Universidade Federal de Goiás
Instituto de Ciências Biológicas
Pós-graduação em Ecologia e Evolução

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Variação espacial dos múltiplos caminhos que conectam ambiente e biodiversidade

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Variação espacial dos múltiplos caminhos que conectam ambiente e biodiversidade

Elisa Barreto Pereira

Orientador: Dr. Thiago F. Rangel

Tese apresentada à Universidade Federal de Goiás como parte das exigências do Programa de Pós-graduação em Ecologia e Evolução para a obtenção do título de Doutora.

Goiânia - GO

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ATA DE DEFESA DE TESE

Ata nº 93 da sessão de **Defesa de Tese de Elisa Barreto Pereira**, que confere o título de **Doutora em Ecologia e Evolução**, na área de concentração em **Ecologia e Evolução**.

Aos **doze dias do mês de março de dois mil e vinte (12/03/2020),** a partir das **13h30min**, no **Auditório do ICB V,** do **Instituto de Ciências Biológicas,** realizou-se a sessão pública de Defesa de Tese intitulada **"Variação espacial dos múltiplos caminhos que conectam ambiente e biodiversidade"**. Os trabalhos foram instalados pelo Orientador, **Professor Doutor Thiago Fernando Lopes Valle de Britto Rangel - PPGEE/ICB/UFG,** com a participação dos demais membros da Banca Examinadora: **Professora Doutora Catherine Helen Graham - Swiss Federal Institute for Forest, Snow and Landscape Research - SWL),** membro titular externo; **Professor Doutor José Alexandre Felizola Diniz Filho - PPGEE/ICB/UFG**, membro titular interno; **Professor Doutor Luis Mauricio Bini - ICB/UFG**, membro titular interno**;** e **Dr. André Menegotto Domingos - Pós-Doc/ICB/UFG**, membro titular externo. Durante a arguição os membros da banca **não fizeram** sugestão de alteração do título do trabalho. A Banca Examinadora reuniu-se em sessão secreta a fim de concluir o julgamento da tese, tendo sido a candidata **aprovada** pelos seus membros. Proclamados os resultados pelo **Professor Doutor Thiago Fernando Lopes Valle de Britto Rangel**, Presidente da Banca Examinadora, foram encerrados os trabalhos e, para constar, lavrou-se a presente ata que é assinada pelos Membros da Banca Examinadora**.**

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It was a long and joyful journey.

Looking back, it is curious to see how things turned out.

The setbacks pushed me further.

Misfortunes changed my luck.

Obligations have become a real joy.

And now I have much more to be grateful for.

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SUMÁRIO

RESUMO

A biodiversidade não está distribuída igualmente ao redor do globo, e um grande desafio em ecologia e evolução é desvendar os processos que geram e mantém os padrões espaciais de diversidade. O longo histórico de pesquisa sobre o tema indica que os atuais padrões de biodiversidade resultam de uma complexa rede de interação entre múltiplos fatores atuando ao longo do tempo e do espaço. Nesta tese, nós exploramos como as relações que compõe parte desta rede variam ao longo do espaço geográfico em escala global e propomos uma série espaço-temporal do paleoclima, que tem o potencial de elucidar parte da variação espacial da biodiversidade. Iniciamos desenvolvendo uma análise de caminhos espacialmente explícita para explorar a não-estacionaridade espacial das relações entre condições ambientais atuais e passadas com a riqueza de espécies e a diversidade filogenética de mamíferos terrestres (primeiro capítulo). Mostramos que o ambiente se relaciona de forma diferente com cada dimensão da diversidade, explicando porque a riqueza de espécies nem sempre é um indicativo da quantidade de diversidade filogenética em uma comunidade. Em seguida, utilizamos a mesma abordagem metodológica para revisitar tradicionais teorias ecológicas de como o clima e a produtividade influenciam a riqueza de tetrápodes terrestres (segundo capítulo). Mostramos que a temperatura e a precipitação têm efeitos diretos e indiretos, via produtividade, na riqueza de espécies e mapeamos explicitamente onde cada condição ambiental é mais determinante para a riqueza de cada grupo taxonômico. A partir do reconhecimento de que ainda sabemos pouco sobre a biogeografia de ilhas de mamíferos terrestres, geramos uma base de dados global de mamíferos insulares e estimamos como a riqueza e o endemismo estão relacionados com características físicas e ambientais das ilhas, enquanto acomodando a não-estacionaridade entre regiões biogeográficas (terceiro capítulo). Mostramos que área e isolamento da ilha estão entre os fatores que mais influenciam a biodiversidade de mamíferos, enquanto efeitos ambientais variaram com o grupo taxonômico, a região biogeográfica e a medida da diversidade. Os resultados dos três primeiros capítulos apontam para a grande importância do clima atual e passado para a geração e manutenção dos padrões espaciais de biodiversidade. Portanto, propomos uma série espaço-temporal global do clima nos últimos 5 milhões de anos (Plioceno-Pleistoceno) para ajudar na compreensão da forte relação diversidade-clima (quarto capítulo).

Palavras-chave: Análise de caminhos, biogeografia de ilhas, clima, dimensões de diversidade, endemismo, gradientes de diversidade, mamíferos, não-estacionaridade, paleoclima.

ABSTRACT

Biodiversity is not evenly distributed around the globe, and a major challenge in ecology and evolution is to unravel the processes that generate and maintain spatial patterns of diversity. Decades of research on the subject indicates that current patterns of biodiversity result from a complex network between multiple factors acting over time and space. In this thesis, we explore how the relationships that make up part of this network vary across geographical space on a global scale and propose a spatiotemporal series of paleoclimate, which has the potential to elucidate the spatial variation of biodiversity. We begin by developing a spatially explicit path analysis to explore the spatial non-stationarity of the relationships between current and past environmental conditions with species richness and phylogenetic diversity of terrestrial mammals (first chapter). We show that environmental conditions relate differently to each dimension of diversity, explaining why species richness is not always an indicative of the amount of phylogenetic diversity in a community. Then, we employ the same methodological approach to revisit traditional ecological theories of how climate and productivity influence the richness of terrestrial tetrapods (second chapter). We show that temperature and precipitation have direct and indirect effects, via productivity, on species richness and we explicitly map where each environmental condition is most determinant for the richness of each taxonomic group. Based on the recognition that we still know little about islands biogeography of terrestrial mammals, we generated a global database of island mammals and estimated how richness and endemism are related to the physical and environmental characteristics of the islands, while accommodating non-stationarity between biogeographic regions (third chapter). We show that island’s area and isolation are among the strongest drivers of mammalian biodiversity, while environmental effects varied with taxonomic group, biogeographic region and measure of diversity. The results from the first three chapters point to the great importance of current and past climate for the generation and maintenance of spatial patterns of biodiversity. Therefore, we propose a global spatiotemporal series of the climate during the last 5 million years (Pliocene-Pleistocene), which holds the potential to advance our understanding of the strong diversity-climate relationship (fourth chapter).

Keywords: Climate, dimensions of diversity, endemism, gradients of diversity, island biogeography, mammals, non-stationarity, paleoclimate, path analysis.

INTRODUÇÃO

A diversidade biológica não está igualmente distribuída no espaço geográfico, e desvendar quais os processos que geram e mantém os padrões espaciais de biodiversidade é um dos objetivos centrais em ecologia e evolução. O longo histórico de pesquisa sobre o tema levou à proposição de várias hipóteses (Mittelbach *et al.* 2007; Fine 2015) e à identificação de consistentes padrões de variação entre biodiversidade e ambiente (Field *et al.* 2009). Entretanto, é difícil separar os diferentes mecanismos por trás das relações entre biodiversidade e ambiente (i.e. condições físicas e ambientais) porque eles não são mutuamente exclusivos, podem levar a padrões semelhantes e são dependentes da escala de estudo (e.g. Currie et al. 2004, Hortal et al. 2008). Nesta tese, exploramos outros dois fatores que também dificultam o estudo das relações biodiversidade-ambiente, a não-estacionaridade e os múltiplos caminhos pelos quais o ambiente pode influenciar a biodiversidade.

A relação biodiversidade-ambiente pode ser não-estacionária, ou seja, pode variar ao longo do espaço (Hawkins 2012; Gouveia *et al.* 2013), do tempo (Dornelas *et al.* 2013; Fritz *et al.* 2016) e da filogenia (Machac *et al.* 2017; Graham *et al.* 2018). Esta não-estacionaridade pode ser tanto na direção do efeito (positivo versus negativo) quanto na intensidade da relação, e pode levar um preditor a ser mais ou menos importante entre regiões geográficas, momentos no tempo e grupos de organismos. Uma forma tradicional de acomodar a não-estacionaridade tem sido, por exemplo, subdividir análises espaciais globais em unidades biogeográficas (e.g. biomas, domínios; Qian 2010) e análises de grandes grupos taxonômicos em seus clados constituintes (e.g. subdividir mamíferos em carnívoros, morcegos, artiodáctilos, primatas; Machac et al. 2017). Porém, abordagens mais espacial e taxonomicamente explicitas têm indicado que a não-estacionaridade pode ser ainda mais acentuada do que o antecipado pelas abordagens tradicionais (Cassemiro *et al.* 2007; Davies *et al.* 2018).

Explorar a variação nas relações entre preditor e resposta tem inúmeras vantagens para o avanço do conhecimento científico. Por exemplo, o estudo da variação espacial das relações biodiversidade-ambiente, um dos focos desta tese, possibilita identificar locais onde os preditores incluídos no modelo não são bons descritores da diversidade biológica. A observação desses locais pode oferecer pistas sobre quais os preditores faltantes no modelo (Foddy 2004) e pode revelar locais em que uma teoria recebe maior ou menor suporte (Cassemiro *et al.* 2007). Consequentemente, a não-estacionaridade espacial das relações pode ajudar a compreender inconsistências entre resultados de estudos conduzidos em diferentes locais (e.g. Mittelbach et al. 2001, Fei et al. 2018).

Relações ambiente-diversidade também tendem a ser vistas de forma simplificada por geralmente assumirem apenas relações diretas entre preditor e resposta, enquanto na realidade os preditores tendem influenciar a diversidade por vias diretas e indiretas (Belmaker & Jetz 2015; Marin *et al.* 2018). Por exemplo, o clima pode influenciar a riqueza de espécies não apenas diretamente, mas também indiretamente mediada pela produtividade (efeito de mediação; Grace 2006). Apesar da complexa rede de interação entre múltiplos preditores ser frequentemente reconhecida, ela é geralmente desconsiderada pela maior parte dos estudos e abordagens estatísticas. Análises de caminhos ou modelos de equações estruturais oferecem o ferramental ideal para testar os múltiplos caminhos pelos quais o ambiente pode influenciar a diversidade biológica, pois essas análises possibilitam particionar os efeitos diretos e indiretos enquanto controla por covariáveis (Grace *et al.* 2010).

Nesta tese buscamos inferir quais os determinantes atuais e históricos da diversidade de grupos de vertebrados terrestres em grandes escalas geográficas. Para isso, exploramos a importância relativa de diferentes preditores (e potencialmente, processos) que se relacionam com diferentes dimensões da diversidade biológica. Nos dois primeiros capítulos da tese nós usamos uma nova combinação de análise de caminhos (*path analysis*) e regressões geograficamente ponderadas (*geographically weighted regression – GWR*) para estimar a não-estacionaridade espacial dos efeitos diretos e indiretos do ambiente sob a biodiversidade. No terceiro capítulo, utilizamos abordagens tradicionais de subdividir o conjunto de dados por região geográfica e grupo taxonômico para estimar as relações entre condições ambientais e físicas de ilhas com a diversidade de mamíferos. No último capítulo, propomos um conjunto de dados paleoclimáticos que pode ajudar a compreender a origem da não-estacionaridade espacial, temporal e filogenética entre clima e diversidade biológica.

Desenvolvimento da tese

Diversos estudos têm mostrado que apesar das diferentes dimensões da biodiversidade serem muitas vezes fortemente correlacionadas, seja por causas matemáticas e/ou biológicas, existem locais em que elas divergem consideravelmente (Tucker & Cadotte 2013). Tais divergências não estão aleatoriamente distribuídas no espaço geográfico, o que sugere a ocorrência de diferentes processos ecológicos e evolutivos (Stevens & Tello 2018). No **primeiro capítulo** da tese exploramos as relações entre fatores ambientais presentes e passados com a riqueza de espécies e a diversidade filogenética de mamíferos terrestres utilizando a análise de caminhos espaciais. Os resultados desse trabalho mostraram que riqueza de espécies, diversidade filogenética e fatores ambientais se relacionam de maneira diferente no espaço geográfico, com a maioria das relações variando em magnitude e em direção. Observamos que os efeitos ambientais na diversidade filogenética são predominantemente mediados por seus efeitos na riqueza de espécies. Porém, uma vez que a riqueza de espécies é controlada, as relações entre ambiente e diversidade filogenética indicam o efeito do ambiente na composição de espécies. Também pudemos detectar que temperatura média anual e evapotranspiração efetiva são os principais determinantes da diversidade de mamíferos na maior parte do globo, e que há uma divisão longitudinal na importância relativa dessas variáveis.

Este último resultado contrasta com a hipótese de água-energia, que propõe a existência de uma variação latitudinal na importância de água e de energia, sendo a primeira mais limitante nos trópicos e a segunda na região temperada (Hawkins *et al.* 2003). Portanto, no **segundo capítulo** da tese nós utilizamos a análise de caminhos espacial para revisitar a hipótese de água-energia (Hawkins *et al.* 2003) e as várias hipóteses de como clima e produtividade influenciam a riqueza de espécies (Hutchinson 1959; Rohde 1992; Brown *et al.* 2004; Currie *et al.* 2004; Evans *et al.* 2005) de tetrápodes terrestres global. Nosso modelo possibilitou estimar os efeitos diretos de temperatura, precipitação e produtividade sobre a riqueza de espécies, bem como os efeitos indiretos do clima via produtividade, resultando em um mapa dos locais em que cada um desses fatores é mais importante para determinar a diversidade de cada um dos tetrápodes terrestres. Nós confirmamos que o clima influencia a riqueza direta e indiretamente, apoiando a ideia de que a energia térmica e a disponibilidade de água influenciam a riqueza, não apenas através de taxas metabólicas e tolerâncias fisiológicas das espécies (Brown *et al.* 2004; Currie *et al.* 2004), como geralmente reconhecido, mas também pela quantidade de energia produtiva. Observamos que répteis apresentaram relações espécie-energia mais distintas entre os tetrápodes, com um claro padrão latitudinal de importância relativa de água versus temperatura, como o proposto pela teoria de água-energia. Para todos os quatro grupos de tetrápodes terrestres, os efeitos diretos do clima foram majoritariamente mais fortes do que os efeitos indiretos mediados pela produtividade, sugerindo que gradientes de riqueza parecem resultar principalmente por restrições fisiológicas do organismo do que pelos limites impostos pela quantidade de energia produtiva no ambiente.

O estudo de mamíferos nos dois primeiros capítulos da tese me levou à observação de que sabemos consideravelmente pouco sobre a diversidade de mamíferos em ilhas em grandes escalas espaciais. Portanto, no **terceiro capítulo** da tese geramos uma base de dados globais da riqueza de espécies e do número de espécies endêmicas e investigamos a relação entre características de ilhas e a biodiversidade insular de mamíferos terrestres. Nossos resultados indicam que área e isolamento são fortes preditores da diversidade insular entre todas as regiões biogeográficas do mundo, em consonância com a teoria da biogeografia das ilhas (MacArthur & Wilson 1967; Rosindell & Phillimore 2011). O isolamento atual e passado deixou fortes marcas na biodiversidade dos mamíferos, resultando em menor riqueza, mas maior endemismo, conforme o esperado pelo provável aumento no intercâmbio de espécies e fluxo gênico entre ilha e continente. A capacidade de voo influenciou a importância relativa do isolamento atual e passado, visto que a diversidade de morcegos está mais fortemente ligada ao isolamento atual e a de mamíferos não-volantes está mais associada ao isolamento passado. O clima teve relações variadas com a diversidade, dependendo do grupo taxonômico, da região biogeográfica e da medida da diversidade, com uma tendência de efeitos mais fortes no endemismo do que na riqueza.

Os três primeiros capítulos da tese demonstraram como condições climáticas, inclusive as passadas, são importantes preditores dos padrões de biodiversidade atuais. No entanto, ainda sabemos relativamente pouco sobre como a variação espaço-temporal do paleoclima ao longo do tempo afetou dinâmicas ecológicas e evolutivas devido à escassez de estimativas espacial e temporalmente explícitas do clima na escala de milhões de anos. No **quarto capítulo** da tese, em parceria com um time de pesquisadores em paleoclimatologia, nós preenchemos essa lacuna ao propor o PaleoClimSeries, um conjunto de dados espaço-temporal global do clima nos últimos 5 milhões de anos (Plioceno-Pleistoceno) derivado do *downscaling* espacial de um modelo de circulação geral oceânico-atmosférico de complexidade intermediária, o PLASIM-GENIE (Holden *et al.* 2019). Esse conjunto de dados tem o potencial de avançar nossa compreensão sobre os mecanismos ecológicos e evolutivos por trás da forte relação entre biodiversidade e clima que observamos nos capítulos anteriores, o que é de extrema importância para prever com maior precisão a resposta da biodiversidade às mudanças climáticas.

INTRODUCTION

Biological diversity is not equally distributed across geographic space and unraveling the processes that generate and maintain spatial patterns of biodiversity is one of the main goals in ecology and evolution. The long research tradition on the topic has led to the proposition of several hypotheses (Mittelbach et al. 2007; Fine 2015) and the identification of consistent patterns of variation between biodiversity and the environment (Field et al. 2009). However, it is difficult to separate the different mechanisms behind the biodiversity-environment (i.e. physical and environmental conditions) because they are not mutually exclusive, they can lead to similar patterns and are dependent on the scale of the study (e.g. Currie et al. 2004, Hortal et al. 2008). In this thesis, we explore two other factors that also hinder the study of biodiversity-environment relationships: non-stationarity and the multiple paths by which the environment can influence biodiversity.

Biodiversity-environment relationship may be non-stationary, that is, it can vary over space (Hawkins 2012; Gouveia et al. 2013), time (Dornelas et al. 2013; Fritz et al. 2016) and phylogeny (Machac et al. 2017; Graham et al. 2018). Non-stationarity may occur in the direction of effect (positive versus negative) and in the strength of the relationship, and can lead a predictor to be more or less important among geographic regions, moments in time and groups of organisms. A traditional way of accommodating non-stationarity has been, for example, subdividing global spatial analyzes into biogeographic units (e.g. biomes, domains; Qian 2010) and analyzes of large taxonomic groups in their constituent clades (e.g. subdividing mammals into carnivores, bats, artiodactyls, primates; Machac et al. 2017). However, more spatially and taxonomically explicit approaches have suggested that non-stationarity may even be more drastic than anticipated by traditional approaches (Cassemiro et al. 2007; Davies et al. 2018).

Exploring the variation in the relationship between predictor and response has numerous advantages for advancing scientific knowledge. For example, the study of the spatial variation of biodiversity-environment relationships, one of the focuses of this thesis, makes it possible to identify places where the predictors included in the model are not good descriptors of biological diversity. These sites can offer clues as to which predictors are missing from the model (Foddy 2004) and can reveal places where a theory receives more or less support (Cassemiro et al. 2007). Consequently, the spatial non-stationarity of relationships may help to understand inconsistencies between studies conducted in different locations (e.g. Mittelbach et al. 2001, Fei et al. 2018).

Environment-diversity relationships also tend to be simplified by generally assuming only direct relationships between predictor and response, whereas predictors tend to influence diversity through direct and indirect pathways (Belmaker & Jetz 2015; Marin et al. 2018). For example, climate can influence species richness not only directly, but also indirectly mediated by productivity (mediation effect; Grace 2006). Although the complex network of interactions between multiple predictors is often recognized, it is generally overlooked by most studies and statistical approaches. Path analysis or structural equation models offer the ideal tools to test the multiple paths through which the environment can influence biological diversity, as these analyzes make it possible to partition the direct and indirect effects while controlling for covariates (Grace et al. 2010).

In this thesis we seek to infer which are the current and historical determinants of the diversity of terrestrial vertebrate groups in large geographic scales. To this end, we explore the relative importance of different predictors (and potentially, processes) that relate to different dimensions of biological diversity. In the first two chapters of the thesis we used a new combination of path analysis and geographically weighted regressions (GWR) to estimate the spatial non-stationarity of the direct and indirect effects of the environment on biodiversity. In the third chapter, we use traditional approaches to subdivide the data set by geographic region and taxonomic group to estimate the relationship between environmental and physical conditions of islands with the diversity of mammals. In the last chapter, we propose a set of paleoclimatic data that can help to understand the origin of spatial, temporal and phylogenetic non-stationarity between climate and biological diversity.

Thesis development

Several studies have shown that although the different dimensions of biodiversity are often strongly correlated, whether due to statistical and/or biological reasons, there are places where they diverge considerably (Tucker & Cadotte 2013). Such mismatches are not randomly distributed across geographic space, which suggests the occurrence of different ecological and evolutionary processes (Stevens & Tello 2018). In the **first chapter** of the thesis we explore the relationships between present and past environmental factors with the richness of species and the phylogenetic diversity of terrestrial mammals using a spatial path analysis. Our results showed that species richness, phylogenetic diversity and environmental factors related differently in geographic space, with most relationships varying in magnitude and direction. We observed that the environmental effects on phylogenetic diversity are predominantly mediated by their effects on species richness. However, once the species richness is controlled, the relationships between environment and phylogenetic diversity indicate the effect of the environment on species composition. We were also able to detect that average annual temperature and effective evapotranspiration are the main determinants of mammal diversity in most parts of the globe, and that there is a longitudinal division in the relative importance of these variables.

This last result contrasts with the water-energy hypothesis, which proposes the existence of a latitudinal variation in the importance of water and energy, the first being more limiting in the tropics and the second in the temperate region (Hawkins et al. 2003). Therefore, in the **second chapter** of the thesis we use spatial path analysis to revisit the water-energy hypothesis (Hawkins et al. 2003) and the various hypotheses of how climate and productivity influence species richness (Hutchinson 1959; Rohde 1992; Brown et al. 2004; Currie et al. 2004; Evans et al. 2005) of global terrestrial tetrapods. Our model made it possible to estimate the direct effects of climate (temperature and precipitation) and productivity on species richness, as well as the indirect effects of climate via productivity, resulting in a map of the locations where each of these factors is most important to determine the diversity of each of the terrestrial tetrapods. We confirm that climate influences richness directly and indirectly, supporting the idea that thermal energy and water availability influence richness, not only through metabolic rates and physiological tolerances of species (Brown et al. 2004; Currie et al 2004), as generally recognized, but also for the amount of productive energy. We observed that reptiles showed more distinct relationships among the tetrapods, with a clear latitudinal pattern of relative importance of water versus temperature, as proposed by the water-energy theory. For all four groups of terrestrial tetrapods, the direct effects of the climate were mostly stronger than the indirect effects mediated by productivity, suggesting that gradients of richness seem to result mainly from physiological tolerance and metabolic rates than from the limits imposed by the amount of productive energy. in the environment.

The study of mammals in the first two chapters of the thesis led me to the observation that we know considerably little about the diversity of mammals on islands at large spatial scales. Therefore, in the **third chapter** of the thesis, we generate a global database of species richness and the number of endemic species and investigate the relationship between island characteristics and the insular biodiversity of terrestrial mammals. Our results indicate that area and isolation are strong predictors of island diversity among all biogeographic regions of the world, in line with the theory of island biogeography (MacArthur & Wilson 1967; Rosindell & Phillimore 2011). Current and past isolation has left strong marks on the biodiversity of mammals, resulting in lower richness, but greater endemism, as expected by the likely increase in species exchange and gene flow between island and continent. Flight ability influenced the relative importance of current and past isolation, since the diversity of bats is more strongly linked to current isolation and that of non-flying mammals is more associated with past isolation. The climate had varied relations with diversity, depending on the taxonomic group, the biogeographic region and the measure of diversity, with a tendency for stronger effects on endemism than on richness.

The first three chapters of the thesis demonstrated how climatic conditions, including past ones, are important predictors of current biodiversity patterns. However, we still know relatively little about how the spatiotemporal variation of paleoclimate over time has affected ecological and evolutionary dynamics due to the scarcity of spatially and temporally explicit estimates of climate on the scale of millions of years. In the **fourth chapter** of the thesis, in collaboration with a team of researchers in paleoclimatology, we fill this gap by proposing PaleoClimSeries, a global spatio-temporal data set for the last 5 million years (Pliocene-Pleistocene) derived from the spatial downscaling of an intermediate complexity atmosphere-ocean general circulation model, the PLASIM-GENIE (Holden et al. 2019). This data set has the potential to advance our understanding of the ecological and evolutionary mechanisms behind the strong relationship between biodiversity and climate that we noted in previous chapters, which is extremely important to more accurately predict biodiversity's response to climate change.

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CAPÍTULO 1

Environmental factors explain the spatial mismatches between species richness and phylogenetic diversity of terrestrial mammals

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ABSTRACT

Aim Explore the spatial variation of the relationships between species richness (SR), phylogenetic diversity (PD) and environmental factors to infer the possible mechanisms underlying patterns of diversity in different regions of the globe.

Location Global

Time period Present day

Major taxa studied Terrestrial mammals

Methods We used a hexagonal grid to map SR and PD of mammals and four environmental factors (temperature, productivity, elevation and climate-change velocity since the Last Glacial Maximum). We related those variables through direct and indirect pathways using a novel combination of Path Analysis and Geographically Weighted Regression to account for spatial non-stationarity of path coefficients.

Results SR, PD and environmental factors relate differently across the geographic space, with most relationships varying in both, magnitude and direction. Species richness is associated with lower phylogenetic diversity in much of the tropics and in the Americas, which reflects the tropical origin and the recent diversification of some mammalian clades in these regions. Environmental effects on PD are predominantly mediated by their effects on SR. But once richness is controlled for, the relationships between environmental factors and PD (i.e. PD_{SR}) highlight environmentally driven changes in species composition. Environmental- PD_{SR} relationships suggest that the relative importance of different mechanisms driving biodiversity shifts spatially. Across most of the globe, temperature and productivity are the strongest predictors of richness, while PD_{SR} is best predicted by temperature.

Main conclusions Richness explains most spatial variation in PD, but both dimensions of biodiversity respond differently to environmental conditions across the globe, as indicated by the spatial mismatches in the relationships between environmental factors and these two types of diversity. We show that accounting for spatial non-stationarity and environmental effects on PD while controlling for richness uncovers a more complex scenario of drivers of biodiversity than previously observed.

Key words: biodiversity measures, dimensions of biodiversity, geographically weighted regression, Last Glacial Maximum, latitudinal gradient, Mammalia, non-stationarity, path analysis, spatial patterns, structural equation modelling.

INTRODUCTION

Biodiversity encompasses multiple dimensions, such as phylogenetic and functional diversity, and species richness, which have varying degrees of spatial co-variation (Stevens & Tello, 2018). Environmental factors correlate differently with each dimension of biodiversity and this variation offers opportunities to explore the multiple mechanisms that underlie different biodiversity dimensions (Safi *et al.*, 2011; Oliveira *et al.*, 2016). However, most studies exploring environmental correlates of diversity have assumed that relationships are consistent across regions (e.g., a single regression is run), when they actually might vary considerably (Cassemiro *et al.*, 2007; Gouveia *et al.*, 2013). The standard assumption of spatial stationarity may lead to erroneous conclusions about the magnitude of different relationships. For example, spatial stationary analyses may deem a variable of little or nil effect if its direction shifts regionally from positive to negative (Fotheringham *et al.*, 2002). Here we relaxed the stationarity assumption to explore the spatial variation of the relationships between environment, species richness and phylogenetic diversity of terrestrial mammals.

Mammals have a clear latitudinal gradient of higher species richness (SR) and phylogenetic diversity (PD) in the tropics, but the spatial patterns of each dimension are not always congruent, with some areas having more, or less, PD than expected based on richness alone (Davies & Buckley, 2011). Spatially structured differences between SR and PD reflects differences in species composition, which are likely influenced by environmentally-driven ecological and evolutionary processes (Davies *et al.*, 2007; Safi *et al.*, 2011; Penone *et al.*, 2016). Thus, comparing how SR and PD relate to each other and to environmental factors offers clues about the underlying mechanisms behind diversity patterns (Davies *et al.*, 2007). Path analysis (or Structural Equation Modeling in general) offers a way to explore the complex interactions between assemblage’s richness, phylogenetic diversity and environment, as it can disentangle the direct and indirect effects on a variable while controlling for covariates (Grace *et al.*, 2010). We designed a path model that is not only able to relate SR and PD (Fig. 1, path *i*) and to identify environmental factors responsible for promoting higher or lower PD and SR, but also to separate how much of the total environmental effect on phylogenetic diversity is due to (1) changes in species richness (Fig. 1, paths *a*-*d* mediated by path *i*) and (2) changes in species composition (i.e., PD controlled for richness; Fig. 1, paths *e*-*h*). The relationship between environmental factors and PD controlled for richness (hereafter, PD_{SR}) should offer insights on the relative influence of speciation and extinction in the generation of biodiversity patterns (Davies *et al.*, 2007).

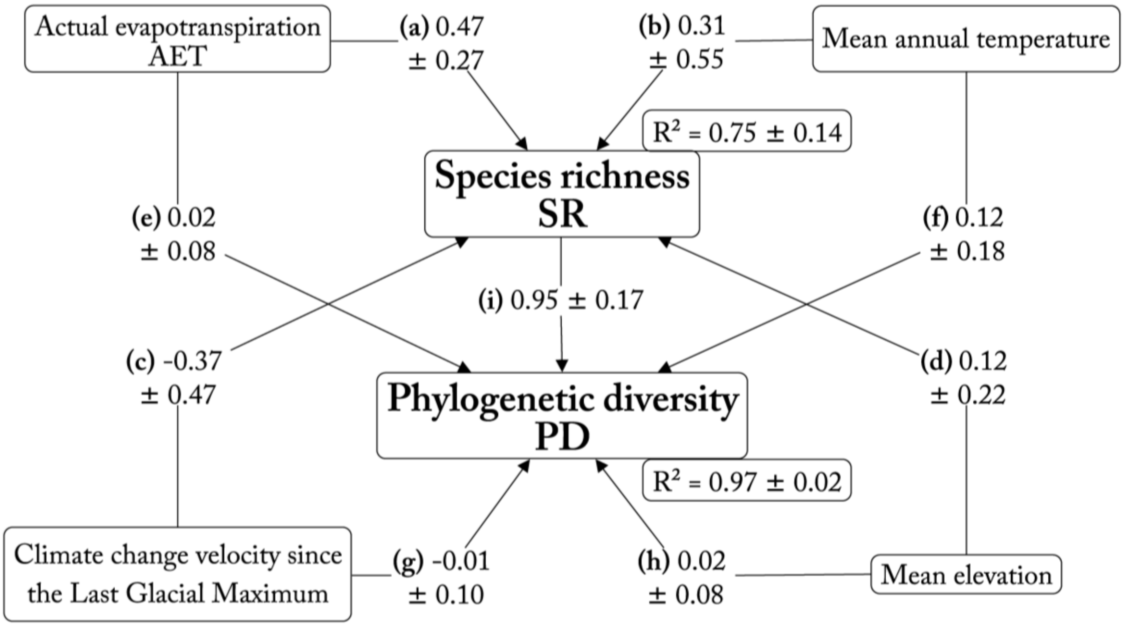

Figure 1 - Path model of hypothesized relationships among environmental factors, species richness (SR) and phylogenetic diversity (PD) of terrestrial mammals. Numbers indicate mean and standard deviation of standardized path coefficients across the entire globe.

In assemblages composed of closely related species, such as those resulting from rapid speciation, selective extinction of older lineages, or reduced lineages interchange, individual species contribute to a small fraction of the phylogenetic diversity (Cardillo, 2011; Tucker & Cadotte, 2013). In contrast, in assemblages composed of distantly related species, such as those with lower diversification rates and frequent interchange of distantly related species, each additional species yields a greater relative increase in phylogenetic diversity (Cardillo, 2011; Tucker & Cadotte, 2013). In the tropics, phylogenetic diversity (PD) should be lower than expected for the species richness (SR) because diversification rate seems to be higher (Rolland *et al.*, 2014) and mammals species tend to conserve tropical niches (Cooper *et al.*, 2011; Olalla-Tárraga *et al.*, 2011). Conversely, the relationship between PD-SR should be stronger (Fig.1, path *i*) in regions that harbor high diversity of early diverging mammalian lineages, such as in Africa when compared to the Neotropics (Davies & Buckley, 2012). Thus, mapping the strength of the PD-SR relationship highlights ecological and evolutionary processes that influence phylogenetic composition of assemblages.

Mammalian richness is strongly and positively related to productivity (Davies *et al.*, 2011; Oliveira *et al.*, 2016), and this relationship has been maintained for millions of years (Fritz *et al.*, 2016). Areas of higher productivity support larger population sizes, potentially reducing extinction and increasing speciation rates, which culminates in higher species richness (Coelho *et al.*, 2018; Storch *et al.*, 2018). Thus, productivity should relate positively to richness across the entire globe (Fig. 1, path *a*), but the magnitude of such relationship might vary across the globe (Gouveia *et al.*, 2013; Alves *et al.*, 2018). The relationship between AET and phylogenetic diversity when holding richness constant (i.e., PD_{SR}; Fig. 1, path *e*) will vary in direction depending on the relative importance of AET in reducing extinction and increasing speciation rates. A humped relationship between PD_{SR} and AET observed in global parrots was interpreted as a result of decreasing extinction when AET is low and increasing speciation when AET is high (Davies *et al.*, 2007). Therefore, we expect the AET–PD_{SR} relationship to vary in both magnitude and direction across the globe, being positive where AET it is low and negative where it is high.

Mammalian richness also positively relates to temperature (Belmaker & Jetz, 2015), which is hypothesized to be the result of an acceleration in metabolic, mutation and speciation rates (Rohde, 1992; Brown *et al.*, 2004) or of most lineages having a tropical origin and conserved niches (Wiens & Donoghue, 2004). In both cases, the association between temperature and richness (Fig. 1, path *b*) should be consistently positive across the globe and any shifts in the magnitude of the relationship might follow a latitudinal gradient similar to that of temperature itself. However, the relationship between PD_{SR} and temperature (Fig. 1, path *f*) will vary depending on the mechanism at play, and there is no clear expectation of which mechanisms predominate in a particular region. If acceleration in speciation rates predominates, then PD_{SR} should relate negatively with temperature. On the contrary, a positive relationship between temperature and PD_{SR} is expected when the main effect of temperature on diversity is associated with constrained thermal tolerance to colder environments and traits are conserved, as has being noticed in mammals (Olalla-Tárraga *et al.*, 2011).

Spatially structured environmental relationships with SR and PD_{SR} are also expected in mountainous regions and in areas of past climatic instability. Mountains are cradles of biodiversity because they promote higher speciation rates by range fragmentation and lower extinction rates by acting as climatic refugia (Fjeldså *et al.*, 2011; Rangel *et al.*, 2018). Rapid speciation adds short terminal branches to the phylogenetic tree, and therefore, it is expected that spatial analysis will detect a clear pattern of positive relationship between elevation and richness in mountainous regions (Fig. 1, path *d*). However, the relationship between elevation and PD_{SR} (Fig. 1, path *h*) should be negative if mountains are acting more as species cradles and positive if their main effect is on offering refugia and buffering extinction (Davies *et al.*, 2007; Voskamp *et al.*, 2017). Climatic instability since the Last Glacial Maximum (LGM) is also expected to have left imprints on SR and PD_{SR} given that it triggered extinction and range contractions, leading to reductions in species richness (Fig. 1, path *c*) (Sandel *et al.*, 2011; Svenning *et al.*, 2015). The effect of climate-change velocity on PD_{SR} depends on which lineages persisted and recolonized the region (Fig. 1, path *g*). Thus, climate-change velocity should relate positively with PD_{SR} where more distantly related species persisted and/or recolonized the region, but negatively where these species are more closely related (e.g. phylogenetic conservatism of traits that enable species to survive or recolonize) (Svenning *et al.*, 2015). A spatially explicit analysis may capture these different imprints of past climatic change on biodiversity, especially where changes were more extreme, such as in the formerly glaciated areas in North America and Europe (Hortal *et al.*, 2011; Gouveia *et al.*, 2013).

MATERIALS AND METHODS

Spatial grid

We built a geodesic dome from an icosahedron, triangulating its faces to compose a global hexagonal grid. Our grid is suitable for spatial analyses of global datasets because it minimizes geographic distortions in distances, shapes and areas caused by map projection (Sahr *et al.*, 2003). The 20,163 *quasi* equal-area cells in our hexagonal grid span on average 6,917.84 (± 858.62 s.d.) km^2. Most importantly, variation in grid cell area does not correlate with latitude.

Diversity measures

We mapped the geographic distribution of terrestrial mammals by recording their presence in each grid cell. We used SAM (*Spatial Analysis in Macroecology,* Rangel *et al.*, 2006, 2010) to calculate the overlap between species range polygons (IUCN, 2017) and grid cells. Species richness map was estimated by the total count of species recorded in each grid cell. We removed 392 cells from analysis because they had less than 5 species.

We used mammal phylogenetic trees provided by Kuhn *et al.* (2011), which solved the polytomies that comprise approximately 50% of the most complete mammal super-tree (Bininda-Emonds *et al.*, 2007; Fritz *et al.*, 2009). We used public databases of taxonomic synonyms to match the 5,020 species on the phylogenetic trees to the species in the IUCN's geographic distribution database, resulting in a final dataset of 4,751 mammal species with phylogenetic and geographic data. We mapped phylogenetic diversity by summing the branch lengths connecting all species present in each cell (Faith, 1992).

Environmental predictors

To incorporate environmental productivity, temperature, elevation and climatic stability into our analyses we compiled, respectively, the following variables: (1) mean actual evapotranspiration (AET; Trabucco & Zomer, 2010), (2) mean annual temperature (Fick & Hijmans, 2017), (3) mean elevation (USGS, 1996), and (4) climate-change velocity since the Last Glacial Maximum, which is a proxy of the speed at which species must shift their ranges to track a given changing climate (Sandel *et al.*, 2011). Mean elevation was chosen instead of a measure of elevation heterogeneity to increase the chances of detecting the effect of mountains on biodiversity when using a spatial analysis based on circular kernels (see the *statistical analysis* subsection). We rescaled these four environmental variables to our hexagonal grid using the “raster” package in R software (Hijmans, 2016), and excluded from the final dataset the cells missing environmental information, resulting in a final dataset of 17,151 cells.

Statistical analysis

We designed a path model according to a hypothesis of how the environmental factors likely influence richness and phylogenetic diversity, as well as how PD is influenced by SR (Fig. 1). The path model can assess (1) the direct effect of each variable on richness and PD, while controlling for the effect of the remaining variables (paths *a*-*i*), (2) the indirect effect of the environment on PD given its influence on richness (paths *a*-*d* multiplied by path *i*), and (3) the total environmental effect on PD (i.e., sum of all direct and indirect path coefficients connecting environmental factors to PD). We *Z*-transformed all variables to allow direct comparison among estimated path coefficients, as in partial regression coefficients.

Standard path analysis (and Structural Equation Modeling - SEM) of spatially distributed samples assumes that the relationship among variables is the same across space, which is unrealistic for very complex historical phenomena at large spatial scales (Hortal *et al.*, 2011; Gouveia *et al.*, 2013). To relax this assumption, we developed a Geographically Weighed Path Analysis (GWPath), which allows path coefficients to vary regionally (code available in the supplementary material). Contrary to the traditional path analysis that uses ordinary least square regression, GWPath uses

Geographically Weighted Regressions (GWR) to fit the regressions that compose the path model. Thus, the path analysis was repeated for each grid cell, around which a distance-based Gaussian weighting function (kernel) was set, to assign greater weight to nearby cells than distant ones (Fotheringham *et al.*, 2002; Fig. S1). We implemented GWPath by using the "gwr" function of "spgwr" R package (Bivand & Yu, 2017) within the framework of a path analysis.

The challenge of Geographically Weighted methods is to parameterize the bandwidth (radius) of the spatial kernel function. On one hand, if the bandwidth is too large, the analysis converges back to the spatial stationarity assumption, preventing variation of estimated coefficients. On the other hand, if the bandwidth is too narrow, the model overfits residual variation and the coefficients shift drastically even among nearby cells (Fotheringham *et al.*, 2002), leading to the formation of islands of coefficients that are easily detectable by visual inspection. We evaluated bandwidths ranging from 500 to 3,000 km, at 100 km intervals, visually inspecting spatial patterns in estimated coefficients for signs of artifacts caused by overfitting. We found the bandwidth of 1,000 km to be ideal for capturing large-scale patterns in coefficient variation while avoiding overfitting, as found in other studies using GWR on environmental drivers of large-scale biodiversity data (Davies *et al.*, 2011; Ficetola *et al.*, 2017).

Phylogenetic uncertainty

To account for uncertainty in the evolutionary history of mammals we replicated the GWPath analyses 1,000 times, each time using the phylogenetic diversity calculated from a differently randomly sampled phylogeny from a posterior distribution of 10,000 fully resolved trees (Kuhn *et al.*, 2011). We calculated mean and standard deviation of each path coefficient among replicates, which capture, respectively, the average effect and uncertainty in coefficient estimates due to phylogenetic uncertainty (Rangel *et al.*, 2015). The ratio between the mean and standard error of estimated coefficients follows Student's *t*-distribution, so that $t > |1.96|$ have statistically large effects relative to the magnitude of phylogenetic uncertainty.

RESULTS

Phylogenetic diversity of mammal assemblages is largely determined by the number of species it contains (SR), but the magnitude of the relationship between these two dimensions of biodiversity shifts across the geographic space (standardized path coefficients averaged across space 0.95±0.17, path *i* in Fig. 1) because of how phylogenetically related the species are. As predicted, changes in SR are associated with smaller changes on phylogenetic diversity (PD) in the tropics, ranging from 0.69 in South America, Central Africa and eastern Asia to 1.59 in the Sahara Desert, Arabian Peninsula and northern Eurasia (Fig. 2). Central North America is an exception to the latitudinal pattern, as its SR explains less of its PD.

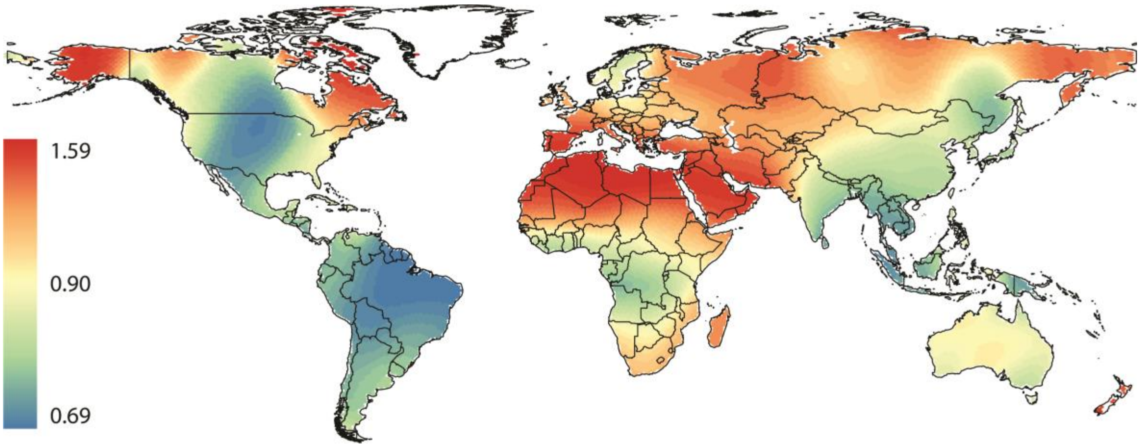

Figure 2 – Standardized path coefficients estimating the regional relationship between species richness (SR) and phylogenetic diversity (PD) of terrestrial mammals (path *i* on

Figure 1).

Spatially varying relationships are observed for all tested paths relating environmental factors to richness and phylogenetic diversity (Figs. 1 and 3). Unsurprisingly, much of how the environment relates to PD (i.e., total effects) is a consequence of how it relates to richness (Figs. S2-S4), because the PD of an assemblage is largely determined by the number of species it contains (Figs. 1 and 2). However, when richness is held constant, there are considerable differences in the way the environment relates to PD (i.e., PD_{SR}; paths *e* to *h* in Fig. 1) and to SR (paths *a* to *d* in Fig. 1), highlighting environmentally driven changes in species composition. Our results are robust to phylogenetic uncertainty, as most of the uncertainty in estimated path coefficients (i.e., cells with high standard errors) are in regions of small effect sizes (grey regions in Fig. 3 and white regions in Fig. 4).

The way environment relates to richness and to PD_{SR} vary greatly over space, not only in magnitude but also in direction (Figs. 1 and 3). Less variation in the direction of the relationships are found for how richness relates to AET (+) and climate-change velocity (-), and for PD_{SR} and temperature (+) (Fig. 3). In general, PD_{SR} has more spatially varying relationships with environmental factors than does richness (Fig. 3), suggesting that environmental influences on diversification might have a more complex spatial pattern than previously anticipated based solely on richness patterns.

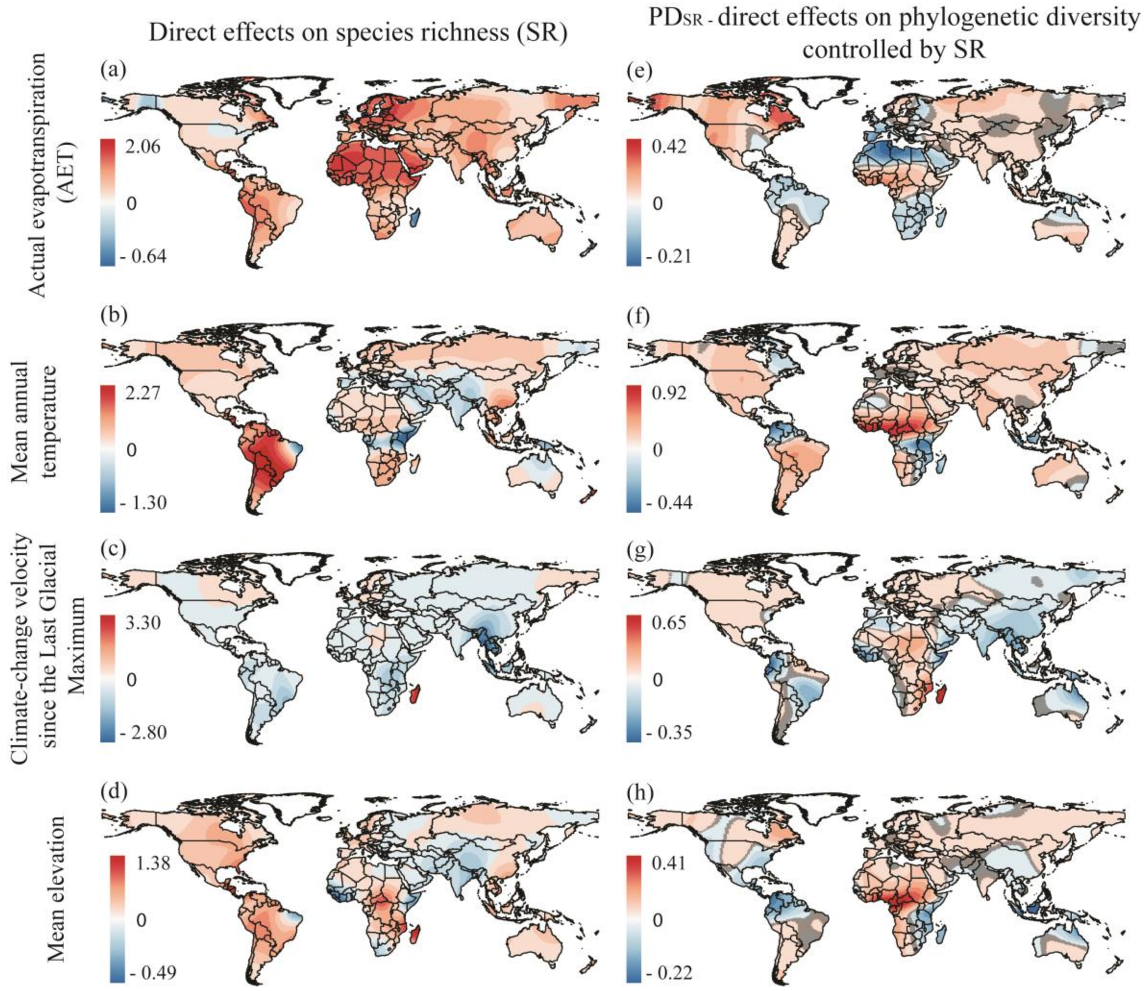

Figure 3 – Map of standardized path coefficients of environmental determinants of terrestrial mammalian richness (first column, a to d), and phylogenetic diversity controlled for richness (seccond column, e to h). Panels labels correspond to path labels in Figure 1. Gray areas indicate large phylogenetic uncertainty, where the direction of the coefficient could not be inferred accurately.

Temperature and AET are mostly positively associated with richness, but unlike our prediction, there are regions where both measures of energy relate negatively with richness (Fig. 3a and b). A notable exception to the positive relationships between temperature and richness is in the Rift Valley region (Fig. 3b), just where mammalian richness peaks. As expected, the relationships between AET and temperature with PD_{SR} shifts in direction (Fig. 3e and f). But contrary to our prediction, there is no clear pattern of how AET relates to PD_{SR} given the amount of AET, as there are positive and negative relationships in highly productive areas, such as the tropical region of Africa and South America, respectively (Fig. 3e). The strongest effects of AET are concentrated in the energy-limited Sahara Desert, where it is associated with an increase in richness and decrease in PD_{SR}, whereas the strongest effects of temperature are concentrated in South America for richness (Fig. 3b) and on sub-Sharan regions for PD_{SR} (Fig. 3f).

Mountainous areas do not present a marked difference in coefficients of the relationship between elevation, richness and PD_{SR} as we predicted. The closest to our expectations are the negative coefficients between elevation and PD_{SR} in the Himalayan region (Fig. 3h), consistent with the hypothesis that mountains trigger rapid speciation events. However, contrary to our expectations, elevation relates negatively with richness in this area (Fig. 3d). Climate-change velocity is associated with decreases in mammalian richness across most of the globe, except in Madagascar and parts of North America and Europe where climate-change velocity was greatest (Fig. 3c). In these areas, climate-change velocity correlates positively with PD_{SR} (Fig. 3g). However, in general, the PD_{SR}-climate change velocity relationships vary considerably in direction across the globe without a clear pattern (Fig. 3g).

Among the environmental factors being considered, mammalian richness is most strongly influenced by AET and temperature across most of the globe, with temperature playing a more important role in most of the New World and AET being more important in the Old World (Fig. 4a). Temperature is the environmental factor that explains most spatial variation of PD_{SR} over the globe (Fig. 4b). Small differences on total environmental effects on phylogenetic diversity and on richness arise where SR is a weaker predictor of PD – much of the tropics and North America (Fig. 2) - and where environmental effects on PD_{SR} are strong (Fig. 3). Thus, when considering total environmental effects on PD, temperature becomes more important in South America and in central Africa, while climate-change velocity is more important in parts of Asia, Madagascar and central Africa (Fig. 4c).

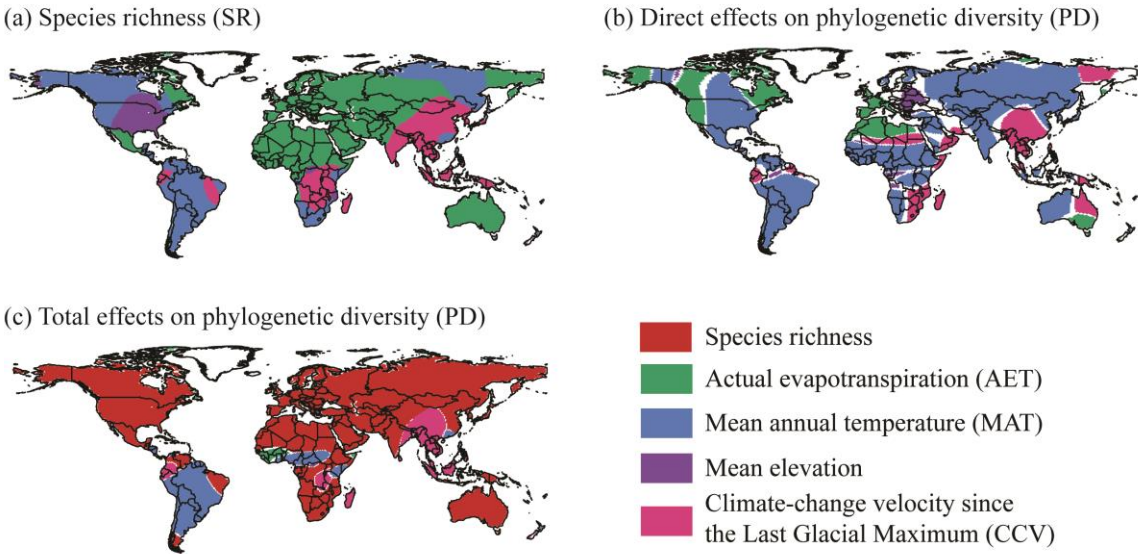

Figure 4 – Categorical maps showing the strongest environmental correlates of terrestrial mammal (a) species richness (SR) and (b) phylogenetic diversity (PD), controlling for indirect effects via SR. (c) Depicts the total effects on PD when controlling and accounting for SR. Phylogenetic uncertainty prevents inference over white regions.

DISCUSSION

Our spatial path analysis confirmed that while much of the relationship between environmental factors and phylogenetic diversity (PD) can be explained by species richness (SR), once SR is held constant, the environmental-PD_{SR} relationships offer insights on the relative importance of speciation and extinction on the phylogenetic composition of the assemblages. All the relationships tested in our path model shift across the geographic space in a more complex pattern that has been revealed by regional analyses (Safi *et al.*, 2011), and suggests that there are spatial changes in the relative importance of the different mechanisms driving mammalian diversity. Models may fail to identify relevant environmental effects on biodiversity if they have a strong effect in only a specific region or only via indirect paths (Hortal *et al.*, 2011; Calatayud *et al.*, 2016) and if the direction of the relationship (and potentially, the mechanism) changes across the globe (Fotheringham *et al.*, 2002; Gouveia *et al.*, 2013). Our analytical framework, which combines the path analysis and GWR, provides a new approach for exploring spatially complex phenomena. And because path analysis is a special case of Structured Equation Modeling, the framework can be further expanded to include geographically structured latent variables.

Species richness, phylogenetic diversity and their relationship

Phylogenetic diversity (PD) of an assemblage is strongly determined by species richness (SR), but the relative change in PD between two regions is not always consistent with the relative change in richness between the same two regions (Tucker & Cadotte, 2013). Here we found that, at the regional scale, after controlling for environmental factors, tropical regions harbor relatively less mammalian PD than expected for SR. This “deficit” of tropical PD indicates that tropical regions host more closely related species than temperate regions. A notable exception is North America, which also has less PD than expected. The relatively smaller coefficient values of the PD-SR relationship in the tropics is consistent with the proposition that a substantial proportion of tropical mammalian biota has originated *in situ* (Rolland *et al.*, 2014; Marin & Hedges, 2016). Our results also support the hypothesis that diversification is faster in the tropics, which might be a consequence of multiple non-mutually exclusive mechanisms, such as area effects, time for speciation, stronger biotic interactions or increased mutation rates (reviewed in Mittelbach *et al.*, 2007). However, there is still much controversy about latitudinal variation in the rates of diversification. Studies of mammals have found all possible results: greater diversification in the tropics (Purvis *et al.*, 2011; Rolland *et al.*, 2014; Machac & Graham, 2017), absence of latitudinal differences (Soria-Carrasco & Castresana, 2012) and lower diversification in the tropics (Weir & Schluter, 2007).

The smaller PD-SR coefficients we observe in the tropics may also be related to species richness because adding a random species to a species-rich assemblage should promote a smaller increment to the assemblage’s PD than adding the same species to a species-poor assemblage. In essence, there is a higher probability that the new species is more closely related to one of the species in the rich assemblage than to one of the species in the poor assemblage often resulting in a non-linear and asymptotic relationship between PD and SR at large spatial scales. However, the non-linearity problem is reduced in our spatial analysis because the regressions are performed at the regional scale, where there is limited variation in species richness (Fig. S1). Nonetheless, some non-linearity could persist, and the PD-SR coefficients should be interpreted with caution.

Richness accounts for less PD in the New World than in the Old World, in line with our expectations, which reflects the fact that the American mammalian fauna was strongly impacted by more recent events, such as the megafaunal extinction during the Quaternary and the Great American Biotic Interchange that followed the formation of the Isthmus of Panama 2.7 Ma ago (Webb, 2006; Barnosky & Lindsey, 2010). The faunal interchange between North and South America triggered the explosive radiation of Canidae, Cervidae, Mustelidae and Muridae families (Webb, 2006) that may explain why richness is associated with lower phylogenetic diversity in the Americas than in the Old World, where many lineages, especially those in the African continent, are the result of early and gradual diversification (Davies & Buckley, 2012; Marin & Hedges, 2016). The highest coefficients of the PD-SR relationship were found in the Sahara and Arabian deserts and in high-latitude Eurasia, suggesting the occurrence of species with more dissimilar evolutionary histories, consistent with the observation that mammalian species tend to co-occur with phylogenetically distantly related species in these areas (Villalobos *et al.*, 2017).

Environmental correlates of species richness and phylogenetic diversity

Environmental conditions relate differently to assemblages' richness and phylogenetic diversity controlled by richness (PD_{SR}) across the space, varying in direction and magnitude, and supporting the idea that spatial mismatches between SR and PD are at least partially governed by environmentally-driven ecological and evolutionary processes (Davies *et al.*, 2007; Voskamp *et al.*, 2017). We found that AET and temperature relate positively with mammalian richness in most places, consistent with the hypotheses that energy contributes to the generation and maintenance of species (Evans *et al.*, 2005). The species-energy relationship is one of the strongest associations known in ecology and there are many possible mechanisms proposed to explain it, such as tolerance limits, available niches, metabolic rates and amount of energy flowing through food webs (Evans *et al.*, 2005); disentangling the importance of these mechanisms remains a challenge.

We found higher temperatures to be associated with less phylogenetically diverse assemblages in some tropical areas, as would be expected if the main effect of temperature was an acceleration in metabolic and mutation rates that culminates in faster rates of speciation (Rohde, 1992; Brown *et al.*, 2004). However, in most of the globe we found that higher temperatures are mainly associated with assemblages that are phylogenetically more diverse. Recent studies have found a conflicting effect of temperature on the diversification rates of mammals (Belmaker & Jetz, 2015; Marin *et al.*, 2018), suggesting that either temperature is not the best measure of ambient energy and other measures - such as solar radiation - should be considered (Clarke & Gaston, 2006), or that other mechanism may connect temperature to high richness. One possible alternative is that most clades originated in the tropics and only a few groups were able to adapt to colder environments (Wiens & Donoghue, 2004), thus explaining why lower temperatures are associated with less phylogenetic diverse assemblages. These results are supported by the evidence of tropical niche conservatism in mammals (Cooper *et al.*, 2011; Olalla-Tárraga *et al.*, 2011) and the positive association between temperature and clade age (Marin *et al.*, 2018).

Productive energy, here measured as AET, is considered to drive mammalian richness by supporting more resources and individuals (Wright, 1983), instead of by offering greater diversity of ecological niches (Oliveira *et al.*, 2016). The greater number of individuals potentially reduces extinction and accelerates speciation rates, leading to higher diversification rates and ultimately, higher species richness (Brown, 1981; Coelho *et al.*, 2018), as we found to be the case across most of the globe. The relative importance of productivity on speciation and extinction rates seems to change across the geographic space, given that the relationship between AET and PD_{SR} shift in direction across the geographic space, as found for parrots (Davies *et al.*, 2007). In much of North America and Eurasia, higher AET is associated with more phylogenetically diverse assemblages, suggesting that the main role of productivity in these regions is associated with the reduction in extinction rates. On the contrary, negative AET-PD_{SR} relationships were found in regions with limited productivity, such as the Sahara Desert and Saudi Arabia, and in highly productive areas, such as tropical South America, suggesting a higher relative importance of productivity in driving faster speciation rates. Thus, the relative importance of AET in driving rates of speciation and extinction does not seem to be linked to the amount of AET on the region, as previously hypothesized (Davies *et al.*, 2007). Instead, spatially structured relationships between AET and diversity may reflect historical differences associated with pool-specific or clade-specific adaptations to environmental gradients, given that the effect of AET on mammalian diversification rates varies depending on the taxa and on age of the lineages (Oliveira *et al.*, 2016; Machac *et al.*, 2017), both of which are spatially structured (Davies & Buckley, 2011; Hawkins *et al.*, 2012).

Climate-change velocity has left considerable imprints on mammalian richness and PD_{SR}, as expected giving that past climatic instability is associated with local extinctions and range shifts (Davies *et al.*, 2009; Hortal *et al.*, 2011). Species richness decreases with climate-change velocity across most of the globe, consistent with what has been observed for multiple taxonomic groups (Svenning *et al.*, 2015). In northern North America and Europe, where change since the LGM has been strongest, higher velocity of climate-change is associated with increases in both, species richness and PD_{SR}, suggesting that phylogenetically distant lineages are recolonizing areas that were covered with ice during the last glaciation. This finding contrasts with the pattern observed with Scarabaeinae dung beetles (Hortal *et al.*, 2011) and to what would be expected given that cold tolerance is phylogenetically conserved in mammals (Olalla-

Tárraga *et al.*, 2011). Increases in phylogenetically distant mammal species where climate-change velocity was greatest might be associated with the colonization by highly vagile species belonging to different clades (Torres-Romero *et al.*, 2017). Unexpectedly, climate-change velocity left strong imprints in the geographical patterns of SR and PD_{SR} in areas that have not experienced strong climatic changes since the LGM, as previously found to be the case for amphibian richness (Gouveia *et al.*, 2013). For instance, our spatial analysis shows that climate-change velocity is the strongest environmental variable explaining PD_{SR} in Madagascar, consistent with a previous study that noticed that climate-change velocity is a strong predictor of the richness of some mammalian groups on the island (Descombes *et al.*, 2018).

Contrary to our expectations, we did not find marked shifts in the slopes of the relationship between elevation and diversity in mountainous regions. The higher elevation in the Himalayas is directly linked to less PD_{SR}, consistent with the higher diversification rates of mammals in the region (Oliveira *et al.*, 2016) and the fact that mountains are important centres of speciation (Rangel *et al.*, 2018). However, as elevation is associated with a decrease in richness in the area, its association with less phylogenetic diversified communities may result from environmental filtering as the main mechanism driving diversity in mountains. In addition, we also note that the relative importance of mountains may be underestimated in our analysis, because (1) the poor spatial resolution of species ranges causes inaccurate description of global biodiversity patterns along slopes of mountains, (2) the size of grid cells used in the analysis is unable to capture fine-scale biodiversity patterns and their environmental correlates (Hortal *et al.*, 2008), and (3) the isotropic assumption of our model (i.e., circular kernel function) precludes accurate analysis of spatial patterns that are long and narrow, such as those generated by the Andes and Himalayas.

Among the advantages of using a spatially explicit approach is the identification of which predictor has the greatest effect on a response variable in each region. From the set of predictors used here, we noticed an east-west geographical change in the primary factor determining mammalian richness, being temperature most important in much of the New World and AET in the Old World. The limiting factor to species richness is expected to shift latitudinally in response to limitations in water and energy from the tropics to northern latitudes (Hawkins *et al.*, 2003), but as AET is a measure of the balance between water and energy, we cannot directly test this hypothesis. In contrast to the effects on species richness, in much of the globe, temperature is the most important environmental factor for phylogenetic diversity once richness is controlled for (PD_{SR}). This is similar to Davies' *et al.* (2007) findings for parrots that while SR is strongly linked to productive energy, PD_{SR} is mostly associated with ambient energy. This suggests that mammal diversification seems to be more associated with temperature than productivity, supporting the claim that it is linked to warmer, but not necessarily more productive areas (Davies & Buckley, 2011; Safi *et al.*, 2011). Non-stationary spatial patterns, such as the ones we found, may arise because particular clades in each region might relate differently to the environment as a consequence of their ecology and biogeographical and diversification histories (Buckley *et al.*, 2010; Machac *et al.*, 2017). Indeed, different diversity-environmental relationships are known to occur among mammalian groups (Buckley *et al.*, 2010; Oliveira *et al.*, 2016).

CONCLUDING REMARKS

Previous studies have shown that even though species richness (SR) and phylogenetic diversity (PD) are strongly correlated, the spatial patterns in mammalian SR does not account for the variation in PD and such mismatches provide insights into ecological and evolutionary processes (Davies & Buckley, 2011; Safi *et al.*, 2011; Penone *et al.*, 2016). Here we demonstrate that regionally structured mismatches between richness and phylogenetic diversity of terrestrial mammals are associated with the group biogeographical history and with the different ways that both dimensions of biodiversity relate to current and past environmental factors. We found more complex spatial patterns than previously anticipated based on per-realm analysis (Davies *et al.*, 2007; Gouveia *et al.*, 2014; Voskamp *et al.*, 2017), supporting our claim that Geographically Weighted Path Analysis and other GWR-based methods are promising tools to explore complex systems with varying relationships over the space, overcoming the need to arbitrarily split the data into geographical sub-regions. We argue that spatial variation in environmental-diversity relationships might emerge from either different mechanisms being at play or from different species pools having specific adaptations to environmental gradients (Ricklefs, 2006; Hawkins *et al.*, 2012; Fergnani & Ruggiero, 2017). Such spatial variation in the relative importance of different environmental factors may explain why results differ among studies and why a theory might receive more, or less support, depending on where the study was conducted (Cassemiro *et al.*, 2007).

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Data accessibility statement

The R code to perform Geographically Weighed Path Analysis and a spatial file containing the global hexagonal grid cell with all variables and results of this study is available online in the Dryad repository, doi:10.5061/dryad.nq8hg19

CAPÍTULO 2

Spatial variation in the direct and indirect effects of climate and productivity on species richness of terrestrial tetrapods

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ABSTRACT

Climate and productivity are among the strongest predictors of species richness across taxonomic groups and geographic regions. However, most studies do not explicitly consider the spatial variation in environment-richness relationships and how climate and productivity are interrelated. Here we used a spatial path analysis to estimate and map the direct and indirect effects of temperature, precipitation and primary productivity on species richness of terrestrial tetrapods across the globe. We found that all relationships to shift in magnitude, and even in direction, among taxonomic groups, geographic regions and connecting paths. Direct effects of temperature and precipitation are generally stronger than both indirect effects mediated by productivity and direct effects of productivity. Therefore, richness gradients seem primarily driven by climate effects on organismal physiological limits and metabolic rates rather than by the amount of productive energy. Reptiles had the most distinct relationships across tetrapods, with a clear latitudinal pattern in the importance of water versus temperature.

Keywords: biodiversity gradients, climate, geographically weighted regression, metabolic theory, non-stationarity, path analysis, productivity, species-energy, structural equation modeling, water-energy hypothesis.

INTRODUCTION

Diversity gradients of biodiversity are known to result from multiple factors operating non-independently and at different scales[1–3]. Current environmental factors, especially those related to climate and productivity, are among the strongest predictors of richness for terrestrial and aquatic organisms across multiple regions and spatial scales[4,5]. However, most studies rarely consider how climate and productivity are interrelated and that their relative importance to diversity patterns potentially varies across geographic space[4,6]. Here we use a spatial path analysis to revisit hypothesis on how climate and productivity relate to species richness of terrestrial tetrapods by allowing direct and indirect effects to vary geographically. The four terrestrial tetrapods groups (amphibians, birds, mammals and reptiles) are well suited for exploring variation these relationships because of their differences in physiology (ecto- and endo-therms), rate of niche evolution, and dispersal ability[7–10].

Several hypotheses have been proposed to explain why species richness tend to be greater in warmer, wetter and more productive environments[5,11,12]. The more individuals hypothesis proposes that species richness increases with productivity because more individuals can be supported if there is a greater amount of energy present in the food web, thus, increasing the number of viable populations and reducing extinction rates[13–16]. Productive energy is also proposed to increase richness by providing greater diversity of niches and thus facilitating the coexistence of more species in this increased niche space[17–19]. Climate, on the other hand, is expected to influence species richness given the physiological and thermal tolerances of organisms, especially ectotherms[8,11]. Additionally, the metabolic theory and the evolutionary speed hypothesis propose a positive temperature-richness relationship because higher thermal and kinetic energies are linked to faster metabolic, mutation and speciation rates[20–22].

Disentangling the different mechanisms behind the strong species-climate and species-productivity relationships is difficult because they are not mutually exclusive[11,12,18] and productivity is strongly dependent on climate[23]. As productive energy is not a simple increasing function of temperature and precipitation[23], the positive climate-richness relationships might not hold true when indirect pathways through productivity are considered. Even though these two pathways (Fig. 1) are usually acknowledged, indirect paths are generally ignored in statistical analysis[4,24]. Thus, it is yet unclear to what extent the effects of precipitation and temperature on richness are direct via physiological tolerances of organisms and metabolic rates; and to what extent they are indirect, mediated by productivity (i.e., mediation effect[25]).

Additional complexity is added to the study of climate and productivity-richness relationships because they vary among taxonomic groups and geographic regions[4,7,26]. In the warm tropics, where temperature is not usually a physiological limitation, water availability should be a stronger limiting factor of species richness. In contrast, the lower inputs of thermal energy in temperate regions should lead to temperature being the primary limiting factor of species richness there (water-energy hypothesis[4]).

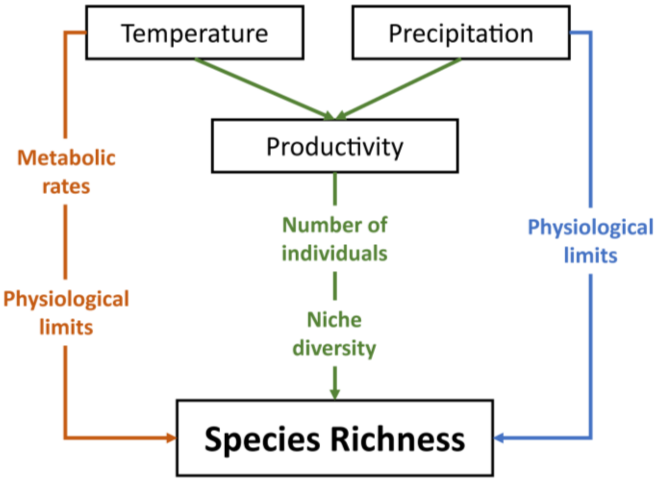

Figure 1 – Path model depicting the analyzed directional relationships and the underlying hypotheses linking different energy measures to species richness.

Here we tackled the spatial non-stationarity of direct and indirect pathways connecting climate, productivity and species richness using a spatial path analysis. Our approach consists in a distance-weighted moving window[27] to locally calibrate path models along continuous global gradients, removing the need to arbitrarily split the data into geographical sub-regions or latitudinal bands. This approach allow us to comprehensively test the long standing climate and productivity-based hypothesis at broad spatial scales and to map where in the globe each environmental condition has a stronger effect on diversity, potentially identifying new patterns that could only be revealed because of the exploratory nature of the analysis.

We expect to find the well-known positive direct effects of all predictors on species richness[7,11,26], with the strength of the relationships following the opposite spatial pattern of the predictor itself (e.g. stronger species-temperature relationships outside the tropics). Given the strong limiting effect imposed by climate on organismal physiological tolerances and metabolic rates, we hypothesize that direct effects will be mostly stronger than the indirect ones. The strong physiological dependence of ectotherms on climatic conditions[8] should lead to reptiles being more strongly influenced by the direct effect of temperature[26,28,29] and amphibians by the direct effect of precipitation[30] across most of the globe. In contrast, endotherms are hypothesized to be mostly constrained by the amount of productive energy[7,8,31]. Summing up direct and indirect pathways to diversity, we expect overall stronger effects of precipitation on richness in the tropics and temperature in the temperate region, as proposed by the water-energy hypothesis[4]. Such latitudinal pattern is expected to be stronger for amphibians and reptiles (ectotherms) than for mammals and birds (endotherms)[7,26].

RESULTS

As we expected, the spatial path analysis revealed that direct effects of all three predictors are mainly positive, but it also uncovered unexpected exceptions. We found negative effects of precipitation on species richness of birds and mammals in North America, and of reptiles at high latitudes and in parts of Australia (Figs. 2h and S4,5,7). In contrast, amphibian richness was scaled positively with precipitation everywhere (Fig. 2g). Temperature was negatively associated with richness of birds, mammals and amphibians in much of the tropics, especially in Africa and Asia (Figs. 2c and S4-S6), and also in South America and Australia for birds (Fig. S4). In contrast, temperature was directly associated with increases in species richness of reptiles globally, with stronger coefficients outside the tropics (Fig. 2d). Productivity was only found to scale negatively with richness of reptiles, and this negative relationship was mostly above the Tropic of Cancer (Fig. 2a-b). For all taxonomic groups, the spatial path analysis revealed a latitudinal gradient in the strength of the relationship between productivity and species richness, with stronger coefficients located at higher latitudes (Fig. 2a-b).

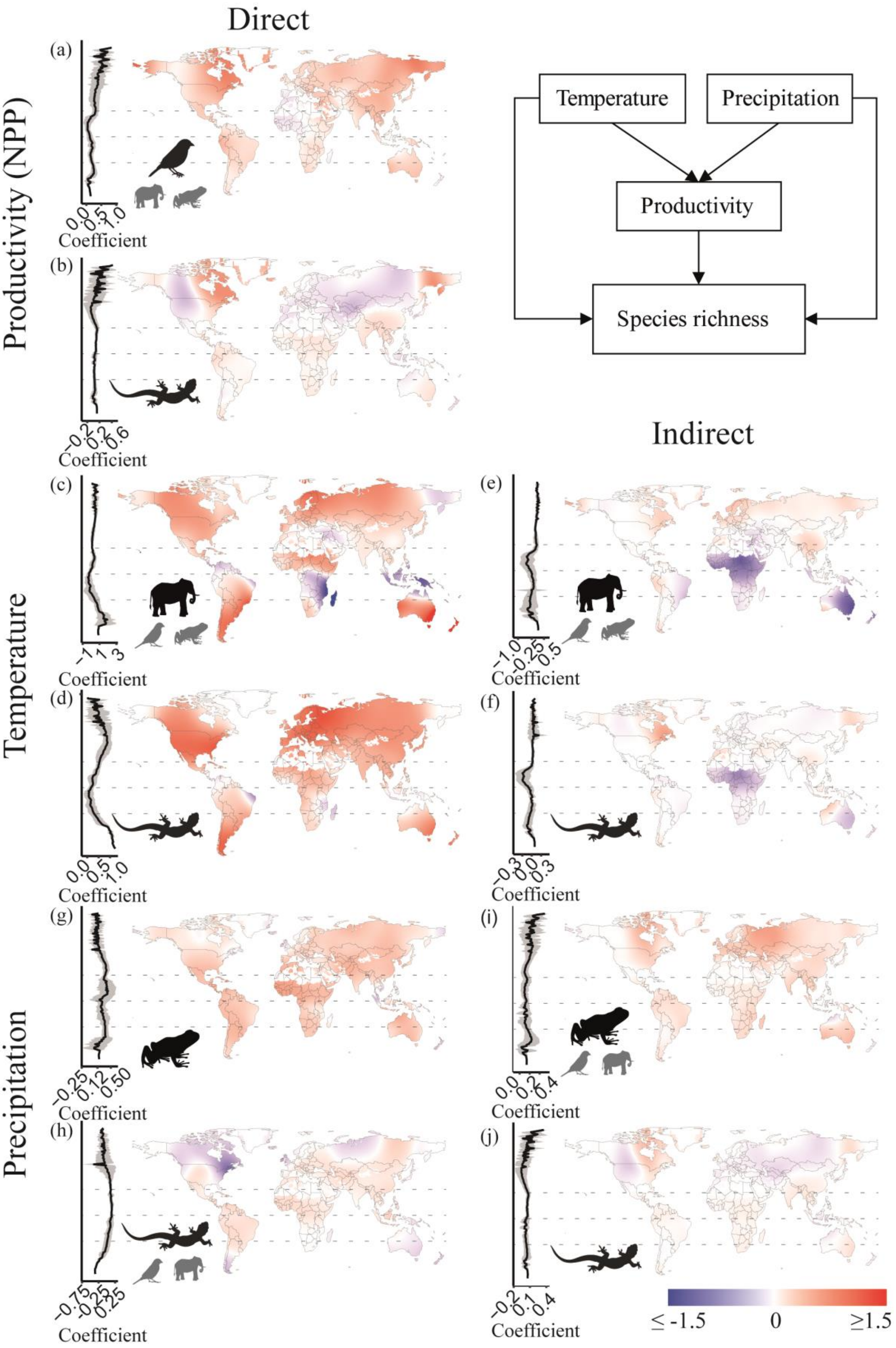
Direct
Productivity (NPP)
(a)
0.0
0.5
1.0
Coefficient
Temperature
Precipitation
Productivity
Species richness
(b)
-0.2
0.2
0.6
Coefficient
Indirect
Temperature
(c)
-1
1
3
Coefficient
(e)
-1.0
-0.25
0.5
Coefficient
(d)
0.0
0.5
1.0
Coefficient
(f)
-0.3
0.0
0.3
Coefficient
Precipitation
(g)
-0.25
0.12
0.50
Coefficient
(i)
0.0
0.2
0.4
Coefficient
(h)
-0.75
-0.25
0.25
Coefficient
(j)
-0.2
0.1
0.4
Coefficient
≤ -1.5
0
≥1.5

Figure 2 – Direct (a-d, g, h) and indirect (e, f, i, j) coefficient strengths between species richness of terrestrial tetrapods and three measures of energy – productivity (a-b), temperature (c-f) and precipitation (g-j) – according to the geographically weighted path model. Path coefficients are standardized and are mapped using the same color scale, allowing direct comparison of their magnitudes. For each path, we show the two most contrasting results among the four taxonomic groups analyzed. Black silhouette indicates for which organism group the result are mapped, and smaller gray silhouettes indicate the other groups showing similar results. The full set of coefficient maps for all four taxonomic groups is available in the supporting information (Figs. S4-S7). Next to each map is the path coefficient across latitude, plotted with the mean (black line) and the standard deviation (longitudinal variation, grey area). Dotted lines indicate the Tropic of Cancer, the Equator, and the Tropic of Capricorn, respectively from top to bottom. Silhouette images were taken from Freepik.com.

Temperature and precipitation were also related to species richness indirectly via productivity, with such indirectly effects being often weaker than direct ones (maps on the left panels compared to those on the right panels in Fig. 2; Fig. S8). Indirectly, the effect of temperature on richness was weakly positive above the Tropic of Cancer and negative or zero beneath it for birds, mammals and amphibians (Figs. 2e and S4-S6). For reptiles, the indirect effect of temperature on richness was mainly negative and weaker than for the other groups (Figs. 2f and S4-S7) because productivity was a weak predictor of its species richness (Fig. 2b). In general, there were more areas of negative relationship between temperature and richness indirectly via productivity than directly (Fig. 2e-f compared to 2c-d and Figs. S4-S6).

As with temperature, the direct and indirect (via productivity) effects of precipitation on species richness have different spatial patterns. Indirect effects of precipitation on richness were consistently positive for all groups except for reptiles, where the relationship was mostly negative at high latitudes and nearly zero elsewhere (Figs. 2i-j and S4-S7). In general, the direct and indirect effects of precipitation on reptile richness was weaker than in the other groups (Fig. 2j compared to 2i and Figs. S4-S7). The consistent indirect positive effects of precipitation on richness of birds, mammals and amphibians arises from the mainly positive effect of precipitation on productivity, which in turn is associated with an increase in species richness of these taxonomic groups (Figs. S4-S6).

The relative strength of productivity, precipitation and temperature on species richness was not the same everywhere and was different for the four taxonomic groups (Figs. 3 and S9). As we expected, when comparing the total effects (i.e., sum of direct and indirect effects) of the three predictors, amphibian richness was more dependent on precipitation (shades of pink in Fig. 3c) and reptile richness on temperature (shades of yellow in Fig. 3c). For reptiles, we found a clearer latitudinal pattern of precipitation being more important in much of the tropics and temperature being of predominant importance outside the tropics (Fig. 3d), a pattern that only emerges when the indirect effects are accounted for (Fig. S9). For mammals and birds our model showed that temperature and productivity are relatively more predictive above the Tropic of Cancer, whereas temperature and precipitation are more predictive below the Tropic of Cancer (Figs. 3a-b and S4-S5).

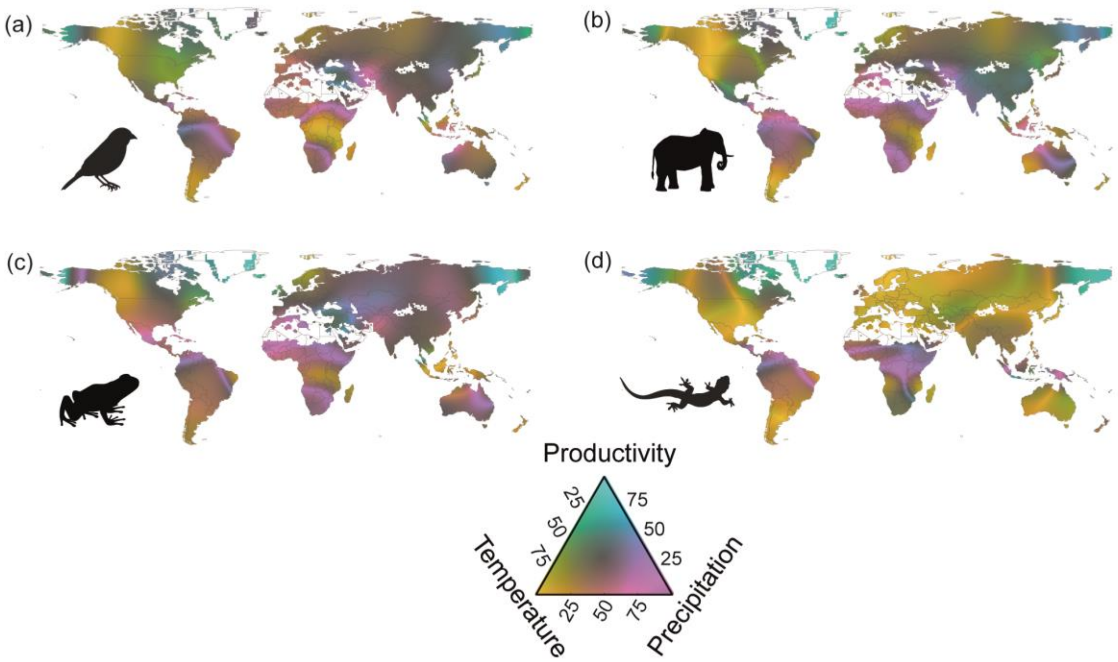

Figure 3 – Relative importance of productivity, temperature and precipitation to the species richness of terrestrial tetrapods when considering both, the direct and indirect effects of temperature and precipitation through productivity. Colors indicate how much, in percentage, a measure of energy is important to explain species richness based on the magnitude of the summed, standardized path coefficients. Shades of green indicate productivity; yellow indicate temperature and pink indicate precipitation as relatively more important. The black silhouette indicates which organismal group the result belongs to. Silhouette images were taken from Freepik.com.

DISCUSSION

The relationship between climate and species richness is one of the most ubiquitous in ecology[5,18], yet it is uncertain how much of the climatic effects on diversity are direct or indirect via productivity and how spatially stationary these relationships are. Using a novel approach, we explicitly maped the intricate network that connects climate and productivity to species richness of terrestrial tetrapods and revealed that climate is a stronger driver of richness, either directly or indirectly, than productivity in most areas. Also, we found direct and indirect pathways to have distinct spatial patterns, causing the emergence of a clear latitudinal gradient in the relative importance of water versus temperature for reptiles. Overall, we revealed that climate and productivity-richness relationships vary considerably in magnitude, and sometimes even in direction, across the globe depending on the type of energy, pathways connecting energy to richness (i.e., direct and indirect) and taxonomic group. All these levels of variation, combined with those related to spatial[32,33] and temporal scales[34], suggests that when dissecting the species-energy relationships, the pattern reverals itself more complex.

The direct effect of temperature, precipitation and productivity on species richness is mainly positive, in agreement with many proposed hypotheses[11,18]. Nevertheless, by allowing relationships to vary geographically without arbitrarily splitting data into geographical sub-regions, our analysis revealed spatially structured exceptions to the well-known positive species-energy relationships for all three measures of energy. Only reptiles had a negative productivity-richness relationship above the Tropic of Cancer, offering insights into why this group richness is commonly lower than of other tetrapods in this region[35]. The negative NPP-richness relationship recovered for reptiles could be explained by the evidence that this group abundance also scales negatively with NPP[36], which in turn should increase extinction rates[15]. Our result also helps understand the idiosyincrasis in NPP-richness relationship among lizards clades[37], as clades whose richness relates positively to NPP are mostly distributed within the geographic areas where we uncovered positive relationships (red areas in Fig. 2b).

The direct effect of temperature on richness of birds, mammals and amphibians was negative in parts of the tropical region, where temperatures are highest. This suggests that the tropics may be too warm for these groups, consistent with a threshold in species richness at higher levels of solar radiation across Europe for these same taxonomic groups[26]. The negative temperature-richness relationship may also be influenced by precipitation being kept constant in the model; a direct link in the path model measures the direct effect of a predictor while holding the remaining ones constant[25]. Temperature and precipitation most likely interact to determine diversity, so that when temperatures are high, species richness increases only if there is enough moisture[4,38,39]. The same likely holds true for the negative relationship between precipitation and richness of reptiles, birds and mammals in temperate regions, especially in North America. Precipitation does not promote an increase in species richness in these areas if it is not warm enough; a similar pattern found for angiosperms[39].

This balance between thermal energy and water availability seems to be less ubiquitous (straightforward) for reptiles and amphibians. The temperature-reptile richness and precipitation-amphibian richness relationships were positive nearly everywhere. The positive relationship between reptile richness and temperature, even when statistically holding precipitation constant, can be explained the group’s strong dependence on external thermal energy for metabolic maintenance and reproduction[28,29,40]. Also, reptiles have strongly conserved thermal niches, which appears to constrain the number of species able to survive and diversify in colder environments[10,41]. In contrast, amphibians are more strongly constrained by water availability because of their high vulnerability to desiccation and the dependence of water for the reproduction of many species[30,42].

Our spatial path analysis confirmed that temperature and precipitation influence species richness not only directly[11,21], but also indirectly mediated by the effect of climate on productivity[4]. Spatial patterns of indirect effects are complex because NPP results from the interaction among multiple climatic conditions and is not a straightforward increasing function of temperature and precipitation, especially in the tropics[23,43]. At large spatial scales, temperature and precipitation are often found to be stronger drivers of richness patterns than productivity ([23] and references therein). However, the greater importance of climate could be a consequence of its effect on species richness both, directly and indirectly via productivity. Partitioning both pathways, we revealed a general pattern of direct effects of climate often being stronger than (1) their indirect effects via productivity and (2) the direct effects of productivity. These results suggest that species richness is more strongly driven by the physiological tolerance of organisms and by climatic conditions influencing metabolic and, ultimately, speciation rates[11,21], rather than by the diversity of niches and/or the amount of energy flowing through the food webs[15,18].

The complex spatial patterns revealed by our analysis help explain the lack of consensus among tests for the relative importance of climatic and productive energy (i.e. the water-energy hypothesis[4]), as they are conducted across different regions, using pre-defined spatial unities and only accounting for direct effects[7,26]. Our spatial path analysis revealed that only reptiles present a clear latitudinal pattern of water being more important in the tropics and thermal energy everywhere, once the productivity-mediated indirect effects are acknowledged. This finding contrasts with previous assessments, which did not recover such latitudinal gradient[4,26] or found it to be the weakest among the tetrapods[7]. For the other tetrapods, we found amphibians to be constrained by water across most of the globe, especially in the Paleartic region, whereas birds and mammals are more constrained by temperature and productivity above the Tropic of Cancer; below it, temperature and precipitation become more important for these groups.

Variation in strength and direction of species-energy relationships across the globe (i.e., spatial non-stationarity) may be associated with several factors other than the spatial variance of the energy variables itself. For example, non-stationarity could be associated to historical factors of each region[44,45] or to the proportion of ecological groups within a region, as different groups may respond differently to energy conditions, such as of specialists *versus* generalists[46] or thermoregulators *versus* thermoconformers[47,48]. Spatial variation in species-energy relationships can also emerge if different processes prevail in different regions. For instance, whereas at high latitudes the effect of temperature might be more strongly related to thermal tolerances and to overcoming tropical niche conservatism[49], at mid latitudes it may be more strongly associated with diversification rates[50]. Expanding our spatial path model to incorporate other variables, such as diversification rates and abundance[2,51,52], is a promising way forward to explore the spatial variations of different underlying processes.

METHODS

Datasets

We used range maps of the global distribution of each of the four terrestrial tetrapod groups from publicly available databases[35,53], totaling 10,425 species of birds, 5,408 mammals, 6,515 amphibians and 10,066 reptiles after the exclusion of introduced species. We overlaid range maps with a grid composed of squared cells of 110 x 110 km at the Equator using the Behrman equal-area projection and calculated the number of species whose range overlapped with each cell to derive richness maps for each taxonomic group.

We selected mean annual precipitation as a measure of water availability; mean annual temperature as a measure of thermal energy; and mean annual net primary production (NPP) and fraction of photosynthetically active radiation (fPAR) as measures of productive energy. We obtained data on temperature and precipitation from CHELSA[54] at 0.008º x 0.008º resolution and aggregated it at 1º x 1º resolution. NPP estimates the amount of biomass produced per unity area and time, whereas fPAR measures the fraction of the incident PAR that is absorbed by plants[23]. At large spatial scales, NPP can be estimed using different approaches that yield fairly similar results[23]. We summarized mean annual NPP and fPAR over the years of 2003 to 2015 obtained from remotely sensed imagery of the MODIS sensor onboard the NASA TERRA satelite (MOD17A2 product). We gathered fPAR data from the Dynamic Habitat Indices[55] and divided the annual cumulative $fPAR_8$ over the 46 measures taken within each year. We computed the mean annual value of each environmental variable to each cell in our grid using the “raster” package[56] in R statistical environment.

Analysis

Path analysis is useful for exploring the complex web that connects environmental drivers and biodiversity by partitioning the total association between predictors and response variables (i.e., total effects) into direct and indirect effects. We designed a path model based on the proposed hypothesis of how different measures of energy may relate directly and indirectly with species richness (Fig. 1). As it is unrealistic to assume that these relationships are the same across the geographic space[4,6], we relaxed the assumption of spatial stationarity by using a Geographically Weighted Path Analysis

(GWPath; code available in Appendix S1 in Supporting Information). Under the GWPath framework, path coefficients can vary regionally because of a distance-based Gaussian weighting function that assigns greater weights to nearby cells, similar to a Geographically Weighted Regression (GWR[27]). We implemented GWPath using the “gwr” function of “spgwr” R package[57].

Deciding on the radius of the spatial kernel function (bandwidth) for GWPath is non-trivial, because if the radius is too large the analysis converges back to the spatial stationarity assumption, and if it is too narrow the model overfits residual variations[27]. Overfitting can be identified by visual inspection because it leads to drastic shifts in the coefficients even among nearby cells, causing the formation of coefficient islands. We visually inspected the results for signs of artifacts caused by overfitting from bandwidths ranging from 700 to 2,000 km, at 100 km interval. We found that a bandwidth of 1,000 km was ideal to capture large-scale patterns in coefficient variation, as it yields results similar to those from coarser bandwidths while avoiding overfitting. The same bandwidth was also used by other studies using GWR on environmental drivers of large-scale biodiversity data[45,58].

Our path model is composed by two multiple regressions: (1) species richness ~ productivity + precipitation + temperature and (2) productivity ~ precipitation + temperature (Fig. 1). To compare coefficients among taxonomic groups, geographic regions and connecting paths, we fitted the same path model to each vertebrate group across the entire geographic space using standardized response and predictor variables (z-scores). We ran all analyzes twice, once using NPP as the measure of productive energy and once using fPAR. Given that results were qualitatively and quantitatively similar (see Figs. S1 to S20 in Supporting Information), we chose to display and discuss the results from the model with NPP in the main text. We log-transformed all variables because of the potential non-linearity of species-energy relationships, which led to an increase in the coefficient of determination (R^2) in most focal cells for all taxonomic groups but mammals (Fig. S1). We assessed multicollinearity among predictors by calculating Variance Inflation Factors (VIF) and Condition Numbers (CN) at each focal cell. Both measures indicate that multicollinearity is not a problem in our analysis, as VIF scores were lower than 8 [mean 1.56 ± 1.06 std. dev.; Fig. S2] and CN were lower than 40 [mean 10.80 ± 7.87 std. dev.; Fig. S3] (Dormann *et al.* 2013).

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CAPÍTULO 3

Determinants of richness and endemism of mammals on islands worldwide

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ABSTRACT

Aim To conduct a global test of the relative importance of island environmental and physical characteristics on mammal species richness and endemism.

Location Five thousand five hundred ninety-four islands worldwide.

Time period Present.

Major taxa studied Terrestrial mammals.

Methods We derived a global database of insular mammals from IUCN range maps and calculated species richness, number of single island endemics (SIE) and proportion of SIE. We gathered data on island area, current and past isolation, temperature, elevation, precipitation and velocity of climate change since the last glacial maximum from publicly available databases. We fitted generalized linear and mixed models to quantify the effects of island characteristics on the three diversity measures, while accommodating differences in biogeographic realm. Analyzes were also performed separately for bats and non-volant mammals.

Results Island area had a positive effect on mammal diversity, being a stronger driver of SIE than richness for non-volant species. Island isolation, both current and past, was associated with lower richness but greater endemism. Flight capacity influenced the relative importance of past versus current isolation, as bats responded more strongly to current and non-volants to past isolation. Environmental effects on biodiversity varied depending on taxonomic group, biogeographic realm and the measure of diversity, with a tendency for greater effects on endemism than on richness. Unexpectedly, climate change velocity was positively associated with endemism.

Main conclusions In line with island biogeography theory, we found area and isolation were among the strongest drivers of overall mammalian biodiversity. In addition, our results support the growing evidence on the importance of past conditions (i.e. connectivity and velocity of climate change) on current patterns, particularly on non-volant species.

Key-words Endemism, island biogeography, isolation, last glacial maximum, single island endemic, species-area relationship.

INTRODUCTION

Islands are numerous discrete land areas distributed around the world with broad variation in sizes, shapes, environmental conditions and degree of isolation (Weigelt *et al.*, 2013). These characteristics make islands a remarkable system for ecological and evolutionary studies, which has stimulated the development of central theories in the field for decades (MacArthur & Wilson, 1967; Warren *et al.*, 2015; Santos *et al.*, 2016). Multiple processes operating over space and time, often influenced by the physical and environmental characteristics of the islands, appears to have resulted in consistent patterns of variation in insular biodiversity (Whittaker & Fernández-Palacios, 2007). However, most work has been done on specific island archipelagos. Global evaluation of these emergent patterns are scarce (e.g. Kalmar & Currie 2006; Kreft *et al.* 2007; Pyron & Burbrink 2014) and we still lack such an assessment for mammals.

Large-scale studies of insular mammal diversity have so far been mostly centered on the island rule (e.g. Faurby & Svenning 2016) and on community structure (Cardillo *et al.*, 2008; Cardillo & Meijaard, 2010), while studies on the relationship between biodiversity and characteristics of islands, were limited to a few biogeographic regions and taxonomic groups (e.g. Lawlor 1986; Lomolino 1986; Millien-Parra & Jaeger 1999; Presley & Willig 2010; Lavery *et al.* 2016). While accommodating possible variations across biogeographic realms, we investigated the effects of islands on mammalian richness and endemism. To obtain insights into evolutionary dynamics we measured insular endemism as the number of single island endemics (SIE) and the proportion of SIE (pSIE) (Whittaker *et al.*, 2008).

Area and isolation are key drivers of island biodiversity (Whittaker & Fernández-Palacios, 2007). The influential Equilibrium Model of Island Biogeography proposed by MacArthur & Wilson (1967) poses that number of species on an island results from an equilibrium between the opposing forces of extinction and immigration in response to area and isolation. Lower extinction and higher immigration rates are expected on larger and less isolated islands, as they can support larger population sizes (MacArthur & Wilson, 1967) and are easier targets for propagules (i.e. target-area effect) that can colonize or repeatedly immigrate to the island (i.e. rescue effect) (Lomolino, 1990). Over long time periods, speciation also plays a role in generating insular biodiversity (Heaney, 2000). Speciation rates are greater on larger islands due to intra-island reproductive isolation and lower on less isolated islands because of the greater frequency of gene flow between an island and the mainland or among nearby islands (Losos & Schluter, 2000; Rosindell & Phillimore, 2011). All these processes lead to the emergence of positive species-area and negative species-isolation relationships, and to positive effects of both, area and isolation, on endemism (Whittaker & Fernández-Palacios, 2007).

Greater richness and endemism on larger islands may also arise from the confounding effect of heterogeneity, either in habitat, topography and/or climate, which tends to be greater on larger islands (Ricklefs & Lovette, 1999; Steinbauer *et al.*, 2012). More heterogeneous environments facilitate the co-existence of a wide range of species with different environmental requirements through niche partitioning (Hortal *et al.*, 2009; Stein *et al.*, 2014). Additionaly, over evolutionary time, greater heterogeneity may increase speciation rates as a result of increased reproductive isolation and ecological specialization (Kisel & Barraclough, 2010; Stein *et al.*, 2014).

In addition to heterogeneity in environmental conditions on islands, insular diversity should be influenced by average environmenal conditions. On continental areas at large spatial scales, climate is a major determinant of biodiversity (Hawkins *et* *al.*, 2003). Species numbers tend to be greater in warmer, wetter, more productive and climatically more stable environments, as these conditions are associated with organismal physiological tolerances, range dynamics, diversification rates, niche conservatism, energy, among others (Field *et al.*, 2009). However, it is yet unclear to what extent the strength of the climate-diversity relationships on islands resembles that of the continent, especially because of the comparatively low number of island biogeography studies conducted at spatial scales large enough to encompass the same range of climatic conditions often included in continental studies. Global analysis of island biogeography on plants (Kreft *et al.*, 2007; Weigelt *et al.*, 2015), birds (Kalmar & Currie, 2006) and snakes (Pyron & Burbrink, 2014) found climatic effects on biodiversity to be as strong as those reported for continents.

Islands are not static over time. Past geological and climatic conditions left strong imprints on current patterns of island biodiversity, especially endemism (Weigelt *et al.*, 2016; Norder *et al.*, 2018). Physical characteristics and environmental conditions of the islands have shifted considerably since the Last Glacial Maximum (LGM), 21,000 years ago. As sea level dropped approximately 120m, changes in island configurations exposed land bridges that connected 75% of the world islands larger than 1km^2 to continents (Weigelt *et al.*, 2013), facilitating biotic and genetic interchange. Such increased connectivity during the LGM strongly influenced the mammalian fauna in the Japanese archipelago resulting in greater species numbers and lower endemism than would be expected if islands had remained unconnected (Millien-Parra & Jaeger, 1999). Changes in climate since the LGM also influence mammalian biodiversity through range shifts and increased the probability of extinction (Dynesius & Jansson, 2000). Evidence from continental areas and major islands point to greater endemism and phylogenetic endemism in areas that experienced higher velocity of climate change (Sandel *et al.*, 2011; Rosauer & Jetz, 2015).

Drivers of insular biodiversity may differ between bats and non-volant mammals. The flight capacity of bats facilitates dispersal over water, essentially creating land bridges that are inaccessible to other mammals (Lawlor, 1986). Indeed, it has been shown that biogeographical patterns of bats are substantially different in continental and insular areas (Lawlor, 1986; Rosauer & Jetz, 2015). For instance, bats are the only mammalian group to occupy the largely isolated islands of Hawaii and New Zealand. Therefore, we expect that the effects of area and isolation will be weaker for bats than for non-volant mammals, and that for bats the effect of past isolation will be weaker than that of current isolation (but see Rosauer & Jetz 2015).

Here we investigate how mammalian richness and endemism relate to island attributes worldwide. We seek to establish the relative importance of island characteristics as predictors of richness and endemism of bats and non-volant mammals, while accounting for the deep historical effects recorded in biogeographical realms (Holt *et al.*, 2013). We demonstrate that island area and isolation, both current and past, are the most consistent predictors of mammalian biodiversity on islands, although regional process, at the scale of realms, also play a substantial role in structuring biodiversity patterns of insular mammals.

METHODS

Mammalian biodiversity data

We used the Global Administrative areas version 3.6 (GADM, 2018) to subset the spatial polygons of all non-freshwater islands larger than 1km² and smaller than

Greenland. We overlapped the mammalian range maps from IUCN (IUCN, 2017) and the geographic contour of islands to estimate (1) species richness of native mammals, (2) number of single island endemics (SIE) and (3) proportion of SIE (pSIE). Visual inspection of the spatial overlap between island and species polygons confirmed that they largely agree on geographic location, shape and area, suggesting that IUCN data have sufficient resolution to derive data for macroecological studies on island biodiversity. At very small spatial scales, we identified few mismatches in the overlap of island and species polygons that could lead to errors in automatically assigning species presence to islands. These problems were mainly centered in regions with clusters of nearby islands (e.g., Patagonia and Scandinavia) and on islands near the continental shore. We carefully inspected and manually corrected any alignment inconsistencies using QGIS 3.6 (Open Source Geospatial Foundation Project, 2019) and opted for a highly conservative approach of excluding any island with the slightest doubt about species attribution. The final dataset consisted of 6,099 islands worldwide, of which 132 contained at least one SIE.

We removed introduced species from the database by excluding species polygons recorded as introduced and by removing from the database the occurrence of species listed as invasive for each particular island in the Database of Island Invasive Species Eradication (DIISE, 2015). We also removed fully aquatic and marine semi-aquatic species because they are not expected to respond to the environmental and physical characteristics of the islands in the same way as terrestrial species. We ensured that native species that were most likely extinct due to human activity were included in database by adding occurrence records from other data sources (Faurby & Svenning, 2016; Upham, 2017; Faurby *et al.*, 2018).

We contrasted the patterns of mammal biodiversity that we estimated using IUCN range polygons against published datasets that were compiled for specific regions (Millien-Parra & Jaeger, 1999; Meiri *et al.*, 2008; Hanna & Cardillo, 2014; Lavery *et al.*, 2016; Upham, 2017). The correlation among datasets was high (0.95 ± 0.05), which indicates that reliability of our global dataset. In addition, based on the IUCN range polygons we categorized species as being present only on mainland, on mainland and islands, and only on islands. The resulting list was a perfect match to a similar categorization from another mammalian database (Faurby *et al.*, 2018), which reinforces the accuracy of our database.

Physical and environmental characteristics of islands

For each island in our database, we gathered physical and environmental characteristics expected to influence biodiversity: area (in km²), $\log_{10}$-transformed sum of surrounding landmass proportion (SLMP) within buffer distances of 100, 1,000 and 10,000 km around island perimeter (*sensu* Weigelt *et al.* 2013), mean annual temperature (in degrees Celsius) and precipitation (in millimeters), standard deviation of mean annual temperature and precipitation within the island, standard deviation in elevation within the island, island connectivity to the mainland during the Last Glacial Maximum (GMMC), and climate change velocity in temperature since the Last Glacial Maximum (CCVT, in meters/year). We obtained island area, SLMP, GMMC and CCVT from a public island characterization database (Weigelt *et al.*, 2013) by matching the coordinates to island polygons. We multiplied SLMP by –1 and coded GMMC as 0 being connected and 1 being disconnected to the mainland during the LGM, so both metrics represent isolation (i.e. higher SLMP and GMMC represent greater isolation). Hereafter we will refer to those variables as “current isolation” and “past isolation”. We derived temperature and precipitation data from CHELSA (Karger *et al.*, 2017) and elevation data from the Global Digital Elevation Model GTOPO30 (USGS, 1996) by calculating mean and standard deviation per island using QGIS 3.6.

Islands were classified into the 12 global mammalian zoogeographical regions (Holt *et al.* 2013, Figure 1), hereafter “realm”. Due to the lower number of sample units per realm on the analyzes of pSIE, we grouped the islands into four larger realms based on Holt *et al.* (2013): (1) Australian, (2) Oriental + Oceanina + Madagascan + Afrotropical + Saharo-Arabian, (3) Paleartic + Neartic + Eurasia + Sino-Japanese , (4) Panamanian + Neotropical (Figure 2). We removed 505 islands from the dataset because it was not possible to derive all environmental variables or to assign a realm with confidence, usually because they were small (< 1km²) or located on a biogeographical boundary. The final dataset comprised 5,594 islands of which 124 contained SIE.

Data analysis

We standardized all quantitative predictors (mean = 0 and standard deviation = 1) to enable comparison among regression coefficients and we transformed those that were non-normally distributed by using natural logarithm base 10 or square root to reduce asymmetry. Multicollinearity among predictors was calculated with the variance inflation factor (VIF) and was generally low (mean 1.86 ± 1.06 std. dev., Table S1). Highest VIF values were observed for standard deviation in precipitation in models where SIE was the response variable (VIF ~7), but this predictor was maintained in the final models as its exclusion did not change the results.

We tested if islands that harbor only bats, only non-volant species, or both, tend to differ in latitude, physical and environmental characteristics using ANOVA tests (Figs. S1 and S2). We related the biodiversity of the islands to their physical and environmental characteristics by fitting Generalized Linear Models (GLM's) to SIE and Generalized Linear Mixed-effect Models (GLMM) to species richness and pSIE using the packages glmmTMB (Brooks *et al.*, 2017), lme4 (Bates *et al.*, 2015) and MASS (Venables & Ripley, 2002) in R. SIE was modeled using GLM because there was not enough variation in the data to fit a GLMM. Species richness and SIE were modeled using a negative binomial error distribution and pSIE was modeled using a binomial error distribution with species richness used as prior weights. Only islands with at least one SIE were included in the models fitted for SIE and pSIE (n = 124). Analyzes were conducted for all mammals and separately for bats and non-volant species. To improve the fit of negative binomial models, we removed one (1) from the species richness and from the number of SIE of all islands when modeling the biodiversity of all mammal species as an alternative to using a zero-truncated model. This approach yielded similar results as that of a zero-truncated model, which is only available for GLMM's.

We fitted GLMM's with realm as random effect to enable the estimation of different intercept and slopes for each realm, as this reduces type I error when compared to models with only random intercept (Schielzeth & Forstmeier, 2009). Inclusion of realms as random effect accommodated the regional differences that are expected due to historical factors (Bunnefeld & Phillimore, 2012; Holt *et al.*, 2013; Ficetola *et al.*, 2017) and that might cause spatial autocorrelation at regional scales (Dormann *et al.*, 2007). None of the models had zero-inflation or overdispersion, which was tested by simulating standardized residuals from the fitted models in DHARMa R package (Hartig, 2019). We estimated spatial autocorrelation in the residuals using Moran's I correlogram based on the geodesic distances among islands in SAM (Rangel *et al.*, 2010) and it was only detected at very small spatial scales (Tables S2-S10 and Fig. S1). Conditional and marginal pseudo coefficients of determination (R^2) were calculated following Nakagawa *et al.* (2017) using MuMIn (Kamil Barton, 2019) R package. In the main text, we present the more conservative pseudo-R^2 estimates that resulted from trigamma (for GLMM's) and delta methods (for GLM's). All other R^2 estimates can be found in the supplementary material (Tables S11-S13).

RESULTS

Diversity patterns

Mammalian richness on islands ranged from one to 234 species, with most islands being home to only one (42.9%) or two (20.8%) species (Figure 1). New Guinea, Borneo, Madagascar, Sumatra, Sulawesi and Java had the richest mammalian faunas, each containing more than 100 species (Figure 1). The richest fauna of bats was found in Borneo (92 species; Figure S2), whereas Madagascar and New Guinea hosted the richest faunas of non-volant mammals (169 and 167 species, respectively; Figure S3). We identified 782 species that are endemics to a single island (SIE), most of which are non-volant species (86.1%). Madagascar and New Guinea concentrated the largest number of SIE, which accounted for 87.6% and 55.5% of their mammalian fauna (Figures 2 and S2-3). As found for species richness, most islands with SIE hosted only one (63.6%) or two (14.4%) SIE species (Figure 2).

We tested whether islands that harbor only bats, only non-volant mammals, or both, differ in their physical and environmental characteristics (Figure S6-7). Compared to islands where either bats or non-volant mammals exist, islands where these two groups co-occur were larger, less isolated and have greater spatial variation in temperature, precipitation and elevation (Figure S6). Islands occupied only by bats had the opposite characteristics and were also warmer and wetter (Figure S6). Islands where only non-volant mammals occur have experienced significantly greater climate-change velocity since the LGM and were located at higher latitudes than those islands that supports only bats or both (Figure S6). Differences among islands regarding the occurrence of SIE were largely similar to that of species richness (Figure S7).

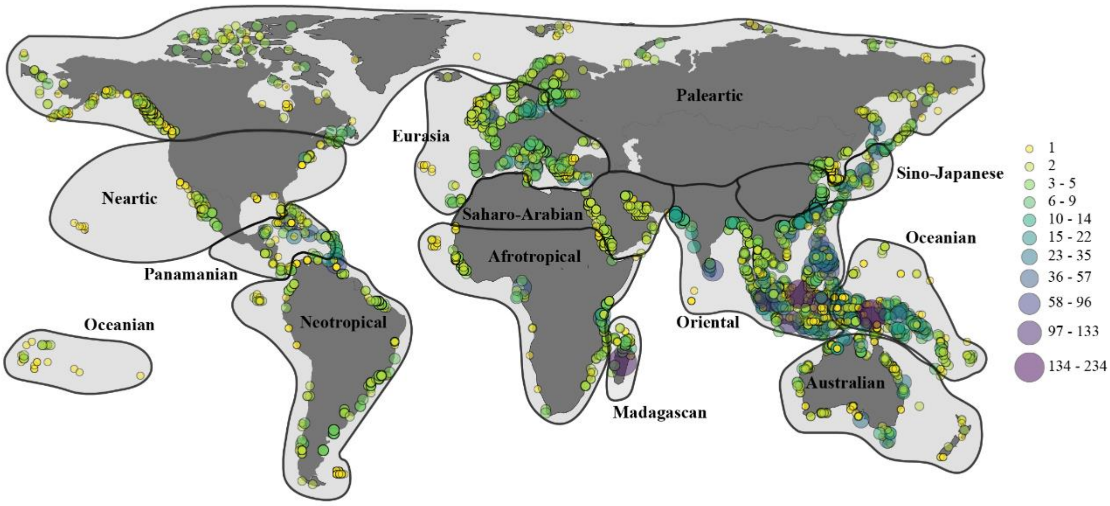

Figure 1 – Number of mammal species on the 5,594 islands included in this study, with an indication of the biogeographic region to which each island belongs. Maps with the richness of only bats and of only non-volant species are available in the supplementary material (Figs. S2-3).

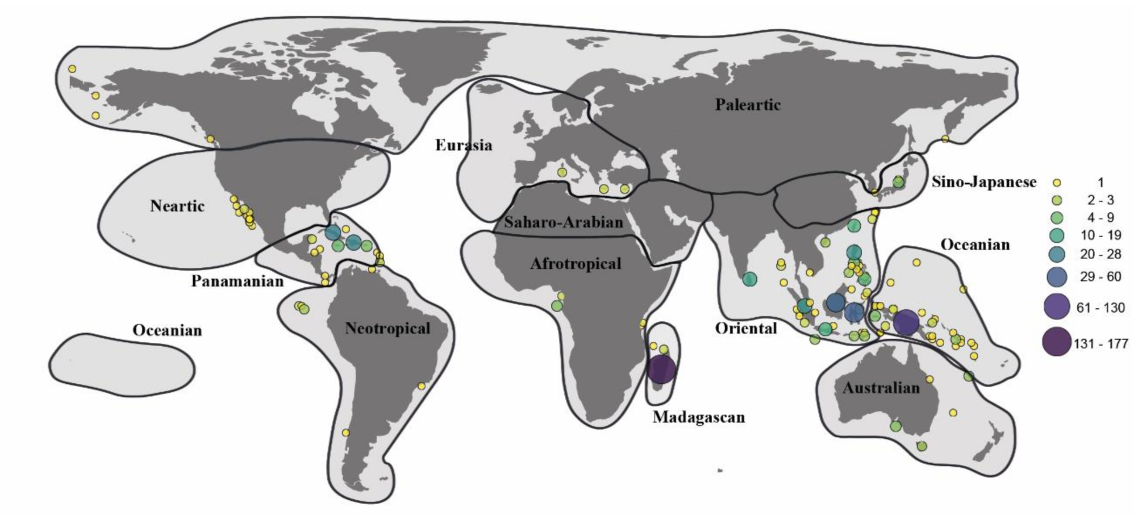

Figure 2 – Number of single island endemic (SIE) mammal on the 124 islands included in this study, with an indication of the biogeographic region to which each island belongs. Maps with the number of SIEs for bats and for non-volant species are available in the supplementary material (Figs. S4-5).

Drivers of island diversity

Our models explained between 27% and 90% of the variation in island biodiversity, with species richness being better explained (mean $R^2 = 0.89 \pm 0.06$ std. dev., Table 2) than endemism (mean $R^2 = 0.43 \pm 0.15$ std. dev. for SIE and $R^2 = 0.55 \pm 0.22$ std. dev. for pSIE; Table 2). The mixed models fitted for richness and pSIE revealed that a large proportion of the explained variation is attributed to the variance among biogeographic realms (comparison of marginal versus conditional R^2 in Table 2). Overall, we found that species richness responded more strongly to area (+), current and past isolation (-) and mean temperature (+ for bats and - for non-volants), whereas the other predictors had comparatively little or no effect on richness (Figs. 3a). In contrast, we found that endemism (SIE and pSIE) was strongly related to a more varied set of predictors, including climate velocity (+) and mean precipitation (-), for example (Figure 3b and 3c).

Table 2 – Pseudo coefficients of determination (pseudo-R^2) of the generalized linear models used to model the number of single island endemics (SIE) and the mixed models used to model species richness and the proportion of SIE (pSIE) of all mammals and of bats and non-volants separately. In mixed models, the marginal R^2 describes the proportion of the variance in biodiversity that can be explained only by the physical and environmental characteristics of the islands (i.e. fixed factors), and the conditional R^2 describes the proportion explained by the entire model, including fixed factors and the realm (i.e. random factor).

	Species richness		**SIE**		**pSIE**
	Conditional	Marginal	Conditional	Marginal	
All mammals	0.83	0.19	0.45	0.23	0.68
Bats	0.94	0.21	0.27	0.26	0.30
Non-volant	0.90	0.19	0.57	0.21	0.68

We found that area and isolation are the physical factors with strongest relationship with mammalian biodiversity (Figure 3), with consistent relationships with species richness across biogeographic realms (Figure 4). Island area was positively associated with species richness and SIE, as expected, but had no relationship with pSIE (Figure 3). Area had a similar effect on SIE ($\beta = 0.51 \pm 0.2$ std. error) and on richness of bats ($\beta = 0.54 \pm 0.13$ std. error), whereas among all mammals and non-volants, area was twice as strong a predictor of SIE ($\beta = 1.23 \pm 0.18$ std. error) than of species richness ($\beta = 0.69 \pm 0.12$ std. error for all mammals and $\beta = 0.63 \pm 0.13$ std. error for non-volants).

The effect of area on richness of all mammals and of bats was significantly higher the more isolated the island (Figure 3a).

As expected, islands that are currently isolated, or have been isolated in the past, have a negative relationship with richness and positive relationship with endemism, being stronger drivers of pSIE, followed by SIE and richness (Figure 3). For instance, the positive relationship between pSIE and current isolation was twice stronger than that on SIE and up to six times stronger than the negative relationship with richness (Figure 3). Flight capacity influenced the relative importance of past versus current isolation, as richness and pSIE of non-volants responded more strongly to past than current isolation (Figure 3). Conversely, bats were more strongly related to current isolation, whereas past isolation had no significant effect on the biodiversity of the group (Figure 3).

Environmental factors emerged as stronger predictors of endemism (SIE and pSIE) than of richness (Figure 3). Smaller environmental-richness slopes resulted partially from the variation in strength and in direction of these relationships among biogeographic realms (Figure 4). For example, richness of all mammals had a strong negative relationship with temperature in the Afrotropics, but a positive one in Oceania (Figure 4a). Variation in temperature within the island was the environmental factor with the most consistent direction of effect across realms, being positively associated with richness, but with a small effect size (Figure 4). We found mean precipitation to relate negatively with endemism, whereas variation in precipitation within the island had a positive relationship with endemism of bats (Figure 3). Unlike what is commonly observed for continental areas, endemism (SIE and pSIE) had a positive association with climate change velocity and a negative association with variation in elevation (Figure 3a and 3b).

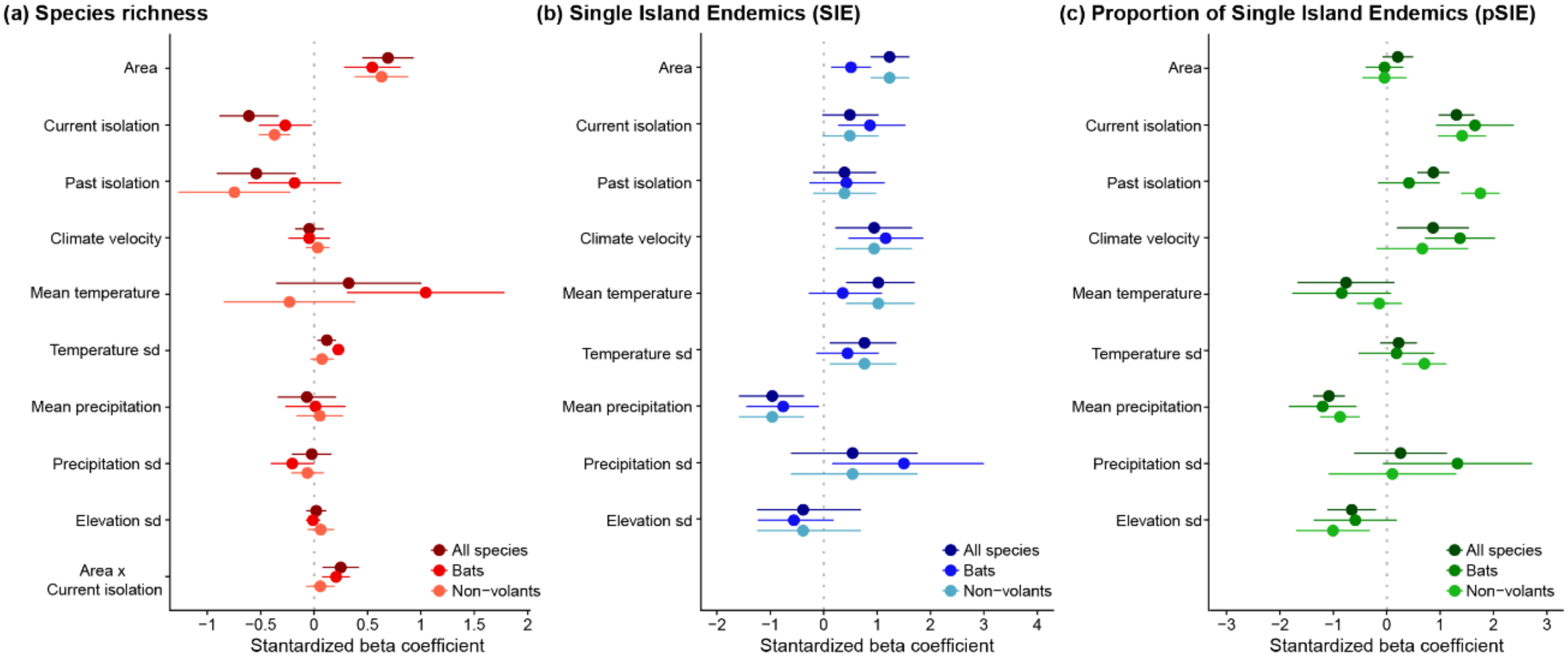

Figure 3 – Standardized beta coefficients of the generalized linear models used to model the number of single island endemics (SIE) and the mixed models used to model species richness and the proportion of SIE (pSIE) of all mammals and of bats and non-volants separately. Dots indicate estimated beta and error bars represent 95% confidence intervals. Beta coefficients, standard errors and z-values are available in Tables S13 to S15 in the supplementary material.

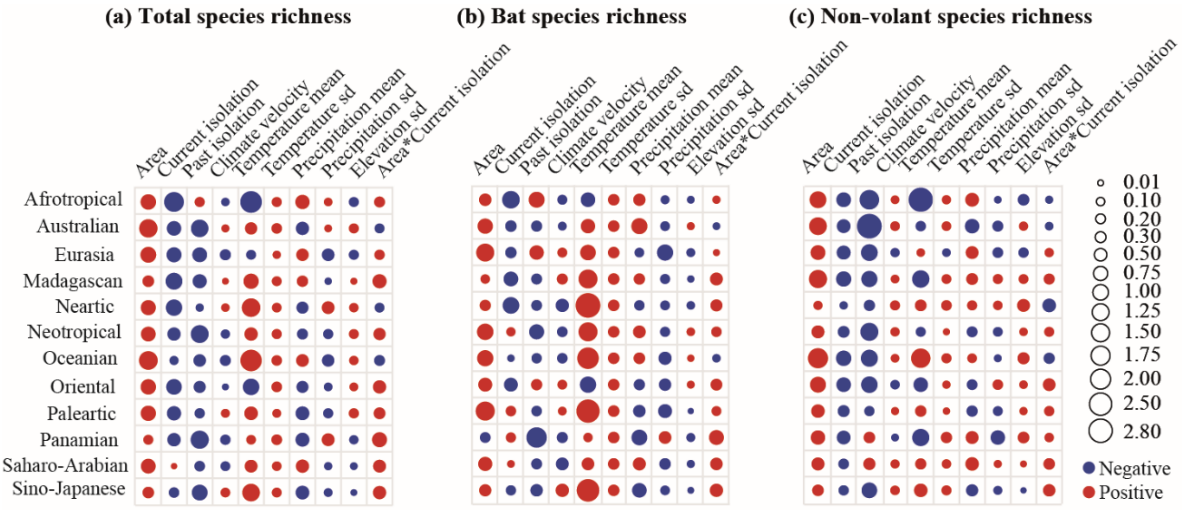

Figure 4 –Standardized beta coefficients per biogeographic realm for species richness of (a) all mammals, (b) bats and (c) non-volant species estimated from the generalized linear mixed models with biogeographic realm as a random factor. Dot size represents effect size and color represent direction of effect (blue is negative and red is positive). Coefficients are available in Tables S16 to S18 in the supplementary material.

DISCUSSION

Global patterns of biodiversity of insular mammals is well explained by the physical, biogeographical and environmental characteristics of the islands that are also often good predictors for other groups at large spatial scales, such as birds (Kalmar & Currie, 2006), plants (Kreft *et al.*, 2007; Cabral *et al.*, 2014), snakes (Pyron & Burbrink, 2014), and even human languages (Gavin & Sibanda, 2012). This is especially the case for species richness, whose models explained, on average, 89% of the variation in the diversity and pointed to the strong effects of area and isolation. As expected, a large proportion of the explained variation in global richness is attributed to the realms, because they capture the historical effects that acted on the origin and maintenance of mammalian pools (Ficetola *et al.*, 2017; Mazel *et al.*, 2017). In contrast to richness, our set of predictors explained about half of the variance in SIE and pSIE, probably because endemism is also partially driven by factors that act on smaller spatial scales, such as intra-archipelagic dynamics (Cabral *et al.*, 2014). The remaining variance in endemism may also be associated with island's age, which influences the time for speciation and colonization and also the carrying capacity in the case of oceanic islands (Whittaker *et al.*, 2008). Unfortunately, however, we still lack information on the age of most islands.

Mammals are a textbook example of how island area is positively associated with species richness and SIE, whereas isolation is negatively related to richness, but positively with SIE (MacArthur and Wilson 1967, Whittaker and Fernández-Palacios 2007). The positive species-area and SIE-area relationships comes close to be a universal law of ecology (Triantis et al. 2008, 2012) and is well documented for mammals, both on true islands (e.g. Lawrence 1986; Presley & Willig 2010) and mountain tops (e.g. Brown 1971, Lomolino, Mark et al. 1989). Our results strongly support the universality of the positive species-area relationship by recovering global positive association across realms (except for the richness of bats in the Panamian), unlike relationships observed for other predictors. Also, the negative or weak relationship between within-island elevation and diversity makes it improbable that the strong positive effects of area arise from a confounding effect of habitat heterogeneity (Ricklefs and Lovette 1999).

The contrasting relationships of island isolation with richness (negative) and endemism (positive) left a strong positive imprint on the proportion of SIE and are in line with the expected reduction in immigration and gene flow with increasing isolation (Lomolino 1990, Rosindell and Phillimore 2011). Measures of island isolation at global scale should incorporate elements of the landscape in addition to distance to the mainland (Weigelt and Kreft 2013), especially when studying mammals, whose neighboring islands might be a more important source of colonizers than the closest mainland (Millien-Parra and Jaeger 1999). Indeed, we were able to capture the strong effects of current isolation by using a measure based on the proportion of surrounding landmass (Weigelt and Kreft 2013), giving support for the growing body of evidence on the importance of archipelago configuration and the spatial structure of islands as drivers of biodiversity (Cabral et al. 2014, Gascuel et al. 2016).

The strength of the relationship between area and isolation and biodiversity varied with the group's vagility as well as the type of diversity measured, and is likely to reflect the relative importance of different processes (Triantis et al. 2008). The flight capacity of bats enables them to move more easily between and within islands and mainland (Fleming, Theodore, & Racey 2009) thus maintaining an effective population rescue that decreases their chances of extinction, but hinders speciation events (Heaney 2000, Rosindell and Phillimore 2011). Accordingly, we found that bats had weaker SIE-area association than non-volants, suggesting that intra-island diversification is weaker on organisms with greater vagility. Also, island area had a greater influence on number of SIE than on the richness of non-volants, as expected from increased *in situ* speciation resulting from a weaker rescue effect.

The relative importance of past versus current island isolation among bats and non-volants also points to differences in vagility driving global spatial patterns of insular biodiversity, especially on the proportion of SIE (pSIE). Non-volant mammals still carry strong imprints of past isolation, whereas bats have largely overcome such historical effects and are more positively associated with current than past isolation. This finding contrasts with that of phylogenetic endemism of mammals across the mainland and large islands globally, for which a dominance of past versus current isolation was found even for bats (Rosauer and Jetz 2015). One explanation for the contrasting result could be that phylogenetic patterns are better at holding the effects of historical events than patterns based on species diversity. Also, the study on phylogenetic endemism was not focused exclusively on islands, and different continental versus insular processes get mixed up.

The greater dispersal capacity of bats over water likely resulted in their sole occupancy of smaller, more isolated islands with narrow spatial variation in environmental conditions. In addition, bats are more common on warmer and wetter islands, as expected given their tropical origin and strong niche conservatism (Villalobos et al. 2013). Few Chiropteran lineages have been able to overcome the energy constraints imposed by low temperatures limiting their ability to colonize temperate regions and high elevations (Buckley et al. 2010, Stevens 2011). Indeed, we found temperature effects on bat richness to be greatest in colder regions, such as the Neartic and Paleartic realms.

Environmental factors are more strongly associated with insular endemism than richness. However, the environment-diversity relationship on islands is context-dependent, with strong variation across measures of biodiversity (e.g. richness vs endemicity) and geographic regions (Kalmar and Currie 2006). The weaker effect of climate on richness likely emerges because, by controlling for the effect of realms, we broke down the global latitudinal patterns into relatively similar climatic conditions, revealing heterogeneous within-realm relationships. Increased heterogeneity in precipitation and temperature within island tended to relate to greater SIE, possibly because greater variation in climate facilitate of niche partitioning and reproductive isolation via ecological specialization (Kisel and Barraclough 2010, Stein et al. 2014). The positive association between SIE and climate velocity since the LGM contrasts with findings for endemism on the mainland (Sandel et al. 2011) and challenge the expectation that climate instability would favor the occurrence of generalist broad-ranged species (Dynesius and Jansson 2000). Endemism might increase with climatic instability on islands if environmental changes were comparatively milder on the focal island than on nearby islands and mainland, thus species that went extinct everywhere else might have persisted on the focal island (Cronk 1997).

Given the broad agreement between our results and various expectations from island biogeography theory, we argue that IUCN-derived diversity measures appear robust to explore patterns of insular biodiversity at large spatial scales (Cardillo et al. 2008), despite the consequences of human activities (e.g. Upham 2017; van der Geer *et al.* 2017) and the general lack of knowledge about island species - a recent study shows that half of the mammal species on the well-known island of Luzon were unknown only a few years ago (Heaney et al. 2016).

In line with island biogeography theory, insular area and isolation are important predictors of total mammal species richness. However, richness of endemic mammals on islands are also associated with environmental predictors. Our results add to the growing evidence on the importance of the islands' past connectivity and current spatial structure to understand current biodiversity patterns. Also, we found that the dispersal capacity greatly influences the biogeographic patterns of mammals.

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CAPÍTULO 4

PaleoClimSeries: a spatial time series of the global climate over the last 5 million years (Pleiocene-Pleistocene)

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Status: Aguardando geração de todas as variáveis bioclimáticas para ser enviado para Global Ecology and Biogeography como um data paper

ABSTRACT

Motivation: Climate plays an important role in the generation and maintenance of biodiversity by driving processes such as diversification and range shifts. Current biodiversity patterns are often found to be strongly correlated with past climatic dynamics, especially in regions and periods when climate change was most pronounced, such as at northern latitudes or during the Last Glacial Maximum. However, we still know little about how the spatiotemporal variation in paleoclimate over deep time affected ecological and evolutionary dynamics, mostly because of the scarcity of user-friendly, freely available, spatially and temporally explicit, high resolution, global and deep time paleoclimate estimates. Here we address this gap by presenting PaleoClimSeries, a global spatiotemporal dataset of the last 5 Ma, derived from the intermediate complexity atmosphere-ocean general circulation model PLASIM-GENIE using emulation and downscaling techniques. PaleoClimSeries holds the potential to advance our understanding of the ecological and evolutionary mechanisms behind the strong relationship between biodiversity and climate, and hence to predict with greater confidence biodiversity responses to anthropogenic climatic change.

Main types of variable contained: Spatiotemporal series of 17 bioclimatic variables related to temperature and precipitation over the Pliocene-Pleistocene (i.e. last 5 million years).

Spatial location and grain: Global, downscaled from ~5º x 5º to the spatial resolution requested by the user.

Time period and grain: Last 5 million years at 1000-year resolution, interpolated to the temporal resolution requested by the user.

Major taxa and level of measurement: Not applicable.

Software and data format: Command-line compiled executable program and accompanying data files to derive estimates of paleoclimate at the spatial location, time period and resolution requested by the user. Each paleoclimate variable is exported to an individual file, in table format, with geographic locations in rows and time periods in columns.

Keywords: Climate-change velocity, downscaling, paleoemulator, PLASIM-GENIE, general circulation models, niche modelling, Pleistocene, Pliocene, paleo reconstruction, stability.

INTRODUCTION

Climate has played an important role in the history of life on Earth. It is the major predictor of variation in multiple dimensions of biodiversity over space and time (Svenning *et al.*, 2015). Diversity tends to be greater in warmer, wetter, more productive and climatically more stable environments (Currie *et al.*, 2004; Field *et al.*, 2009; Sandel *et al.*, 2011). Climate has direct and indirect effects on diversification rates (Condamine *et al.*, 2019), range shifts (Jansson & Dynesius, 2002), metabolic rates (Brown *et al.*, 2004), among other biological processes. Irrespective of the underlying mechanism behind the strong climate-diversity relationship, it is certain that past climatic regimes played an important role in determining current biodiversity patterns (Svenning *et al.*, 2015; Rangel *et al.*, 2018).

Understanding how historical climatic conditions influenced the origin and maintenance of biodiversity is constrained by the scarcity of high-resolution spatiotemporal paleoclimatic estimates. Most of the spatially explicit estimates that are freely available and of easy access to ecologists (Table 1) consist of sparse climate estimates in specific time slices, and only recently have global spatiotemporal estimates become available (Fordham *et al.*, 2017; Gamisch, 2019). In addition, the spatial and temporal heterogeneity and non-linearity of climate dynamics does not allow for an assumption of constant and unidirectional change. Thus, studying the historical effect of climate on biodiversity patterns using only coarse spatial or temporal resolution could miss or obscure important patterns (Fordham *et al.*, 2019).

Despite such limitations, the use of time-sliced paleoclimate estimates has demonstrated that past climate change (particularly since the Last Glacial Maximum, 21 ka) affected species richness (Araújo *et al.*, 2008; Hortal *et al.*, 2011), endemism

(Graham *et al.*, 2006; Sandel *et al.*, 2011), lineage survival and diversification (Carnaval *et al.*, 2009), functional diversity and ecosystem functioning (Ordonez & Svenning, 2015), genetic diversity (Hewitt, 2000), phylogenetic diversity (Rosauer & Jetz, 2015), species and lineages turnover (Dobrovolski *et al.*, 2012), species interaction (Dalsgaard *et al.*, 2011) and community structure (Rowan *et al.*, 2016).

Spatially explicit time series of paleoclimate at the scale of millennia would enable us to dig deeper into the ecological and evolutionary mechanisms driving biodiversity, and to advance further towards mechanistic approaches to model biodiversity (Cabral *et al.*, 2017; Descombes *et al.*, 2018; Nogués-Bravo *et al.*, 2018; Rangel *et al.*, 2018). Indeed, several questions remain unanswered due to the lack of such spatiotemporal data. For instance, how deep in time does the relationship between climate change and diversity hold? How did paleoclimatic fluctuations affect diversification and population dynamics? How did stability and spatial prevalence of environmental conditions over time influence biodiversity? What is the maximum rate of climate change that still allows for some evolutionary rescue? Such knowledge is paramount to predict how biodiversity may respond to current anthropogenic climatic change (Fordham *et al.*, 2016). In order to help fill the gap, here we propose the PaleoClimSeries, a spatially explicit temporal series of the Pliocene-Pleistocene period (i.e. 5 Ma) downscaled from a newly available paleoclimatic emulator (Holden *et al.*, 2019).

Table 1 – Summary of the freely available global paleoclimatic estimates at the spatial scales of interest for macroecological studies. Databases are in increasing order of oldest time period covered. Database references: [1]Karger *et al.* (2017), [2]Fordham *et al.* (2017), [3]Fick & Hijmans (2017), [4]Lima-Ribeiro *et al.* (2015), [5]Brown *et al.* (2018), [6]Gamisch (2019).

Database	**Time series or snapshots**	**Time range**	**Time resolution**	**Smallest spatial scale**
CHELSA[1]	Snapshot PMIP3 simulations with downscaling	LGM (21ka)	21ka	0.008º x 0.008º
PaleoView[2]	Transient CCSM3 simulation with downscaling	LGM (21ka)	Every 10 years	2.5° x 2.5°
WorldClim[3]	Snapshot PMIP2 simulations with downscaling	Last Interglacial (~120 – 140ka)	6ka, 21ka, ~120 - 140ka	0.008º x 0.008º 0.04° x 0.04°
ecoClimate[4]	Snapshot PMIP3 simulations with downscaling	Pliocene (~3.3 to 3Ma)	6ka, 21ka, ~3.3 - 3Ma	0.5° x 0.5°
PaleoClim[5]	Snapshot HadCM3 simulations with downscaling	Pliocene (3.3Ma)	787ka, 3.264 - 3.025Ma, 3.3Ma	0.04° x 0.04°
Oscillayers[6]	Pattern-scaled WorldClim LGM anomalies, temporally scaled by oxygen isotope data	Plio-Pleistocene (5.4Ma)	Every 10ka	0.04° x 0.04°

PaleoClimSeries

Data generation

Most global paleoclimatic reconstructions at fine spatial resolution come from the downscaling of simulations from General Circulation Models (GCMs), such as the Paleoclimate Modeling Intercomparison Project (PMIP3) and the Coupled Model Inter-comparison Project (CMIP5) (Taylor *et al.*, 2012). However, GCM simulations become intractable when reconstructing climate on a million-year scale, causing the general lack of spatiotemporal climatic estimates for deep time at fine spatial scales. Our PaleoClimSeries overcomes this limitation downscaling paleoclimate reconstructions from an intermediate complexity atmosphere-ocean GCM based on emulation technique, namely PLASIM-GENIE (Planet Simulator-Grid-Enabled Integrated Earth system model, Holden *et al.*, 2016; Holden *et al.*, 2019). This allows us to retain the effects of climate dynamics with sufficient spatial detail for macroecological studies. The emulator allows us to reconstruct deep-time climate in a computationally feasible way by applying statistical emulation techniques to represent the output of process-driven simulations. In the case of paleo PLASIM-GENIE, paleoclimate is reconstructed by using climate forcing, given by orbital configuration, ice-sheet state and level of atmospheric CO_2 to drive emulators of dimensionally-reduced PLASIM-GENIE outputs (Holden *et al.*, 2019).

We derived paleoclimate estimates at finer spatial resolution than the original coarse resolution of the underlying climate model (~5º x 5º) for each bioclimatic variable, at each time step, by downscaling the paleoclimate estimates using anomaly adjustments (Osborn *et al.*, 2016). For each time step, we linearly interpolated onto the spatial grid the climate anomalies between the emulated estimate for that time (E_t) and the emulated estimate for the current time (E_0). The interpolation was performed using a distance-based weighted mean from the centroid of the downscaled cell to the corners of the cell in the original resolution. To preserve a realistic spatial heterogeneity in estimated paleoclimate we applied additive anomaly adjustment (Eq. 1) using current climate C_0, derived from WorldClim (Fick & Hijmans, 2017):

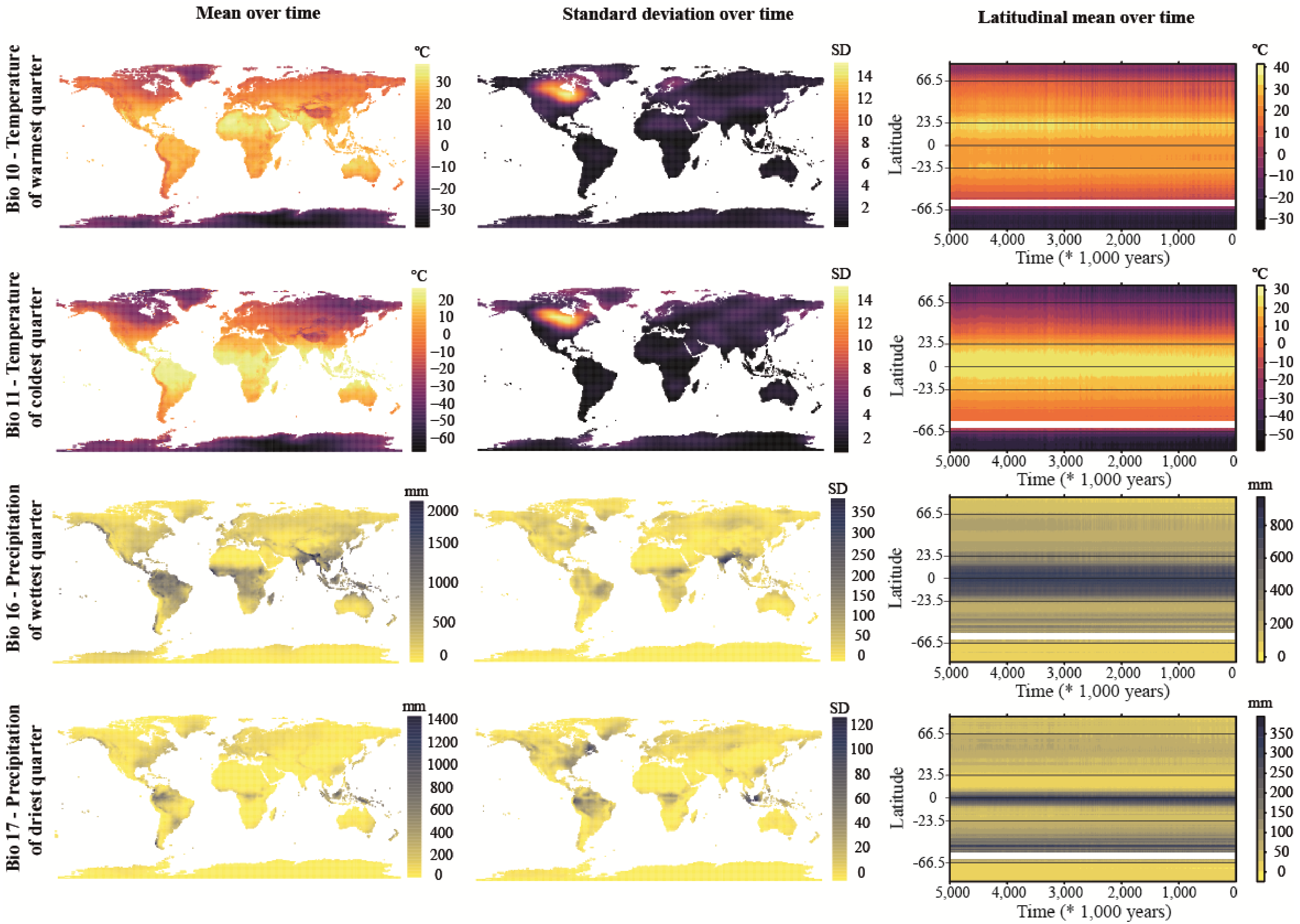
$$C_t = C_0 + (E_t - E_0) \qquad \text{Equation 1}$$

However, in very dry regions the additive anomaly adjustment applied to precipitation may generate negative estimates if the underlying climate model fails to represent observed extremes of climate. Thus, we applied multiplicative anomaly adjustment (Eq. 2) in regions where $E_0 > C_0$.

$$C_t = C_0 \times (E_t / E_0) \qquad \text{Equation 2}$$

The multiplicative anomaly adjustment better captures arid regions that are not well captured by the emulator and prevents the occurrence of unrealistic negative precipitation estimates in hyper-arid deserts and overestimates in wetter areas. For instance, the multiplicative term enabled us to reconstruct the hyper-aridity of the Atacama Desert and the seasonally hyper-wet monsoons. We use the additive adjustment for precipitation when the $E_0 < C_0$ because this prevents the possibility of unrealistically high precipitation when $E_t / E_0 >> 1$. Note that both approaches yield similar downscaled estimates in regions where $E_0 \approx C_0$.

PaleoClimSeries can be generated for any geographic region, including marine environments, at any time period within the last 5 Ma, at the desired spatial and temporal grains (see section 2.3 on data availability). Here, for demonstration and comparison to available datasets, we downscaled the estimates for land areas onto a global grid of 1º x 1º (~ 110 km² cells at Equator) at 1,000-year interval (5,000 time slices), which is the native temporal resolution of the climate model (Figure 1). We used WorldClim as our baseline for current observed climate (Fick & Hijmans, 2017), but it is also possible to use other databases of contemporary climate upon user’s interest. Videos of the spatial-time dynamics of climatic change over the past 5 million years are available in the supplementary material.


Mean over time

Standard deviation over time

Latitudinal mean over time

Bio 10 - Temperature of warmest quarter

Bio 11 - Temperature of coldest quarter

Bio 16 - Precipitation of wettest quarter

Bio 17 - Precipitation of driest quarter

Figure 1 – Representation of the PaleoClimSeries over space and time for four bioclimatic variables, one in each row: temperature of the warmest quarter (Bio 10), temperature of the coldest quarter (Bio 11), precipitation of the wettest quarter (Bio 16) and precipitation of the driest quarter (Bio 17). The first and second panels illustrate mean and standard deviation in climatic conditions of each geographic cell over the past 5 million years at a 1,000-year interval. The Hovmöller plots in the third panel illustrate the mean climatic condition per latitude at each time step.

Uncertainties and limitations

As for other downscaled estimates from GCM's, PaleoClimSeries is subject to the uncertainties and limitations of its underlying emulated GCM (see section 9 in Holden *et al.,* 2019). We accommodate aspects of model uncertainty in PaleoClimSeries by reporting the mean and the standard error of the estimated climate over 50 runs of the stochastic GCM emulator (Figure 2). This constitutes an estimate of the error incurred in statistically emulating the underlying simulations, which is an additional source of error, technically distinct from errors in the simulator itself. Nevertheless, the magnitudes and spatial patterns of these two sources of uncertainty have been shown to be generally similar, an important exception being that the emulator understates the uncertainty in global climate sensitivity (Holden et al 2019). We suggest that users take advantage of these uncertainty estimates by incorporating them into their analysis, for example, by conducting sensitivity tests to assess how robust their results are in the face of the uncertainty in climatic conditions.

The spatial downscaling converts the relatively low-resolution GCM output into the regional resolution that is often required for macroecological studies by capturing the first-order effect of topographic complexity, but at the cost of assuming that the lapse rate within a downscaled cell is constant over time. As for temporal resolution, we emphasize that time series downscaled to grains smaller than 500 years will not capture sub-millennial variation because they are driven only by orbital-timescale forcing.

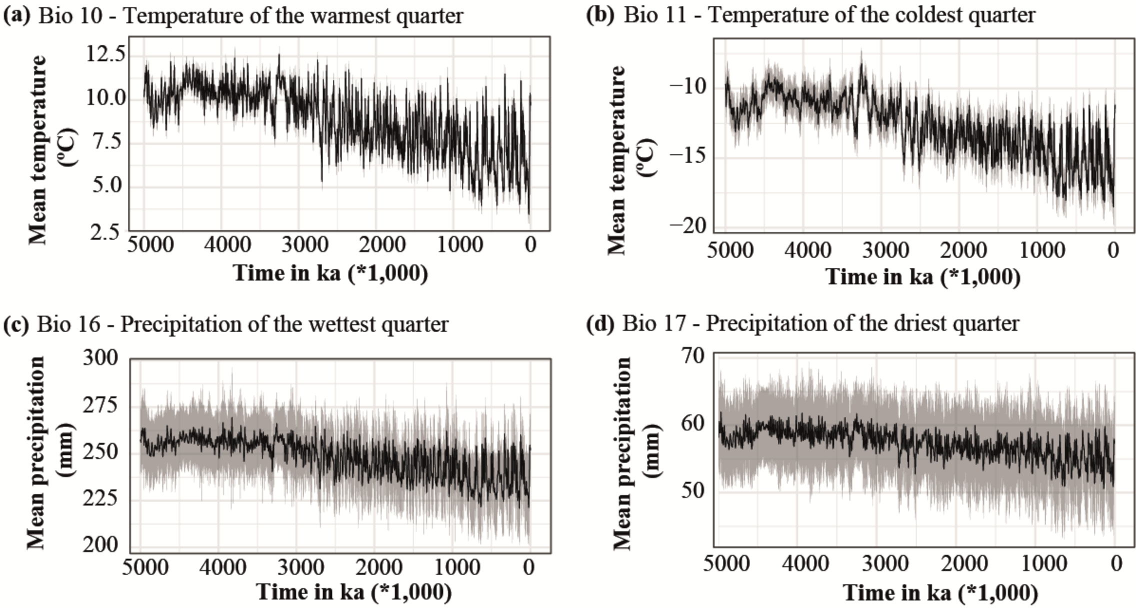


Figure 2 – Representation of PaleoClimSeries time series of four bioclimatic variables averaged across the globe for each time step: (a) temperature of the warmest quarter (Bio 10), (b) temperature of the coldest quarter (Bio 11), (c) precipitation of the wettest quarter (Bio 16) and (d) precipitation of the driest quarter (Bio 17). Black lines indicate mean and shading indicate standard error of the climate estimate across multiple GCM emulations.

Data availability

We made available at [*website under development*] and in the supplementary material an executable software coupled with the PLASIM-GENIE reconstructions and 17 bioclimatic variables from Worldclim to work as the baseline current observed climate for the spatial downscaling (Fick & Hijmans, 2017). The software downscales the requested bioclimatic variables according to user settings (e.g. geographical coordinates, spatial and temporal grains) and returns two tables per variable, one with mean climate estimates with time in columns and geographic cells in rows and another with standard error from multiple runs of the GCM emulators. In all files the rows are in the same order as the coordinates provided by the user. Tables can easily be converted into spatial files (e.g. raster) and visualized and explored using GIS libraries.

COMPARISONS AGAINST OTHER PALEOCLIMATE ESTIMATES

Most spatially explicit global paleoclimatic estimates are restricted to a few points in time that are separated by millennia (Table 1): Mid Holocene (6 ka), Last Glacial Maximum (21 ka), Last Interglacial (~120 to 140 ka), Isotope Stage 19 in the Pleistocene (~787 ka), mid-Pliocene warm period (3.3 Ma) and Plio-Pleistocene (5 Ma). We compared the mean estimates of all 17 blioclimatic variables[1] from our PaleoClimSeries with those from other databases at these six well studied snapshots of time (Table 1) using Pearson's correlation coefficient (*r*) at the spatial resolution of 1° x 1°. For databases with multiple estimates for the same bioclimatic variable and time due to variations in the underlying GCM, downscaling method or current climate baseline (i.e. ecoClimate), we measured the correlation with all available estimates and reported mean and standard deviation of Pearson's r.

PaleoClimSeries largely agree with estimates from other paleoclimatic reconstructions. Correlation coefficients ranged from 0.99 to 0.73 (mean 0.94 ± 0.07 standard deviation) across all bioclimatic variables and snapshots of time (Table 2).

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[1] So far, the manuscript includes the comparison of four variables. The remaining 13 are being generated.

Weakest correlations were found with Oscillayers for bio10 at 5Ma (r = 0.73) and with ecoClimate for bio16 and 17 at 6ka, 21ka and 3.3Ma (mean r = 0.80 ± 0.03 sd).

Correlation of ecoClimate estimates for bio16 and bio17 with the other databases (i.e. PaleoClim, WorldClim and Oscillayers) was similar to ours (mean r = 0.80 ± 0.02 sd).

We also compared our PaleoClimSeries estimates with those of the only other spatially explicit time series of the last 5Ma, the Oscillayers (Gamisch, 2019). We correlated the paleoclimate of the two databases every 10,000 years, which is the finest temporal resolution available in Oscillayers. Overall, our estimates are in good agreement (Fig. 3; mean 0.96 ± 0.03 sd over the 19 bioclims). Bio11 had the highest correlation coefficients and bio10 had the lowest coefficients over the 5 Ma series (Fig. 3). For most bioclim variables, strength of correlation become more variable among deeper times (Fig. 3, but see bio17). This behaviour is to be expected because model assumptions are likely to become increasingly untenable as we go deeper in time [for more details, see section 9 of Holden *et al.*, (2019) and section 4.2 in Gamisch (2019)]. Compared to Oscillayers, our PaleoClimSeries is generated from a more dynamically realistic model, incorporates the uncertainty of its underlying GCM, and is available at finer temporal resolution. Additionally, PaleoClimSeries has the advantage of being generated quickly and easily upon the user’s request of spatial and temporal extent and grains and the variable of interest, without the need to download large files.

Table 2 – Pearson's correlation coefficient (r) between PaleoClimSeries estimates and that of other freely available datasets for six snapshots of time: Mid Holocene (6ka), Last Glacial Maximum (21ka), Last Interglacial (~120 to 140ka), Isotope Stage 19 in the Pleistocene (787ka), mid-Pliocene warm period (3.3Ma) and Plio-Pleistocene (5Ma).

Bio	**Description**	**6ka**			**21ka**			**120-140ka**		**785ka**		**3.3ma**		**5ma**
		World Clim	**eco Climate**	**Oscillayers**	**World Clim**	**eco Climate**	**Oscillayers**	**World Clim**	**Oscillayers**	**Paleo Clim**	**Oscillayers**	**Paleo Clim**	**eco Climate**	**Oscillayers**
1	Annual Mean Temp													
4	Temp Seasonality													
5	Max Temp of Warmest Month													
6	Min Temp of Coldest Month													
7	Temp Annual Range													
8	Mean Temp of Wettest Quarter													
9	Mean Temp of Driest Quarter													
10	Mean Temp of Warmest Quarter	0.98	0.99±0.00	0.97	0.97	0.97±0.01	0.98	0.92	0.97	0.98	0.99	0.95	0.98±0.00	0.73
11	Mean Temp of Coldest Quarter	0.99	0.99±0.00	0.98	0.98	0.97±0.00	0.99	0.98	0.99	0.99	0.99	0.99	0.99±0.00	0.93
12	Annual Prec													
13	Prec of Wettest Month													
14	Prec of Driest Month													
15	Prec Seasonality													
16	Prec of Wettest Quarter	0.96	0.81±0.01	0.93	0.93	0.80±0.02	0.97	0.92	0.97	0.94	0.98	0.94	0.82±0.00	0.95
17	Prec of Driest Quarter	0.97	0.73±0.04	0.88	0.88	0.67±0.06	0.96	0.92	0.97	0.93	0.98	0.90	0.78±0.00	0.93
18	Prec of Warmest Quarter													
19	Prec of Coldest Quarter													

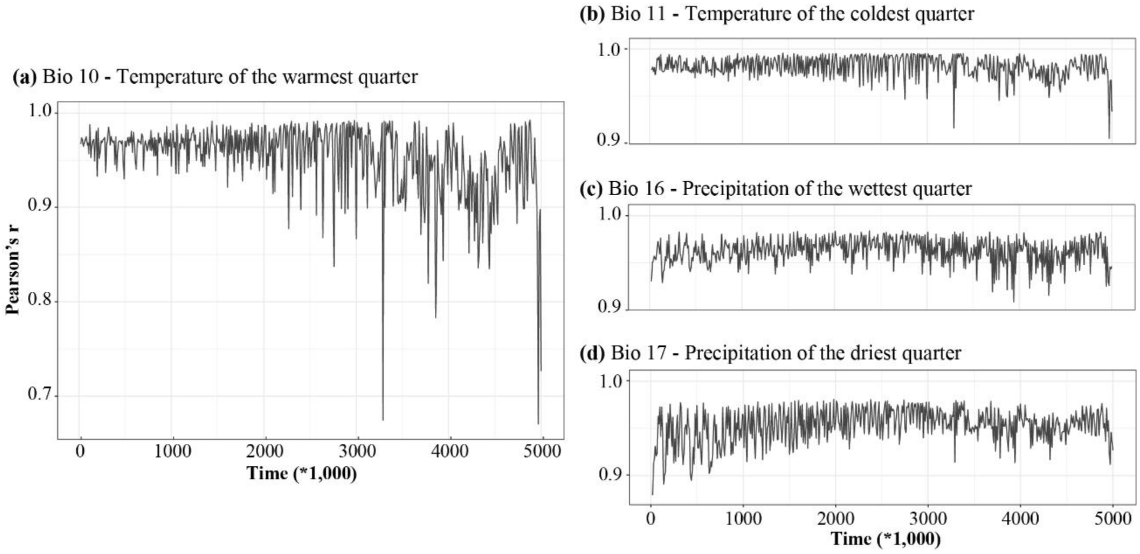

Figure 3 – Pearson's correlation coefficient (r) between PaleoClimSeries and Oscillayers (Gamisch 2019) for each 10,000 years.

APPLICABILITY

PaleoClimSeries can be used to explore a series of long-standing ecological, biogeographical and macroecological hypotheses of great relevance to understand the drivers of biodiversity and forecast organismal response to future climatic change. Our paleoclimate spatiotemporal series are highly relevant to studies that simulate the origin and maintenance of diversity (Gavin *et al.*, 2017; Nogués-Bravo *et al.*, 2018; Rangel *et al.*, 2018) and that model ecological niches and geographic distribution of organisms and biomes through time (Graham *et al.*, 2006; Kozak *et al.*, 2008; Costa *et al.*, 2018). Additionally, PaleoClimSeries is a promising tool for studies on population and genetic dynamics (Carstens & Richards, 2007) and for the study of human evolution (Diniz-Filho *et al.*, 2019). Importantly, the time frame of PaleoClimSeries offers the possibility to move from the inference of climate stability as a driver of species persistence (i.e. reduction of extinction rates and range shifts) to a driver of species generation (i.e. increase in speciation rates) (Svenning *et al.*, 2015).

DATA ACCESSIBILITY

PaleoClimSeries is available in the supplementary material of this paper and at [*website under development*]. All data used to compare PaleoClimSeries estimates are freely available online.

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CONSIDERAÇÕES FINAIS

Nesta tese mostramos como os padrões espaciais de múltiplas dimensões da diversidade biológica estão relacionados de forma direta e indireta às condições ambientais, biogeográficas e físicas atuais e passadas. Em especial, destacamos como as relações são não-estacionárias e como essa variação pode nos ajudar a compreender os diferentes processos por trás da geração e manutenção da biodiversidade. Adicionalmente, nós propomos uma série espaço-temporal do clima nos últimos 5 milhões de anos, o que tem o potencial de ajudar a compreender a origem do não-estacionaridade nas relações ambiente-diversidade.

Nos dois primeiros capítulos da tese, mostramos que a não-estacionaridade espacial não segue o mesmo padrão geográfico de unidades biogeográficas, como biomas e domínios, e também que o ambiente se relaciona à biodiversidade de formas direta e indireta. Estas duas características adicionam mais complexidade ao estudo das relações ambiente-diversidade e se mostram promissoras para explorar em mais detalhes os padrões emergentes bem conhecidos em macroecologia, como por exemplo, a tendência de a riqueza de espécies ser maior em ambientes mais quentes, úmidos, produtivos e estáveis. Inclusive, nossos resultados indicaram que até mesmo essas relações amplamente estudadas apresentaram não-estacionaridade na direção e/ou no tamanho do efeito. Por exemplo, as relações entre riqueza e energia apresentam variações geográficas tão drásticas quanto a mudança na direção do efeito (positivo e negativo) de temperatura, precipitação e produtividade primária dependendo do grupo taxonômico. No terceiro capítulo da tese, identificamos padrões emergentes globais de como a diversidade de mamíferos em ilhas se relacionam às características desses ambientes. Nossos resultados oferecem suporte ao grande corpo teórico da biogeografia de ilhas ao recuperar os fortes e consistentes efeitos de área e isolamento entre regiões geográficas. Porém, nossos resultados também avançam no conhecimento de ilhas ao indicar a grande importância da capacidade de dispersão e de características ambientais passadas, como a velocidade de mudança climática e a conectividade da ilha em relação ao último máximo glacial.

De maneira geral, nossos estudos sugerem a necessidade de encontrar um equilíbrio entre a generalidade e a especificidade dos modelos que descrevem padrões macroecológicos. Considerando a maturidade alcançada pela macroecologia na detecção e confirmação de muitos padrões emergentes nos últimos 30 anos, nós argumentamos pela necessidade de procurar variações nesses padrões emergentes e explorar as possíveis causas dessas variações.

CONCLUDING REMARKS

In this thesis we show how spatial patterns of multiple dimensions of biological diversity are directly and indirectly related to current and past environmental, biogeographic and physical conditions. We highlight how these relationships are non-stationary and how the variation can help us understand the different processes behind the generation and maintenance of biodiversity. In addition, we propose a spatiotemporal series of the climate over the past 5 million years, which has the potential to help understand the origin of non-stationarity in environment-diversity relationships.

In the first two chapters of the thesis, we show that spatial non-stationarity does not follow the same geographical pattern as biogeographic units, such as biomes and domains, and also that the environment is directly and indirectly related to biodiversity. These two characteristics add more complexity to the study of environment-diversity relationships and are promising way forward to explore in more detail the emergent patterns that are well known in macroecology, such as the tendency for species richness to be greater in warmer, wetter, more productive and more stable environments. Our results signaled that even these widely studied relationships are non-stationary in their direction and/or in their effect size. For example, the relationship between temperature, precipitation and primary productivity with species richness change in direction (positive and negative) depending on the taxonomic group. In the third chapter of the thesis, we identified emerging global patterns of how the diversity of mammals on islands is related to the characteristics of these environments. Our results support the island biogeography theory by recovering strong and consistent effects of area and isolation between geographic regions. However, our results also advance the knowledge of islands by indicating the great importance of the dispersion capacity and past environmental characteristics, such as the velocity of climate change and island's connectivity since the last glacial maximum.

In general, our studies suggest the need to find a balance between the generality and the specificity of the models that describe macroecological patterns. Considering the maturity reached by macroecology in detecting and confirming many emergent patterns over the past 30 years, we advocate for the need to search for variations in the well-known emergent patterns and to explore the possible causes of these variations.

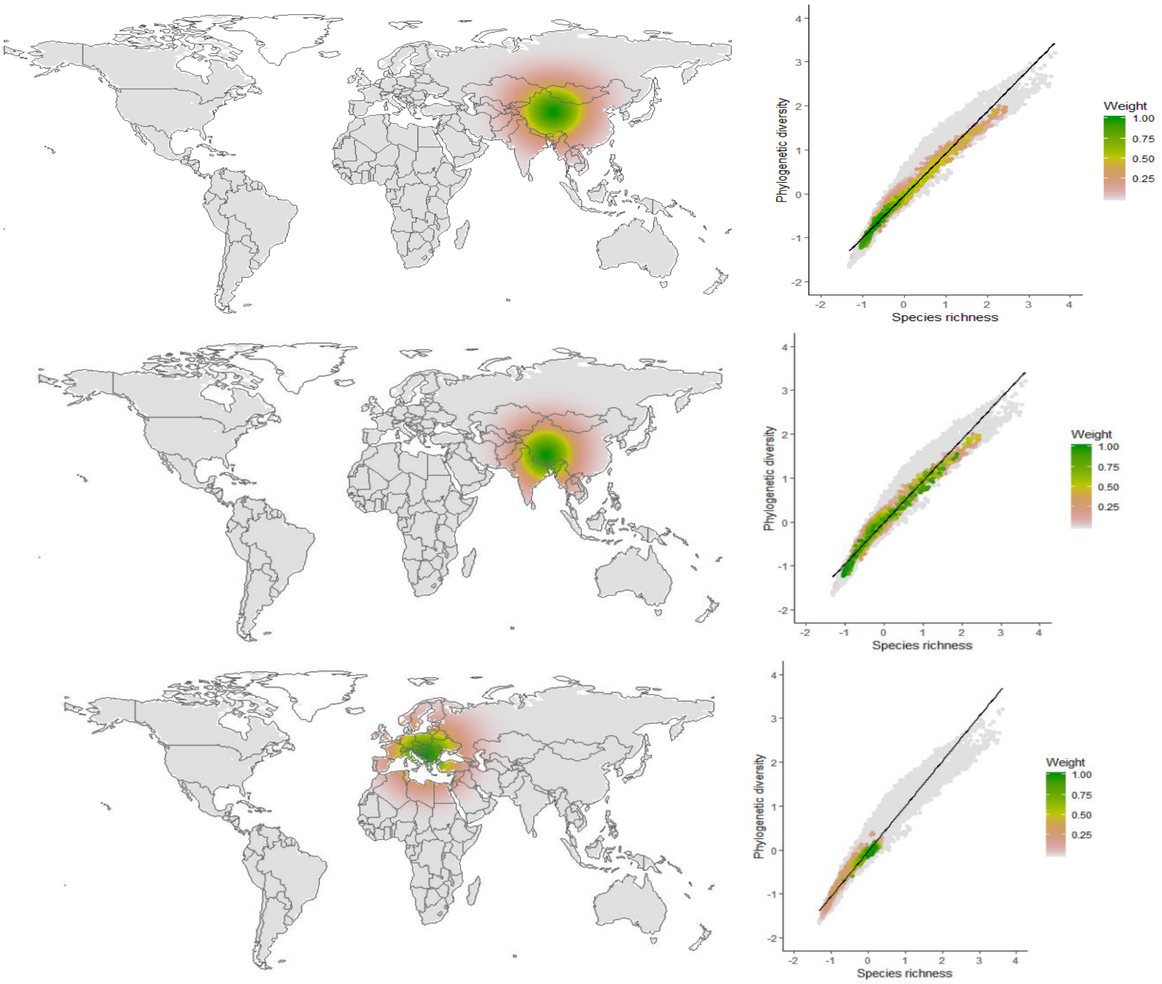
MATERIAIS SUPLEMENTARES

Capítulo 1

Supporting information from

“Environmental factors explain the spatial mismatches between species richness and phylogenetic diversity of terrestrial mammals”

Elisa Barreto, Catherine H. Graham & Thiago F. Rangel



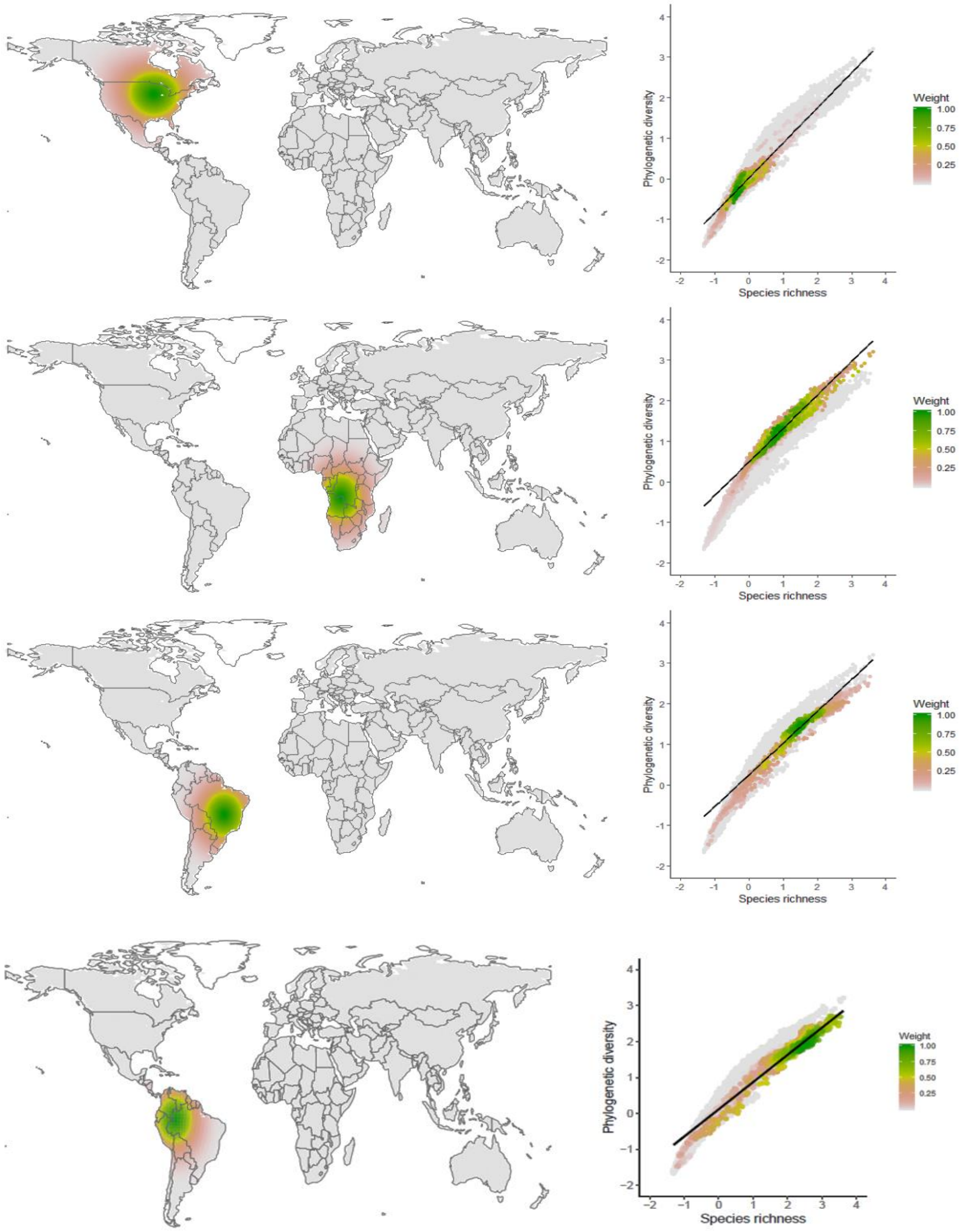


Figure S1 – Visual example of the distance-based Gaussian weighting function used to assign greater weight to nearby cells to fit the linear regression model.

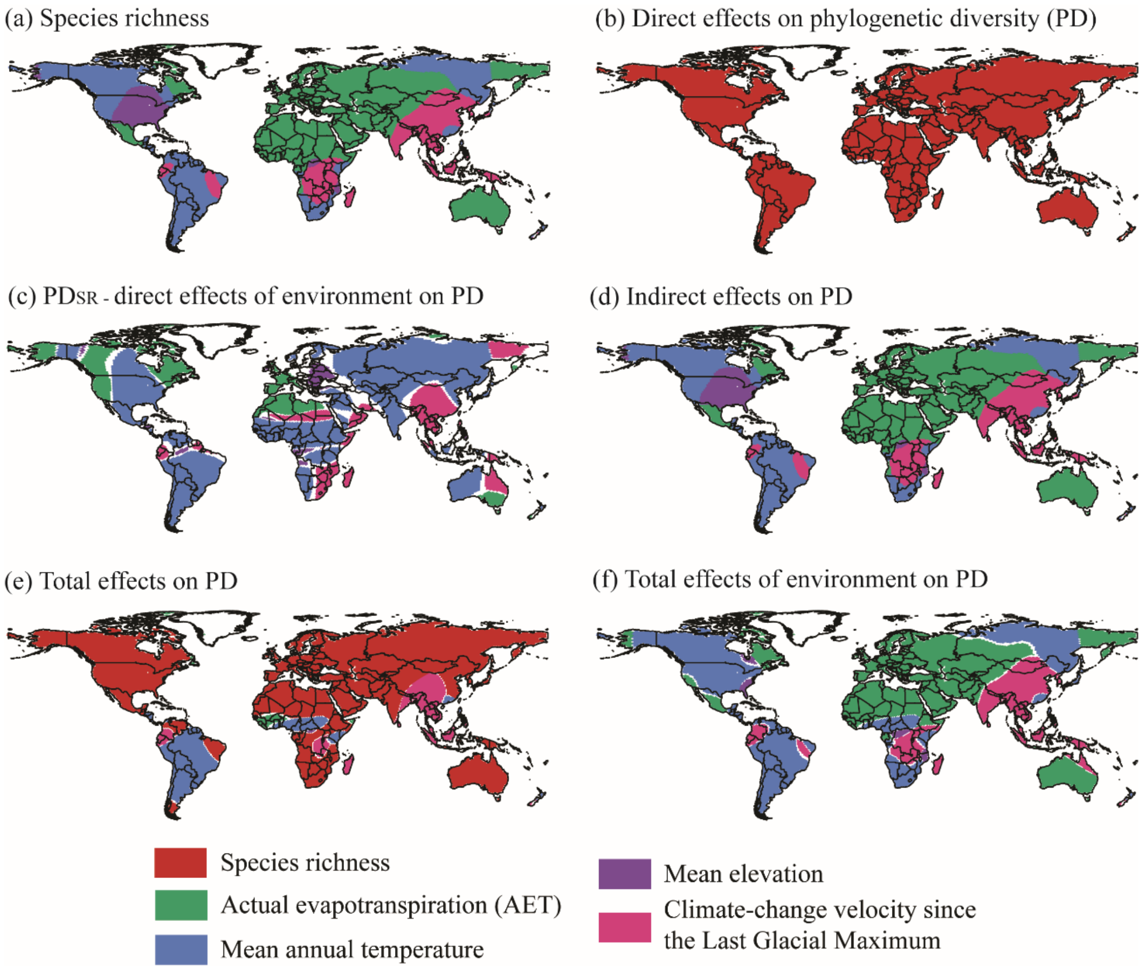
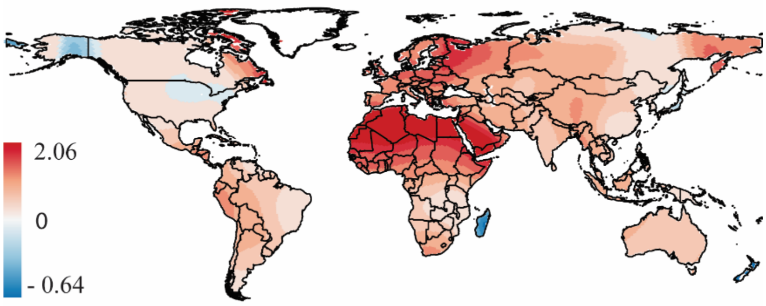


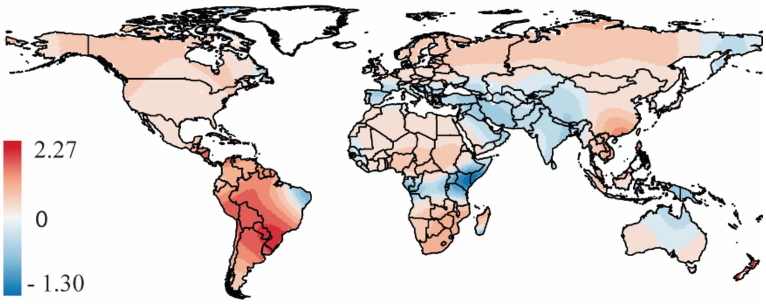
Figure S2 – Categorical map showing the strongest environmental correlates of terrestrial mammal diversity. Each cell of the map indicates the variable with the highest path coefficient in at least 95% of the 1,000 results obtained with distinct phylogenetic hypothesis. Phylogenetic uncertainty prevents inference over white regions of maps.

Indirect effects on phylogenetic diversity

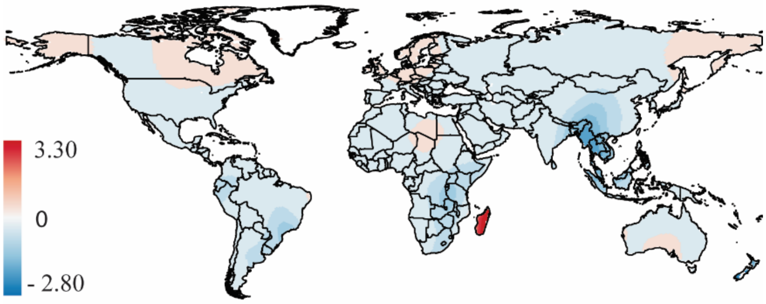
(a) Actual evapotranspiration (AET)



(b) Mean annual temperature



(c) Climate-change velocity since the Last Glacial Maximum



(d) Mean elevation

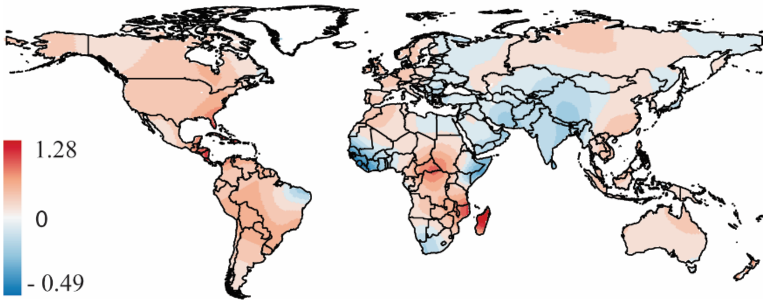
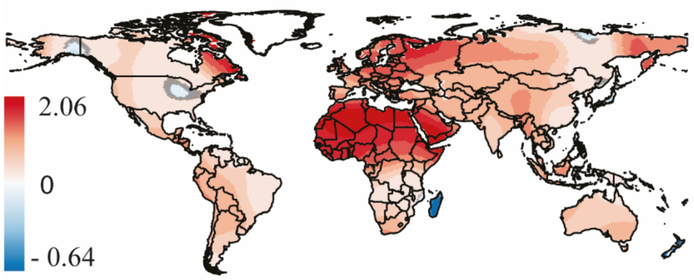
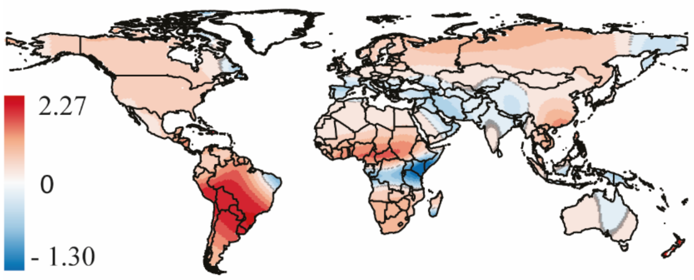


Figure S3 – Standardized path coefficients of the indirect environmental effects on phylogenetic diversity given its effects on species richness. Coefficients are averaged across 1,000 results from distinct phylogenetic hypothesis. Phylogenetic uncertainty does not significantly change the result.

(a) Actual evapotranspiration (AET)



(b) Mean annual temperature



(c) Climate-change velocity since the Last Glacial Maximum

(d) Mean elevation

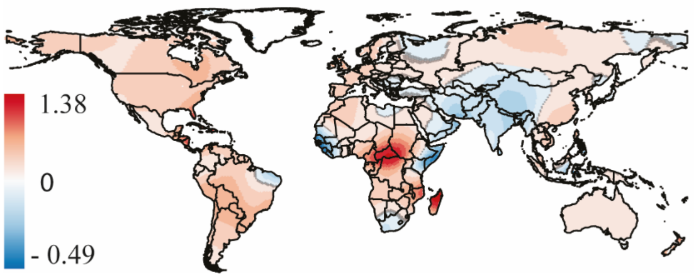


Figure S4 – Standardized path coefficients of the total environmental effects on phylogenetic diversity (i.e., sum of direct and indirect paths). Coefficients are averaged across 1,000 results from distinct phylogenetic hypothesis. Phylogenetic uncertainty does not significantly change the result.

Capítulo 2

Supporting information from

"Spatial variation in the direct and indirect effects of climate and productivity on species richness of terrestrial tetrapods"

Elisa Barreto, Thiago F. Rangel, Marco Túlio Pacheco Coelho, Fernanda Cassemiro, Niklaus E. Zimmermann & Catherine H. Graham

Figs. S1 to S9: Path model using Net Primary Production (NPP) as proxy of productive energy.

Figs. S10 to S20: Path model using Fraction of Photosynthetically Active Radiation (fPAR) as proxy of productive energy.

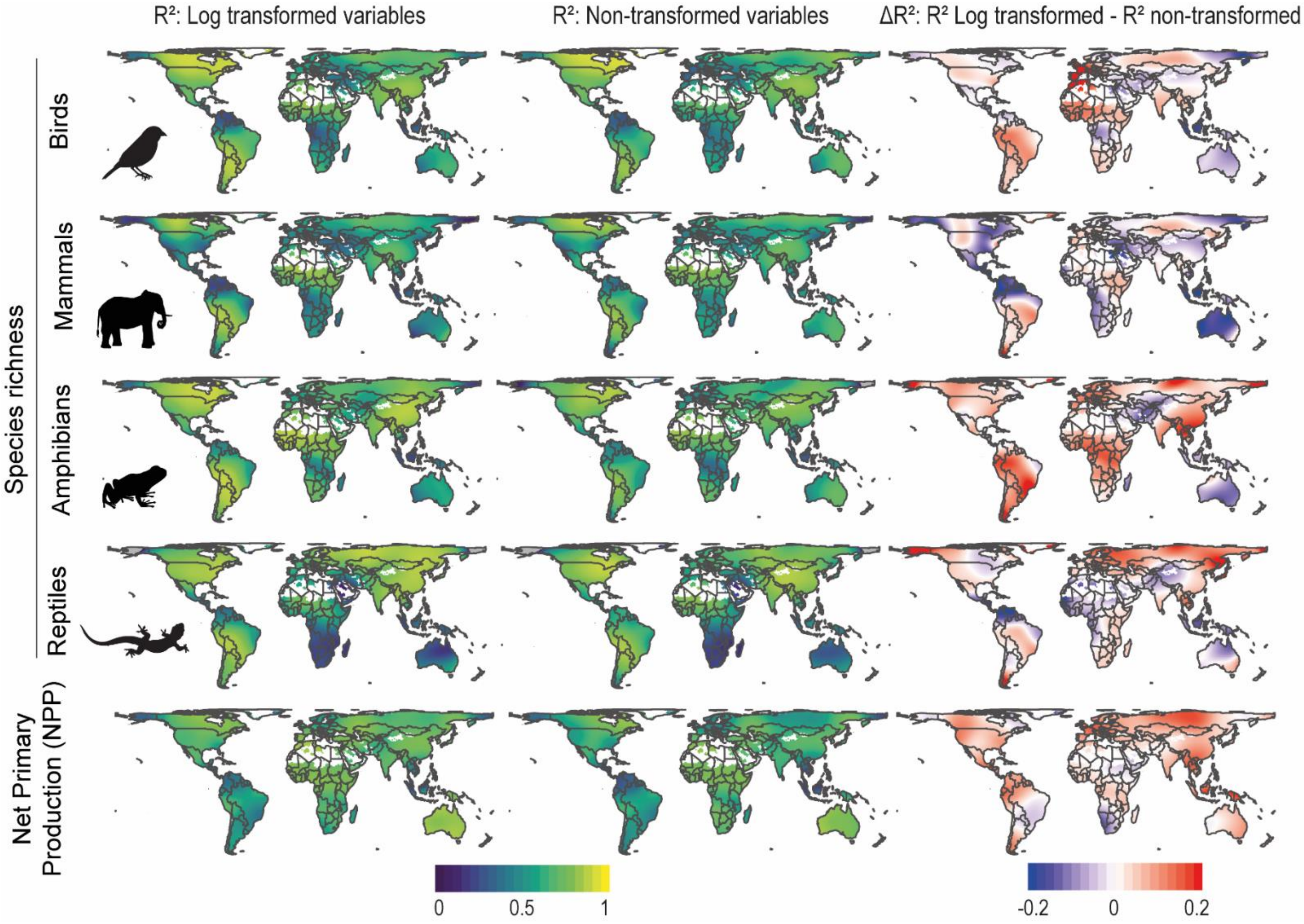

R²: Log transformed variables
R²: Non-transformed variables
ΔR²: R² Log transformed - R² non-transformed
Species richness
Birds
Mammals
Amphibians
Reptiles
Net Primary Production (NPP)
0
0.5
1
-0.2
0
0.2

Figure S1 – Local coefficient of determination (R^2) of regression models using log-transformed variables (first panel) and untransformed variables (second panel) for each of the response variables indicated in the rows. Maps on the third panel show the difference between the R^2 of the models with log-transformed and untransformed variables. Areas in blue indicate places where the model with untransformed variables has higher R^2, areas in red indicate places where model with log-transformed variables has higher R^2. The black silhouette indicates to which organismal group the result belongs. Silhouette images were taken from Freepik.com.

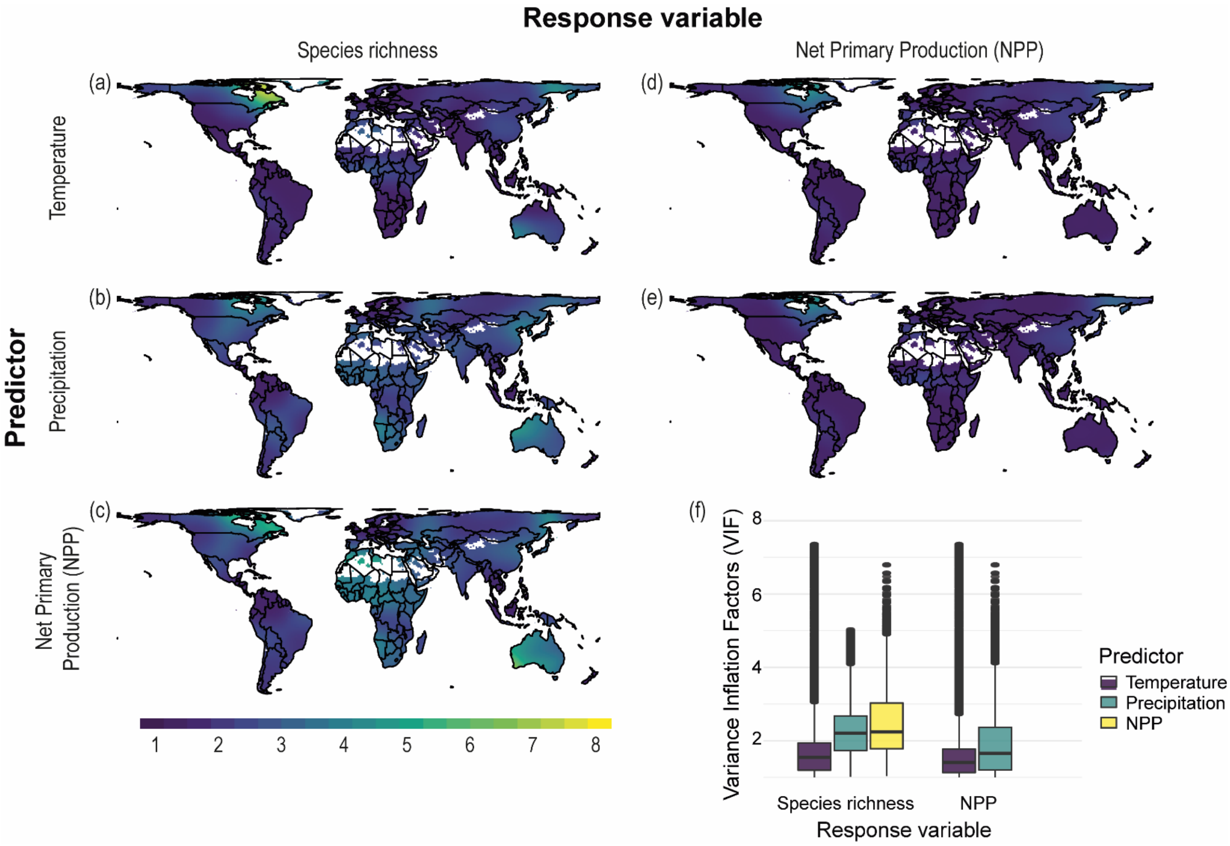


Figure S2 – Variance Inflation Factors (VIF) at each focal cell for the regressions of species richness (first panel; a-c) and Net Primary Production (seccond panel; d-e) as a function of the predictors indicated in the rows. Summary of VIF's across space is shown in the boxplot f.

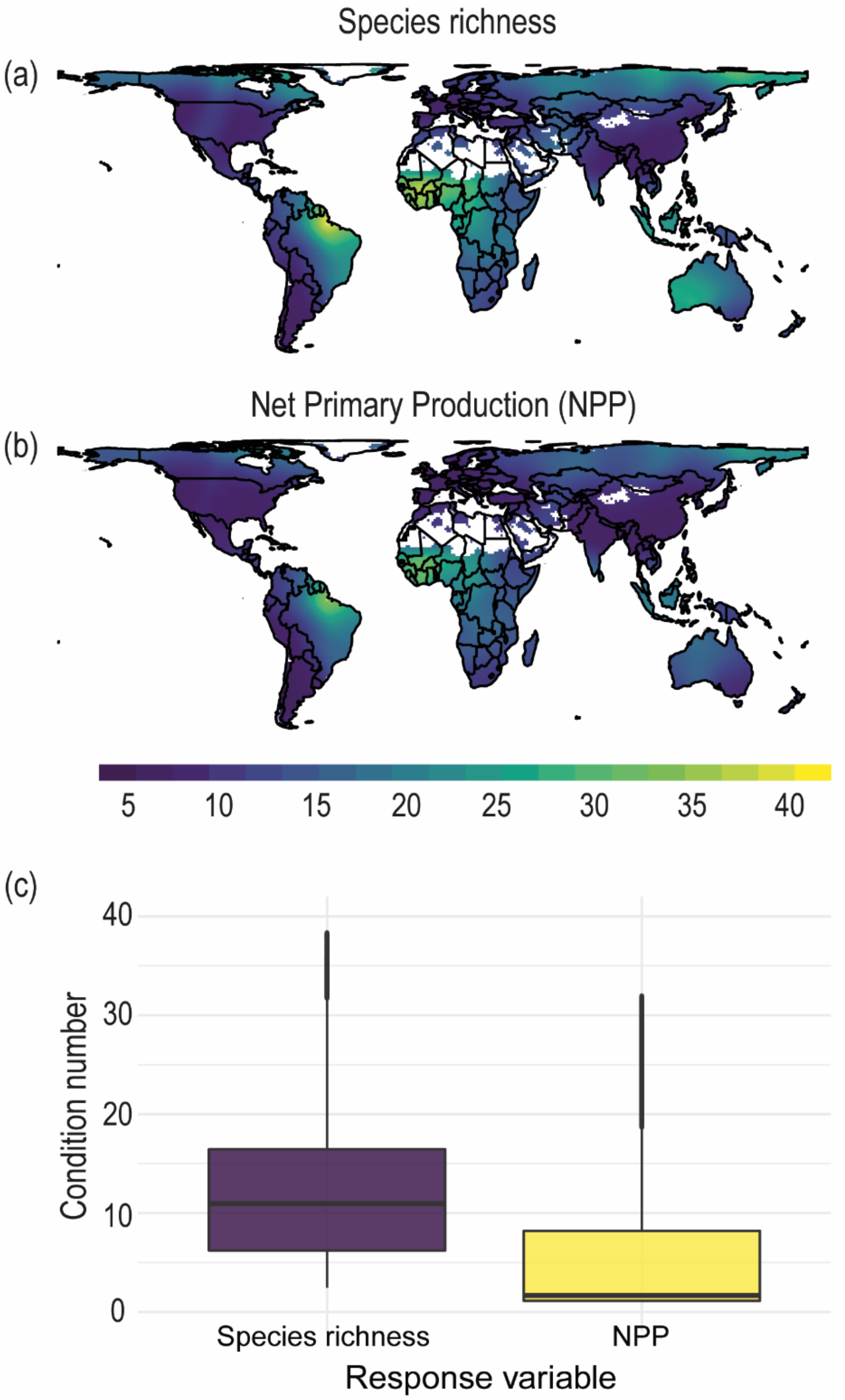


Figure S3 – Condition number at each focal cell for the regressions of species richness (a) and Net Primary Production (b) as a function of the environmental predictors. Summary of CN’s across space is shown in the boxplot c.

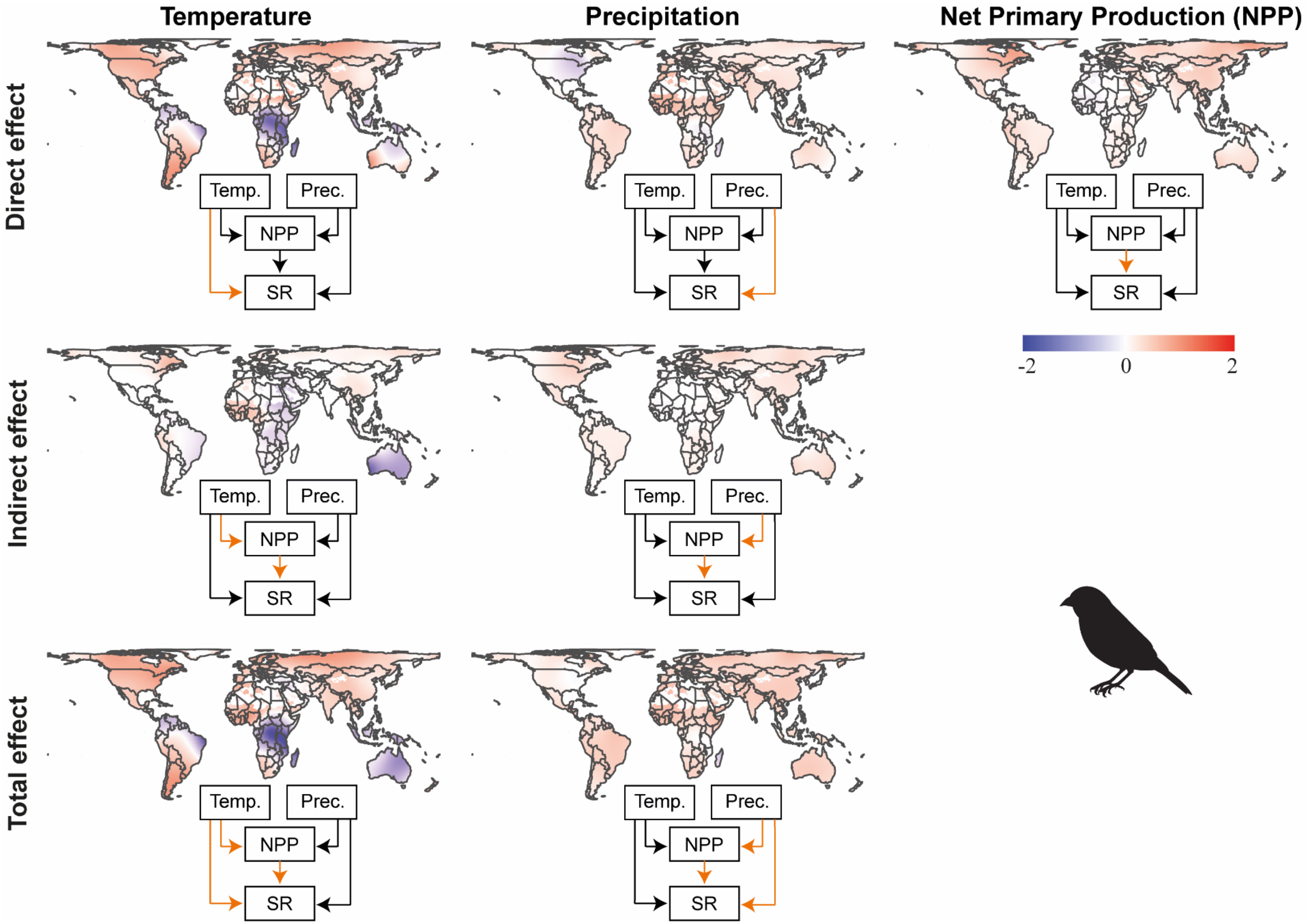


Figure S4 – Direct, indirect and total path coefficients between species richness of birds and the three measures of energy: temperature (first panel), precipitation (second panel) and productivity (third panel). Path coefficients are standardized and are mapped using the same color scale, allowing for the direct comparison of their magnitudes. Orange arrows in the model indicate which paths the coefficients refer to. Silhouette image was taken from Freepik.com.

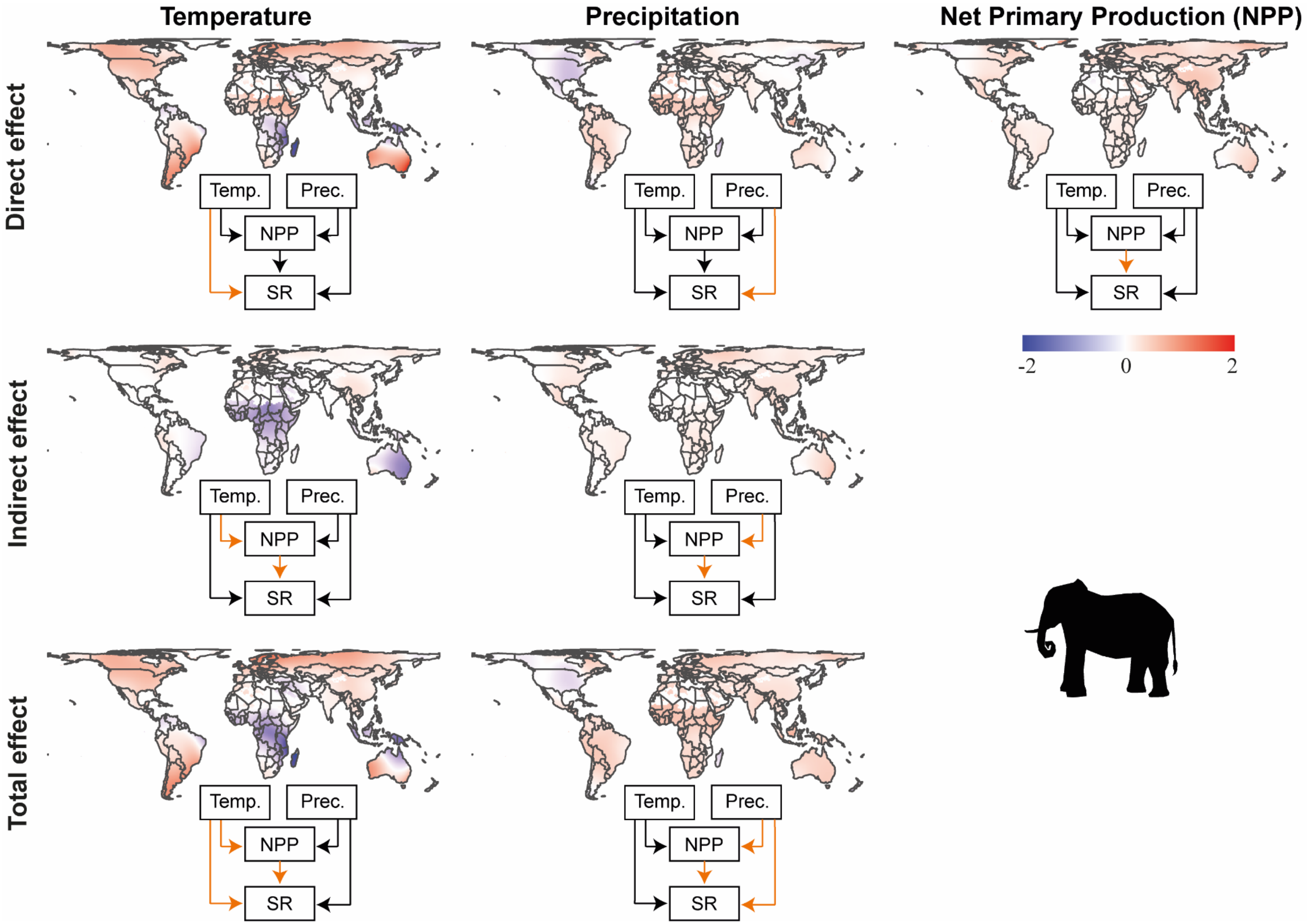


Figure S5 – Direct, indirect and total path coefficients between species richness of mammals and the three measures of energy – temperature (first panel), precipitation (second panel) and productivity (third panel). Path coefficients are standardized and are mapped using the same color scale, allowing for the direct comparison of their magnitudes. Orange arrows in the model indicate which paths the coefficients refer to. Silhouette image was taken from Freepik.com.

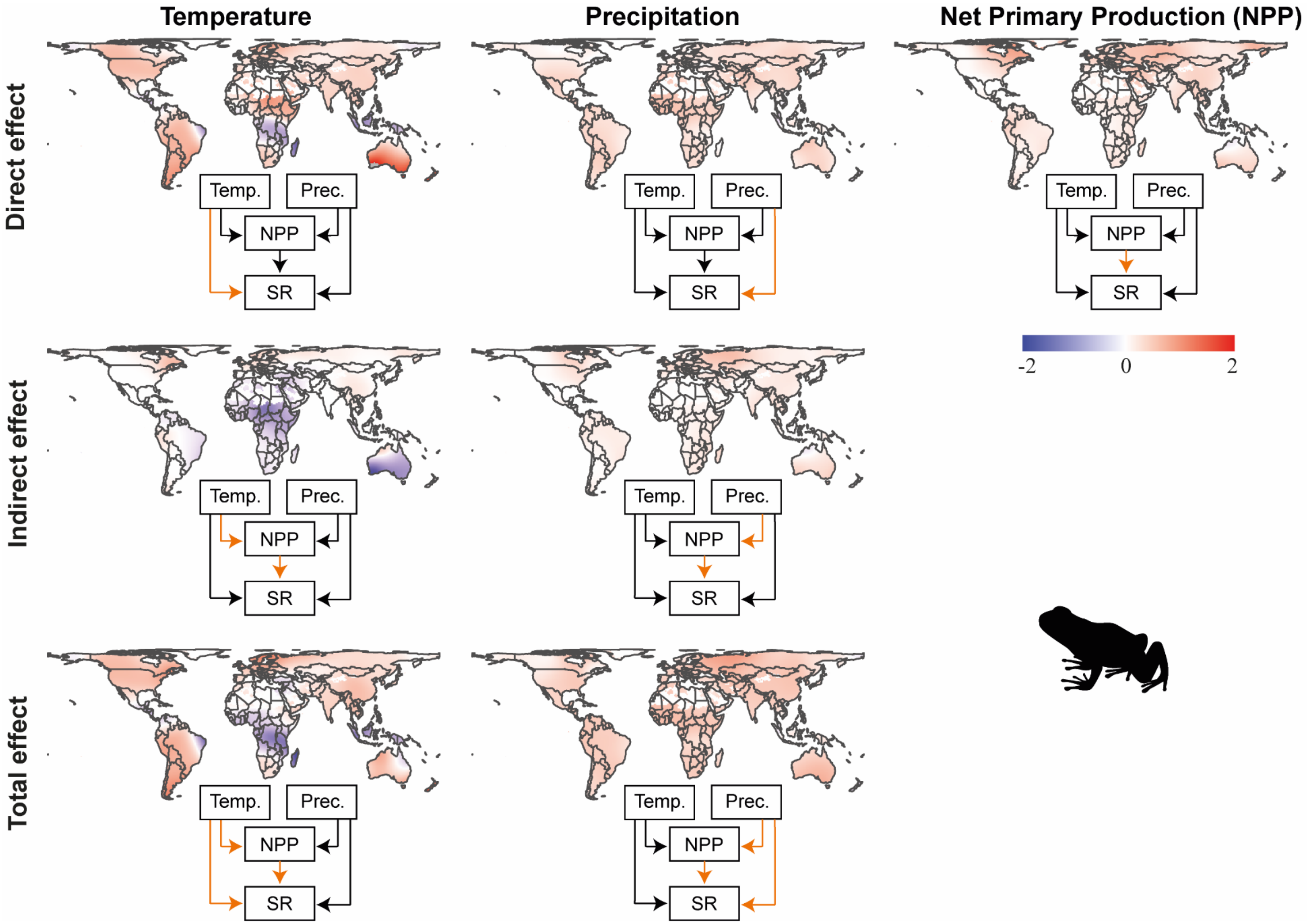


Figure S6 – Direct, indirect and total path coefficients between species richness of amphibians and the three measures of energy – temperature (first panel), precipitation (second panel) and productivity (third panel). Path coefficients are standardized and are mapped using the same color scale, allowing for the direct comparison of their magnitudes. Orange arrows in the model indicate which paths the coefficients refer to. Silhouette image was taken from Freepik.com.

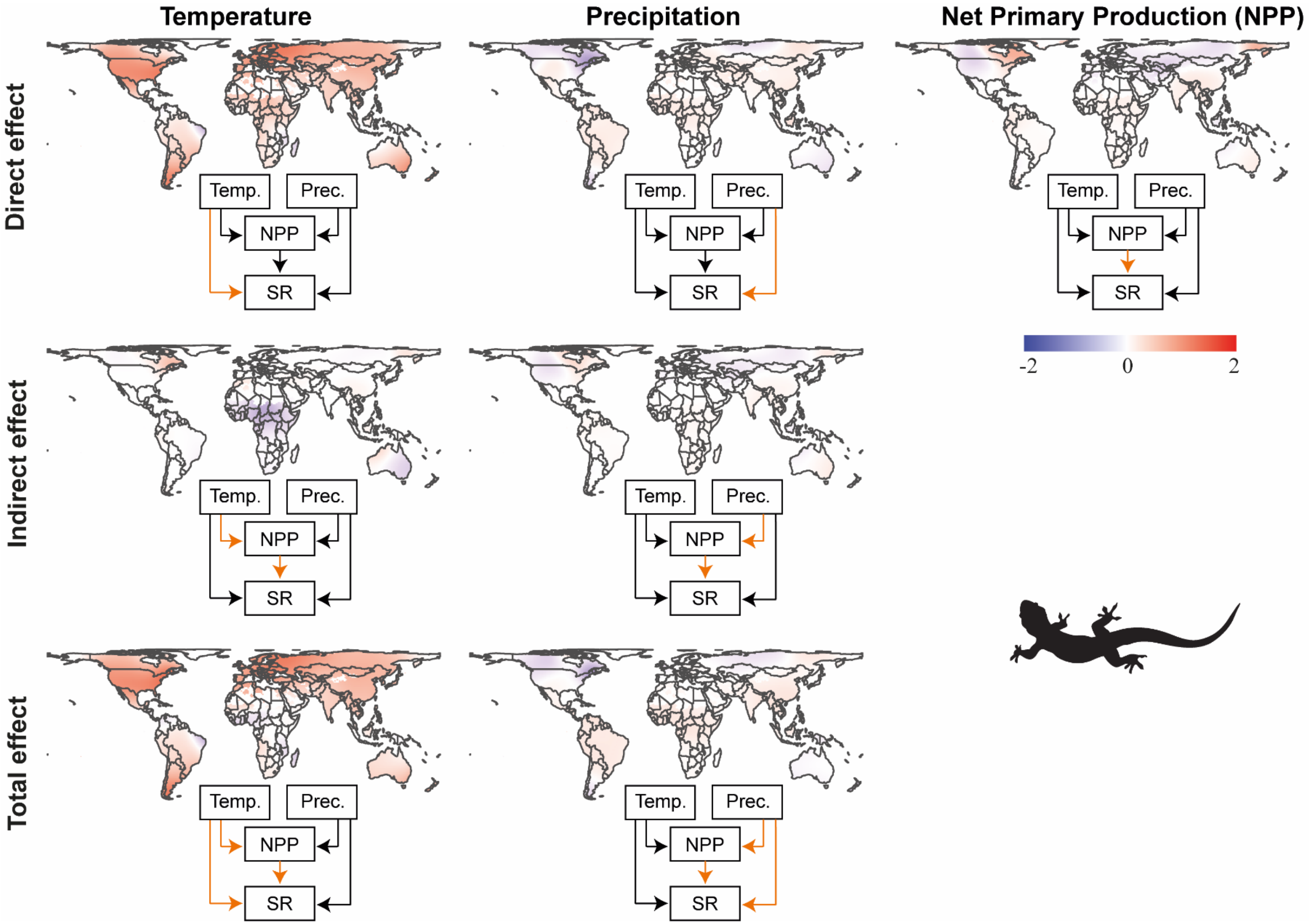


Figure S7 – Direct, indirect and total path coefficients between species richness of reptiles and the three measures of energy – temperature (first panel), precipitation (second panel) and productivity (third panel). Path coefficients are standardized and are mapped using the same color scale, allowing for the direct comparison of their magnitudes. Orange arrows in the model indicate which paths the coefficients refer to. Silhouette image was taken from Freepik.com.

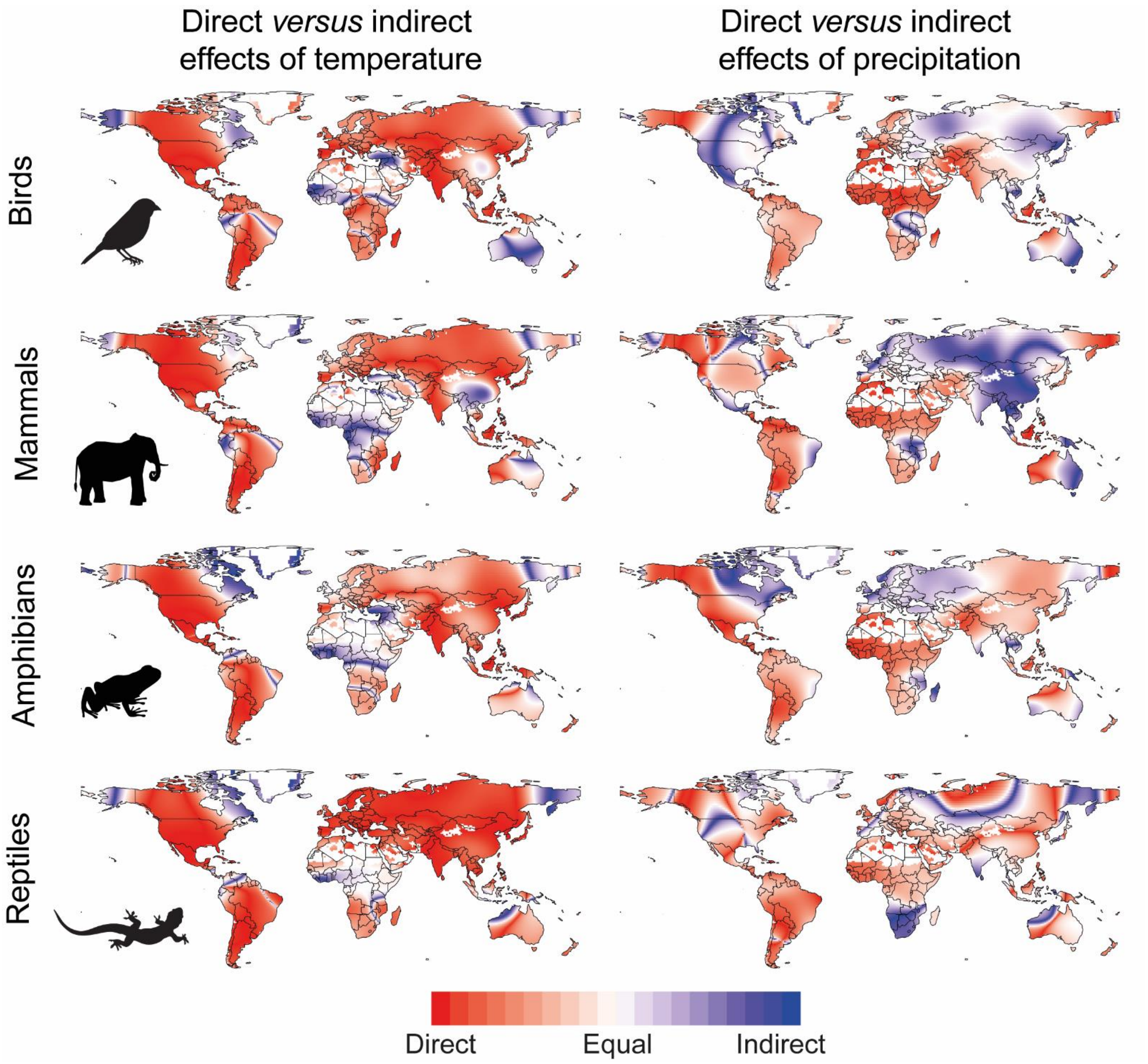


Figure S8 - Relative importance of the direct and indirect effects of temperature and precipitation on the species richness of terrestrial tetrapods. Red indicates that a higher percentage of the total effects is due to the direct effects of the energy measure on species richness, whereas blue indicates that indirect effects predominate and white indicates that direct and indirect effects are equally important. Intensity of the colors indicate the prevalence of direct versus indirect effects. The black silhouette indicates to which organismal group the result belongs. Silhouette images were taken from Freepik.com.

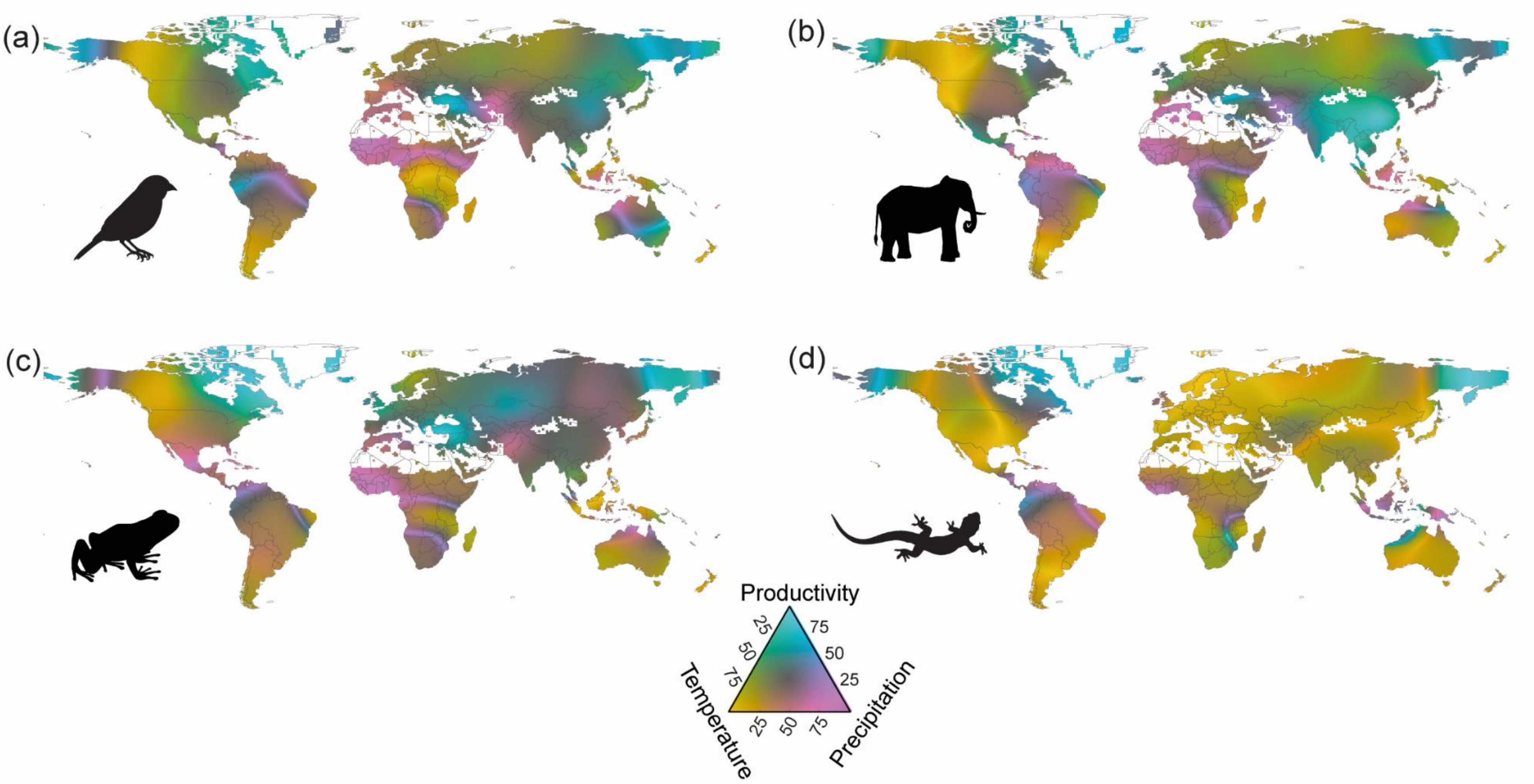


Figure S9 - Relative importance of the direct effects of productivity, temperature and precipitation to the species richness of terrestrial tetrapods. Colors indicate how much, in percentage, a measure of energy is important to explain species richness based on the magnitude of the standardized path coefficients. Shades of green indicate productivity; yellow indicate temperature and pink indicate precipitation as relatively more important. The black silhouette indicates to which organismal group the result belongs. Silhouette images were taken from Freepik.com.

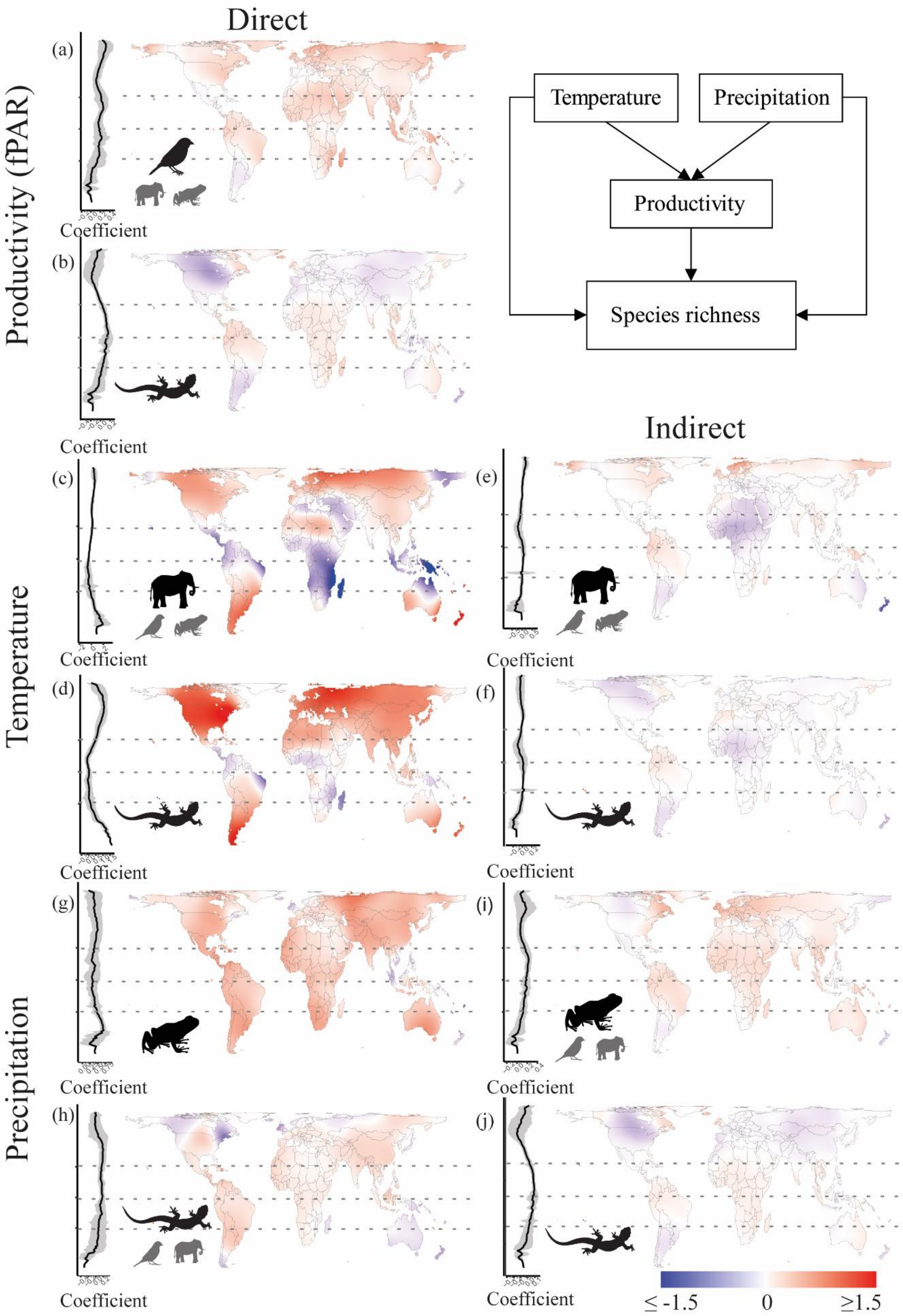

Direct
Indirect
Productivity (fPAR)
Temperature
Precipitation
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)
(j)
Coefficient
Temperature
Precipitation
Productivity
Species richness
≤ -1.5
0
≥1.5

Figure S10 – Direct (a-d, g, h) and indirect (e, f, i, j) coefficient strengths between species richness of terrestrial tetrapods and three measures of energy – productivity (a-b), temperature (c-f) and precipitation (g-j) – according to the geographically weighted path model. Path coefficients are standardized and are mapped using the same color scale, allowing direct comparison of their magnitudes. For each path, we show the two most contrasting results among the four taxonomic groups analyzed. Black silhouette indicates for which organism group the result are mapped, and smaller gray silhouettes indicate the other groups showing similar results. The full set of coefficient maps for all four taxonomic groups is available in the supplementary material (Figs. S4-S7). Next to each map is the path coefficient across latitude, plotted with the mean (black line) and the standard deviation (longitudinal variation, grey area). Dotted lines indicate the Tropic of Cancer, the Equator, and the Tropic of Capricorn, respectively from top to bottom. Silhouette images were taken from Freepik.com.

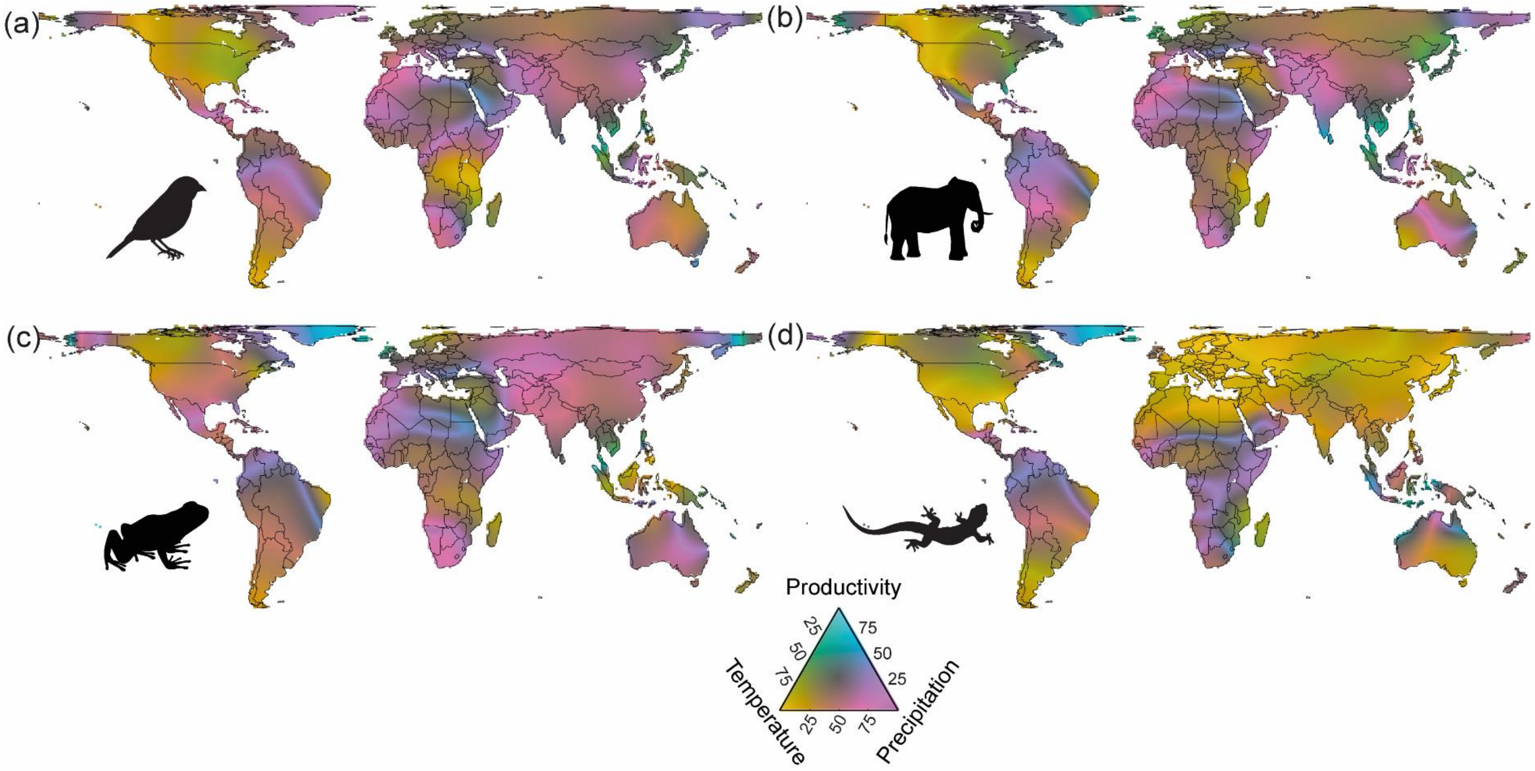


Figure S11 – Relative importance of productivity, temperature and precipitation to the species richness of terrestrial tetrapods when considering both, the direct and indirect effects of temperature and precipitation through productivity. Colors indicate how much, in percentage, a measure of energy is important to explain species richness based on the magnitude of the summed, standardized path coefficients. Shades of green indicate productivity; yellow indicate temperature and pink indicate precipitation as relatively more important. The black silhouette indicates which organismal group the result belongs to. Silhouette images were taken from Freepik.com.

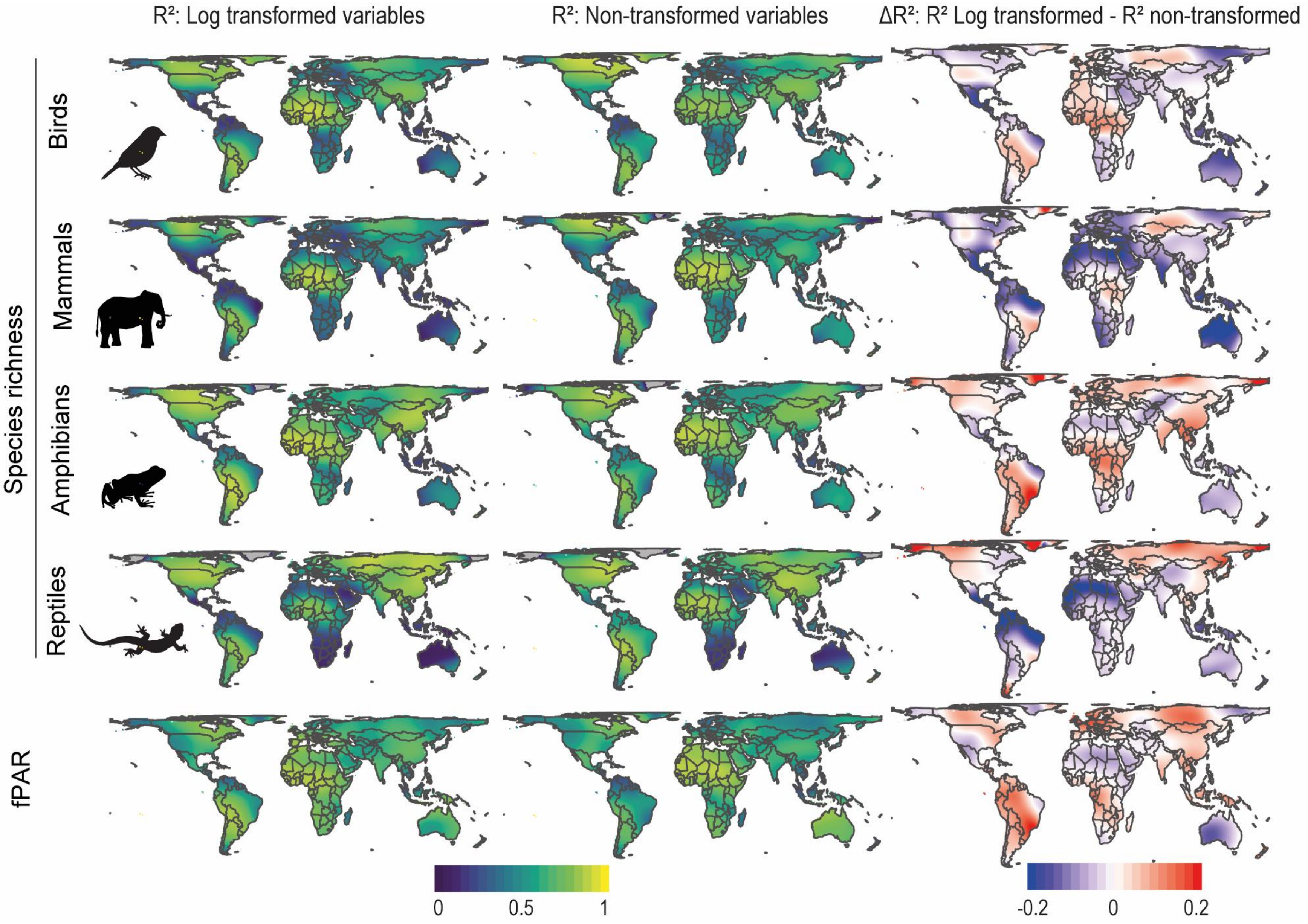

R²: Log transformed variables
R²: Non-transformed variables
ΔR²: R² Log transformed - R² non-transformed
Species richness
Birds
Mammals
Amphibians
Reptiles
fPAR
0
0.5
1
-0.2
0
0.2

Figure S12 – Local coefficient of determination (R^2) of regression models using log-transformed variables (first panel) and untransformed variables (second panel) for each of the response variables indicated in the rows. Maps on the third panel show the difference between the R^2 of the models with log-transformed and untransformed variables. Areas in blue indicate places where the model with untransformed variables has higher R^2, areas in red indicate places where model with log-transformed variables has higher R^2. The black silhouette indicates to which organismal group the result belongs. Silhouette images were taken from Freepik.com.

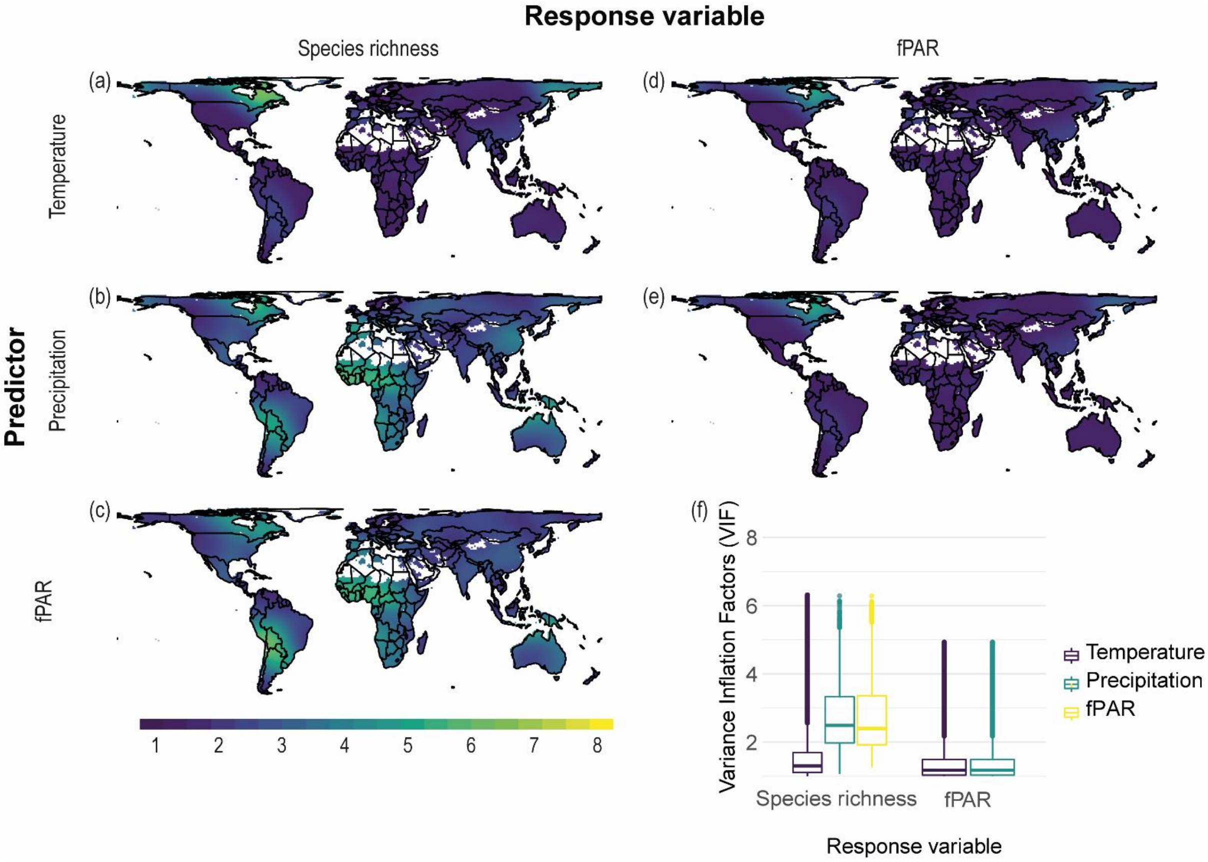


Figure S13 – Variance Inflation Factors (VIF) at each focal cell for the regressions of species richness (first panel; a-c) and Fraction of Photosynthetically Active Radiation (fPAR) (seccond panel; d-e) as a function of the predictors indicated in the rows. Summary of VIF's across space is shown in the boxplot f.

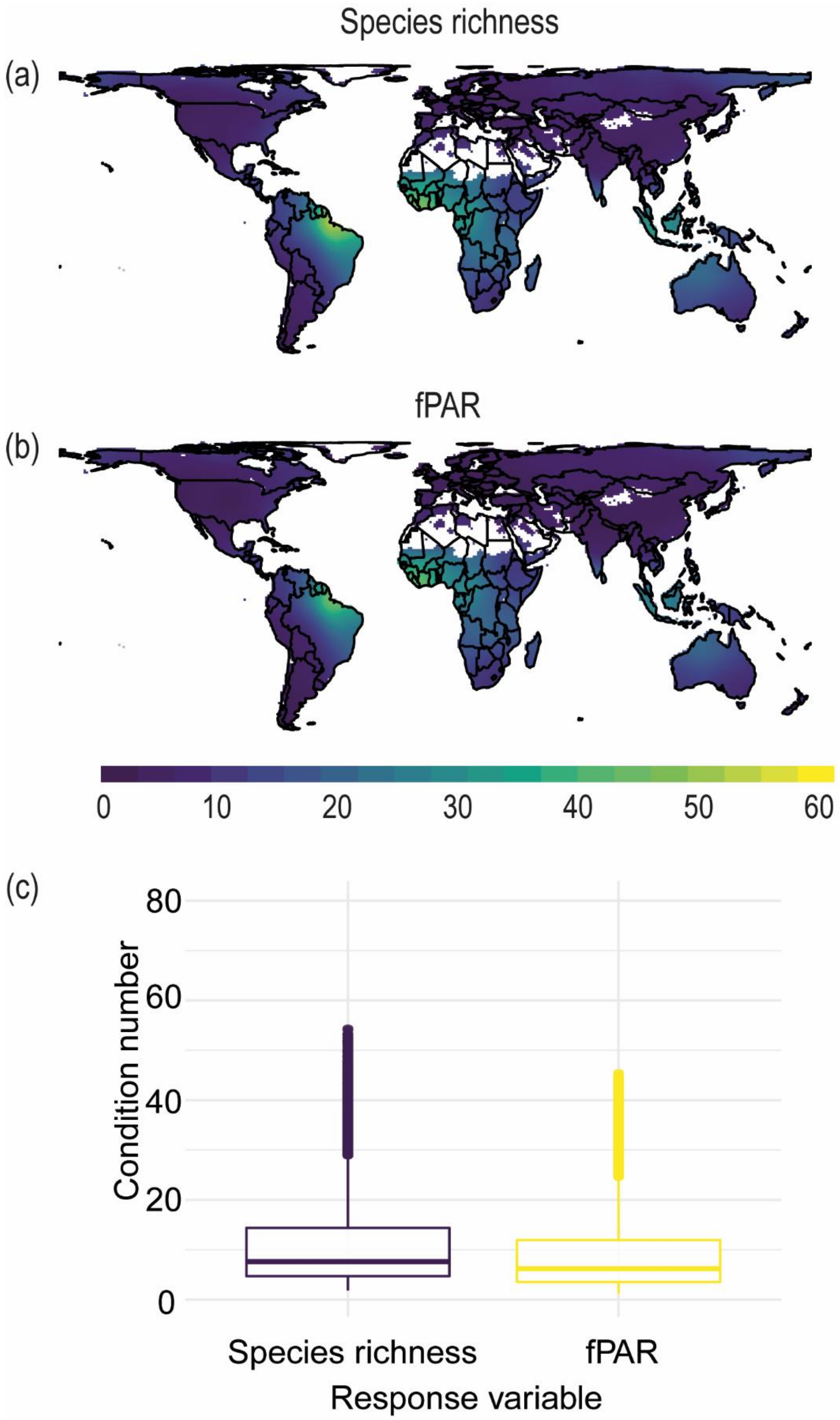


Figure S14 – Condition number at each focal cell for the regressions of species richness (a) and Fraction of Photosynthetically Active Radiation (fPAR) (b) as a function of the environmental predictors. Summary of CN’s across space is shown in the boxplot c.

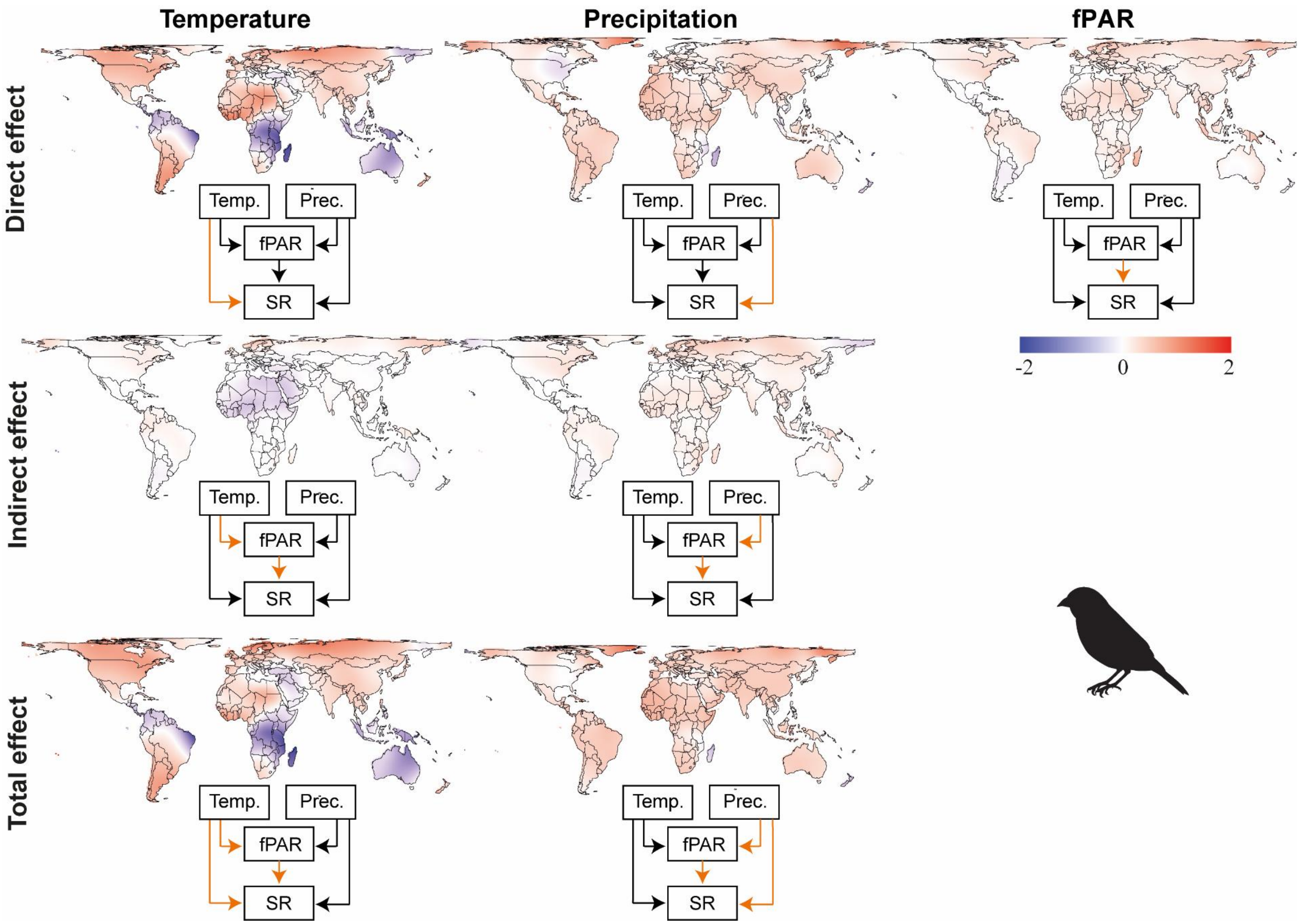


Figure S15 – Direct, indirect and total path coefficients between species richness of birds and the three measures of energy: temperature (first panel), precipitation (second panel) and productivity (third panel). Path coefficients are standardized and are mapped using the same color scale, allowing for the direct comparison of their magnitudes. Orange arrows in the model indicate which paths the coefficients refer to. Silhouette image was taken from Freepik.com.

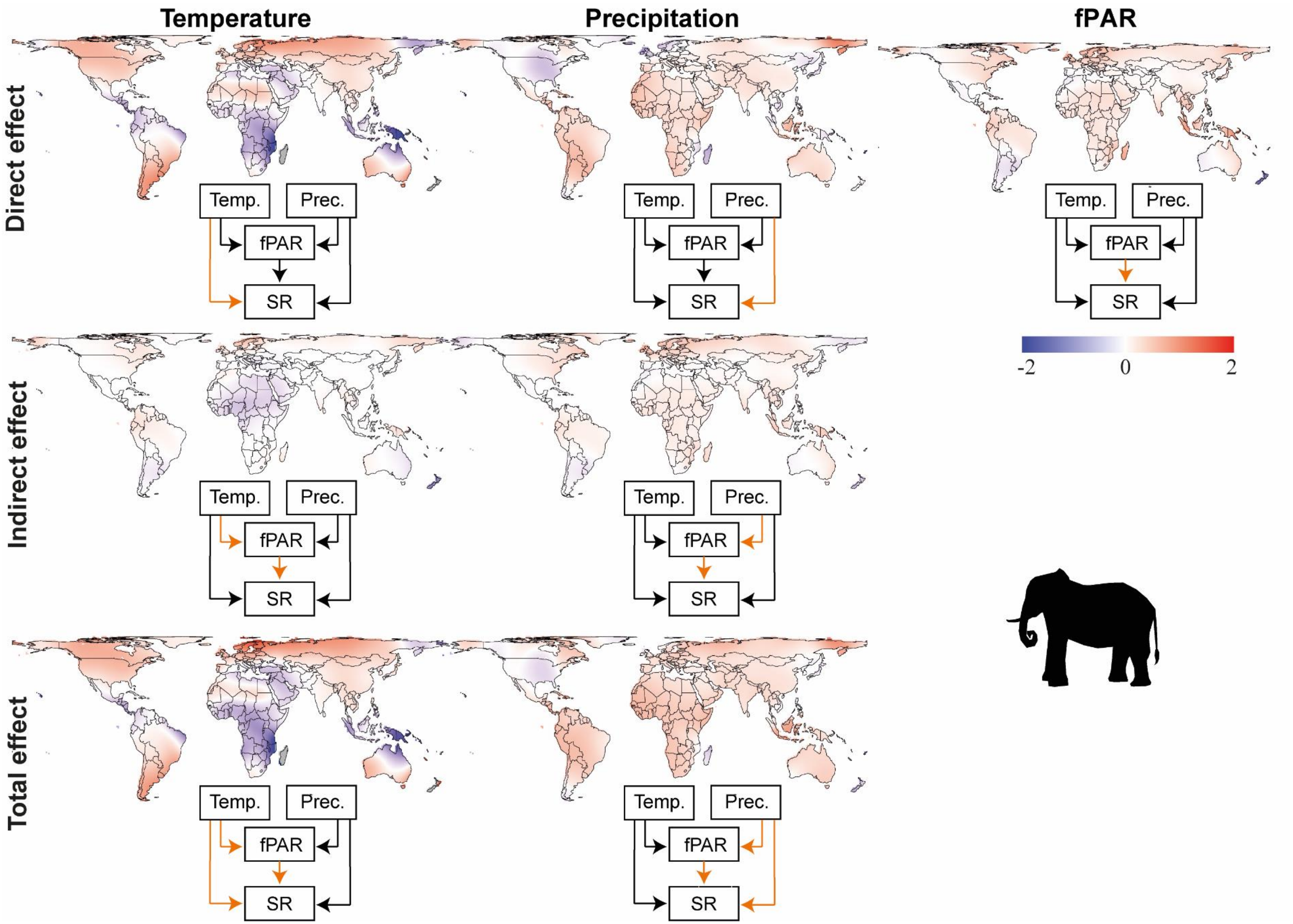


Figure S16 – Direct, indirect and total path coefficients between species richness of mammals and the three measures of energy – temperature (first panel), precipitation (second panel) and productivity (third panel). Path coefficients are standardized and are mapped using the same color scale, allowing for the direct comparison of their magnitudes. Orange arrows in the model indicate which paths the coefficients refer to. Silhouette image was taken from Freepik.com.

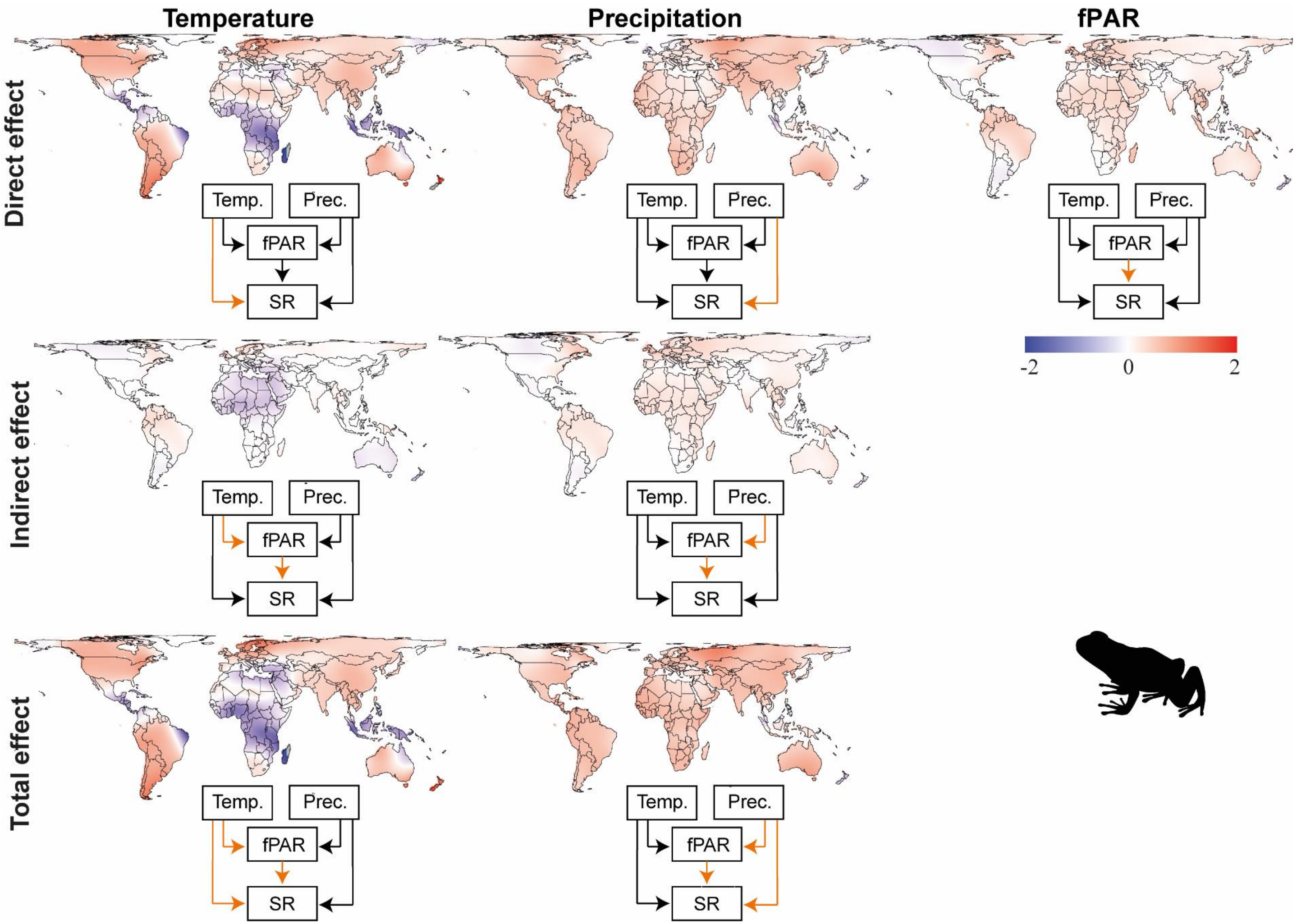


Figure S17 – Direct, indirect and total path coefficients between species richness of amphibians and the three measures of energy – temperature (first panel), precipitation (second panel) and productivity (third panel). Path coefficients are standardized and are mapped using the same color scale, allowing for the direct comparison of their magnitudes. Orange arrows in the model indicate which paths the coefficients refer to. Silhouette image was taken from Freepik.com.

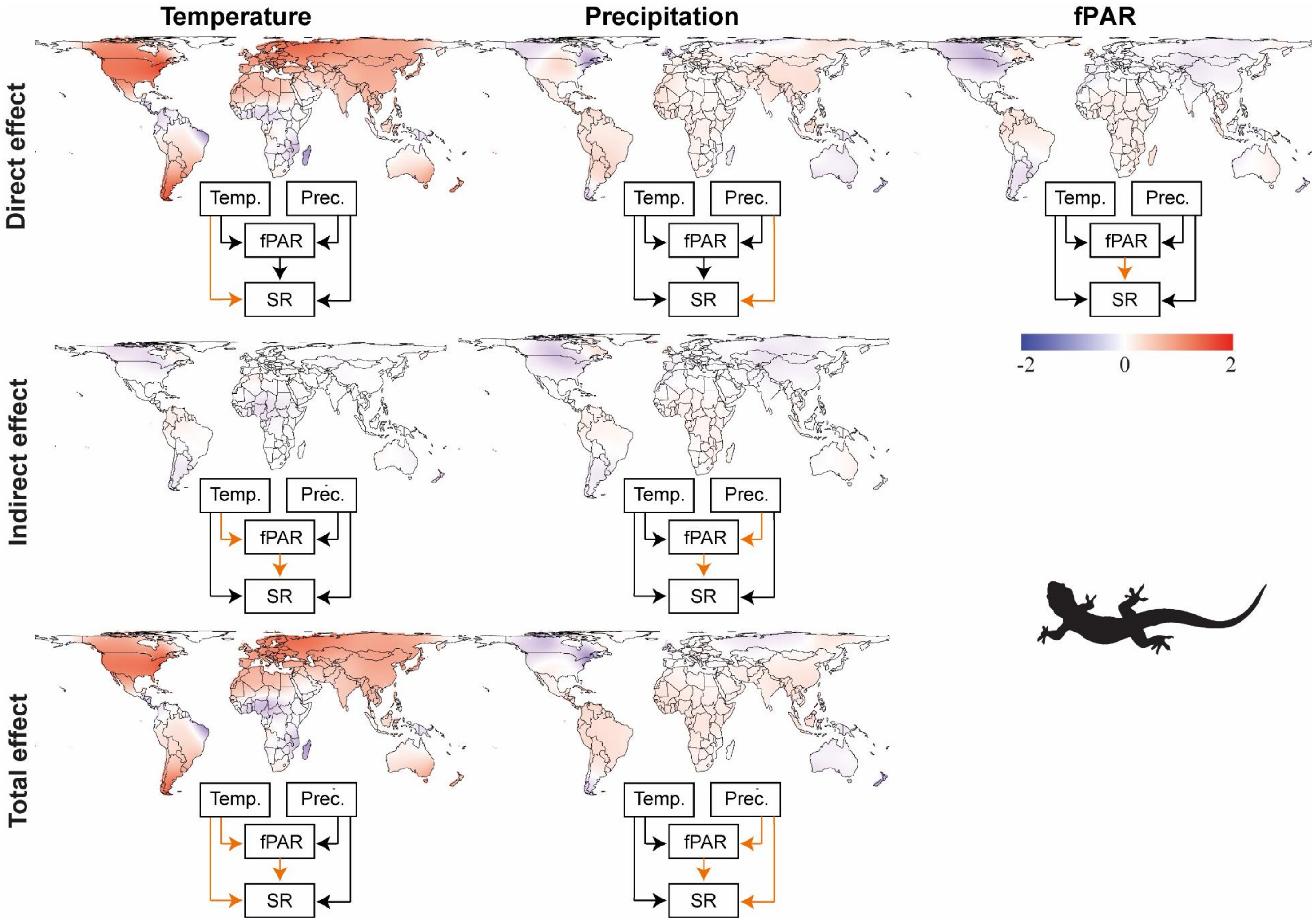


Figure S18 – Direct, indirect and total path coefficients between species richness of reptiles and the three measures of energy – temperature (first panel), precipitation (second panel) and productivity (third panel). Path coefficients are standardized and are mapped using the same color scale, allowing for the direct comparison of their magnitudes. Orange arrows in the model indicate which paths the coefficients refer to. Silhouette image was taken from Freepik.com.

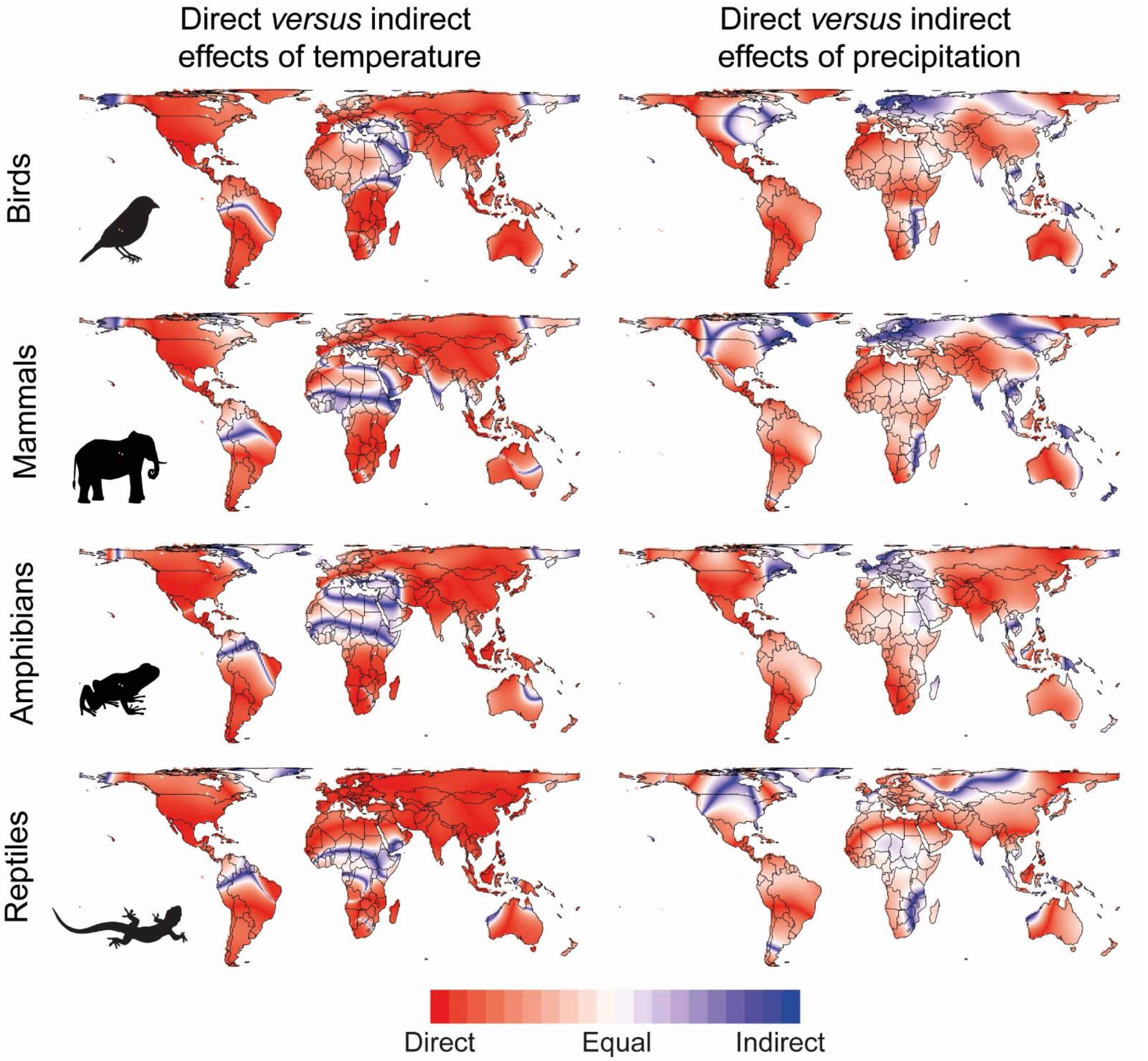


Figure S19 - Relative importance of the direct and indirect effects of temperature and precipitation on the species richness of terrestrial tetrapods. Red indicates that a higher percentage of the total effects is due to the direct effects of the energy measure on species richness, whereas blue indicates that indirect effects predominate and white indicates that direct and indirect effects are equally important. Intensity of the colors indicate the prevalence of direct versus indirect effects. The black silhouette indicates to which organismal group the result belongs. Silhouette images were taken from Freepik.com.

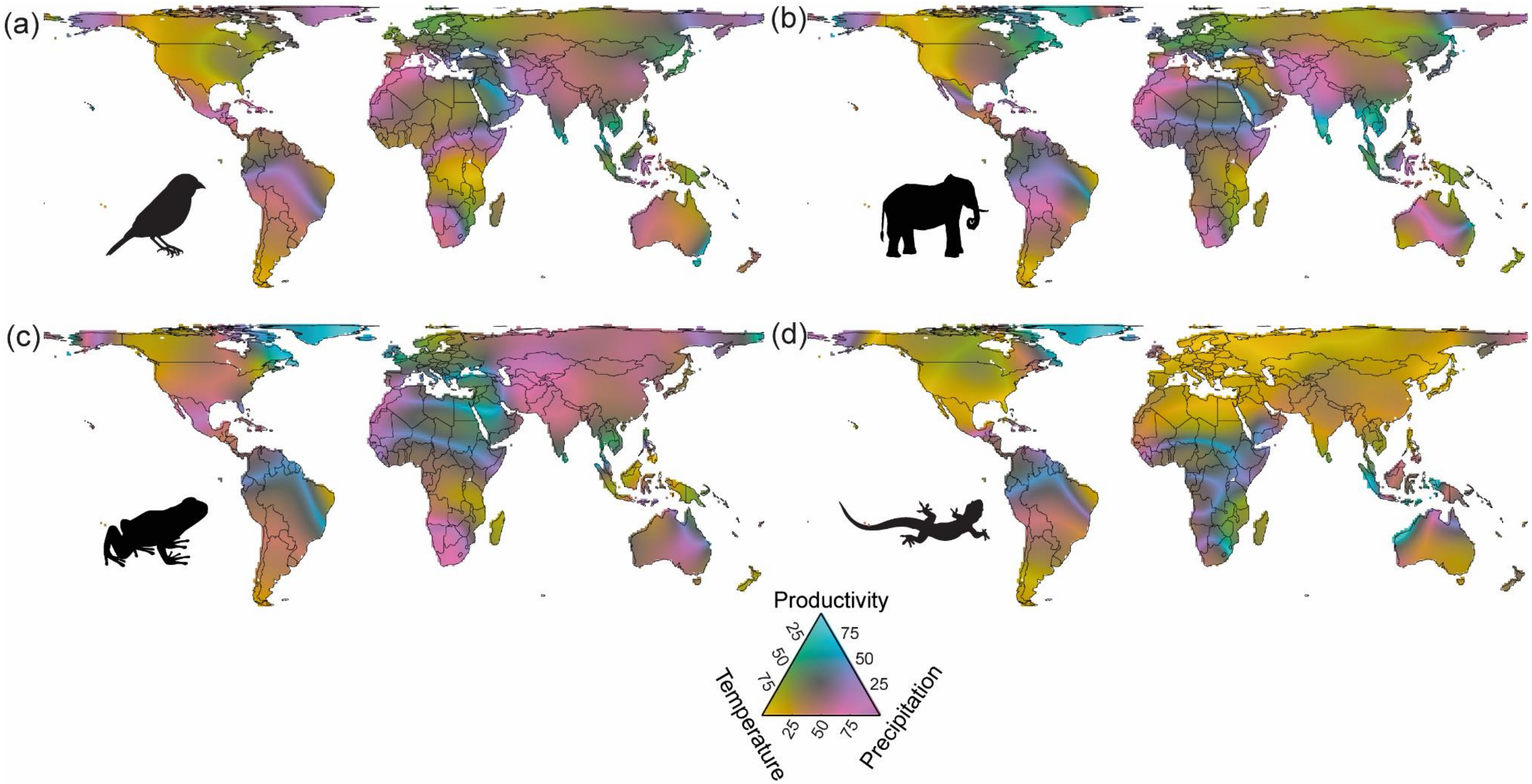


Figure S20 - Relative importance of the direct effects of productivity, temperature and precipitation to the species richness of terrestrial tetrapods. Colors indicate how much, in percentage, a measure of energy is important to explain species richness based on the magnitude of the standardized path coefficients. Shades of green indicate productivity; yellow indicate temperature and pink indicate precipitation as relatively more important. The black silhouette indicates to which organismal group the result belongs. Silhouette images were taken from Freepik.com.

Capítulo 3

Supporting information from

"Determinants of richness and endemism of mammals on islands worldwide"

Elisa Barreto, Catherine H. Graham, Loïc Pellissier & Thiago F. Rangel

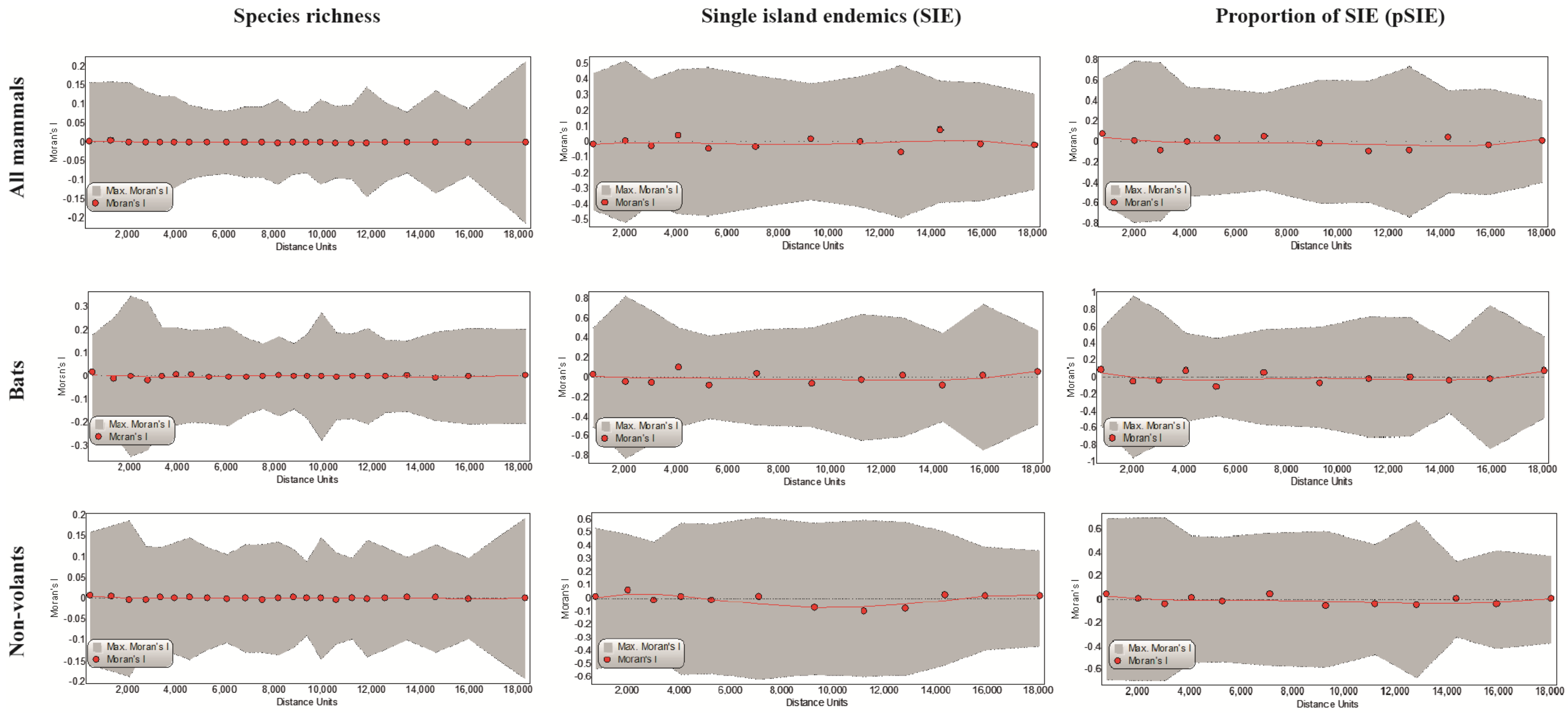


Figure S1 – Moran's I (red dots) and maximum Moran's I (grey area) among residuals of models fitted for species richness (first panel), number of single island endemics (second panel) and proportion of single island endemics (third panel) at each distance class.

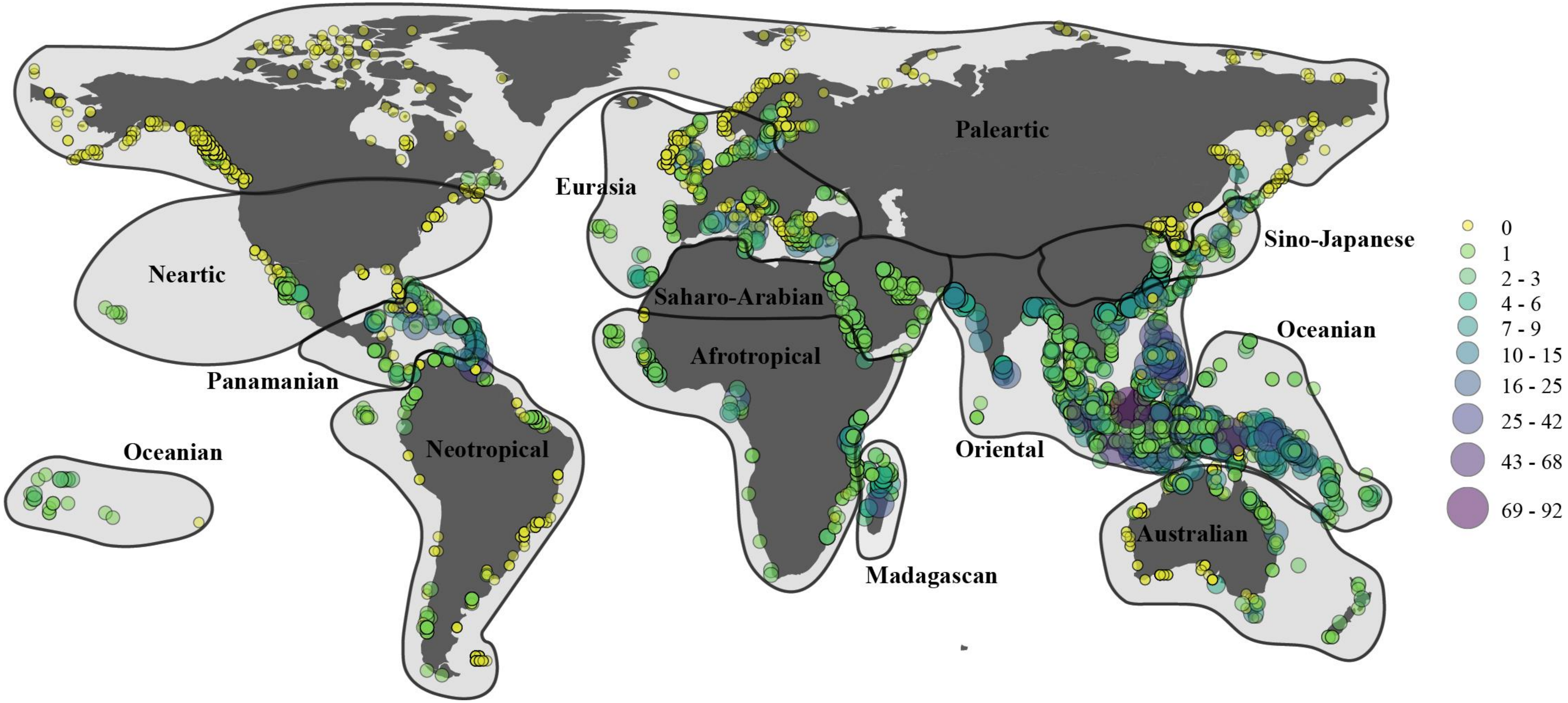


Figure S2 – Number of bat species on the 5,594 islands included in this study, with an indication of the biogeographic region to which each island belongs.

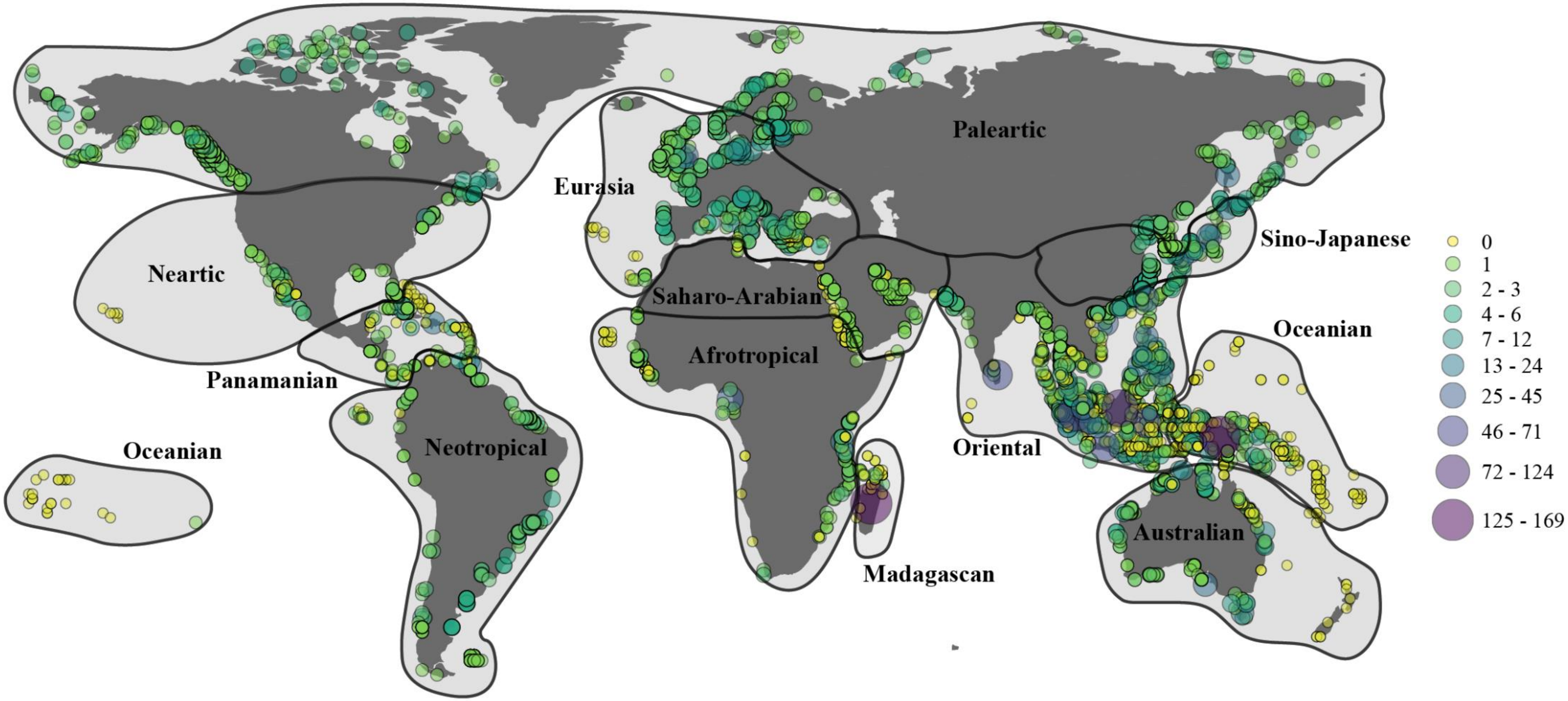


Figure S3 – Number of non-volant mammal species on the 5,594 islands included in this study, with an indication of the biogeographic region to which each island belongs.

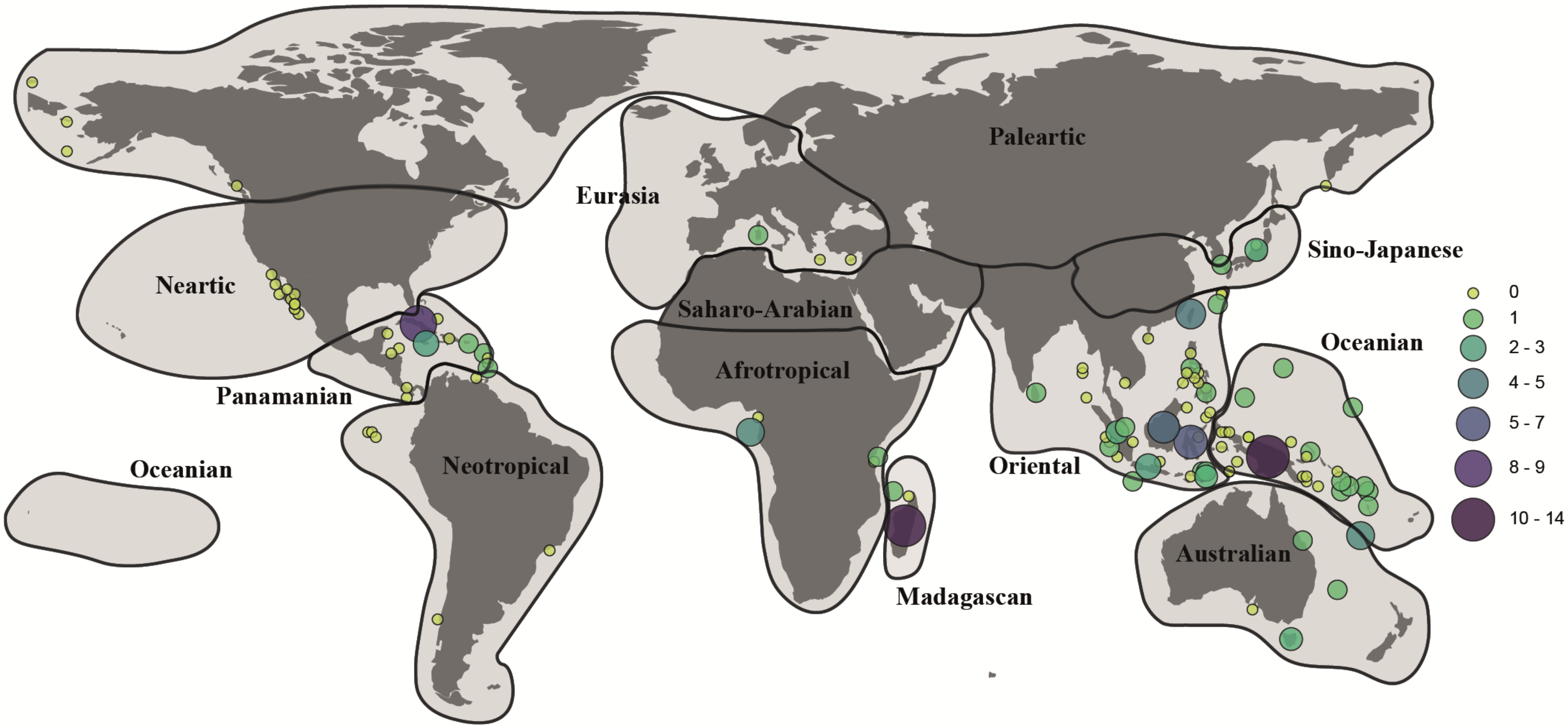


Figure S4 – Number of single island endemic (SIE) bats on the 124 islands included in this study, with an indication of the biogeographic region to which each island belongs.

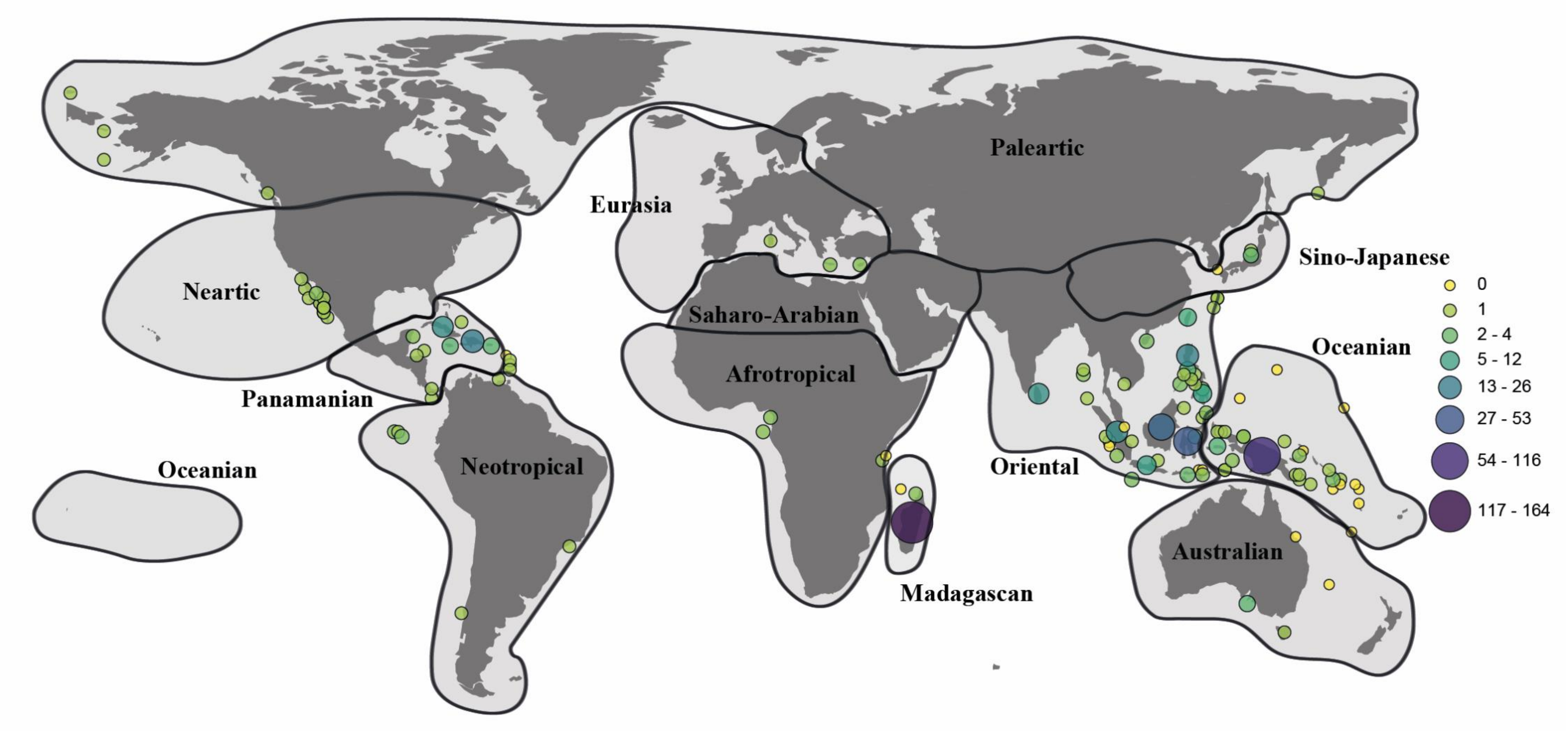


Figure S5 – Number of single island endemic (SIE) non-volant mammals on the 124 islands included in this study, with an indication of the biogeographic region to which each island belongs.

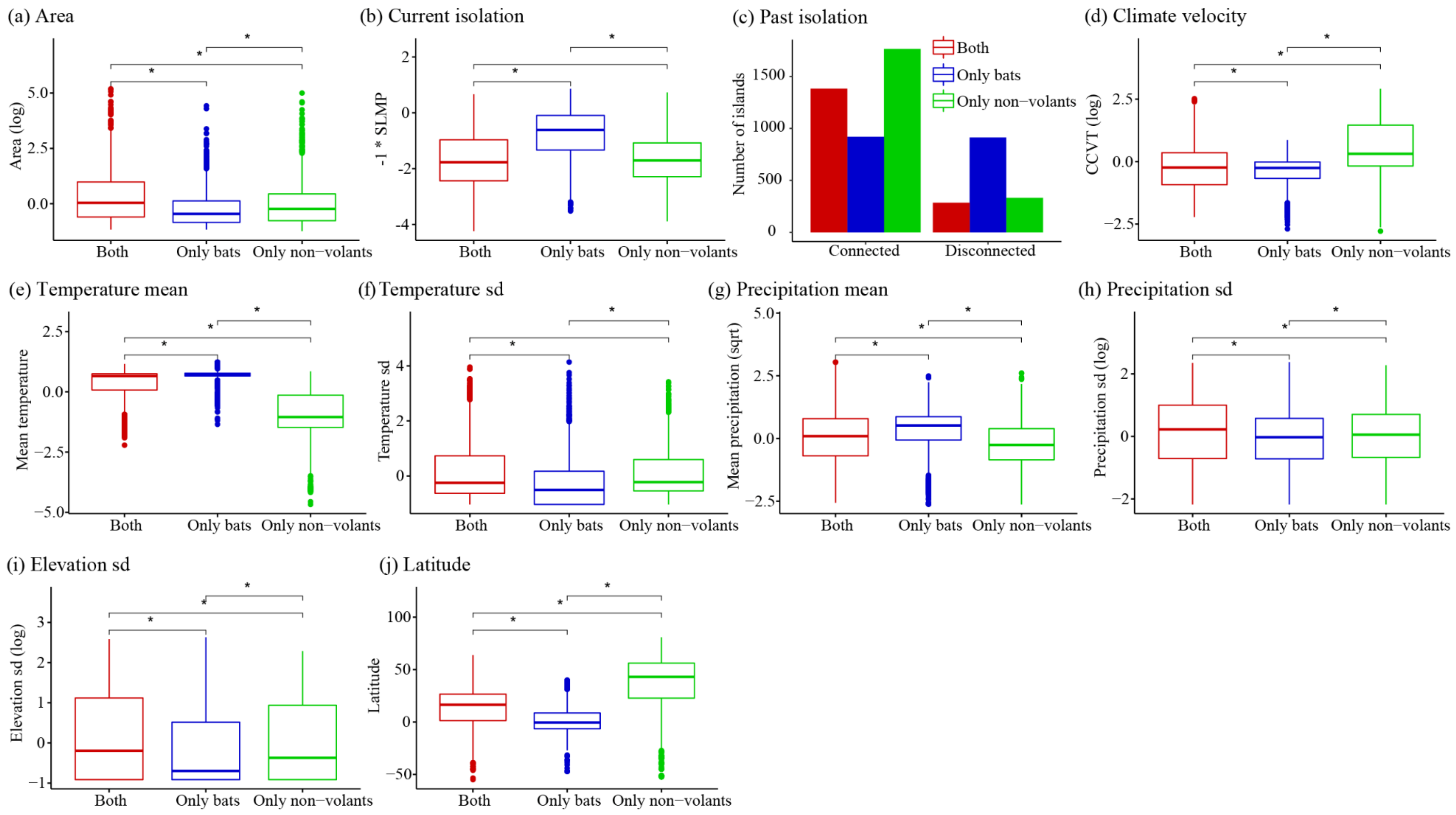


Figure S6 – Comparison among islands that harbor only bats (blue), only non-volant mammals (green), or both (red), regarding their physical and environmental characteristics and their latitude using ANOVA tests. Asterisks represent $p < 0.05$ between pairwise comparisons. All variables are standardized to mean = 0 and standard deviation = 1.

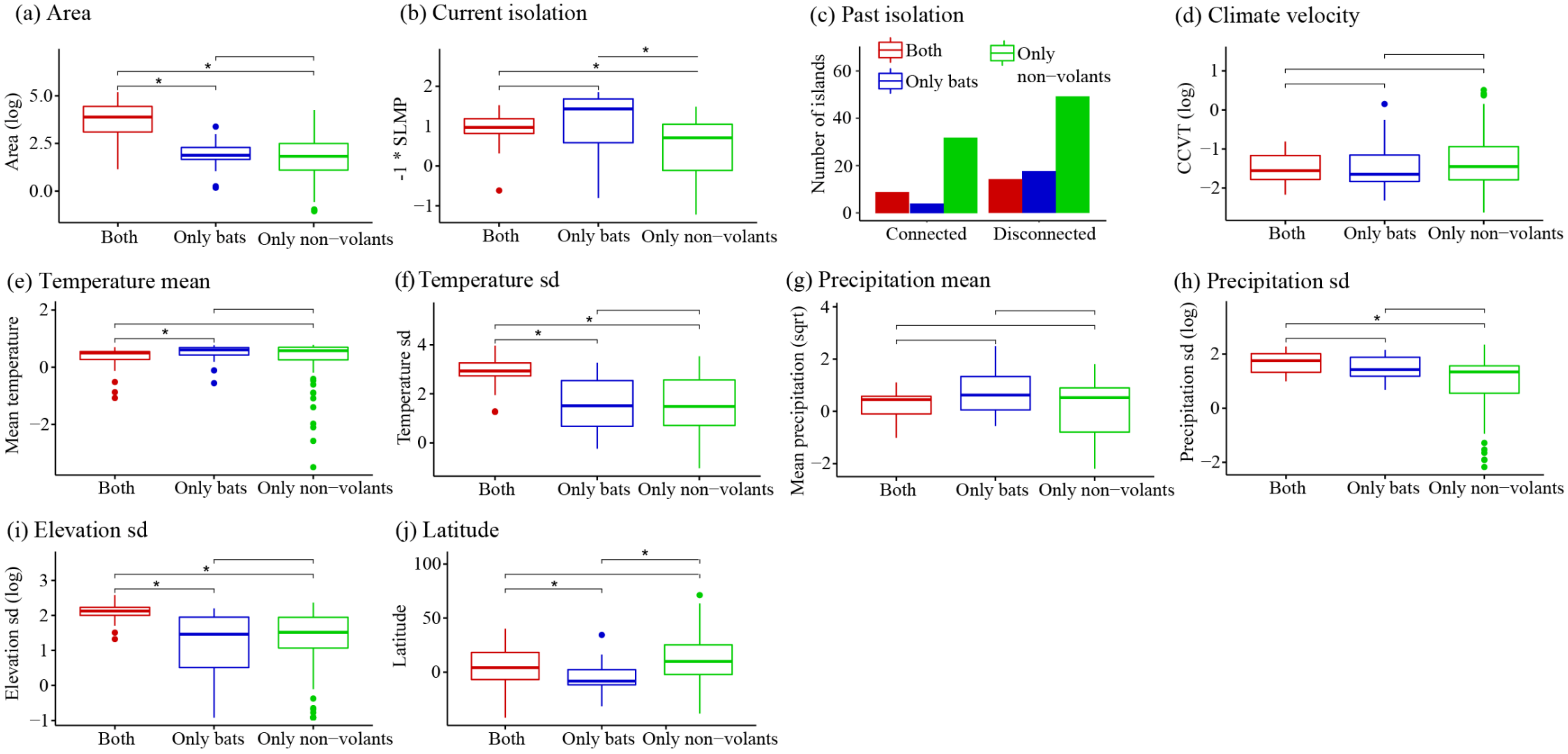


Figure S7 – Comparison among islands that harbor only endemic species of a single island (SIE) of bats (blue), only non-volant mammals (green), or both (red), regarding their physical and environmental characteristics and their latitude using ANOVA tests. Asterisks represent $p < 0.05$ between pairwise comparisons. All variables are standardized to mean = 0 and standard deviation = 1.

Table S1 - Variance inflation factor (VIF) of each predictor of the generalized linear models and mixed models.

Predictor	**All mammals**			**Bats**			**Non-volants**		
	Species richness	**SIE**	**pSIE**	**Species richness**	**SIE**	**pSIE**	**Species richness**	**SIE**	**pSIE**
Area	2.24	1.44	1.44	2.12	4.00	3.09	2.06	3.31	1.18
Current isolation	1.01	1.23	1.23	1.26	1.47	1.68	2.02	1.60	1.26
Past isolation	1.01	1.29	1.29	1.00	1.58	1.70	1.00	1.44	1.11
Climate velocity	1.07	1.25	1.25	1.06	1.96	1.92	1.10	2.01	1.18
Temperature mean	1.01	1.07	1.07	1.01	1.40	2.06	1.01	1.37	1.15
Temperature sd	1.15	2.62	2.62	1.11	5.09	4.46	1.21	5.03	3.15
Precipitation mean	1.03	1.40	1.40	1.02	3.30	2.46	1.02	3.89	1.49
Precipitation sd	1.11	1.40	1.40	1.07	7.11[1]	3.81	1.09	7.57[1]	1.36
Elevation sd	1.05	2.36	2.36	1.07	4.11	3.11	1.08	5.10	3.32
Area * Current isolation	2.19			1.90			1.10		

[1] Results remained the same without this predictor.

Table S2 – Spatial autocorrelation among residuals of the generalized linear mixed model fitted for species richness of all mammals measured with Moran’s I per distance class.

Distance class	**Count**	**Distance (km)**	**Moran's I**	**Standard Error**	**P-value**	**Maximum I (Imax)**	**I/Imax**
1	$>1\times10^6$	486.95	0.00	0.00	0.04	0.16	0.01
2	$>1\times10^6$	1357.56	0.01	0.00	<.001	0.16	0.03
3	$>1\times10^6$	2096.44	<.001	0.00	0.59	0.16	0.00
4	$>1\times10^6$	2764.52	<.001	0.00	0.43	0.13	0.01
5	$>1\times10^6$	3369.93	<.001	<.001	0.67	0.12	-0.01
6	$>1\times10^6$	3957.86	0.00	<.001	0.35	0.12	-0.01
7	$>1\times10^6$	4576.45	<.001	0.00	0.81	0.10	<.001
8	$>1\times10^6$	5304.49	<.001	0.00	0.61	0.09	-0.01
9	$>1\times10^6$	6107.25	<.001	0.00	0.93	0.08	0.00
10	$>1\times10^6$	6837.99	<.001	0.00	0.52	0.09	-0.01
11	$>1\times10^6$	7521.91	<.001	0.00	0.99	0.09	0.00
12	$>1\times10^6$	8189.16	0.00	0.00	0.19	0.11	-0.01
13	$>1\times10^6$	8775.82	<.001	0.00	0.43	0.09	0.01
14	$>1\times10^6$	9325.67	<.001	0.00	0.47	0.08	-0.01
15	$>1\times10^6$	9914.68	<.001	0.00	0.84	0.11	0.00
16	$>1\times10^6$	10553.96	0.00	0.00	0.17	0.10	-0.02
17	$>1\times10^6$	11179.99	0.00	<.001	0.21	0.10	-0.02
18	$>1\times10^6$	11805.08	0.00	0.00	0.07	0.14	-0.01
19	$>1\times10^6$	12542.59	<.001	<.001	0.95	0.11	0.00
20	$>1\times10^6$	13462.98	<.001	<.001	0.31	0.08	0.01
21	$>1\times10^6$	14622.78	<.001	<.001	0.74	0.14	0.00
22	$>1\times10^6$	15953.11	<.001	<.001	0.57	0.09	-0.01
23	$>1\times10^6$	18299.25	<.001	<.001	0.37	0.21	0.00

Table S3 – Spatial autocorrelation among residuals of the generalized linear mixed model fitted for species richness of bats measured with Moran’s I per distance class.

Distance class	Count	Distance (km)	Moran's I	Standard Error	P-value	Maximum I (Imax)	I/Imax
1	>1×10^6	486.95	0.02	0.00	0.00	0.18	0.10
2	>1×10^6	1357.56	-0.01	0.00	0.00	0.25	-0.05
3	>1×10^6	2096.44	<.001	0.00	0.75	0.35	0.00
4	>1×10^6	2764.52	-0.02	0.00	0.00	0.32	-0.06
5	>1×10^6	3369.93	<.001	0.00	0.47	0.21	0.00
6	>1×10^6	3957.86	0.01	0.00	0.00	0.21	0.04
7	>1×10^6	4576.45	0.01	0.00	<.001	0.20	0.03
8	>1×10^6	5304.49	-0.01	0.00	<.001	0.21	-0.02
9	>1×10^6	6107.25	0.00	0.00	0.10	0.22	-0.01
10	>1×10^6	6837.99	0.00	0.00	0.00	0.17	-0.02
11	>1×10^6	7521.91	0.00	0.00	0.12	0.14	0.01
12	>1×10^6	8189.16	0.01	0.00	<.001	0.17	0.03
13	>1×10^6	8775.82	<.001	0.00	0.80	0.14	<.001
14	>1×10^6	9325.67	0.00	0.00	0.19	0.19	0.01
15	>1×10^6	9914.68	<.001	0.00	0.84	0.28	0.00
16	>1×10^6	10553.96	0.00	0.00	<.001	0.19	-0.02
17	>1×10^6	11179.99	<.001	0.00	0.75	0.19	0.00
18	>1×10^6	11805.08	<.001	0.00	0.31	0.21	0.00
19	>1×10^6	12542.59	0.00	0.00	0.15	0.16	0.01
20	>1×10^6	13462.98	0.00	0.00	0.01	0.15	0.02
21	>1×10^6	14622.78	-0.01	0.00	0.00	0.20	-0.04
22	>1×10^6	15953.11	0.00	<.001	0.22	0.21	-0.01
23	>1×10^6	18299.25	0.00	<.001	<.001	0.20	0.02

Table S4 – Spatial autocorrelation among residuals of the generalized linear mixed model fitted for species richness of non-volant mammals measured with Moran's I per distance class.

Distance class	Count	Distance (km)	Moran's I	Standard Error	P-value	Maximum I (Imax)	I/Imax
1	$>1\times10^6$	486.95	0.01	<.001	<.001	0.16	0.04
2	$>1\times10^6$	1357.56	0.00	<.001	<.001	0.18	0.02
3	$>1\times10^6$	2096.44	0.00	<.001	<.001	0.19	-0.02
4	$>1\times10^6$	2764.52	0.00	<.001	<.001	0.13	-0.03
5	$>1\times10^6$	3369.93	0.00	<.001	0.00	0.12	0.02
6	$>1\times10^6$	3957.86	<.001	<.001	0.84	0.13	<.001
7	$>1\times10^6$	4576.45	0.00	<.001	0.01	0.15	0.02
8	$>1\times10^6$	5304.49	<.001	<.001	0.70	0.12	0.00
9	$>1\times10^6$	6107.25	0.00	<.001	0.05	0.11	-0.02
10	$>1\times10^6$	6837.99	<.001	<.001	0.63	0.13	-0.01
11	$>1\times10^6$	7521.91	0.00	<.001	<.001	0.13	-0.03
12	$>1\times10^6$	8189.16	<.001	<.001	0.68	0.14	0.00
13	$>1\times10^6$	8775.82	0.00	<.001	<.001	0.12	0.03
14	$>1\times10^6$	9325.67	<.001	<.001	0.45	0.09	0.01
15	$>1\times10^6$	9914.68	<.001	<.001	0.88	0.15	0.00
16	$>1\times10^6$	10553.96	0.00	<.001	<.001	0.11	-0.03
17	$>1\times10^6$	11179.99	<.001	<.001	0.47	0.10	-0.01
18	$>1\times10^6$	11805.08	0.00	<.001	0.04	0.14	-0.02
19	$>1\times10^6$	12542.59	<.001	<.001	0.64	0.12	-0.01
20	$>1\times10^6$	13462.98	0.00	<.001	0.09	0.10	0.01
21	$>1\times10^6$	14622.78	0.00	<.001	0.14	0.13	0.01
22	$>1\times10^6$	15953.11	0.00	<.001	0.02	0.10	-0.02
23	$>1\times10^6$	18299.25	0.00	<.001	0.30	0.19	-0.01

Table S5 – Spatial autocorrelation among residuals of the generalized linear model fitted for number of single island endemics (SIE) of all mammals measured with Moran's I per distance class.

Distance class	Count	Distance (km)	Moran's I	Standard Error	P-value	Maximum I (Imax)	I/Imax
1	1250	765.11	-0.02	0.04	0.74	0.44	-0.05
2	1248	2026.84	0.01	0.03	0.63	0.52	0.01
3	1248	3047.19	-0.03	0.03	0.57	0.40	-0.07
4	1250	4076.19	0.04	0.03	0.16	0.46	0.09
5	1248	5274.06	-0.05	0.04	0.29	0.48	-0.09
6	1248	7139.62	-0.04	0.03	0.43	0.42	-0.08
7	1248	9297.07	0.02	0.03	0.42	0.37	0.05
8	1250	11223.10	0.00	0.03	0.76	0.42	0.00
9	1248	12835.51	-0.07	0.03	0.08	0.49	-0.14
10	1248	14359.23	0.07	0.03	0.02	0.39	0.19
11	1248	15928.30	-0.02	0.03	0.72	0.38	-0.05
12	1250	18072.24	-0.03	0.03	0.59	0.31	-0.08

Table S6 – Spatial autocorrelation among residuals of the generalized linear model fitted for number of single island endemics (SIE) of bats measured with Moran's I per distance class.

Distance class	Count	Distance (km)	Moran's I	Standard Error	P-value	Maximum I (Imax)	I/Imax
1	1250	765.11	0.03	0.04	0.29	0.50	0.06
2	1248	2026.84	-0.04	0.03	0.29	0.83	-0.05
3	1248	3047.19	-0.06	0.03	0.15	0.68	-0.08
4	1250	4076.19	0.10	0.03	0.00	0.50	0.21
5	1248	5274.06	-0.08	0.04	0.04	0.42	-0.19
6	1248	7139.62	0.04	0.03	0.16	0.48	0.08
7	1248	9297.07	-0.07	0.03	0.08	0.50	-0.14
8	1250	11223.10	-0.03	0.03	0.44	0.64	-0.05
9	1248	12835.51	0.02	0.03	0.40	0.61	0.03
10	1248	14359.23	-0.08	0.03	0.04	0.45	-0.18
11	1248	15928.30	0.02	0.03	0.32	0.75	0.03
12	1250	18072.24	0.05	0.03	0.04	0.47	0.11

Table S7 – Spatial autocorrelation among residuals of the generalized linear model fitted for number of single island endemics (SIE) of non-volant mammals measured with Moran’s I per distance class.

Distance class	Count	Distance (km)	Moran's I	Standard Error	P-value	Maximum I (Imax)	I/Imax
1	1250	765.11	0.01	0.04	0.58	0.54	0.02
2	1248	2026.84	0.06	0.03	0.03	0.49	0.13
3	1248	3047.19	-0.01	0.03	0.89	0.43	-0.03
4	1250	4076.19	0.01	0.04	0.52	0.58	0.02
5	1248	5274.06	-0.02	0.04	0.82	0.57	-0.03
6	1248	7139.62	0.02	0.03	0.48	0.62	0.03
7	1248	9297.07	-0.07	0.03	0.09	0.58	-0.12
8	1250	11223.10	-0.10	0.03	0.00	0.60	-0.17
9	1248	12835.51	-0.08	0.03	0.04	0.59	-0.13
10	1248	14359.23	0.03	0.03	0.26	0.51	0.06
11	1248	15928.30	0.02	0.03	0.30	0.39	0.06
12	1250	18072.24	0.02	0.03	0.37	0.36	0.05

Table S8 – Spatial autocorrelation among residuals of the generalized linear mixed model fitted for proportion of single island endemics (pSIE) of all mammals measured with Moran’s I per distance class.

Distance class	Count	Distance (km)	Moran's I	Standard Error	P-value	Maximum I (Imax)	I/Imax
1	1250	765.11	0.08	0.04	0.01	0.63	0.13
2	1248	2026.84	0.01	0.03	0.59	0.79	0.01
3	1248	3047.19	-0.09	0.03	0.01	0.78	-0.12
4	1250	4076.19	0.00	0.04	0.73	0.53	0.01
5	1248	5274.06	0.03	0.04	0.25	0.51	0.06
6	1248	7139.62	0.05	0.03	0.08	0.47	0.11
7	1248	9297.07	-0.02	0.03	0.79	0.61	-0.03
8	1250	11223.10	-0.10	0.03	0.00	0.60	-0.17
9	1248	12835.51	-0.09	0.03	0.01	0.74	-0.13
10	1248	14359.23	0.04	0.03	0.14	0.50	0.08
11	1248	15928.30	-0.03	0.03	0.46	0.51	-0.06
12	1250	18072.24	0.01	0.03	0.53	0.40	0.03

Table S9 – Spatial autocorrelation among residuals of the generalized linear mixed model fitted for proportion of single island endemics (pSIE) of bats measured with Moran's I per distance class.

Distance class	Count	Distance (km)	Moran's I	Standard Error	P-value	Maximum I (Imax)	I/Imax
1	1250	765.11	0.08	0.04	0.01	0.58	0.14
2	1248	2026.84	-0.06	0.03	0.16	0.96	-0.06
3	1248	3047.19	-0.04	0.03	0.30	0.79	-0.05
4	1250	4076.19	0.08	0.03	0.02	0.52	0.15
5	1248	5274.06	-0.11	0.04	0.00	0.46	-0.25
6	1248	7139.62	0.06	0.03	0.05	0.56	0.10
7	1248	9297.07	-0.08	0.03	0.04	0.60	-0.13
8	1250	11223.10	-0.03	0.03	0.56	0.71	-0.04
9	1248	12835.51	0.00	0.03	0.77	0.71	0.00
10	1248	14359.23	-0.04	0.03	0.28	0.43	-0.10
11	1248	15928.30	-0.02	0.03	0.69	0.85	-0.02
12	1250	18072.24	0.07	0.03	0.01	0.48	0.15

Table S10 – Spatial autocorrelation among residuals of the generalized linear mixed model fitted for proportion of single island endemics (pSIE) of non-volant mammals measured with Moran's I per distance class.

Distance class	Count	Distance (km)	Moran's I	Standard Error	P-value	Maximum I (Imax)	I/Imax
1	1250	765.11	0.05	0.04	0.11	0.69	0.07
2	1248	2026.84	0.01	0.03	0.69	0.70	0.01
3	1248	3047.19	-0.04	0.03	0.37	0.70	-0.05
4	1250	4076.19	0.02	0.04	0.50	0.54	0.03
5	1248	5274.06	-0.02	0.04	0.81	0.54	-0.03
6	1248	7139.62	0.05	0.03	0.10	0.56	0.08
7	1248	9297.07	-0.05	0.03	0.18	0.58	-0.09
8	1250	11223.10	-0.04	0.03	0.34	0.47	-0.08
9	1248	12835.51	-0.05	0.03	0.25	0.68	-0.07
10	1248	14359.23	0.01	0.03	0.60	0.33	0.03
11	1248	15928.30	-0.04	0.03	0.36	0.42	-0.09
12	1250	18072.24	0.01	0.03	0.58	0.37	0.03

Table S11 – Pseudo-R^2 of the generalized linear mixed models fitted for species richness of all mammals, bats and non-volants with biogeographic realm as random effect.

	All mammals		**Bats**		**Non-volants**	
	Marginal R^2	**Conditional R^2**	**Marginal R^2**	**Conditional R^2**	**Marginal R^2**	**Conditional R^2**
Trigamma	0.19	0.83	0.21	0.94	0.19	0.90
Delta	0.20	0.87	0.22	0.95	0.20	0.92
Lognormal	0.21	0.90	0.22	0.96	0.20	0.93

Table S12 – Pseudo-R^2 of the generalized linear models fitted for number of single island endemics (SIE) of all mammals, bats and non-volant.

	All mammals	**Bats**	**Non-volants**
Trigamma	0.68	0.30	0.68
Lognormal	0.85	0.66	0.85
Delta	0.79	0.51	0.79

Table S12 – Pseudo-R^2 of the generalized linear mixed models fitted for proportion of single island endemics (pSIE) of all mammals, bats and non-volants with biogeographic realm as random effect.

	All mammals		**Bats**		**Non-volants**	
	Marginal R^2	**Conditional R^2**	**Marginal R^2**	**Conditional R^2**	**Marginal R^2**	**Conditional R^2**
Theoretical	0.37	0.52	0.33	0.34	0.23	0.63
Delta	0.23	0.45	0.26	0.27	0.21	0.57

Table S13 – Standardized regression coefficients (β) of the generalized linear mixed models used to model species richness of all mammals, bats and non-volants on islands worldwide. Z-values in bold indicate significant β coefficients considering a significance level of $p < 0.05$.

	All mammals		**Bats**		**Non-volants**	
	β ± Std. error	**Z-value**	**β ± Std. error**	**Z-value**	**β ± Std. error**	**Z-value**
Intercept	-0.08 ± 0.35	-0.22	-0.15 ± 0.37	-0.39	-0.27 ± 0.38	-0.71
Area	0.69 ± 0.12	**5.66**	0.54 ± 0.13	**4.04**	0.63 ± 0.13	**4.94**
Current isolation	-0.61 ± 0.14	**-4.30**	-0.27 ± 0.13	**-2.13**	-0.37 ± 0.08	**-4.91**
Past isolation	-0.54 ± 0.19	**-2.87**	-0.18 ± 0.22	-0.82	-0.75 ± 0.27	**-2.79**
Climate velocity	-0.04 ± 0.07	-0.65	-0.05 ± 0.1	-0.46	0.03 ± 0.06	0.60
Temperature mean	0.32 ± 0.35	0.94	1.05 ± 0.38	**2.78**	-0.23 ± 0.31	-0.74
Temperature sd	0.12 ± 0.04	**2.67**	0.23 ± 0.03	**7.83**	0.07 ± 0.05	1.37
Precipitation sd	-0.02 ± 0.09	-0.23	-0.2 ± 0.1	**-1.98**	-0.06 ± 0.08	-0.81
Precipitation mean	-0.07 ± 0.14	-0.48	0.01 ± 0.14	0.09	0.05 ± 0.11	0.48
Elevation sd	0.02 ± 0.05	0.44	-0.01 ± 0.04	-0.30	0.06 ± 0.06	0.99
Area * Current isolation	0.25 ± 0.09	**2.85**	0.21 ± 0.07	**3.09**	0.06 ± 0.07	0.85

Table S14 – Standardized regression coefficients (β) of the generalized linear models used to model the number of single island endemics (SIE) of all mammals, bats and non-volants on islands worldwide. Z-values in bold indicate significant β coefficients considering a significance level of $p < 0.05$.

	All mammals		**Bats**		**Non-volants**	
	β ± Std. error	**Z-value**	**β ± Std. error**	**Z-value**	**β ± Std. error**	**Z-value**
Intercept	-4.05 ± 0.63	**-6.45**	-3.2 ± 0.66	**-4.88**	-4.05 ± 0.63	**-6.45**
Area	1.23 ± 0.18	**6.76**	0.51 ± 0.2	**2.60**	1.23 ± 0.18	**6.76**
Current isolation	0.49 ± 0.25	1.96	0.87 ± 0.32	**2.69**	0.49 ± 0.25	1.96
Past isolation	0.39 ± 0.29	1.33	0.42 ± 0.35	1.22	0.39 ± 0.29	1.33
Climate velocity	0.94 ± 0.36	**2.65**	1.16 ± 0.37	**3.17**	0.94 ± 0.36	**2.65**
Temperature mean	1.02 ± 0.3	**3.41**	0.36 ± 0.34	1.05	1.02 ± 0.3	**3.41**
Temperature sd	0.76 ± 0.31	2.48	0.45 ± 0.3	1.48	0.76 ± 0.31	**2.48**
Precipitation sd	0.54 ± 0.58	0.93	1.5 ± 0.72	**2.09**	0.54 ± 0.58	0.93
Precipitation mean	-0.96 ± 0.3	**-3.17**	-0.76 ± 0.34	**-2.23**	-0.96 ± 0.3	**-3.17**
Elevation sd	-0.38 ± 0.47	-0.82	-0.56 ± 0.35	-1.58	-0.38 ± 0.47	-0.82

Table S15 – Standardized regression coefficients (β) of the generalized linear mixed models used to model the proportion of single island endemics (pSIE) of all mammals, bats and non-volants on islands worldwide. Z-values in bold indicate significant β coefficients considering a significance level of $p < 0.05$.

	All mammals		**Bats**		**Non-volants**	
	β ± Std. error	**Z-value**	**β ± Std. error**	**Z-value**	**β ± Std. error**	**Z-value**
Intercept	-1.83 ± 0.36	**-5.04**	-3.6 ± 0.75	**-4.83**	-0.71 ± 0.62	-1.15
Area	0.21 ± 0.15	1.42	-0.04 ± 0.18	-0.23	-0.04 ± 0.21	-0.20
Current isolation	1.31 ± 0.17	**7.64**	1.65 ± 0.37	**4.44**	1.41 ± 0.23	**6.11**
Past isolation	0.87 ± 0.15	**5.75**	0.42 ± 0.29	1.42	1.75 ± 0.18	**9.53**
CCVT	0.87 ± 0.34	**2.53**	1.37 ± 0.33	**4.12**	0.67 ± 0.44	1.52
Temperature mean	-0.76 ± 0.46	-1.65	-0.84 ± 0.47	-1.79	-0.14 ± 0.22	-0.65
Temperature sd	0.22 ± 0.17	1.27	0.18 ± 0.36	0.50	0.71 ± 0.21	**3.34**
Precipitation mean	-1.08 ± 0.15	**-7.17**	-1.2 ± 0.32	**-3.71**	-0.87 ± 0.19	**-4.63**
Precipitation sd	0.26 ± 0.44	0.58	1.33 ± 0.71	1.86	0.11 ± 0.61	0.17
Elevation sd	-0.65 ± 0.23	**-2.84**	-0.59 ± 0.4	-1.48	-1.01 ± 0.35	**-2.85**

Table S16 – Standardized regression coefficients (β) per biogeographic realm from the generalized linear mixed models used to model species richness of all mammals on islands worldwide.

	Intercept	**Area**	**Current isolation**	**Past isolation**	**Climate velocity**	**Temperature mean**	**Temperature sd**	**Precipitation mean**	**Precipitation sd**	**Elevation sd**	**Area*Current isolation**
Afrotropical	1.17	0.75	1.63	-0.13	-0.04	-2.12	0.13	0.57	0.05	-0.12	0.19
Australian	-1.52	1.30	0.60	1.12	0.03	0.32	0.16	-0.43	0.02	0.12	-0.12
Eurasia	-0.05	0.81	0.68	0.65	-0.20	-0.12	0.04	0.34	-0.35	-0.13	0.15
Madagascan	0.60	0.25	1.00	0.54	0.00	0.72	0.11	0.23	-0.01	0.01	0.55
Neartic	-0.80	0.68	0.91	0.04	0.04	1.35	0.10	-0.29	0.37	0.09	-0.11
Neotropical	-0.75	0.64	0.44	1.20	-0.08	0.44	0.13	-0.19	-0.13	0.11	0.31
Oceanina	-1.83	1.39	0.07	0.34	-0.19	2.05	0.16	0.36	-0.33	0.08	-0.19
Oriental	1.29	0.74	0.78	0.30	0.00	-0.93	0.17	-0.29	-0.05	0.06	0.43
Paleartic	-0.35	0.72	0.57	0.14	0.06	0.48	0.06	-0.51	-0.13	0.13	0.27
Panamanian	-0.76	0.12	0.45	1.26	-0.15	0.10	0.17	-0.52	0.38	-0.08	0.68
Saharo-Arabian	0.78	0.64	0.00	0.17	-0.11	0.38	0.10	0.44	-0.03	-0.02	0.39
Sino-Japanese	1.50	0.25	0.16	0.81	0.10	1.14	0.11	-0.50	-0.06	0.00	0.43

Table S17 – Standardized regression coefficients (β) per biogeographic realm from the generalized linear mixed models used to model species richness of bats on islands worldwide.

	Intercept	**Area**	**Current isolation**	**Past isolation**	**Climate velocity**	**Temperature mean**	**Temperature sd**	**Precipitation mean**	**Precipitation sd**	**Elevation sd**	**Area*Current isolation**
Afrotropical	1.15	0.32	1.05	-0.77	-0.11	-0.56	0.23	0.29	-0.06	-0.02	0.03
Australian	-0.28	0.67	0.23	0.19	-0.06	0.54	0.23	0.78	-0.10	0.03	-0.02
Eurasia	-0.42	1.13	0.22	-0.55	0.11	0.72	0.23	-0.10	-0.81	-0.06	0.01
Madagascan	0.56	0.09	0.59	0.18	0.19	1.33	0.23	0.21	-0.12	-0.01	0.36
Neartic	-1.99	0.21	0.88	0.17	-0.40	2.83	0.23	-0.14	-0.10	-0.05	0.28
Neotropical	-1.56	0.85	-0.08	0.64	-0.16	1.34	0.23	0.34	-0.13	0.04	0.15
Oceanina	-0.88	0.81	0.01	0.14	-0.15	1.94	0.23	0.23	-0.39	0.01	-0.04
Oriental	1.82	0.48	0.47	-0.21	0.10	-0.83	0.23	-0.20	-0.30	0.02	0.25
Paleartic	-0.72	1.36	-0.15	0.15	0.05	2.40	0.23	-0.32	-0.48	0.00	0.11
Panamanian	-0.96	-0.16	-0.13	1.65	-0.19	0.08	0.23	-0.73	0.34	-0.06	0.62
Saharo-Arabian	0.51	0.50	-0.02	0.18	-0.35	0.33	0.23	0.37	-0.23	-0.03	0.32
Sino-Japanese	1.34	0.29	0.13	0.32	0.41	2.22	0.23	-0.56	-0.10	0.00	0.41

Table S18 – Standardized regression coefficients (β) per biogeographic realm from the generalized linear mixed models used to model species richness of non-volant mammals on islands worldwide.

	Intercept	**Area**	**Current isolation**	**Past isolation**	**Climate velocity**	**Temperature mean**	**Temperature sd**	**Precipitation mean**	**Precipitation sd**	**Elevation sd**	**Area*Current isolation**
Afrotropical	0.20	0.85	0.54	1.36	0.04	-2.48	0.07	0.43	-0.01	-0.22	-0.03
Australian	-2.55	1.01	0.43	2.62	0.09	-0.13	0.09	-0.51	-0.17	0.07	-0.04
Eurasia	0.23	0.56	0.46	0.84	-0.07	0.04	-0.04	0.33	-0.15	-0.13	0.07
Madagascan	-1.25	1.08	0.62	0.75	0.05	-0.95	0.10	0.24	0.11	0.10	0.17
Neartic	0.29	0.07	0.03	0.19	0.11	0.22	0.14	0.11	0.08	0.33	-0.41
Neotropical	-0.20	0.34	0.23	1.06	0.07	-0.10	0.01	-0.16	-0.09	0.04	0.10
Oceanina	-2.48	1.48	0.64	0.88	0.04	1.32	0.11	0.09	-0.02	0.26	-0.19
Oriental	-0.17	0.71	0.53	0.81	-0.08	-0.52	0.03	-0.15	0.14	0.04	0.31
Paleartic	0.55	0.39	0.24	0.12	0.03	0.20	0.01	-0.19	-0.10	0.03	0.12
Panamanian	0.74	0.50	0.43	-0.21	-0.02	-0.92	0.19	0.33	-0.51	0.22	0.08
Saharo-Arabian	0.76	0.34	0.15	-0.26	0.06	0.18	0.08	0.40	0.03	0.00	0.21
Sino-Japanese	0.96	0.22	0.13	0.67	0.09	0.40	0.11	-0.26	-0.06	0.00	0.29

Table S19 – Standardized regression coefficients (β) per biogeographic realm from the generalized linear mixed models used to model the proportion of single island endemics (pSIE) of all mammals on islands worldwide.

	Intercept	Area	Current isolation	Past isolation	Climate velocity	Temperature mean	Temperature sd	Precipitation mean	Precipitation sd	Elevation sd
Australian	-1.83	0.19	-1.31	-0.87	1.08	-0.51	0.22	-1.08	-0.22	-0.65
Ori+Ocea+ Mad+Afro+Sah	-1.83	0.31	-1.31	-0.87	1.36	-1.49	0.22	-1.08	1.16	-0.65
Pale+Nea+Eur+ SinJ	-1.83	0.15	-1.31	-0.87	0.61	0.01	0.22	-1.08	-0.11	-0.65
Panam+Neotrop	-1.83	0.18	-1.31	-0.87	0.39	-1.07	0.22	-1.08	0.23	-0.65

Table S20 – Standardized regression coefficients (β) per biogeographic realm from the generalized linear mixed models used to model the proportion of single island endemics (pSIE) of bats on islands worldwide.

	Intercept	Area	Current isolation	Past isolation	Climate velocity	Temperature mean	Temperature sd	Precipitation mean	Precipitation sd	Elevation sd
Australian	-3.60	-0.04	-1.65	-0.42	1.37	-0.84	0.16	-1.20	1.33	-0.59
Ori+Ocea+Mad+ Afro+Sah	-3.60	-0.04	-1.65	-0.42	1.37	-0.84	0.33	-1.20	1.33	-0.59
Pale+Nea+Eur+ SinJ	-3.60	-0.04	-1.65	-0.42	1.37	-0.84	0.11	-1.20	1.33	-0.59
Panam+Neotrop	-3.60	-0.04	-1.65	-0.42	1.37	-0.84	0.14	-1.20	1.33	-0.59

Table S21 – Standardized regression coefficients (β) per biogeographic realm from the generalized linear mixed models used to model the proportion of single island endemics (pSIE) of non-volant mammals on islands worldwide.

	Intercept	**Area**	**Current isolation**	**Past isolation**	**Climate velocity**	**Temperature mean**	**Temperature sd**	**Precipitation mean**	**Precipitation sd**	**Elevation sd**
Australian	-0.46	0.01	-1.41	-1.75	0.74	-0.14	0.71	-0.87	-0.79	-1.01
Ori+Ocea+ Mad+Afro+ Sah	-1.76	0.28	-1.41	-1.75	1.24	-0.14	0.71	-0.87	1.00	-1.01
Pale+Nea+ Eur+SinJ	-0.53	-0.17	-1.41	-1.75	0.48	-0.14	0.71	-0.87	-0.42	-1.01
Panam+ Neotrop	-0.10	-0.30	-1.41	-1.75	0.19	-0.14	0.71	-0.87	0.73	-1.01