly species using two temporally distinct datasets on species distribution and climate (for 1988 and 2006; chapter V). I found higher R/P ratios in lentic than in lotic species and a tendency for faster tracking of climatic changes in lentic species. These results lend further support to the hypothesis that lentic species show a stronger dispersal ability than lotic species on average.

Overall, these findings provide additional evidence for the HSDH, suggesting that habitat stability strongly influences the evolution of dispersal ability, which has now been documented for aquatic and terrestrial systems, and based on macroecological, phylogenetic, phylogeographical and theoretical approaches (Denno *et al.* 1991; Roff 1994; Zera & Denno 1997; Travis & Dytham 1999; Ribera *et al.* 2001; Ribera *et al.* 2003; Hof *et al.* 2006; Marten *et al.* 2006; Abellan *et al.* 2009).

3. Perspectives

3.1 Predicting the future of biodiversity: challenges and needs

Predicting future scenarios for biodiversity is a challenge, because any validation of models projecting the future is difficult, if not impossible. On the other hand, the challenge is due to the complexity of nature and of the factors determining occurrence, survival, reproduction or dispersal of living organisms. However, predicting future scenarios of biodiversity is a fundamental goal of ecological research in the era of global change and the current biodiversity crisis. This combination of challenges and needs calls for rigorous scientific approaches and careful interpretations of results. From this seemingly trivial but nevertheless important statement, several conclusions arise:

- All studies aiming to predict future scenarios of biodiversity, e.g. by means of species distribution modelling (SDM), should carefully assess the uncertainty of the methods and data used. This may provide estimates of the consistency and the reliability of the projections (chapter II, supplementary chapter A). The requirement of uncertainty assessments also implies that when modelling species distributions, e.g. based on their climatic envelopes, studies should make use of the broadest selection of data and methods available (Araújo & New 2007), unless there is a valid *a priori* reason to include or exclude certain data or methods.

- Predictions of biodiversity scenarios may be improved by the integration of different methodological approaches, as the strength of one method may compensate for the weakness of another. For example, SDMs rely on a calibration of the relationships between occurrences and environmental variables for each single species, which is problematic for species with very few occurrences. Macroecological modelling does not rely on species-by-species fitting of environmental envelopes, but assumes an influence of environmental conditions on species richness *per se*, thus being able to provide future scenarios of biodiversity where SDMs may not be applicable (Kerr *et al.* 2007; Algar *et al.* 2009). These multi-species approaches may further be improved by methods of simulation-based macroecological modelling, taking into account processes such as speciation, extinction and dispersal (Rangel *et al.* 2007; Rahbek *et al.* 2007; Gotelli *et al.* 2009). Furthermore, combining SDMs with process-based approaches such as models of (meta-) population and community dynamics may help to overcome the general neglect of demographic processes or biotic interactions in SDMs or macroecological modelling (e.g. Keith *et al.* 2008; Anderson *et al.* 2009).

- Since the direct validation of future biodiversity scenarios is not possible, insights into past dynamics of species distributions in response to climatic fluctuations may be used for an improved calibration of models (Nogués-Bravo 2009). Examples from the marine realm illustrate how time series data from the past can be used to calibrate models for future projections (MacKenzie & Köster 2004; MacKenzie *et al.* 2007). Further, the existence of occurrence or distribution data for different time periods (chapter IV; Menendez *et al.* 2006; Gonzalez-Megias *et al.* 2008; Pöyry *et al.* 2009) gives the opportunity to

directly assess the influence of climatic changes on changes in species distributions, species richness and turnover. Empirical estimates of species dispersal over time, extracted from these data, may also improve SDMs by overcoming unrealistic assumptions of no or unlimited dispersal (see also below).

3.2   Habitats, dispersal and climate change

The habitat-stability-dispersal hypothesis (HSDH) has received additional support by my findings (chapter IV, V, supplementary chapter B). However, direct empirical data on dispersal distances of a sufficient sample of species adapted to habitats of different stability are still lacking. Systematic assessments of the variation in population genetic and phylogeographical structuring across a range of species may serve as a first step in this direction (Marten *et al.* 2006; Papadopoulou *et al.* 2008; Abellan *et al.* 2009).

The consistently documented link between habitat stability and dispersal ability may help to improve studies using SDMs for projecting species distributions in response to climate change. These studies usually rely on simplified dispersal scenarios, such as unlimited or no dispersal (e.g. Thomas *et al.* 2004; Levinsky *et al.* 2007). Even though it is widely acknowledged that these scenarios are unrealistic assumptions (Guisan & Thuiller 2005), a lack of data on dispersal abilities enforces the use of these oversimplified scenarios. If habitat is a robust determinant of dispersal ability, establishing simple links between habitat preferences, habitat stability, and dispersal ability may help to improve model parametrisation with regard to species dispersal, and hence to improve the biological validity of SDMs (chapter IV; see e.g. Williams *et al.* 2005 for an example trying to use more realistic dispersal scenarios by linking modes of dispersal to dispersal distances).

Dispersal ability may also be important for niche dynamics in space and time. To successfully cope with climatic changes, species with a higher tendency of climatic niche stability (and thus a lower adaptability) should have evolved a stronger dispersal ability. In contrast, species with a higher tendency of niche lability (and thus a higher adaptability) should be able to "afford" being weak dispersers. A test of this prediction may help to understand how the interactions of ecological and evolutionary processes such as dispersal and adaptation may influence species responses to climate change.

3.3 Ecological niches: What are we measuring?

The recent boost of studies investigating the link between phylogenetic relatedness and niche similarity is partly due to the increasing availability of phylogenetic trees, distribution data and powerful computer software. However, the availability of data and technical resources may sometimes distract us from reflections about whether we try to answer questions that we can actually *not* answer with the data at hand. In my analyses on phylogenetic signal in amphibian climatic niches, for instance, I quantified climatic niches by calculating niche positions from species occurrence records and climatic variables extracted from grid cells that cover areas of up to 50,000 km^2. These grid cells may contain steep climatic gradients and their area by far exceeds the range of many species, so it is doubtful that I correctly characterised the niches of many small-ranging species. Therefore, I refrained from trying to infer complex evolutionary mechanisms such as speciation (Graham *et al.* 2004; Kozak & Wiens 2006) or the phylogenetic structuring of local or regional communities (Webb *et al.* 2002; Cavender-Bares *et al.* 2004). Instead, I was only able to explore coarse trends and provide a baseline for further studies on much finer phylogenetic and geographical resolutions. For these studies, high-quality data on species occurrences are of fundamental importance. However, data quality can not be improved by downscaling coarse range maps that are based on SDMs or expert knowledge to finer resolutions; instead, more and better data obtained from field surveys are urgently needed to overcome the problem of data deficiency.

The inference of ecological niches from environmental variables across species ranges may be questionable in general, which is be partly due to a lack of understanding of the conceptual background of the niche and its realisation in geographical space (Colwell & Rangel 2009; see also discussion in chapter III for the problem of the distinction between realised and fundamental climatic niches and the issue of niche quantification in this context). We urgently need more empirical studies assessing the relationships between a species' (fundamental and realised) ecological niche and its geographical distribution (for conceptual papers, see Pulliam 2000; Soberón 2007; Soberón & Nakamura 2009; Colwell & Rangel 2009).

Finally, I am tempted to add the – also self-critical – note that the increasing disassociation of analyses using highly advanced techniques from solid conceptual thinking and profound biological knowledge may not be sustainable for the advancement of ecological and global change research in the long run.

3.4 Interaction of different threats: challenges for conservation

Different threats impacting biodiversity require different conservation measures. My analysis on the spatial variation of different threats for amphibians illustrates this challenge (Beebee & Griffiths 2005; Mendelson *et al.* 2006b; Gascon *et al.* 2007). The measures necessary for amphibian conservation include, among others, conventional protected area approaches, the prohibition of industrial and agrochemical pollutants, the prevention of *Bd* spread through hygienic measures for herpetologists, captive breeding programs, and international agreements on the reduction of greenhouse gas emission.

Although the number of studies on the mechanistic interactions among different threats for biodiversity is increasing, the relevant processes remain poorly understood in many cases, which impedes the application of appropriate conservation approaches. For amphibians, e.g., the interaction of climate change and *Bd* spread is still controversial (Pounds *et al.* 2006; Mendelson *et al.* 2006a; Pounds *et al.* 2007; Lips *et al.* 2008; Rohr *et al.* 2008), and the abiotic and biotic factors influencing host susceptibility to *Bd* are far from being understood (Bielby *et al.* 2008; Garner *et al.* 2009; Richmond *et al.* 2009). Little is also known about how interacting effects of land-use climate change influence the potential responses of species to rapid climate change (chapter I).

To fill these gaps of knowledge, a unified research framework is needed that considers climate change together with the other main drivers of species extinctions, in particular habitat destruction, invasive species, and infectious diseases (chapter I). The development of such a framework imposes challenges for climate change biologists and conservationists, as it requires integrative approaches in theory and application. However, this avenue appears to be the only one to effectively mitigate the current biodiversity crisis.

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PART 2

Chapters I-V
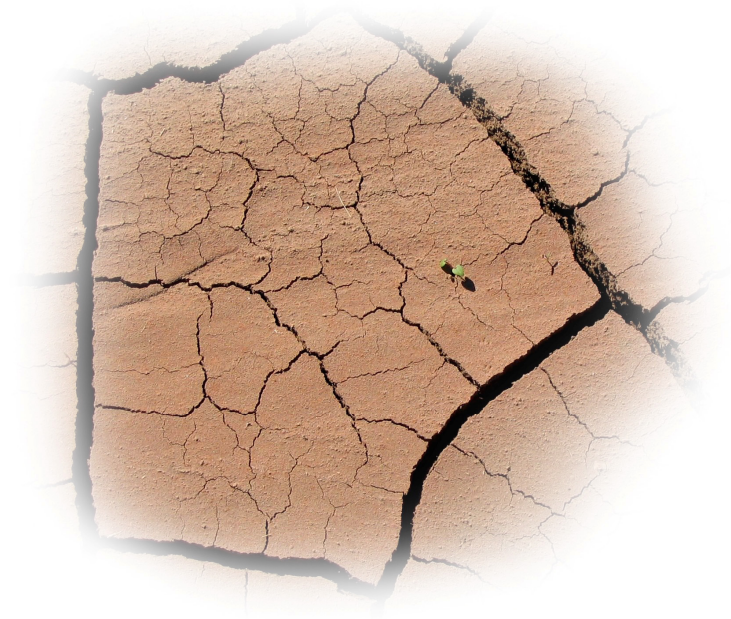
Chapter I

Rethinking species' ability to cope with rapid climate change

Manuscript in preparation

Rethinking species' ability to cope with rapid climate change

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Abstract

It is generally assumed that current climate change is exceptional partly because of its unprecedented velocity. This being true, species and ecosystems would now face new challenges given their exposure to such extremely fast climatic changes. However, new geophysical research suggests that dramatic changes in temperature, wind regime, and sea-level during the Late Pleistocene occurred extremely rapidly over just a few years. These climatic changes may have been faster than contemporary ones, which raises questions about the ability of extant species to adapt to ongoing climate change. We argue that the advances in geophysical research will fundamentally change the way we perceive species' ability to cope with climate change and call for a revision of how we model and interpret the effects of climate change on biodiversity.

Planet Earth has undergone severe climatic changes in the past, most recently during the glacial-interglacial cycles of the Pleistocene. It has generally been assumed that climate changes during and after the Pleistocene were gradual while contemporary climate warming occurs at an unprecedentedly rapid rate, a factor predicted to have dramatic consequences for biodiversity (IPCC 2007). However, recent geophysical studies are now challenging this view. Based on high resolution Greenland ice core data, Steffensen *et al.* (2008) showed that moisture source temperature changed up to 4°C per year near the end of the last glacial period (14,700yr B.P.). Brauer *et al.* (2008) reported an abrupt increase in storminess within a single year in Western Germany during the Younger Dryas cold climate period (12,700yr BP), and linked this event to the inception of deglaciation (see also Bakke *et al.* 2009). Similarly, sea levels around the Yucatán Peninsula underwent a rapid rise of 2-3 meters (most likely approximately 36 mm per year) during the last interglacial period (121ky B.P.) (Blanchon *et al.* 2009). Although the existence of abrupt historic climate change has previously been acknowledged (Alley *et al.* 2003), these new studies not only confirm these changes as being general, but also document, on a much finer temporal resolution, that these changes were more rapid than previously anticipated, especially by researchers modelling the effect of current and future climate change on biodiversity. Thus, these new geophysical findings have profound implications for climate research and pose a challenge to existing paradigms in climate change impact studies.

Studies that assess the impact of climate change on biodiversity tend to adopt the view that past climatic changes were gradual rather than abrupt. The most recent report of the Intergovernmental Panel of Climate Change (IPCC), while recognizing that rapid climate changes occurred in the past, states that "it is very likely that the global warming of 4°C to 7°C since the Last Glacial Maximum occurred at an average rate about 10 times slower than the warming of the 20th century" (IPCC 2007, p. 435). This perception is based upon the fact that Earth's temperature has increased by 0.74°C from 1906 to 2005 and that sea levels have risen 3.1 mm per year in the decade between 1993 and 2003 (IPCC 2007). Climate projections for the end of the century (2090-2099) range from a global mean temperature change of 1.8-4°C to a sea level rise of 0.18-0.59 m (IPCC 2007). Focus on the speed of climate change during the last century has presumably given rise to the view that past climatic changes were much slower and that the current and anticipated "extraordinary" rate of future global warming is predicted to have a significant effect on Earth's biodiversity (e.g. Thomas *et al.* 2004).

In this context, it is worth noting that the rapid climate change in the Quaternary period (spanning approximately 2.6 million years ago to the present) did not cause a broad-spectrum mass extinction; instead it appeared to have primarily affected a few specific groups, mainly large mammals and European trees (Koch & Barnosky 2006). The fact that relatively few taxa became extinct, compared to periods of mass extinctions, indicates that most extant species exposed to contemporary climate changes must have coped successfully with the abrupt climatic changes of the past.

Species' responses to climate change are usually condensed to: adaptation, dispersal and extinction (Holt 1990). The prevailing consensus, when modelling the effect of climate change on species distributions, is that current climate change simply outpaces micro-evolutionary processes so that there is no time for evolutionary adaptation (Jump & Penuelas 2005). Dispersal is regarded as the likely main response of species to past climatic changes and has been widely identified as a response to recent climate change, usually via range shifts from lower to higher latitudes and altitudes (Parmesan & Yohe 2003). However, if the rapid rates of historical climate change described above are acknowledged, dispersal in terms of large range shifts (Fig. 1 A) over these short time periods become quite improbable as the main response of species to past climatic changes. Likewise, microevolutionary adaptations comprising small-scale changes in genetic diversity in a population over a few generations are even more difficult to imagine as a potential response to rapidly changing historical climate regimes.

The fact that extant species did not become extinct during the last period of drastic, rapid climate change indicates that species must have used strategies other than shifts of geographical distributions or evolutionary adaptation to cope with changing climate. Adaptation to rapid changes in environmental conditions is not exclusively reliant on relatively slow microevolutionary processes based on genetic changes in populations. Instead, the phenotypic variability of populations, in the form of physiological, phenological or morphological traits, may have allowed species to cope with rapid climatic changes within their range (Nussey *et al.* 2005). Alternatively, retreats to nearby areas with suitable microclimates (Fig. 1 B, C), permitting species to endure adverse climatic conditions appear to have played a role for various taxa and regions (Willis *et al.* 2000).

The recent reports on the exceptionally rapid climatic changes in the Late Quaternary and the fact that extant species have coped successfully with past climatic changes give rise to the question of whether estimates of extinction risk due to current

and future climate change are exaggerated. When addressing this question one should bear in mind that the ability of species to cope with fast climate change is different today than it was in the past, with current landscapes and ecosystems severely modified by humans (Sala *et al.* 2000). These modifications have brought about land-use change and concomitant habitat destruction, degradation, and fragmentation at large spatial scales, which impose severe pressures on species. These modifications also have a huge impact on species' potential strategies to cope with climate change thus increasing the negative impact of climate change *per se*. First; these land-use changes may reduce the possibilities of species to survive climate change in suitable microclimatic "pockets". Smaller and fewer habitat patches by definition contain fewer microclimatic pockets suitable for species' endurance during climate change (Fig. 1 D-F). Secondly, smaller habitat patches sustain smaller populations, which show lower genetic and phenotypic variability (Jump & Penuelas 2005) – a pre-requisite for rapid adaptive responses. Thus, habitat fragmentation reduces species' potential to respond with trait shifts due to lower phenotypic variability across species ranges. Furthermore, fragmentation also impedes short- and long-distance dispersal processes (Fig. 1 D-F) (Fahrig & Merriam 1994), reducing immigration probability, which further reduces genotypic and phenotypic variability (Young *et al.* 1996) and in turn the ability of species to adapt to changing environmental conditions.

The fact that extant species have demonstrably survived rapid, historic climatic changes is good news. It suggests that species' ability to cope with drastic climate change is better than hitherto recognised, perhaps due to the phenotypic variability of populations, or to their ability to survive in microclimatic pockets in a heterogeneous landscape. In other words, species are probably more resilient to climatic changes than typically anticipated in most assessments of the negative effect of climate change on biodiversity (Willis & Bhagwat 2009). To understand the potential responses (e.g. dispersal or adaptation) of species to changing environments, a unified framework that considers climate change together with the main drivers of species extinctions, such as habitat destruction, invasive species, and diseases, is needed. The development of such a framework imposes a challenge for climate change biologists and conservationists focusing on how to effectively mitigate the biodiversity crisis and ecosystem changes caused by global changes of land-use and climate.
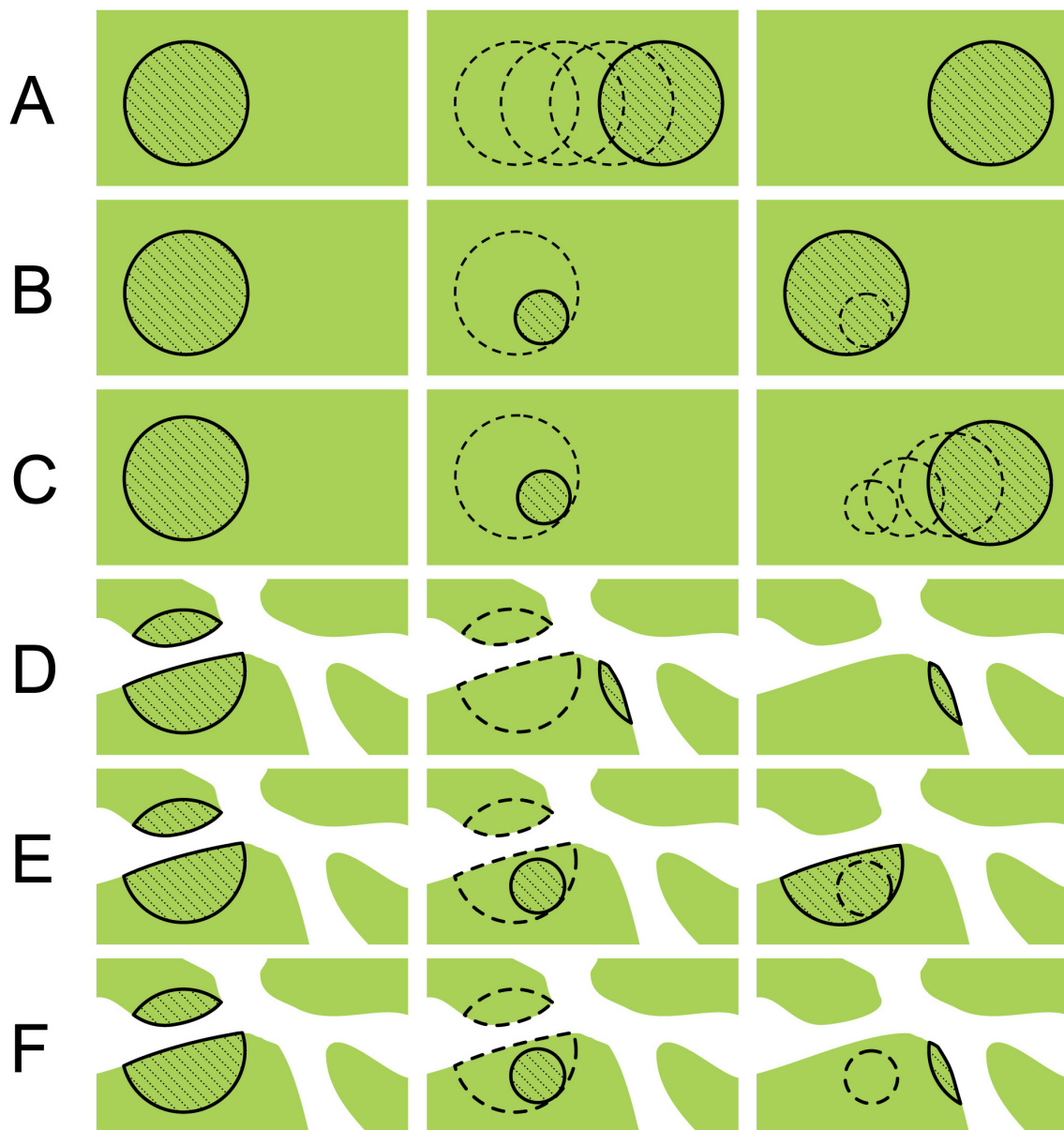
Figure 1 | Changes in species' ranges as a result of climatic changes in a pristine world prior to human impact on e.g. habitat continuity (A-C), and in a world of habitat destruction and fragmentation (D-F), with adaptation excluded as a determining factor. **A,** Species track climatic changes by gradual range shifts. In case of extremely rapid climate change, as suggested by recent studies (see text), species may (**B**) endure adverse climatic conditions in small areas of suitable microclimates within their ranges and expand when suitable climatic conditions return, or (**C**) endure in small areas of suitable microclimates within their ranges, and thereafter track suitable climate conditions. **D-F** are parallels to **A-C** in a world of habitat destruction and fragmentation. Here, the available area containing suitable microclimatic conditions is smaller, which reduces the probability of endurance (central panels) and the probability of successful range shifts (right-hand panels).

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"Disease is the bullet that's killing the frogs.
But climate change is pulling the trigger.
Global warming is wreaking havoc on
amphibians, and soon will cause
staggering losses of biodiversity."

J. Alan Pounds

Chapter II

Future threats for
global amphibian diversity

Manuscript in preparation

Future threats for global amphibian diversity

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Abstract

Amphibians are experiencing population declines far exceeding those of other vertebrate groups. The exact causes of these declines are still a matter of controversy but most likely include climate change, land-use change and the spread of Chytridiomycosis, a disease caused by the pathogenic chytrid fungus *Batrachochytrium dendrobatidis* (or *Bd* for short). Here, we provide a global assessment of the geography of these potential threats and their interactions. We show that the highest proportions of species negatively affected by climate change are projected to occur in Africa, parts of northern South America, and the Andes. Regions with highest projected climate and land-use change impacts show a strong tendency of congruence, but show little overlap with regions of high *Bd* prevalence. Other threats like pollution and direct exploitation may affect the exact geography of impacts, but in absolute terms only add to the already considerable threats identified. Our findings highlight that the existing declines of amphibians will most likely be exacerbated in the 21st century as multiple drivers of extinction risk may impose a far more alarming jeopardy for global amphibian diversity than previous, mono-causal assessments have suggested.

30% of the world's amphibian species are listed as threatened in the IUCN Red List, making of this group the most endangered vertebrate group globally (Stuart *et al.* 2004; IUCN *et al.* 2008; Wake & Vredenburg 2008). Numerous species are experiencing population declines in many regions of the world (Pounds & Crump 1994; Lips 1998; Alford & Richards 1999; Houlahan *et al.* 2000; Schloegel *et al.* 2006; Whitfield *et al.* 2007; Ryan *et al.* 2008; Rovito *et al.* 2009). Important causes for amphibian declines are anthropogenic land-use changes leading to habitat destruction, degradation and fragmentation, climate change, the fatal disease chytridiomycosis which is transmitted by the chytrid fungus *Batrachochytrium dendrobatidis* (*Bd*), direct exploitation for food, medicine and the pet trade, environmental pollution, increase in UV-B irradiation due to anthropogenic ozone depletion, and the spread of invasive species (Blaustein & Kiesecker 2002; Collins & Storfer 2003; Beebee & Griffiths 2005).

Numerous studies have assessed how these threats affect amphibian species and interact at local and regional scales (Pounds & Crump 1994; Berger *et al.* 1998; Becker *et al.* 2007; Bosch *et al.* 2007; Wake 2007; Laurance 2008; Lips *et al.* 2008). A recent continental assessment has used species distribution models to project climate change impacts on American amphibian diversity (Lawler *et al.* 2010). Attempts have also been made to assess the relative importance of different threats on a global scale (Stuart *et al.* 2004; Bielby *et al.* 2008; Sodhi *et al.* 2008). Several hypotheses have been proposed on the potential interactions between major threats, namely *Bd* and climate change, yet no final accord has been reached (Pounds *et al.* 2006; Pounds *et al.* 2007; Alford *et al.* 2007; Lips *et al.* 2008; Rohr *et al.* 2008). First models of the geography of *Bd* under climate change have been provided (Ron 2005; Rödder *et al.* 2009; Rödder *et al.* 2010), but to date an integrative, global-scale assessment on the spatial interactions of the most severe threats climate change, *Bd* and land-use change is missing.

Using a dataset of 5,527 amphibian species we here demonstrate how the spatial interaction of the three most important threats (climate change, *Bd*, and land-use change, see Methods) may impact amphibian diversity between now and 2080 in a geographically heterogeneous way (see Fig. 1 for the spatial variation of threat intensity).

Regions with high projected impact of climate change on diversity (regions of overlap of the 25% grid cells with the highest proportion of species losing climatic suitability in 2080 with the 25% grid cells of highest species richness) were for frogs in the northern Andes and parts of the Amazon and the Cerrado in South America, large

areas of Africa and a small region in South East Asia (Fig. 1A, Fig. S1 in the Supplementary Material). Values for the proportion of losers per grid cell range up to 73% (= 96 species) (Fig. 1A). For salamanders, western North America, northern Central America and southern and southeastern Europe are the regions projected to be most heavily impacted by climate change, as are some scattered grid cells in northern South America for caecilians (Fig. 1A, Fig. S1). For salamanders, the maximum proportion of losers (species projected to lose climatic suitability) in the most species-rich grid cells reaches 72% (18 species, Fig. 1A).
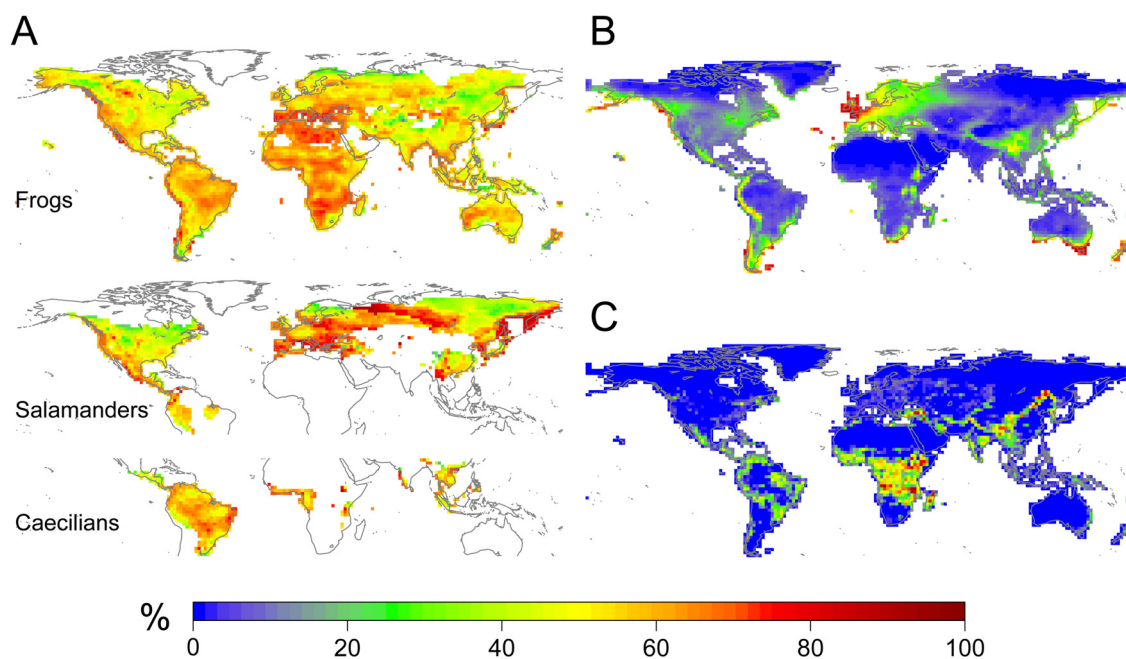
Figure 1 | Geographical variation of threat intensity, projected for 2080. A, proportion of "climate losers" (= proportion of species per grid cell projected to lose climatic suitability, arithmetic mean across 14 GCMs, 3 emission scenarios, and 3 modeling algorithms); **B**, probability of occurrence of *Bd* (as projected by climate-based species distribution models, arithmetic mean across 3 GCMs and 2 emisson scenarios, data from Rödder *et al.* 2010); **C**, land-use change (= proportion of grid cell area projected to be converted from a natural to an anthropogenic state, arithmetic mean across 4 scenarios, data from Alcamo *et al.* 1998); see Methods for further details. White areas in panel **A** indicate the absence of the amphibian order from the respective regions.

The regions with the strongest projected impacts of climate change did not overlap with the regions of the highest probability of occurrence of *Bd* for frogs and caecilians (Fig. 2A); the observed overlap (OV_{obs}) of the two threats was significantly lower than the overlap expected by chance for frogs (OV_{exp}, $G = 6.19$, $p = 0.013$) and did not differ from random overlap for caecilians ($G = 0.51$, $p = 0.48$; Table 1). They did, however, overlap for salamanders ($OV_{obs} > OV_{exp}$, $G = 11.0$, $p < 0.001$, Table 1, Fig. 2A). Within

the 25% grid cells with the highest frog species richness, the difference between observed and expected overlap was even stronger (G = 37.5, $p < 0.001$; Table 1). Regions of high projected climate change impacts largely overlapped with those showing high projected land-use change impacts for frogs ($OV_{obs} > OV_{exp}$; all grid cells, G = 15.3, $p < 0.001$; 25% richest grid cells, G = 10.6, $p = 0.001$; Table 1, Fig. 2B), but not for salamanders and caecilians ($OV_{obs} \approx OV_{exp}$; all grid cells, $G_{Salamanders} = 0.90$, $p = 0.34$, $G_{Caecilians} = 0.036$, $p = 0.85$; 25% richest grid cells, $G_{Salamanders} = 1.2$, $p = 0.27$, $G_{Caecilians} = 0.71$, $p = 0.40$; Table 1, Fig. 2B). The regions with high probability of occurrence of *Bd* did not overlap with the regions of high projected land-use change impact ($OV_{obs} < OV_{exp}$, G = 4.28, $p = 0.038$; Table 1, Fig. 2C), also when considering the regions of highest species richness ($OV_{obs} \approx OV_{exp}$; Table 1). This supports previous studies that have outlined the varying intensity of projected climate and land-use change across space (Jetz *et al.* 2007; Lee & Jetz 2008) or ecosystems (Sala *et al.* 2000).
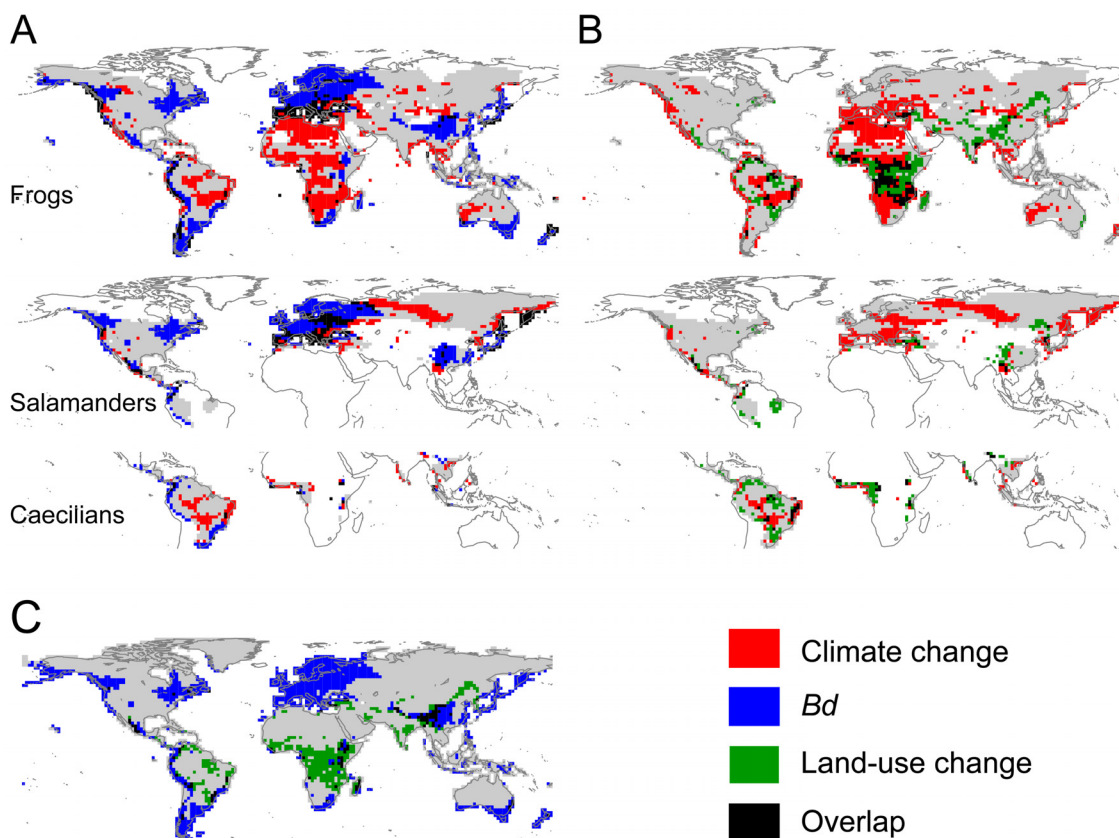
Figure 2 | Spatial overlap of regions exposed to high impact of different threats, projected for 2080. A, climate change and *Bd*; **B**, climate change and land-use change; **C**, land-use change and *Bd*. Regions under high impact are defined as (1) the 25% grid cells with the highest projected proportion of "climate losers", (2) the 25% grid cells with the highest projected probability of *Bd* occurrence, (3) the grid cells with a projected land-use conversion from a natural to an anthropogenic state of at least 25%. White areas in panels **A** and **B** indicate the absence of the amphibian order from the respective regions.

Table 1 | Null model results and G-statistics for the analyses of spatial overlap of different threats.

	overlap$_{obs}$*	overlap$_{exp}$[†] ±CI	G[‡]
ALL GRID CELLS			
Climate change and *Bd*			
Anura	241	280 ±20	6.19*
Caudata	212	170 ±15	10.96***
Gymnophiona	19	22 ±6	0.51 n.s.
Climate change and land-use			
Anura	161	117 ±14	15.27***
Caudata	22	27 ±7	0.9 n.s.
Gymnophiona	35	34 ±7	0.0355 n.s.
***Bd* and land-use**			
World	111	134 ±15	4.28*
25% RICHEST REGIONS			
Climate change and *Bd*			
Anura	25	58 ±10	37.47***
Caudata	66	55 ±7	5.18*
Gymnophiona	5	3 ±2	1.13 n.s.
Climate change and land-use			
Anura	127	95 ±12	10.61**
Caudata	2	4 ±3	1.21 n.s.
Gymnophiona	2	3 ±3	0.71 n.s.
***Bd* and land-use**			
Anura	62	67 ±10	0.44 n.s.
Caudata	15	12 ±3	0.74 n.s.
Gymnophiona	4	4 ±2	0.003 n.s.

Threats are the projections of the proportion of "climate losers" (climate change), *Bd* probability of occurrence (*Bd*), and land-use change (land-use). Threat overlap analyses were done separately for all grid cells and within the 25% grid cells of highest species richness for the respective amphibian order.

*number of grid cells being among the 25% of the grid cells projected to be most heavily impacted by the two respective threats

[†]expected overlap (arithmetic mean and 95% confidence intervals) as derived from 10,000 null model simulations; for the null models, grid cells projected to be most threatened were randomly distributed across the available grid cells (which differ for frogs, salamanders and caecilians) and grid cells where threats overlapped were counted

[‡]G-statistics tests if the expected and observed values of overlap differ significantly from each other (replicated goodness of fit, Sokal & Rohlf 1995; Lund & Rahbek 2002); significance levels: ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$, n.s. = not significant

To the best of our knowledge, no study has so far quantitatively coupled species-specific climate change models with projections of land-use change and the potential spread of a highly infectious pathogen on a global scale. We stress, however, that various issues of data- and method inherent uncertainties and of some underlying biological assumptions in the models need to be borne in mind when interpreting our results (see Methods and Supplementary Text). Nevertheless, this note of caution should not hide the fact that the future of amphibian biodiversity appears to be threatened (Beebee & Griffiths 2005; Wake & Vredenburg 2008). Firstly, several threats that have been documented to cause amphibian declines, such as exploitation, pollution, the spread of invasive species or UV-B irradiation (Collins & Storfer 2003; Beebee & Griffiths 2005), could not be considered in this study. They give reason for additional concern, especially because of negatively interacting effects (Blaustein & Kiesecker 2002; Collins & Storfer 2003; Bancroft *et al.* 2008). Secondly, our coarse-resolution approach may obscure more severe impacts on local scales that could have global effects. For instance, small areas may harbor rich endemic amphibian faunas whose species may be highly susceptible to *Bd* infection and show particularly high values of climate suitability for *Bd* in combination with the actual occurrence of the fungus. Such local coincidences cannot be detected by our coarse-scale assessment, but could actually result in the global extinction of many endemic species.

Thirdly, the 25%-approach as used in our analyses does not imply that the amphibian faunas of the remaining regions are not impacted. Nevertheless, even in the unlikely case that the only regions where amphibians are threatened by 2080 are those identified by the arbitrary thresholds used here, more than half of the total range of each of the three amphibian orders would be under severe impact of either of the three threats (Fig. 3). When only considering the regions with the highest species richness, about two thirds of the area harboring the richest frog and salamander faunas (half of the area for caecilians) can be assumed to be heavily impacted by 2080.

The phenomenon of spatial threat additivity revealed by our analysis may be particularly problematic for amphibians. Their biology makes amphibians vulnerable to a variety of threats (Wells 2007; Wake & Vredenburg 2008). For instance, many amphibian species rely on different habitats because of their multi-stage life cycle (Wilbur 1980). If threats are spatially additive, this may be worse for amphibians than for other organisms only relying on a single habitat: if, e.g., one particular area is affected by land-use change and another area by the water-mediated spread of a

pathogenic fungus, organisms relying on both habitats will suffer in both areas, while a coincidence of the two threats in one area and the absence of both in the other area would potentially be less problematic be more beneficial. In fact, amphibians without an aquatic stage appear to be less vulnerable than those relying on an aquatic stage (Lips 1998; Lips *et al.* 2003; Bielby *et al.* 2008; Sodhi *et al.* 2008).
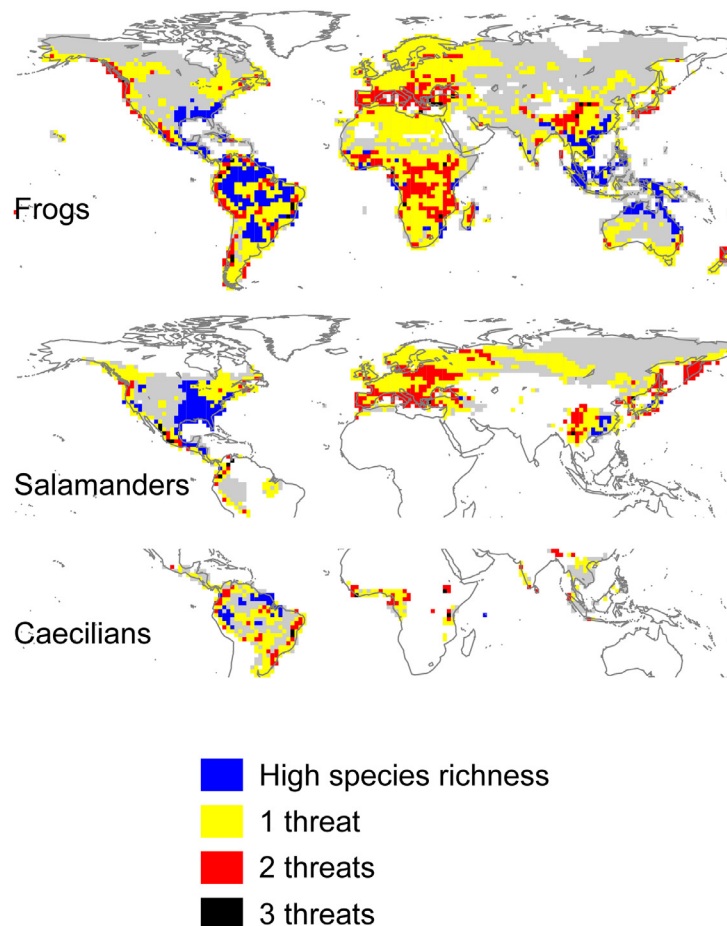
Figure 3 | Spatial additivity of threats in 2080. Yellow, red and black colors indicate regions exposed to one, two or three high threat projections, respectively. Blue colors indicate regions of high species richness not projected to be exposed to high impact (by any of the three threats).

Regions under high threat are defined as (1) the 25% grid cells with the highest projected proportion of "climate losers", (2) the 25% grid cells with the highest projected probability of *Bd* occurrence, (3) the grid cells with a projected land-use conversion from a natural to an anthropogenic state of at least 25%. Regions of high species richness are defined as the 25% grid cells with the highest species richness for the respective amphibian order. White areas indicate the absence of the amphibian order from the respective regions.

The problem of spatial additivity and mechanistic interaction of multiple threats imposes major challenges for sustainable approaches of amphibian conservation. Very different measures on different temporal, spatial and political scales are needed (Beebee & Griffiths 2005; Mendelson *et al.* 2006; Gascon *et al.* 2007). These range from conventional protected area approaches via the prohibition of industrial and agrochemical pollutants or the prevention of *Bd* spread through hygienic measures for herpetologists and captive breeding programs to international agreements on the reduction of greenhouse gas emission. The global spatial additivity of threats for amphibian diversity as documented by our analyses underlines the pessimistic long-term perspectives for the global amphibian diversity (Stuart *et al.* 2004; Beebee & Griffiths 2005; Mendelson *et al.* 2006). We call for more quantitative spatial assessments on the intensity and interactions of threats and stress the need of multi-level conservation approaches.

Methods summary

To identify the regions with the highest projected impacts of climate change on amphibian species, we fitted bioclimatic models for 5,527 species using ensemble forecasting (Araújo & New 2007). We used climatic data from 14 different general circulation models (GCMs) of the 4th IPCC report (IPCC 2007; Meehl *et al.* 2007) under three emission scenarios and applied three common bioclimatic modeling algorithms. For each of 5041 2×2 degrees latitude-longitude cells, we identified the species projected to lose climatic suitability ("losers") in 2080 compared with current conditions. We then mapped the proportion of losers out of the total number of species per grid cell across the world. As the regions with the highest projected impact of climate change, we identified the 25% of the grid cells with the highest proportion of losers, separately for frogs, salamanders and caecilians. We also identified the regions with the highest species richness, as well as the regions with the highest probability of occurrence of *Bd* (data from Rödder *et al.* 2010) and with the highest projected land-use change in 2080 (data from Alcamo *et al.* 1998), again using a 25%-threshold.

To assess the spatial overlap of the regions of highest impact from different threats, we used null model simulations and a G-statistics approach (replicated goodness of fit, Sokal & Rohlf 1995; as proposed in Lund & Rahbek 2002). For the null models, we randomly distributed the regions projected to be most threatened (which were defined as explained above) across the available grid cells (which differ for frogs, salamanders and

caecilians), and counted the cells where threats overlap – separately for projected climatic impacts on amphibian diversity, *Bd* probability of occurrence and land-use change. We ran 10,000 simulations after which we compared the observed overlap values with those of the simulations. The G-statistics tests if the expected and observed values of overlap differ significantly from each other.

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Methods

Data. We conducted species distribution modeling for 5527 amphibian species from the three amphibian orders Anura (frogs and toads), Caudata (salamanders and newts) and Gymnophiona (caecilians), which for simplicity are henceforth referred to as frogs, salamanders and caecilians. Distribution data were compiled from the 'Global Amphibian Assessment' (IUCN *et al.* 2004). Polygons of species' ranges were resampled to a 2 × 2 degree latitude-longitude grid (referred to as the 2°-grid in the following) including 5041 terrestrial cells (for maps of species richness, see Fig. S2 in the Supplementary Material).

Climatic data were obtained from the World Climate Research Programme's (WCRP's) Coupled Model Intercomparison Project phase 3 (CMIP3) multi-model dataset (Meehl *et al.* 2007) of the 4th Intergovernmental Panel on Climate Change (IPCC) report. Data were derived from 14 coupled Atmosphere-Ocean General Circulation Models (GCMs) and three emission scenarios (see Table S1 for an overview of the used datasets). Using this series of GCMs we encompass a wide range of equilibrium climate sensitivity (ECS, 2.1°C to 4.3°C; see Table S1 for details) and an array of original spatial resolutions, from 1.1 × 1.1 to 3.75 × 3.75 degrees latitude-longitude in the original sets. Outputs for each model were obtained for three SRES (IPCC 2000) emission scenarios (A1B, A2 and B1, but note that A2 and B1 scenarios were not available for all of the GCMs, Table S1; see IPCC 2007, p. 18, for a detailed description of the different scenario storylines). Inclusion of these three scenarios ensures that the models cover a wide range of likely climatic changes.

For each of the GCMs and emission scenarios, five climatic variables were obtained for present time (averaged across a 30-year time period from 1970 to 1999), which was the baseline used to calibrate the models, as well as for a 30-year time period from 2070 to 2099, subsequently referred to as 2080. The variables used were mean annual rainfall and precipitation seasonality, annual temperature range, minimum temperature and maximum temperature. These variables are known to impose constraints on amphibian physiology and survival (Carey & Alexander 2003; Wells 2007) and are often used to model amphibian species distributions and richness (e.g. Araújo *et al.* 2006; 2008). All climate variables were resampled to the 2°-grid. This resolution approximates the average of the original GCM resolutions.

By using a global extent approach and given our scale of analysis in terms of grain size, we (1) avoid asserting artificial data quality by inappropriate downscaling of the climatic data, and (2) minimize the problem of false absences in the species distribution data (e.g. Hurlbert & Jetz 2007) as many species in the dataset have only been identified in a few localities, with no knowledge about the true extent of occurrence of the species (IUCN *et al.* 2008). However, the coarse resolution precludes detailed local assessments of threat interactions and processes; therefore we focus on documenting coarse spatial patterns here.

As projections of the probability of occurrence of *Bd* we used climate-based consensus projections by Rödder *et al.* (2010). Their projections (standardized probability of occurrence given by a consensus of MaxEnt SDMs across 3 GCMs and 2 emission scenarios) were resampled to the 2°-grid by weighted averaging (Fig. S3). For the subsequent analyses, we used a consensus map calculated as arithmetic means across the all projections (Fig. 1B). Generally, averaging across different scenarios may be problematic. However, for practical reasons and because separate maps of the variation of *Bd* probability of occurrence for each combination of used GCM × scenario did not show strong differences in the spatial pattern (Fig. S3), we stick to the consensus map.

For the projections of potential land-use change, we used data from the Millennium Ecosystem Assessment (MA, Alcamo *et al.* 1998; Millennium Ecosystem Assessment 2005b). The MA uses four scenarios representing a variety of socio-economic and political futures to estimate future changes in the Earth's land-cover ("Adapting Mosaic", "Global Orchestration", "Order from Strength", and "TechnoGarden"; for more information on the MA data and the description of scenarios, see Millennium Ecosystem Assessment 2005a; Jetz *et al.* 2007). The MA maps provide information on current and future distributions of 18 different land-cover types at a 0.5° latitude-longitude resolution. For a quantification of potential land-use change we identified grid cells that are projected to change from a natural to an anthropogenic land-cover state (change of any land-cover type to land-cover type 3 "cropland/permanent pasture") and calculated the proportion of area changed for each cell of our 2°-grid for 2080, as a consensus map (arithmetic mean across all four scenarios, Fig. 1C) and separately for each of the four scenarios (Fig. S4). As for *Bd* projections, for practical reasons and because a separate use of different MA scenarios does virtually not affect the results, we used the consensus map in the subsequent analyses.

Modeling. Three different modeling algorithms, Euclidean distance (ED), Mahalanobis distance (MD) and MaxEnt (MX), were used to run species distribution models (SDMs). These presence-only algorithms were selected due to the large number of species with uncertain distributions to be modelled. The two distance methods measure the similarity of each species' occurrence to the mean (or centre) of the available climatic space. Accordingly species' niches are defined as circular (for ED) or elliptical (for MD) shapes in climatic hyperspace (Farber & Kadmon 2003). BioEnsembles, a new computer software which is able to optimize and take advantage of high-speed parallel processing, was used to run the ED and MD models (Rangel *et al.* 2009). MaxEnt version 3.2.4 (Phillips *et al.* 2006; Phillips & Dudik 2008), a machine-learning technique based on the principle of maximum entropy, was used to run the MX models. In MaxEnt, we used a regularization multiplier of 0.5 (a model parameter which allows for adjustment of the degree of model overfitting), since this value represents a balance between being able to fit models for species with very few records while avoiding an unreliable degree of overfitting. For each of the 5,527 species, we ran each possible modeling combination (3 modeling algorithms × 14 GCMs × 3 scenarios × 2 time periods), which resulted in 1,260,156 models (note that for some GCMs only two scenarios were available, Table S1). Standard SDM validation procedures were not applicable in our study (but note that a validation for future scenarios is in any case not possible). However, we cautiously assessed patterns of variation in model results that may have resulted from different sources of uncertainty, such as species with small numbers of occurrence records, different modeling algorithms, variation among GCMs that may result from different resolutions and equilibrium climatic sensitivities, as well as different emission scenarios (see Supplementary Text, also for discussion on model-inherent assumptions). All analyses were performed separately for frogs, salamanders and toads.

Processing of modeling results. For two reasons we used a no-dispersal scenario as the basic underlying assumption for the further processing of the modeling results. Firstly, it is unlikely that amphibians will be able to fully track changes in climatic conditions by shifts of their distributional ranges (Smith & Green 2005), in particular when thinking of the coarse spatial scale of our analyses (see also our discussion of coarse data implications in Supplementary Text). Secondly, and more importantly, the ranges of many species are extremely small (see Fig. S1 for range-size frequency distributions). Since SDM range projections can become unreliable for species with few

occurrence records (Stockwell & Peterson 2002; McPherson *et al.* 2004; Wisz *et al.* 2008) we refrained from projecting a species' range into areas where the species does not currently occur. Furthermore, because of various uncertainties (see Supplementary Text) we decided not to use thresholds to transfer raw model outputs (i.e. probabilities of occurrence) into presences or absences. Instead, we used the change in climatic suitability per grid cell within species' current ranges. The change in climatic suitabilities was then calculated as the difference of the climatic suitabilities between current and future conditions (standardized MX probability of occurrence or 1 *minus* the standardized raw distance for ED and MD, respectively; see Fig. S5 for an example). This procedure was repeated for each model combination (algorithm × GCMs × scenarios) for each species. Despite the standardization of values of suitability change to a range from 0 to 1, the values are not quantitatively comparable across the different modeling algorithms, which is due to general differences in distance-based (ED, MD) and machine-learning (MX) algorithms as well as to and software-inherent differences (for histograms and maps of the mean changes of suitability per grid cell, calculated across the means of all species, see Fig. S6 and Fig. S7). Therefore we used a qualitative approach to identify the regions with the strongest projected impacts of climate change on amphibian diversity: for each model combination, we counted the number of species per grid cell that (1) lose climatic suitability ("climate losers" - negative change in climatic suitability between current and future conditions), (2) gain climatic suitability ("climate winners" - positive change in climatic suitability between current and future conditions) and (3) show no change in climatic suitability between current and future conditions. Note that doing so implies that species with the smallest change in climatic suitability will be counted as "climate loser" or "climate winner", and that species may be identified as losers in one grid cell and as winners in another. However, as we do not intend to forecast species extinctions we believe our approach is valid.

To identify the regions with the strongest projected impacts of climate change on amphibian diversity, we built consensus maps of the proportion of climate losers and then identified the 25% of all grid cells with the highest proportion of losers (Fig. S1). Consensus maps were derived by calculating arithmetic means of the proportion of climate losers across all model combinations (algorithm × GCM × scenario) for 2080 (Fig. 1A).

Many studies have shown that species distribution modeling results can vastly differ when using different GCMs, emission scenarios and algorithms (e.g. Araújo *et al.* 2005;

Pearson *et al.* 2006). To assess the uncertainties around the consensus, we mapped the proportion of losers separately as arithmetic means (1) across all combinations of GCM × algorithm per scenario (Fig. S8), (2) across all combinations of GCM × scenario per algorithm (Fig. S9 A-C), and (3) across all combinations of GCM × scenario per combination of two algorithms (Fig. S9 D-F). Furthermore, following a novel uncertainty assessment protocol (Diniz-Filho *et al.* 2009), we assessed the proportion of variation explained by different sources of uncertainty (algorithm, GCM, scenario, their interactions, and the residual uncertainty) by variance partitioning (SS proportion in 3-way ANOVAs; Fig. S10), and mapped these proportions of uncertainty (Fig. S11, see Diniz-Filho *et al.* 2009 and Supplementary Text for details). In addition, we identified the 25% grid cells with the highest proportion of climate losers separately for each model combination and calculated the number of models per grid cell that identified this grid cell as one of the 25% with the highest proportion of losers. These overlap maps were constructed for each possible algorithm combination (ED × MD × MX; ED × MD, ED × MX, MD ×MX; ED, MD, MX) to also assess the amount of uncertainty that is associated with the use of one, two or three modeling algorithms (Fig. S12).

Spatial overlap of different threats. To investigate the spatial overlap of different threats for amphibian diversity, we identified the regions with the highest projected impact for each of the respective threat: 25% of all grid cells with the highest proportion of climate losers (Fig. S13 A), 25% of all grid cells with the highest probability of occurrence of *Bd* (Fig. S13 B), and the grid cells with a projected land-use change of at least 25% of the total area (Fig. S13 C). All of these calculations were based on the consensus maps which were derived as explained above.

To assess the spatial overlap of the regions of highest projected impact from different threats (Fig. 2), we used null model simulations (Table 1, Fig. S14) and a G-statistics approach (replicated goodness of fit, Sokal & Rohlf 1995; as proposed in Lund & Rahbek 2002). For the null models, we randomly distributed the regions projected to be most threatened (which are defined as explained above) across the available grid cells (which differ for frogs, salamanders and caecilians), and counted the cells where threats overlapped – separately for projections of climatic impacts on amphibian diversity, *Bd* probability of occurrence and land-use change. We ran 10,000 simulations after which we compared the observed overlap values with those of the simulations (Table 1, Fig. S14). With the G-statistics test we determined which of the expected and

observed values of overlap differ significantly (see also Table 1 and Lund & Rahbek 2002 for details).

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Supplementary Material

Supplementary Text | Assessment of uncertainties

In the analyses quantifying the amount of uncertainty resulting from different sources in the ensemble modeling, we found that the interaction between GCMs and modeling algorithm accounted for the largest level of uncertainty (c. 60% explained variance in a three-way ANOVA, Fig. S10 – see Methods for details). Among the main effects, the variation among GCMs was the largest source of uncertainty (c. 20% explained variance), followed by the variation among algorithms (c. 10%). This pattern was consistent among the different amphibian orders (Fig. S10). Mapping the different sources of variance revealed no distinct spatial pattern (Fig. S11).

When mapping the 25% grid cells with the highest projected proportion of losers separately for each modeling combination (GCM × scenario × algorithm, Fig. S12), an overlay of all model combinations showed only an intermediate consistency among the different models for some of the regions projected to be most heavily impacted. When removing the models of the Mahalanobis Distance (MD), the consistency increased considerably (Fig. S12 E), especially for regions projected to be most heavily impacted, which then reached consistency values of up to 50-60%. In fact, a visual inspection of a large sample of species-specific maps indicated that the MD results were much less reliable than the results obtained from the ED and MX models. However, since the spatial pattern of the regions projected to be exposed to high climate change impact does not considerably change when excluding the MD models (Fig. S13 and S16), we decided to leave them in the consensus projections.

The overall pattern of the spatial variation of the proportion of climate losers did not differ among the three SRES emission scenarios, with only the proportion values differing among the different scenarios, where the A2 scenario generally showed higher proportions of losers than the A1B and the B1 scenario (Fig. S8). Removing the species with very small range sizes did not result in any considerable changes in the spatial patterns (Fig. S15).

We emphasize that beyond the uncertainties resulting from the large number of models used in the ensemble modeling analyses there are several fundamental assumptions and uncertainties inherent in the methods used that need to be taken into account. These refer in particular to (1) assumptions inherent in the species distribution

modeling approach, (2) assumptions and uncertainties in the climate-based modeling of *Bd*, and (3) the coarseness of the data and analyses used. These points call for a cautious interpretation of the results.

Firstly, several fundamental, biologically rather unrealistic assumptions are inherent in climate-based species distribution models, such as the equilibrium of the species' distributions with current climatic conditions, neglect of biotic interactions in determining distributions, simplified dispersal assumptions (null- and full- dispersal scenarios), and neglect of species' evolutionary potential to adapt to novel climatic conditions (Guisan & Thuiller 2005). As a result of this, many studies have outlined pathways to overcome the shortcomings of species distribution models (e.g. Araújo & Guisan 2006; Keith *et al.* 2008; Anderson *et al.* 2009). However, for a global and taxonomically comprehensive analysis like ours we rely on the coarse distribution and climate data at hand which does not allow for more innovative approaches. Therefore, we provide an uncertainty assessment of our models in concert with a cautious interpretation of our results (see above). In particular, we stress that projections and scenarios as used and produced in our analyses are not to be taken as predictions.

Secondly, the occurrence and spread of *Bd* is, of course, not only dependent on climate, and the interaction between climate change and *Bd* outbreaks remains heavily debated (Pounds *et al.* 2006; Pounds *et al.* 2007; Alford *et al.* 2007; Bosch *et al.* 2007; Lips *et al.* 2008). Although a certain climatic optimum has been documented, the evolutionary potential to adapt to novel climatic conditions may be particularly high for microbial pathogens such as *Bd* (Fisher *et al.* 2009). Furthermore, several of the regions with a high climate-based projected probability of *Bd* occurrence that harbor a rich amphibian fauna, such as Madagascar, have as yet not been exposed to *Bd* (Kriger & Hero 2009). Thus, the *Bd* models would rely on the introduction of *Bd* to these regions. However, reports on the rapid spread of *Bd* during the last decades (James *et al.* 2009) and the contribution of humans to this spread (Kriger & Hero 2009) give rise to serious concerns even for the regions not yet colonized by *Bd*. Furthermore, little is yet known about the factors influencing the susceptibility of amphibians to *Bd* infection (Berger *et al.* 2005; Woodhams *et al.* 2007; Fisher *et al.* 2009; Richmond *et al.* 2009). While some species suffer dramatically and the first extinctions due to *Bd* infection have been documented (Schloegel *et al.* 2006; Skerratt *et al.* 2007), other species are apparently able to cope with the pathogen (Woodhams *et al.* 2006).

Thirdly, the data on land-use change are very rough estimates based on various socioeconomic and environmental development scenarios (Millennium Ecosystem Assessment 2005). As a general caveat, one has to bear in mind that our analyses as well as the underlying climate, species distribution and land-use data are of coarse resolution. For example, it is unlikely that we accurately characterize the climatic niche of a narrowly-ranging species by averaging temperature values across 2° grid cells of an area covering c. 48,000 km² at the equator (see also discussion in Hof *et al.* 2010). However, due to the high uncertainty inherent in model or scenario data (such as our climate and land-use data), scaling down the resolution to 1° or even 0.5° would imply an artificial accuracy of the analyses that by no means can be supported by the underlying source data. Hence, using a rather coarse resolution may actually be more appropriate for this type of analyses. Moreover, as we restrict our aim to the coarse quantification of the spatial interactions of different threat projections, we believe our analyses are robust.

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Supplementary Tables

Table S1 | Overview of the climatic (GCM) data used.

Model	ecs*	resolution (°lat × °lon)	scenarios[†]
CCSM3, USA	2.7	1.4 × 1.4	A1B, A2, B1
MRI-CGCM2.3.2, Japan	3.2	2.8 × 2.8	A1B, A2, B1
CGCM3.1(T47), Canada	3.4	3.75 × 3.75	A1B, A2, B1
CGCM3.1(T63), Canada	3.4	1.9 × 1.9	A1B, B1
GFDL-CM2.0, USA	2.9	2.0 × 2.5	A1B, A2, B1
GFDL-CM2.1, USA	3.4	2.0 × 2.5	A1B, A2, B1
CSIRO-Mk3.0, Australia	3.1	1.9 × 1.9	A1B, A2, B1
ECHAM5/MPI-OM, Germany	3.4	1.9 × 1.9	A1B, A2, B1
UKMO-HadCM3, UK	3.3	2.5 × 3.75	A1B, A2, B1
UKMO-HadGEM1, UK	4.4	1.3 × 1.9	A1B, A2
IPSL-CM4, France	4.4	2.5 × 3.75	A1B, A2, B1
MIROC3.2(hires), Japan	4.3	1.1 × 1.1	A1B, B1
MIROC3.2(medres), Japan	4	2.8 × 2.8	A1B, A2, B1
PCM1, USA	2.1	2.8 × 2.8	A1B, A2

*equilibrium climate sensitivity, the annual mean surface air temperature change experienced by the climate system after it has attained a new equilibrium in response to a doubling of CO_2 concentration (unit: degrees Celsius) (IPCC 2007)
[†]scenarios used in the species distribution modeling; for some GCMs only two scenarios were available by the time of data download

Supplementary Figures
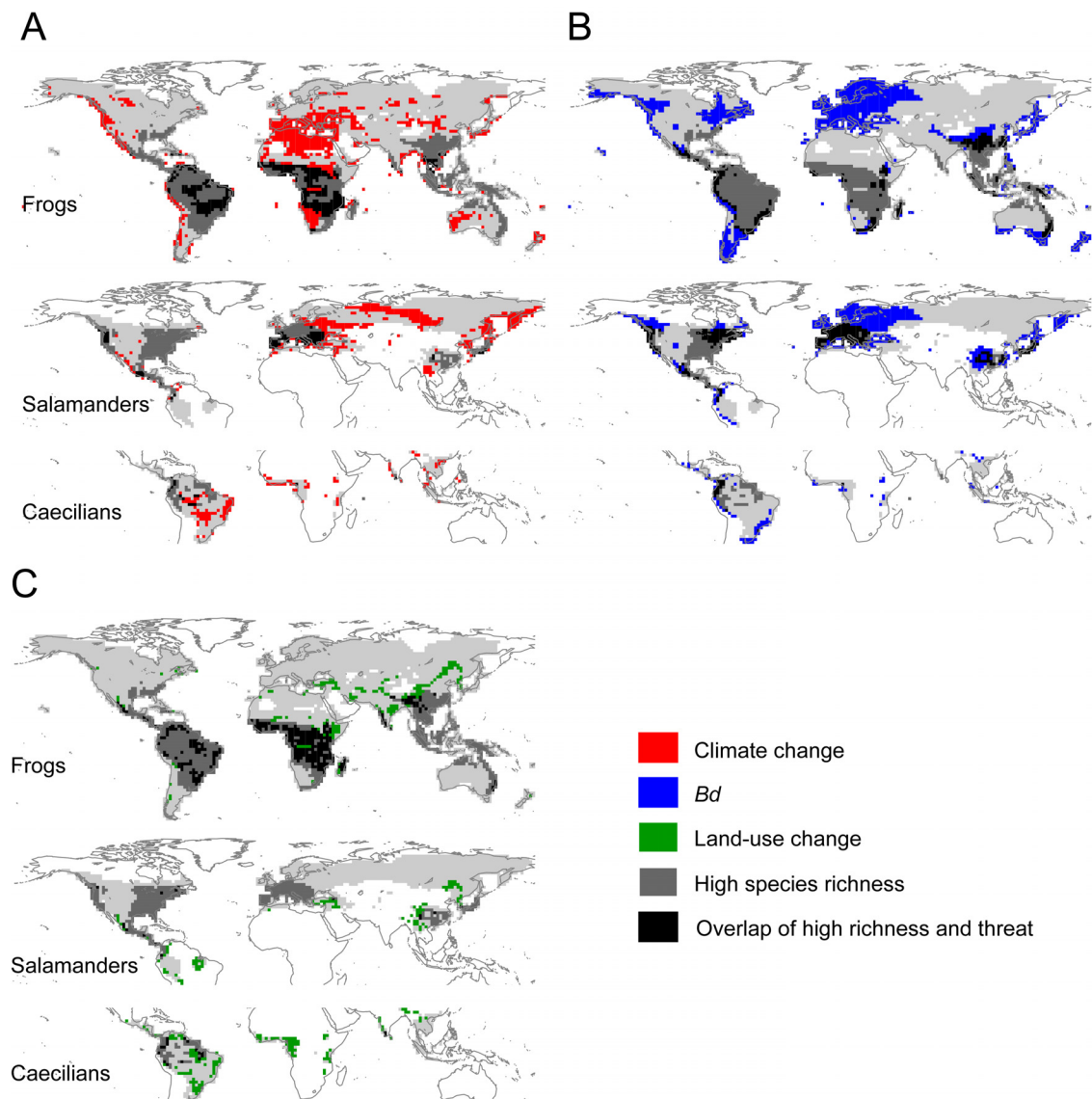
Figure S1 | Overlap of regions of high species richness and high impact of climate change, *Bd*, and land-use change by 2080. Regions of high species richness (dark grey) are defined as the 25% grid cells with the highest species richness; regions exposed to high impact are defined as, **A**, the 25% grid cells with the highest projected proportion of "climate losers" (red), **B**, the 25% grid cells with the highest projected probability of *Bd* occurrence (blue), **C**, the grid cells with a projected land-cover conversion from a natural to an anthropogenic state of at least 25% (green). Overlap of high richness with the respective threat is given in black. White areas indicate the absence of the amphibian order from the respective areas.
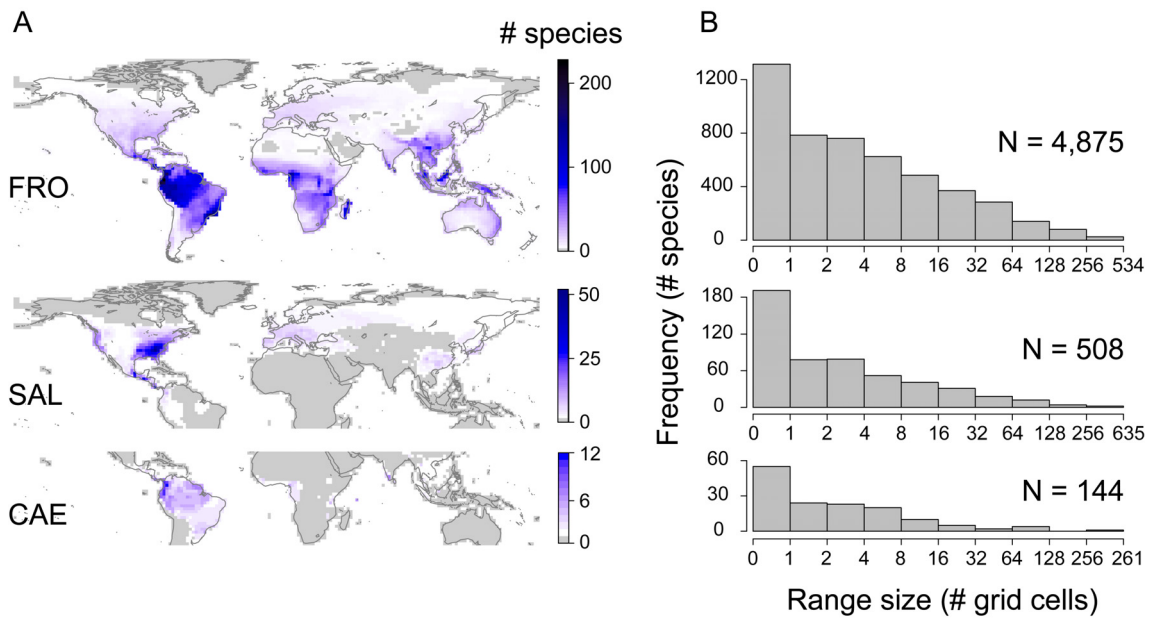
Figure S2 | Species richness and range sizes of amphibians. A, Spatial variation of amphibian species richness; **B**, range-size frequency distributions. Note the differences in the color scale in panel **A** and the scaling of the x-axis in panel **B**.
FRO, frogs; SAL, salamanders, CAE, Caecilians. Grey areas in panel **A** indicate the absence of the amphibian order from the respective areas.
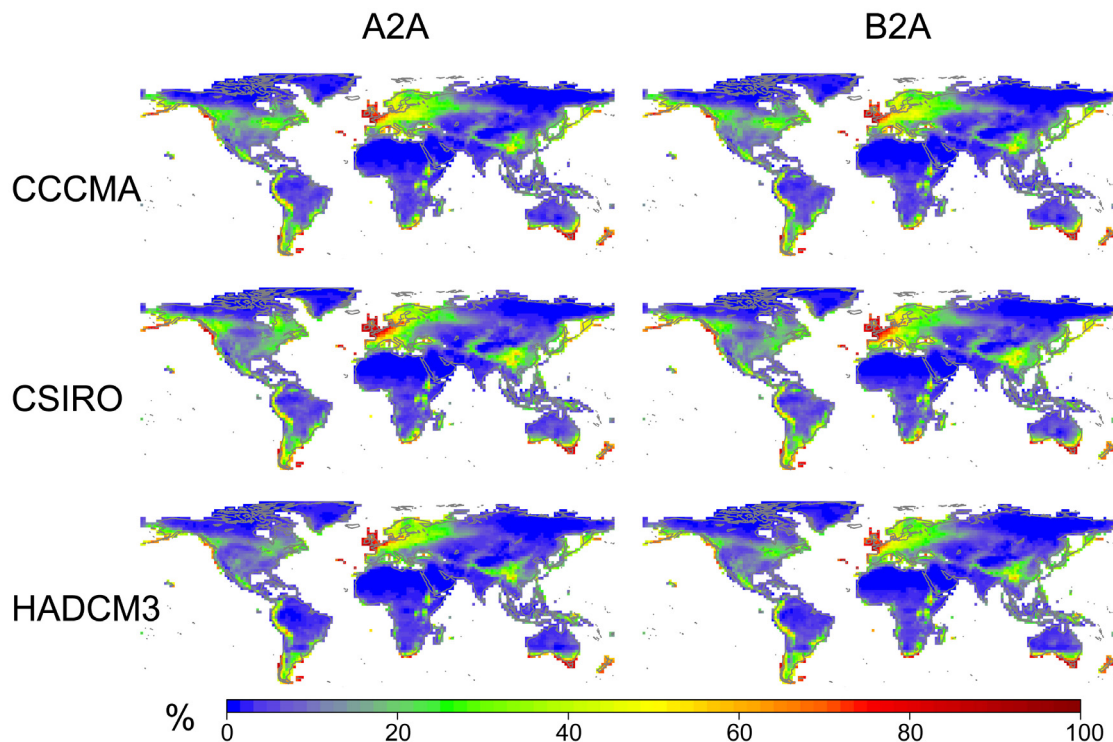
Figure S3 | Probability of occurrence of *Bd*, projected for 2080. Values of probabilities of occurrence are obtained on climate-based species distribution models using MaxEnt (results from Rödder *et al.* 2010; rescaled to the 2°-grid). Different panels show the combinations of emission scenarios (columns) and GCMs (rows) used.
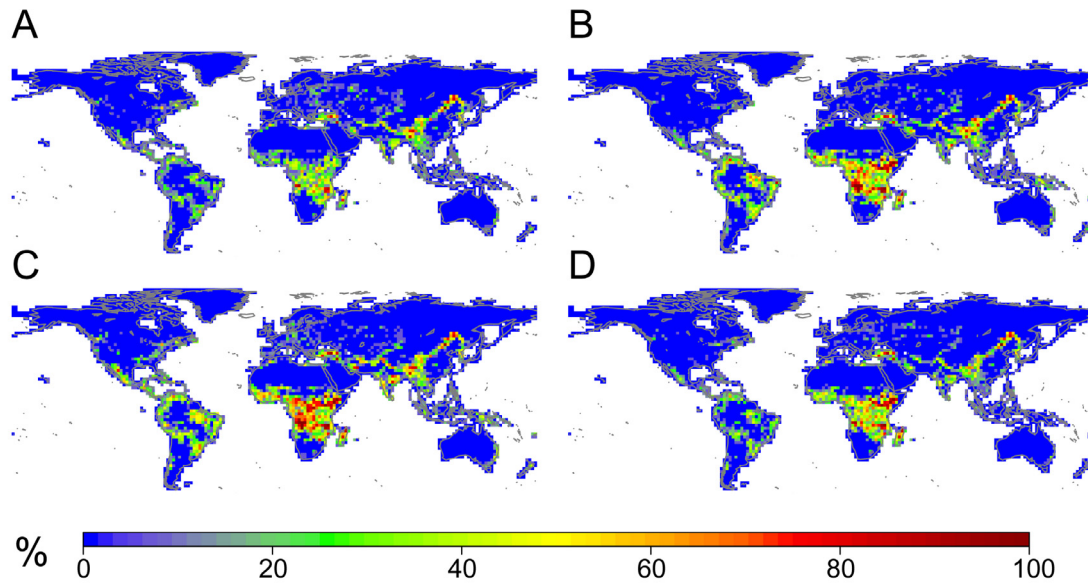
Figure S4 | Projections of land-use change for 2080. Colors indicate the proportion of the area of one 2°-grid cell projected to be converted from a natural to an anthropogenic land-use state (data from Alcamo *et al.* 1998), for each the four MA scenarios (Millennium Ecosystem Assessment 2005). **A**, Adapting Mosaic; **B**, Global Orchestration; **C**, Order from Strength; **D**, TechnoGarden.
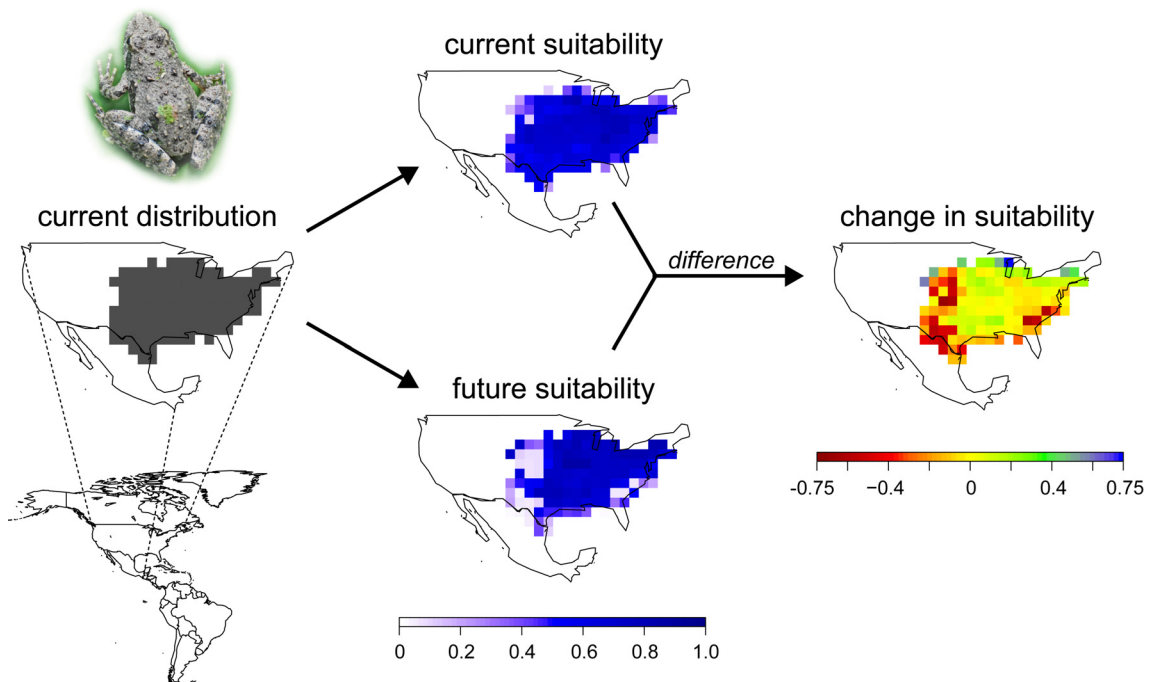
Figure S5 | Calculation of change in climatic suitability. From the current distribution (left-hand panel), SDMs are fitted using climatic variables for current and future conditions. SDMs assign a certain climatic suitability (= probability of occurrence) to each grid cell (central panels; darker colours indicate higher suitabilities). The change in suitability is calculated as the difference between current and future suitabilities (right-hand panel). The exemplary species is the Northern Cricket Frog (*Acris crepitans*), which occurs throughout the eastern USA (picture courtesy: J. Oldenettel).
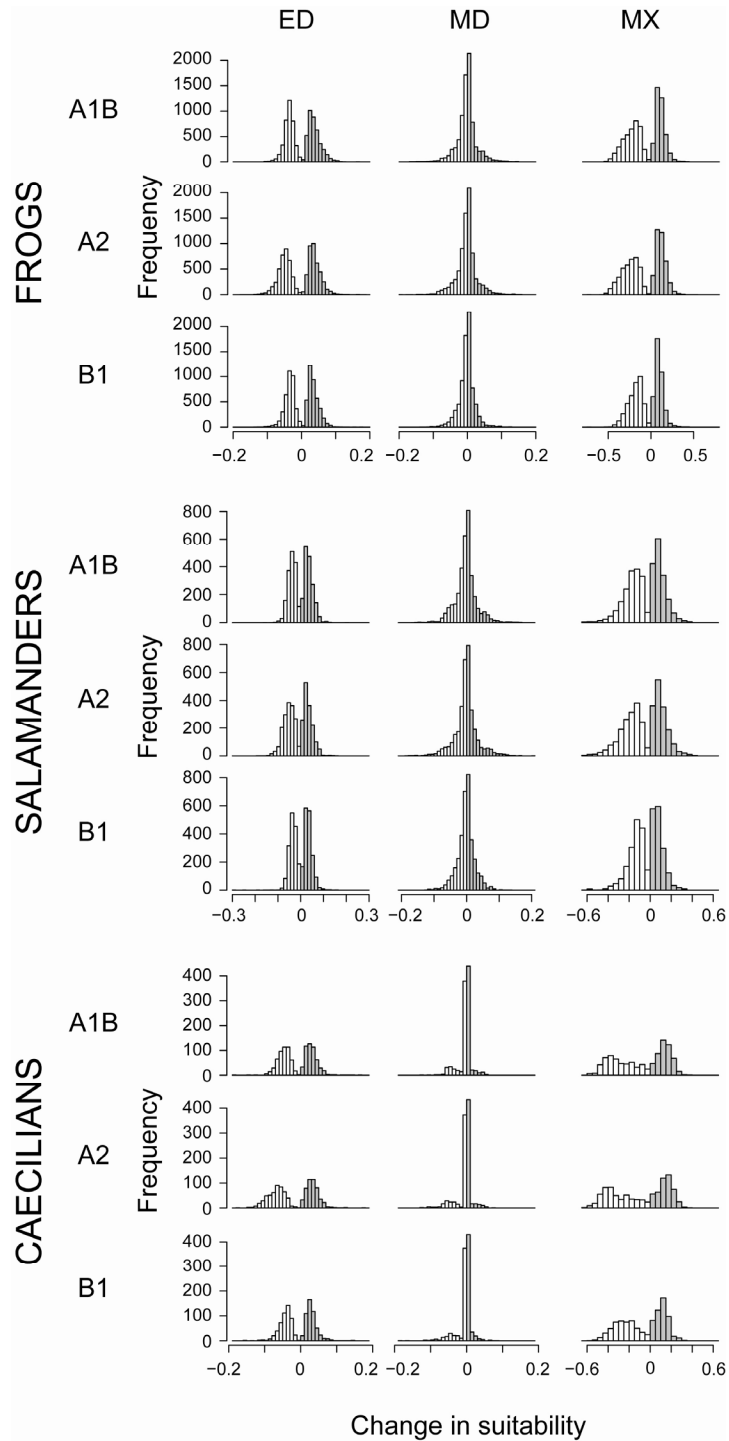
Figure S6 | Mean changes in climatic suitability for climate losers and winners, projected for 2080. Values are calculated as arithmetic means across 14 GCMs of mean changes in climatic suitability across all species per grid cell that lose (white bars) or win (grey bars) climatic suitability (for an explanation of the calculation of climatic suitabilities, see Fig. S2). Each panel shows a separate combination of emission scenario (rows) and modeling algorithm (columns).
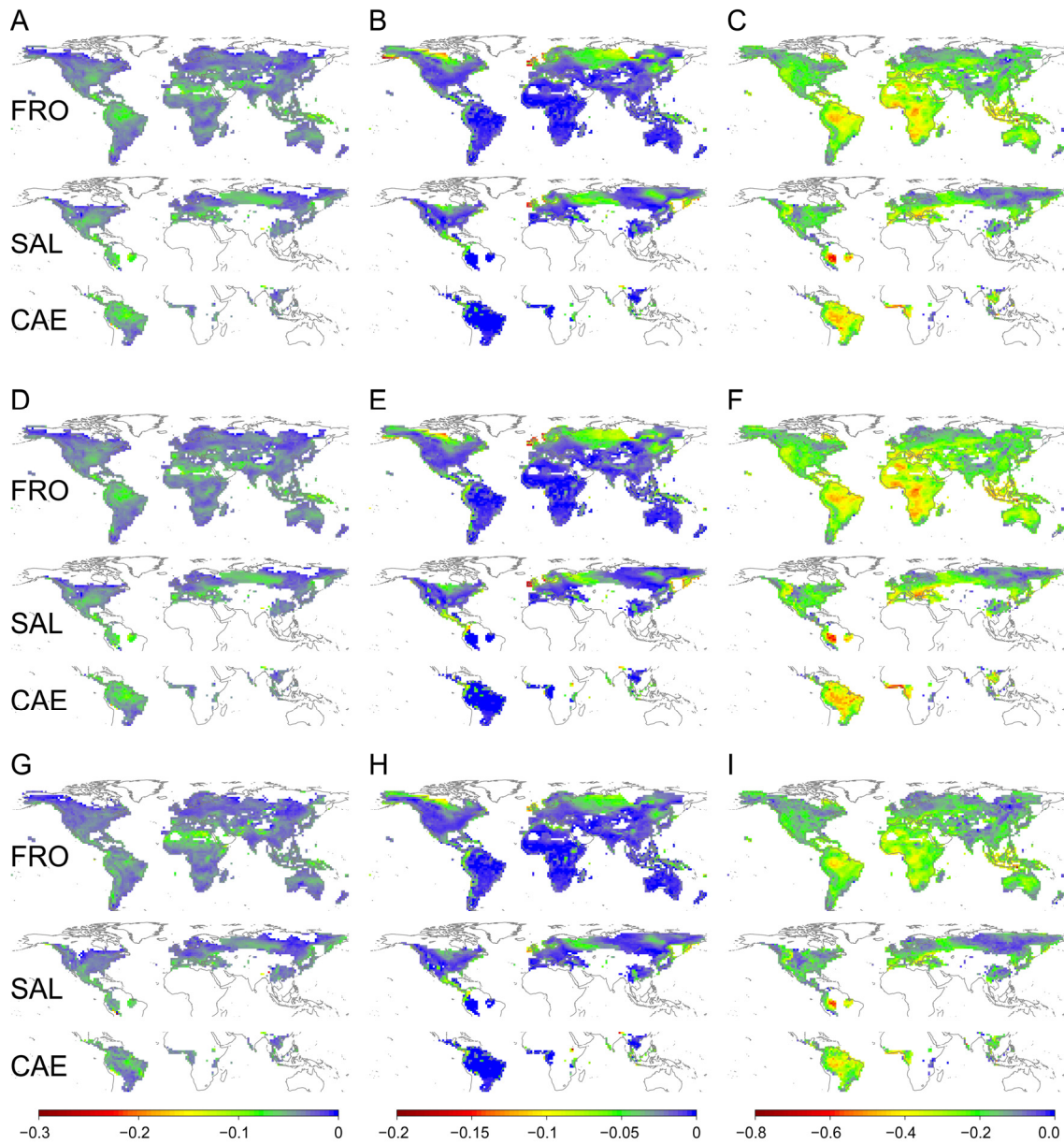
Figure S7 | Spatial variation of mean changes in climatic suitability for climate losers, projected for 2080. Values are calculated as arithmetic means across 14 GCMs of mean changes in climatic suitability across all species per grid cell that lose climatic suitability. Each panel shows a separate combination of emission scenario (rows) and modeling algorithm (columns). **A**, ED × A1B, **B**, MD × A1B; **C**, MX × A1B; **D**, ED × A2; **E**, MD × A2, **F**, MX × A2; **G**, ED × B1; **H**, MD × B1, **I**, MX × B1; FRO, frogs; SAL, salamanders; CAE, caecilians. Note the different color scaling for the different modeling algorithms (columns).
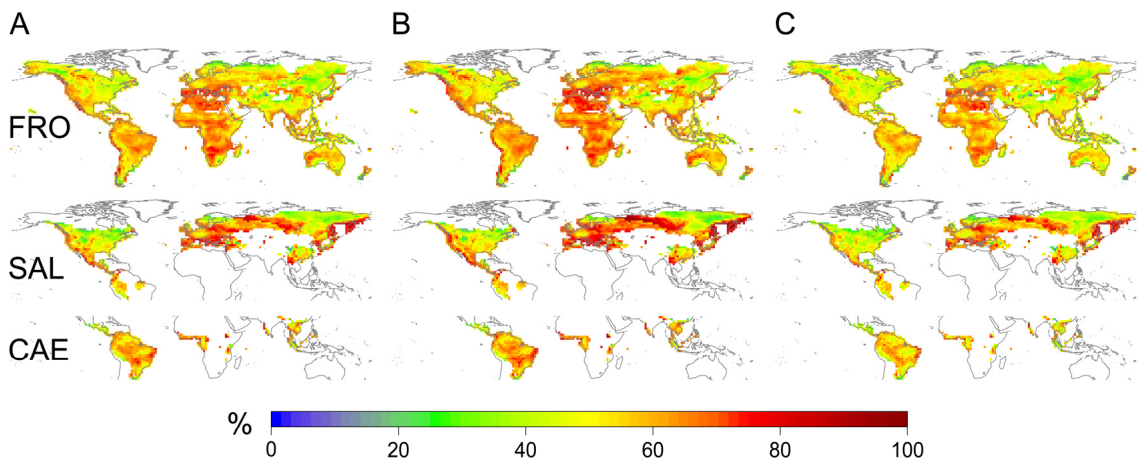
Figure S8 | Proportions of climate losers projected for 2080, based on different emission scenarios. Values are calculated as arithmetic means across 14 GCMs and 3 modeling algorithms, separately for different emission scenarios. **A**, A1B scenario; **B**, A2 scenario; **C**, B1 scenario; FRO, frogs; SAL, salamanders, CAE, caecilians.
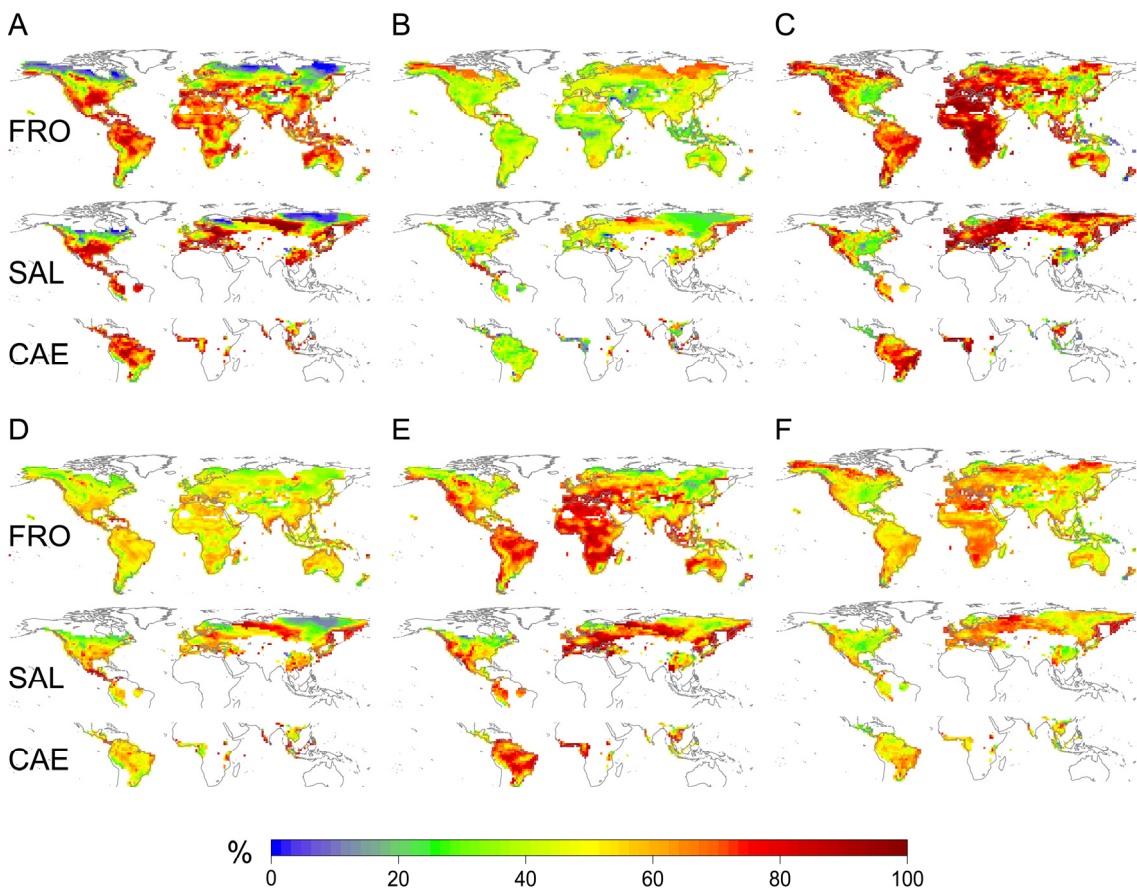
Figure S9 | Proportions of climate losers projected for 2080, based on different modeling algorithms. Values are calculated as arithmetic means across 14 GCMs and 3 emission scenarios, separately for each modeling algorithm (A-C), and for combinations of two modeling algorithms (D-F). **A**, ED; **B**, MD; **C**, MX; **D**, ED × MD; **E**, ED × MX, **F**, MD × MX; FRO, frogs; SAL, salamanders, CAE, caecilians; ED, Euclidean Distance; MD, Mahalanobis Distance; MX, MaxEnt.
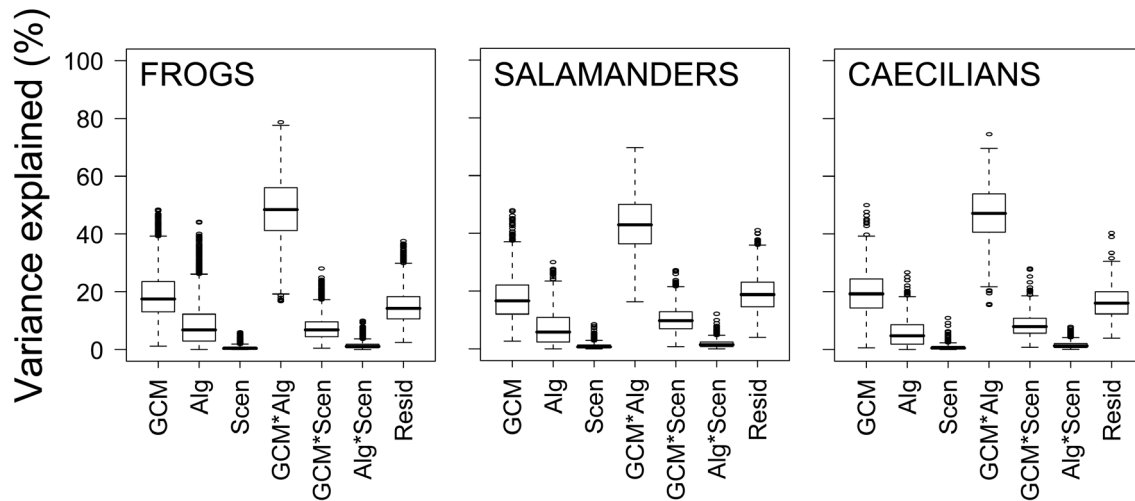
Figure S10 | Partitioning of uncertainty in ensemble modeling of the proportions of climate losers for 2080. Uncertainty is given as the proportion of variance in the proportion of "climate losers" per grid cell explained by different sources of uncertainty: GCM, algorithm (Alg), emission scenario (Scen), their interactions, and residual variance (Resid). Variance proportions (proportions of Sum of Squares) are obtained from 3-way ANOVAs (see Methods and Supplementary Text for further details).
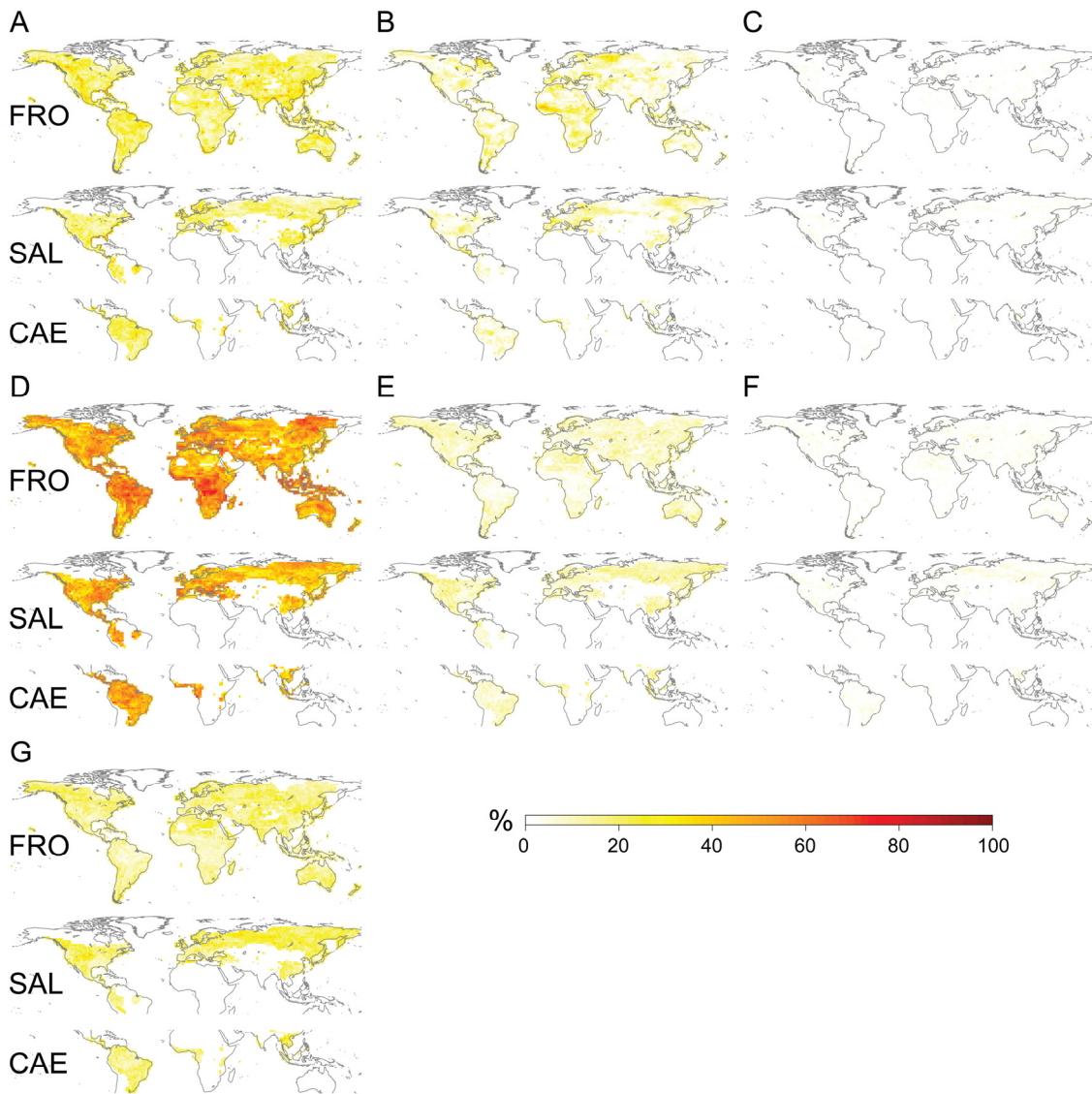
Figure S11 | Spatial variation of the uncertainty in the consensus projections of climate losers for 2080. Uncertainty is given as the proportion of variance in the proportion of "climate losers" per grid cell explained by different sources of uncertainty. **A**, GCM; **B**, algorithm; **C**, emission scenario; **D**, GCM × algorithm; **E**, GCM × scenario, **F**, Algorithm × scenario; **G**, residual variance. FRO, frogs; SAL, salamanders, CAE, Caecilians. Variance proportions (proportions of Sum of Squares) are obtained from 3-way ANOVAs (for further details, see Methods and Diniz-Filho *et al.* 2009).
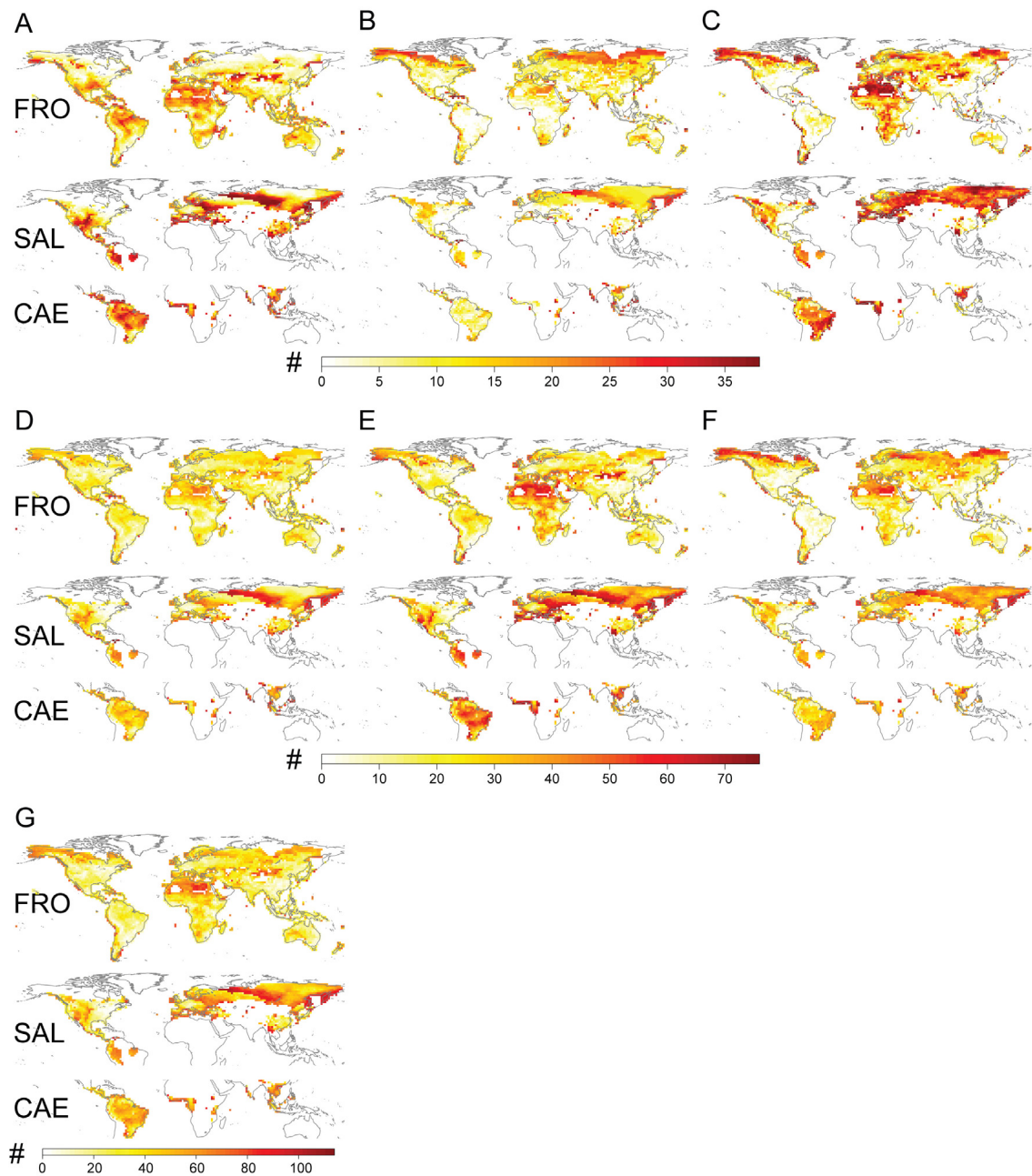
Figure S12 | Consistency of models projecting regions to be exposed to high climate change impact by 2080. Consistency is indicated as number of model combinations (algorithm × GCM × scenario) projecting a certain grid cell as being among the 25% cells with the highest proportion of climate losers. **A**, ED; **B**, MD; **C**, MX (n =38); **D**, ED + MD; **E**, ED + MX; **F**, MD + MX (n = 76); **G**, all model combinations (n = 114). Darker colours indicate higher consistency (larger number of models projecting this grid cell to be exposed under high impact). FRO, frogs; SAL, salamanders, CAE, caecilians; ED, Euclidean Distance, MD, Mahalanobis Distance, MX, MaxEnt.
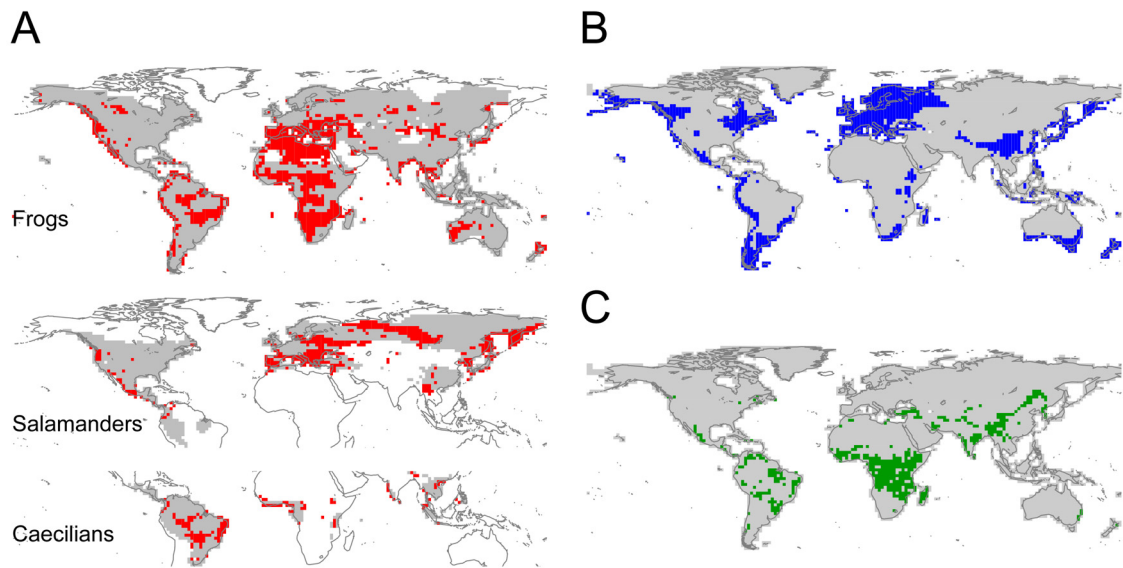
Figure S13 | Regions projected to be exposed to high impact of climate change, Bd, and land-use change by 2080. Regions projected to be exposed to high impact are defined as, **A**, the 25% grid cells with the highest projected proportion of "climate losers" (red), **B**, the 25% grid cells with the highest projected probability of *Bd* occurrence (blue), **C**, the grid cells with a projected land-cover conversion from a natural to an anthropogenic state of at least 25% (green). Overlap high richness with the respective threat is given in black. White areas in panel A indicate the absence of the amphibian order from the respective regions.
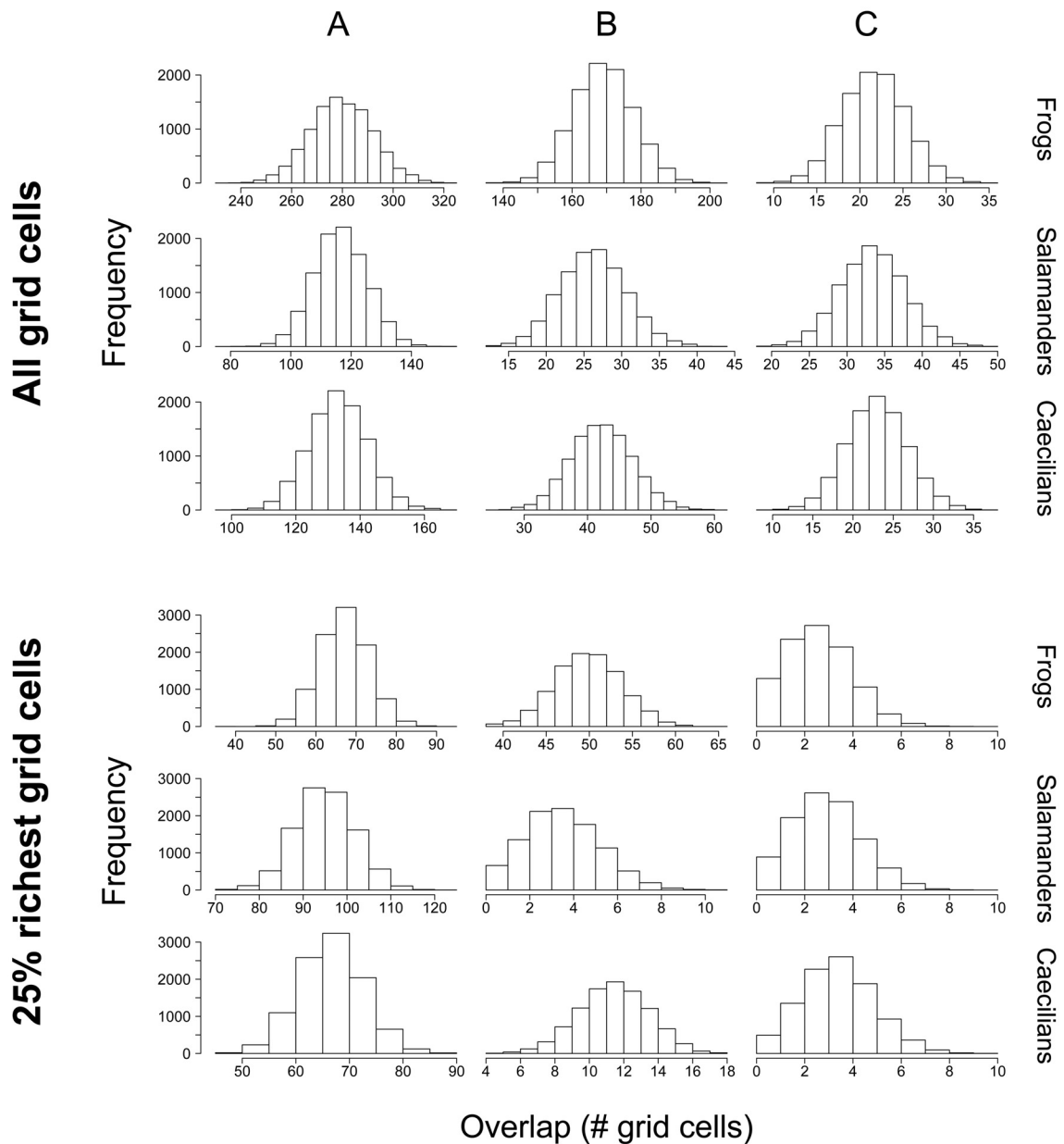
Figure S14 | Results of null models simulating random spatial overlap among different threats. For the null models, we randomly distributed the regions projected to be exposed to high impact (defined by 25%-thresholds, see Methods, Fig. 2, Fig. S13 and Fig. S15) across the available grid cells (which differ for frogs, salamanders and caecilians). Here, histograms of the values obtained from 10,000 simulations are shown (see also Table 1 and Fig. 2). **A**, climate change × *Bd*, **B**, climate change × land-use; **C**, *Bd* × land-use.
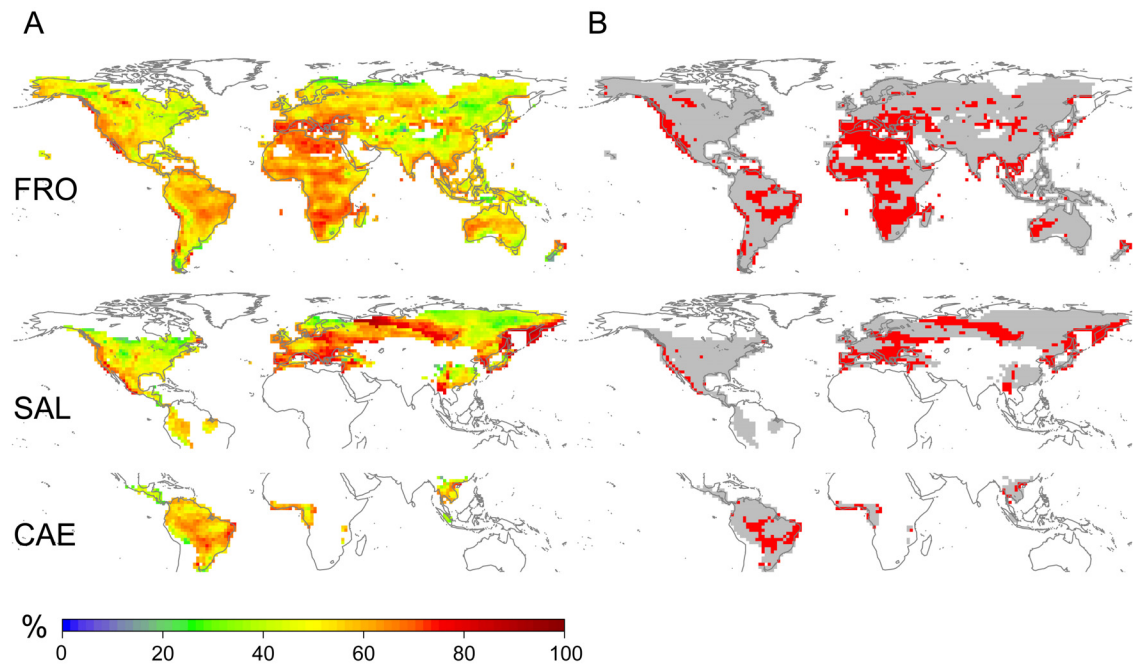
Figure S15 | Proportion of climate losers for species of the upper range-size quartile, projected for 2080. A, raw values calculated as arithmetic means across 14 GCMs, 3 emission scenarios, and 3 modeling algorithms, only including the species within the upper range-size quartile; **B**, 25% grid cells with the highest proportion of climate losers (red). The upper range size quartile is comprised of the 25% species with the largest range sizes (numbers of grid cells occupied by species in the upper range size quartile: frogs, 11; salamanders, 8; caecilians, 6). FRO, frogs; SAL, salamanders, CAE, caecilians.
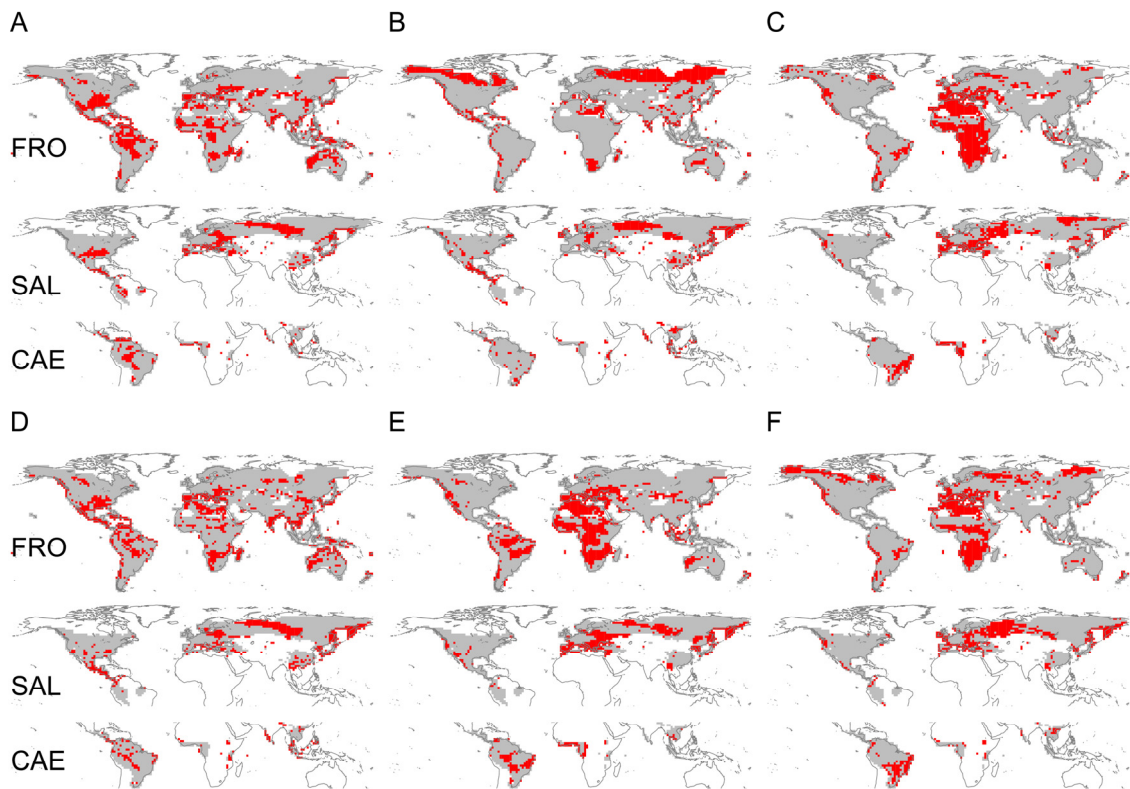
Figure S16 | Regions projected to be exposed to high climate change impact by 2080, based on different modeling algorithms. Regions of high climate change impact (red) are defined as the 25% grid cells with the highest proportions of climate losers, based on values calculated as arithmetic means across 14 GCMs and 3 emission scenarios, separately for each modeling algorithm (**A-C**), and for combinations of two modeling algorithms (**D-F**). **A**, ED; **B**, MD; **C**, MX; **D**, ED × MD; **E**, ED × MX, **F**, MD × MX; FRO, frogs; SAL, salamanders, CAE, caecilians; ED, Euclidean Distance; MD, Mahalanobis Distance; MX, MaxEnt (see Fig. S7 for raw values).
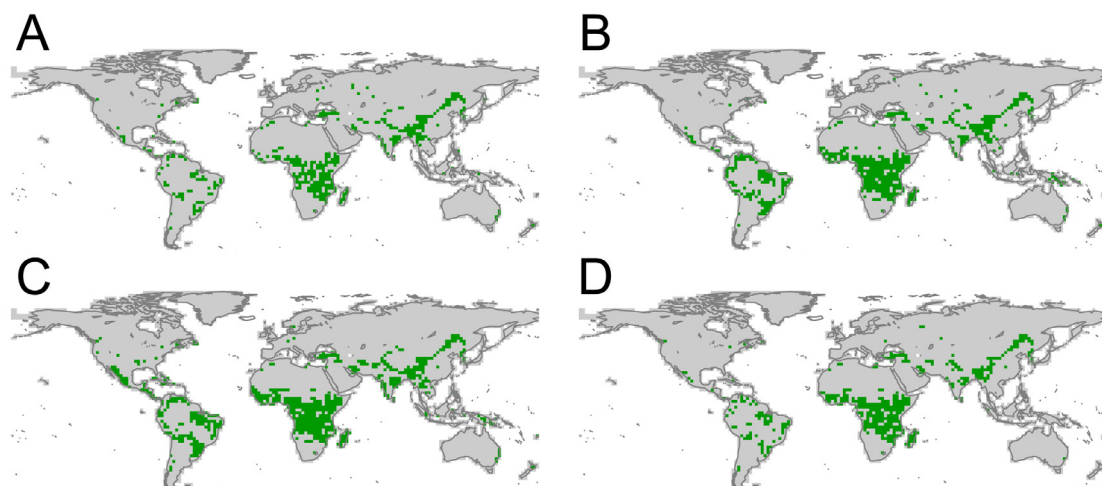

Figure S17 | Regions projected to be exposed to high land-use change impact by 2080. Regions exposed to high land-use change impact (green) are defined as the grid cells with a conversion from a natural to an anthropogenic land-cover state of at least 25% of the total grid cell area. Different panels show the values for each the four Millennium Ecosystem Assessment scenarios (Millennium Ecosystem Assessment 2005). **A**, Adapting Mosaic; **B**, Global Orchestration; **C**, Order from Strength; **D**, TechnoGarden (see Fig. 14 for raw values).

Chapter III

Phylogenetic signals in the climatic niches of the world's amphibians

Phylogenetic signals in the climatic niches of the world's amphibians

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Abstract

The question of whether closely related species share similar ecological requirements has attracted increasing attention, because of its importance for understanding global diversity gradients and the impacts of climate change on species distributions. In fact, the assumption that related species are also ecologically similar has often been made, although the prevalence of such a phylogenetic signal in ecological niches remains heavily debated. Here, we provide a global analysis of phylogenetic niche relatedness for the world's amphibians. In particular, we assess which proportion of the variance in the realised climatic niches is explained on higher taxonomic levels, and whether the climatic niches of species within a given taxonomic group are more similar than between taxonomic groups. We found evidence for phylogenetic signals in realised climatic niches although the strength of the signal varied among amphibian orders and across biogeographical regions. To our knowledge, this is the first study providing a comprehensive analysis of the phylogenetic signal in species climatic niches for an entire clade across the world. Even though our results do not provide a strong test of the niche conservatism hypothesis, they question the alternative hypothesis that niches evolve independently of phylogenetic influences.

Introduction

The question of whether related species are also ecologically similar is as old as modern biology (Darwin 1859). Recently, the question has gained increased interest (Wiens 2008; Losos 2008a; 2008b; Dormann *et al.* 2009; Vieites *et al.* 2009a), partly because of its implications for understanding global biodiversity gradients (Wiens & Donoghue 2004), and partly because it helps in comprehending how species might adapt to ongoing climate changes (e.g. Botkin *et al.* 2007). Understanding the extent to which there is a phylogenetic signal in ecological niches (the tendency for related species to resemble each other's ecological characteristics more than species randomly drawn from a phylogeny; Blomberg & Garland 2002; Losos 2008a) helps to formulate hypothesis about niche evolution. This is particularly true if one adopts the view that estimation of the signal strength in climatic niches may serve as a surrogate measure for the rate of climatic niche evolution (Garland 1992; Blomberg *et al.* 2003; Rheindt *et al.* 2004; but see Revell *et al.* 2008; Ackerly 2009). It needs to be added, though, that establishing such a phylogenetic signal does not demonstrate the existence of phylogenetic niche conservatism, which is the tendency of related species' niches to be even more similar than expected given their phylogeny (Losos 2008a). However, the existence of strong signals in climatic niches do challenge the alternative hypothesis that niches evolve quickly (e.g. Broennimann *et al.* 2007) and independently of phylogeny (e.g. Dormann *et al.* 2009).

Despite the relevance of the climatic niche concept to contemporary ecology (Araújo & Guisan 2006; Soberón 2007), quantitative analyses on the strength of the phylogenetic signal in climatic niche similarities are scarce (but see, e.g., Prinzing *et al.* 2001). As pointed out by Losos (2008a), most studies investigating phylogenetic signals in ecological niches only include few species at rather small geographic extents. Thus, the need for taxonomically and geographically comprehensive analyses on phylogenetic signals in climatic niches is timely. Here, we provide the first of such analyses and test for the existence and strength of phylogenetic signals in climatic niches for an entire class of organisms, the amphibians, on a global scale. Ideally, one would test hypotheses about niche evolution using measures of the fundamental niche (*sensu* Hutchinson 1957), since the fundamental niche is the product of the genetics, morphology and physiology of the species, thus being the "feature" which evolves. In a climatic context, the fundamental niche would be the range of combinations of climatic

variables in which the species could potentially exist (Austin *et al.* 1990; Soberón 2007). Unfortunately, estimates of the fundamental climatic niches for large numbers of species are difficult to obtain. Therefore we have to rely on surrogates estimated with the climate envelope of species, i.e. the combination of climatic variables (e.g. means and extremes of precipitation and temperature) that best describes a species' geographical range. This characterisation can, however, at best represent the realised climatic niche of a species, and will never entirely portray the fundamental climatic niche (see discussion in Araújo & Guisan 2006; Colwell & Rangel 2009; Soberón & Nakamura 2009).

Here, we first used a family-level phylogeny of the world's amphibians to test for the existence of phylogenetic signals in species climate niches. Then we tested for the existence of phylogenetic signals and measured their strength separately for the three orders of amphibians and for each one of seven biogeographical regions.

Material and methods

We used distributions for 5527 amphibian species from all three amphibian orders (Anura, Caudata, Gymnophiona, see Table S1 in the Supplementary Material for an overview of the numbers of species included in the dataset). Distribution data were compiled from the 'Global Amphibian Assessment' (IUCN *et al.* 2004). This dataset comprises distribution maps (extent of occurrence polygons) for each species based on documented records and expert knowledge. Although it is the most comprehensive global dataset available for amphibian distributions, many species are listed as "data deficient", due to a lack of knowledge on their real distributions. Climatic data (originally 19 bioclimatic variables at 10' resolution) were compiled from the WorldClim database (Hijmans *et al.* 2005). Distribution and climate data were resampled to a 2×2 degree latitude-longitude grid including 5017 terrestrial cells.

A taxonomic topology for genus, subfamily, family and higher taxonomic levels was compiled from the 'Amphibian Tree of Life' (Frost *et al.* 2006) and the online database 'Amphibian Species of the World' (ASW; Frost 2007). The taxonomic nomenclature of this database is based on a phylogenetic super tree considering the most recent studies of amphibian phylogeny and is thus building upon direct inferences of the evolutionary history of the species. Despite criticism on several aspects of the original 'Amphibian Tree of Life' phylogeny (see e.g. Wiens 2007), the ASW taxonomy is the most comprehensive taxonomic database for amphibians to date and is being used frequently

in conservation and evolutionary studies (e.g. Blackburn 2008; Corey & Waite 2008; Santos *et al.* 2009).

Quantifying climatic niches

Climatic niches were characterised using an ordination approach termed 'outlying mean index' (OMI; Dolédec *et al.* 2000). In contrast to other ordination techniques, OMI does not make assumptions about the shape of the species' response curves to the environment and gives equal weight to sites independent of their species richness. OMI gives the species average position ("niche position") within environmental space, which represents a measure of the distance between the environmental conditions used by the species and the mean environmental conditions of the study area. It also quantifies the variability of environmental conditions used by each species ("niche breadth"), given by the standard deviation along the respective OMI axes (for more details, see Dolédec *et al.* 2000; as well as Thuiller *et al.* 2004 for a case study using OMI). Here, environmental conditions were measured as a function of eight climatic variables: mean diurnal range of temperature, minimum temperature of the coldest month, annual range of temperature, mean temperature of the warmest quarter, annual precipitation, precipitation seasonality, precipitation of the driest quarter, and precipitation of the warmest quarter (for a detailed description of the derivation of these variables, see Hijmans *et al.* 2005). These variables include a range of climatic factors (temperature extremes, amount and seasonality of precipitation) which are known to impose constraints on the occurrence and survival of amphibians (Carey & Alexander 2003; Wells 2007), and are often used to model the geographical distributions of individual species (e.g. Araújo *et al.* 2006) and species richness (e.g. Araújo *et al.* 2008). In the OMI analysis, we used the first and second axes of the ordination since they explained 82% to 96% of the total inertia (Table S2). OMI analyses were performed using the ade4 package in R (Chessel *et al.* 2004; R Development Core Team 2008). A randomisation test was performed to examine if niche positions along climate gradients could have arisen by chance (Dolédec *et al.* 2000); one thousand permutations were obtained for testing niche positions of each species occurring in each one of the biogeographical regions (see below). From the OMI analysis, we also obtained measures of niche breadth along the first and second OMI axes (for more details, see Dolédec *et al.* 2000; Thuiller *et al.* 2004).

Species may share ecological traits because of their shared evolutionary history, but also because they occur in similar places (see Freckleton & Jetz 2009, and references therein). For practical reasons, to account for possible confounding effects arising from spatial autocorrelation in niche characteristics and to explore the potential geographic variation in phylogenetic signal strength, all analyses except the one for the family-level phylogeny (see below) were performed separately for each amphibian order and biogeographical realm. Biogeographical realms were classified following the divisions of Sclater (1858) and Wallace (1876), later renamed by Olson *et al.* (2001): Afrotropics, Australasia, Indo-Malay, Nearctic, Neotropics, Palaearctic, Antarctica, and Oceania (referred to here as "regions"; see Table S1 for an overview of the numbers of species for each species set). Because there are no amphibians in Antarctica and only a few across the scattered islands of Oceania, these regions were removed from the analyses. Madagascar harbours a rich amphibian fauna that is quite distinct from the Afrotropical fauna (Duellman 1999; Vieites *et al.* 2009b); therefore, we added Madagascar as a seventh region. Nevertheless, we are aware that the spatial extent of the regions is still too large to completely rule out any confounding spatial influence on niche similarity. However, the geographic and phylogenetic resolution of our data does not allow for more sophisticated approaches (as recently proposed by Freckleton & Jetz 2009).

Testing for phylogenetic signals in climatic niche similarity

To test for phylogenetic signals in climatic niche similarity, we used Blomberg's randomisation test and K statistic, variance component analyses (VCA), analysis of similarity (ANOSIM) and Wilcoxon rank sum tests. Blomberg's randomisation test for phylogenetic signal assesses whether a given phylogenetic tree (including topology and branch lengths) better fits a set of data assigned to the tree tips (climatic niche positions in our case) as compared with the fit obtained when the data have been randomly permuted across the tree tips (Blomberg *et al.* 2003). The K statistic indicates the strength of phylogenetic signal, as compared with an expectation based on the tree structure and assuming Brownian motion character evolution. K values equal to 1 indicate a phylogenetic signal resembling the Brownian motion evolution model, values of $K > 1$ or < 1 indicate a stronger or weaker signal than the one expected by the Brownian motion model of character evolution (Blomberg *et al.* 2003). Since no complete phylogeny is yet available for the world's amphibians, we used the global family-level phylogeny from Roelants *et al.* (2007). Climatic niches of families were

calculated as arithmetic means of niche positions (separately for each OMI axes) across all species belonging to the respective family. Blomberg's randomisation and *K* analyses were performed using the picante package within R, with 1000 randomisations to assess significance (Kembel *et al.* 2009).

With VCA we quantified how much of the niche variance on the species level (among-species variance) can be explained at different taxonomic levels (Venables & Ripley 1999; Prinzing *et al.* 2001). As taxonomic levels we used the genus, subfamily and family grouping as well as the higher taxonomic categories above the family level as given by Frost *et al.* (2006). A large proportion of the among-species variance in niche position explained at higher taxonomic levels would indicate a phylogenetic signal in climatic niche similarity. On the other hand, all the variance localised among the species would indicate the absence of a phylogenetic signal. We applied VCA with a restricted maximum likelihood approach, using the functions lme and varcomp in the ape package within R (Paradis *et al.* 2004). We also performed null models to assess if the results of the VCA could be produced by chance alone. The null models simulate the case of no phylogenetic signal – running VCA based on a randomised phylogeny. To generate the null models, we randomised the taxonomic assignments of the species and calculated the variance components as the mean of one thousand randomisations. Again, we ran this analysis separately for the three amphibian orders within each region.

With ANOSIM – a non-parametric test analogous to ANOVA – we tested if niche similarities within groups were larger than between groups (Clarke 1993). The procedure started with a calculation of within- and between-group niche dissimilarities, as follows. Euclidean distances between niche positions were calculated for pairwise combinations of all possible pairs of species. The Euclidian distances – reflecting niche dissimilarity between pairs of species – were then compared within and between taxonomic groups aggregated at the genus and family levels. When the mean within-group niche dissimilarity is smaller than between-group niche dissimilarity, this is interpreted as indicating the presence of a phylogenetic signal in climatic niche similarity; when the mean is larger, it means the phylogenetic signal is lost. Based on 999 permutations, we tested whether within- and between-group niche dissimilarities were more different than expected by chance. ANOSIM was run with the vegan package of R (Oksanen *et al.* 2009), again separately for each one of the biogeographical regions (see also Fig. S1 in the Supplementary Material for an illustration of the procedure, and Fig. S2 for examples of two species sets).

We also calculated the amount of niche overlap along the first and second OMI axis within and between groups (families and genera). To do so, according to the protocol of the ANOSIM analysis, we calculated the pairwise niche overlap for all possible species pairs, again separately for each order and biogeographical region. Species occurring in only one grid cell have by definition a niche breadth of zero and are therefore excluded from the overlap analyses. We then grouped the pairwise niche overlap values into a within-taxon and between-taxon group (the taxon being the family or genus). Fore each dataset (amphibian order per region), the within- and between-group separation was done (i) for the entire species pool and (ii) separately for each taxon (see also Table 2 for details). Wilcoxon rank sum tests (Hollander & Wolfe 1999) were used to test if within-group overlap was larger than between-group overlap, which would indicate a phylogenetic signal.

By applying different methods to test for phylogenetic signal we try to decrease the risk that the outcomes are biased by the uncertainties or problems of a certain method. Results indicating the same tendency for different methods (although not quantitatively comparable) would strengthen the general value of results and support stronger inference. To ensure that the results were not systematically biased by species with niche characterisations that could have arisen by chance, VCA and ANOSIM analyses were performed (1) including all species and (2) including only species with climatic niches significantly better characterised by OMI than expected by chance.

Results

In the global analyses on the family level, we found a phylogenetic signal in climatic niches for the first and second OMI axes ($P = 0.001$ and $P = 0.026$, respectively). Signal strength differed considerably among the two axes, the first axis showing a signal stronger than expected from a Brownian motion evolution model ($K = 1.45$), the second axis showing a signal lower than that ($K = 0.44$).

The analysis conducted with VCA showed that a high proportion of among-species variance in climatic niche position is explained at higher taxonomic levels (Fig. 1). Results were consistent independently of whether the whole set of species or the sub-set with significant OMI values was considered. In most cases, the analyses of the species for which climatic influences were significant showed an even stronger phylogenetic signal (Fig. S3); this indicates that there were no biases arising from potentially unreliable niche characterisations. Therefore, results for the full analyses are presented.
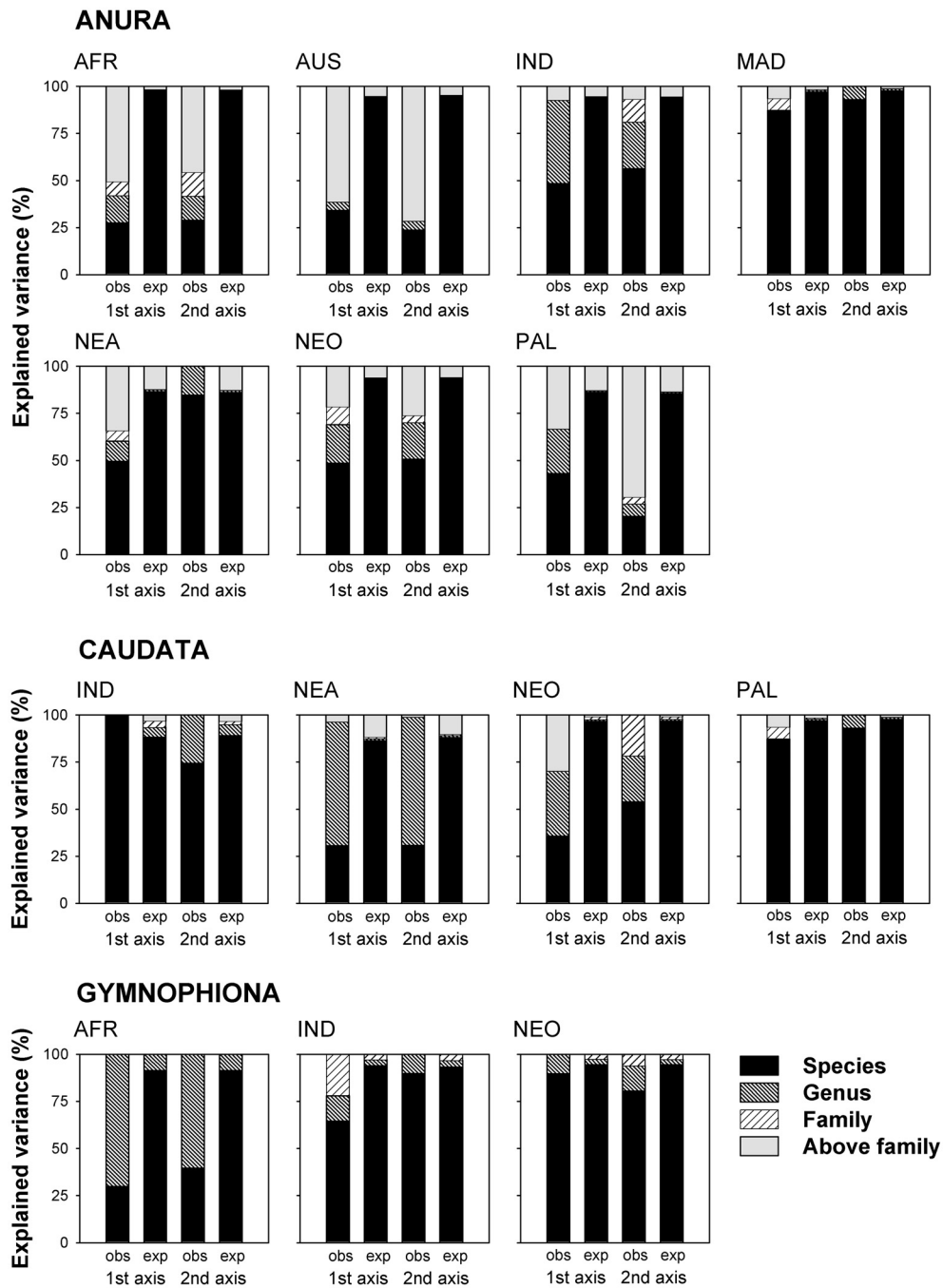
Figure 1 | Results of the variance component analyses (VCA). Variance components are calculated as the proportion of among-species variance in climatic niche positions that is explained at different taxonomic levels (species, genus, family, above-family; see key). The bars are organised from lower (species) to higher (above-family) taxonomic levels. A completely black bar indicates that all variance lies at the species-level, and none is explained at higher taxonomic levels. The analyses were performed separately for the three orders and each of the biogeographical regions (AFR, Afrotropics; AUS, Australasia; IND, Indo-Malay; MAD, Madagascar; NEA, Nearctic; NEO, Neotropics; PAL, Palaearctic). Within one species set (represented by a box), the first and third bars give the observed ("obs") values (for the first or second OMI axis, respectively), and the second and fourth bars give the values for the according null model ("exp"). Null models were conducted by randomising the phylogenetic assignment for the species pool, thus representing the null expectation of no phylogenetic signal in climatic niche similarity (see text for further details).

The observed proportions of explained variance at higher taxonomic levels were consistently larger than those yielded by the null models, which simulated the case of no phylogenetic signal (the only exception were Indo-Malayan Caudata). However, when comparing different regions and orders, we found considerable variation (Fig. 1): For Anura, variance explained above the species level ranged from 7% (Madagascar) up to 76% (Australasia), with most values exceeding the mean value of 49% (averaged across all regions and both OMI ordination axes). For Caudata, values ranged from 0% (Indo-Malay) to 87% (Palaearctic), and the mean was 50%. For Gymnophiona, extreme values for niche variance explained above the species level were 10% (Indo-Malay and Neotropics) and 70% (Afrotropics), with a mean of 34%.

Tests of niche differences with ANOSIM revealed that within-group niche distances were significantly smaller than between-group distances in the vast majority of cases (Table 1). This outcome matches the findings of the VCA, also indicating the presence of a phylogenetic signal in climatic niches at both the genus and the family levels for most regions and taxa. Again, running the analyses with all species or using only those species for which OMI performed significantly well rendered highly consistent results (Table S3). Despite the consistent trend of within-group niche distances being smaller than between-group distances, we found a small number of cases deviating from the overall pattern. At the family level, 3 out of 13 analyses showed larger within-group distances than between-group distances. At the genus level, within-group distances were larger than between-group distances only for two out of 14 data sets (see Table 2 for details).

Niche overlap analyses showed that in the majority of cases within-group overlap was larger than between-group overlap (Table 2). In the comparison of pooled within- and between groups, within-family overlap was significantly larger than between-family overlap in 8 out of 13 datasets along the first OMI axis and in 7 out of 13 datasets along the second OMI axis. On the genus level, within-group overlap was significantly larger than between-group overlap in 10 out of 14 datasets along the first OMI axis and in 9 out of 14 datasets along the second OMI axis. Comparing within- and between-group overlap separately for each family or genus per region, still the majority of datasets showed the overall pattern. As for the other analyses, the results varied considerably among regions, taxa, and the two OMI axes.

Table 1 | Climatic niche distances for amphibians on the family and genus levels within different biogeographical regions.

| | n | Mean niche distance* | | | | ANOSIM[†] | |
		Within	SD	Between	SD	r_{ANOSIM}	*P*
FAMILIES							
Anura							
AFR	16	2.04	1.18	2.37	1.35	**0.14**	**<0.001**
AUS	9	2.03	1.64	3.18	1.87	**0.35**	**<0.001**
IND	12	2.42	1.42	2.50	1.39	**0.034**	**<0.001**
MAD	3	1.65	0.94	1.83	1.03	**0.10**	**0.003**
NEA	8	2.31	1.41	2.35	1.35	0.022	0.143
NEO	19	2.08	1.41	2.37	1.54	**0.11**	**<0.001**
PAL	11	2.37	1.47	2.73	1.57	**0.14**	**<0.001**
Caudata							
IND	2	1.53	0.89	1.37	0.79	-0.10	0.785
NEA	7	2.46	1.73	2.40	1.56	-0.0045	0.522
NEO	3	2.13	1.48	2.87	1.77	**0.25**	**<0.001**
PAL	4	2.92	1.88	3.61	2.02	**0.21**	**<0.001**
Gymnophiona							
AFR	-	-	-	-	-	-	-
IND	2	2.58	1.55	2.56	1.51	-0.0040	0.44
NEO	2	2.14	1.26	2.24	1.50	0.0012	0.462
GENERA							
Anura							
AFR	50	1.96	1.12	2.35	1.34	**0.16**	**<0.001**
AUS	37	2.69	1.84	2.92	1.88	**0.074**	**0.002**
IND	67	2.04	1.43	2.50	1.39	**0.19**	**<0.001**
MAD	16	1.62	0.94	1.74	0.99	**0.069**	**0.02**
NEA	17	2.37	1.51	2.34	1.35	-0.0042	0.454
NEO	126	1.98	1.51	2.33	1.52	**0.16**	**<0.001**
PAL	41	2.08	1.50	2.69	1.56	**0.25**	**<0.001**
Caudata							
IND	6	1.43	0.78	1.47	0.87	0.0089	0.445
NEA	20	1.37	1.22	2.57	1.66	**0.44**	**<0.001**
NEO	9	1.69	1.31	2.38	1.57	**0.28**	**<0.001**
PAL	17	2.31	1.78	3.42	1.99	**0.35**	**<0.001**
Gymnophiona							
AFR	7	1.12	1.17	2.90	1.67	**0.62**	**<0.001**
IND	4	2.66	1.61	2.51	1.49	-0.052	0.725
NEO	10	2.12	1.32	2.17	1.31	0.029	0.321

*Mean distances were calculated by averaging all Euclidean distances in niche positions in climatic space between species pairs within a family or genus ("Within") or between species pairs that do not share the same family or genus ("Between"). Furthermore, we give the respective standard deviations ("SD") and the number of families or genera ("n") within each region used in the analysis. For further details on how the distance values were calculated, see Fig. S1.
[†]The ANOSIM statistic (r_{ANOSIM}) and the associated *P* values give estimations on the likelihood that the observed differences were significantly different from 0. (For more details, see text). Values are

given separately for the three amphibian orders and for each biogeographical region. ANOSIM values showing significantly larger niche distances for between-group than for within-group species pairs are indicated in bold. Note that the analyses could not be conducted on the family level for Afrotropical Gymnophiona, as all species occurring there belong to the same family.

AFR, Afrotropics; AUS, Australasia; IND, Indo-Malay; MAD, Madagascar; NEA, Nearctic; NEO, Neotropics; PAL, Palaearctic.

Discussion

Our analyses provide evidence in support of the idea that phylogenetically related species have similar realised climatic niches, even though the strength of the phylogenetic signal varied considerably across amphibian orders and biogeographical regions. To our knowledge, this is the first study investigating phylogenetic niche signals across an entire class of organisms on a global scale, nevertheless accounting for regional variation. Thus it provides a starting point to address questions related to evolutionary niche dynamics of amphibians.

Overall, we found a phylogenetic signal in amphibians' realised climatic niches, as was first shown at the family level by Blomberg's randomisation test and K statistic. However, the strength of the signal differed considerably for the two niche axes. Both the VCA and the niche overlap analyses, which were done separately for the different regions and orders, supported the existence of a phylogenetic niche signal among amphibians in the majority of the datasets. Applying a different methodology (ANOSIM) again supported the general finding of a phylogenetic signal. Admittedly, the values for the ANOSIM statistic (r_{ANOSIM}, see Table 1) are relatively low in many cases, even though the P values indicated statistical significance. These low values may often be attributable to the high species numbers in some regions (e.g. Neotropical or Indo-Malayan Anura), resulting in high significance levels even though the differences might be weak. However, the general tendency confirmed by four different methods and across the majority of the species sets analysed supports the conclusion that the trend is robust.

Only a few studies have measured phylogenetic niche signals of clades at large geographical scales. For European plants, Prinzing et al. (2001) found that 28–75% of among-species niche variance (niche positions along environmental gradients) was explained at higher taxonomic levels. This result is roughly concordant with our findings. For Central European spiders, 20–40% of the variance in niche position in shading and moisture was explained at higher taxonomic levels (Entling et al. 2007). However, the spiders' phylogenetic signal in ecological traits was consistently lower

than in morphological traits (>70% of morphological variance explained above the species level). For dietary niches of European birds, Brändle *et al.* (2002) found that about 70% of the variance was explained at higher taxonomic levels. Even though there are a limited number of studies to compare our results with, our findings are consistent with results previously reported for phylogenetic signals in climatic niches, and also with those in morphological traits or dietary niches.

Despite an overall and robust trend of detection of phylogenetic signals in climatic niches, we found considerable variation in the strength of the signal among biogeographical regions and the three amphibian orders. Further analyses are needed to examine such variation in detail. In the context of this study we can only discuss some of the limitations of the analysis and some of the most striking findings.

As mentioned before our analyses are based on characterizations of species realised climatic niches. Such niches are incomplete representations of species' true limits of tolerance to climate variables and so cannot entirely portray fundamental climatic niches (Soberón 2007). Obviously the possibility of existence of strong mismatches between the observed realised and the fundamental niches decrease the likelihood of detecting a phylogenetic (i.e. evolutionary) signal and it is impossible to rule out that such mismatches may have caused weak phylogenetic signal in some of our data sets. Nevertheless, given (i) this conceptual mismatch between realised and fundamental climatic niches, and (ii) that except for the global family-level analysis we use a taxonomy (albeit based on recent phylogenies) that introduced further uncertainties (see below), one could expect that any phylogenetic signal would be obscured. Given this potential for ambiguity, identifying a consistent pattern across most of the regions even with the data and methods used rather strengthens the conclusion that a phylogenetic signal exists in amphibian climatic niches.

However, the coarse spatial resolution of the data may on the other hand weaken the information content of the results. Many of the grid cells (which cover areas of almost 50,000 km^2 at the equator) contain strong climatic gradients and exceed the range of many species. Assigning closely related species within one grid cell to the same climatic niche although they actually have very different climatic preferences could inflate the phylogenetic signal. In fact, within areas of rather small extent, closely related species may show strong tendencies of niche divergence (e.g. Graham *et al.* 2004; Knouft *et al.* 2006; Kozak & Wiens 2007). However, an inflation of the phylogenetic signal should not occur if such species with different niches within the same grid cell belong to

different genera or families – assigning them to the same niche position would in this case rather weaken the phylogenetic signal in our analyses. In any case, we cannot fully discard the potential inflation of the phylogenetic signal's strength here, but we emphasize that with our analyses we do not and cannot unravel complex evolutionary mechanisms such as speciation (Kozak & Wiens 2006) or the phylogenetic structuring of local or regional communities (Webb *et al.* 2002), all of which require data at a much finer spatial and phylogenetic resolution.

Besides methodological factors, geographic, taxonomic and climatic idiosyncrasies contribute to the observed variation in the strength of the phylogenetic signal. For Anura, e.g., only Nearctic genera showed a result contradictory to the overall pattern of the ANOSIM analysis, the within-group similarity being slightly lower than the between-group similarity. This result was driven by the low niche similarity within the genus *Lithobates*, which is the largest genus in the Nearctic Anura (30 species). An examination of the different species reveals that some are widely distributed (e.g. *L. sylvatica*, *L. catesbeiana*), but others (e.g. *L. dunni*, *L. onca*, *L. sevosus*) have small ranges located in very different regions within the Nearctic and thus have very different climatic niches. This combination of high species richness and a high within-genus variety of climatic niches may have contributed to the low phylogenetic signal in the Nearctic Anuran genera. Furthermore, taxonomic misclassifications may also influence the failure of detection of a phylogenetic signal (Blomberg *et al.* 2003). This is a general issue for our analyses, of course, but may be particularly important for Nearctic Anura, as classification of *Lithobates* as a genus remains controversial (see, e.g., Hillis & Wilcox 2005; Frost *et al.* 2006; Che *et al.* 2007).

A rather weak phylogenetic signal was also detected at the family level of Nearctic Caudata as indicated by the VCA and the niche overlap analysis (Fig. 1, Table 2). Here, the family Plethodontidae comprises more than three times as many species as the other families combined (143 vs. 43 species). The highly diverse Plethodontid salamanders occupy a great variety of niches (Vieites *et al.* 2007), whereas the niches of species within each Plethodontid genus are very similar (e.g. for *Hydromantes*, *Desmognathus*, or *Batrachoseps*). Indo-Malayan Caudata showed no clear pattern, possibly because of the low species richness of Caudata in this region (25 species) and because for many species the distributions used represent only a small part of their entire distribution. Thus, this species set is rather negligible. However, we stress that in the vast majority of cases, the total ranges of species are contained within one biogeographical region.

Table 2 | Climatic niche overlap analyses for amphibians on the family and genus levels, along the first and second OMI axes (OMI1 and OMI2), within different biogeographical regions.

		OMI1			OMI2		
	n*	Pooled[†]	$n_{W > B}$[‡]	$n_{W < B}$[‡]	Pooled	$n_{W > B}$	$n_{W < B}$
FAMILIES							
Anura							
AFR	15 (2)	**W > B*****	10 (0)	0 (5)	**W > B*****	6 (4)	1 (4)
AUS	9 (0)	**W > B*****	7 (1)	0 (1)	**W > B*****	6 (2)	0 (1)
IND	12 (1)	**W > B*****	7 (1)	2 (2)	**W > B*****	7 (1)	1 (3)
MAD	3 (2)	W < B (n.s.)	0 (0)	0 (3)	**W > B*****	1 (1)	1 (0)
NEA	8 (3)	**W > B****	1 (2)	0 (5)	W > B (n.s.)	0 (3)	0 (5)
NEO	19 (1)	**W > B*****	8 (3)	3 (5)	W > B (n.s.)	9 (1)	3 (6)
PAL	11 (3)	W > B (n.s.)	3 (4)	1 (3)	**W > B****	4 (2)	3 (2)
Caudata							
IND	2 (1)	**W > B***	1 (1)	0 (0)	W > B (n.s.)	0 (1)	0 (1)
NEA	7 (1)	W < B***	2 (3)	1 (1)	W < B***	3 (2)	1 (1)
NEO	2 (1)	**W > B*****	2 (0)	0 (0)	W < B (n.s.)	0 (1)	0 (1)
PAL	4 (1)	**W > B***	1 (1)	0 (2)	**W > B*****	2 (0)	0 (2)
Gymnophiona							
IND	1 (1)	W < B (n.s.)	0 (0)	0 (1)	W < B (n.s.)	0 (0)	0 (1)
NEO	2 (0)	W > B (n.s.)	0 (1)	0 (1)	**W > B*****	1 (0)	0 (1)
GENERA							
Anura							
AFR	47 (34)	**W > B*****	16 (18)	0 (13)	**W > B*****	12 (10)	2 (23)
AUS	34 (17)	**W > B*****	17 (7)	1 (9)	**W > B*****	9 (11)	1 (13)
IND	60 (32)	**W > B*****	22 (21)	0 (17)	**W > B*****	25 (17)	4 (14)
MAD	16 (8)	W > B (n.s.)	3 (2)	2 (9)	**W > B*****	3 (3)	1 (9)
NEA	15 (15)	**W > B***	2 (6)	0 (7)	W > B (n.s.)	4 (2)	0 (9)
NEO	112 (52)	**W > B*****	39 (27)	4 (42)	**W > B*****	32 (34)	5 (41)
PAL	38 (18)	**W > B*****	5 (19)	0 (14)	**W > B*****	8 (13)	1 (16)
Caudata							
IND	5 (2)	W > B (n.s.)	0 (3)	0 (2)	W > B (n.s.)	0 (3)	0 (2)
NEA	18 (7)	**W > B*****	4 (6)	1 (7)	W < B*	6 (3)	1 (8)
NEO	7 (6)	**W > B*****	5 (0)	0 (2)	**W > B***	0 (4)	0 (3)
PAL	16 (13)	**W > B*****	4 (2)	0 (10)	**W > B*****	4 (1)	0 (11)
Gymnophiona							
AFR	4 (7)	W > B (n.s.)	0 (2)	0 (2)	W < B (n.s.)	0 (0)	0 (4)
IND	2 (3)	W < B (n.s.)	1 (0)	0 (1)	W > B (n.s.)	1 (1)	0 (0)
NEO	9 (7)	**W > B*****	1 (1)	0 (7)	**W > B*****	2 (2)	0 (5)

*Number of groups (families or genera, respectively) included in the overlap analyses. Values in brackets give the number of groups for which tests could not be performed (e.g. groups that included a single species only or that only consisted of species occurring in a single grid cell)

[†]For the pooled comparisons, all within- (W) and all between-group (B) values of niche overlap (families or genera, respectively) were pooled and then compared using Wilcoxon rank sum tests. "W > B" indicates that within-group overlap was larger than between-group overlap (which would indicate a phylogenetic signal). Asterisks indicate significance levels, ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$, n.s., not significant.

‡Numbers of groups (families or genera) showing within-group niche overlap being larger or smaller than between-group overlap (numbers in brackets indicate the number of within- or between-group comparisons that were not significant).
AFR, Afrotropics; AUS, Australasia; IND, Indo-Malay; MAD, Madagascar; NEA, Nearctic; NEO, Neotropics; PAL, Palaearctic.

Some authors question whether establishing the existence of a phylogenetic signal is a useful pursuit (Wiens & Graham 2005; Wiens 2008). In parallel, calls for "further research into the extent and occurrence of PNC [phylogenetic niche conservatism], and phylogenetic signal more generally" (Losos 2008a, p. 1001) are also common. Testing for the existence of a phylogenetic signal is important as the assumption underlies several types of studies, such as the investigation of diversity gradients and the building of species distribution models for climate change prediction, and because its generality is still under debate.

Although the aim of our study was to test for a phylogenetic signal in climatic niches, our analyses provide a baseline for further investigations on climatic niche conservatism in amphibians. Phylogenetic niche conservatism can be defined as the tendency of closely related species to be more similar than expected based on phylogenetic relationships (Losos 2008a); put more broadly, it is the temporal constancy of the ecological niche (Pearman *et al.* 2008; Nogués-Bravo 2009). Niche conservatism is a topic of recent growing interest (Peterson *et al.* 1999; Prinzing *et al.* 2001; Wiens 2004; Wiens & Graham 2005; Kozak & Wiens 2006; Dormann *et al.* 2009; Freckleton & Jetz 2009; Vieites *et al.* 2009a). Overall, its generality or even existence remains a matter of controversial debate (Pearman *et al.* 2008; see, e.g., Losos 2008a). Based on our findings, we can draw two conclusions with regards to phylogenetic niche conservatism and temporal niche constancy in amphibians. First, as recently pointed out by Losos (2008a, p. 997), a "lack of phylogenetic signal is sufficient to indicate that PNC does not occur." Thus, based on our detection of a phylogenetic signal in climatic niches, the niche conservatism hypothesis cannot be rejected. Second, for several regions, we found high values of among-species niche variance explained above the family level (Afrotropical and Palaearctic Anura: >30%, Australasian Anura: >60%). This result lends support to the suggestion of the existence of considerable constancy in climatic niches for a period of time that reaches back to the late Cretaceous or even earlier (>65 Mya ago), when many of the above-family splits took place (Roelants *et al.* 2007). However, further studies are needed using finely resolved phylogenetic and

climatic data to test for the occurrence and strength of phylogenetic conservatism in amphibian climatic niches.

Acknowledgements

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Supplementary Material

Supplementary Tables

Table S1 | Numbers of species included in the analyses for the three amphibian orders within the seven biogeographical regions and for the world.

	Anura	Caudata	Gymnophiona
AFR	672		26
AUS	526		
IND	813	26	42
MAD	219		
NEA	145	186	
NEO	2428	224	76
PAL	331	97	
World	4875	508	144

Note that for Anura and Caudata, the values for the world slightly differ from the bare sum of the species occurring in the different regions because a few species occur in two of the regions for these orders. Empty fields indicate the absence of the entire order from the respective region. AFR, Afrotropics; AUS, Australasia; IND, Indo-Malay; MAD, Madagascar; NEA, Nearctic; NEO, Neotropics; PAL, Palaearctic.

Table S2 | Cumulative explained inertia of the first and second OMI ordination axes, given as proportions of the total inertia, separately for the three amphibian orders and biogeographical regions.

Region	Axis	Anura	Caudata	Gymnophiona
AFR	1	0.70		0.91
	2	0.89		0.95
AUS	1	0.74		
	2	0.94		
IND	1	0.67	0.77	0.54
	2	0.89	0.92	0.82
MAD	1	0.76		
	2	0.96		
NEA	1	0.74	0.84	
	2	0.94	0.95	
NEO	1	0.69	0.71	0.78
	2	0.83	0.90	0.91
PAL	1	0.60	0.69	
	2	0.83	0.88	

Note that missing values reflect an absence of the entire order in the region.
AFR, Afrotropics; AUS, Australasia; IND, Indo-Malay; MAD, Madagascar; NEA, Nearctic; NEO, Neotropics; PAL, Palaearctic.

Table S3 | Climatic niche distances for amphibians on the family and genus levels, considering only those species for which climatic influence was significant.[*]

	Mean niche distance				ANOSIM	
	Within	**SD**	**Between**	**SD**	r_{ANOSIM}	***P***
FAMILIES						
Anura						
AFR	2.05	1.30	2.52	1.48	0.18	**<0.001**
AUS	2.01	1.83	3.23	2.10	0.34	**<0.001**
IND	2.62	1.66	2.77	1.68	0.053	**<0.001**
MAD	1.08	0.82	1.40	1.11	0.13	0.062
NEA	2.42	1.43	2.43	1.41	0.003	0.41
NEO	2.31	1.55	3.04	1.93	0.23	**<0.001**
PAL	2.41	1.50	2.77	1.61	0.13	**<0.001**
Caudata						
IND	1.22	0.92	1.12	0.98	-0.03	0.541
NEA	2.41	1.89	2.40	1.62	0.032	0.205
NEO	1.86	1.68	4.99	1.67	0.77	**0.012**
PAL	2.80	1.77	3.65	1.97	0.26	**<0.001**
Gymnophiona						
AFR	-	-	-	-	-	-
IND	-	-	-	-	-	-
NEO	2.14	1.26	2.24	1.50	0.30	0.368
GENERA						
Anura						
AFR	2.00	1.20	2.48	1.47	0.18	**<0.001**
AUS	2.78	2.02	2.98	2.12	0.057	**0.043**
IND	2.14	1.62	2.77	1.67	0.22	**<0.001**
MAD	1.02	0.78	1.23	0.98	0.096	0.098
NEA	2.44	1.47	2.42	1.41	-0.0035	0.522
NEO	2.09	1.53	2.97	1.90	0.29	**<0.001**
PAL	2.18	1.54	2.73	1.60	0.21	**<0.001**
Caudata						
IND	1.11	0.87	1.20	0.95	0.15	0.27
NEA	1.44	1.29	2.53	1.78	0.36	**<0.001**
NEO	1.73	1.49	2.63	2.18	0.19	**0.039**
PAL	2.19	1.52	3.40	1.93	0.38	**<0.001**
Gymnophiona						
AFR	0.69	1.82	2.40	1.46	0.55	**0.047**
IND	-	-	-	-	-	-
NEO	1.85	1.18	2.34	1.44	0.20	**0.032**

[*]Note that the analyses could not be conducted at the family level for Afrotropical and Indo-Malayan Gymnophiona because all species occurring there belong to the same family. Accordingly, the analyses could not be conducted for Indo-Malayan genera of Gymnophiona. For details, see text and Table 2.
AFR, Afrotropics; AUS, Australasia; IND, Indo-Malay; MAD, Madagascar; NEA, Nearctic; NEO, Neotropics; PAL, Palaearctic.

Supplementary Figures
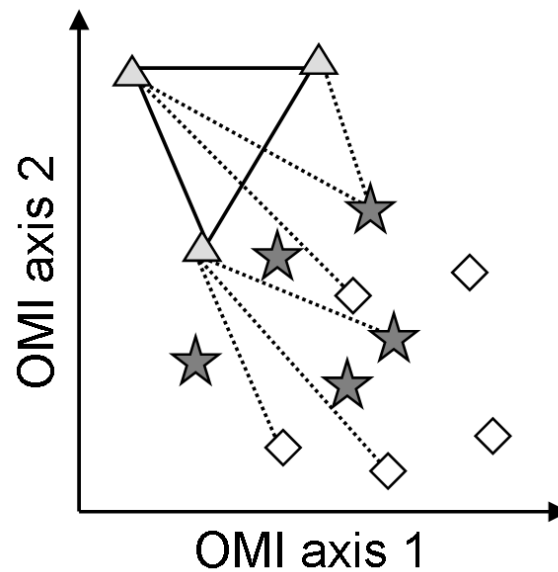
Figure S1 | Illustration of the calculation of within- and between-group niche distances. We show the hypothetical example of three groups (e.g. three different genera, indicated by the different symbols – triangles, stars, and diamonds). Each point represents the niche position of one species within a two-dimensional climatic space (given by the first and second OMI axis). Lines represent the Euclidean distances between niche positions (= niche distances) among species. Straight lines indicate niche distances between species belonging to the same group. All distances between species within this group are averaged, with the result giving the mean within-distance for this group. Dotted lines indicate niche distances among the species of one group and the species of all the other groups (note that only a small selection of all possible dotted lines is shown). The average of all these values gives the mean between-distance for this group. This procedure is repeated for every group. Finally, the mean within-group distance for the whole species set is calculated by averaging all the mean within-group distances from all the groups. Accordingly, the mean between-group distance for the whole dataset is calculated. These mean values for within- and between-group niche distances are given in Table 2. The ANOSIM statistic tests if the differences between within-group and between-group distances are significantly different from zero, using a rank-similarity algorithm, based on a given number of permutations (see text for further details).
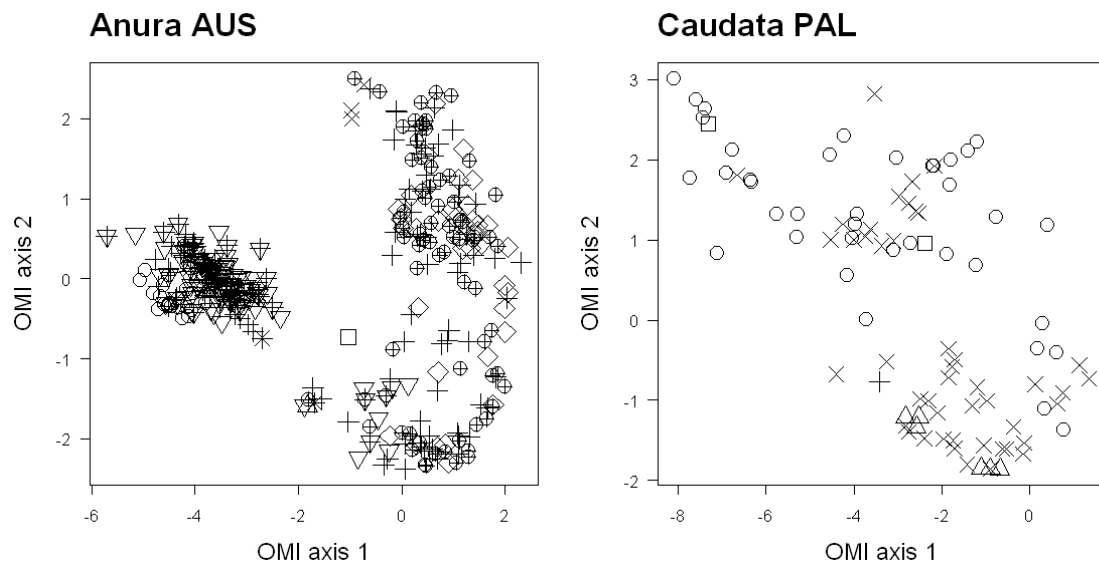
Figure S2 | Examples for OMI plots according to the setup of Fig. S1. Each point represents the niche position of one species within a two-dimensional climatic space (given by the first and second OMI axis). Different symbols indicate different families. AUS, Australasia; PAL, Palaearctic.

ANURA

CAUDATA

GYMNOPHIONA

Species
Genus
Family
Above family
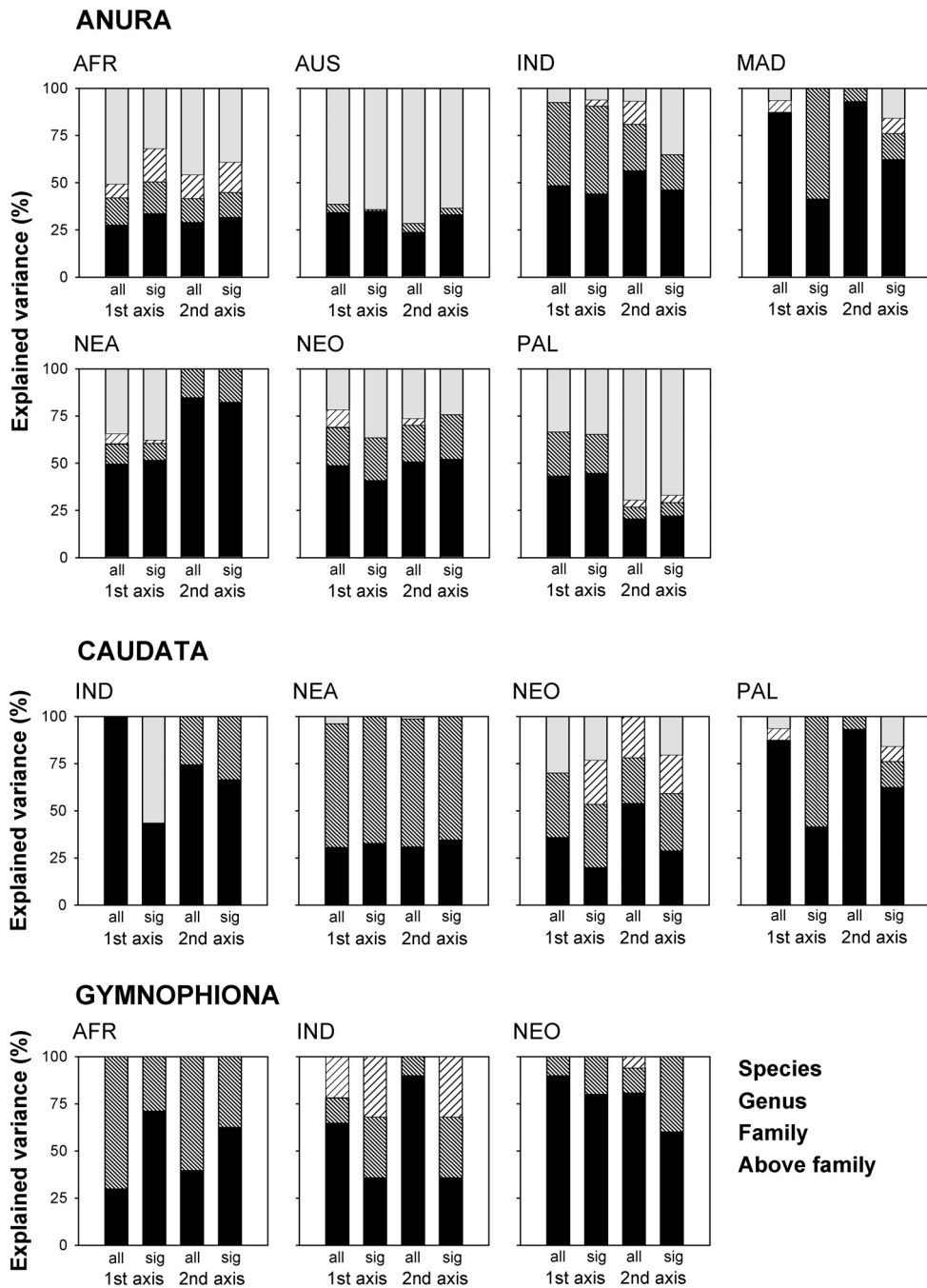
Figure S3 | Comparison of the variance component analyses (VCA) for all species (indicated by "all") and for those species for which climatic influence was significant (indicated by "sig"). For further details, see text and Fig. 1. AFR, Afrotropics; AUS, Australasia; IND, Indo-Malay; MAD, Madagascar; NEA, Nearctic; NEO, Neotropics; PAL, Palaearctic.

# Habitat availability cannot explain the species richness patterns of European lentic and lotic freshwater animals

Habitat availability cannot explain the species richness patterns of European lentic and lotic freshwater animals

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Abstract

Aim. In Europe the relationships between species richness and latitude differ between lentic (standing water) and lotic (running water) species. Freshwater animals are highly dependent on suitable habitat, and thus, the distribution of available habitat should strongly influence large-scale patterns of species richness. We tested whether habitat availability can account for the differences in species richness patterns between European lentic and lotic freshwater animals.

Location. Europe

Methods. We compiled occurrence data of 1959 lentic and 2445 lotic species as well as data on the amount of lentic and lotic habitats across 25 pre-defined biogeographical regions of European freshwaters. We used the range of altitude of every region as a proxy for habitat diversity. We investigated the relationship between species richness and habitat availability and diversity with univariate and multiple regression analyses.

Results. Species richness increased with habitat availability in lentic species, but not in lotic species. Species richness increased with altitudinal range in lotic species, but decreased in lentic species. In both groups habitat availability and diversity could not account for previously reported latitudinal patterns in species richness. In lotic species, richness declined with latitude whereas there was no relationship between habitat

availability and latitude. In lentic species, richness showed a hump-shaped relationship with latitude whereas there was an increase of available habitat with latitude.

Main conclusions. Habitat availability and diversity are poor predictors of species richness of the European freshwater fauna across large scales. Our results indicate that the distributions of European freshwater animals are probably not in equilibrium and may still be influenced by history, namely the recurrent glaciations of Europe and possible differences in post-glacial re-colonization. The distributions of lentic species appear to be closer to equilibrium than those of lotic species. This lends further support to the hypothesis that lentic species have a higher propensity of dispersal than lotic species.

Introduction

Habitat is the template for the evolution of species traits, e.g. the propensity for dispersal (Southwood 1962; 1977). Lentic habitats are generally more ephemeral than lotic habitats (Dobson & Frid 1998) and because there is a negative relationship between the persistence of a habitat and the propensity for dispersal of its inhabitants (Southwood 1962; Wiener & Tuljapurkar 1994; Dingle & Drake 2007), lentic species should have evolved a higher propensity for dispersal than lotic species. Therefore, several recent studies suggested that in freshwater animals, lentic (standing water) species are stronger dispersers than lotic (running water) species (e.g. Ribera & Vogler 2000; Ribera *et al*. 2001; 2003; Marten *et al*. 2006; Hof *et al*. 2006; see Ribera 2008 for an overview).

Analysing distribution data of the European freshwater fauna published by Illies (1966a; 1978), Hof *et al*. (2008) showed that there are strong differences in the patterns of species richness between lentic and lotic species: Lentic species show a hump-shaped relationship with latitude with a peak in central Europe, whereas richness of lotic species decreases with increasing latitude. The authors attributed these patterns to differences in postglacial re-colonization of both groups as a result of the different dispersal abilities of lentic and lotic species (Hof *et al*. 2008). By definition, freshwater animals are confined to aquatic habitats and so their distribution is totally dependent on the distribution of suitable habitat. In terrestrial animals there is commonly a positive relationship between species richness and area (Rosenzweig 1995) or suitable habitat, respectively (MacArthur 1964; Storch *et al*. 2003). The same holds true for freshwater

organisms (Hugueny 1989; Rosenzweig & Sandlin 1997; Allen *et al.* 1999). The distribution of freshwater habitats should therefore be a strong predictor of freshwater species richness in Europe and the observed differences in the relationship of species richness with latitude between lentic and lotic species may simply reflect differences in the distribution of lentic and lotic habitats across Europe. In their analysis, Hof *et al.* (2008) tested for a relationship between the size of the biogeographical regions and species richness. However, it is doubtful that area *per se* is a good proxy for suitable habitat. In the present study, we analysed the spatial distribution and amount of lentic and lotic water bodies across Europe in relation to the observed patterns of species richness of lentic and lotic freshwater animals.

Illies (1961) divided watercourses into different segments (e.g. krenal, rhithral, potamal) that usually occur in a similar order downstream, from relatively high altitudes (springs, brooks) to relatively low altitudes (river mouths). The different segments have different physical (e.g. water current) and chemical (e.g. oxygen, nutrients) properties and species compositions, and there is a high species turnover between different river segments (Illies 1961; Dobson & Frid 1998). Lentic water bodies also have different characteristics at different altitudes. In Europe, lakes at low altitudes usually have lower alkalinity, lower pH, and lower concentrations of nitrogen and phosphorus, whereas lakes at higher elevations are deeper and have lower concentrations of organic matter and nutrients (Nõges 2009). Consequently, regions with a large altitudinal range should contain more different types of freshwater habitats. In our analysis, we thus included the altitudinal range of a region as a simple proxy for habitat diversity.

To summarize, we want to address the following questions: (1) Are there differences in the distribution and quantity of lentic and lotic habitats across Europe? (2) Is there a relationship between the availability of habitat and species richness in European freshwater animals? (3) Does species richness increase with the altitudinal range as a proxy for habitat diversity within a region? (4) Do differences in habitat availability and habitat diversity account for the different species richness patterns of lentic and lotic freshwater animals?

Material and methods

Data on the distribution and habitat use of all European freshwater species were compiled from Illies (1978). Together with leading experts in the field of freshwater zoology, Illies (1966a; 1978) defined 25 zoogeographic regions of European freshwater

and recognised 42 types of habitat. The majority of these habitat types are very specialised. There are, e.g., more than 20 types of parasitism and many specific cases of habitat use such as in Tardigrada and Culicidae (five habitat types). The categories lentic and lotic consist of seven (lakes, ephemeral small water bodies, phytotelmata, inland saline waters, bogs, thermal waters, swamps) and three (springs, brooks and rivulets, rivers and streams) of the 42 habitat types. For all European freshwater species, the book provides data on their presence/absence in each of the regions and their habitat use. For further information on the compilation of the dataset and on habitat categories see Hof *et al.* (2008). For the present analysis, we used only species occurring exclusively in these seven (lentic) and three (lotic) habitats (number of species per region in Table S1 in the Supplementary Material). The habitat data correspond to the species used in the data set.

Data on standing and running waters were compiled from the Global Lakes and Wetland Database (GLWD; Lehner & Döll 2004) and from the Digital Chart of the World Server (Environmental Systems Research Institute 1993, http://www.maproom.psu.edu/dcw). Our data set included all European lentic waters with a surface area greater than 0.1 km² and lotic waters of a Strahler stream order of two and higher (Strahler 1952). We defined lotic habitat availability as the sum of the length of all parts of a river within a region (henceforth called river length) and lentic habitat availability as the sum of the perimeter of all standing waters (henceforth called lake perimeter). Lake perimeter is a more suitable proxy of lentic habitat availability than lake area (Bohle 1995; see also discussion in Ribera *et al.* 2003).

Altitudinal data were compiled from the GTOPO30 data set (EROS 1996). It includes a digital elevation model with a grid spacing of 30 arc seconds. For our analysis, we determined the altitudinal range of every region as the difference between maximum and minimum elevation. We used GLOBAL MAPPER 7.04 (Global Mapper Software LLC, Parker, CO, USA, 2006) and ArcGIS 9.2 (Environmental Systems Research Institute, Redlands, CA, USA, 2006) for all GIS analyses.

Since our habitat dataset does not include very small, temporary lentic water bodies, we excluded from the analysis all lentic species that occur exclusively in such habitats (based on Illies' classification). We also excluded those lotic species that occur exclusively in springs. The final data set included 1959 lentic and 2445 lotic species (taxonomic overview in Table S2). Although this classification of species differs slightly from that in Hof *et al.* (2008), it had no relevance on the general outcomes of

the analyses: lentic (R^2=0.33, P=0.012) and lotic (r^2=0.33, P=0.003) species richness of the reduced dataset showed virtually the same relationship with latitude as the one including all lentic (R^2=0.32, P=0.015) and lotic (r^2=0.32, P=0.003) species. The relationships between lentic and lotic species richness and latitude were consistent among taxonomic groups (Fig. S1 and S2).

Lake perimeter, river length, and altitudinal range were $\log_{10}$-transformed in order to approximate normality. We fitted multiple general linear models (type I sum of squares) to evaluate the effect of habitat availability and habitat diversity on species richness. After inclusion of habitat availability and diversity, we subsequently added latitude and its squared term into the model in order to test whether the spatial structure remained in the data (cf. Legendre & Legendre 1998) after accounting for habitat availability. A significant and negative regression coefficient of the squared latitude after accounting for habitat availability would indicate that a hump-shaped relationship remained between lentic species richness and latitude. All final models showed no spatial autocorrelation of residuals and it was therefore not necessary to include space in our tests. We used R version 2.7 (R Development Core Team 2008) for all statistical analyses.

Results

With respect to the questions posed in the introduction the results were as follows:

(1) Habitat availability of lentic habitats increased with increasing latitude (r^2=0.44, P<0.001), whereas there was no relationship between lotic habitat availability and latitude (r^2=0.06, P=0.25; Fig. 1, Fig. 2). Habitat availability was significantly and positively correlated with the size of the bioregions. The relationship was stronger for lotic (r^2=0.98, P<0.001) than for lentic habitats (r^2=0.56, P<0.001).

(2) Species richness tended to increase with habitat availability in lentic species (r^2=0.14, P=0.06), but not in lotic species (r^2=0.01, P=0.65, Fig. 2). Total species richness of freshwater animals was not correlated with the size of a bioregion (r^2=0.09, P=0.14). Tested separately, lentic species richness increased with the size of a bioregion (r^2=0.19, P=0.03), whereas there was no correlation in lotic species (r^2=0.01, P=0.60).

(3) Species richness increased with the altitudinal range of a region in lotic species (r^2=0.19, P=0.03), but tended to decrease in lentic species (r^2=0.15, P=0.06). Habitat availability and diversity together accounted for 20.3 and 19.5 per cent of the variance in lentic and lotic species richness, respectively.
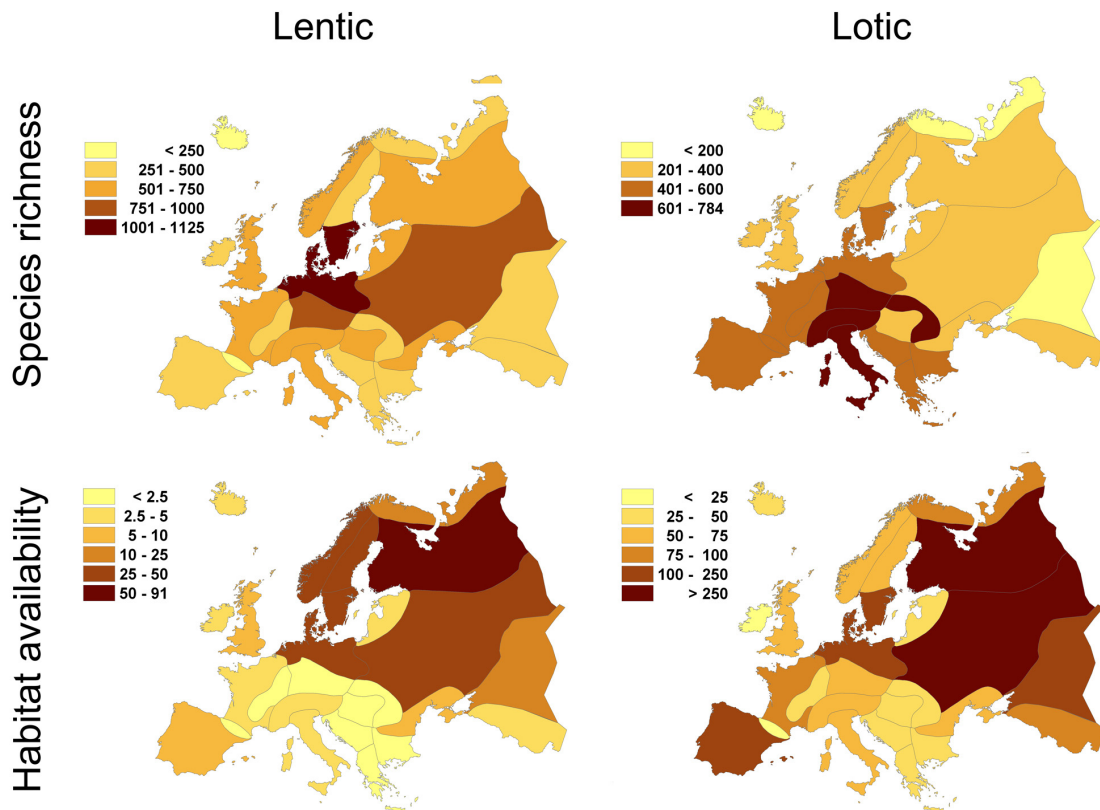
Figure 1 | Species richness and habitat availability of lentic and lotic animals in Europe.
Lentic habitat availability is defined as the perimeter of all standing water bodies (km$\times10^3$), and lotic habitat availability as the sum of the length of all parts of a river (km$\times10^3$) within a bioregion. The 25 biogeographical regions of the European freshwater fauna were defined by Illies (1966a; 1978).

(4) After accounting for habitat availability, altitudinal range was still positively correlated with species richness in lotic but not in lentic species (Table 1). Adding latitude and its squared term into the model showed that after controlling for habitat and altitudinal range, there was still a monotonic decrease of species richness with latitude in lotic species (r^2=0.16, P=0.050), and a hump-shaped relationship between species richness and latitude in lentic species (regression coefficient of squared latitude negative; R^2=0.32, P=0.015, Fig. 3, Table 1). The patterns of habitat availability did not correspond to the patterns of species richness (Fig. 1). In lentic species there was an increase of available habitat with increasing latitude (vs. hump-shaped relationship of richness and latitude), and in lotic species there was no relationship between habitat availability and latitude (vs. decline of species richness with increasing latitude; Fig. 2).

Table 1 | Species richness in dependency of habitat availability and latitude (general linear models, type 1 SS).

	MSS	F	Regression coefficient	P
Lotic species				
River length	9353	0.32	44.70	0.579
Altitudinal range	181389	6.17	269.6	**0.022**
Latitude	175575	5.97	62.27	**0.024**
Latitude²	51247	1.74	-0.66	0.202
Residuals	29409			
Lentic species				
Lake perimeter	174180	5.69	202.12	**0.027**
Altitudinal range	27090	0.88	93.79	0.358
Latitude	64429	2.10	178.2	0.162
Latitude²	332661	10.9	-1.70	**0.004**
Residuals	30614			

Significant correlations (P<0.05) are given in bold. (MSS: Mean sum of squares; n = 25). River length and lake perimeter were log10-transformed. Note the significant and negative regression coefficient for Latitude² in lentic species.

Discussion

Differences in species diversity are most commonly attributed to area (MacArthur & Wilson 1967; Connor & McCoy 1979; Rosenzweig 1995), contemporary climatic conditions (Wright 1983; Currie 1991; Hawkins *et al.* 2003), or historical factors (Haffer 1969; Latham & Ricklefs 1993; Dynesius & Jansson 2000). With respect to habitat area we found a positive, albeit weak, relationship between species richness and habitat availability in lentic species (r^2=0.14), but not in lotic species (r^2=0.01). These values are very low compared to values reported for species-area relationships in terrestrial as well as aquatic species (Barbour & Brown 1974; Connor & McCoy 1979; Hugueny 1989; Watters 1992; Oberdorff *et al.* 1995; 1997; Rosenzweig & Sandlin 1997). Furthermore, the latitudinal species richness patterns of both lentic and lotic animals remained virtually the same after controlling for habitat (Table 1, Fig. 3). Hence, the patterns of species richness of lentic and lotic species across Europe do not reflect the distribution of the respective freshwater habitats. We conclude that the availability of habitat is a poor predictor of the broad scale patterns of species richness in freshwater animals across broad spatial scales.
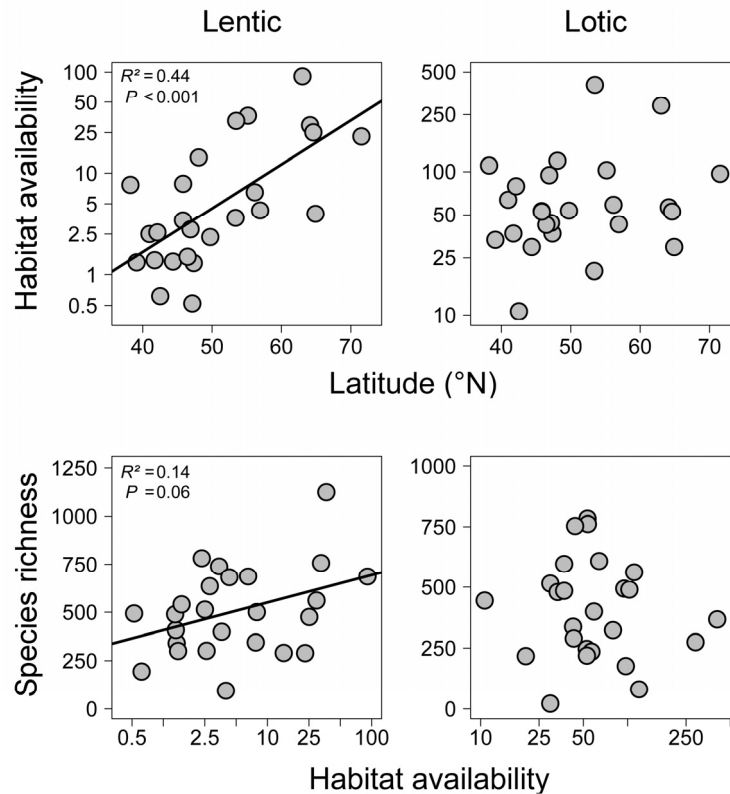
Figure 2 | Habitat availability vs. latitude (above), and species richness vs. habitat availability for lentic (left) and lotic species. Every point represents one of the 25 biogeographical regions of European freshwater species defined by Illies (1966a; 1978). Habitat availability is log_{10} transformed. Lentic habitat availability is defined as the perimeter of all standing water bodies (km*10^3), and lotic habitat availability as the sum of the length of all parts of a river (km*10^3) within a bioregion. *n*=25.

Ribera *et al*. (2003) found that total area is a good predictor of total species richness of aquatic Coleoptera, but not of the species richness of lentic and lotic species, when tested separately. In our analysis, total species richness of European freshwater animals was not correlated with the total area of a bioregion. When tested separately, lentic, but not lotic, species richness increased with the total area of a bioregion. The relationship between lentic species richness and total area was a bit stronger (r^2=0.19, *P*=0.03) than that between lentic species richness and available lentic habitat (r^2=0.14, *P*=0.06). Both relationships, however, are rather weak and there is only a small, non-significant difference between them. We thus conclude that neither of them is a good predictor of the species richness of European lentic freshwater animals.
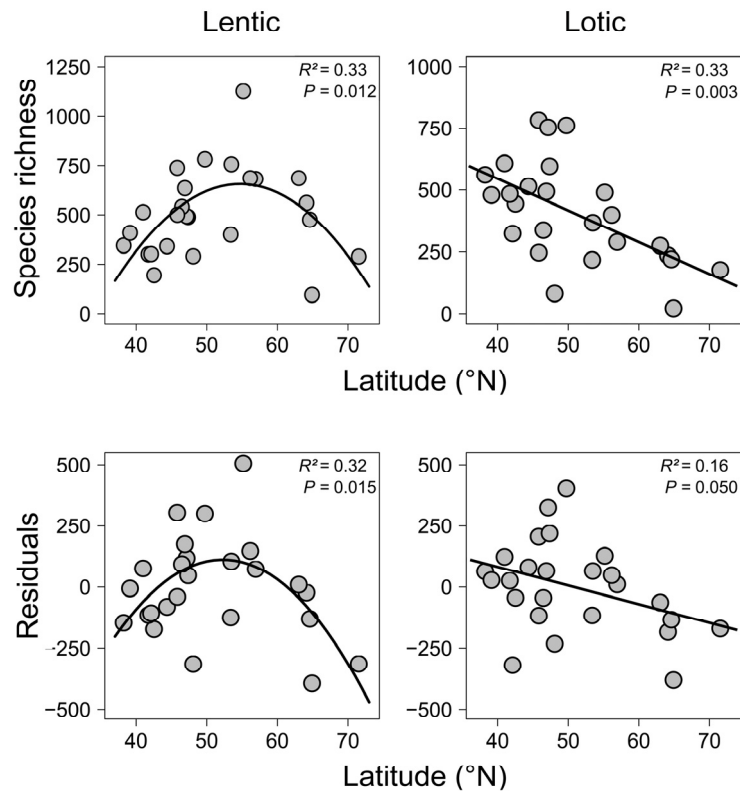
Figure 3 | Species richness (above) and residuals vs. latitude in lentic (left) and lotic species, after controlling for habitat availability and habitat diversity (i.e. altitudinal range), *n*=25.

Illies (1966b) argued that montane regions such as the Pyrenees or the Alps have relatively fewer species than other regions probably because they largely lack typical lowland habitats such as eutrophic lakes or potamal river segments and consequently lack species that occur in these kinds of habitats. The diversity of both lentic and lotic habitats should thus be highest in regions that span a wide altitudinal range (Illies 1961; 1966b; Dobson & Frid 1998; Nõges 2009; see also Introduction). In our analysis the altitudinal range of a region accounted for 15.0 and 19.5 per cent of the variation in lentic and lotic species richness, respectively. Lotic species richness increased with the altitudinal range of a region as expected, but lentic species richness tended to decrease. The relationship, however, was rather weak in both groups, and in lentic species it disappeared in the multivariate analysis. This might indicate that altitudinal range is not a suitable proxy for diversity of lentic habitats or that its effects are superimposed by other relationships. The altitudinal ranges of the regions are highest in southern and northern Europe and show a minimum in central Europe whereas lentic species richness shows the opposite trend: it peaks in central Europe and then gradually declines both northwards and southwards. Given the rather weak correlation and the complex history

of the European continent with its recurrent glaciations during the ice-ages, it is likely that the peak of lentic species richness in central Europe is predominantly caused by other factors than habitat diversity (see Hewitt 1999; 2000; Hof *et al*. 2008). The observed negative trend between species richness and altitudinal range could merely present a random pattern caused by their opposing relationships with latitude.

Our habitat data set does not (and cannot) include *all* European water bodies but only those with a surface area bigger than 0.1 km² (lentic) and rivers of a Strahler stream order of two and higher (lotic). Any river, however, is fed from its tributaries, so its presence will be due to the presence of smaller ones (Bohle 1995; Dobson & Frid 1998). As a consequence, every river in our data set will stand for a similar number of smaller ones that are not included. Kristensen *et al.* (1995) estimated that there were about 500,000 – 700,000 water bodies with a surface area of 0.01 to 0.1 km² in Europe, 65 – 90 % of which are estimated to be located in northern Europe (Scandinavia and northern Russia). These water bodies are thus not likely to explain the peak of species richness in central Europe. Furthermore, in our analysis we removed all lentic species from the original data set that exclusively occur in small temporary pools, i.e. in habitats that are too small to be included in our habitat data set. We also excluded all lotic species that exclusively occur in springs. Hence our data set includes only species typical for the water bodies that were included in our data sets on habitat availability. Nevertheless, species richness of these removed species showed similar relationships to habitat availability (Fig. S3 and S4). Hence, small water bodies that are not included in our habitat data set are not responsible for the observed patterns of lentic and lotic species richness.

Available energy, measured e.g. as mean annual temperature or primary productivity, has been suggested to be a strong predictor of species richness, and shown to decrease with increasing latitude (Wright 1983; Currie 1991; Hawkins *et al.* 2003). With respect to our data, it may appear as if the decrease of lotic species richness with latitude followed a decrease of available energy. We tested species richness against climatic data taken from Worldclim (Hijmans *et al.* 2005). However, because of the rather coarse resolution of our species distribution data, climatic data have to be averaged over relatively large bioregions, which makes it very difficult to disentangle the effect of energy from a possible influence of space (i.e. history). We therefore decided not to follow up these tests. Higher resolved species distribution data are required to test how energy is related to lentic and lotic species richness in Europe.

Nevertheless, because European lentic and lotic species show strikingly different patterns of species richness, energy alone has to be ruled out as a *universal* determinant of species richness of European freshwater animals (Hof *et al.* 2008). Moreover, it certainly cannot account for the differences in the distribution of lentic and lotic species richness.

If neither habitat availability nor energy are likely to be responsible for the observed differences in the distribution of species richness of lentic and lotic animals, this may suggest that the distribution of certain taxa of freshwater species in Europe is not in equilibrium with current environmental conditions and to some extent is still influenced by historical factors (Svenning & Skov 2004; Araújo *et al.* 2008). It is well known that the European biota were strongly influenced by the glacial cycles during the Pleistocene (Hewitt 1999; 2000) and signals of these impacts remain detectable in present-day patterns of species richness and composition as well as in the distribution of genotypes (Svenning & Skov 2004; Araújo *et al.* 2008). Many European species spent the last glacial maximum in refugia on the Mediterranean peninsulas (Holdhaus 1954; Taberlet *et al.* 1998; Hewitt 1999). When the ice masses retreated, species re-colonized central and northern Europe out of these refugia (Hewitt 1999). Lentic species are expected to have a higher propensity for dispersal than lotic species which is expressed by larger geographical ranges (Ribera & Vogler 2000; Hof *et al.* 2006; Reyjol *et al.* 2007), faster colonization (Ribera *et al.* 2003), lower beta diversity (Hof *et al.* 2008), a lower population differentiation (Bohonak *et al.* 2004; Marten *et al.* 2006) but higher intra-population and overall genetic diversity (Zickovich & Bohonak 2007). Since re-colonization is strongly dependent on the dispersal ability of a species (Diamond 1972; Svenning & Skov 2007; Araújo *et al.* 2008), the higher dispersal ability of lentic species may have allowed them to re-colonize central and northern European regions faster than lotic species.

This is supported by the fact that the proportion of lentic to lotic species increases from southern towards northern Europe, while beta-diversity between regions decreases (Hof *et al.* 2008). Furthermore, the positive species-area (or species-habitat) relationship in lentic species may indicate that the distributions of lentic species are closer to equilibrium with the current distribution of their habitats than those of lotic species. The hump-shaped relationship between lentic species richness and latitude and the decrease of lotic species richness with increasing latitude are consistent when individual taxa are tested separately (Fig. S1 and S2 in the Supplementary Material). Re-colonization

routes of lentic species from different refugia may have met in central Europe (see Hewitt 2000, for terrestrial animals), which may have led to a mixing of species and the observed peak of richness there. Lotic species, on the other hand, probably re-colonized central and northern Europe much slower, and therefore the extent of mixing is less pronounced or even lacking.

Our study corroborates former results that suggested non-equilibrium situations for European biota (Svenning & Skov 2004; Araújo *et al.* 2008). We emphasize that consideration of species' ecological traits (Ribera *et al.* 2003; Vogler & Ribera 2003; Marten *et al.* 2006; McPherson & Jetz 2007), as well as the history of the region studied (Graham *et al.* 2006; Svenning & Skov 2007) is indispensable in order to understand large-scale species richness patterns and differences among taxa in this regard.

Acknowledgements

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Supplementary Material

Supplementary Tables

Table S1 | Number of lentic and lotic species per bioregion

Region	Number of lentic species	Number of lotic species
Ibero-Macaronesian Region	345	562
Pyrenees	195	445
Italy, Corsica, and Malta	514	609
Alps	739	784
Dinaric Western Balkan	341	515
Hellenic Western Balkan	409	480
Eastern Balkan	301	485
Western Highlands	490	597
Central Highlands	782	762
The Carpathians	494	754
Hungarian Lowlands	541	338
Pontic Province	501	247
Western Plains	635	494
Central Plains	1125	490
Baltic Province	682	290
Eastern Plains	757	368
Ireland and Northern Ireland	400	218
Great Britain	686	400
Iceland	95	22
Borealic Uplands	561	236
Tundra	290	177
Northern Sweden	476	220
Taiga	686	275
The Caucasus	302	324
Caspic Depression	291	81

Table S2: Number of species per taxon in the data sets of European lentic and lotic freshwater animals.

Phylum		Lentic	Lotic
Annelida		14	5
Arthropoda	Arachnida	366	300
	Crustacea	270	79
	Insecta	749	1798
Chordata	'Pisces'	38	72
	Amphibia	6	4
	Reptilia	0	1
Mollusca	Bivalvia	10	16
	Gastropoda	89	78
Nematoda		61	14
Platyhelminthes		93	50
Porifera		1	0
Rotifera		262	19
Tardigrada		0	8
Cnidaria		0	1
Total		**1959**	**2445**

Supplementary Figures
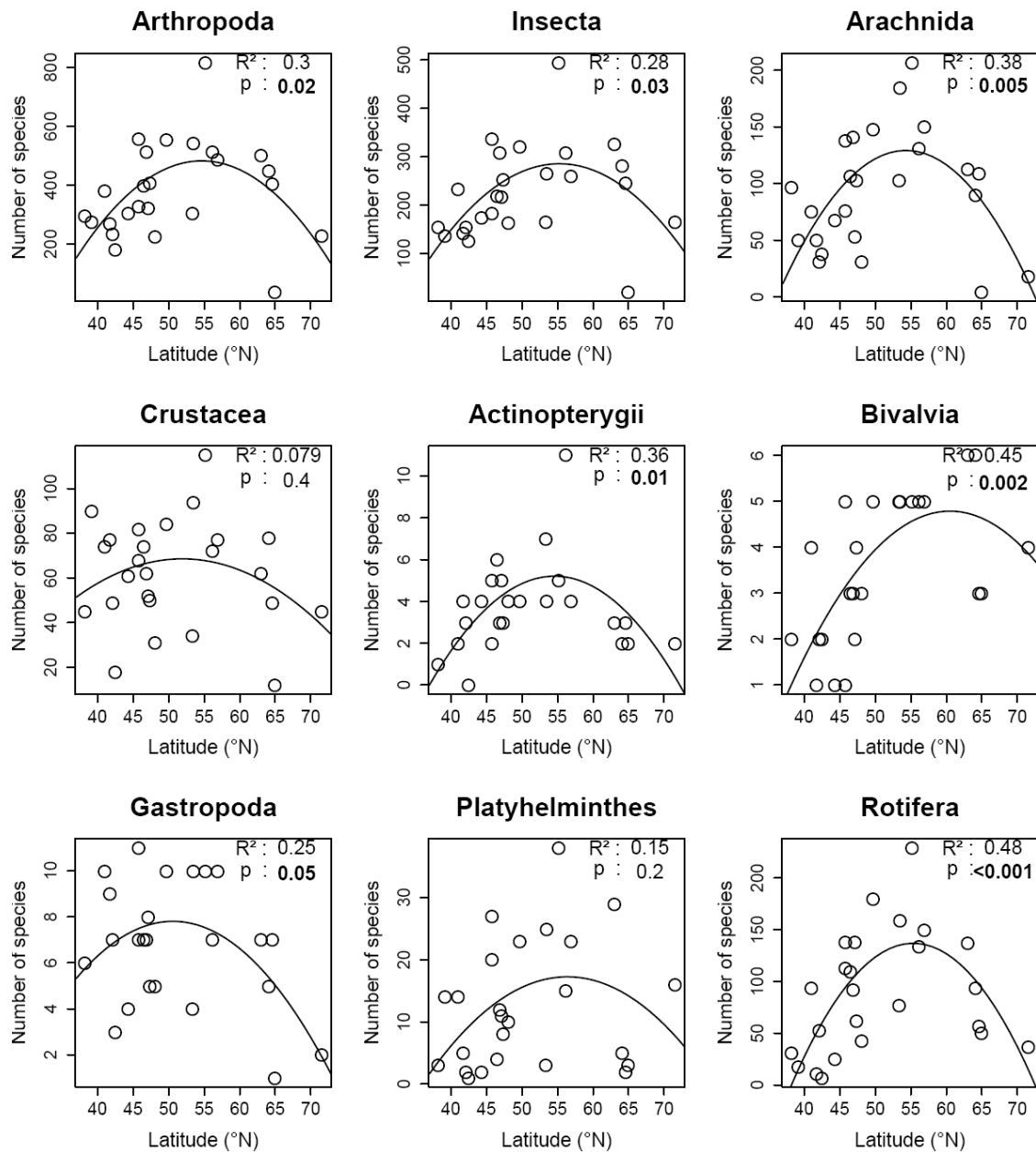
Figure S1 | Species richness vs. latitude in different lentic taxa. In Actinopterygii, Bivalvia and Gastropoda, Region 6 was removed because of its unusually high number of species which only occur in Lake Ochrid.
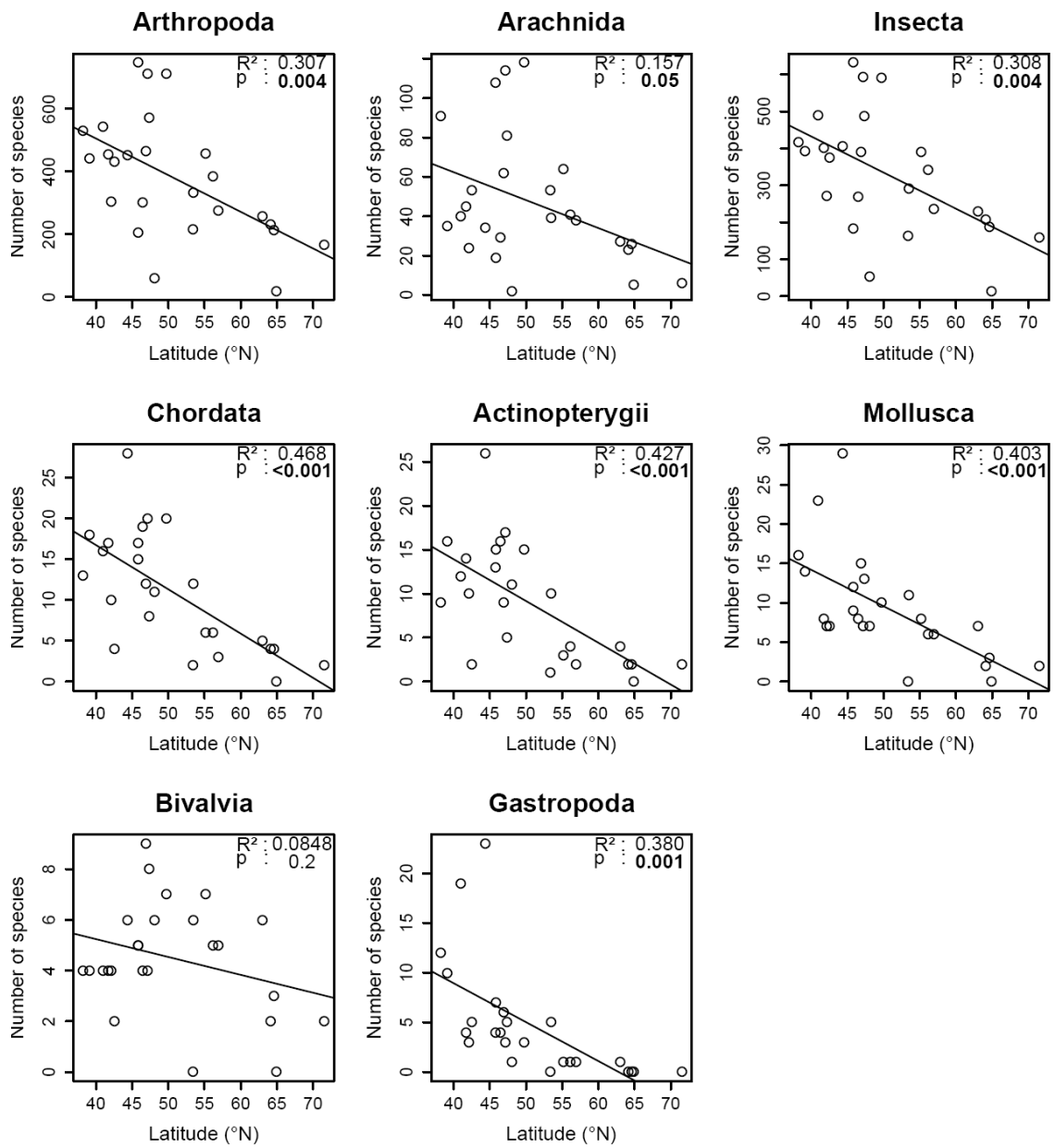
Figure S2 | Species richness vs. latitude in different lotic taxa.
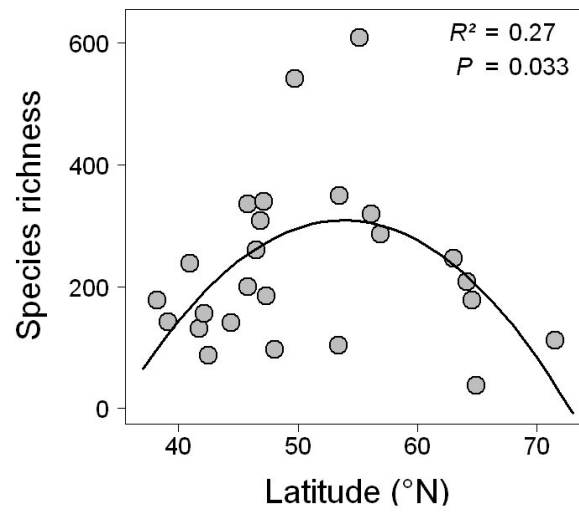
Figure S3 | Species richness of lentic species that exclusively occur in small and ephemeral water bodies vs. latitude. These species were removed from the original data set and were not included in the analyses.
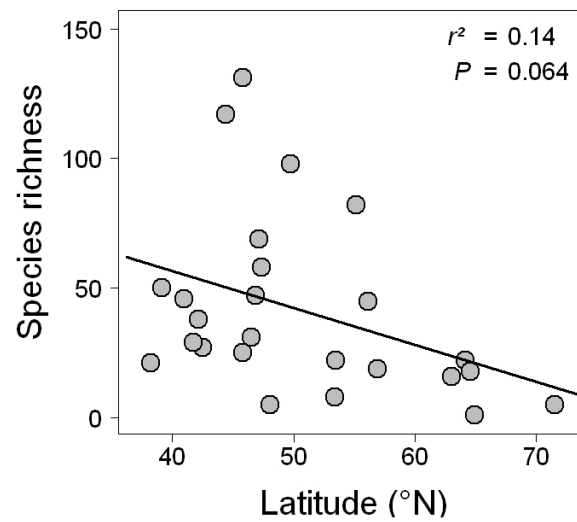
Figure S4 | Species richness of lotic species that exclusively occur in springs vs. latitude. These species were removed from the original data set and were not included in the analyses.

Chapter V

The effect of habitat stability on dispersal and species' ability to track climate change

Manuscript in preparation

The effect of habitat stability on dispersal and species' ability to track climate change

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Abstract

Habitat shapes life history traits and ecological characteristics of species. The persistence of habitats should influence the dispersal of species, selecting for stronger dispersal in habitats of lower temporal stability. As standing freshwater bodies (lentic habitats) are on average less persistent over time than running waters (lotic habitats), lentic species should show a higher propensity for dispersal than lotic species. Assuming that climatic conditions are an important determinant of species distributions, we hypothesise that the distributions of lentic species should be closer to equilibrium with current climatic conditions and that lentic species should more rapidly track climatic changes. We tested these hypotheses using two datasets (from 1988 and 2006) of European dragonfly distributions and the according climatic data. Species distribution models showed that range filling (the ratio of realised vs. potential range size) was consistently higher for lentic than for lotic species. When using data from 1988 to model distributions in 2006, models consistently overpredicted the ranges of lotic species, and more strongly than for lentic species. These results confirm the proposed hypotheses, lending support to the assumption that habitat persistence shapes

the evolution of dispersal. Further, we conclude that lentic species may be more successful in tracking climate change.

Introduction

Habitat is an important template for the evolution of life history traits and hence ecological characteristics of species (Southwood 1962). Freshwater habitats can be divided into standing water bodies such as lakes and ponds (= lentic habitats) and running water bodies such as streams, rivers and creeks (= lotic habitats). Lentic habitats are, on average, less persistent over time than lotic habitats (Dobson & Frid 1998; Ribera 2008). This should have consequences for the evolution of dispersal abilities of species adapted to these habitat types: if their habitats are more likely to disappear within shorter periods of time, lentic species should have evolved a higher propensity for dispersal than lotic species (Ribera & Vogler 2000). Several studies have provided support for predictions of this hypothesis – hereafter referred to as the habitat-stability dispersal hypothesis (HSDH). Various macroecological, phylogenetic and phylogeographical studies have shown that lentic species have larger range sizes (Ribera & Vogler 2000; Hof *et al.* 2006) and a lower genetic diversity among populations (Marten *et al.* 2006; Papadopoulou *et al.* 2008; Abellan *et al.* 2009) than lotic species. Furthermore, re-colonisation of northern European regions after the last glaciation was most probably faster for lentic than for lotic species (Ribera *et al.* 2003; Hof *et al.* 2008; Dehling *et al.* 2010). However, at least the molecular evidence for the HSDH is controversial (e.g. Short & Caterino 2009) and comparisons of dispersal capacities of lentic and lotic species, e.g. by quantitative assessments of range changes, remain scarce.

Here, we provide a test of the HSDH for European dragonflies using species distribution models (SDMs). SDMs are useful for projecting species' potential ranges based on observed distribution data (Elith & Leathwick 2009), and have been extensively used for projecting potential future distributions of species under climate change scenarios (e.g. Levinsky *et al.* 2007). If contemporary climate is an important determinant of species distributions, distributions of species with stronger dispersal abilities should be closer to equilibrium with contemporary climatic conditions (Araújo & Pearson 2005). Therefore these species should show higher levels of range filling and should be able to rapidly track climatic changes. Range filling, the ratio of the realised vs. potential range size (R/P) given by SDMs, has been used to infer the degree of

species' equilibrium with climatic conditions (Svenning & Skov 2004; Munguía *et al.* 2008), with a higher R/P ratio indicating higher degree of equilibrium. The HSDH therefore predicts that R/P ratios of lentic species should be higher than R/P ratios of lotic species. Furthermore, lotic species should track changes in the climatic conditions more slowly than lentic species. If so, then SDMs should overestimate lotic more often than lentic species ranges when comparing range changes with climatic changes between two distinct time periods.

Material and Methods

As distribution data we used the range maps of all species of European dragonfly published in Askew (1988) and Dijkstra & Lewington (2006) (Table S1 in Supplementary Material). Maps were transferred into the UTM (Universal Transverse Mercator) 50 × 50 km grid of Europe used for the Atlas Flora Europaeae (see Supplementary Material for details). We further compiled larval habitat preferences (lentic, lotic, generalist) and taxonomic data for all species from the abovementioned sources.

Climatic data were obtained from the CRU TS 2.1 data set (Mitchell & Jones 2005). It covers the years 1901-2002 and includes mean monthly temperature and total monthly precipitation at a resolution of 0.5 × 0.5° latitude-longitude. Climatic data were resampled to the 50 × 50 km grid by weighted averaging, using a grid of Europe from Nogués-Bravo & Araújo (2006, http://www.biochange-lab.eu/). To relate the species distribution data to climatic conditions, we averaged climatic data across time spans matching the 1988 and 2006 species distribution datasets. As climatic variables we used mean annual temperature and total annual precipitation (see Supplementary Material for further details).

We ran SDMs for all species using BIOMOD (Thuiller *et al.* 2009) with eight different modelling techniques (see Table 1 and Fig. 1 for the techniques used). Model outputs were transformed into presences and absences using two different thresholds (ROC and Kappa). For more details on the different SDM techniques as well as on the standard features of BIOMOD, see Thuiller *et al.* (2009). Potential distributions for 1988 and 2006 were obtained by calibrating the models using the species distribution and climatic data for the respective time periods and projecting distributions back into geographical space for the same time period, using the 50 × 50 km grid. These projections were used to calculate the ratio of realised vs. potential range sizes (R/P

ratio), for 1988 and 2006. Six species in each dataset were excluded from the analyses because they occurred in less than 20 grid cells (Table S1), and SDMs with fewer records are less reliable (see e.g. Stockwell & Peterson 2002). Models calibrated in 1988 were also used to project distributions for 2006. To assess how well species tracked climatic changes from 1988 to 2006 we calculated proportions of true positives (TP) and true negatives (TN) comparing projected and observed distributions for 2006. To assess the influence of habitat type (lentic and lotic) on R/P ratios and TP and TN proportions, we excluded 13 generalist species. We used Wilcoxon rank sum tests to assess the effect of habitat type on R/P ratios and proportions of TP and TN. To test for confounding effects of phylogeny, we used two-way ANOVAs with family, habitat and their interactions as independent variables (type I sum of squares). As range size *per se* may also affect SDM performance and R/P ratios, we plotted the effect of habitat on R/P ratios and proportions of TP and TN separately for range size quartiles. All analyses were run in R (version 2.8.1; R Development Core Team 2008).

Results

R/P ratios were higher for lentic than for lotic species, independent of the SDM method used ($P < 0.05$, Fig. 1). Phylogeny had a weak influence on R/P ratio, but the effect of habitat type remained significant in most cases for 2006, and marginally significant in most cases for 1988 (table1). Range size had an influence on R/P ratio, but for the first to third range size quartiles lentic species still showed higher R/P ratios (Fig. S2 and S3 in Supplementary Material).

Comparisons of observed and projected distributions for 2006 showed an overprediction of lotic species ranges in six of eight modelling techniques (significantly smaller proportion of TP than TN, Fig. 2). The same pattern was observed in most cases for lentic species, but the difference tended to be smaller, indicating a stronger tendency of overprediction for lotic species. The tendency of smaller TP than TN proportions for lotic species was supported in most of the cases in the 1st, 2nd and 3rd range size quartile, whereas in the 4th quartile TP proportions were larger than TN proportions (Fig. S4). The tendency of smaller differences between TP and TN proportions for lentic than for lotic species was less pronounced when accounting for range size (Fig. S4).
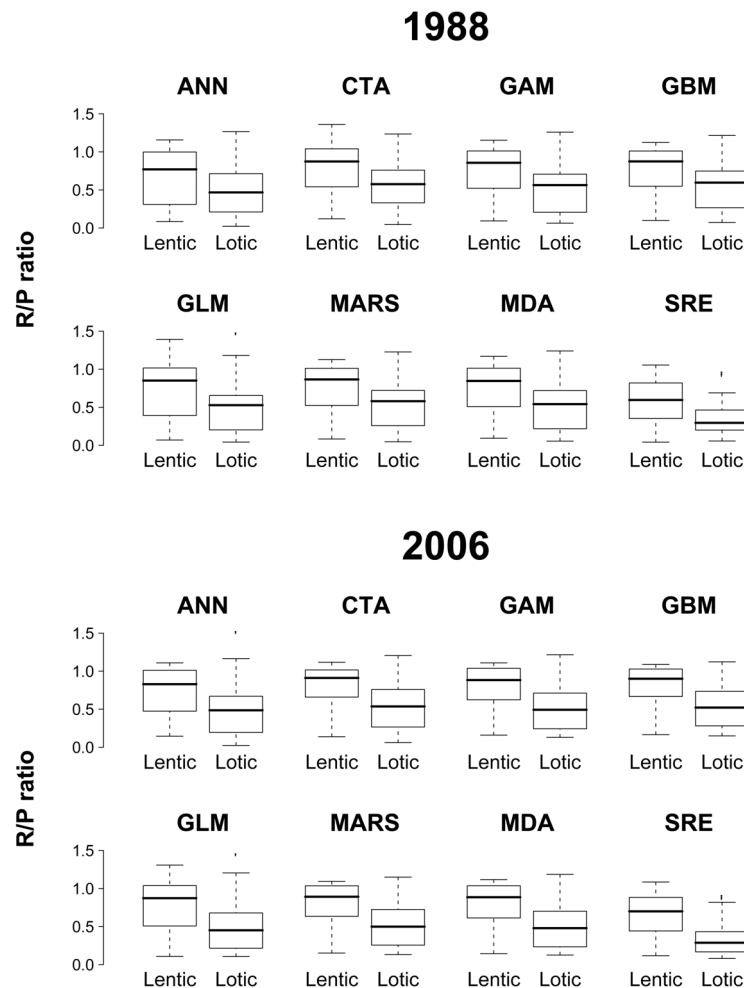
1988

2006

Figure 1 | Effect of habitat type (lentic = standing waters, lotic = running waters) on R/P ratios of European dragonflies for different SDM techniques, for 1988 and 2006. Range projections were translated into presences and absences from probabilities of occurrence using ROC-based thresholds (see Fig. S1 for calculations using Kappa-based thresholds). Differences were significant ($P < 0.05$) in all cases (Wilcoxon rank sum test). See Fig. S1 for SDM acronyms and an explanation of box-and-whisker plots.

Discussion

Higher range filling levels in lentic dragonfly species (Fig. 1) support the hypothesis that distributions of lentic species distributions are closer to climatic equilibrium than distributions of lotic species. This is further underlined by the tendency of stronger overprediction for lotic species ranges when comparing range projections and observed ranges for 2006 (Fig. 2). Both findings support the HSDH, suggesting that lower habitat stability selects for stronger dispersal abilities (Ribera & Vogler 2000; Hof *et al.* 2006). Species with the largest range sizes did not show the difference in R/P ratios between

lentic and lotic species (Fig. S2-S4). However, SDMs cannot project ranges larger than the geographical domain; hence species with very large ranges are expected to have high R/P ratios. Furthermore, note that only a small number of lotic species reach very large range sizes (twenty lentic but only three lotic species in the fourth range-size quartile), which precludes meaningful comparisons. Phylogenetic effects influenced the differences in range filling in some cases (Table 1), but the influence of habitat was still detectable after controlling for phylogeny (family). We though call for studies using species-level phylogenies to eventually discard potentially confounding phylogenetic effects.

Table 1 | Two – way ANOVA (type I sum of squares) for effects of family and habitat on range filling (realised vs. projected range size) for 1988 and 2006.

	Family		Habitat		Family×Habitat		Residuals
	F	*P*	F	*P*	F	*P*	MS[†]
1988							
ANN*	1.18	0.32	2.29	0.13	0.76	0.55	0.13
CTA	1.58	0.14	*3.02*	*0.086*	0.99	0.42	0.10
GAM	1.51	0.16	*3.77*	*0.056*	0.87	0.49	0.11
GBM	1.43	0.19	*3.80*	*0.055*	0.86	0.49	0.098
GLM	1.43	0.19	2.51	0.12	0.59	0.67	0.14
MARS	1.35	0.23	*3.39*	*0.070*	0.80	0.53	0.11
MDA	1.38	0.21	*3.46*	*0.067*	0.79	0.53	0.11
SRE	1.85	0.073	**5.97**	**0.017**	0.87	0.49	0.073
2006							
ANN	2.19	0.032	*2.95*	*0.090*	1.12	0.35	0.13
CTA	1.76	0.090	**7.23**	**0.009**	1.45	0.22	0.086
GAM	1.99	0.052	**7.68**	**0.007**	1.45	0.22	0.089
GBM	1.96	0.056	**7.91**	**0.006**	1.46	0.22	0.080
GLM	1.77	0.088	**5.45**	**0.022**	1.12	0.35	0.12
MARS	1.80	0.083	**6.92**	**0.010**	1.36	0.26	0.090
MDA	1.83	0.077	**7.07**	**0.010**	1.42	0.24	0.095
SRE	2.72	0.008	**8.22**	**0.005**	2.59	0.04	0.066

Significant effects (*P* < 0.05) of habitat type after correcting for the effect of family are given in bold, marginally significant effects (*P* < 0.1) are given in italic fonts.
*see Fig. S1 for SDM technique acronyms
†residual mean squares

The availability of lentic and lotic habitats can also confound the observed differences in range filling, e.g. in cases where climatic conditions are suitable, but no freshwater habitats are present. This case is assumed if habitat availability is a strong

predictor of freshwater species richness. However, for the geographical extent and resolution of our study, the distribution of freshwater bodies is a weak predictor for dragonfly species richness (Keil *et al.* 2008). Furthermore, the explanatory power of habitat availability for species richness of lotic habitats is exceptionally low (Dehling *et al.* 2010). Therefore the effect of the distribution of habitat availability should be of minor importance. The influence of other factors such as pollution, anthropogenic land-cover changes, or the occurrence of predators (Hassall & Thompson 2008) could also affect the results of our analyses. However, as these factors do either not differentially affect lotic and lentic species or habitats (land-cover changes) or most likely act at a different geographical scale than the scale of our analyses (pollution, predators), we assume such effects are negligible for the extent and resolution of our analyses.

Our results support findings of previous studies that lotic species are weaker dispersers than lentic species (Marten *et al.* 2006; Hof *et al.* 2006; Abellan *et al.* 2009). If so, lentic species should be able to track climatic changes more rapidly than lotic species (Heino *et al.* 2009). Our analyses support this prediction, along with studies that relate contrasting large-scale diversity patterns in European lentic and lotic species to their re-colonisation capacity after the last ice age (Ribera & Vogler 2000; Ribera *et al.* 2003; Hof *et al.* 2008). It is widely accepted that the glacial-interglacial cycles of the Pleistocene are still mirrored in contemporary patterns of species richness in Europe (Svenning & Skov 2007; Araújo *et al.* 2008). As dragonflies are assumed to be strong dispersers compared to other invertebrates, they are also expected to be able to track climatic changes more successfully (Hickling *et al.* 2005; Clausnitzer *et al.* 2009). The differential dispersal abilities of species adapted to different habitat types suggest that similar generalizations for entire taxa may be misleading, though.

Dispersal ability is of major importance for species to successfully respond to climate change. SDM studies aiming to project species distributions under future climate change projections usually adopt very coarse dispersal scenarios, i.e. unlimited or no dispersal (e.g. Levinsky *et al.* 2007). That these scenarios are unrealistic is widely acknowledged, but as long as species-specific dispersal data are vastly lacking, multi-species SDMs rely on simplifications. If habitat is indeed a generally important determinant of dispersal ability (Southwood 1962), establishing even simplified links between habitat preferences, habitat stability, and dispersal ability may, with an accordant model parametrisation, help to overcome the oversimplistic dispersal

assumptions currently used in models that project species responses to future climate change.
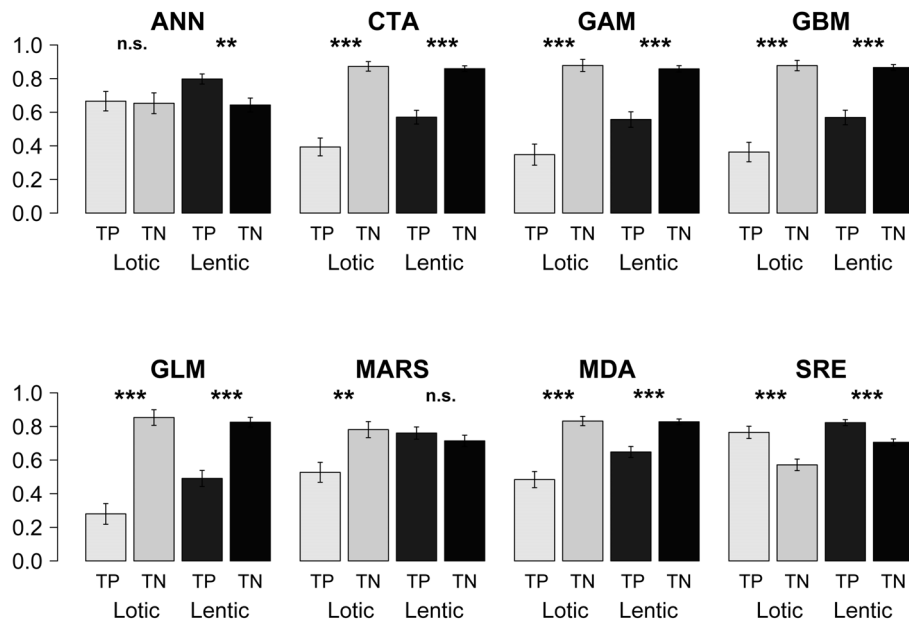
Figure 2 | Proportion of true positives, TP, and true negatives, TN, for lotic and lentic dragonflies according to different SDMs. TP and TN where calculated comparing the ratio of projected vs. observed presence (TP) or absence (TN) records for 2006, averaged across all lotic and lentic species, respectively. Models were calibrated with 1988 distribution and climate data and then projected for 2006. Error bars give the standard error of the mean. See Fig. S1 for SDM acronyms. Significance levels (Wilcoxon rank sum tests), ***$P < 0.001$, ** $P < 0.01$, n.s., not significant.

Acknowledgements

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Supplementary Material

Supplementary Text | Material and Methods

Species distribution maps. The different sources of range maps (Askew 1988; Dijkstra & Lewington 2006) may differ in their accuracy. The maps in Dijkstra & Lewington (2006), for instance, use different colours to indicate the status of the species. Following Keil *et al.* (2008) we only used the purple (main area of distribution) and blue (uncommon/scattered occurrence but not declining) areas in Dijkstra & Lewington (2006) as distribution records. Records from the inner Alps, where major differences between the different map sources could be attributed to differences in mapping accuracy were excluded. Since distribution data are generally less reliable in eastern Europe, we ignored all distribution records located east of the eastern borders of Finland, the Baltic countries, Poland, Hungary, Slovakia, Romania, Bulgaria and Greece. Nevertheless, we stress that dragonflies, due to their size, habitats and behaviour, range among the taxa with the best data record in space and time across Europe. Therefore, we believe that the accuracy of the maps is sufficient for our analyses.

Time periods of climatic data used. To relate the species distribution datasets to climatic conditions, we averaged climatic the climatic variables (mean annual temperature and total annual precipitation) for time periods from 1971 to 1984 and from 1989 to 2002 for comparisons with the 1988 and 2006 species distribution datasets. CRU TS 2.1 and other single climatic data sets of comparable quality do not cover all the years of interest for the respective time periods of this study (1970-2006). Using two data sets of different origin that cover all the years of interest though appeared to be problematic, due to potential mismatches in accuracy. We believe that despite the small gap between the climatic and species distribution data, this approach is sound for two reasons: firstly, including four additional years would most probably not significantly change the average calculated over 14 years (we repeated the analyses using a time span of 10 years for the climatic data which did not significantly change the results [not shown here]). Secondly, the data records used to generate the range maps of dragonfly distributions do not correspond exactly to the date these maps were published but rather to a larger period of time before the date of publication.

Supplementary Tables

Table S1 | List of 112 dragonfly species with range size (number of grid cells occupied), larval habitat and taxonomic information (suborder and family).

Species	Range size		Habitat	Suborder	Family
	1988	**2006**			
Aeshna affinis	906	1171	lentic	Anisoptera	Aeshnidae
Aeshna caerulea	524	497	lentic	Anisoptera	Aeshnidae
Aeshna crenata	24	48	lentic	Anisoptera	Aeshnidae
Aeshna cyanea	1544	1462	lentic	Anisoptera	Aeshnidae
Aeshna grandis	1139	1165	lentic	Anisoptera	Aeshnidae
Aeshna isosceles	1038	920	lentic	Anisoptera	Aeshnidae
Aeshna juncea	1266	1228	lentic	Anisoptera	Aeshnidae
Aeshna mixta	1435	1596	lentic	Anisoptera	Aeshnidae
Aeshna serrata	55	56	lentic	Anisoptera	Aeshnidae
Aeshna subarctica	458	626	lentic	Anisoptera	Aeshnidae
Aeshna viridis	333	341	lentic	Anisoptera	Aeshnidae
Anax imperator	1422	1593	lentic	Anisoptera	Aeshnidae
Anax parthenope	848	1146	lentic	Anisoptera	Aeshnidae
Boyeria irene	377	352	lotic	Anisoptera	Aeshnidae
Brachythemis leucosticta	30	30	lentic	Anisoptera	Libellulidae
Brachytron pratense	1145	1100	lentic	Anisoptera	Aeshnidae
Calopteryx haemorrhoidalis	444	385	lotic	Zygoptera	Calopterygidae
Caliaeschna microstigma	117	118	lotic	Anisoptera	Aeshnidae
Calopteryx splendens	1370	1414	lotic	Zygoptera	Calopterygidae
Calopteryx virgo	1797	1530	lotic	Zygoptera	Calopterygidae
Calopteryx xanthosoma	383	339	lotic	Zygoptera	Calopterygidae
Cercion lindeni*†	758	843	generalist	Zygoptera	Coenagrionidae
Ceriagrion tenellum	763	695	lentic	Zygoptera	Coenagrionidae
Coenagrion armatum	468	319	lentic	Zygoptera	Coenagrionidae
Coenagrion caerulescens	316	235	lotic	Zygoptera	Coenagrionidae
Coenagrion hastulatum	1044	902	lentic	Zygoptera	Coenagrionidae
Coenagrion hylas*†	2	0	generalist	Zygoptera	Coenagrionidae
Coenagrion johanssoni	375	363	lentic	Zygoptera	Coenagrionidae
Coenagrion lunulatum	764	557	lentic	Zygoptera	Coenagrionidae
Coenagrion mercuriale	611	558	lotic	Zygoptera	Coenagrionidae
Coenagrion ornatum	244	223	lotic	Zygoptera	Coenagrionidae
Coenagrion puella*†	1688	1634	generalist	Zygoptera	Coenagrionidae
Coenagrion pulchellum*†	1359	1378	generalist	Zygoptera	Coenagrionidae
Coenagrion scitulum	276	570	lotic	Zygoptera	Coenagrionidae
Cordulia aenea	985	1098	lentic	Anisoptera	Corduliidae
Cordulegaster bidentata	199	350	lotic	Anisoptera	Cordulegastridae
Cordulegaster boltoni	1230	1120	lotic	Anisoptera	Cordulegastridae
Cordulegaster heros*	8	101	lotic	Anisoptera	Cordulegastridae
Cordulegaster insignis*†	10	17	lotic	Anisoptera	Cordulegastridae
Cordulegaster picta†	41	14	lotic	Anisoptera	Cordulegastridae
Crocothemis eythraea	907	1306	lentic	Anisoptera	Libellulidae
Diplacodes lefebvrei	29	26	lentic	Anisoptera	Libellulidae
Enallagma cyathigerum*†	1918	2037	generalist	Zygoptera	Coenagrionidae
Epallage fatime	43	64	lotic	Zygoptera	Euphaeidae
Ephitheca bimaculata	332	469	lentic	Anisoptera	Corduliidae

Table S1 continued

Erythromma najas*†	1053	1216	generalist	Zygoptera	Coenagrionidae
Erythromma viridulum*†	911	1298	generalist	Zygoptera	Coenagrionidae
Gomphus flavipes	466	276	lotic	Anisoptera	Gomphidae
Gomphus graslini	33	103	lotic	Anisoptera	Gomphidae
Gomphus pulchellus	411	555	lentic	Anisoptera	Gomphidae
Gomphus schneideri†	49	15	lotic	Anisoptera	Gomphidae
Gomphus simillimus	358	297	lotic	Anisoptera	Gomphidae
Gomphus vulgatissimus	944	1162	lotic	Anisoptera	Gomphidae
Hemianax ephippiger	58	320	lentic	Anisoptera	Aeshnidae
Ischnura elegans*†	1554	1633	generalist	Zygoptera	Coenagrionidae
Ischnura genei*†	42	42	generalist	Zygoptera	Coenagrionidae
Ischnura graellsi	243	166	lentic	Zygoptera	Coenagrionidae
Ischnura pumilio	1106	1453	lentic	Zygoptera	Coenagrionidae
Lestes barbarus	1364	1431	lentic	Zygoptera	Lestidae
Lestes dryas	1477	1428	lentic	Zygoptera	Lestidae
Lestes macrostigma	418	141	lentic	Zygoptera	Lestidae
Lestes sponsa	1425	1506	lentic	Zygoptera	Lestidae
Lestes virens	1074	1298	lentic	Zygoptera	Lestidae
Lestes viridis*†	1406	1261	generalist	Zygoptera	Lestidae
Leucorrhinia albifrons	301	394	lentic	Anisoptera	Libellulidae
Leucorrhinia caudalis	303	389	lentic	Anisoptera	Libellulidae
Leucorrhinia dubia	976	975	lentic	Anisoptera	Libellulidae
Leucorrhinia pectoralis	214	508	lentic	Anisoptera	Libellulidae
Leucorrhinia ribucunda	558	736	lentic	Anisoptera	Libellulidae
Libellula depressa	1690	1662	lentic	Anisoptera	Libellulidae
Libellula fulva	1150	1003	lentic	Anisoptera	Libellulidae
Libellula quadrimaculata	1602	1659	lentic	Anisoptera	Libellulidae
Lindenia tetraphylla	168	59	lotic	Anisoptera	Gomphidae
Macromia splendens	23	61	lotic	Anisoptera	Corduliidae
Nehalennia speciosa	292	194	lentic	Zygoptera	Coenagrionidae
Onychogomphus costae*	5	29	lotic	Anisoptera	Gomphidae
Onychogomphus forcipatus	1040	1363	lotic	Anisoptera	Gomphidae
Onychogomphus uncatus	392	314	lotic	Anisoptera	Gomphidae
Ophiogomphus cecilia	588	562	lotic	Anisoptera	Gomphidae
Orthetrum albistylum	511	617	lentic	Anisoptera	Libellulidae
Orthetrum brunneum	1050	1164	lotic	Anisoptera	Libellulidae
Orthetrum cancellatum	1515	1683	lentic	Anisoptera	Libellulidae
Orthetrum chrysostigma*†	36	44	generalist	Anisoptera	Libellulidae
Orthetrum coerulescens*†	1307	1492	generalist	Anisoptera	Libellulidae
Orthetrum nitidinerve	43	86	lentic	Anisoptera	Libellulidae
Orthetrum trinacria	21	27	lentic	Anisoptera	Libellulidae
Oxygastra curtisi	400	269	lotic	Anisoptera	Corduliidae
Pantala flavescens*†	0	6	generalist	Anisoptera	Libellulidae
Paragomphus genei	41	42	lotic	Anisoptera	Gomphidae
Platycnemis acutipennis	415	312	lotic	Zygoptera	Platycnemididae
Platycnemis latipes	362	301	lotic	Zygoptera	Platycnemididae
Platycnemis pennipes*†	1468	1398	generalist	Zygoptera	Platycnemididae
Pyrrhosoma nymphula*†	1811	1649	generalist	Zygoptera	Coenagrionidae
Selysiothemis nigra	33	59	lentic	Anisoptera	Libellulidae
Somatochlora alpestris	351	293	lentic	Anisoptera	Corduliidae
Somatochlora arctica	489	686	lentic	Anisoptera	Corduliidae
Somatochlora flavomaculata	541	796	lentic	Anisoptera	Corduliidae
Somatochlora meridionalis	165	329	lentic	Anisoptera	Corduliidae
Somatochlora metallica	1409	1316	lentic	Anisoptera	Corduliidae

Table S1 continued

Somatochlora sahlbergi*†	3	10	lentic	Anisoptera	Corduliidae
Sympecma annulata	172	219	lentic	Zygoptera	Lestidae
Sympetrum danae	1170	1147	lentic	Anisoptera	Libellulidae
Sympetrum depressiusculum	222	344	lentic	Anisoptera	Libellulidae
Sympetrum flaveolum	1511	1110	lentic	Anisoptera	Libellulidae
Sympetrum fonscolombei	1095	1521	lentic	Anisoptera	Libellulidae
Sympecma fusca	1453	1398	lentic	Zygoptera	Lestidae
Sympetrum meridionale	815	1025	lentic	Anisoptera	Libellulidae
Sympetrum sanguineum	1503	1463	lentic	Anisoptera	Libellulidae
Sympetrum striolatum	1783	1827	lentic	Anisoptera	Libellulidae
Sympetrum vulgatum	1006	1022	lentic	Anisoptera	Libellulidae
Trithemis annulata	90	250	lentic	Anisoptera	Libellulidae
Zygonyx torridis*	5	23	lotic	Anisoptera	Libellulidae

* species not included in the analyses of the 1988 data
† species not included in the analyses of the 2006 data

Supplementary Figures
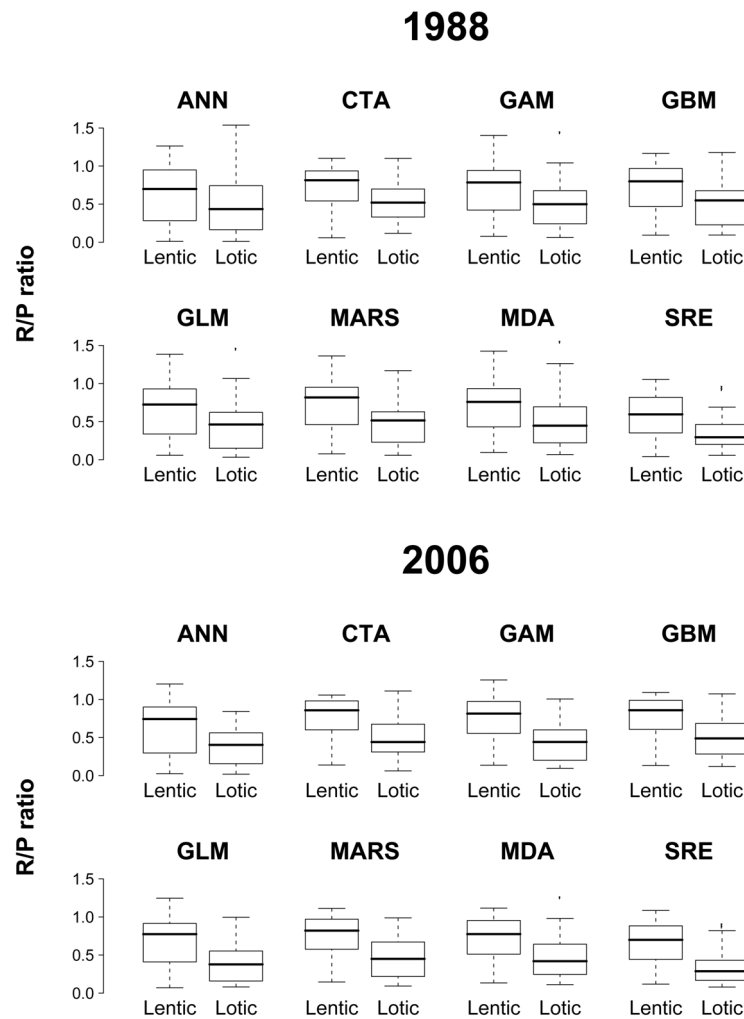
1988

2006

Figure S1 | Box-and-whisker plots of the effect of habitat type (lentic = standing waters, lotic = running waters) on R/P ratios of European dragonflies using different SDM techniques, for 1988 and 2006. Projected range sizes were transformed into presences and absences from probabilities of occurrence using Kappa-based thresholds. The differences were statistically significant ($P < 0.05$) in all cases except for ANN models in 1988 (P = 0.18, Wilcoxon rank sum test). Box-and-whisker plots give the following variables: horizontal black line, median; box, range between 1st and 3rd quartile; vertical dashed lines, maximum or minimum values (if no outliers, indicated by small circles) *or* 1.5 times the interquartile range below the first and above the third quartiles. SDM technique acronyms: artificial neural networks, ANN, classification tree analyses, CTA, generalised additive models, GAM, generalised boosted models, GBM, generalised linear models, GLM, multiple adaptive regression splines, MARS, mixture discriminant analyses, MDA, surface range envelopes, SRE.

Figure S2 | Box-and-whisker plots of the effect of habitat type on R/P ratios of European lentic and lotic dragonflies for different SDM techniques, 1988. Projected range sizes were translated into presences and absences from probabilities of occurrence using ROC-based thresholds. R/P ratio comparisons were plotted separately for each of the four range size quartiles of the species in the dataset (the first consisting of the 25% of the species with the smallest range sizes, the fourth quartile consisting of the 25% of the species with the largest range sizes). Note that the number of lentic and lotic species per range size quartile was not equally distributed: ([quartile, N_{lentic}, N_{lotic}] 1st, 13, 10; 2nd, 13, 10; 3rd, 17, 6; 4th, 20, 3). See Fig. S1 for SDM technique acronyms and for an explanation of the box-and-whisker plots.
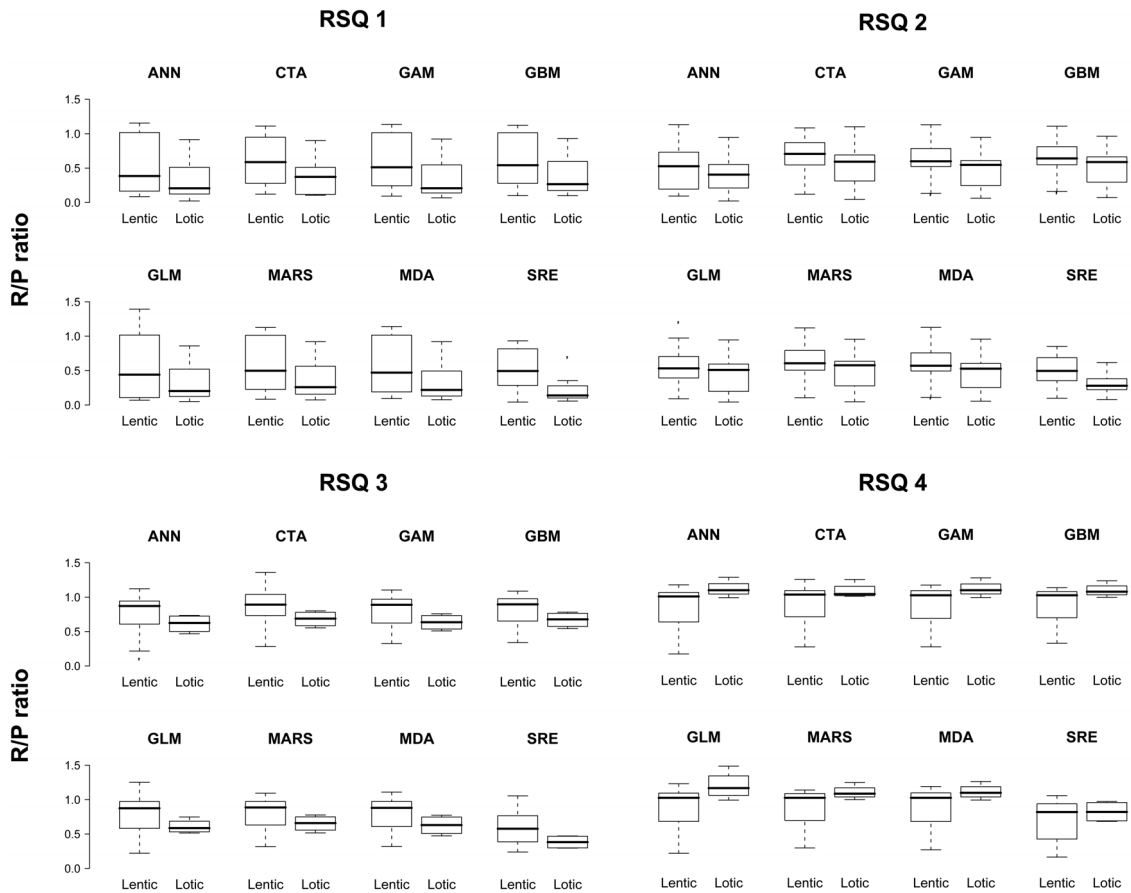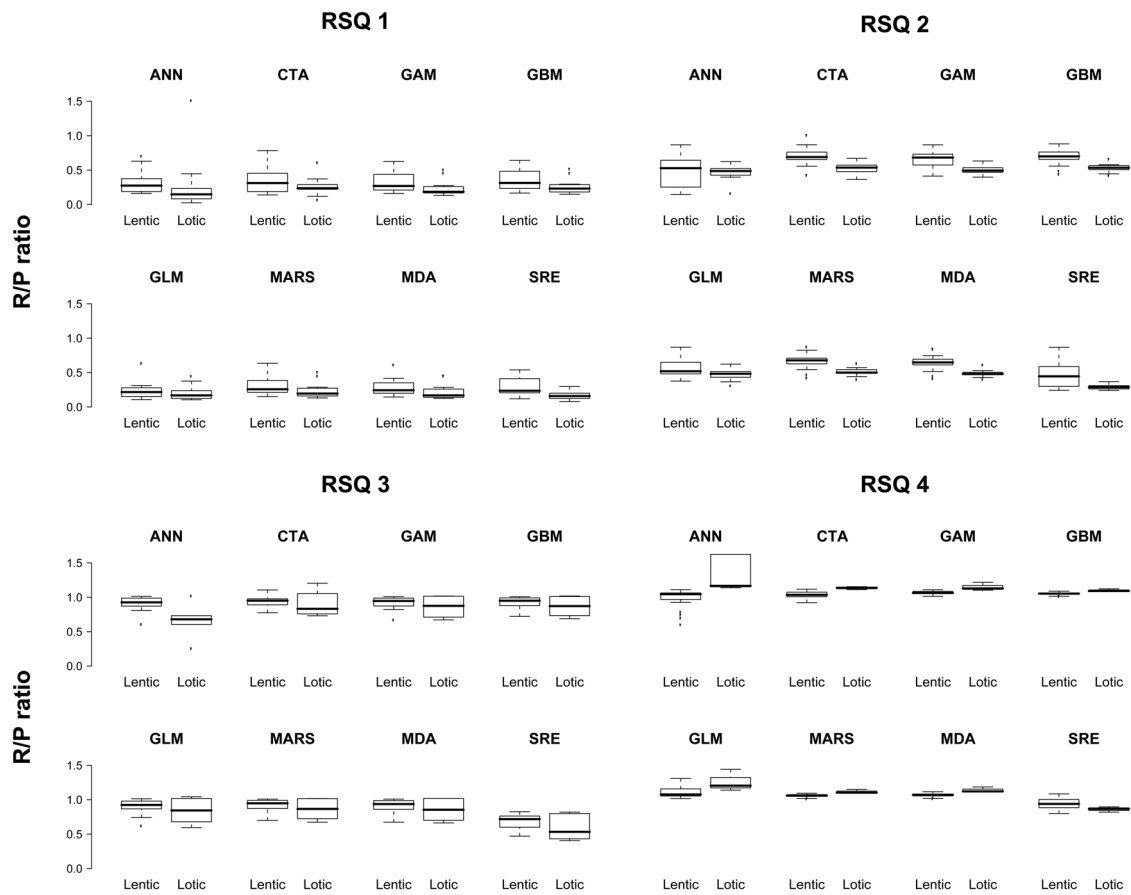
Figure S3 | Box-and-whisker plots of the effect of habitat type on R/P ratios of European lentic and lotic dragonflies for different SDM techniques, 2006. Projected range sizes were translated into presences and absences from probabilities of occurrence using ROC-based thresholds. R/P ratio comparisons were plotted separately for each of the four range size quartiles of the species in the dataset (the first quartile consisting of the 25% of the species with the smallest range sizes, the fourth quartile consisting of the 25% of the species with the largest range sizes). Note that the number of lentic and lotic species per range size quartile was not equally distributed: ([quartile, N_{lentic}, N_{lotic}] 1st, 12, 11; 2nd, 14, 9; 3rd, 17, 6; 4th, 20, 3). See Fig. S1 for SDM technique acronyms and for an explanation of the box-and-whisker plots.

Figure S4 | Proportion of true positives, TP, and true negatives, TN, for European lotic and lentic dragonflies according to different species distribution models. TP and TN proportions were plotted separately for each of the four range size quartiles of the species in the dataset (the first quartile consisting of the 25% of the species with the smallest range sizes, the fourth quartile consisting of the 25% of the species with the largest range sizes). Note that the number of lentic and lotic species per range size quartile was not equally distributed: ([quartile, N_{lentic}, N_{lotic}] 1st, 12, 11; 2nd, 14, 9; 3rd, 17, 6; 4th, 20, 3). See Fig. 2 for details on TP and TN calculation; see Fig. S1 for SDM technique acronyms.

APPENDIX

Supplementary chapters A-C

Supplementary chapter A

Latitudinal variation of diversity in European freshwater animals is not concordant across habitat types

RESEARCH PAPER

Latitudinal variation of diversity in European freshwater animals is not concordant across habitat types

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ABSTRACT

Aim We analysed the variation of species richness in the European freshwater fauna across latitude. In particular, we compared latitudinal patterns in species richness and β-diversity among species adapted to different habitat types.

Location Europe.

Methods We compiled data on occurrence for 14,020 animal species across 25 pre-defined biogeographical regions of European freshwaters from the *Limnofauna Europaea*. Furthermore, we extracted information on the habitat preferences of species. We assigned species to three habitat types: species adapted to groundwater, lotic (running water) and lentic (standing water) habitats. We analysed latitudinal patterns of species richness, the proportion of lentic species and β-diversity.

Results Only lentic species showed a significant species–area relationship. We found a monotonic decline of species richness with latitude for groundwater and lotic habitats, but a hump-shaped relationship for lentic habitats. The proportion of lentic species increased from southern to northern latitudes. β-Diversity declined from groundwater to lentic habitats and from southern to northern latitudes.

Main conclusions The differences in the latitudinal variation of species richness among species adapted to different habitat types are in part due to differences in the propensity for dispersal. Since lentic habitats are less persistent than lotic or groundwater habitats, lentic species evolved more efficient strategies for dispersal. The dispersal propensity of lentic species facilitated the recolonization of central Europe after the last glaciation. Overall, we stress the importance of considering the history of regions and lineages as well as the ecological traits of species for understanding patterns of biodiversity.

Keywords
β-Diversity, dispersal, Europe, freshwater, glaciations, history, latitude, species richness.

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INTRODUCTION

Although it has been known about for more than 200 years, the decrease of species richness with latitude is still poorly understood (Fischer, 1960; for recent reviews see Willig *et al.*, 2003; Hillebrand, 2004; Mittelbach *et al.*, 2007). Besides the mid-domain effect (Colwell & Lees, 2000), three classes of hypotheses have been proposed to explain this pattern: (1) the species–energy hypothesis, which states that species richness is determined by energy availability (Currie, 1991; Hawkins *et al.*, 2003); (2) the species–area hypothesis, which points to the importance of space for species richness (Terborgh, 1973; Rosenzweig, 1995); and (3)

the historical hypothesis which emphasizes the importance of history, in particular climatic fluctuations (Fischer, 1960; Dynesius & Jansson, 2000; Graham *et al.*, 2006). In Europe the climatic fluctuations during the Pleistocene had dramatic impacts on diversity patterns, since the east–west orientation of the major mountain ranges impeded rearrangements of distributional areas in response to climatic fluctuations (see, e.g., Whittaker *et al.*, 2007, and references therein).

Habitat is an important template for the evolution of species traits, in particular for dispersal ability (Southwood, 1962; 1977). For freshwater ecosystems, studies initiated by I. Ribera and co-workers highlighted the importance of interactions between

C. Hof *et al.*

habitat stability, dispersal ability and patterns of species distributions (Ribera & Vogler, 2000; Ribera *et al.*, 2001, 2003; see also Hof *et al.*, 2006; Marten *et al.*, 2006; Ribera, 2008). Our study is an extension of this work covering a broader range of taxonomic groups and habitat types and analyzing β-diversity among biogeographical regions. It is, like the foregoing investigations, based on the following hypothetical framework: On geological time-scales lentic habitats (standing waters) are less stable than lotic (running waters) or groundwater habitats (Gibert *et al.*, 1994; Dobson & Frid, 1998; Griebler & Mösslacher, 2003; Ribera, 2008). The majority of the larger lakes in Europe, for instance, date back to the Pleistocene (Schwoerbel, 1999). On the contrary, several European river systems originated in the Mesozoic (Hantke, 1993). Depending on size, lentic waters may even disappear within decades as sediments accumulate in the basins (Hutchinson, 1957; Harper, 1992). Overall, lentic habitats are likely to vanish within shorter periods of time than lotic habitats. Hence, one would expect species living in lentic habitats to be characterized by a higher propensity for dispersal than species living in lotic or groundwater habitats (Dobson & Frid, 1998; Ribera & Vogler, 2000; Ribera *et al.*, 2003; Marten *et al.*, 2006; Ribera, 2008).

From this, we deduce two predictions concerning latitudinal patterns of species richness and β-diversity in European freshwater animals. Firstly, if lentic species have a higher propensity for dispersal, they should have more rapidly recolonized central and northern regions. Hence we expect that species richness of lentic habitats should decrease with latitude at a lower rate compared with lotic or groundwater habitats. This implies also that the proportion of lentic species increases with latitude. Furthermore, dispersal influences species turnover (β-diversity) (Soininen *et al.*, 2007a,b). Therefore, we secondly expect lower levels of β-diversity among regions for lentic compared with lotic and groundwater species.

METHODS

The data for the present analyses were extracted from the *Limnofauna Europaea* (Illies, 1978). The biogeographical regions of Europe outlined in this book were used for all analyses (Table 1). For each region, data on latitude (northern and southern boundary), longitude (western and eastern boundary) and maximum altitude were compiled from http://earth.google.com/. From this information we calculated the mean latitude and longitude of each region. Areas of regions were estimated by weighing pieces of paper cut from a copied map. Note that four of the 25 regions are open at their eastern border, which may

Table 1 Geographical data and species richness of all habitats, and of the different habitat types of the 25 biogeographical regions of Europe as defined in the *Limnofauna Europaea* (Illies, 1978).

						Species richness			
Region code	Region	Latitudinal centre (°N)	Longitudinal centre (°E)	Maximum altitude (m)	Area (km²)	All habitats	Groundwater habitats	Lotic habitats	Lentic habitats
IBE	Ibero-Macaronesian region	38.23	−12.24	3717	560,736	2543	99	633	741
PYR	Pyrenees	42.53	0.54	3404	49,548	1684	82	510	395
ITA	Italy, Corsica and Malta	40.98	12.97	3380	264,311	3284	135	709	1018
ALP	Alps	45.81	10.82	4808	210,580	4479	96	989	1426
DIN	Dinaric western Balkans	44.37	17.71	2656	161,032	2543	170	683	682
HEL	Hellenic western Balkans	39.13	23.76	2917	173,419	2258	100	566	729
EAB	Eastern Balkans	41.73	25.07	2925	177,548	2161	74	564	623
WEH	Western highlands	47.36	5.53	1886	156,903	2776	101	706	888
CEH	Central highlands	49.74	12.50	1602	260,129	4922	133	927	1717
CAR	Carpathians	47.15	22.07	2655	185,806	3842	130	884	1112
HUN	Hungarian lowlands	46.48	19.72	500	169,290	3187	67	421	1098
PON	Pontic province	45.83	30.18	1545	264,258	2819	50	345	939
WEP	Western plains	46.90	0.61	1000	404,644	3690	106	609	1280
CEP	Central plains	55.17	9.27	500	540,902	5465	77	627	2213
BAP	Baltic province	56.93	24.23	318	210,580	3163	13	347	1263
EAP	Eastern plains	53.48	38.66	1000	2,320,511	3792	27	445	1442
IRE	Ireland and Northern Ireland	53.39	−8.01	1041	82,580	1669	9	249	691
GBR	Great Britain	56.16	−3.44	1344	235,354	3490	33	492	1350
ICE	Iceland	64.91	−19.02	2110	103,226	475	2	28	204
BOR	Borealic uplands	64.13	13.06	2469	309,677	2153	4	276	1004
TUN	Tundra	71.53	44.68	1590	330,219	1365	6	193	540
NSW	Northern Sweden	64.60	17.44	1200	231,225	1954	12	254	849
TAI	Taiga	63.03	39.71	1000	1,606,190	2896	9	312	1221
CAU	Caucasus	42.12	44.07	5642	363,354	2089	65	391	606
CAS	Caspic depression	48.08	47.03	500	627,612	1591	5	144	532

introduce some bias due to the distribution of singletons or the calculation of areas. All these areas are located in the European part of Russia. Therefore, we used the Ural Mountain chain as the eastern boundary of these regions. It is well known that the Ural Mountains act as a biogeographical boundary, which is not crossed by most of the species occurring in central Asia or Siberia.

For each region we compiled species presences or absences. The taxonomy as well as recent changes in species names were updated using the Fauna Europaea Web Service (2004). Our initial compilation listed 14,457 species, and after considering taxonomic changes and uncertain species the final list comprised 14,020 species of fish, annelids, water mites, crustaceans, insects, molluscs, nematodes, rotifers, flatworms and several taxa of fewer than 150 species (for an overview on species numbers of these major taxonomic groups, see Table S1 in Supplementary Material). The *Limnofauna Europaea* provides information of the habitat requirements for most of the species listed. From the more than 40 habitat categories given in the *Limnofauna* we grouped species into three major habitat types: groundwater, lotic (running waters from springs to large streams) and lentic habitats (standing waters from phytotelmata to large lakes). For a number of reasons we had to exclude 46% of the total species pool: (1) we had to exclude the 2663 species for which no habitat preferences where available; (2) we excluded 1958 generalists for which a habitat assignment was impossible; (3) we excluded 1025 parasitic species, as they rather rely on a specific host than on a certain type of habitat; (4) we excluded the 476 species occurring in brackish waters or with very special habitat requirements (e.g. leaf miners of aquatic plants, species living in mosses like tardigrades etc.).

Geographical variables and species richness of the different habitat types were tested for normality using the Kolmogorov–Smirnov test (StatSoft Inc., 2002). All variables except area approximated a normal distribution. Area was $\log_{10}$-transformed in all analyses, after which it also attained normality. We calculated simple linear regressions to test for the effect of area on species richness across the 25 regions. To analyse the relationship between species richness and latitude, we used multiple linear regressions. We always tested for the effect of latitude on species richness after correcting for all other geographical variables (for a visual inspection of the relationships between species richness and latitude, longitude, altitude and area see Fig. S1). The plot of species richness vs. latitude suggested a hump-shaped

Table 2 Slope and correlation coefficients for the relationship between species richness and area ($\log_{10}$-transformed) for the three different habitat types (simple linear regressions, $n = 25$).

Habitat type	Slope	R	P
Groundwater habitats	−29.16	0.044	0.32
Lotic habitats	−48.58	0.0050	0.74
Lentic habitats	+537.4	0.19	0.031

relationship. Therefore, we also included squared latitude as an independent variable in some analyses. To investigate the relationship between the proportion of lentic species and latitude, we used a multiple generalized linear model (binomial error term, logit link function, forward selection; Crawley, 2002). Patterns of β-diversity among regions were investigated by means of additive partitioning of species diversity (Crist *et al.*, 2003) for each of the three habitats. For this analysis, regions were grouped into four latitudinal bands according to their latitudinal centres (< 45° N, between 45° N and 50° N, between 50° N and 60° N, > 60° N; see Fig. 2). Areas of regions were used as weights.

RESULTS

We found a significant species–area relationship only for lentic habitats (Table 2). The relationship of species richness and latitude differed between lentic habitats compared with lotic and groundwater habitats. In the latter species groups, species richness declined monotonically with latitude, whereas lentic species exhibited a hump-shaped relationship (Table 3, Fig. 1, Fig. S2). Species richness of lentic species peaked in central Europe, within a region covering the Netherlands, the northern part of Germany, the southern part of Scandinavia and parts of Poland (region CEP, see Table 1 and Fig. 2). The proportion of lentic species increased significantly from southern to northern latitudes (deviance = 647.2, $P < 0.0001$; Fig. 3). Even after considering the other geographical variables this pattern remained significant (Table 4). Additive partitioning of species diversity revealed a decline of β-diversity from groundwater to lotic to lentic species (Fig. 2). Furthermore, for each of the three habitat types, β-diversity decreased from southern to northern latitudes (Fig. 2).
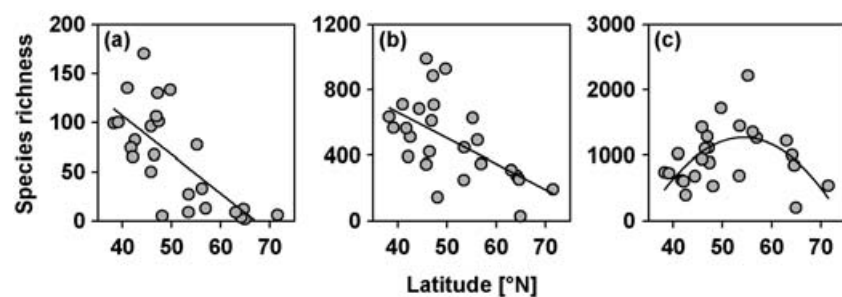

Figure 1 Relationship between latitude and species richness for freshwater species occurring within three different habitat types: (a) groundwater habitats, (b) lotic habitats, (c) lentic habitats. Each point represents the number of species occurring in the respective habitat within one of the 25 regions shown in Fig. 2.

Table 3 Multiple linear regressions of species richness for freshwater animals within 25 European biogeographical regions vs. geographical variables (type I sum of squares; StatSoft Inc., 2002) according to different habitat types. Significant relationships are indicated in bold.

	β	MSS	F	P		β	MSS	F	P
Groundwater habitats					**Lentic habitats**				
Area	0.001	2589	1.7	0.206	Area	0.48	894,966	6.8	**0.017**
Longitude	−0.13	557	0.37	0.551	Longitude	−0.18	289,230	2.2	0.154
Altitude	0.14	9485	6.3	**0.021**	Altitude	−0.037	225,321	1.7	0.206
Latitude	0.37	19,174	12.7	**0.002**	Latitude	5.4	73,866	0.56	0.462
Latitude^2	−1.0	349	0.23	0.636	Latitude^2	−5.4	820,983	6.3	**0.022**
Residuals		1510			Residuals		131,343		
Lotic habitats									
Area	0.15	7008	0.16	0.690					
Longitude	−0.17	39,051	0.91	0.352					
Altitude	0.31	222,965	5.2	**0.034**					
Latitude	2.8	289,894	6.8	**0.018**					
Latitude^2	−3.3	90,277	2.1	0.163					
Residuals		42,815							

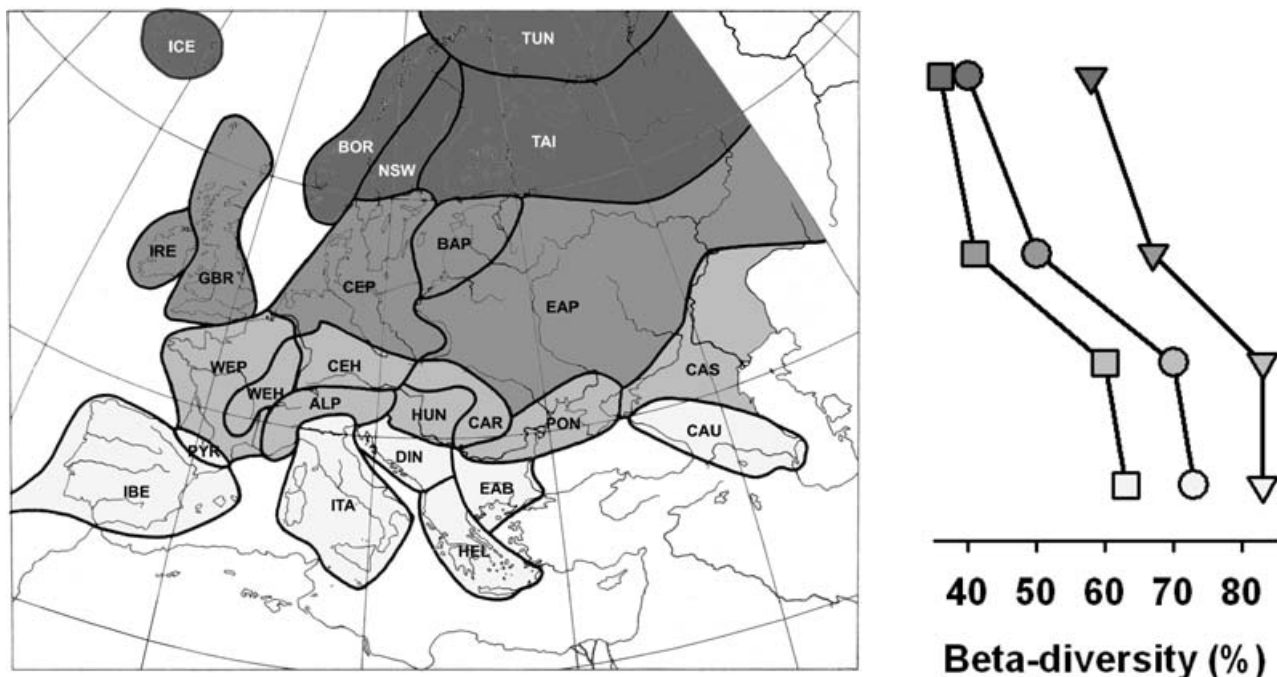MSS, mean sum of squares; β, standardized regression coefficient.

Figure 2 β-Diversity of freshwater animals within four bands of regions across Europe. We calculated β-diversity for each band and habitat using additive partitioning of species richness (Crist *et al.*, 2003). A value of 100% would indicate that all species occur in only one region of a band and a value of 0% that all species occur in all regions of a band. Regions of a band are marked by the same colour. β-Diversity decreased from groundwater species to lentic species for all four bands and β-diversity decreased with latitude for all habitat types (square, lentic habitats; circle, lotic habitats; triangle, groundwater). Region codes are listed in Table 1.

DISCUSSION

Our analyses showed (1) a monotonic decline of species richness with latitude for groundwater and lotic habitats, but a hump-shaped relationship for lentic habitats; (2) an increase in the proportion of lentic species with increasing latitude; and (3) a decline in β-diversity from groundwater to lotic to lentic habitats and from southern to northern latitudes.

The observed patterns in species richness might be caused by a variation in the sampling effort among regions (Bardgett *et al.*, 2005; Moerman & Estabrook, 2006). As many, if not most, ecologists and taxonomists reside in central Europe, the fauna of this region is very well known (Illies, 1966; Bardgett *et al.*, 2005). We argue that this bias does not sufficiently explain the observed variation of richness. First, since the fauna of groundwater habitats is not very well known (Gibert *et al.*, 1994; Griebler &
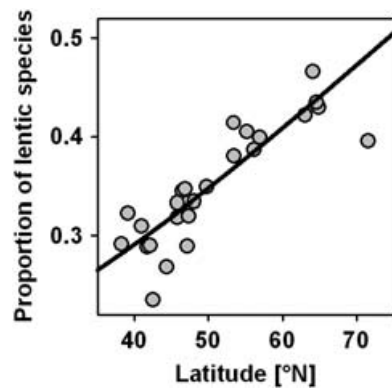
Figure 3 Proportion of lentic species in relation to latitude. Each point represents the proportion of species occurring in lentic habitats of the 25 regions shown in Fig. 2. The curve visualizes a generalized linear model (deviance = 647.2; $P < 0.0001$; $y = e^{-1.93 + 0.026 \times \text{latitude}} (1 + e^{-1.93 + 0.026 \times \text{latitude}})^{-1}$).

Table 4 Relationships between the proportion of lentic species within 25 biogeographical regions of Europe vs. geographical variables (multiple generalized linear model, binomial error term, logit link function, forward selection, Crawley, 2002, $n = 25$).

	Estimate	Deviance	P
Area	0.13	134	< 0.001
Longitude	−0.0029	16.9	< 0.001
Altitude	−0.000028	238	< 0.001
Latitude	0.037	324	< 0.01
Latitude^2	−0.00013	1.03	0.31

Mösslacher, 2003), sampling should particularly influence the species numbers within this group. However, species richness of the groundwater fauna declined with latitude (Fig. 1a). Second, the number of species recorded in only one sample (singletons) is a good indicator of the sampling effort (Novotný & Basset, 2000). In our case the number of singletons in a region has two components: species with a restricted geographical range (endemics) and species accidentally recorded in only one region. The latter is an indication of the sampling effort. If the hump-shaped pattern is a consequence of the extensive sampling in central Europe, then we would expect: (1) that species groups with a hump-shaped relationship have a high proportion of singletons; and (2) that there is also a hump-shaped relationship between the number of singletons and latitude. However, the hump-shaped relationship occurs in species adapted to lentic habitats (Table 3, Fig. 1c), which have a rather low proportion of singletons compared with lotic and groundwater species (Table S2). Furthermore, for all three species groups the number of singletons declines with increasing latitude (Fig. S3).

Although the areas of the biogeographical regions differed by a factor of more than 40 (Table 1), area was a poor predictor of species richness for species adapted to lotic and groundwater

habitats. One may argue that terrestrial surface area is not a good surrogate for area covered by freshwaters. For groundwater habitats, though, the terrestrial surface area roughly approximates habitat area, as groundwater is a type of freshwater habitat that should be available almost everywhere below the surface (Gibert *et al.*, 1994; Griebler & Mösslacher, 2003). However, for groundwater species, the relationship between species richness and area was negative (Table 2). If one accepts that our failure to find a species–area relationship for groundwater or lotic habitats is not due to a bias, the difference in the significance between lotic and lentic habitats becomes interesting. A non-significant relationship between area and species richness may be due to non-equilibrium conditions (MacArthur & Wilson, 1963; Ricklefs & Bermingham, 2004), which points to differences in the equilibrium conditions between groundwater and lotic vs. lentic biota. We will return to this point below.

Many papers have documented that species richness increases with several surrogates of energy available to the communities of plants or animals (Wright, 1983; Currie, 1991; Badgley & Fox, 2000; Hawkins *et al.*, 2003). Even if the geographical resolution of our data is not sufficient for a meaningful evaluation of the energy-availability hypothesis, the monotonic decline of species richness with latitude that was observed for lotic and groundwater habitats is consistent with a latitudinal decline of energy availability. Nevertheless, the surprising difference in the latitudinal variation of species richness among species adapted to different habitats rejects the energy-availability hypothesis as a *general* explanation.

We are aware of four possible explanations for the observed differences in diversity patterns among habitats: (1) evolutionary idiosyncrasies; (2) differences in habitat availability; (3) differences in the location of refugia; and (4) differences in the dispersal propensity of species among habitats. These are discussed in turn below.

(1) We pooled a wide variety of taxa with very different phylogenetic backgrounds. This could lead to differences in diversity patterns between habitats if certain taxa of species adapted to a particular habitat dominate certain regions. To investigate if such evolutionary idiosyncrasies are responsible for the decrease of species richness with latitude in lotic and groundwater habitats, we tested whether the observed correlations are expected by chance, i.e. whether the phylogenetic assignment drives the pattern. For this, we randomized habitat preference across species and calculated the correlation coefficient for the relationship between species richness and latitude (for a detailed explanation see Fig. S4). For both lotic and groundwater habitats, the correlation coefficient expected by chance was negative, but all simulated coefficients were larger than the observed coefficients. Consequently, evolutionary idiosyncrasies are not sufficient to explain the decrease of species richness with latitude.

(2) The availability of the habitat types across the 25 biogeographical regions might also explain the observed differences in the latitudinal variation of species richness. This argument is partly related to our discussion of the species–area relationship. For groundwater habitats, terrestrial area approximates the available

C. Hof *et al.*

habitat area. Our failure to find a species–area relationship for this habitat type suggests that the availability of habitats is not sufficient to explain the diversity patterns of freshwater species. Ribera *et al.* (2003) also argued consistently against this habitat-availability hypothesis. Nevertheless, further investigations are needed for a convincing test of this hypothesis.

(3) After the last glaciation many species recolonized central Europe from Mediterranean refugia (de Lattin, 1957; Hewitt, 1999). However, recent studies have demonstrated the existence of glacial refugia north of the Alps (Stewart & Lister, 2001; Pauls *et al.*, 2006; Kristjánsson & Svavarsson, 2007). Furthermore, a considerable number of species may have colonized central Europe from eastern regions (e.g. Banarescu, 1990; Kotlík *et al.*, 2004). Irrespective of the location of the refugia, the recolonization of Europe should be biased towards species with a high dispersal propensity. The decrease of β-diversity from southern to northern regions may also be a legacy of the recolonization of the higher latitudes after the Pleistocene (Hewitt, 1999; 2000).

(4) Lentic species are assumed to show a higher propensity for dispersal than lotic species. The differences in β-diversity among species adapted to groundwater, lotic and lentic habitats are perfectly consistent with the proposed differences in the dispersal propensity of species associated with these habitats, because with an increasing propensity for dispersal one expects a decrease in β-diversity (Soininen *et al.*, 2007a,b). From this, in turn, one may deduce the hypothesis that the decrease of species richness with latitude in lotic as well as groundwater habitats is due to a low recolonization rate. The increase in the proportion of lentic species with latitude supports this argument. Consequently one might argue that the communities of lotic and groundwater habitats have not yet reached equilibrium in central and northern Europe. In contrast, lentic species may have reached equilibrium, which is also suggested by a significant species–area relationship (see above). Furthermore, low dispersal rates facilitate speciation (Bohonak, 1999; Marten *et al.*, 2006), which should lead to a higher speciation rate in lotic as well as groundwater species compared to lentic species (Ribera & Vogler, 2004). The rugged topographic relief of the Mediterranean regions may have further contributed to a higher speciation rate (Mayr, 1942; Hewitt, 1999). The high levels of β-diversity in southern Europe are concordant with a higher speciation rate in the Mediterranean. However, we found this difference in lotic and lentic species. Therefore, differences in the speciation rate of lentic and lotic species do not sufficiently explain the observed difference in the relationship between species richness and latitude among lentic and lotic species.

None of these four factors that may have influenced the difference in the relationship between species richness and latitude among the different habitat types can account for the hump in species richness of lentic freshwater animals in central Europe. We propose three possible processes that might have generated this pattern. First, a considerable number of lentic species could have gone extinct in the southern refugia after the last glaciation, when the Mediterranean climate shifted to semi-arid conditions (Salinas *et al.*, 2000; Oliva-Paterna *et al.*, 2003). Note that this argument is not consistent with the foregoing, that habitat availability is not supposed to drive the observed patterns. Second, if lentic species are stronger dispersers, more species from eastern refugia may have reached central Europe. At the end of the last Ice Age, huge proglacial lakes provided pathways of recolonization for lentic species (e.g. Schäfer, 1997). However, our data indicate a decrease in the proportion of lentic species from west to east (Table 4). Consequently, this explanation also seems to be rather unlikely. Third, the mid-domain effect predicts a hump in species richness in the centre of a geographical domain (Colwell & Lees, 2000). This model places geographical ranges of species randomly across the available space. Furthermore, it assumes that biota are close to equilibrium. Indeed, due to their higher dispersal ability, lentic species should be near equilibrium conditions (see also above), so the mid-domain effect might be useful to approach an explanation of the species richness peak in lentic species in central Europe.

With our study, we underline that to understand differences in the spatial variation of biological diversity among taxa one has to consider the history of regions and lineages (Graham *et al.*, 2006; Rahbek *et al.*, 2007; Reyjol *et al.*, 2007; Svenning & Skov, 2007) as well as the ecological traits of species (Ribera *et al.*, 2003; Vogler & Ribera, 2003; Hof *et al.*, 2006; Marten *et al.*, 2006; McPherson & Jetz, 2007; Ribera, 2008). Furthermore, our analyses support previous studies which document that various European groups of plants and animals are not in equilibrium with current climate (Svenning & Skov, 2004; Araújo & Pearson, 2005; Araújo *et al.*, 2008).

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Table S1 Taxonomic groups included in the analyses.

Table S2 Habitat types used in the *Limnofauna Europaea*.

Figure S1 Relationships between species richness and geographical variables.

Figure S2 Relationships between latitude and residuals of the regression of species richness and area.

Figure S3 Relationships between number of singletons and latitude.

Figure S4 Distribution of simulated correlation coefficients of the relationship between species richness and latitude for randomized habitat preference.

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BIOSKETCHES

Christian Hof is broadly interested in biodiversity research, particularly in the fields of macroecology, biogeography and conservation biology. Parts of this study were part of his MSc thesis at the Department of Animal Ecology of the University of Marburg. He is now a PhD student at the Center for Macroecology of the University Copenhagen, where he investigates the impacts of climate change on global biodiversity.

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Supplementary chapter B

Partitioning and mapping uncertainties in ensembles of forecasts of species turnover under climate change

Partitioning and mapping uncertainties in ensembles of forecasts of species turnover under climate change

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Forecasts of species range shifts under climate change are fraught with uncertainties and ensemble forecasting may provide a framework to deal with such uncertainties. Here, a novel approach to partition the variance among modeled attributes, such as richness or turnover, and map sources of uncertainty in ensembles of forecasts is presented. We model the distributions of 3837 New World birds and project them into 2080. We then quantify and map the relative contribution of different sources of uncertainty from alternative methods for niche modeling, general circulation models (AOGCM), and emission scenarios. The greatest source of uncertainty in forecasts of species range shifts arises from using alternative methods for niche modeling, followed by AOGCM, and their interaction. Our results concur with previous studies that discovered that projections from alternative models can be extremely varied, but we provide a new analytical framework to examine uncertainties in models by quantifying their importance and mapping their patterns.

Environmental niche models, or species distribution models (SDM), are frequently used to forecast shifts in species geographic distributions under climate change (Peterson et al. 2002, Thomas et al. 2004a, Thuiller et al. 2005a, b, Araújo et al. 2006, Lawler et al. 2009). When species ranges closely match their potential niche, associations between species ranges and environmental factors can be reliably used to estimate the ecological requirements of species (Araújo and Guisan 2006, Soberón 2007). Estimated associations can then be utilized to forecast species range shifts and related changes in biodiversity patterns under climate change scenarios.

It is widely acknowledged that SDMs provide a simplified representation of the processes governing the geographic distributions of species (Pearson and Dawson 2003, Guisan and Thuiller 2005). Actually, multiple ecological and evolutionary processes, operating at different spatial and temporal scales, are expected to determine contemporary distributions of most species (Araújo et al. 2008, Pearman et al. 2008), and several of these processes are poorly represented in the models (Guisan and Thuiller 2005). In addition to ecological uncertainties, there are several sources of methodological uncertainty that have been discussed in a number of recent studies (Thuiller et al. 2004, Araújo et al. 2005a, b, Pearson et al. 2006, 2007,

Marmion et al. 2009). Nevertheless, and despite computational and methodological advances, the decision as to which model to use is often ad hoc (Araújo and New 2007), and there is little agreement regarding the relative performance of alternative niche-based techniques and overall modeling strategies for forecasting species distributional changes under climate change (Araújo and Rahbek 2006, Dormann 2007, Peterson et al. 2007, Phillips 2008).

Methodological uncertainties may arise because of differences in data sources and statistical methods used for niche and climate modeling (Heikkinen et al. 2006). If it is not possible to clearly establish which models are more adequate to a particular problem, a potential solution to take inter-model variability into account is to fit multiple models, or ensembles, and combine them into some sort of consensus forecast (for reviews see Araújo and New 2007, Leutbecher and Palmer 2008). Recent studies suggested that improvements in the forecasts could be achieved if ensembles were obtained and the results were appropriately analyzed (Araújo et al. 2005a, 2006, Marmion et al. 2009, Roura-Pascual et al. 2009). For instance, some widely used methods for niche modeling, such as GARP, Neural Networks, and Random Forests do generate multiple projections and combine them into a single consensus solution (Lawler et al. 2009, O'Hanley 2009, see also

Table 1 in Araújo and New 2007). The new version of the BIOMOD software allows different methods to be fitted and projections to be compared and combined (Thuiller et al. 2009).

However, existing approaches sparsely sample all possible uncertainties from models (Araújo and New 2007). For example, it is difficult to fully explore uncertainties arising from data uncertainty or from the large numbers ensembles of AOGCM (Atmosphere-Ocean General Circulation Models) that are currently being generated. There is indeed a possibility that some sources of methodological and technological uncertainty, such as climate models and emission scenarios, might be more important than how the parameters of particular method are estimated (Thomas et al. 2004b, Berthelot et al. 2005, Stainforth et al. 2005). Techniques for handling and combining large ensembles of forecasts are also in their infancy and consensus projections may hide variability arising from disparate sources of uncertainty with existing tools being unable to successfully disentangle them. Thus, a more detailed analysis of the sources of uncertainties and their patterns is important to improve modeling strategies and to define over which sources an ensemble is necessary.

Here, we develop a new quantitative approach to analyze uncertainties in large ensembles of forecasts and disentangle the contribution of individual sources of variation entering the models. This approach is based on a spatially-explicit decomposition of total sum of squares of the ensemble-forecasted values of faunal turnover. Thus, our approach provides maps of uncertainty and allows an investigation of the regions more affected by particular sources of uncertainty. Buisson et al. (2009) proposed an alternative approach to partition the variance in ensembles of forecasts of species distributional changes that also allows an exploration of the geographic components of uncertainty. We applied our approach to understand the uncertainties in forecasts of species turnover maps of New World birds under climate change. Our study provides a comprehensive ensemble forecasting experiment to assess the relative contribution of seven species distribution models, five climate models, and two emission scenarios. Although other sources of uncertainty exist, our approach can be quickly expanded in the future to incorporate other sources of variation and thus it provides a fine perspective that enables new insights on how to better evaluate shifts in biodiversity patterns and what are the greatest challenges at different levels of the modeling process.

Material and methods

Data

Data on the extent of occurrence (range filling) for 3837 species of the New World birds were downloaded from the NatureServe <www.natureserve.org/getData/birdMaps.jsp> and resampled to a grid of $1° \times 1°$ latitude/longitude. A similar approach for deriving species presence and absence maps from extent of occurrence data was adopted by Lawler et al. (2009). Although we acknowledge that this is not the most commonly used approach to model species distributions (which is usually based on more detailed data of species occurrences and fine scale environmental data), this allows a first understanding of continental patterns in species turnover based on a very large number of species.

Climatic data for species distribution modeling were derived from five coupled Atmosphere-Ocean General Circulation Models (AOGCMs), including CCSM3, CSIRO-Mk3.0, UKMO-HadCM3, ECHAM5/MPI-OM and MIROC. Although other AOGCMs are available, this selection covers a wide range of different predictions and was defined to maximize the different degree of predicted climate warming. The AOGCMs used here have different equilibrium climate sensitivity values ranging from 2.7°C to 4.3°C. Equilibrium climate sensibility is the annual mean surface air temperature change experienced by the climate system after it has attained a new equilibrium in response to a doubling of CO_2 concentration, and are within the range of all AOGCMs available from IPCC. These models also tried to encompass projections with different spatial resolutions, ranging from $1.1° \times 1.1°$ to $3.75° \times 3.75°$ latitude/longitude in the original set. Data were extracted from the World Climate Research Program's (WCRP) Coupled Model Intercomparison Project phase 3 (CMIP3) multi-model dataset (Meehl et al. 2007).

Outputs for each model were obtained for two emission scenarios (A1 and B1) that are available for all AOGCMs selected above. In general, scenarios A1 and B1 can be roughly classified as "pessimistic" and "optimistic", respectively, according to the CO_2 emissions. The A1 storyline and scenario family assumes a future of very rapid economic

Table 1. Median proportions of the total sum of squares from the three-way ANOVA performed for each grid cell covering the New World, evaluating the relative contributions of method for niche modeling, AOGCM and emission scenario to the variability in forecasting species turnover. Minimum and maximum values in the maps are also given (see also Fig. 3). Geographical patterns in each variance component are estimated by Moran's I coefficient in the first distance class and by correlogram intercept (in km).

Source	SS(%)		Geographical patterns	
	Median	Min-max	Moran's I*	Correlogram intercept (km)
Method	66.10	3.8–94.7	0.489	4014
AOGCM	13.80	1.2–47.4	0.399	3088
Scenario	0.01	0.0–20.0	0.155	643
Method × AOGCM	11.80	1.3–40.9	0.259	643
Method × Scenario	0.70	0.0–15.7	0.219	1646
AOGCM × Scenario	3.10	0.0–34.3	0.242	1646
Third-order interaction	2.30	0.2–15.2	0.199	643

*All Moran's I significant at $p < 0.01$.

growth and rapid introduction of more efficient technologies, but low population growth. A major underlying theme is a substantial reduction in regional differences in per capita income and, more specifically, the A1 scenario used here assumes a balanced mix of technologies and supply sources, with technology improvements and resource assumptions, including that no single energy source is overly dominant (IPCC 2000). The other scenario used herein (B1), also starts from the same low population growth rate, but it differs from A1 in assuming rapid changes in economic structures toward a service and information economy, with reductions in material intensity, and the introduction of clean and resource-efficient technologies. The emphasis is on global solutions to economic, social, and environmental sustainability, including improved equity, but without additional climate initiatives (IPCC 2000).

For each one of the AOGCMs and emission scenarios, four variables were obtained for both present time (baseline used to calibrate the models, the average values from 1970 to 1999) and future (estimated 2070–2099 interval, 2080 for simplicity hereafter). Variables used were mean annual rainfall and variability, average temperature of the warmest and coldest months. Rather than only using all these variables simultaneously to predict the geographic ranges of all species, the 15 combinations ($2^P - 1$, where $p = 4$) of these four variables (Fig. 1) were used in independent models, accounting them for eventual differences in ecological processes driving geographic distributions of species across the New World. These variables encompass the major hypotheses which are often raised to explain patterns of species richness at global scale (Hawkins et al. 2003).

Modeling species distributions

For each species, data were randomly divided into calibration and validation sets comprising 75 and 25% of the species' range, respectively, and the procedure was repeated 50 times, maintaining the observed prevalence of species in each partition (i.e. for presence only methods, 75% of the cells within the species' range, randomly defined, were used for modeling, whereas for presence–absence methods the analyses were conducted using a random sample of 75% of cells both inside and outside species' range). Beyond creating independent – or at least partially independent – sets for model calibration and validation, partition also allows to take data uncertainty into account, especially considering that range filling maps tend to have larger commission errors (Hawkins et al. 2008). Thus, each calibration dataset was used to project species distributions, according to seven SDMs described below (which were estimated with the 15 combinations of four environmental variables) on each combination of AOGCM and emission scenario previously defined. For species with range size >10 cells (12% of species), rather than performing a cross-validation 50 times, each of the n cells was deleted once and analyses were repeated n times (roughly equivalent to a Jackknife procedure – Pearson et al. 2007).

We fitted seven species distribution models (SDMs) and projected species potential distributions for baseline and
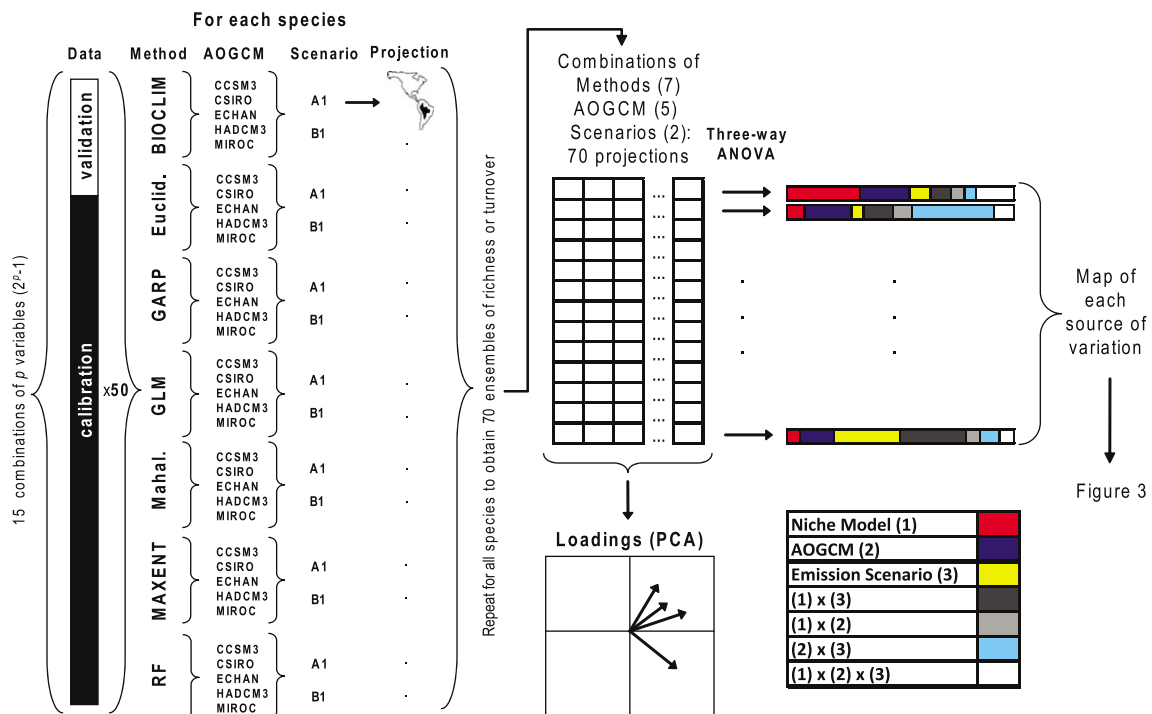

Figure 1. A schematic representation of the analytical framework used to evaluate spatial patterns of uncertainty in ensemble forecasting. Forecasting is generated using 15 combinations of the four bioclimatic variables, based on 50 random replications of calibration/validation datasets, for each method for niche modeling. Projections are based on the five AOGCMs for the two emission scenarios (A1 and B1). Then a three-way ANOVA is applied to each cell and the proportion of the total sum of squares accounted by each source can be mapped. A PCA can be used to evaluate the similarity among the ensemble-based vectors.

future climates (Fig. 1). The modeling methods used included a range of SDMs that are both conceptually and statistically different (Segurado and Araújo 2004, Elith et al. 2006, Tsoar et al. 2007, Philips and Dudík 2008), such as simple surface range envelope models like BIOCLIM (Busby 1991), and Euclidian and Mahalanobis (EUC and MAHAL) distances (Farber and Kadmon 2003). We also fitted Generalized Linear Models (GLM) (McCullagh and Nelder 1989) and more complex machine learning approaches such as Random Forest (RF) (Breiman 2001), Genetic Algorithm for Rule Set Production (GARP) (Stockwell and Noble 1992), and Maximum Entropy (MAXENT) (Phillips et al. 2006, Phillips and Dudík 2008). We developed new computer software – BioEnsembles – in which all these methods were implemented. This software was designed to optimize and take advantage of high-speed parallel processing, both within (multi-processors computers) and between (grid architecture) computers.

Notice that the fitting and projection of alternative models using data partition and the 15 combinations of variables are used here to explore uncertainties from the initial conditions and model parameterization (sensu Araújo and New 2007). However, because of the large number of maps for each species, both the data-splitting procedures and variable selection were not included into the current analysis of sources of uncertainty. Rather, maps resulting from reshuffling data and variables were summed to generate the vector of ensemble frequencies of occurrence of the species for each of the combinations of SDM, AOGCM and emission scenarios (see below).

The True Skill Statistics (TSS) (Allouche et al. 2006), varying between −1 and 1, was used as a fit statistic. It was calculated for each model based on the confusion matrix expressing matches and mismatches of observed and predicted occurrences in the validation data set. This matrix was computed after using ROC curves to convert continuous predictions into presence-absence. Models with TSS smaller than zero were discarded.

Also, it was not possible to fit all methods for all species using different combinations of variables (for example, lack of convergence in GLM or impossibility of inverting the covariance matrix when computing Mahalanobis distances). Most methods cannot deal with species occurring in a single cell (ca 1.2% of the species). Because of these restrictions, not all 3837 species were used for all SDM methods and AOGCMs (Supplementary material Table S1, Fig. S1). Thus, for each method and AOGCM, up to 750 models (50 dataset partitions modeled using 15 combinations of variables) were generated for each species. Finally, this combination of models generates an ensemble-based frequency of species distributions in the future and species are considered to occur in a given cell if at least 50% of the models predict its occurrence there (i.e. a majority consensus rule) (Araújo et al. 2005a, 2006).

Rather than evaluating each species' ensemble distribution independently, we calculated species turnover for each combination of SDM, AOGCM, and scenario, which was based on the number of potential species gained (G) or lost (L) within each cell and given by $(G+L)/(S+G)$ (Thuiller 2004). Notice that species turnover was calculated by comparing potential ranges as modeled in 2070–2099 and the modeled ranges on baseline period, rather than observed ranges.

Evaluating the consistency between projections

Species turnover maps (7 SDM × 5 AOGCMs × 2 emission scenarios, each one based on a maximum number of 750 models for each species) were averaged across each cell, generating a turnover consensus map, as well as standard deviations and coefficients of variation that allow mapping where uncertainty in projections is larger.

To evaluate the origins of variability around this consensus, we submitted the correlation matrix among the 70 projections to a Principal Component Analysis (PCA), as suggested by previous authors (Thuiller 2004, Araújo et al. 2005a, 2006). This allows evaluating the similarity of the projections (values of turnover as predicted by combinations of SDM, AOGCM and emission scenarios) by the loadings (i.e. the Pearson's correlation coefficients between predicted values and the scores) of the interpretable axes, which were defined by the broken-stick criterion (Legendre and Legendre 1998).

The loadings of the PCA can be used to express the relative position (similarity) of the maps from different SDM, AOGCMs and scenarios, whereas the PCA scores are the main directions of covariation among the maps throughout the projections variability. If the first principal component has a large relative eigenvalue, it tends to be highly correlated with the average consensus map and can be used as a consensus map as well (Araújo et al. 2005a, 2006, Marmion et al. 2009).

Mapping the sources of variation around the consensus solution

Although it is trivial to map the mean (consensus) turnover in each cell based on maps generated by different SDM, AOGCMs, and emission scenarios, as well as their variance or coefficient of variation, it is much more difficult to understand the main sources of variation around the consensus. The PCA described above can be used to evaluate similarity of maps, but it does not necessarily allow a formal partition of the sources contributing to the differences among the maps. To address this problem we performed a three-way Analysis of Variance (ANOVA) without replication (Sokal and Rohlf 1995, Legendre and Legendre 1998) for each cell, using species turnover as the response variable and SDM, AOGCM and emission scenarios as factors. We then obtained the sum of squares which can be attributed to each of these sources and their interaction (SDM × AOGCM, SDM × emission scenario, AOGCM × emission scenario and SDM × AOGCM × emission scenario). Notice that because this is a three-way ANOVA without replication, it is impossible to disentangle residual variance (i.e. part of variation not explained by SDM, AOGCM and emission scenario) and variance determined by the full (triple) interaction among these three sources. Because the levels in each factor (or source of variation) are a "sample" of possibilities (i.e. other AOGCMs and SDM), we could think in all these factors as random effects, although as pointed out above they were

selected to cover most of the range of variation within each factor.

We estimated the variance components as the simple proportions of the sum of squares attributable to the three sources (and their interaction) in respect to the total sum of squares. As we performed the analyses for each cell in the grid covering the New World (Fig. 1), it was possible to map each variance component and, in this way, identify regions of low and high uncertainty and the main sources accounting for this uncertainty. Notice that ANOVA was applied here to a turnover metrics, which varies between 0 and 1, so that violations in the assumptions of normality are not unlike. This may be not a problem when dealing with other metrics, but it is difficult to check for this problem in every grid cell. However, we believe that our results are robust to these problems and performing a square root/arcsin transformation of turnovers prior to the ANOVA (which are likely to improve the models) did not qualitatively affect the patterns in maps and the relative magnitude of variance components. The correlation between variance components from transformed and untransformed turnover metrics was always higher than 0.95 (median magnitudes all the same up to the second decimal place).

We explicitly quantified the spatial patterns in each variance components using correlograms, based on Moran's I spatial autocorrelation coefficients calculated for 10 geographic distance classes (Legendre and Legendre 1998). Magnitude of spatial pattern was established by Moran's I in the first distance class and by the correlograms' X-intercept (i.e. the distance at which autocorrelation becomes negative). Spatial analyses were performed in SAM (Spatial Analysis in Macroecology) software, freely available at <www.ecoevol.ufg.br/sam> (Rangel et al. 2006).

Results

A consensus map of mean species turnover across the 70 ensembled combinations of SDM, AOGCM and emission scenario (Fig. 2A), shows relatively high turnover (up to 56%) in northern parts of North America, in the Amazon and across the Andean region in South America, in Central America, throughout Mexico and in southeastern US. However, there was a high variation among projections, mainly in north and northwestern North America and parts of the Amazon, with coefficients of variation going up to 90% (Fig. 2B).

The first axis of the principal component analysis applied to the correlation matrix among the 70 turnover maps explained only 29.3% of the correlation structure, whereas the second principal component explained 23.5% of the variation. The first five axes selected by a broken-stick criterion explained 67.5% of the variation among turnover maps, indicating thus a marked level of heterogeneity among them. Spatial patterns and magnitude of turnover were quite different among combinations of SDM, AOGCM and emission scenarios (Supplementary material Table S2). Thus, it is difficult to disentangle by a simple visual inspection of the loading structure which sources of variation contributed more to the variability in the
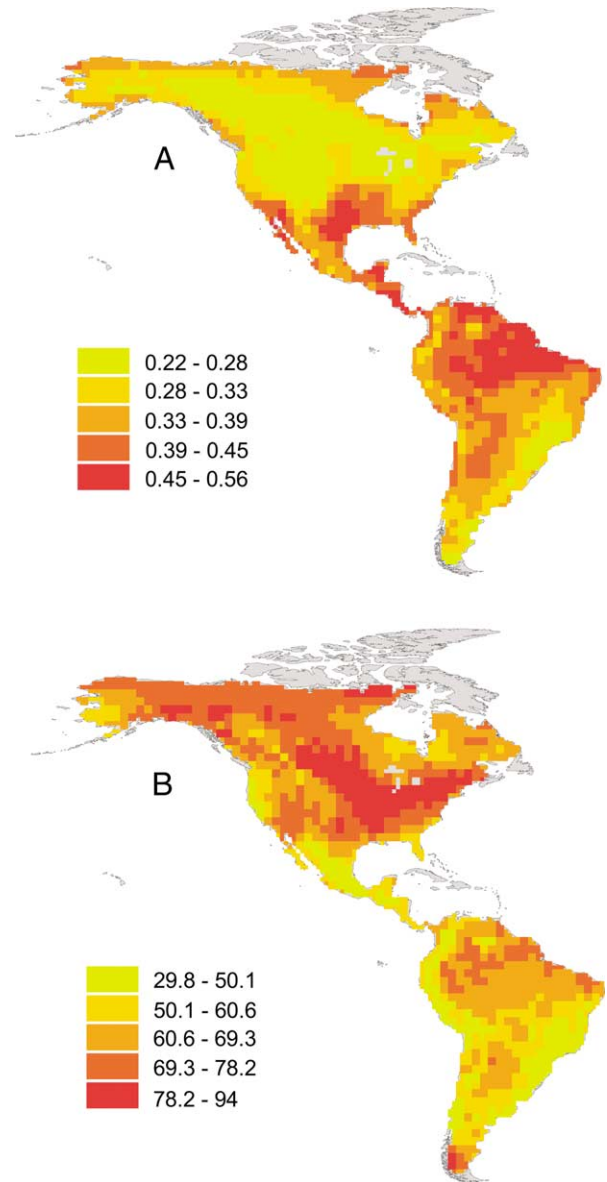

Figure 2. Consensus patterns of species turnover (A) and coefficients of variation, in percentage, among the 70 turnover maps (B) based on 3837 species of New World birds.

ensemble of forecasts (although this may be useful for a posteriori comparisons – see below).

The three-way ANOVA applied to each cell indicated that the distinct sources of variation have different contributions to the geographically-structured variation around the consensus solution observed in Fig. 2A. Out of the main effects, SDM explained a high proportion of the total sum of squares with a median value of 66%, ranging from 4 up to 95% (Table 1). High proportions of the total sum of squares that can be attributable to this factor were found in all North America and in the Amazon (Fig. 3A).

There is a high correlation (r = 0.88) between the Moran's I coefficients in the first distance class and the median proportion of variation accounted for by each source of uncertainty (Table 1). Thus, factors accounting for most of the variability among the forecasts are also the
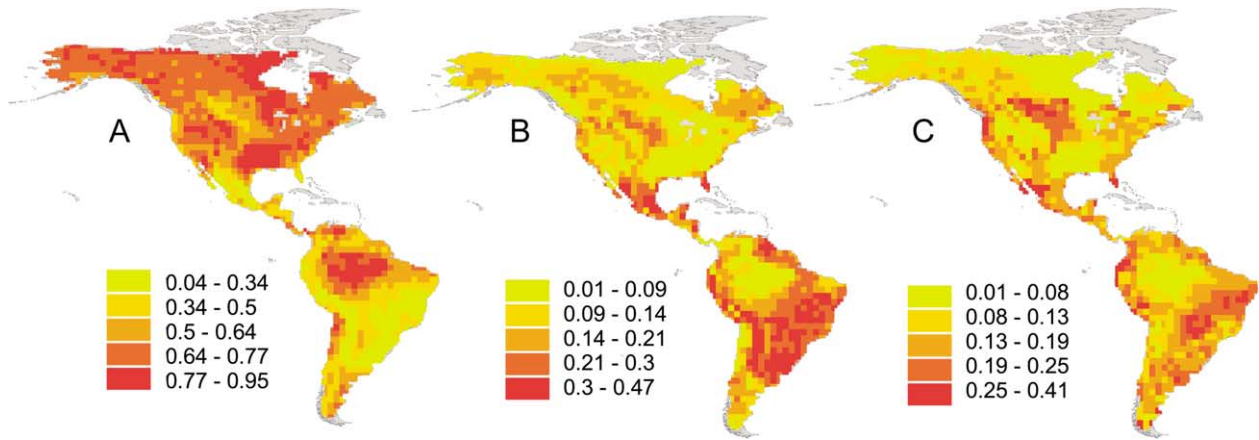
Figure 3. Proportion of the total sum of squares accounted for by SDM (A), AOGCM (B) and the interaction between these factors (C).

ones with the strongest spatial patterns. For instance, the variance component associated to SDM (the main source of variation according to the decomposition of the total sum of squares) is structured at broad geographical scales, with a large Moran's I in the first distance class and positive coefficients extending up to ca 4000 km (Table 1).

On the other hand, although AOGCM did not have a very high median value (Table 1), the proportion of the total sum of squares attributable to this source can be as high as 47% in most of South America, as well as in Central America (Fig. 3B). Geographical patterns expressed in the correlograms are also relatively strong (Moran's I in the first distance class equal to 0.399) and positive autocorrelation can be found up to 3000 km (Table 1).

Among the interactions, the most important was the one between SDM and the AOGCM, with proportions ranging from 1.3 to 40.9%, with a median of 11.8% (Table 1). The highest values for this interaction were found in central North America and in the dry regions of eastern part of South America (Fig. 3C). This variance component has
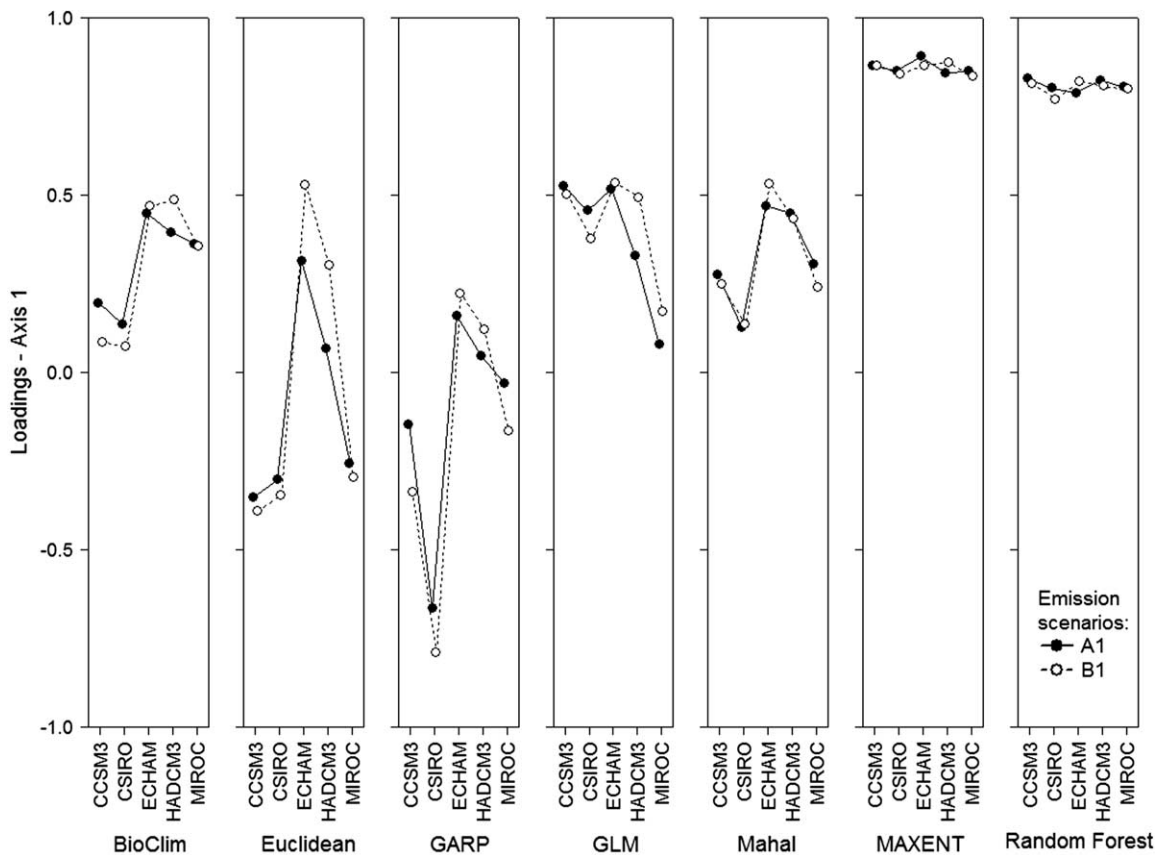

Figure 4. Loadings of the first principal component extracted from a matrix of species turnover forecasted by different methods for niche modeling, AOGCMs and emission scenarios.

spatial autocorrelation only at the smallest distance classes, with positive Moran's I (0.259) in the first distance class (up to 640 km) (Table 1).

The proportion of the total sum of squares revealed wide differences in species turnover patterns derived from distinct SDM and AOGCMs, and these components are geographically structured. These differences in maps can now be analyzed in more detail by examining the loadings of the first principal component. This analysis works here as a multivariate version of "a posteriori" comparisons in ANOVA (Sokal and Rohlf 1995), expressing the relative importance of each vector of prediction to the consensus map (Fig. 4). According to the loadings of the first principal component, the main difference among methods can be seen between a cluster of RF and MAXENT (with higher loadings in PC1) against Euclidean and GARP (with lowest loadings, but with high variation), with BIOCLIM, MAHAL and GLM occupying an intermediate position. All methods, except for RF and MAXENT, produce different results when using different AOGCMs, which explains the interaction term and makes it more difficult to interpret the effects of AOGCM alone (methods for modeling approaches, because of their larger effects, are easier to interpret).

Discussion

Partitioning uncertainties

Our study provides an illustration of how variation in ensembles of forecasts can be partitioned, thus offering a tool for investigating the origins of the uncertainties entering the models. Even if we accept that ensemble forecasts generate more accurate (Araújo et al. 2005a), or at least more conservative projections (Marmion et al. 2009), it is still important to identify the main sources of variation that affect the averaged projections (Brook et al. 2009, Elith and Graham 2009).

Previous studies (Thuiller 2004, Araújo et al. 2005a, 2006) used principal component analysis, or other classification analyses, as exploratory tools to describe the relative similarity among maps produced using different SDM or AOGCMs, allowing then a qualitative assessment of the relative importance of uncertainty sources. However, when several sources of uncertainty are explored, variability among projections might display complex patterns that might be difficult to interpret with the visual inspection of PCA loadings. Furthermore, formal quantitative assessments of uncertainty are necessary if they are to be systematically addressed and conveyed to model users.

Dormann et al. (2008) pioneered the use of ANOVA designs to uncouple uncertainties in SDM. They showed that the variability among statistics used to evaluate models projections of great grey shrike's distributions was, on average, 60% attributable to the use of distinct SDM. Our approach differs from Dormann et al. (2008) in that we quantify variance in the projected distribution maps rather than in the model fit statistics, which have more complex properties and are difficult to interpret in the context of model "transferability" (i.e. projecting the results of SDM in a different region or time; Araújo et al. 2005b, Araújo

and Rahbek 2006, Randin et al. 2006). A manuscript recently accepted for publication in Global Change Biology and kindly supplied by one of the authors (Buisson et al. 2009) proposed an alternative approach to partition the variance in ensemble-based forecasts of species turnover that also allows an exploration of the geographic components of uncertainty, as performed here. However, Buisson et al. (2009) used a GLM to evaluate only the main sources of uncertainty, but they did not explore the interactions between SDM and AOGCMs, and indeed our results showed that differences among SDMs are not the same when their projections are based on different AOGCMs (Fig. 4).

It is important to notice that the relative importance of each source of uncertainty depends of the variation among the levels within each factor. For all factors analyzed here, we tried to maximize the variation among levels by selecting SDM, AOGCMs, emission scenarios and data (species) with different characteristics. For example, the PCA reveals that differences among forecasts derived from different SDM are in line with current knowledge on how these methods work and how they are classified (Elith and Graham 2009). It is understood that SDM tend to differ in model fit, but it is less clear what is the link between fit and "transferibility" of the models (see below). So, if one uses sophisticated methods such as MAXENT and RF (i.e. assuming that a good fit indicates high transferability – see below), the relative importance of SDM may be reduced (Buisson et al. 2009). Indeed, if only these two methods are used, the median proportion of variation accounted by SDM falls from 66.1 to only 4.2% (whereas the median proportion accounted by AOGCM increases from 13.8 to 53%). Clearly, discussions around the relatively magnitude of these sources of uncertainty (Thomas et al. 2004b, Thuiller et al. 2004) must take into account which amount of variation within a factor the levels used (different SDM or AOGCM) cover in a comparative analysis.

Our results based on the turnover of New World birds clearly showed that the choice of the SDM contributed the most to uncertainty in the range of predictions, when compared with AOGCM and emission scenarios. These results are in line with previous studies showing that different niche modeling approaches may produce markedly different predictions of species range changes under climate change (Thuiller et al. 2004, Araújo et al. 2005a, b, 2006, Araújo and Rahbek 2006, Pearson et al. 2006). Our approach further revealed that the AOGCM would contribute with more uncertainty than the emission scenarios, and its interaction with SDM could be as important as the effects of AOGCM alone.

The discrepancy among the results obtained with different SDM has certainly motivated a large body of literature on comparison of methods that tries to find the "best" predictions (Manel et al. 1999, Thuiller 2003, Brotons et al. 2004, Segurado and Araújo 2004, Elith et al. 2006, Lawler et al. 2006, Meynard and Quinn 2007, Peterson et al. 2007, Tsoar et al. 2007) and discusses how to evaluate modeling approaches, both in terms of model fit (Fielding and Bell 1997, Liu et al. 2005, Lobo et al. 2008, Peterson et al. 2008) and model transferability (Araújo et al. 2005b, Randin et al. 2006, Peterson et al. 2007, Fitzpatrick et al. 2008, Peterson and Nakazawa 2008, Phillips 2008).

It is important to highlight that, in most cases, fit-statistics provide measures of the adjustment of projections to the data used for calibration, but in other cases, fit statistics measure how well model projections fit data sets apart for evaluation. The problem is the lack of independence as evaluation data are frequently spatially and/or temporally autocorrelated with the data used for calibration. Therefore, fit statistics provide an inflated and sometimes spurious measure of the models' suitability to be transferred into independent settings (Araújo et al. 2005b, Araújo and Rahbek 2006, Randin et al. 2006, Peterson et al. 2008).

In addition to such statistical considerations on model fit and transferability, there is also a discussion about the components of the niche that are captured by each model (Araújo and Guisan 2006, Soberón 2007, Jiménez-Valverde et al. 2008), as well as the relative roles of multiple ecological and evolutionary processes driving current species' ranges in deterministic and stochastic ways and how they can be incorporated into the methods (Araújo and Luoto 2007, De Marco et al. 2008, Rickebusch et al. 2008, Anderson et al. 2009).

Thus, supposing that further studies on all these issues will be able to discard some of the SDMs or AOGCMs (considering the criteria of model fit and transferability, or unreliable AOGCMs), we can expect that the uncertainties around the ensemble-based forecasts would be reduced. In a very optimistic (and most unlikely) scenario, if researchers found a definitive solution about which SDM should be selected (the main source of variation according to our results), then the level of uncertainty could be drastically reduced.

Mapping uncertainties

In addition to allowing a quantitative evaluation of the relative importance of different sources of variation around a consensus solution discussed above, our approach also allows mapping the variance components. This can be important because it adds another dimension (geography) to evaluate the uncertainties, giving more information on where the consensus can be achieved with low variation and where more research is needed to minimize variance.

In principle, four independent combinations of the two characteristics of the variance component maps, their geographic structure and their magnitude, could be found, forming a "two-by-two" scheme. Finding which of these combinations exist for a particular analysis possesses some interesting implications for practical decisions regarding forecasting. The first combination is given by a high level of variability which is also geographically-structured. In this case, uncertainty is not spatially random, which can shed light to the problems in each factor generating uncertainty. For example, AOGCMs can give different predictions in regions with a particular environmental characteristic, whereas all methods for SDM can provide similar solutions in a given region and differ in others (Beaumont et al. 2007). These geographically-structured components also show that when analyzing a given region more emphasis can be given in a particular source of uncertainty. Although short-distance spatial autocorrelation in the variance components is inevitable, because of autocorrelation in climate and distributional data, broad-scale patterns may indicate more complex patterns that require ecological or methodological interpretations.

The second combination can be given by a high, but geographically random variance component. This is the most challenging combination because it will be hard to predict regions of high or low uncertainty or establish which levels within a factor (i.e. SDM) can be used alone without increasing uncertainty. In this case, the differences among models cannot be associated with geographically-structured factors (e.g. environmental characteristics), so that it is more difficult to understand variation among projections. Under this combination, the use of ensemble-based forecasts is probably the best analytical strategies for forecasting.

The third combination, a geographic structure in a variance component with low mean, is unlikely to appear in real data. If the effect is small, there is also small variation among cells and it is unlike that any spatial pattern appears. Finally, the forth combination, given by low variability among results within cells which is also geographically random, indicates that the source of uncertainty is not important at all.

For the New World birds, we found a correlation between geographic structure and the relative proportion of variation accounted for by each source of uncertainty, reinforcing that the two characteristics of the variance component maps (i.e. magnitude and spatial pattern of the component) are not independent, so that the second and third combinations described above are not found.

The map of coefficient of variation in turnover shows that most differences among ensemble-based projections were found in the northern temperate region of the New World, and in the Amazon. A visual inspection of the maps averaged across SDM and AOGCMs further revealed why these differences arise (see also Supplementary material Fig. S2, Fig. S3). For example, some methods, such as RF, MAXENT, EUC and GLM, did not predict high turnovers in central Amazon (although this still depends on AOGCMs for some methods), which explains why the variance component of niche modeling techniques in this region is much higher (up to 90%) than for other regions of the New World (Fig. 3A). In general, MAXENT, RF and GLM predict smaller turnover across the continent than other methods, and the other methods vary a lot in their prediction of turnover in the northern part of the continent. Indeed, Fig. 3 suggest that if predictions of turnover rates are to be made for a few regions in the New World, such as the southeastern coast of Brazil, methods for niche modeling tend to give similar results and their differences are of minor concern. On the other hand, if one is interested in predictions for northern hemisphere of the New World or Amazon, especially northern US and Canada, AOGCMs are not an important source of uncertainty (so any one could be used) and one should focus on why methods are giving different answers. These patterns can also have implications for conservation decisions and it is important to notice, for example, that regions with higher SDM uncertainty are also those with high turnover levels detected by Lawler et al. (2009), based on random forest.

Concluding remarks

Our analyses support previous findings that SDM is the main source of uncertainty in forecasts of species range shifts under climate change and clearly highlights the importance of ensemble forecasting because of the current difficulties in the statistical evaluating model fit and transferability. This conclusion does not oppose the view that reductions of uncertainty in ensembles forecasts still demand a better evaluation of the individual SDM that compose the ensembles. Although the effects of SDM, AOGCMs and emission scenarios have been continuously evaluated in the literature, our approach provides a quantitative evaluation of the magnitude and geographical structure of these sources of uncertainty. Also, it can be easily expanded to encompass more complex designs addressing a larger spectrum of sources of variation in ensemble forecasting. Moreover, mapping uncertainty brings a new avenue for research, as it reveals that even when a given study compares sources of uncertainty they are not necessarily the same across different parts of the globe.

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Supplementary chapter C

Range size patterns in European freshwater trematodes

Manuscript under revision in Ecography

Range size patterns in European freshwater trematodes

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Abstract

While patterns in geographic range sizes in free-living species have received much attention, little is known on the corresponding patterns in parasites. For the first time, we report on patterns in geographic range sizes and dimensions of endoparasites, using published species lists of freshwater trematodes in 25 biogeographical regions of Europe. In general, the range sizes of trematodes showed a typical hollow curve frequency distribution, with most species having small ranges. Contrary to expectations, there were no differences in range sizes among trematodes using hosts with high (birds) and limited (e.g. fish) dispersal capacity. This suggests that the well known importance of host dispersal capacity for parasite dispersal at small local spatial scales is overridden by other factors on larger continental scales. Regression analyses and Rohde plots showed that the relationship between the latitudinal centre and range size was hump-shaped in all host groups except for reptiles, for which it was linear. Most of the variation fell within the expectations given by null models, suggesting that the patterns mainly result from the geographic properties of the European continent and the biogeographical regions. Finally, trematode ranges tended to stretch more in east-west than in north-south directions, indicating dispersal barrier effects for parasite faunas, probably due to the orientation of major geographical features such as the Alps.

Introduction

There is substantial variation in the size of the geographic ranges of species, spanning up to 12 orders of magnitude (Brown *et al.* 1996). Species with very limited distributions, e.g. confined to oceanic islands, lie at one end of the spectrum. At the other end are cosmopolitan species with extremely large range sizes, spreading over much of the globe. This includes many marine animals like algae, jellyfish, fish, seabirds and cetaceans have wide distributions throughout the marine realm (Gaston 2003). Within any taxonomic group, this variation in the size of geographic ranges can be visualised with a frequency distribution of the species-specific range sizes. Most groups of plants and animals show a unimodal distribution of range sizes with a strong right skew, sometimes called the "*hollow curve*" (Willis 1922; MacDonald 2003). This means that the majority of species within a taxon have small to medium geographic range sizes and only a few species have very large ranges.

While the hollow curve distribution of species' geographic range sizes is a universal pattern, the mean size of geographic ranges differs among major phylogenetic lineages. Within the vertebrates, freshwater fish have the smallest range sizes, followed by, in increasing order, amphibians, reptiles, mammals and birds (Anderson 1977; 1984a; 1984b; Anderson & Marcus 1992; Brooks *et al.* 2001). There are also patterns in range size variation within taxonomic groups. For example, the range sizes of species tend to decrease from high to low latitudes, a phenomenon known as Rapoport's rule (Stevens 1989). Geographic ranges may not only vary in extent but also in shape, i.e. ranges do not necessarily have the same extent in all dimensions. For example, Major biogeographical barriers or large-scale climatic zones can restrict the contours of species' ranges (Brown & Maurer 1989). However, geographic patterns in species richness may also simply result from the geometric properties of the study area, resulting in the so-called mid-domain effect, which can be tested using null models (Colwell & Hurtt 1994; Colwell & Lees 2000; Colwell *et al.* 2004).

Whereas patterns in geographic range sizes of free-living species have received much interest, little is known about the geographic range sizes of parasites. Some studies have found a positive correlation between the range sizes of hosts and the numbers of parasite species infecting these hosts (Dritschilo *et al.* 1979; Gregory 1990; Brändle & Brandl 2001; Krasnov *et al.* 2004). However, to our knowledge only two related studies to date have investigated patterns in geographic range sizes of parasites themselves. The geographic ranges of ectoparasitic fleas (Siphonaptera) from small

mammals show the same hollow curve distribution as seen in free-living species (Krasnov *et al.* 2005; 2008). The geographic range size of flea species was negatively correlated with their degree of host specificity, i.e. highly host specific flea species had smaller ranges than generalists that infect a wide range of host species (Krasnov *et al.* 2005). However, host specificity is not the only determinant of the size of geographic ranges of parasites. As parasites, depend on their hosts for dispersal, the dispersal capacity of the hosts should be strong determinants of the size of geographic ranges of parasites. In parasites with complex life cycles, like digenean trematodes, definitive hosts should be most relevant in this respect, as adult worms inside definitive hosts are the main dispersal stage of the parasites. The first intermediate hosts of trematodes are molluscs, which have a very limited dispersal capacity (planktonic larval stages are not infected). The second intermediate hosts are invertebrates, amphibians or fish, all of which again have limited dispersal capacity. Definitive hosts of trematodes are always vertebrates, which carry the adult parasites and disperse the parasites via their eggs shed with faeces. In general, the dispersal capacity of parasites in bird definitive hosts is considered to be higher than that of parasites utilising fish and other less vagile definitive hosts (Esch *et al.* 1988), an assumption supported by data on population genetics (Criscione & Blouin 2004). Hence, we expect parasites using freshwater fish as definitive hosts to have, on average, the smallest range sizes, and parasites utilising birds to have the largest range sizes within a regional assemblage of trematodes.

In this study, we investigate patterns in range sizes and dimensions in European freshwater trematodes. Besides determining the frequency distributions of trematode range sizes, we investigate whether the range sizes of trematode species are determined by the dispersal capacity of their definitive hosts. To the best of our knowledge, both have not been investigated in endoparasites. Also, other patterns in range sizes of parasites like Rapoport's rule or the dimensional shapes of parasites' ranges have, as far as we know (other than the flea study mentioned above), not been studied to date. Based on the published distributions of trematodes over 25 biogeographical regions in Europe, we ask the following questions: 1) Do the range sizes of trematodes exhibit the typical hollow curve distribution known from free-living species?, 2) Do the mean range sizes of trematodes differ depending on the type of definitive host they use?, 3) Are the range sizes of trematodes larger at higher latitudes (Rapoport's rule)?, and 4) Do the shapes of the ranges of trematodes in Europe follow major topographic features like the Alps?

Materials and methods

The data set used for the analyses was extracted from the *Limnofauna Europaea* (Illies 1978), using the data on presence/absence of digenean trematodes in each of 25 bioregions. All trematode species included in these tables spend at least the first part of their life cycle in freshwater habitats, i.e. the first intermediate host is always a freshwater mollusc. For each trematode species, we extracted information on the type of definitive hosts used from the original tables in the book: 1) fish, 2) amphibians, 3) reptiles, 4) mammals, 5) birds and mammals (in the case of trematode species that can use either), and 6) birds. Species with unknown type of definitive host were excluded from the analyses. In addition to information on the parasites we acquired geographic data on the 25 biogeographical regions. For each biogeographical region, as defined in the book, we determined the northern and southern as well as the eastern and western boundaries using http://earth.google.com/ and calculated the latitudinal and longitudinal ranges of each region from these data (Table 1; see Hof *et al.* 2008 for a map). In addition, using GIS, we calculated the area of each bioregion (Table 1).

Based on these data, we calculated various geographic range measures for each trematode species: 1) number of biogeographical regions in which each species was recorded; 2) total area occupied by each trematode species; 3) latitudinal and longitudinal range (degrees), using the boundaries of the northern-, southern-, western- and eastern-most regions in which each species occurred; and 4) dimensional shapes of each range (maximum north-south and east-west extent in km), using great circle calculations. Since the distance between longitudinal bands depends on latitude, we identified the eastern and western longitudinal extremes of the range and calculated the distance between them at the mean latitude of the species' range.

To visualise the geographic ranges of the European freshwater trematode species, we plotted the frequency distribution of range sizes, separately for each major host group, using the total number of regions occupied by each species as this measure is least vulnerable to area overestimation (see discussion). We tested for differences in the mean range of trematode species utilising different definitive host groups with one-way ANOVAs (type 3 SS), using log-transformed data of 1) number of regions occupied by each species, 2) total area occupied, 3) latitudinal range and 4) longitudinal range. Post-hoc comparisons were conducted with Tukey's HSD tests (for unequal n).

To investigate the relationships between the latitudinal centres of each species' range and the total area occupied by the species (log-transformed), we used regression

analyses and Rohde plots (named after Rohde 1993, although this type of plot was originally introduced by Graves 1985). For the regression analyses, we included simple and squared latitudinal centre as independent variables, since plots of log(area) vs. latitudinal centre suggested a hump-shaped relationship. For the Rohde plots, we divided the geographic domain into latitudinal bands of 3° width. Within each of these bands, we calculated the mean log(area) of all species whose latitudinal centre falls within this band (for details, see Rohde *et al.* 1993).

Table 1 | Latitudinal and longitudinal range as well as area of the 25 different biogeographical regions, as defined in Illies (1978), used for the analyses.

Region code	Region	Latitudinal range [°]	Longitudinal range [°]	Area [km²]
IBE	Ibero-Macaronesian region	11.12	33.28	623512
PYR	Pyrenees	1.08	4.28	47177
ITA	Italy, Corsica and Malta	10.55	11.13	259796
ALP	Alps	4.32	11.53	230555
DIN	Dinaric western Balkan	5.03	8.15	169565
HEL	Hellenic western Balkan	8.42	8.95	148864
EAB	Eastern Balkan	5.97	8.07	166136
WEH	Western highlands	6.88	5.28	163624
CEH	Central highlands	4.35	11.53	265879
CAR	The Carpathians	5.34	9.83	187997
HUN	Hungarian lowlands	3.52	7.30	171969
PON	Pontic province	5.35	16.08	245422
WEP	Western plains	9.00	11.48	403351
CEP	Central plains	10.70	25.40	551551
BAP	Baltic Province	6.00	13.20	205697
EAP	Eastern plains	12.72	40.02	2320724
IRE	Ireland and Northern Ireland	3.95	5.18	91572
GBR	Great Britain	12.42	10.38	246186
ICE	Iceland	3.08	11.00	110541
BOR	Borealic uplands	12.33	16.42	321639
TUN	Tundra	10.95	48.62	415856
NSW	Northern Sweden	9.40	13.42	258423
TAI	Taiga	11.37	38.68	1647955
CAU	The Caucasus	6.60	12.57	379397
CAS	Caspic depression	10.22	20.85	780402

Because the shape of Europe constrains the possible locations and shapes of geographic ranges, a hump-shaped relationship between latitude and range size is expected even in the absence of ecological processes (Colwell & Hurtt 1994). To account for the effect of such geometric constraints, we compared the observed patterns to a null model. For each host group, we used a modification of the 'spreading dye'

algorithm (Jetz & Rahbek 2001) to generate a set of random cohesive ranges. This algorithm keeps the range size distribution constant (in this case the number of occupied regions), while randomizing the geographic location of each range. We then used the generated ranges to calculate slopes and intercepts for regressions of log(area) vs. latitudinal centre (including both the linear and quadratic term of the latter). This procedure was repeated 1000 times, and the coefficients were averaged to generate composite models for the null expectation of area-latitude plots. We also added 95% confidence intervals of the null model to all Rohde plots, based on the 2.5 and 97.5 quantile values from the 1000 sets of simulated ranges.

To visualise the geographical orientation of ranges, we plotted the east-west extent of ranges versus their north-south extent (km). If the orientation of ranges were random, we would expect these values to cluster around a diagonal line with slope = 1 (Brown & Maurer 1989). To account for the shape of the European continent and the location of biogeographical regions, we also added a line indicating the orientations of the null ranges generated above.

As the analyses of Rapoport's rule and of geographical orientation of ranges along the north-south and east-west axes combine data from various trematode lineages, we tested for potential phylogenetic effects. Unfortunately, no complete phylogeny of trematodes is currently available. Instead we used the latest taxonomy used in a current comprehensive revision of the Trematoda (Gibson *et al.* 2002, Jones *et al.* 2005, Gibson *et al.* 2008) to test for effects of superfamily, family or genus on area, latitudinal centre, east-west or north-south extent of the parasite ranges used in the analyses. We tested each taxonomic level separately, using one-way ANOVAs, as nested designs combining all taxonomic levels in a single analysis were not possible due to many missing cells resulting in incomplete designs.

Results

Overall, our analyses included data on 564 freshwater trematode species (see Fig. 1 for numbers per definitive host groups). In general, all four measures of geographic range considered here were highly correlated with each other (all $p < 0.001$; area - number of regions: $r^2=0.84$; area – latitudinal range: $r^2=0.83$; area - longitudinal range: $r^2=0.77$; number of regions - latitudinal range: $r^2=0.70$; number of regions - longitudinal range: $r^2=0.71$; latitudinal range - longitudinal range: $r^2=0.77$).
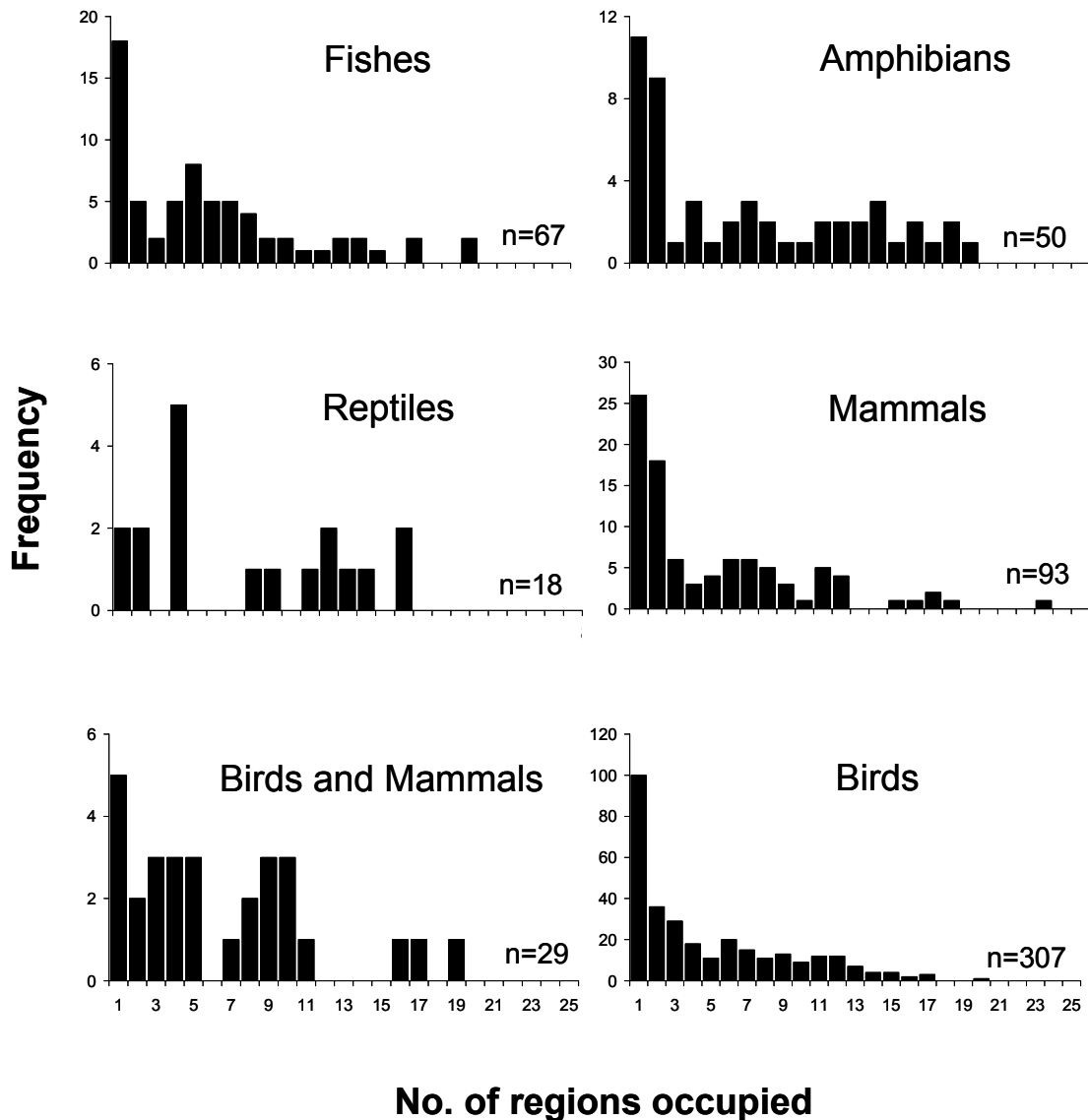
Figure 1 | Frequency distribution of species-specific range sizes of European freshwater trematodes utilising different types of definitive hosts. Note that data are non-transformed. Numbers of trematode species in each group are indicated on the figure.

The species-range size distributions showed that most trematode species occupy only a few bioregions (Fig. 1). Overall, this pattern was less clear in trematodes of definitive host groups for which only limited numbers of parasite species are available (reptiles, birds & mammals, Fig. 1). In general, the range size distributions among host groups were similar, with trematodes from none of the definitive host groups having particularly large ranges. This was reflected in the mean geographic range sizes or dimensions of trematode species among the different types of definitive hosts. Although trematode species utilising mammals or birds as definitive hosts had the smallest geographic ranges (Fig. 2), the difference was not or only marginally significant, depending on the measure of range size used (ANOVAs: Area: $F_{5,558}= 1.66$, $p = 0.14$;

number of regions: $F_{5,558}$= 2.59, p = 0.02; latitudinal range: $F_{5,558}$= 2.34, p= 0.04; longitudinal range: $F_{5,558}$= 1.92, p = 0.09). Subsequent post-hoc comparisons in the two significant ANOVAs showed no significant differences among any of the different comparisons (in all comparisons $p \geq 0.53$ (no. of regions) or p$\geq$0.47 (latitudinal range)).
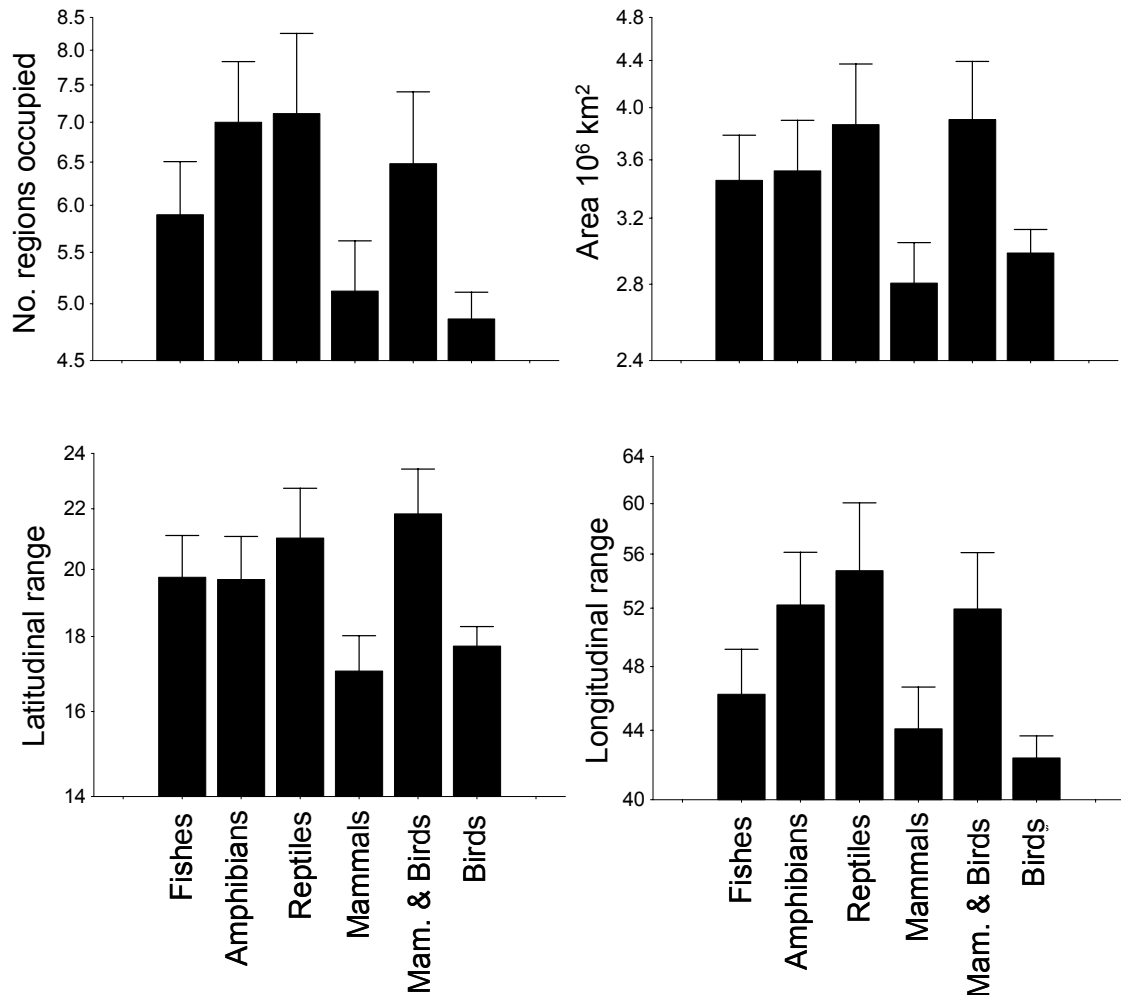

Figure 2 | Mean (+SE) geographic range sizes (number of regions occupied, log area occupied, latitudinal and longitudinal range) of European freshwater trematodes utilising different types of definitive hosts. Note the truncated y-axes in all cases. For the number of trematode species per type of definitive host see Fig. 1.

We found the relationship between latitudinal centre and area to be hump-shaped in all host groups except for reptiles, for which it was linear (Fig. 3 & 4; Table S1 in Supplementary Material). The linearity of the relationship for reptiles may arise because only a part of the latitudinal gradient is realized: no trematode species are associated with reptiles above 55° N (Fig. 3 upper left). Both the regression analyses and the Rohde plots showed that most of the variation falls within the expectations due to geometric constraints. However, comparing observed and simulated values, most

observed relationships are steeper than expected from the null model simulations. This is also indicated by the differences in the slopes and intercepts between observed and simulated relationships (Table S1).
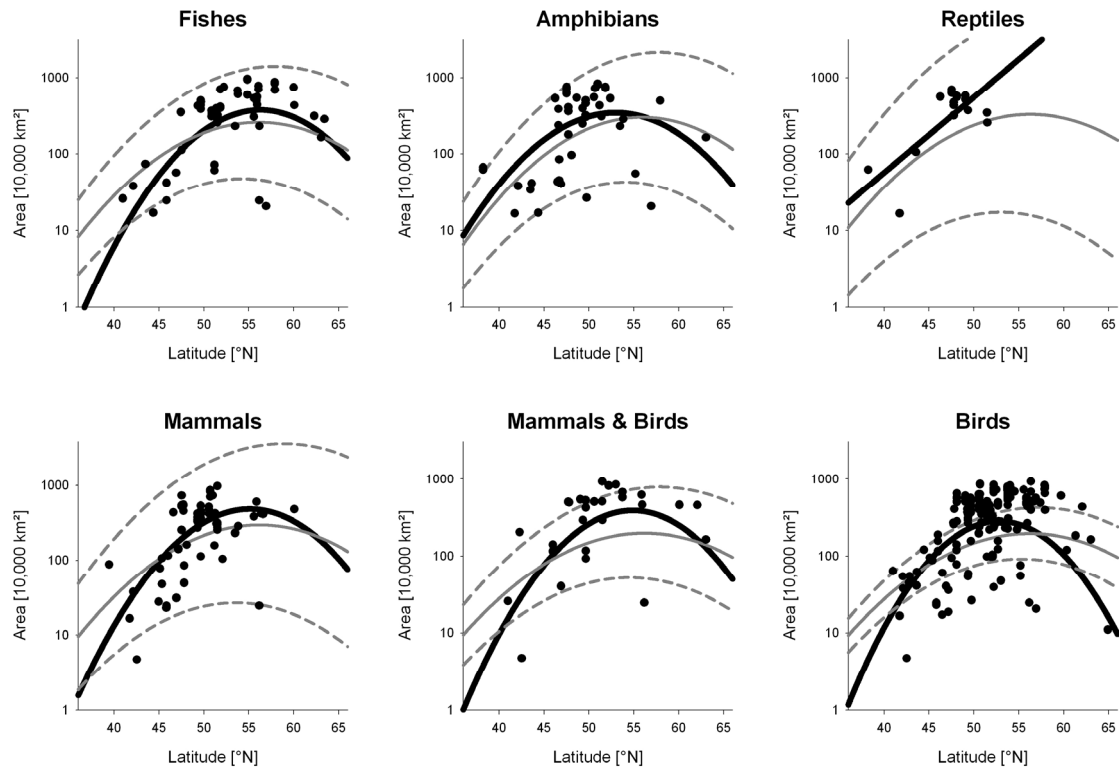

Figure 3 | Relationships between the latitudinal centre (°N) and range size (area*10.000 km²) for the six groups of definitive hosts showing values for each trematode species (black points). Black lines indicate the observed relationships fitted from these points (area vs. linear and squared term of latitudinal centre; reptiles: area vs. linear term of latitudinal centre only). Grey lines indicate the relationships rendered by the null model simulations, based on slopes and intercepts from 1000 simulations (straight line) and the according 95% confidence intervals (For values of observed and simulated slopes and intercepts, see Table S1).

Trematodes in all six types of definitive hosts showed similar trends in the shape of their ranges. All ranges tended to stretch more in east-west than in north-south directions (Fig. 5), as the vast majority of points fall below the diagonal line indicating equal north-south and east-west extents. Furthermore, most of the points also fall below the lines indicating the pattern expected from the null models – most species have range shapes that stretch even more towards east-west vs. north-south than expected given the geographic extent and shape of the European continent and the biogeographical regions (Fig. 5, Fig. S1).
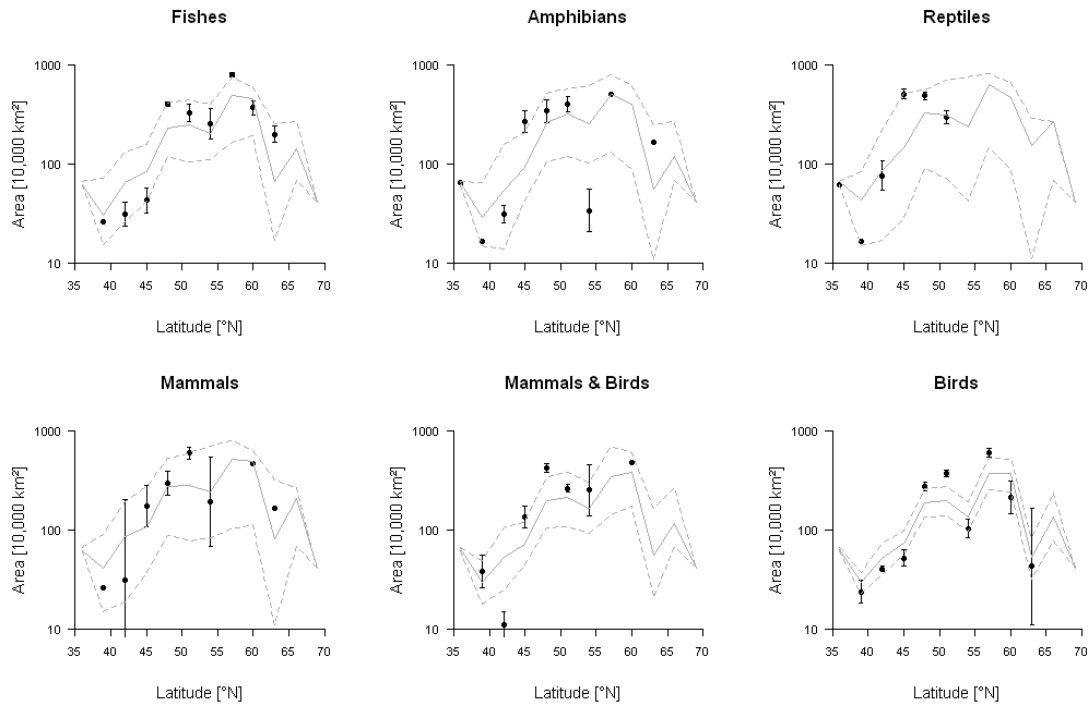
Figure 4 | Relationships between the latitudinal centre (°N) and range size (area*10.000 km^2) for the six groups of definitive hosts using Rohde plots. Black points are the mean values of log10(area), calculated from those species whose latitudinal centres fall within latitudinal bands of 3° width. Error bars indicate the standard errors of the mean. Grey lines indicate the values rendered by the null model simulations (straight line) and their respective 95% confidence intervals (dashed lines). For the number of trematode species per type of definitive host see Fig. 1. For details on null model setup, see text.

Tests for potential phylogenetic effects in the latter two analyses (Fig. 3-5) showed significant overall ANOVAs in only a few cases. However, subsequent post-hoc tests did not reveal significant differences among particular taxonomic groups, which suggests that potential differences among groups were two small to be detectable in post-hoc comparisons. While this does not completely rule out any differences among groups it indicates that potential differences are very small and that phylogenetic effects should not be confounding the analyses. The only significant tests occurred in the host group with the least data available in terms of the number of parasite species, the trematodes of reptiles, where post-hoc tests identified a particular genus (*Patagium*) and family (Auridistomidae, *Patagium* being the only genus in this family) as being significantly different from others. However, excluding this genus from the analyses resulted in similar results and thus we decided to present the full data.
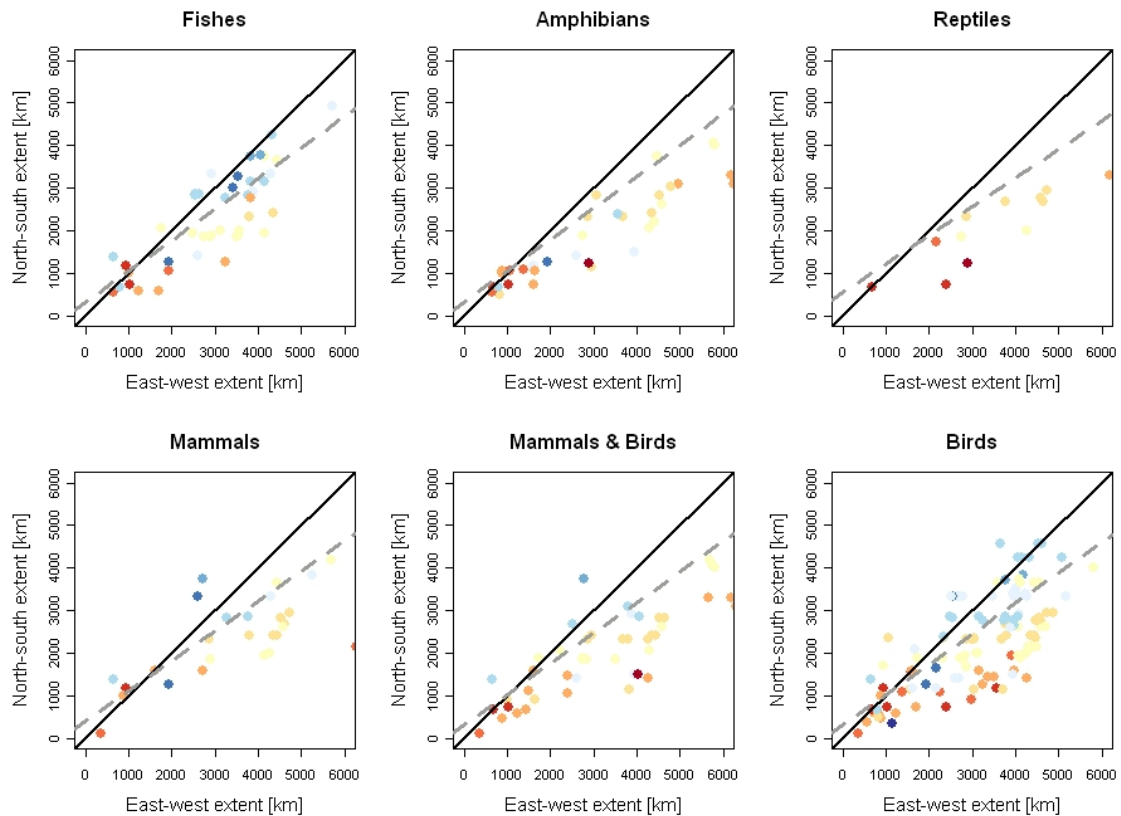
Figure 5 | Relationships between the maximum north-south and east-west extent (km) of the geographic ranges of European freshwater trematodes utilising different types of definitive hosts. Black straight lines (slope = 1) indicate ranges of equal extent in north-south and east-west direction. Grey dashed lines indicate the regression line rendered from the null model simulations. Colours indicate the latitudinal centres of the species' ranges, ranging from southern (dark red) via central (light red and blue) to northern (dark blue) latitudes.

Discussion

The geographic range sizes of parasites in all definitive host groups showed the typical right-skewed pattern observed in free-living species: most parasite species occupy small ranges, and only a few species occupy large ones. The range size measures for each parasite species are likely to be overestimates as parasite species occurring within a bioregion do not necessarily occur everywhere within this region. This may particularly affect the range size measures of parasites occurring in large regions as it results in large total range sizes. However, the number of regions occupied should be the least problematic measure in this respect and thus the general trend of a right-skewed pattern seems to be robust. Fleas (Siphonaptera) ectoparasitic on small mammals show a similar pattern (Krasnov *et al.* 2005) and their geographic range size is negatively correlated with their degree of host specificity: generalist flea species, infecting a wide range of host species, had larger ranges than highly specific species

(Krasnov *et al.* 2005). Host specificity may also underlie the pattern observed in European trematode species, although we cannot test this formally as no information on host specificity is currently available. The extreme right skew of trematode range sizes might suggest that the majority of trematodes are relatively host specific and analyses of regional parasite faunas of vertebrates indicate that the majority of helminth species are indeed relatively host specific (Gregory *et al.* 1991; Poulin 1992; Poulin 2007). Being restricted to a single or just a few host species means that the spatial distribution of a parasite species strongly depends on the dispersal capacities of its particular host species. Dispersal capacity is probably limited in the majority of potential hosts as vertebrates also generally show hollow curve distributions of their geographic range sizes (Gaston 2003). Hence, the dispersal potential of parasites should be limited by that of their hosts, and consequently their geographic ranges have to be relatively small in the majority of cases, resulting in the observed hollow curve shapes for the frequency distributions of their geographic range sizes. Dispersal limitations of the intermediate hosts involved in the complex life cycles of trematodes might further restrict the parasites' dispersal. Host specificity is universally high for the first intermediate (mostly gastropods) host (Galaktionov & Dobrovolskij 2003) and gastropods are usually restricted in their dispersal capacity as adults (planktonic stages are not infected).

Contrary to expectation, parasites utilizing host groups presumed to have high dispersal capacities, like birds, did not have, on average, larger range sizes than those utilizing host groups with smaller dispersal capacity. Of course, the resolution of the available data might have been too coarse to detect any differences. However, considering the well known importance of definitive host type for parasite dispersal, we would have expected strong differences among groups well exceeding the resolution of our data. For example, findings from parasite community structure in fish hosts on local scales indicate the dispersal capacity of the definitive host to be crucially important for parasite dispersal (Esch *et al.* 1988). In addition, phylogeographical evidence suggests that parasites using birds should achieve a greater geographic range (especially considering the large migrations of water birds in Europe). Typically, freshwater parasites using fish as definitive hosts show pronounced genetic structure among different populations on a scale of a few hundred kilometres, whereas those using birds do not, suggesting that the latter have much greater dispersal potential (Criscione & Blouin 2004). Perhaps the structuring forces acting on local scales are overcome by other forces on regional to continental scales as used in our analysis. Several non-

exclusive mechanisms might be at work on these larger spatial scales. For instance, hosts with a high dispersal capacity may often also carry a high number of parasite species, as the number of parasite species exploiting a particular host species increases with that host's geographic range size (Dritschilo *et al.* 1979; Gregory 1990; Shenbrot *et al.* 2007). Hence, a few highly mobile and widely distributed host species (e.g. migratory fish) might distribute many parasite species on a large spatial scale, although the host group in general (e.g. fish) has a relatively small dispersal capacity. In addition, the actual infection levels (e.g. prevalence, or percentage of hosts infected) of parasite species in host populations may be of importance. Interestingly, mean helminth prevalence in fish hosts, i.e. the proportion of individual hosts in a population that are infected, seem to be higher than in bird hosts based on comprehensive compilations of published data (Poulin 1998a; 1998b). Hence, the higher dispersal capacity of birds might be offset by their relatively low levels of infection, decreasing the chances for a parasite species to disperse. Another mechanism blurring the expected pattern could be that there are simply more specialist parasites using birds compared to those using fish. These specialists would be confined to the dispersal ranges of their single definitive hosts, most of which would have limited dispersal capacity themselves as suggested by small ranges, and this may again offset any advantage associated with the high dispersal capacity of the host group in general. However, consistent comparative data from the different host groups are not available to test these ideas.

Regression analyses and Rohde plots showed that the relationship between latitudinal centre and range size was hump-shaped in all host groups (except for reptiles). We acknowledge that both of these methods have their pitfalls and that the coarse resolution of the data limits the analyses. Also, using latitude alone does not allow identifying underlying structuring environmental factors like climate (Hawkins & Diniz-Filho 2004). However, we think that the data are still valuable for a simple analysis of latitudinal patterns; especially since such patterns have never been studied in endoparasites before. Should more detailed distributional data become available in the future, more elaborate and detailed analyses will be feasible, expanding on our basic findings. However, the graphs suggest that latitude does not seem to have an important effect on range size patterns as most of the variation falls within the expectations given by the null models. Hence, the pattern arises due to the geographic shape and extent of the European continent and the biogeographical regions, with land masses being interrupted along a latitudinal band by the Mediterranean Sea in the south. Species with

the mid-point of their range in the south may thus have a restricted dispersal capacity simply due to the geographical topology. In addition, mid-domain effects due to the geographic extent of the continent and the bioregions probably add to the phenomenon (Colwell & Hurtt 1994; Colwell & Lees 2000; Colwell et al. 2004). However, although the latitudinal distribution of range size largely followed the expectations from the null models, most host groups showed somewhat steeper slopes in the observed values versus the null model simulations. This might indicate that other factors besides non-biological domain effects additionally mediate the latitudinal distribution of range sizes. For example, host specificity may play a role in that generalist trematodes may occur in more regions than null models suggest because a higher number of potential hosts should translate into a higher dispersal capacity (see above).

The pattern of range sizes stretching more in east-west than in north-south directions remained after controlling for geometric constraints of the study area with null models and is similar to the one observed in European birds (Brown & Maurer 1989). If the orientation of ranges was only determined by the shape of Europe, we would expect the data to follow the null model expectations. However, the orientation is longer in the East-West direction than expected, which is probably an effect of the orientation of major climatic zones and major topographical features like mountain chains (e.g. the Alps), which run in an east-west direction in Europe (Brown & Maurer 1989). They act as a dispersal barrier for both free-living and parasite species. Interestingly, the effect in our data was most pronounced in trematodes with centres of distribution in the south to mid Europe. This probably points to the particular importance of the southern mountain chains like the Alps and Pyrenees as biogeographical barriers for hosts and parasites. In contrast, the pattern was more or less absent in trematode species with northern distributional centres. This may be interpreted as a legacy of the ice ages with highly dispersive northern species re-colonising large parts of northern Europe after a large-scale eradication of northern faunas (Hof et al. 2008).

Any large scale analysis of geographical patterns depends on the quality of the underlying data. As discussed above, the coarse resolution of the data might be of particular concern. However, we think using these data is valid considering that the simple biogeographical patterns we investigate should not be too sensitive in this respect (see above) and considering that such patterns have never been investigated in endoparasites before. There are certainly data sets of better quality but for trematodes this data base is probably as good as it can get. Hence, we believe the data presented

make a valuable start to investigate biodiversity patterns in this group. Other critical issues with the data set might be sampling effort and synonyms. Potential differences in sampling effort among bioregions could affect our measures of trematode range sizes. However, the trematode fauna of Europe is probably one of the best known in the world, and it has been the focus of much interest, particularly with respect to vertebrates, for a very long time. In addition, a quantitative analysis of the proportion of singletons per bioregion (species present in a single bioregion only) shows a relatively even distribution of singletons among bioregions (Thieltges *et al.* in prep.). As singletons can be good indicators of sampling effort (Novotny & Basset 2000), this suggests that sampling effort is relatively uniform among the 25 bioregions and thus not confounding our study. Synonyms among the named parasite species in the data set might be problematic but the original data set was compiled by experts in their field and therefore the nomenclature should be consistent across the bioregions. It is also difficult to see how the spatial distribution of synonymous species could occur in a way that leads to the patterns observed in our analyses. Hence, we think the data set and our analyses are sufficiently robust to test for the observed patterns.

In conclusion, the geographic range size patterns of European freshwater trematodes show a typical hollow curve distribution, with most species having small ranges. Interestingly, varying within-range dispersal capacity among host groups (e.g. high in birds and low in fish) did not affect the range sizes of parasites, suggesting that the dispersal capacity of definitive hosts is of much less importance on large spatial scales than small-scale studies have suggested. Range sizes of trematodes showed a hump-shaped distribution along a latitudinal gradient similar to null model expectations, suggesting that the observed pattern is caused by the extent and shape of the geographic domain and that no latitudinal trend exists. Finally, trematode ranges tended to stretch more in east-west than in north-south directions, even when the geographic domain was considered by null models, pointing to geographic features like the Alps as major barriers for the dispersal of parasites. Our analysis was confined to trematodes and it will be interesting in futures studies to investigate other parasite groups (e.g. cestodes, nematodes, ectoparasites etc.) to see if the patterns hold true more generally.

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Supplementary Material

Supplementary Tables

Table S1 | Values for models fitted for the relationship between latitudinal centre and log10(area).

	Observed values						Null model simulations		
	Intercept	Slope	*P*	Slope²	*P²**	R²	Intercept	Slope	Slope²
Fishes	-14.7	0.76	<0.001	-0.0067	<0.001	0.43	-5.14	0.41	-0.0037
Amphibians	-9.12	0.59	0.015	-0.0056	0.003	0.25	-6.61	0.47	-0.0042
Reptiles	1.79	0.099	<0.001			0.58	-5.02	0.41	-0.0037
Mammals	-14.0	0.75	0.009	-0.0068	0.003	0.42	-5.03	0.41	-0.0037
Mam. & birds	-15.3	0.80	<0.001	-0.0073	<0.001	0.52	-3.83	0.36	-0.0032
Birds	-17.1	0.89	<0.001	-0.0085	<0.001	0.34	-3.94	0.36	-0.0032

Observed values are calculated as coefficients from the model area vs. linear and squared term of latitudinal centre. *P* values indicate if the slopes of the terms were significant. For reptiles, since the quadratic term was not significant, area was fitted to the linear term of latitudinal centre only. R² values indicate the explained variance for the full models. For the setup of null model simulations, see text.
*Values for the squared term of latitudinal centre
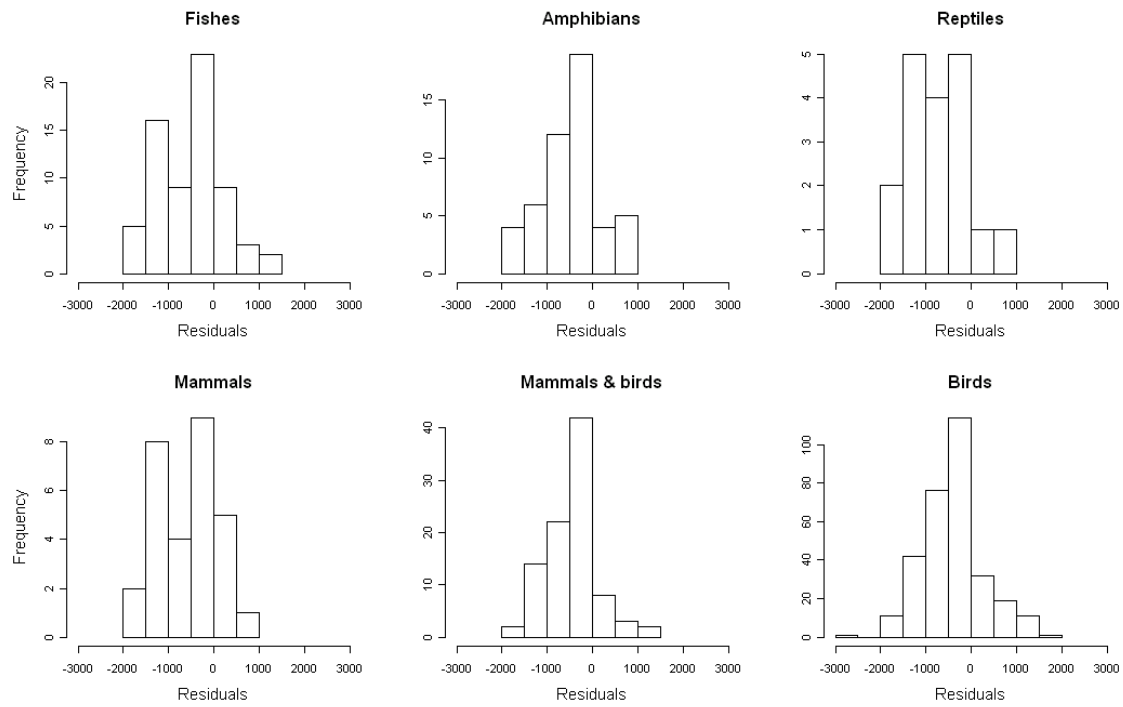
Supplementary Figures

Figure S1 | Frequency distributions of the residuals of the observed values of north-south vs. east-west extent against the line fitted from the null model simulations. Negative values are those that fall below the null model line, i.e. that have a larger east-west than north-south extent than expected from the geographic shape and extent of the European continent and the biogeographical regions. Positive values are those that fall above the null model line

Curriculum vitae

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Education

2007 – 2010	**PhD student**, Center for Macroecology, Evolution and Climate, University of Copenhagen (Denmark) and Biodiversity and Global Change Lab, Museo Nacional de Ciencias Naturales, CSIC, Madrid (Spain)
2006	Graduation as "**Diplom-Biologe"** (equivalent to a M.Sc. in Biology)
1999 – 2006	**Studies of Biology**, University of Marburg (Germany); majors: Animal Ecology, Nature Conservation, Zoology
1989 – 1998	**Abitur** (university-entrance qualification) at the Westerwald-Gymnasium Altenkirchen/Ww (Germany)

Publications

Hof, C., Rahbek, C. & Araújo, M.B. (2010) Phylogenetic signals in the climatic niches of the world's amphibians. *Ecography* (accepted), DOI: 10.1111/j.1600-0587.2010.06309.x

Dehling, D.M., **Hof, C.**, Brändle, M. & Brandl, R. (2010) Habitat availability cannot explain the species richness patterns of European lentic and lotic freshwater animals. *Journal of Biogeography* (conditionally accepted with minor revisions).

Hof, C. (2010): Biogeography - The Distribution of Life. In: *Grzimek's Animal Life Encyclopedia: Evolution* (ed. by Hutchins, M., Pianka, E. *et al.*). Gale, Cengage Learning.

Diniz-Filho, J.A.F., Bini, L.M., Rangel, T.F.L.V.B., Loyola, R.D., **Hof, C.**, Nogués Bravo, D. & Araújo, M.B. (2009) Partitioning and mapping uncertainties in ensembles of forecasts of species turnover under climate changes. *Ecography* **32**, 897-906.

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Hof, C., Brändle, M. & Brandl, R. (2006) Lentic odonates have larger and more northern ranges than lotic species. *Journal of Biogeography* **33**, 63-70.

Further publication experience: *Author and co-author of four non-peer-reviewed scientific and >20 popular articles and reports.*

Conference, workshop and seminar contributions (selection)

Hof, C. (2009) Frogs in a warming world: global change and the future of amphibian diversity. Oral presentation, Helmholtz-Center for Environmental Research (UFZ), Halle (Germany), 13 November 2009.

Hof, C., Rahbek, C. & Araújo, M.B. (2009) Same clade – same climate. Phylogeny mirrored in the niches of the worlds amphibians. Oral presentation, 39th annual meeting of the Ecological Society of Germany, Austria and Switzerland (GfÖ) in Bayreuth (Germany), 14-18 September 2009.

Hof, C., Rahbek, C. & Araújo, M.B. (2009) Phylogenetic signals in climatic niche similarity of the world's amphibians. Poster, 4th biennial conference of the International Biogeography Society (IBS) in Merida (Mexico), 8-12 January 2009.

Dehling, D.M., Brändle, M., **Hof, C.**, Brandl, R. (2008) Habitat and climate cannot explain species richness patterns of European freshwater species. Oral presentation, EURECO-GfÖ joint meeting in Leipzig (Germany), 15-19 September 2008.

Hof, C. (2008) The climatic niches of amphibians – a global analysis. Oral presentation, 2nd annual conference of the Macroecology Specialist Group of the Ecological Society of Germany, Austria and Switzerland (GfÖ) in Bonn (Germany), 10-11 March 2008.

Hof, C., Brändle, M. & Brandl, R. (2007) Macroecology of freshwater animals: Differences between habitats. Oral presentation, 37th annual meeting of the Ecological Society of Germany, Austria and Switzerland (GfÖ) in Marburg (Germany), 10-14 September 2007.

Hof, C., Brändle, M. & Brandl, R. (2007) Latitudinal variation of European freshwater diversity is not concordant across habitat types. Oral presentation, 92nd annual meeting of the Ecological Society of America in San Jose, California (USA), 5-10 August 2007.

Hof, C. (2007) Distributions, diseases, and dispersal. Predicting the impacts of climate change on global amphibian distributions - an impossible task? Oral presentation, Seminars of the Department of Animal Ecology, University of Marburg (Germany), 25 July 2007.

Hof, C., Brändle, M. & Brandl, R. (2007) Latitudinal patterns in species richness of European freshwater animals are not concordant across habitat types. Poster, 3rd biennial conference of the International Biogeography Society (IBS) in Puerto de la Cruz, Tenerife (Spain), 9-13 January 2007.

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Hof, C., Brändle, M., Marten, A. & Brandl, R. (2006) Latitudinal patterns of species richness in the European freshwater fauna: dispersal matters. Oral presentation, 91st annual meeting of the Ecological Society of America in Memphis, Tennessee (USA), 6-11 August 2006.

Hof, C. (2003) Protected areas of the future: man or nature? Oral presentation, EOS Seminars, Department of Geography, University of California Los Angeles (USA), November 2003.

Grants and awards received

2009	**Poster award** of the International Biogeography Society during the 4th biennial meeting in Merida (Mexico)
2006	**PhD stipend** granted by the **Cusanuswerk** – the German Catholic scholarship foundation for the project "Diversity, Biogeography and Macroecology of the European freshwater fauna" (declined).
2006	**Travelling grant** by the **DFG** (German Research Foundation), to attend the 91st annual meeting of the Ecological Society of America in Memphis, Tennessee (USA), 6-11 August 2006
2004 – 2010	Scholarship granted by **e-fellows.net**
2001 – 2006	**Student scholarship** granted by the **Cusanuswerk** – the German Catholic scholarship foundation

Teaching experience

2009	**Supervision** of the **B.Sc. project** "Predicting susceptibility to infection with the fungal disease Chytridiomycosis among Danish Anurans", Department of Biology, University of Copenhagen
2009	**M.Sc. course "Invasion Biology"**, Department of Biology, University of Copenhagen (guest lecture)
2009	**M.Sc. course "Population Dynamics"**, Department of Biology, University of Copenhagen
2007	**M.Sc. course "Numerical Analyses in Biodiversity studies"**, Department of Biology, University of Copenhagen
2007	**B.Sc. course "Macroecology"**, Faculty of Biology, University of Marburg (Germany)
2006	**Seminar und excursion „Namibia"**, Faculty of Biology, University of Marburg (Germany)
2001 – 2006	**Teaching assistant** at the Faculty of Biology, University of Marburg, (Germany) - various courses in Zoology, Botany and Ecology

Scientific / professional experience, internships

2008	**Co-organisation of a symposium** "Macroecology and Climate Change" during the joint meeting of the European Ecological Federation (EURECO) and the Ecological Society of Germany, Austria and Switzerland (GfÖ) in Leipzig/Germany
2006	**Scientific assistant** (3 months) at the **Helmholtz Centre for Environmental Research** – UFZ (European project "ALTERNet" – WP R3: "Impacts of the main natural and anthropogenic drivers and pressures of biodiversity")

2004	**Internship** (6 weeks) at the **German Federal Agency of Nature Conservation**, Department for Protected Areas.
2003	**Studies and research internship** (4 months) at the Department of Geography, **University of California Los Angeles** (UCLA), USA
1998 – 1999	**Civilian Service** (13 months) with the Verein Jordsand e.V. (Jordsand Society for the Protection of Seabirds and the Conservation of Nature), working as a **nature reserve ranger** at the lower Elbe River
Since 1997	Continuous participation in **local nature conservation projects and scientific field work** for the Society for Nature conservation and Ornithology of Rheinland-Pfalz

Peer reviewing experience

Biodiversity & Conservation, Conservation Letters, Ecography, Global Ecology and Biogeography, Journal of Biogeography, Oikos

PhD courses

2008	METIER Graduate Training Course No. 5: **Ecological Modelling**, Helmholtz Center for Environmental Research (UFZ) Leipzig-Halle (Dr. Karin Frank).
2008	**Species Distribution Modeling** Methods for Conservation Biologists, American Museum of Natural History (Dr. Richard Pearson, Dr. Steven Phillips).
2008	Curso básico de Sistemas de Información Geográfica con software libre (Introductory course on **geographic information systems [GIS]** with free software), Museo Nacional de Ciencias Naturales, Madrid (Dr. Jorge Lobo, Dr. Pablo Sastre).
2007	**Spatial Data Analysis in Macroecology**, Center for Macroecology and Evolution, University of Copenhagen (Prof. Carsten Rahbek, Prof. José Alexandre Diniz-Filho, Thiago Rangel)
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Languages

German mother tongue; fluent in English; basic in Spanish and French; advanced Latin.