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Integrando aspectos filogenéticos e funcionais na Biogeografia da Conservação de vertebrados

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“A corrida agora é entre às forças tecnocientíficas que estão destruindo o ambiente vivo e aquelas que podem ser aproveitadas para salvá-lo. Estamos em um gargalo de superpopulação e consumismo de desperdício. Se a corrida for vencida, a humanidade pode emergir em condição muito melhor do que no começo e com a maior parte da diversidade da vida ainda intacta.”

(The Future of Life – Edward O. Wilson)

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SUMÁRIO

RESUMO

Estimativas recentes mostram que as taxas atuais de extinção são muito maiores do que o indicado pelo registro fóssil, sendo as principais ameaças resultado da atividade humana. Como a crise da biodiversidade age em todas as escalas e não apresenta fronteiras políticas, a aplicação do arcabouço teórico da biogeografia da conservação e do planejamento sistemático para conservação se torna muito útil para a identificação de áreas com alto valor de conservação que sejam significativas em um contexto global, continental ou regional. Além da dimensão taxonômica, as dimensões funcional e filogenética da biodiversidade são componentes importantes para a conservação, e a sua perda implica não somente em perda de espécies, mas também na perda de funções ecossistêmicas e de trajetórias evolutivas. O objetivo desta tese foi avaliar como o impacto humano atual gerado pelo uso da terra, influencia padrões funcionais (relacionados ao risco de extinção, Capítulo 1) e filogenéticos (Capítulo 2) de distribuição, e como informações filogenéticas e de atributos podem ser utilizadas para informar priorização espacial pra conservação (Capítulo 3). Nos capítulos 1 e 2 encontrei que a influência do uso da terra sobre a biodiversidade não está restrita apenas às escalas mais locais e de paisagem, mas também já é perceptível em escalas geográficas amplas. Além disso, verifiquei que o uso da terra tem impacto não somente na dimensão taxonômica, mas também nas dimensões filogenética e funcional da diversidade de vertebrados nessa escala macrogeográfica. Isso demonstra a necessidade de um planejamento de ocupação e manejo de áreas utilizadas para atividades humana em ampla escala também, pois o impacto humano não se dá mais somente em escalas finas. O uso atual da terra representa uma ameaça real maior para algumas linhagens de anfíbios (Capítulo 1) e de primatas (Capítulo 2), como, por exemplo, Microhylidae e Atelidae, respectivamente. Isso reforça a necessidade de utilizarmos abordagens filogenéticas que identifiquem quais linhagens estão mais suscetíveis aos impactos decorrentes de atividades humanas. Ao tentar maximizar a a conservação das dimensões taxonômica, filogenética e funcional da biodiversidade de mamíferos, a congruência entre as áreas selecionadas como prioritárias foi baixa. A integração dos diferentes componentes da biodiversidade para selecionar áreas mais eficientes para a conservação das espécies ainda é um desafio. O desencontro entre as prioridades de conservação para as diferentes dimensões da biodiversidade ressalta a necessidade o desenvolvimento de abordagens mais integrativas para a conservação da biodiversidade.

PALAVRAS-CHAVE: Antromas; Atributos; Biogeografia da conservação; Conservação de anfíbios; Conservação de mamíferos; Coordenadas principais de estrutura filogenética – PCPS; Dimensões da biodiversidade; Espécies ameaçadas; Filogenia; Priorização espacial para conservação; Uso da terra.

ABSTRACT

Recent estimates show that current exticntion rates are much higher than the indicated by fossil records. The causes of this elevated rate are mostly result of human activities. The biodiversity crisis affects all scales and presents no political boundaries, the application of the theoretical and analytical framework of Conservation Biogeography and Systematic Conservation Planning becomes very useful to identify meaningful areas with high conservation value locally and globally. In addition to taxonomic diversity, functional and phylogenetic dimensions of biodiversity are also important components to preserve, and their loss implies not only on species number, but also loss of ecosystem services and evolutionary history. The aim of the thesis was to evaluate how impacts of human land use influences functional (related to extinction risk, Chapter 1) and phylogenetic (Chapter 2) distribution patterns, and how phylogenetic and trait information could be used to inform spatial conservation prioritization (Chapter 3). In the chapter 1 and 2 I found that the influence of land use on the biodiversity is not constrained to local and landscape scales, but has an effect at broad-scales too. Besides, I verified that land use impacts on phylogenetic and functional dimensions on macrogeographical scales. These results show a need of creating a broad scale planning for ocupation and management of areas intended to human activities. Current land use is a major threat to some lineages of amphibians (Chapter 1) and primates (Chapter 2), as for example Microhylidae and Atelidae respectively. That reinforces the need of phylogenetics approaches that identify which lineages are more exposed to human activities. We found low congruence between priority areas for maximize the conservation of taxonomic, functional and phylogenetics dimensions of biodiversity. The integration of the differnt componentes of diversity to conservation still is a chalenge. The mismatch of the conservation priorities across the different dimension highlights the necessity of an integrative approach to biodiversity conservation.

KEYWORDS: Amphibian conservation; Anthromes; Conservation biogeography; Dimensions of biodiversity; Land use; Mammal conservation; Phylogeny; Principal coordinates of phylogenetic structure – PCPS; Spatial conservation prioritization; Threatened species; Traits.

INTRODUÇÃO GERAL

As taxas atuais de perda de biodiversidade têm desafiado os cientistas a desenvolver modelos preditivos capazes de incorporar processos ecológicos e evolutivos e que ajudem a delinear políticas de conservação de maneira que sejam facilmente assimiláveis pelos tomadores de decisão (Bielby *et al.* 2010; Sutherland *et al.* 2006). Estimativas recentes mostram que as taxas atuais de extinção são muito maiores do que o indicado pelo registro fóssil (Pimm *et al.* 2014). As principais ameaças a biodiversidade são a destruição de habitats, introdução de espécies exóticas, sobre-exploração de espécies e recursos, poluição e mudanças climáticas globais. Todas as ameaças citadas anteriormente são resultado da atividade humana, que já alterou aproximadamente 75% da superfície terrestre livre de gelo (Ellis & Ramankutty 2008). A espécie humana tem modificado a forma e o funcionamento de ecossistemas há milênios, e essas alterações já são consideradas tão irreversíveis e marcantes que se julga que o planeta entrou em uma nova era geológica: o “Antropoceno” (Ellis, 2011).

Como a crise da biodiversidade age em todas as escalas espaciais e temporais e não apresenta fronteiras políticas, a aplicação do arcabouço teórico da biogeografia da conservação (Whittaker *et al.* 2005) e do planejamento sistemático para conservação (Margules & Pressey 2000) se torna muito útil para a identificação de áreas com alto valor de conservação que sejam significativas em um contexto global, continental ou regional (Loyola & Lewinsohn 2009). A Biogeografia da Conservação consiste na aplicação do arcabouço teórico e analítico da Biogeografia à problemas relacionadas a conservação da biodiversidade (Whittaker *et al.* 2005). Essa ciência permite que avaliemos questões de conservação em escalas amplas, por exemplo, efeito do uso da terra e das mudanças climáticas na distribuição das espécies, e o uso de diferentes fontes de informação em ampla escala (áreas de endemismo, padrões geográfico diversidade, estrutura filogeográfica) no planejamento sistemático para conservação (Ladle & Whittaker 2011).

Ao longo das últimas décadas, o aumento na disponibilidade de dados referentes à atividades humanas em toda superfície terrestre permitiu que os cientistas avaliassem os efeitos destas atividades sob a biodiversidade em escalas amplas (Harcourt & Parks 2003; Pekin & Pijanowski 2012). Ellis e Ramankutty (2008) fizeram uma reavaliação da cobertura terrestre, propondo os “antromas” ou “biomas antropogênicos“, gerados a partir de um agrupamento que permitiu identificar padrões globais de uso da terra e densidade populacional. A utilização dos antromas representa um novo caminho em direção ao conhecimento da influência humana nos ecossistemas e a modelos investigativos que integram sistemas humanos e ecológicos (Ellis & Ramankutty 2008). Ao contrário dos biomas tradicionais, antromas contam uma história diferente, na qual os ecossistemas naturais estão incorporados dentro dos sistemas humanos (Ellis & Ramankutty 2008). Além disso, os autores apresentam dados de uso da terra biogeograficamente estruturados e possibilitam a inclusão dessa informação de maneira mais refinada em planejamento de conservação em amplas escalas.

Os diferentes tipos de uso da terra pelas populações humanas não são distribuídos uniformemente ao longo da superfície terrestre (Ellis & Ramankutty 2008), gerando pressões antrópicas distintas em regiões diferentes (Harcourt & Parks 2003). Por exemplo, a região tropical, onde se concentra a maior parte da diversidade biológica do planeta, sofre com intenso desmatamento, condenando espécies florestais a extinção local (Hansen *et al.* 2013). Na Asia, a alta densidade populacional gera um conflito de conservaçãoo direto entre populações humanas e espécies selvagens, o que resulta em um aumento da pressão de caça e extrativismo sobre a fauna/flora nativa (IUCN 2013).

A suscetibilidade das espécies frente as diferentes ameaças e, consequentemente, o seu risco de extinção vai depender de suas características ecológicas e afinidades filogenéticas (Bielby *et al.* 2010; Davidson *et al.* 2009; Lee & Jetz 2011). Em espécies de carnívoros e primatas, por exemplo, atributos relacionados à biologia das espécies (distribuição restrita, baixa densidade populacional, taxas reprodutivas baixas e nível trófico) são responsáveis por quase metade da variação total no risco de extinção entre espécies (Purvis *et al.* 2000). Vários estudos já demonstraram que o risco de extinção das espécies não é filogeneticamente aleatório (e.g. Bielby *et al.* 2010; Corey & Waite 2008; Davidson *et al.* 2009a; Purvis 2000), ou seja, algumas linhagens são mais suscetíveis a processos de extinção do que outras. Considerando que atributos intrínsecos das espécies são importantes determinantes do risco de extinção e que espécies próximas filogeneticamente tendem a apresentar maior similaridade em seus atributos (Felsenstein 1985), a utilização de informações proximidade evolutiva entre espécies em estudos de conservação e planejamento sistemático se mostra interessante (Corey & Waite 2008; Hidasi-Neto *et al.* 2013; Loyola *et al.* 2014; Machado & Loyola 2013).

A riqueza de espécies é o componente da biodiversidade mais amplamente explorado por pesquisadores e conservacionistas. Porém, a dimensão taxonômica da diversidade não leva em consideração diferenças funcionais e evolutivas entre as espécies que co-ocorrem em um determinado local. As dimensões funcional e filogenética são componentes importantes da biodiversidade e podem ser perdidas mais rapidamente do que a diversidade de espécies (Flynn *et al.* 2009; Heard & Mooers 2000). A sua perda implica não somente em perda de espécies, mas também na perda de funções ecossistêmicas (Díaz *et al.* 2007) e de trajetórias evolutivas (Faith 1992). Desde o início da década de 90 começou a se discutir a importância da diversidade filogenética em conservação de espécies animais (Faith 1992; Rodrigues & Gaston 2002; Vane-Wright *et al.* 1991), porém a utilização de atributos funcionais de vertebrados para esse mesmo fim é mais recente (Becker *et al.* 2010; Carvalho *et al.* 2010; Hidasi-Neto *et al.* 2013; Loyola *et al.* 2008, 2009; Mazel *et al.* 2014; Sobral *et al.* 2014; Strecker *et al.* 2011; Trindade-Filho *et al.* 2012). Grande parte do arcabouço teórico em ecologia funcional foi desenvolvido baseando-se em comunidades vegetais (Diaz & Cabido 2001; Díaz *et al.* 2007; Navas & Violle 2009; Petchey & Gaston 2006; Pillar *et al.* 2009).

Porém, a crescente disponibilidade de filogenias moleculares (Bininda-emonds *et al.* 2007; Jetz *et al.* 2012; Pyron & Wiens 2011) e base de dados de atributos (Jones *et al.* 2009) para diversos grupos de vertebrados vem facilitando a integração das três dimensões da diversidade (taxonômica, filogenética e funcional) para responder questões de ecologia teórica (Barnagaud *et al.* 2014; Kissling *et al.* 2011; Safi *et al.* 2011) e de prioridades para conservação (Lee & Jetz 2011; Machado & Loyola 2013; Mazel *et al.* 2014; Trindade-Filho & Loyola 2011).

A priorização de algumas áreas para conservação é necessária, pois as decisões relacionadas à conservação são geralmente conduzidas sob restrições de tempo, área e dinheiro (Margules & Pressey 2000). Um dos princípios fundamentais do planejamento sistemático para conservação é garantir a representatividade da biodiversidade. Para isso, é importante usar o máximo de características biológicas possíveis para se desenvolver estratégias de conservação mais compreensivas (Watson *et al.* 2011). Considerando isto, se faz fundamental a incorporação das dimensões funcional e filogenética da diversidade, juntamente com a dimensão taxonômica, em estudos de conservação e planejamento sistemático, desde a escala local até a escala global.

Objetivo e estrutura da tese

O objetivo geral desta tese foi avaliar como o impacto humano atual, gerado pelo uso da terra, influencia padrões funcionais (relacionados ao risco de extinção, Capítulo 1) e filogenéticos (Capítulo 2) de distribuição de vertebrados, e como informações filogenéticas e funcionais podem ser utilizadas para complementar análises de priorização espacial pra conservação (Capítulo 3). Esta tese está estruturada em três capítulos, cada um correspondente a um artigo cientifico, descritos abaixo:

Capítulo 1– Land Use Explains the Distribution of Threatened New World Amphibians better than climate: Neste capítulo o objetivo foi avaliar a influência direta e indireta do clima, do uso da terra, da estrutura filogenética, da riqueza e endemismo na distribuição de anfíbios ameaçados de extinção no Novo Mundo.

Capítulo 2 – Clade-specific impacts of human land use on primates. Este capítulo teve como objetivo avaliar a associação, em ampla escala, entre a distribuição de clados de primatas e diferentes categorias uso da terra, a fim de inferir quais impactos humanos tem mais influencia na ameaça às linhagens de primatas em cada região da sua distribuição.

Capítulo 3 – Spatial conservation priorities are not congruent across different dimensions of diversity in global mammals: O objetivo do terceiro capítulo foi identificar quais são as áreas prioritárias para a conservação de mamíferos terrestres, globalmente, baseando-se em diferentes dimensões da biodiversidade (taxonômica, filogenética e funcional), e verificar se elas são congruentes entre si. Além disso, foi avaliado o quanto da diversidade taxonômica/filogenética/funcional total elas abrigariam, comparando-se isto com a rede atual de unidades de conservação no mundo. Também foi mapeada a relação entre as áreas selecionadas e densidade populacional humana e velocidade de mudanças climáticas.

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CAPÍTULO 1[1]

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Land use explains the distribution of threatened New World amphibians better than climate

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Abstract

Background: We evaluated the direct and indirect influence of climate, land use, phylogenetic structure, species richness and endemism on the distribution of New World threatened amphibians.

Methodology/Principal Findings: We used the WWF’s New World ecoregions, the WWF´s amphibian distributional data and the IUCN Red List Categories to obtain the number of threatened species per ecoregion. We analyzed three different scenarios: urgent, moderate, and the most inclusive scenario. Using path analysis we evaluated the direct and indirect effects of climate, type of land use, phylogenetic structure, richness and endemism on the number of threatened amphibians in New World ecoregions. In all scenarios we found strong support for direct influences of endemism, the cover of villages and species richness on the number of threatened species in each ecoregion. The proportion of wild area had indirect effects in the moderate and the most inclusive scenario. Phylogenetic composition was important in determining the species richness and endemism in each ecoregion. Climate variables had complex and indirect effects on the number of threatened species.

Conclusion/Significance: Land use has a more direct influence than climate in determining the distribution of New World threatened amphibians. Independently of the scenario analyzed, the main variables influencing the distribution of threatened amphibians were consistent, with endemism having the largest magnitude path coefficient. The importance of phylogenetic composition could indicate that some clades may be more threatened than others, and their presence increases the number of threatened species. Our results highlight the importance of man-made land transformation, which is a local variable, as a critical factor underlying the distribution of threatened amphibians at a biogeographic scale.

Introduction

The worldwide decline of amphibian populations has become one of the main priorities on the conservation agenda. Amphibians are protagonists in the current biodiversity crisis, with one third of species threatened with extinction risk [1]. Amphibian decline and extinctions are both geographically and taxonomically structured [1,2]. Threats are concentrated among montane forest and stream associated species in the Neotropics and Australia/New Zealand. Such declines are often propelled by habitat loss and fragmentation, climate change, pollution, and infectious diseases [3] – all threats resulting from the exponential growth of human population [4]. Despite the global influence of humans in amphibian extinction, it is still uncommon to include land use to explain amphibian distribution at the biogeographical scale. Much more common, however, is the use of climatic variables, which have been considered the main drivers of broad scale diversity patterns [5].

Recently, Ellis & Ramankutty [6] reclassified the global land cover into “anthropogenic biomes” or “anthromes”, based on global maps of land use, land cover and human population density. Incorporating anthropogenic biomes into conservation models may reveal patterns that could be markedly different from the traditional perspective of natural biomes, and could integrate human activities into a single view of ecological system. Moreover, anthromes are tractable biogeographical units and offer a more refined way to include land-use changes in geographically broad conservation planning.

The current rate of biodiversity loss has challenged ecologists to develop predictive models which summarize important ecological and evolutionary processes and, most importantly, to provide recommendations for on the ground conservation action that can be readily assimilated by decision and policy makers [7,8]. Current knowledge focuses on phylogenetic and functional diversity [9,10]. Functional diversity represents the extent of functional differences inside a community [11,12], while phylogenetic diversity adds the species evolutionary relatedness into the diversity measure [9]. Where conservation is concerned, phylogenetic and functional diversity are important biodiversity components, as they ensure ecosystem services [13] and represent the evolutionary history of the target group [9]. Considering that all the metrics of phylogenetic/functional diversity aim to synthesize the phylogenetic/functional information, other dimensions of biodiversity end up being neglected. Two areas could have the same phylogenetic/functional diversity, for example, but have a completely different species composition. However, extinction risk is not independent of species identity, evolutionary history and ecological requirements [14,15]; thus, species sharing the same ecological traits and/or phylogenetic affinities may be more prone to go extinct. This suggests that phylogenetic composition, in particular, may be a crucial driver of threatened species distribution at broad spatial scales.

We evaluated the direct and indirect influences of climate, land use, phylogenetic structure, richness and endemism on the distribution of threatened amphibians across the New World using path analysis [16]. We analyzed three distinct scenarios of conservation urgency in order to verify if the drivers of threatened amphibian distribution are the same for different levels of threat.

Methods

Species data and amphibian threat categories

We analyzed the direct and indirect influence of climate, land use (*i.e.* the anthropogenic biomes), phylogenetic structure, species richness and endemism on the distribution of threatened amphibians throughout the New World ecoregions. From the 289 New World ecoregions described by Olson et al. [17], we selected 262 based on the availability of climatic and phylogenetic data. The ecoregions used here ranged from 628 to 1,900,000 square-meters area. The range database we used [18] contains the current amphibian species list occurring in each ecoregion. We compiled the presence or absence of 2472 amphibian species in each ecoregion in a composition matrix W. We then obtained the species richness and the number of endemic species for each ecoregion. Species were classified as endemic if they occur exclusively in one ecoregion. Species richness and endemism were used as independent predictors of threat distribution in the path analysis (see below).

We classified amphibian species following the extinction risk categories proposed by the IUCN Red List Categories and Criteria [19]: Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN), Critically Endangered (CR), Extinct in the wild (EW) and Extinct (EX). For each ecoregion, we calculated the number of species in each category. We ran our analysis based on three different scenarios: (1) the urgent scenario, containing only CR species and those EW and EX, (2) the moderate scenario containing all EN species and those at threat categories higher than EN (i.e. CR, EW, and EX), and (3) the most inclusive scenario, which included all VU species and those at higher threat categories.

Land use data

We used Ellis & Ramankutty's [6] reclassification of global land cover based on land use and human population density. They named the new classification of the global land cover as anthropogenic biomes or anthromes. Using the zonal tabulate area tool in ArcGIS 9.3, we obtained the cover of each anthrome per ecoregion. In order to facilitate the interpretation of our results, we synthesized the cover of the 18 anthromes into six major categories, in decreasing order of human population density: urban (1788 persons/km^2), villages (327 persons/km^2), croplands (33 persons/km^2), rangelands (7 persons/km^2), seminatural (1person/km^2) and wild (0 person/km^2). The cover proportion of each anthrome category per ecoregion was treated as an independent variable in the path analysis (see below). The spatial distribution of the cover of different land uses along the ecoregions can be visualized in Figure 1.

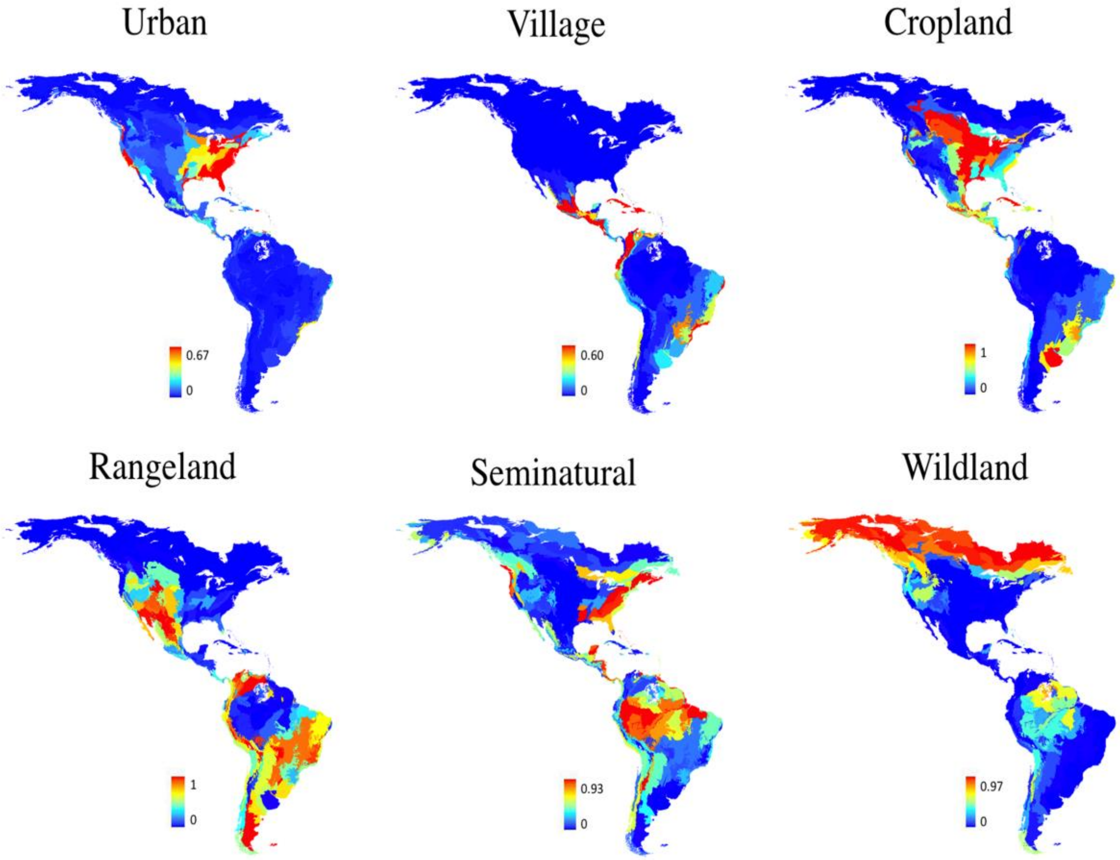


Figure 1 Maps depicting the spatial pattern of the proportion of land use cover in the New World ecoregions.

Climatic data

To describe the climate in each ecoregion, we used nine environmental variables: altitude, annual mean temperature, temperature seasonality (standard deviation of temperature along the year x 100), maximum temperature of the warmest month, minimum temperature of the coldest month, annual mean rainfall, rainfall seasonality (rainfall's coefficient of variation), precipitation of the wettest month and precipitation of the driest month. We decomposed each climatic variable into mean value and the range, totaling 18 climatic variables. All variables were compiled from the WorldClim 1.4 database [20], at the resolution of 2.5 arc-minute (~5 km). Instead of using all nine variables in the analysis, we performed a principal components analysis in order to reduce climate complexity using the two first axes (climate axis 1 and climate axis 2), which concentrated 65% of all climatic variation, as descriptors. Correlations between climatic variables and climate axes are shown in Table 1.

Table 1 Correlation values of each climatic variable with the two first axes of the principal components analysis. M indicates mean values and R indicates range values.

	Climate 1	**Climate 2**
Altitude (M)	0.54	-0.56
Altitude (R)	0.46	-0.83
Annual Mean Rainfall (M)	-0.82	-0.28
Annual Mean Rainfall (R)	-0.49	-0.71
Annual Mean Temperature (M)	-0.87	-0.09
Annual Mean Temperature (R)	0.50	-0.82
Maximum Temperature of Warmest Month (M)	-0.63	0.25
Maximum Temperature of Warmest Month (R)	0.48	-0.80
Minimum Temperature of Coldest Month (M)	-0.88	-0.22
Minimum Temperature of Coldest Month (R)	0.56	-0.72
Precipitation of Driest Month (M)	-0.51	-0.07
Precipitation of Driest Month (R)	-0.49	-0.54
Precipitation of Wettest Month (M)	-0.82	-0.33
Precipitation of Wettest Month (R)	-0.47	-0.74
Rainfall Seasonality (M)	-0.03	-0.26
Rainfall Seasonality (R)	0.14	-0.63
Temperature seasonality (M)	0.75	0.45
Temperature seasonality (R)	0.75	0.02

Phylogenetic structure

To generate a phylogenetic tree of amphibians inhabiting the New World ecoregions we adopted the phylogenetic tree built by Pyron & Wiens [21] .We fixed all branch lengths to unity. A phylogenetic pairwise distance matrix (D_F) based on node counting for the genera contained in matrix W was computed using the software Mesquite 2.73[22].

We scaled-up the phylogenetic relationships between species to the site level, generating a matrix describing the phylogeny-weighted genera composition of each ecoregion, which was defined using the phylogenetic fuzzy-weighting method developed by Pillar & Duarte [23], and implemented in the package SYNCSA-R [24]. For this, phylogenetic pairwise distances in D_F were used in terms of their complement as similarities (S_F). Then, phylogenetic similarities in S_F were used to weigh the number of species per genera in matrix W. This procedure generated a matrix P containing phylogeny-weighted genera composition for each ecoregion. Accordingly, those j taxa most phylogenetically related to i (*e.g.* from the same genus) received a proportionally higher fraction of the presence of i in that ecoregion than more phylogenetically distant taxa (*e.g.* from a different genus), which will receive a proportionally lower fraction, and so on. Note that the sum of the number of species per genera (*i.e.* species richness) in an ecoregion belonging to W will remain exactly the same in P after phylogenetic fuzzy-weighting. Matrix P expresses the phylogenetic composition in the set of ecoregions.

By performing a PCoA [25] on matrix P, based on square-rooted Bray-Curtis dissimilarities between ecoregions [26], we generated principal coordinates of phylogenetic structure (PCPS, Figure S1). Each PCPS is a vector describing an independent phylogenetic gradient in the dataset [27]. The PCPS with the highest eigenvalue describes broader phylogenetic gradients related to the deepest tree nodes across the ecoregions, such as that connecting anurans and salamanders. As the eigenvalues of the other PCPS decrease, finer phylogenetic gradients related to higher nodes (e.g. families, genera) are described. PCPS analysis was done using the SYNCSA-R [24] and the package ape [28]. Then, the associations between amphibian phylogenetic clades and each phylogenetic vector were plotted in a correlation scatter plot.

Path analysis

To remove the effect of area and geographical position of each ecoregion, we did a set of multiple linear regressions between all the variables included in path analysis with latitude, longitude and area. Then, the residuals obtained from these regressions were used to build a causal model linking the different types of variables. Considering that, the final results of the analysis will represent the effect of climate, land use, phylogenetic structure, species richness, endemism on threatened amphibian distribution, with no influence of the area and geographical position of the ecoregions.

We evaluated the influence of the two climatic axes, six anthromes and the three phylogenetic filters in the distribution of threatened amphibians using model selection based on Akaike's information criterion (AIC,[29]), separately for each group of variables, in order to select variables to be used as explanatory variables in path analysis.

Further, we evaluated causal connections between the selected climatic axes, anthromes, phylogenetic structure, species richness, endemism and threatened amphibian distribution using path analysis [25,30]. The goal of this analysis is to evaluate the strength of causal relationships between more than two variables by decomposing the covariation between pairs of variables. We used the analytical approach proposed by Brum et al. 2012 [31].

We built the path model in several steps using the model selection based on AIC. First, using the pre-selected climatic and phylogenetic variables plus species richness, endemism and threatened amphibian distribution, we built a hypothetical model establishing all possible and plausible causal relationships between variables (Figure 2). For this, a hierarchical causal order among explanatory variables was assumed. Climatic variables had the highest causal order, i.e. they are not determined by any other variable present in the model, also called exogenous [16]. All other variables were considered endogenous [16], since they could be determined by some other variable in the model (Figure 2). Threatened amphibian distribution had the lowest causal order, as it could not determine any other variable in the model (Figure 2).

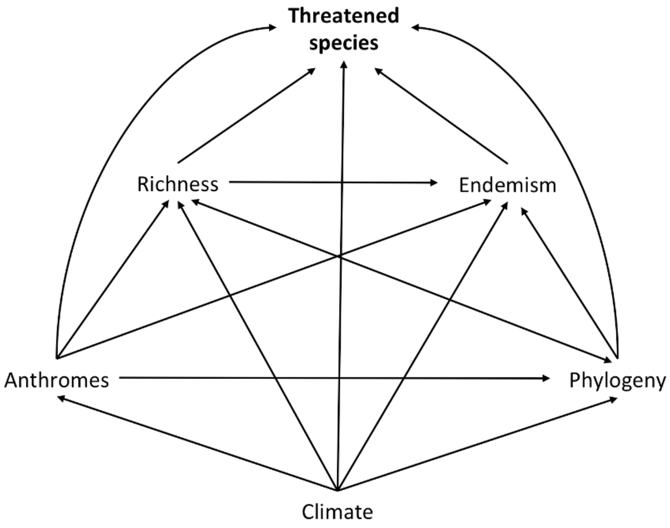


Figure 2 Hypothetical causal model establishing all possible and plausible causal connections between variables.

Our second analytical step consisted in running a model selection to find which variables directly determined the variation in threatened amphibian distribution, based on AIC modeling. After that, we proceeded to iteratively find the explanatory variables determining each endogenous predictor of threatened amphibian distribution. That is, each variable found to determine threatened amphibian distribution was taken as a response variable, and their respective predictors were determined using model selection [31]. Thus, the final path model represented the best model connecting the variables causally structured according to our hypothetical model. We performed all the analytical steps separately for each scenario (urgent, moderate and most inclusive). Then, we obtained three final path models, one for each scenario.

We obtained path coefficients for the so-built models by linear multiple/simple regressions, being the standardized regression coefficient (β) equivalent to the path coefficient [16]. Since none of the variables were normally distributed (all failed in the Shapiro-Wilk normality test), the P values of each path coefficient were calculated by using randomization test [32]. Model selection procedures based on AIC were performed using the software SAM v4.0 [33] and simple and multiple linear regressions were performed using the software Multiv 2.4 [34].

Results

From the 2472 amphibian species present in the ecoregions, 1886 belong to some threat category, 4 species were classified as Extinct, 221 as Critically Endangered, 326 as Endangered, 246 as Vulnerable. It means that the urgent scenario contained 225 species, the moderate scenario 551 species and the most inclusive 797 species. The maps showing the spatial distribution of species richness, endemism and the number of threatened species in each scenario is presented in the Figure 3 and the raw data could be visualized in the Table S1. Principal coordinate analysis for phylogeny-weighted species composition on matrix **P** generated 239 PCPS. The first three PCPS contained, respectively, 41%, 12% and 6% of the total variation of matrix **P**. Only the first three PCPS were submitted to model selection procedure, since most variation in phylogeny-weighted species composition ($\cong$ 60%) was concentrated in these three orthogonal axes. The correlation of phylogenetic clades distribution and PCPS1, PCPS2 and PCPS3 is shown in the Figure 4.

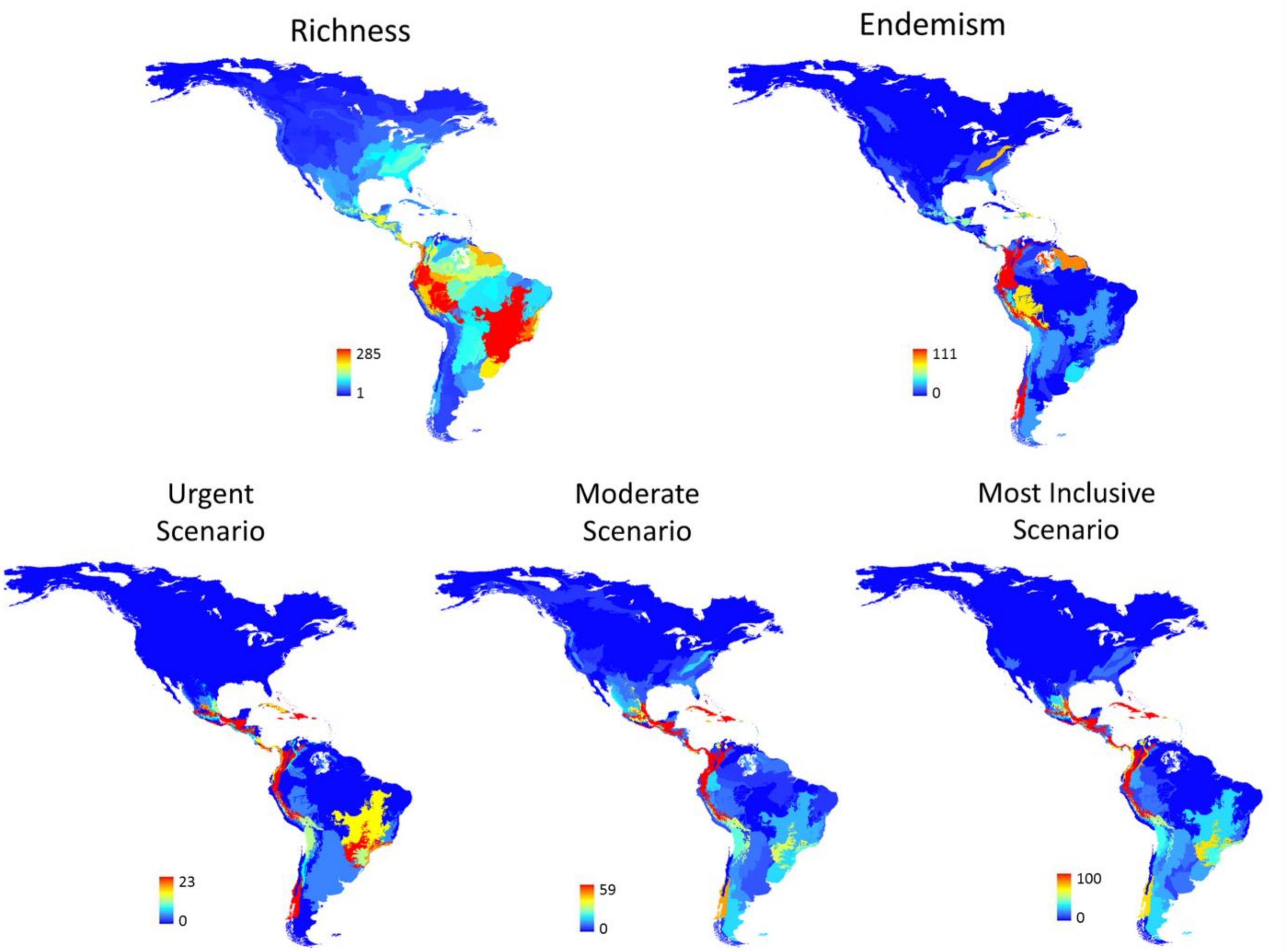


Figure 3 Maps showing the spatial pattern of richness of amphibian species, endemism and the number of threatened amphibian species according to the three different scenarios per ecoregion: the urgent scenario, containing only CR species and those EW and EX, the moderate scenario containing all EN species and those at threat categories higher than EN (i.e. CR, EW, and EX), and the most inclusive scenario, which included all VU species and those at higher threat categories.

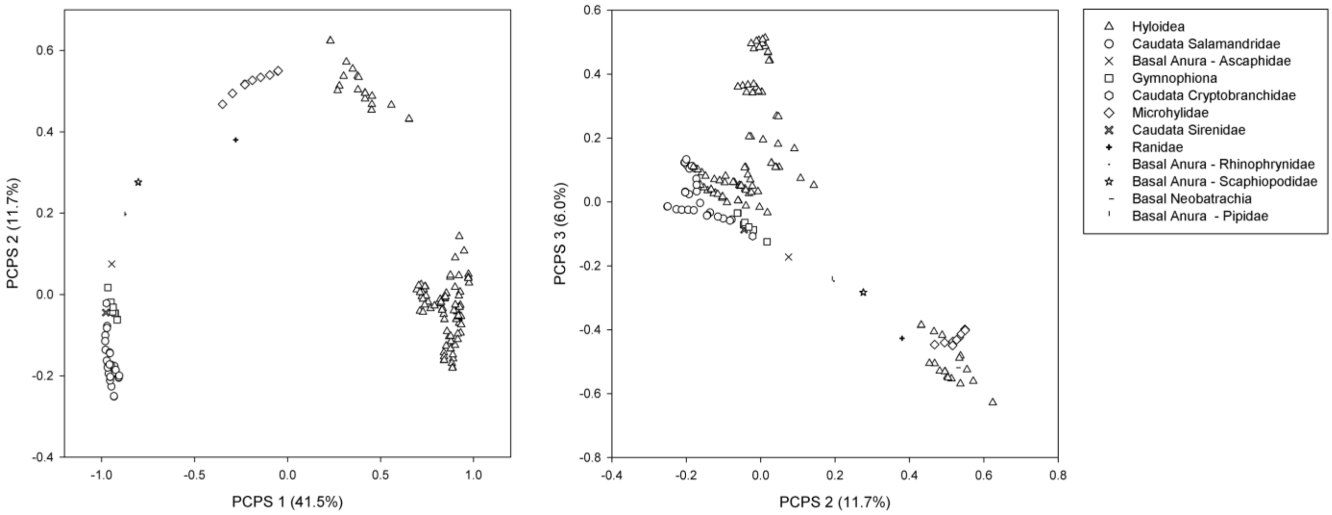
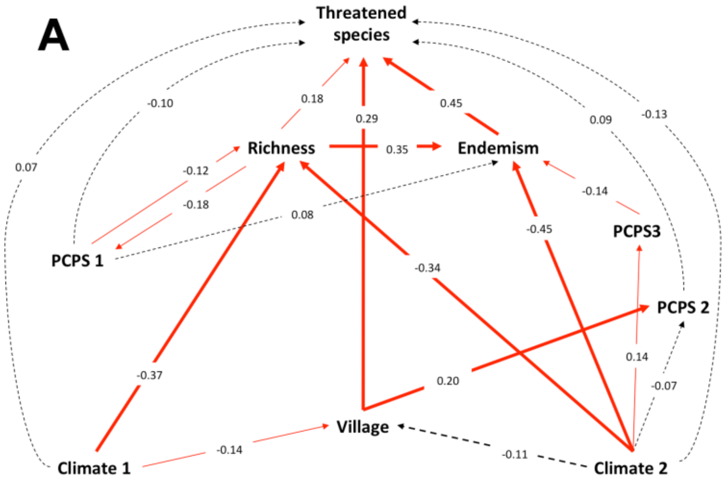
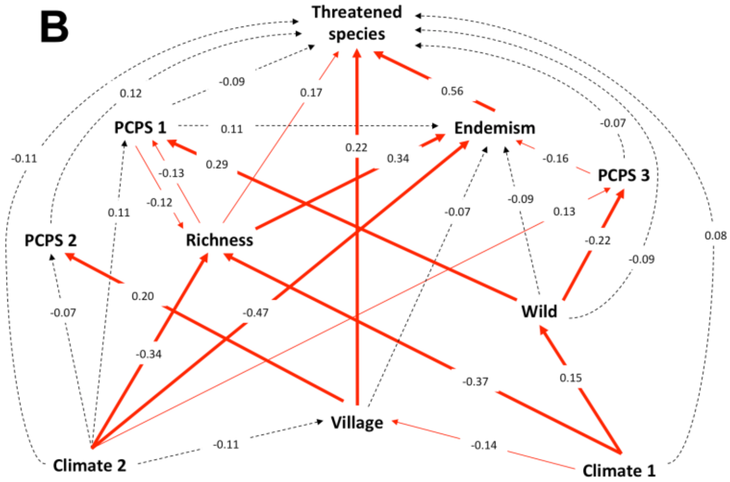


Figure 4 Correlation scatter plot for amphibian phylogenetic clades showing correlation values with three Principal Coordinates of Phylogenetic Structure (PCPS 1, PCPS2 and PCPS3) axes. Each point represents an amphibian genus. Genera are grouped within higher clades represented by different symbols.

Across the New World ecoregions, endemism was the best predictor in our urgent scenario, followed by the proportion of the village anthrome and species richness (Figure 5a). Phylogeny and climate were not important in directly explaining the number of CR and EX species in New World amphibians (Figure 5a), although they exert an indirect effect via species richness, endemism and land use.


A
Threatened species
Richness
Endemism
PCPS 1
PCPS3
PCPS 2
Village
Climate 1
Climate 2
0.07
-0.10
0.18
0.29
0.45
0.09
-0.13
0.35
-0.12
-0.18
0.08
-0.14
-0.45
-0.34
0.14
-0.07
-0.37
0.20
-0.14
-0.11


B
Threatened species
PCPS 1
Endemism
PCPS 3
PCPS 2
Richness
Wild
Village
Climate 2
Climate 1
-0.11
0.12
-0.09
0.17
0.56
0.11
0.22
0.34
-0.07
-0.16
0.29
-0.13
-0.12
0.11
-0.07
-0.09
0.13
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-0.07
-0.47
-0.34
-0.37
0.15
-0.11
-0.14

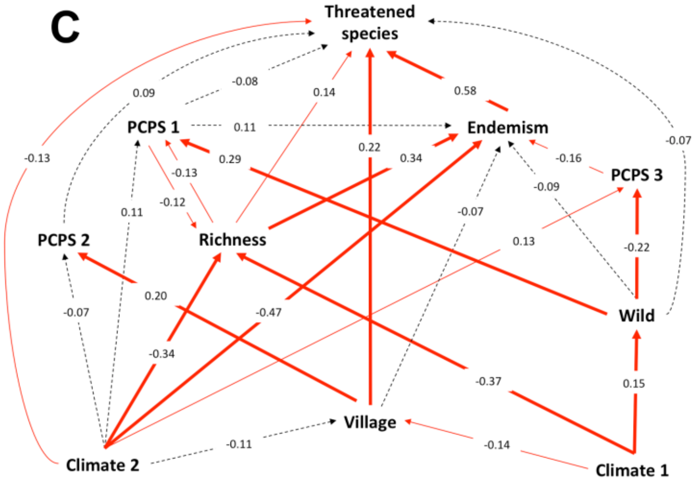
C
Threatened species
PCPS 1
Endemism
PCPS 3
PCPS 2
Richness
Wild
Village
Climate 2
Climate 1
-0.13
0.09
-0.08
0.14
0.58
0.11
0.22
0.34
-0.07
-0.16
0.29
-0.13
-0.09
-0.12
0.11
-0.07
0.13
-0.22
0.20
-0.07
-0.47
-0.34
-0.37
0.15
-0.11
-0.14

Figure 5 The final path model for the most urgent (a), the moderate (b) and the most inclusive (c) scenario, showing the causal relationships between climate axes (Climate) 1 and 2, proportion of village cover (Village) in each ecoregion, principal coordinates of phylogenetic structure (PCPS) 1, 2 and 3, amphibian richness (Richness) per ecoregion, the number of endemic species (Endemism) in each ecoregion and the number of threatened amphibian species in each ecoregion. Black dashed lines represent non-significant relationships between variables. Red lines represent significant path coefficients between variables and the line width represents the P value; narrow lines indicate to $0.05 \geq P \geq 0.01$ and thick lines indicate $P \leq 0.01$. The path coefficients in the arrows are the standardized regression coefficients. The P values were obtained by randomization test.

In our moderate scenario, endemism, the village anthrome and species richness were also the main predictors of threatened amphibian distribution (Figure 5b). The moderate scenario model included a new anthropogenic variable (proportion of wildlands), which did not showed a direct influence on threatened amphibian distribution, but had an association with phylogenetic structure by strongly influencing PCPS1 and PCPS3.

The most inclusive scenario showed climatic factors as determinant of the threatened amphibian distribution, apart from the importance of endemism, proportion of villages and species richness variables (Figure 5c). The effect of endemism in the threatened amphibian distribution was greater than in previous scenarios. A correlation table presenting the correlation coefficients between all the predictor variables and the number of threatened species in each scenario is presented in the Table S2.

Discussion

Despite the reported influence of climate on amphibian distribution [5], our models showed that the diversity components and anthromes are more important as direct predictors than the former one. Our results indicated that maybe climate and land use are acting in different time scales, with the climate operating in evolutionary time scales, influencing the richness, endemism and clade distribution of amphibians in the ecoregions. Now in the Anthropocene, when the current global extent of human transformation of ecosystems has already irreversibly altered the terrestrial biosphere [35], the conversion of wildlands to villages had a direct influence on the distribution of threatened amphibians. These results are straightforward and bring a sound message for amphibian conservation: the need to focus on land-use policies. Although scientists have long recognized and debated the direct and indirect effects of climate change on amphibian distribution, basing conservation actions upon such relationships may become a “Sisyphean task”. The feedback between climate and land use is well documented [36,37]. Therefore, regulating land use may have direct effects on both amphibian extinction and climate change, and may be more feasible task than stopping climatic change.

Our results point toward a better outcome of amphibian conservation efforts if they are to be founded on land-use policies not only at the landscape level, but also at broader spatial scales. However, most current amphibian conservation actions are generally either species or site-specific. Our analysis has a particular caveat when applied to local actions. Although our results indicate that land-use change could drive diversity patterns not only at the landscape level [38] but also at the continental one, our analyses are too coarse to provide on-the-ground conservation support for local decision making. We believe, however, that our approach could act as a first filter to define guidelines for broad-scale conservation planning. Hence, when important regions are identified, our findings could be scaled down to sites within these regions, which would imply result in more manageable planning units [39].

It is largely known that human activities impact amphibian diversity [4]. Nevertheless, different types of land use likely determine distinct negative impacts on amphibian populations and, consequently, their extinction. The village land use category, which is more common in the developing world, synthesizes a variety of human activities, including agriculture and cattle grazing, in a densely populated context (village is the second most-populated anthrome category used in the present study) [6]. One in four people live in agricultural villages [6]. Pekin & Pjanowski [40] also found a negative influence of village settlements for some mammals groups, such as primates, bats and carnivores. An important aspect of our study is that we noticed a strong influence of land use, which is a landscape variable, on a broad scale biodiversity assessment. Thus, to assess the general causes of high levels of amphibian threat and extinction thoroughly, evaluations based on large samples and broad geographic scales are imperative [41].

Amphibian species with small geographical ranges are more prone to extinction than those with broad distributions, since they are more likely to be exposed to threatening process throughout their entire range, generally present a low abundance and they are often habitat or environment specialists [42]. Not surprisingly, the number of endemic species was the main factor increasing the number of threatened species, since they were defined as species occurring in only one ecoregion. The distribution of threatened amphibians was also indirectly associated with the presence/absence of some clades in the ecoregions, as both phylogenetic gradients, PCPS1 and PCPS3, showed significant associations with the species richness and endemism respectively. We found that the richness was higher in ecoregions characterized by all but Hyloidea clades, and the number of endemic species was higher in ecoregions characterized by the presence of Basal Anura, Basal Neobatrachia, Microhylidae, Ranidae and some families from Hyloidea clade. Considering that richness and endemism presented a positive relation with the number of threatened species, these finding suggests some degree of phylogenetic signal at the metacommunity level [23] in relation to the PCPS 1 and PCPS 3. Corey & Waite [2] found a strong signal of extinction threat within the amphibian phylogeny; the Hyloidea, a superfamily of frogs, includes more Critically Endangered species than any other clade in the amphibian phylogeny [2]. We found that the presence of some families of Hyloidea increases the number of endemic species and consequently the number of threatened amphibian species, corroborating with the patterns found by Corey & Waite [2].

Furthermore, land use was important not only via direct effects, but also through indirect effects by determining the spatial distribution of amphibian phylogenetic lineages. That is to say, closely-related species tended to be assembled by similar land use types, suggesting phylogenetic habitat filtering [27] in the geographic distribution of amphibian lineages. The positive relationship between cover of village and PCPS2 indicates that the Microhylidae, Basal Anura, Ranidae clades and some families from Hyloidea clade was more representative in areas with high population density and consequently intensive land use. The advancement of agricultural and colonization frontiers could be leading these clades to extinction, since the land conversion to this activities leads to the use of pesticides and other chemicals due to agricultural activities, and habitat loss as a consequence of forest conversion to pasture or croplands, all of these impacts known to cause amphibian decline and extinction [4].

In conclusion, our results showed that land use was directly more important than climate in determining the distribution of threatened amphibian species across the New World. Nonetheless, a considerable portion of the effect of land use on species threat was phylogenetically structured, meaning that human impact on amphibian distribution affects not only species individually, but may also define the fate of entire lineages of this imperiled group.

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Supporting Information Legends

Table S1 Raw data of richness of amphibian species, endemism and number of threatened amphibian species according to the three different scenarios (urgent, moderate and most inclusive) for each ecoregion, which were used in the analysis. The urgent scenario, containing only CR species and those EW and EX, the moderate scenario containing all EN species and those at threat categories higher than EN (i.e. CR, EW, and EX), and the most inclusive scenario, which included all VU species and those at higher threat categories. The percentage values were calculated in relation to the total ecoregion richness.

Table S2 Pearson correlation coefficient between the number of threatened amphibian species according to the three different scenarios (urgent, moderate and most inclusive), richness of amphibian species, endemism, two climatic axes, proportion of cover of villages and wildlands and the three axes of phylogenetic structure, all in residual form, which were used in the path analyses.

Figure S1 Scaling-up of phylogenetic data from species to the site level employed in this study. Matrices are: SF with phylogenetic pairwise similarities of species, Q′ is a transposed matrix with degrees of species belonging to every other species based on SF, standardized within columns, W with presence of species in sites, P with phylogeny-weighted species composition. Principal coordinates analysis of P using an appropriate dissimilarity measure generates a matrix of principal coordinates of phylogenetic structure (PCPS) composed of sites described by eigenvectors (EV). (Adapted from Duarte et al., 2012)

Table S1. Raw data of richness of amphibian species, endemism and number of threatened amphibian species according to the three different scenarios (urgent, moderate and most inclusive) for each ecoregion, which were used in the analysis. The urgent scenario, containing only CR species and those EW and EX, the moderate scenario containing all EN species and those at threat categories higher than EN (i.e. CR, EW, and EX), and the most inclusive scenario, which included all VU species and those at higher threat categories. The percentage values were calculated in relation to the total ecoregion richness.

Ecoregion name	Richness	Endemism	Urgent scenario	Moderate scenario	Most inclusive scenario
Sierra Madre Occidental pine-oak forests	39	1 (2.6%)	0	0	5 (12.8%)
Sierra Madre Oriental pine-oak forests	39	3 (7.7%)	2 (5.1%)	7 (17.9%)	13 (33.3%)
Allegheny Highlands forests	27	0	0	0	0
Appalachian mixed mesophytic forests	58	1 (1.7%)	0	2 (3.4%)	3 (5.2%)
Appalachian-Blue Ridge forests	67	15 (22.4%)	0	1 (1.5%)	6 (9%)
Central U.S. hardwood forests	55	1 (1.8%)	0	0	1 (1.8%)
East Central Texas forests	29	0	0	1 (3.4%)	1 (3.4%)
Eastern forest-boreal transition	20	0	0	0	0
Eastern Great Lakes lowland forests	22	0	0	0	0
Gulf of St. Lawrence lowland forests	15	0	0	0	0
Mississippi lowland forests	35	0	0	0	0
New England-Acadian forests	20	0	0	0	0
Northeastern coastal forests	29	0	0	0	0
Ozark Mountain forests	39	3 (7.7%)	0	0	1 (2.6%)
Southeastern mixed forests	63	1 (1.6%)	0	2 (3.2%)	2 (3.2%)
Southern Great Lakes forests	33	0	0	0	0
Upper Midwest forest-savanna transition	22	0	0	0	0
Western Great Lakes forests	22	0	0	0	0
Willamette Valley forests	6	0	0	0	0
Alberta Mountain forests	4	0	0	0	0
Alberta-British Columbia foothills forests	5	0	0	0	0
Arizona Mountains forests	12	1 (8.3%)	0	0	1 (8.3%)
Atlantic coastal pine barrens	14	0	0	0	0
Blue Mountains forests	7	0	0	0	0
British Columbia mainland coastal forests	11	0	0	0	0
Cascade Mountains leeward forests	4	0	0	0	0
Central and Southern Cascades forests	20	3 (15%)	0	0	4 (20%)
Central British Columbia Mountain forests	4	0	0	0	0
Central Pacific coastal forests	19	0	0	0	2 (10.5%)

Colorado Rockies forests	7	0	0	0	0
Eastern Cascades forests	4	0	0	0	1 (25%)
Florida sand pine scrub	16	0	0	0	0
Fraser Plateau and Basin complex	5	0	0	0	0
Great Basin montane forests	4	0	0	0	0
Klamath-Siskiyou forests	15	0	0	0	0
Middle Atlantic coastal forests	49	2 (4.1%)	0	0	1 (2%)
North Central Rockies forests	9	2 (22.2%)	0	0	0
Northern California coastal forests	18	1 (5.6%)	0	0	1 (5.6%)
Northern Pacific coastal forests	4	0	0	0	0
Northern transitional alpine forests	5	0	0	0	1 (20%)
Okanagan dry forests	8	0	0	0	0
Piney Woods forests	35	0	0	0	0
Puget lowland forests	12	0	0	0	1 (8.3%)
Queen Charlotte Islands	1	0	0	0	0
Sierra Juarez and San Pedro Martir pine-oak forests	2	0	0	0	0
Sierra Nevada forests	13	3 (23.1%)	0	2 (15.4%)	4 (30.8%)
South Central Rockies forests	6	0	0	0	0
Southeastern conifer forests	53	4 (7.5%)	0	1 (1.9%)	4 (7.5%)
Wasatch and Uinta montane forests	7	0	0	0	0
Alaska Peninsula montane taiga	1	0	0	0	0
Central Canadian Shield forests	12	0	0	0	0
Cook Inlet taiga	1	0	0	0	0
Copper Plateau taiga	1	0	0	0	0
Eastern Canadian forests	12	0	0	0	0
Eastern Canadian Shield taiga	5	0	0	0	0
Interior Alaska-Yukon lowland taiga	1	0	0	0	0
Mid-Continental Canadian forests	6	0	0	0	1 (16.7%)
Midwestern Canadian Shield forests	7	0	0	0	0
Muskwa-Slave Lake forests	3	0	0	0	1 (33.3%)
Northern Canandian Shield taiga	3	0	0	0	0
Northern Cordillera forests	6	0	0	0	1 (16.7%)
Northwest Territories taiga	2	0	0	0	0
Southern Hudson Bay taiga	7	0	0	0	0
Yukon Interior dry forests	4	0	0	0	1 (25%)

Western Gulf coastal grasslands	32	0	0	2 (6.3%)	2 (6.3%)
California Central Valley grasslands	6	0	0	0	0
Canadian Aspen forests and parklands	9	0	0	0	0
Central and Southern mixed grasslands	19	0	0	0	0
Central forest-grasslands transition	44	0	0	0	0
Central tall grasslands	21	0	0	0	0
Edwards Plateau savanna	18	2 (11.1%)	0	0	2 (11.1%)
Flint Hills tall grasslands	15	0	0	0	0
Montana Valley and Foothill grasslands	8	0	0	0	0
Nebraska Sand Hills mixed grasslands	10	0	0	0	0
Northern mixed grasslands	15	0	0	0	0
Northern short grasslands	9	0	0	0	0
Northern tall grasslands	12	0	0	0	0
Palouse grasslands	8	0	0	0	0
Texas blackland prairies	33	3 (9.1%)	0	1 (3%)	3 (9.1%)
Western short grasslands	19	0	0	0	0
Alaska-St. Elias Range tundra	2	0	0	0	1 (50%)
Beringia lowland tundra	1	0	0	0	0
Beringia upland tundra	1	0	0	0	0
Interior Yukon-Alaska alpine tundra	1	0	0	0	0
Pacific Coastal Mountain icefields and tundra	5	0	0	0	1 (20%)
California coastal sage and chaparral	15	0	0	0	1 (6.7%)
California interior chaparral and woodlands	16	1 (6.3%)	0	0	2 (12.5%)
California montane chaparral and woodlands	14	1 (7.1%)	0	0	2 (14.3%)
Baja California desert	8	0	0	0	0
Central Mexican matorral	41	3 (7.3%)	5 (12.2%)	7 (17.1%)	13 (31.7%)
Chihuahuan desert	34	0	0	0	3 (8.8%)
Colorado Plateau shrublands	12	0	0	0	0
Great Basin shrub steppe	9	0	0	0	1 (11.1%)
Gulf of California xeric scrub	2	0	0	0	0
Meseta Central matorral	25	0	1 (4%)	4 (16%)	5 (20%)
Mojave desert	8	2 (25%)	0	2 (25%)	2 (25%)
Snake-Columbia shrub steppe	8	0	0	0	0
Sonoran desert	27	2 (7.4%)	0	0	0
Tamaulipan matorral	17	0	1 (5.9%)	2 (11.8%)	3 (17.6%)

Tamaulipan mezquital	29	0	0	1 (3.4%)	2 (6.9%)
Wyoming Basin shrub steppe	6	0	0	0	0
Araucaria moist forests	172	1 (0.6%)	3 (1.7%)	5 (2.9%)	6 (3.5%)
Atlantic Coast restingas	188	0	1 (0.5%)	2 (1.1%)	4 (2.1%)
Bahia coastal forests	95	0	0	0	3 (3.2%)
Bahia interior forests	145	1 (0.7%)	1 (0.7%)	2 (1.4%)	5 (3.4%)
Bolivian Yungas	53	24 (45.3%)	3 (5.7%)	7 (13.2%)	12 (22.6%)
Caatinga Enclaves moist forests	20	0	0	0	0
Caqueta moist forests	75	2 (2.7%)	1 (1.3%)	1 (1.3%)	1 (1.3%)
Catatumbo moist forests	3	0	0	0	0
Cauca Valley montane forests	58	20 (34.5%)	6 (10.3%)	14 (24.1%)	22 (37.9%)
Central American Atlantic moist forests	35	0	0	2 (5.7%)	3 (8.6%)
Central American montane forests	72	0	9 (12.5%)	28 (38.9%)	41 (56.9%)
Chiapas montane forests	46	1 (2.2%)	8 (17.4%)	12 (26.1%)	20 (43.5%)
Chimalapas montane forests	19	2 (10.5%)	3 (15.8%)	5 (26.3%)	7 (36.8%)
Chocó-Darién moist forests	137	24 (17.5%)	5 (3.6%)	9 (6.6%)	23 (16.8%)
Cordillera La Costa montane forests	40	26 (65%)	2 (5%)	8 (20%)	13 (32.5%)
Cordillera Oriental montane forests	82	25 (30.5%)	2 (2.4%)	11 (13.4%)	27 (32.9%)
Costa Rican seasonal moist forests	40	0	0	3 (7.5%)	4 (10%)
Cuban moist forests	37	2 (5.4%)	6 (16.2%)	21 (56.8%)	28 (75.7%)
Eastern Cordillera real montane forests	194	74 (38.1%)	14 (7.2%)	59 (30.4%)	84 (43.3%)
Eastern Panamanian montane forests	30	1 (3.3%)	0	0	2 (6.7%)
Guianan Highlands moist forests	98	17 (17.3%)	1 (1%)	1 (1%)	4 (4.1%)
Guianan moist forests	126	17 (13.5%)	0	0	3 (2.4%)
Gurupa varzea	31	0	0	0	1 (3.2%)
Hispaniolan moist forests	47	14 (29.8%)	23 (48.9%)	34 (72.3%)	40 (85.1%)
Iquitos varzea	127	1 (0.8%)	0	1 (0.8%)	2 (1.6%)
Isthmian-Atlantic moist forests	116	8 (6.9%)	4 (3.4%)	14 (12.1%)	26 (22.4%)
Isthmian-Pacific moist forests	97	4 (4.1%)	5 (5.2%)	9 (9.3%)	18 (18.6%)
Jamaican moist forests	19	7 (36.8%)	6 (31.6%)	14 (73.7%)	16 (84.2%)
Japurá-Solimoes-Negro moist forests	92	1 (1.1%)	0	0	1 (1.1%)
Juruá-Purus moist forests	63	0	0	0	0
Leeward Islands moist forests	11	0	1 (9.1%)	5 (45.5%)	5 (45.5%)
Madeira-Tapajós moist forests	50	0	0	0	0
Magdalena Valley montane forests	105	52 (49.5%)	12 (11.4%)	34 (32.4%)	57 (54.3%)

Magdalena-Urabá moist forests	46	3 (6.5%)	0	0	1 (2.2%)
Marajá varzea	53	0	0	0	1 (1.9%)
Maranhão Babaþu forests	26	0	0	0	0
Mato Grosso seasonal forests	49	0	0	0	0
Monte Alegre varzea	53	0	0	0	0
Napo moist forests	162	22 (13.6%)	0	3 (1.9%)	6 (3.7%)
Negro-Branco moist forests	67	3 (4.5%)	0	0	1 (1.5%)
Northeastern Brazil restingas	15	0	0	0	0
Northwestern Andean montane forests	213	111 (52.1%)	21 (9.9%)	59 (27.7%)	100 (46.9%)
Oaxacan montane forests	51	4 (7.8%)	8 (15.7%)	19 (37.3%)	24 (47.1%)
Orinoco Delta swamp forests	10	0	0	0	0
Pantanos de Centla	18	0	0	0	0
Guianan freshwater swamp forests	33	0	0	0	0
Alto Paranß Atlantic forests	285	0	6 (2.1%)	10 (3.5%)	12 (4.2%)
Pernambuco coastal forests	35	0	0	0	1 (2.9%)
Pernambuco interior forests	37	0	0	0	1 (2.7%)
Peruvian Yungas	116	64 (55.2%)	8 (6.9%)	24 (20.7%)	32 (27.6%)
Petén-Veracruz moist forests	101	9 (8.9%)	13 (12.9%)	31 (30.7%)	45 (44.6%)
Puerto Rican moist forests	17	11 (64.7%)	6 (35.3%)	11 (64.7%)	11 (64.7%)
Purus varzea	117	0	0	1 (0.9%)	2 (1.7%)
Purus-Madeira moist forests	64	0	0	0	0
Rio Negro campinarana	65	0	0	0	1 (1.5%)
Santa Marta montane forests	18	14 (77.8%)	5 (27.8%)	8 (44.4%)	9 (50%)
Serra do Mar coastal forests	233	4 (1.7%)	5 (2.1%)	6 (2.6%)	8 (3.4%)
Sierra de los Tuxtlas	40	5 (12.5%)	7 (17.5%)	9 (22.5%)	12 (30%)
Sierra Madre de Chiapas moist forests	44	2 (4.5%)	2 (4.5%)	9 (20.5%)	16 (36.4%)
Solimões-Japurá moist forests	131	0	0	1 (0.8%)	2 (1.5%)
South Florida rocklands	15	0	0	0	0
Southern Andean Yungas	49	4 (8.2%)	0	6 (12.2%)	11 (22.4%)
Southwest Amazon moist forests	168	14 (8.3%)	1 (0.6%)	2 (1.2%)	3 (1.8%)
Talamancan montane forests	122	37 (30.3%)	22 (18%)	40 (32.8%)	53 (43.4%)
Tapajós-Xingu moist forests	53	0	0	0	1 (1.9%)
Pantepui	52	28 (53.8%)	0	0	4 (7.7%)
Tocantins/Pindare moist forests	34	0	0	0	0
Trinidad and Tobago moist forests	2	0	0	1 (50%)	1 (50%)

Uatuma-Trombetas moist forests	89	0	0	0	1 (1.1%)
Ucayali moist forests	122	6 (4.9%)	0	1 (0.8%)	4 (3.3%)
Venezuelan Andes montane forests	55	35 (63.6%)	10 (18.2%)	26 (47.3%)	33 (60%)
Veracruz moist forests	58	4 (6.9%)	3 (5.2%)	13 (22.4%)	24 (41.4%)
Veracruz montane forests	27	2 (7.4%)	2 (7.4%)	6 (22.2%)	11 (40.7%)
Western Ecuador moist forests	85	10 (11.8%)	4 (4.7%)	11 (12.9%)	24 (28.2%)
Windward Islands moist forests	6	0	1 (16.7%)	2 (33.3%)	2 (33.3%)
Xingu-Tocantins-Araguaia moist forests	48	0	0	0	1 (2.1%)
Yucatán moist forests	35	0	0	1 (2.9%)	3 (8.6%)
Apure-Villavicencio dry forests	47	3 (6.4%)	1 (2.1%)	2 (4.3%)	2 (4.3%)
Atlantic dry forests	41	0	0	0	0
Bajío dry forests	33	0	0	3 (9.1%)	5 (15.2%)
Balsas dry forests	43	1 (2.3%)	2 (4.7%)	4 (9.3%)	12 (27.9%)
Bolivian montane dry forests	25	2 (8%)	0	1 (4%)	1 (4%)
Cauca Valley dry forests	6	0	0	0	0
Central American dry forests	36	0	2 (5.6%)	2 (5.6%)	3 (8.3%)
Dry Chaco	57	4 (7%)	1 (1.8%)	3 (5.3%)	3 (5.3%)
Chiapas Depression dry forests	33	0	2 (6.1%)	4 (12.1%)	8 (24.2%)
Chiquitano dry forests	54	0	0	0	0
Cuban dry forests	32	0	4 (12.5%)	16 (50%)	23 (71.9%)
Ecuadorian dry forests	13	0	0	0	1 (7.7%)
Hispaniolan dry forests	29	4 (13.8%)	13 (44.8%)	20 (69%)	24 (82.8%)
Jalisco dry forests	25	1 (4%)	1 (4%)	2 (8%)	3 (12%)
Jamaican dry forests	13	0	3 (23.1%)	9 (69.2%)	10 (76.9%)
Lara-Falcón dry forests	10	0	0	0	0
Lesser Antillean dry forests	6	0	1 (16.7%)	2 (33.3%)	2 (33.3%)
Magdalena Valley dry forests	19	0	0	0	0
Maracaibo dry forests	8	0	0	0	0
Marañón dry forests	4	0	1 (25%)	1 (25%)	1 (25%)
Panamanian dry forests	22	0	0	0	1 (4.5%)
Puerto Rican dry forests	6	0	1 (16.7%)	2 (33.3%)	2 (33.3%)
Sierra de la Laguna dry forests	2	0	0	0	0
Sinaloan dry forests	38	1 (2.6%)	1 (2.6%)	2 (5.3%)	7 (18.4%)
Sin· Valley dry forests	42	1 (2.4%)	1 (2.4%)	8 (19%)	12 (28.6%)
Southern Pacific dry forests	68	5 (7.4%)	9 (13.2%)	16 (23.5%)	26 (38.2%)

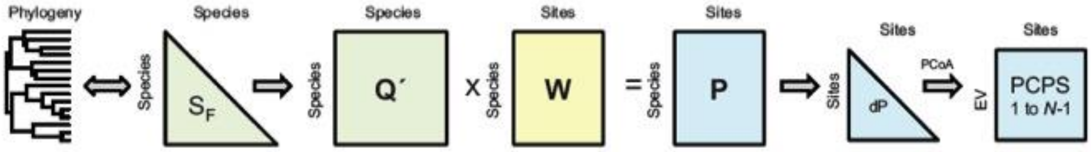
Tumbes-Piura dry forests	11	2 (18.2%)	0	1 (9.1%)	2 (18.2%)
Veracruz dry forests	26	0	0	2 (7.7%)	4 (15.4%)
Yucatán dry forests	19	1 (5.3%)	0	0	0
Bahamian pine mosaic	2	0	0	0	0
Belizian pine forests	14	0	0	0	0
Central American pine-oak forests	103	2 (1.9%)	15 (14.6%)	37 (35.9%)	52 (50.5%)
Cuban pine forests	23	0	1 (4.3%)	7 (30.4%)	14 (60.9%)
Hispaniolan pine forests	30	6 (20%)	11 (36.7%)	20 (66.7%)	24 (80%)
Sierra de la Laguna pine-oak forests	3	0	0	0	0
Sierra Madre del Sur pine-oak forests	13	0	0	0	0
Trans-Mexican Volcanic Belt pine-oak forests	78	8 (10.3%)	9 (11.5%)	25 (32.1%)	33 (42.3%)
Magellanic subpolar forests	12	2 (16.7%)	0	0	1 (8.3%)
Valdivian temperate forests	38	20 (52.6%)	6 (15.8%)	10 (26.3%)	17 (44.7%)
Beni savanna	29	0	0	0	0
Campos Rupestres montane savanna	113	0	2 (1.8%)	2 (1.8%)	3 (2.7%)
Cerrado	199	4 (2%)	4 (2%)	4 (2%)	5 (2.5%)
Guianan savanna	91	5 (5.5%)	0	0	2 (2.2%)
Humid Chaco	60	1 (1.7%)	1 (1.7%)	2 (3.3%)	2 (3.3%)
Llanos	39	1 (2.6%)	0	0	0
Uruguayan savanna	113	6 (5.3%)	1 (0.9%)	3 (2.7%)	6 (5.3%)
Espinal	29	1 (3.4%)	1 (3.4%)	1 (3.4%)	2 (6.9%)
Low Monte	10	0	1 (10%)	3 (30%)	4 (40%)
Humid Pampas	36	0	1 (2.8%)	2 (5.6%)	2 (5.6%)
Patagonian steppe	13	4 (30.8%)	0	4 (30.8%)	6 (46.2%)
Cuban wetlands	16	0	0	3 (18.8%)	8 (50%)
Enriquillo wetlands	9	0	0	2 (22.2%)	5 (55.6%)
Everglades	19	0	0	0	0
Guayaquil flooded grasslands	8	0	0	0	1 (12.5%)
Pantanal	54	0	0	0	0
Paraná flooded savanna	44	0	1 (2.3%)	2 (4.5%)	2 (4.5%)
Southern Cone Mesopotamian savanna	25	0	1 (4%)	1 (4%)	1 (4%)
Central Andean dry puna	14	5 (35.7%)	3 (21.4%)	5 (35.7%)	8 (57.1%)
Central Andean puna	24	4 (16.7%)	1 (4.2%)	4 (16.7%)	9 (37.5%)
Central Andean wet puna	21	11 (52.4%)	3 (14.3%)	7 (33.3%)	10 (47.6%)
Cordillera Central páramo	14	7 (50%)	3 (21.4%)	7 (50%)	7 (50%)

Cordillera de Merida páramo	3	1 (33.3%)	2 (66.7%)	2 (66.7%)	2 (66.7%)
Northern Andean páramo	89	37 (41.6%)	14 (15.7%)	40 (44.9%)	51 (57.3%)
Santa Marta páramo	2	0	2 (100%)	2 (100%)	2 (100%)
Southern Andean steppe	14	4 (28.6%)	2 (14.3%)	3 (21.4%)	4 (28.6%)
High Monte	11	1 (9.1%)	0	2 (18.2%)	4 (36.4%)
Chilean matorral	5	1 (20%)	0	0	0
Araya and Paria xeric scrub	1	0	0	0	0
Caatinga	49	0	0	0	1 (2%)
Caribbean shrublands	14	0	1 (7.1%)	4 (28.6%)	6 (42.9%)
Cuban cactus scrub	24	0	1 (4.2%)	12 (50%)	16 (66.7%)
Guajira-Barranquilla xeric scrub	8	1 (12.5%)	0	0	0
La Costa xeric shrublands	12	0	0	0	0
Motagua Valley thornscrub	23	0	0	0	0
Paraguana xeric scrub	2	0	0	0	0
San Lucan xeric scrub	2	0	0	0	0
Sechura desert	7	3 (42.9%)	0	0	2 (28.6%)
Tehuacán Valley matorral	29	3 (10.3%)	2 (6.9%)	7 (24.1%)	9 (31%)
Amazon-Orinoco-Southern Caribbean mangroves	14	0	0	1 (7.1%)	2 (14.3%)
Bahamian-Antillean mangroves	58	0	8 (13.8%)	25 (43.1%)	33 (56.9%)
Mesoamerican Gulf-Caribbean mangroves	52	0	0	0	5 (9.6%)
South American Pacific mangroves	34	0	0	0	2 (5.9%)
Southern Atlantic mangroves	59	0	1 (1.7%)	1 (1.7%)	1 (1.7%)
Southern Mesoamerican Pacific mangroves	54	0	0	0	3 (5.6%)

Table S2. Pearson correlation coefficient between the number of threatened amphibian species according to the three different scenarios (urgent, moderate and most inclusive), richness of amphibian species, endemism, two climatic axes, proportion of cover of villages and wildlands and the three axes of phylogenetic structure, all in residual form, which were used in the path analyses.

	Urgent	**Moderate**	**Most Inclusive**
Richness	0.46	0.49	0.53
Endemism	0.63	0.73	0.78
Climate 1	-0.05	-0.05	-0.09
Climate 2	-0.50	-0.54	-0.58
Village	0.33	0.27	0.24
Wildlands	-	-0.14	-0.14
PCPS1	-0.14	-0.14	-0.15
PCPS2	0.20	0.21	0.21
PCPS3	-0.15	-0.19	-0.17

Figure S1. Scaling-up of phylogenetic data from species to the site level employed in this study. Matrices are: SF with phylogenetic pairwise similarities of species, Q′ is a transposed matrix with degrees of species belonging to every other species based on SF, standardized within columns, W with presence of species in sites, P with phylogeny-weighted species composition. Principal coordinates analysis of P using an appropriate dissimilarity measure generates a matrix of principal coordinates of phylogenetic structure (PCPS) composed of sites described by eigenvectors (EV). (Adapted from Duarte et al., 2012)



CAPÍTULO 2[2]

Clade-specific impacts of human land use on primates

Short Title: Clade-specific association with land use

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ABSTRACT

Here we applied phylogenetically-based conservation analyses using a novel multivariate approach to better evaluate the effects of human land use on different primate lineages worldwide. Using a 1° x 1° grid, we obtained information on primate species distribution and the cover of six land use categories (Urban, Village, Cropland, Rangeland, Seminatural and Wild). We synthesized the phylogenetic composition into principal coordinates of phylogenetic structure. We correlated phylogenetic composition and land use in each region, and assessed statistical significance via null model. In America, the Atelidae clade was associated to areas with larger coverage of villages whereas Pitheciidae was found on areas with higher cover of wildlands. Moreover, we found some Atelidae, Callitrichidae and Pitheciidae species to be associated with seminatural areas, while other *Alouatta* and *Callicebus* species were more related with higher coverage of rangelands. In Madagascar, Lemuridae was negatively associated with wild areas. Africa did not show any statistically significant association between clades and land use. Asia had an intense association of some Cercopithecidae species with high coverage of villages. Primate lineages are currently facing different land use pressures, what would imply in the need of clade-specific conservation planning.

Key words: Anthropogenic biomes, human impact, primate conservation, principal coordinates of phylogenetic structure – PCPS.

INTRODUCTION

Approximately 75% of Earth’s ice-free land has been altered by humans (Ellis & Ramankutty 2008) and such alterations have modified global patterns of biodiversity. Over the last decades, increased information on human activities across the globe has enabled us to evaluate the effects of such human activities on biodiversity at broad geographical scales (Brum *et al.* 2013; Harcourt & Parks 2003; Pekin & Pijanowski 2012). Commonly, these evaluations have been conducted using species as foci of the research (Davidson *et al.* 2012; Pekin & Pijanowski 2012). However, phylogenetic relationships among taxa are also an important measure for conservation biology (Faith 1992; Vane-Wright *et al.* 1991). Most phylogenetic approaches are limited because they summarize phylogenetic diversity in a single metric, such as the phylogenetic diversity index (PD; Faith 1992), which can obscure which clades are influenced by different sorts of threats. In fact, clades may be affected disproportionally by human disturbances, which, in turn, will determine the relationships among different regions of the phylogeny, providing clues for conservation interventions (Loyola *et al.* 2014). Here we applied phylogenetically-based conservation analyses using a novel multivariate approach to better evaluate what threats impact different lineages.

Much of the variation in species’ extinction risk is associated with spatial patterns of human threats and depends on how different species respond to threats (Cardillo & Meijaard 2012; Purvis; Agapow; *et al.* 2000). Human land-uses are unevenly distributed across the globe (Ellis & Ramankutty 2008), and different types of land use can have different impacts on biodiversity. For example tropical regions, which shelter much of global biodiversity, suffer from intense deforestation, condemning forest species to local extinction (Hansen *et al.* 2013). High human population densities in Asia lead to a direct conservation conflict between human populations and wild species, which result in increased hunting pressure (IUCN 2013).

Phylogenetic relatedness may influence how species respond to human impacts. Closely-related species are likely to show high trait similarity (Felsenstein 1985) and, consequently, could respond similarly to threats. In other words, species with high extinction risk sharing the same phylogenetic affinities and ecological traits may be more prone to go extinct. In contrast, unrelated species might respond differently to human threats. As a result, it may be useful to consider phylogenetic relatedness in conservation assessments and planning (Cardillo & Meijaard 2012; Corey 2010; Hidasi-Neto *et al.* 2013; Loyola *et al.* 2014).

One common way to quantify phylogenetic relatedness is to use diversity metrics based on phylogenetic distance. The most frequently used metric is Faith´s PD (Faith 1992), which sums the branch lengths of the phylogenetic tree connecting all species within a community (Faith 1992). However, phylogenetic diversity metrics synthesize phylogenetic information into one single value. As a consequence, other aspects of phylogenetic diversity are neglected. Hence, it is important to not only know how much diversity is found in a given location, but what that diversity is, especially since different lineages likely respond to different threats (Davidson *et al.* 2012; Pekin & Pijanowski 2012). To address this shortcoming we used a metacommunity phylogenetics approach, which describes the distribution of different phylogenetic lineages across a set of communities using fuzzy sets defined by species' phylogenetic similarities (Duarte 2011; Pillar & Duarte 2010). By using this approach, we could assess the main anthropogenic pressure acting on individual lineages.

Primates represent an important case study on which to apply our methods because nearly half of all the world's primates are currently threatened (IUCN 2013). Primates are mainly threatened by habitat destruction, hunting (for food and other purposes) and live capture for export or local trade (Chapman & Peres 2001; Mittermeier *et al.* 2012). Not surprisingly, the mechanisms underlying the increased extinction risk in primates are directly linked to human population growth and social-economic activities (Benchimol & Peres 2013; Chapman & Peres 2001; Harcourt & Parks 2003). While much has been done on the impact of with human activities on primate species, only few studies evaluated how these impacts influence phylogenetic diversity beyond simply quantify loss of phylogenetic diversity (Sechrest *et al.* 2002; Spathelf & Waite 2007).

In this paper, we did a broad-scale evaluation on the association between land use and primate phylogenetic composition to answer the following question: what human impacts have the strongest influence on primate clades in each continent and Madagascar? For this, we evaluated if there is an association between the distribution of primate lineages and particular types of land use. We discuss the potential threats most likely impact each clade.

METHODS

Primate occurrence data

We obtained primate species occurrences by overlapping the range maps from the Global Mammal Assessment (IUCN 2013) on to a 1° x 1° grid. Only cells with presences were used for further analysis. We split the occurrence data per continent; Madagascar was analyzed separately from continental Africa, due to its historical isolation, which generated a completely distinct biota in this island (Lehman & Fleagle 2006). We used primate species composition in each cell for further analyses.

Phylogenetic composition

We used the phylogenetic hypothesis from Perelman *et al.* (2011), which includes phylogenetic relationship between 186 primate species from 61 genera and estimated divergence time for each node in MYA. Species were arranged as polytomies inside de node of the genera, and genera and species absent in Perelman’s phylogeny were inserted based on literature information (see Supplementary Material). The phylogeny used in the analyses contained 416 primate species, from 72 genera, and the branch lengths were dated in MYA. Then we assessed the phylogenetic composition of primate clades in each continent and Madagascar performing the phylogenetic fuzzy-weighting method developed by Pillar and Duarte (2010), using the package *SYNCSA* (Debastiani & Pillar 2012) and *ape* (Paradis *et al.* 2004) in the R software. This method uses phylogenetic similarities between taxa to scale-up the phylogenetic relationships from taxa to the site level. First, pairwise phylogenetic distances between species were taken form the phylogeny, and then transformed into a phylogenetic similarity matrix ($\mathbf{S}_P$) ranging from 0 to 1. Then, phylogenetic similarities in $\mathbf{S}_P$ were used to weight primate species composition in each cell, using a fuzzy set algorithm (see Pillar & Duarte 2010 for details). This procedure generated a matrix **P** of species by cells containing primate species composition weighted by phylogenetic relationships. Each value in matrix **P** is the probability of a given species to occur in a cell given its phylogenetic similarities to the species that were actually found the cell. We then performed a principal coordinates analysis (PCoA) on matrix **P**, based on square-root of Bray-Curtis distances between cells, which generated principal coordinates of phylogenetic structure (PCPS; Duarte 2011). Each PCPS is a vector describing an independent phylogenetic gradient in the dataset (Duarte 2011). The PCPS with the highest eigenvalue describes broader phylogenetic gradients related to the oldest tree nodes and, as the eigenvalues of the other PCPS decrease, finer phylogenetic gradients related to higher nodes (e.g., families, genera) are described (Duarte *et al.* 2012). Then, the associations between primate phylogenetic clades and each phylogenetic vector in each continent were plotted in a correlation scatter plot.

Land use

We used the Ellis and Ramankutty’s (2008) reclassification of global land cover into “anthropogenic biomes“ or “anthromes“. They identified and mapped 18 anthropogenic biomes using a multi-stage process based on global data for population density, land use and land cover. Using GIS processing, we obtained the cover of each land use per 1°x1° cell. In order to facilitate the interpretation of our results, we synthesized the cover of the 18 categories into six major land use categories, in decreasing order of human population density: urban (1788 persons/km^2), villages (327 persons/km^2), croplands (33 persons/km^2), rangelands (7 persons/km^2), seminatural (1 person/km^2) and wild (0 person/km^2). The proportion of cover of each land use category per cell was treated as separate variables in the analyses.

Statistical analysis

We measured the association between the distribution of primate clades and land use types in each continent using Pearson correlation coefficient (*r*). For each continent, we correlated each land use type with the PCPS axes containing more than 5% of the total variation on the **P** matrix, to avoid including low representative axes in the analysis.

We used a null model to ensure that the observed association between some primate lineages and specific land use types is different of what would be expected if the clades were randomly distributed across the space (Debastiani *et al.* 2014). For this, we built 999 random trees where tree tips (species names) where shuffled across the tree. As a result the phylogenetic distance between any pair of species across the phylogenetic tree changed in each random tree. At each tree randomization, we recalculated the matrix **P** and the PCPS axes.

The PCPS null axes were submitted individually to a procrustean adjustment with the respective observed PCPS, this procedure is necessary for compare two distinct axis of ordination. Procrustes analysis minimizes the differences in the sum of squares between two data sets (Jackson 1995) and allows obtain the fitted PCPS null. The adjusted PCPS null axes, which can be compared with the observed PCPS, were correlated to land use. In the end, we had a distribution of 1000 Pearson correlation values (999 random plus 1 observed) for each PCPS-land use pair (e.g., PCPS1 vs. cover of villages). The rank position of each observed correlation in relation to random correlations defined the probability *P* of the observed coefficient being different of what we could expect by randomizing lineages distribution. As correlation coefficients could be either positive or negative, we used a two-tailed test. Thus, assuming a type I error probability of 0.05, any observed correlation with *P* values lower than 0.025 or higher than 0.975 were considered significant. It is important to note that the null model kept the species occurrence matrix (species by cells) fixed and therefore controlled for spatial autocorrelation (Pillar & Duarte 2010).

RESULTS

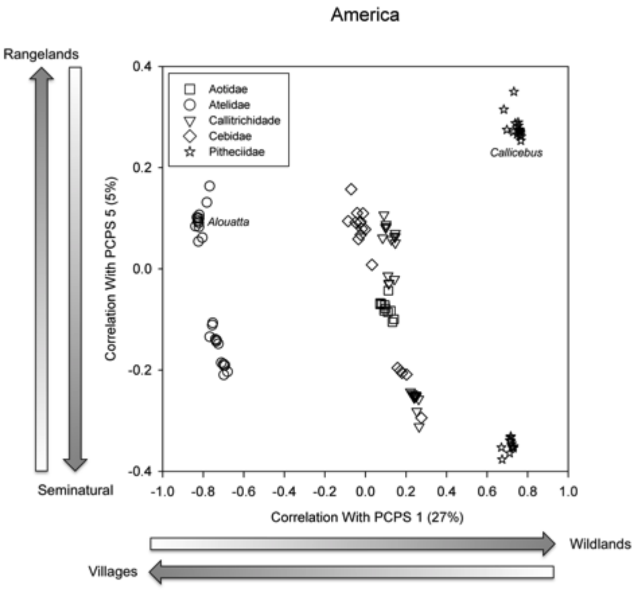
We analyzed the phylogenetic distribution of 416 primate species, being 141 species from five families (Aotidae, Atelidae, Callitrichidae, Cebidae and Pitheciidae) occurring in America, 83 species from four families (Cercopithecidae, Galagidae, Hominidae and Lorisidae) in continental Africa, 93 from five families (Cheirogaleidae, Daubentoniidae, Indriidae, Lemuridae, Lepilemuridae) in Madagascar and 99 species from five families (Cercopithecidae, Hominidae, Hylobatidae, Lorisidae and Tarsiidae) in Asia. All the lineages occurring in America and Madagascar are exclusive of these regions, while Africa and Asia share three families (Hominidae, Lorisidae and Cercopithecidae).

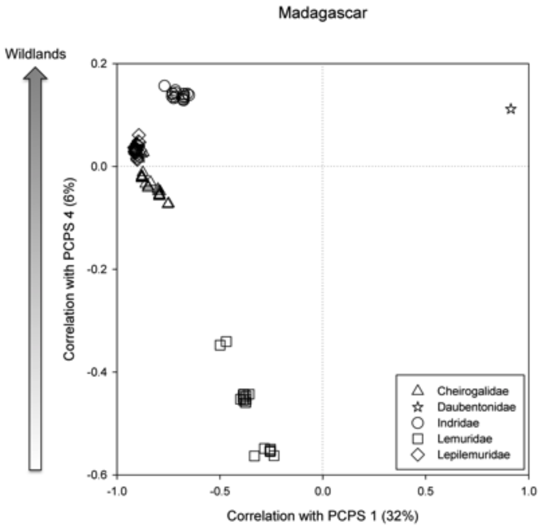
In America, only two axes of primate phylogenetic composition (PCPS1 and PCPS 5) held significant correlation with land use, specifically the cover of villages, rangelands, seminatural lands and wildlands (Table 1). The PCPS 1 was correlated with an opposite gradient of villages and wildlands (Table1), being the Atelidae clade the one more associated to areas with higher villages and Pitheciidae with higher cover of wildlands (Fig. 1). In relation of PCPS 5, this axis was correlated with rangeland and seminatural areas (Table 1).

We found some species from Atelidae, Callitrichidae and Pitheciidae associated with these seminatural areas, while *Alouatta* (Atelidae) and *Callicebus* (Pitheciidae) species were more related with areas with higher cover of rangelands (Fig. 1).

Table 1. Pearson correlation coefficients (*r*) between land use cover and principal coordinates of phylogenetic structure (PCPS) in the regions that presented at least one significant correlation coefficient (America, Madagascar and Asia). The values in bold indicate significance of the correlation coefficient, with P values, obtained by the null model (see main text for explanation), being lower than 0.025 or higher than 0.975. Africa did not present any significant correlation coefficient and was not included in this table.

	Pearson correlation coefficient (*r*)					
	Urban	Village	Cropland	Rangeland	Seminatural	Wildland
America						
PCPS1	-0.175	**-0.346**	-0.412	-0.174	0.338	**0.445**
PCPS5	0.066	0.104	0.181	**0.399**	**-0.385**	-0.238
Madagascar						
PCPS4	0.060	0.010	0.070	-0.131	0.110	**0.253**
Asia						
PCPS4	-0.091	**0.345**	0.102	-0.151	-0.147	-0.009


America
Rangelands
Seminatural
Aotidae
Atelidae
Callitrichidade
Cebidae
Pitheciidae
Callicebus
Alouatta
Correlation With PCPS 5 (5%)
0.4
0.2
0.0
-0.2
-0.4
-1.0
-0.8
-0.6
-0.4
-0.2
0.0
0.2
0.4
0.6
0.8
1.0
Correlation With PCPS 1 (27%)
Wildlands
Villages


Madagascar
Wildlands
Correlation with PCPS 4 (6%)
0.2
0.0
-0.2
-0.4
-0.6
-1.0
-0.5
0.0
0.5
1.0
Correlation with PCPS 1 (32%)
Cheirogalidae
Daubentonidae
Indridae
Lemuridae
Lepilemuridae

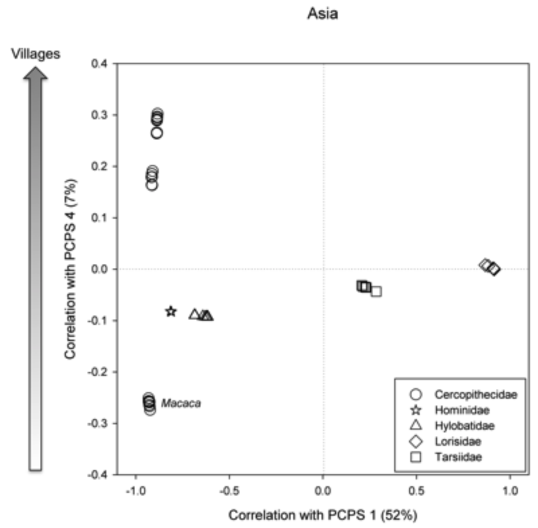

Asia
Villages
Correlation with PCPS 4 (7%)
0.4
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
-0.4
-1.0
-0.5
0.0
0.5
1.0
Correlation with PCPS 1 (52%)
Macaca
Cercopithecidae
Hominidae
Hylobatidae
Lorisidae
Tarsiidae

Figure 1. Correlation scatter plot for primate phylogenetic clades and land use categories showing correlation values with the principal coordinates of phylogenetic structure (PCPS) in America, Madagascar and Asia. Each point represents a primate species and species are grouped within families represented by different symbols. Arrows indicate the direction of the correlation between the principal coordinates of phylogenetic structure (PCPS) and the cover of land-use categories. The names in italic correspond to a specific genus inside the family.

We did not find any clear association between land use cover and distribution of phylogenetic clades in continental African primates. The fourth axis of phylogenetic composition of Madagascarian primates was significantly associated with the cover of wildlands (Table 1). All clades but Lemuridae were associated with areas with higher cover of wildlands (Fig. 1). In Asia, the cover of villages was significantly correlated to phylogenetic composition of primate clades in the axis four (Table 1), being some Cercopithecidae species (all but *Macaca* species) strongly associated with the higher cover of villages (Fig. 1).

DISCUSSION

We found that primate lineages respond differently to human land uses and their response differed among regions. Considering that regions vary greatly regarding their biogeographic history and the intensity of land transformation, and have distinct primate assemblages (Ellis *et al.* 2010; Lehman & Fleagle 2006), it is not surprising that we did not find the same pattern across all regions. Knowledge on clades-specific threats across regions can provide insight needed to design effective clade-specific conservation plans (Corey 2010; Loyola *et al.* 2014). This approach has been used in studies involving amphibians, to identify causes of population decline in Hylidae (Corey 2010) and to quantify and map the efficiency of protected areas in protect biodiversity from threats, e.g. climate change (Loyola *et al.* 2014).

The association between land use and phylogenetic primate composition was stronger in America than in the other regions (see Table 1). Considering the recent intense occupation of the American continent (approx. 100 years, Ellis *et al.* 2010), the extinction debt in the Neotropical primates may not have been paid yet (Kuussaari *et al.* 2009), resulting in greater overlap between the distribution of primate species and the distribution of humans. In particular, the Atelidae clade and some species from Pithecidae are more represented in areas with high cover of villages and rangelands. The advancement of colonization frontiers that result in high human population density and removal of natural vegetation for rangeland could be leading this clades to decline (Ellis & Ramankutty 2008), impacting any species that depends on forests, including primates (Lehman & Fleagle 2006). From the five Neotropical primate species included in the last list of the World's top 25 most endangered primates (Mittermeier *et al.* 2012), three are from the Atelidae family and one is from Pitheciidae. This information highlights the need of a special care with this region and especially with these two families, because without a specific conservation program for these groups and a conscious occupation of the landscape, their population decline can be irreversible.

The fact that we did not find any association between primate clades and land use in Africa does not mean that there is no conservation conflict between primates and human activities in this continent, as we know that deforestation, logging and hunting are serious issues for African primate conservation (Chapman & Peres 2001; Mittermeier *et al.* 2012). There are three possible reasons for this result: firstly, the contact between human and non-human primate populations is very old on this continent, and the extant taxa would be a set resistant survivors from the past changes (Harcourt & Parks 2003). Second, given that African primates use woodlands and wooded grasslands as well as forests (Chapman & Peres 2001), they may be able to use open habitats created by humans. Lastly, the choice of constrain the analyses to axes with at least 5% of variation could have limited the phylogenetic scale that we were able to evaluate. The phylogenetic axes with higher eigenvalues describe broader phylogenetic and, as the eigenvalues decrease, finer phylogenetic gradients are represented (Duarte *et al.* 2012). The coarse phylogenetic scale we analyzed may not be suitable for identifying the relationship between land-use and threat in African primates, perhaps because human pressure occurs at finer phylogenetic scales, or even operates at species level.

Primate lineages from Madagascar were negatively related with wildland cover, what implies in higher cover of other and more populated land uses. Specially, the Lemuridae family, a clade that is highly threatened, was associated with areas with low cover of wildlands. Since the arrival of humans 2000 years ago, the island lost approximately 90% of its original forest cover, driving several species to extinction. Most of the forests in Madagascar were converted to agricultural areas based on the slash-and-burn techniques, and the remaining forests become increasingly fragmented (Lehman & Fleagle 2006), decreasing the habitat suitability and increasing the hunting pressure on the primate populations. The extant species in Madagascar could be the resistant that left and their ranges are just a fraction of what they were once (Harcourt & Parks 2003).

We found a strong association of village cover with phylogenetic structure in Asian primates, mainly related with Cercopithecidae clade. Asia landscape has a long history of agricultural activities (Lehman & Fleagle 2006), leading several primate species to extinction (Zhang & Quan 1981). Tropical Asia presents higher human population density and, consequently, higher cover of villages than any other tropical continent (Ellis & Ramankutty 2008; Harcourt & Parks 2003). The contact with high human densities exposes the primates not only to habitat degradation, but also to hunting pressure (Chapman & Peres 2001). Asian primates are strongly threatened by hunting for several purposes, as for pet trade, meat and traditional medicine (Mittermeier *et al.* 2012). In China and India, *Macaca* species are forced to live at elevation over 3000 m to escape from deforestation and species living near to farms are reputed to raid crops and end up hunted (Srivastava 2006; Zhang & Quan 1981). It shows that in Asia, and especially for the Cercopithecidae family, the direct contact with human population is a critical pathway to primate extinction.

Finally, primate clades are facing different land use pressure around the world, and it implies in the need of clade-specific conservation planning. In two continents (America and Asia) we found significant correlations between the distribution of clades and densely populated land use (village), specially affecting Atelidae and Cercopithecidae species. Knowing that the major threats to biodiversity result from human population growth, and that human population will keep growing, the primate clades that are now facing more densely populated lands should be prioritized, because the conservation conflicts tend to increase.

Here we showed a new way to use phylogenetic information in conservation assessments, far beyond the phylogenetic diversity. The inclusion of phylogenetic composition could benefit conservation studies by showing if a specific lineage is more threatened than another and what is the main threat for each one. Attention should be paid to clades with higher susceptibly, because their extinction could lead not only to the loss of species, but also to a huge loss of evolutionary history and ecosystems services.

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Supplementary Material
Brum et al. 2014 – N&C051-2014

List of the references used to insert the absent primate genera in the phylogeny.

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CAPÍTULO 3[3]

Spatial mismatch among conservation priorities across different dimensions of mammal diversity

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Abstract

A major goal in conservation science is to identify priority areas for conservation, where limited resources can be used to maximize protection of biodiversity. Globally important regions for mammal conservation have been identified, but how they capture the different dimensions of mammal diversity (i.e. phylogenetic, trait and taxonomic patterns of diversity), and how these dimensions relate to each other spatially across the globe is poorly known. Here, we developed conservation schemes to identify and compare important regions for global mammal conservation across the dimensions of biodiversity, under a systematic conservation planning approach. We also evaluate how these regions are congruent and overlap with the geographic range of threatened species, the location of existing protected areas, and the distribution of current and future human impacts. We found that important areas for mammal conservation did not match across the three dimensions of biodiversity and this result carry consequences for policy and decision- making at the global scale. We also found that current protected areas do not protect species richness, phylogenetic diversity, trait diversity and threatened species as much as areas selected across the three dimensions. Some of the areas selected as important for all three dimensions of mammalian biodiversity also hold high human population density, such as the tropical forests in Indonesia, or are in regions projected to experience rapid climate change, such as the Amazon forest and central Australia. These results show the need for conservation action in these regions. The mismatch of the conservation priorities across the different dimension highlights the necessity of an integrative approach to biodiversity conservation.

Introduction

Approximately a quarter of all land mammals are currently threatened, mostly by human activities including habitat loss and harvesting (IUCN 2013; Schipper *et al.* 2008). Recently global phylogenetic, trait and taxonomic patterns of diversity (Davies *et al.* 2008; Fritz & Purvis 2010; Huang *et al.* 2012; Rodrigues *et al.* 2011; Safi *et al.* 2011), extinction risk (Davidson *et al.* 2009; Fritz & Purvis 2010; Purvis; Gittleman; *et al.* 2000) and threat (Jono & Pavoine 2012; Murray *et al.* 2014) have been explored in a variety of geographic and environmental contexts concerning mammal conservation (see also special issue of Phil Trans 2011).

Given that resources are limited, identifying conservation priorities is a key element for developing comprehensive conservation strategies (Margules & Pressey 2000; Rondinini *et al.* 2011). Traditionally, global conservation strategies have been identified based on species endemism and vulnerability (Brooks *et al.* 2006). However, it is important to use as many biological features as possible to develop conservation strategies (Watson *et al.* 2011). Globally important regions for mammal species have been identified (Brooks *et al.* 2006; Jenkins *et al.* 2013; Rodrigues *et al.* 2004), but just a few were based on the different dimensions of mammal biodiversity, i.e. taxonomic, functional and phylogenetic diversities, simultaneously (Mazel *et al.* 2014; Sobral *et al.* 2014)

Biodiversity is complex feature, and maintaining this complexity is the goal of conservation planning (Margules & Pressey 2000). Species richness can not represent alone the other facets of diversity, as differences in ecological traits and evolutionary affinities. The need of integrative approaches in Ecology and Conservation is imperative to better understand the processes and mechanisms generating and maintaining the observed diversity and to better inform spatial priorities for conservation. While taxonomic dimension accounts only for the number and identity of species in a given place, the functional dimension reflects ecological, morphological and physiological strategies of species within an ecological community (Petchey & Gaston 2002), being related to the provision of ecosystem goods and services (Díaz *et al.* 2007). The evolutionary history of species could help us to infer processes in community ecology (Webb *et al.* 2002) and influence species susceptibility to extinction (Davidson *et al.* 2012; Purvis; Agapow; *et al.* 2000). The need for an integrative approach have been argued as the next step in conservation science, although how these dimensions relate to each other across the globe is poorly know.

Even though some studies had showed a high correlation between taxonomic, functional and phylogenetic diversity of global mammals (Huang *et al.* 2012; Safi *et al.* 2011), especially when using diversity indexes affected by species richness (as PD and FD), the congruence of conservation priorities based on the different dimensions still is an interesting endeavor. Recently, Mazel et al. (2014, (Mazel *et al.* 2014)) verified strong geographical mismatches between hotspots of mammal taxonomic/phylogenetic/functional diversity of mammals. Low congruence was also found in prioritization analyses based on taxonomic, functional and phylogenetic diversity of birds and mammals occurring in Brazil (Sobral *et al.* 2014). We then hypothesized that the conservation priorities based on the taxonomic, phylogenetic and functional dimensions of global mammals will present low congruence.

Most of the prioritization analyses for mammals found in the literature incorporate taxonomic, phylogenetic and functional information by using alpha diversity indexes (Huang *et al.* 2012; Mazel *et al.* 2014; Rodrigues *et al.* 2011; Sobral *et al.* 2014). The problem is that selecting priority areas for conservation based on high alpha diversity could lead to an under-representative solution, because alpha diversity indexes do not take into account the differences in species/traits/lineages composition between sites. Here we present a more comprehensive solution to spatial prioritization, using a complementarity-based site selection approach.

By using the hierarchical ranking of cells created by Zonation analyses, we aimed to identify important areas for terrestrial mammal conservation, based on the taxonomic/trait/phylogenetic dimensions separately, how the conservation solutions for the dimensions relate to each other, and how they relate to current protected areas, and current and projected human threats. Following the Strategic Plan 2011–2020 of the Convention on Biological Diversity (CBD 2010), we used a cutoff of 17% to define the spatial extent of our conservation plans.

Results and Discussion

What are the important regions for mammal species across the 3 dimensions of mammalian biodiversity? Are the important regions congruent across the dimensions?

We found that the important areas for mammal conservation presented a different spatial pattern across the three dimensions of biodiversity (Figure 1A-C). For the top 17% of sites having the highest conservation values for mammal conservation, the solution based on taxonomic dimension was spatially scattered, while the phylogenetic and trait-based areas were more spatially aggregated (Figure 1 A-C). The areas with greatest conservation values based on phylogeny and traits were similar, what could be explained by niche conservatism (Wiens & Graham 2005), but there were important differences as well. For example, conservation values for cells in Australia were higher in the phylogeny-based solution than in the trait-based solution. Almost half of the native land mammals from Australia are monotremes or marsupials, lineages from early divergence in mammal's evolution, so the mammals from Australia are phylogenetically distinct from the rest of the world. However, the ecological traits of Australian Marsupials are functionally very similar to placental species, and are classic examples of ecological convergence. This may explain why Australia had more important areas when we considered phylogenetic information rather than trait information in the prioritization analyses, and suggests we are successfully capturing different facets of biodiversity in our prioritization analyses.

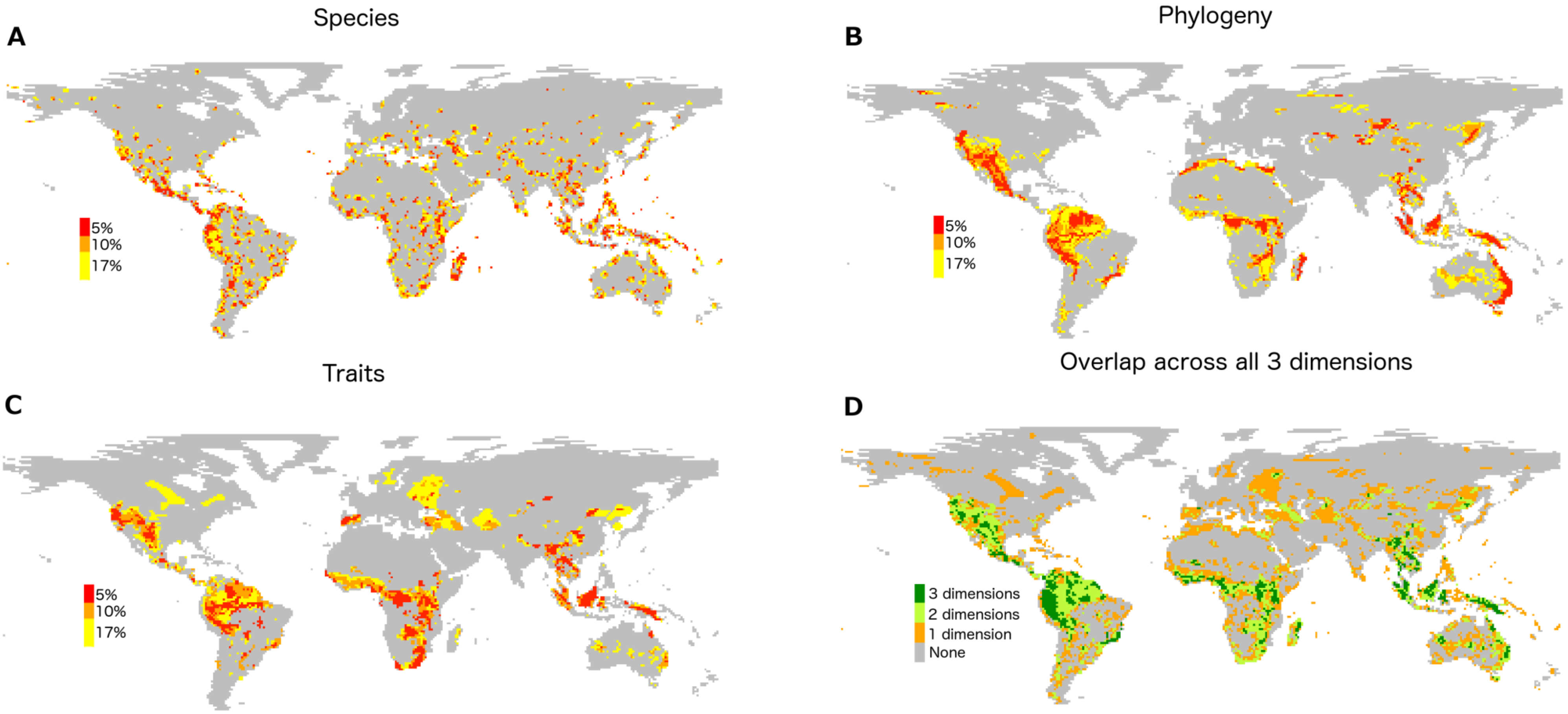


Figure 1: Maps showing the top 17% of cells selected according to zonation prioritization based on (A) species, (B) phylogeny, (C) traits and (D) overlap across the three dimensions. Cells where all 3 dimensions overlap (D) are represented by dark green, those represented by two dimensions in light green, those selected only by one dimension in orange.

The overlap between important areas across the dimensions of biodiversity was low (Figure 1D, Figure 2), with only 4.7% of the global land selected by the three dimensions simultaneously (Figure 1D). Looking at the 17% target, the highest congruence was between phylogeny and trait solutions (around 55%, Figure 2), while the lowest congruence was found when all three dimensions were compared together (around 27%, Figure 2).

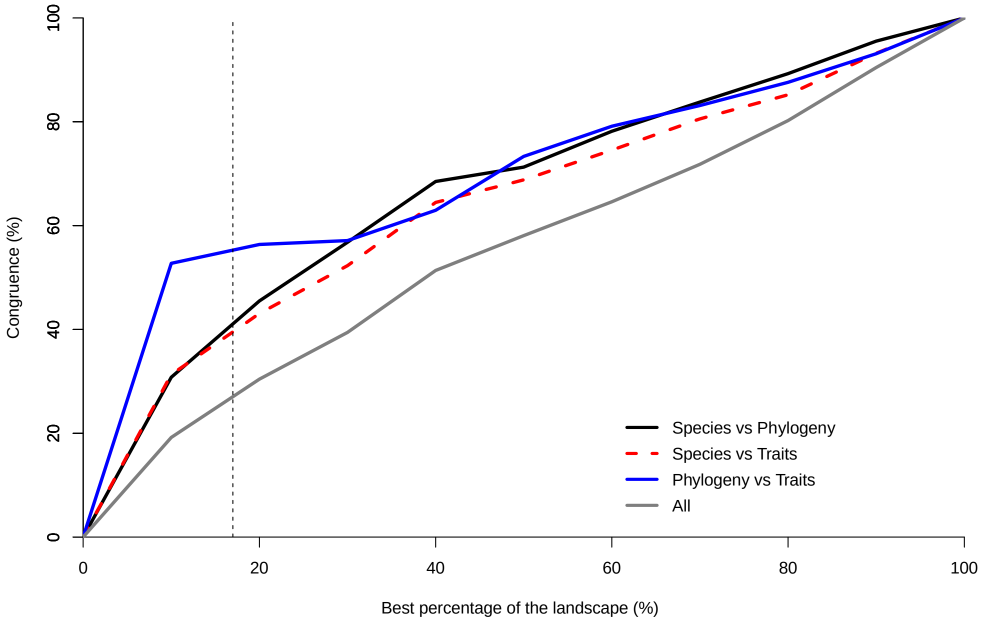


Figure 2: Congruence percentage between the output from Zonation analysis based on species occurrences (Species), phylogeny (Phylogeny) and traits (Traits) along an increasing gradient of landscape quality. The vertical black dashed line indicates the congruence considering the top 17% priority rank.

The performance graph shows the percentage the total distribution (on average) of the species/traits/phylogeny that will be preserved if we protected different proportion of the landscape (Figure 3). It means that if we protected the top 17% of the, on average 65% of the species distribution, 42 and 44% of the lineages and traits distribution, respectively, would be preserved.

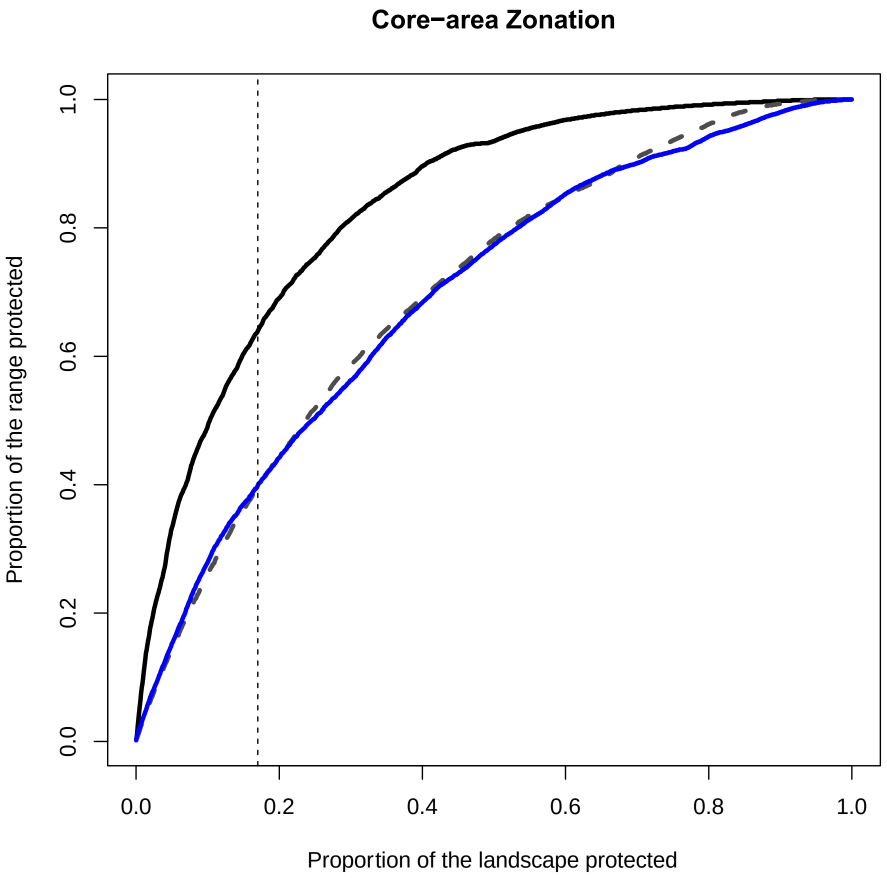


Figure 3: Performance curves showing the mean proportion of the distribution of mammal species (black line), phylogeny (grey line) and traits (blue line), protected against the fraction of protected sites in the landscape. The dotted line indicates the tipping point where 83% of the landscape is lost (therefore retaining the best 17% of its land surface for protection).

How do the important regions relate to current protected areas and current and projected human impacts?

We found that current protected areas showed worse performance in protecting species richness, phylogenetic diversity, trait diversity and threatened species compared to the prioritizations determined by zonation analyses, across all three dimensions (Table 1). We also found that the average conservation values of cells currently under protection were significantly lower than expected by randomly selecting areas around the globe, and this was consistent for all three dimensions (Figure S1). Often protected areas are determined not only by ecological priorities, but also by political and economic factors (Margules and Pressey 2000). This fact could compromise the effectiveness of protected areas to adequately protect global biodiversity, as our results suggest.

Table 1: Values indicating the percentage of global total of species richness, phylogenetic diversity (Faith's PD), trait diversity (Petchey and Gaston's FD), and threatened species contained within the best 17% of the sites based on each dimension, and where all 3 dimensions overlap in zonation analyses and current protected areas (PAs).

	Zonation prioritization				
% of the global total	Species	Phylogeny	Traits	All overlap	Current PAs
Species Richness	99%	83%	71%	70%	62%
Phylogenetic Diversity (PD)	99%	90%	87%	80%	74%
Trait Diversity (FD)	99%	91%	80%	80%	78%
Threatened species	99%	72%	56%	57%	37%

Some of the areas selected as important for the different dimensions of mammalian biodiversity occur where human population density is also high (Figure 4). Human population density is a well-known driver of species threat because it is often associated with habitat loss and degradation, and hunting pressure (Cardillo *et al.* 2004; Harcourt & Parks 2003). This could be a potential threat for the areas with high conservation value selected by our analyses, especially in South and Southeast Asia, a region where both biodiversity and human population densities are high (Figure 4).

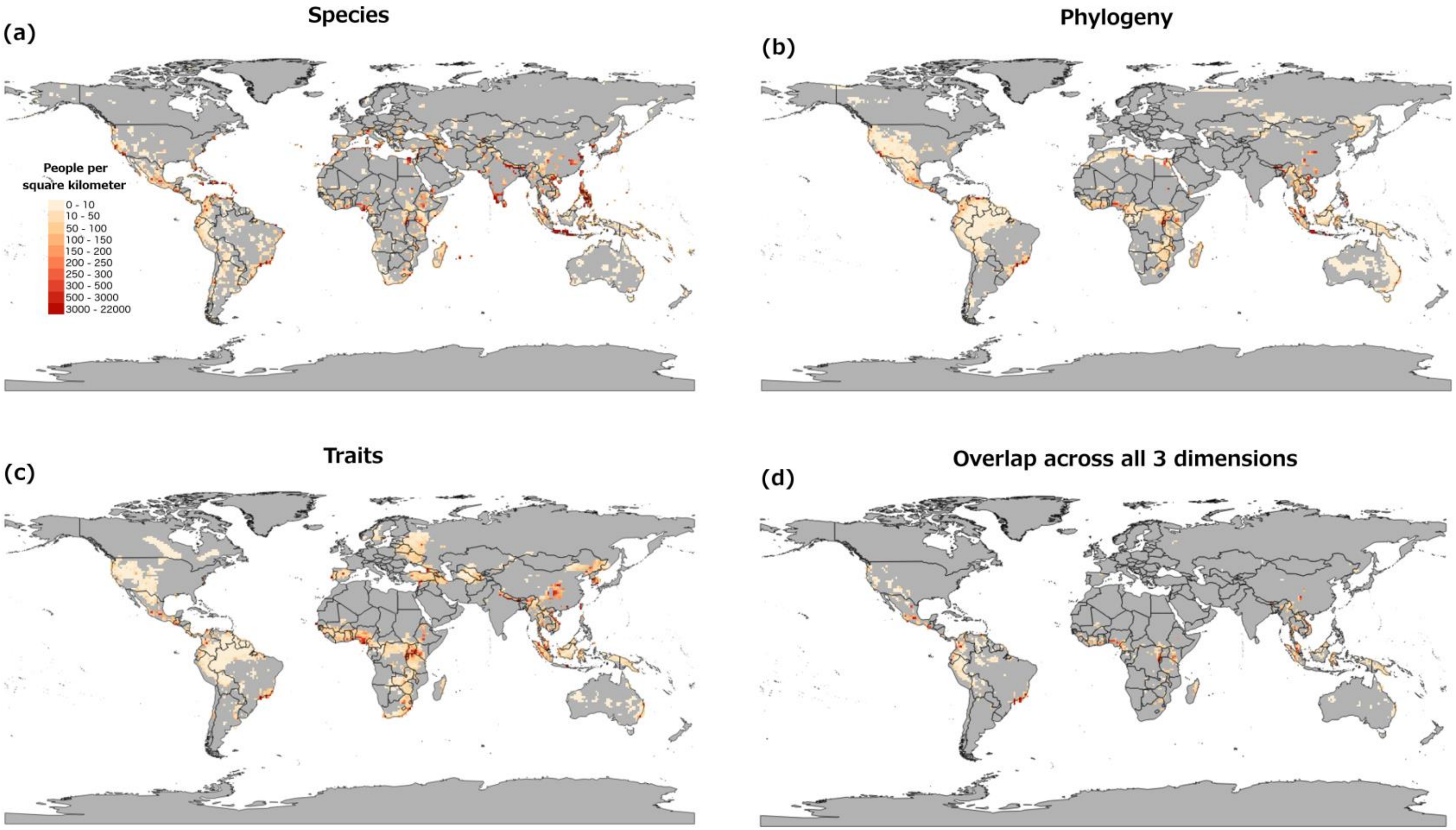
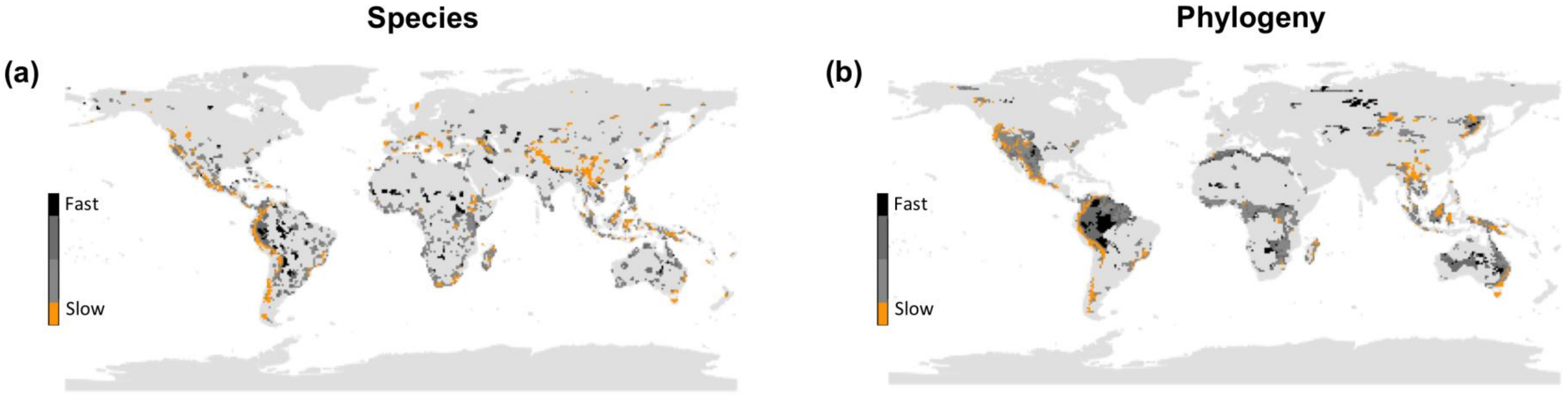


Figure 4. Maps showing human population density values in the top 17% selected according to zonation prioritization based on (a) species, (b) phylogeny, (c) traits, and (d) where all 3 dimensions overlap in zonation analyses.

We mapped climate change velocity in the top 17% of priority areas selected for each dimension and across the 3 dimensions (Figure 5). We find that some areas that harbor a high diversity of species, lineages, and traits, appear to be relatively safe from rapid changes in climate, such as tropical regions of Indonesia, the Atlantic Forest and tropical Andes. However, other highly diverse regions (especially phylogenetically), such as the Amazon forest and central Australia, are likely to experience rapid climate change. Climate change will increasingly affect species in the future by changing the climatic suitable areas and creating novel climates, what could affect species range limits (Moritz & Agudo 2013). Therefore, the maintenance of the different dimensions on the selected areas could be compromised by the repaid change on climate, threatening more these regions.



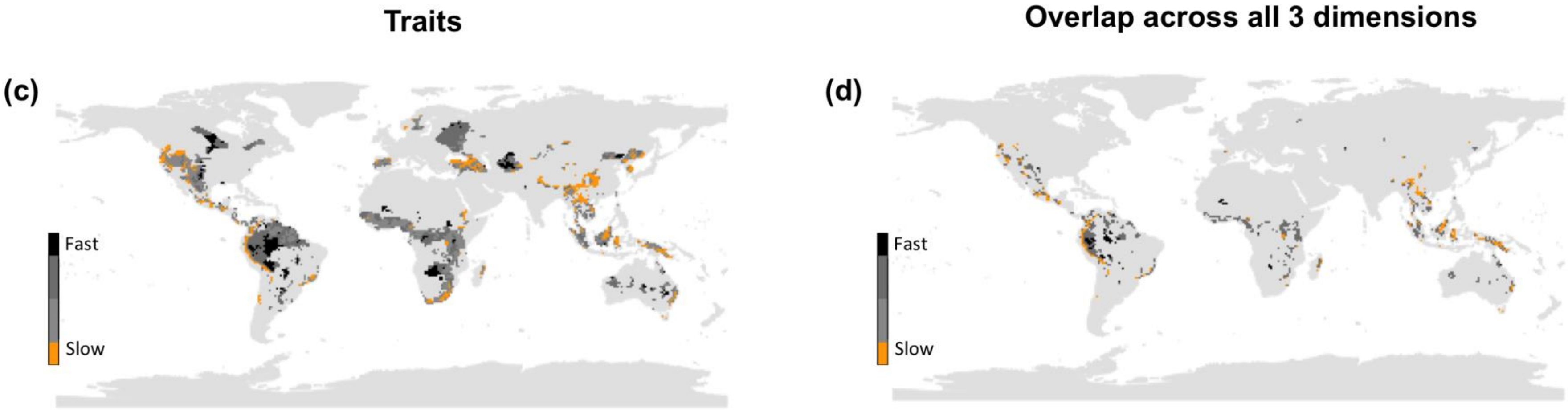


Figure 5. Maps showing the velocity of climate change in the top 17% selected according to zonation prioritization based on (a) species, (b) phylogeny, (c) traits, and (d) where all 3 dimensions overlap.

Conclusion

Spatial conservation priorities based on the different dimensions of biodiversity are different, challenging the conservation scientists to develop more comprehensive strategies. The mismatch of the conservation priorities across the different dimension highlights the necessity of an integrative approach to biodiversity conservation. Besides, the areas that we selected as important to protect taxonomic, phylogenetic and functional dimensions of biodiversity are exposed to different degrees of human population pressure and climate change vulnerability, showing the need for conservation action in these regions.

Methods

Occurrence data

We used the species geographic ranges from Rondinini et al. (2011) to get the mammal species occurrence. We overlapped the distribution maps in a 1° x 1° grid, obtaining a grid cells x species matrix. The occurrence maps of 4547 terrestrial mammals were used in prioritization analyses to find the priority regions for mammal taxonomic dimension.

Traits

We compiled a species-level database for 4547 terrestrial mammals (Davidson *et al.* 2009; Jones *et al.* 2009; Pacifici *et al.* 2013; Tacutu *et al.* 2013; Verde Arregoitia *et al.* 2013). From a total of 23 traits that we collected, we used 14 intrinsic biological traits in the analyses, based on ecological meaning, correlation between them and the percentage of missing values. Traits were related to resource use (activity cycle, habit mode, trophic diet detailed, diet breadth), speed of life history (body mass, litter size, litter per year, gestation length, weaning age, neonate body mass, maximum life span) and population features (social group size, population density). The whole mammal dataset had 63% of data missing. Removing species with missing data in some of the traits may cause statistical bias in the analyses and lead to wrong interpretations (Nakagawa & Freckleton 2008). We thus imputed the dataset using missForest (Package missForest in R, (Stekhoven & Bühlmann 2012)), a nonparametric approach based on random forest. This method has been shown to perform better than others with large databases with correlated variables and to be a valuable alternative to removing missing values (Penone *et al.* 2014; Stekhoven & Bühlmann 2012). Phylogeny was not used in the imputation analysis. As some of the traits had high proportions of data missing, we ran the Zonation analyses on different sets of traits. We found that including traits that had high proportions of missing data before imputations did not change our main results.

To represent the functional dimension in the prioritization analyses, we followed the framework used by Stecker et al. (2011), using a traits x grid cells matrix. To get this information, all trait variables were converted into binary format. For categorical traits, we assigned the presence/absence of each category. We split quantitative traits into 5% quantiles, and then converted them into binary variables. Once our dataset was converted to binary format we then created a binary species by traits matrix. By multiplying the species x traits and species x grid cells (obtained from occurrence data) matrices, we got a traits x grid cells matrix, where each 1 degree grid cell contained the number of species exhibiting a particular trait state (i.e. number of nocturnal species in that cell). Then, we generated a map for each trait state and used them into Zonation analyses to find the priority regions for mammal trait dimension.

Phylogeny

We used phylogenetic eigenvectors, as proposed by Diniz-Fiho et al. (1998, 37), to represent the phylogenetic dimension in the analyses We used an interpolated smoothed tree of Mammals (S.B. Hedges, J. Marin, M. Suleski, M. Paymer, & S. Kumar, *submitted*) to obtain a phylogenetic distance matrix between all the species. Then, we synthesized the phylogenetic information in eigenvectors by doing a principal coordinate analysis (PCoA), based on phylogenetic distances among species ((Diniz *et al.* 1998; Diniz-Filho *et al.* 2012), PVR package).

Eigenvectors from a phylogenetic distance matrix reflect the different phylogenetic relationships among species in independent vectors. The first eigenvectors tend to represent larger distances among species, expressing divergences closer to the root of the phylogeny (Diniz-Filho *et al.* 2012), while the next eigenvectors tend to capture phylogenetic relationships closer to the terminal nodes. We generated multiple eigenvector scores for each species, which represent relatedness of each species to all other species at different phylogenetic levels. We used only axes containing more than 1% of the total variation of the phylogenetic distance matrix, to avoid including low representative axes in the analysis. So, from 4,546 phylogenetic axes generated by the PCoA, we only used 16 eigenvectors in our analyses. They contained around 63% of the total variation in the phylogenetic distance matrix. We tested the sensitivity of our results to the number of eigenvectors using 16, 100, 200 and 250 eigenvectors. Given that the results generated by the different sets were highly correlated, the inclusion of more eigenvectors appeared to not include any significant new information in the analyses. We then decided to use the smallest set (16 eigenvectors).

Considering that for each eigenvector each species present a score, similarly as we did for categorizing the continuous traits, we split the first 16 phylogenetic eigenvectors into 5% quantiles. In each eigenvector species were split in 20 same-size phylogenetic groups (quantiles), grouping species based on their phylogenetic affinity (scores) in a given phylogenetic level (eigenvector). Then, we multiplied the binary matrix of species x phylogenetic groups by the grid cells x species matrix, resulting in a matrix of site x phylogenetic groups, where each 1 degree grid cell contained the number of species belonging to a particular phylogenetic group. Then, we generated a map for each phylogenetic group distribution and used them in Zonation to find the priority regions for mammal phylogenetic dimension.

Prioritization analyses

We identified the important areas for mammal conservation across the dimensions of biodiversity using the Zonation framework and Software (Moilanen *et al.* 2012). Zonation produces a hierarchical prioritization of the landscape based on the biological value of sites (cells), accounting for complementarity. Zonation starts from the full landscape, which in our case was the entire globe, and iteratively removes those cells whose loss causes the smallest marginal loss in overall conservation value of the remaining landscape. Zonation produces a hierarchical prioritization of the landscape based on the order of cell removal, that is recorded and it can later be used to select any given top fraction, for example best 10%, of the landscape. This cell removal order is called conservation value, ranging from 0 to 1, being 0 the first cell removed (least important) and 1 the last cell removed from the landscape (most important).

The basic cell-removal rule is the core-area Zonation (CAZ) algorithm. CAZ calculates the conservation values of each cell based on the marginal loss (i.e. the relative contribution to total diversity) of the species/trait state/phylogenetic group with the higher proportion of its range in that cell. CAZ prioritizes sites by gathering a higher proportion of each dimension (species/traits/phylogeny) distribution, thus favoring rare species/trait state/phylogenetic group in the final solution, even when they occur in otherwise species-poor regions. We analyzed each dimension separately because we wanted to contrast the individual solution generated by each dimension and compare the solutions among each other, to evaluate what each dimensions are capturing individually and how much they converge. Following the Convention on Biological Diversity (CBD 2010), which proposed that 17% of the terrestrial areas should be protected by 2020, we focused our analyses on the top 17% of the landscape, i.e. cells with conservation value greater or equal to 0.83

Protected areas

To compare the selected areas across the tree dimensions with the current protected areas we used the IUCN and UNEP-WCMC data on the protected areas across the globe (IUCN & UNEP 2011), and we considered only those areas classified as I-IV by the IUCN in the analyses. Protected areas were resampled at 1-degree grid cell.

Current and future human threats

To establish the relation between the important areas for mammal conservation across the three dimensions and current and future threats, we used maps of human population density (Bright *et al.* 2012), as the current human threat, and global climate change velocity (Loarie *et al.* 2009), which indicates the speed at which climate is changing based on the instantaneous horizontal velocity of temperature change between 2050 – 2100. We explored the spatial overlap of the selected areas across the dimensions with human population density and climate change velocity to infer possible human threats to these areas.

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Supplementary Material

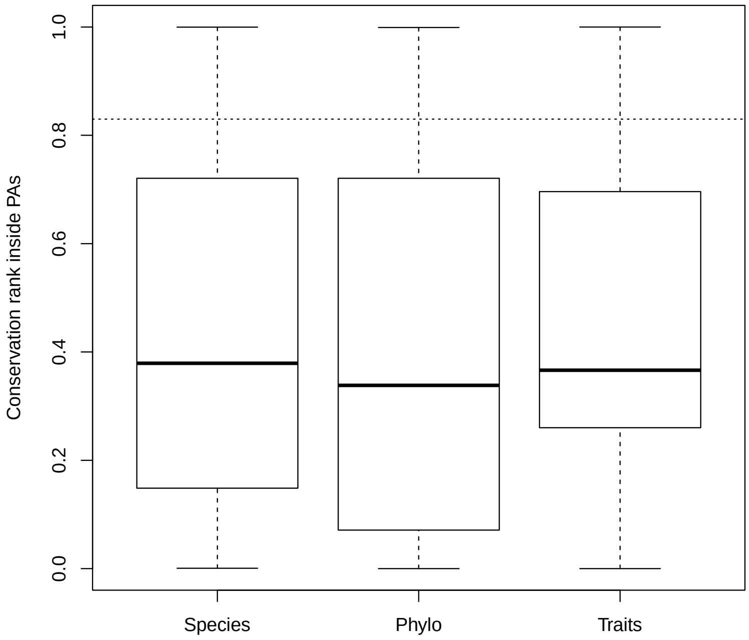

Figure S1: Conservation values of the cells inside current Protected Areas (PAs) from the conservation solutions based on the three dimensions of biodiversity (Species, Phylogeny and Traits). The shaded area indicates the 17% target for conservation, showing that species, phylogenies, and traits that are rare are poorly represented within protected areas.

CONSIDERAÇÕES FINAIS

A influência do uso da terra sobre a biodiversidade não está restrita apenas a escalas local e de paisagem, mas também já é perceptível em amplas escalas geográficas. Além disso, o uso da terra tem impacto não somente na dimensão taxonômica, mas também nas dimensões filogenética e funcional da diversidade de vertebrados nessa escala macrogeográfica. No Capítulo 1, demonstrei que a distribuição de espécies de anfíbios ameaçadas de extinção foi afetada não somente por variáveis ambientais, mas também por impactos humanos derivados do uso e conversão da paisagem. Isso demonstra a necessidade de um planejamento de ocupação e manejo de áreas utilizadas para atividades humana em ampla escala também, pois o impacto humano não se dá mais somente em escalas finas.

O uso atual da terra representa uma ameaça real maior para algumas linhagens de anfíbios e de primatas, como, por exemplo, Microhylidae e Atelidae, respectivamente. Isso mostra que certas linhagens são mais ameaçadas que outras não somente por suas características ecológicas, mas também por estarem mais expostas a impactos humanos específicos, como por exemplo o avanço das fronteiras agropastoris. Isso reforça a necessidade de utilizarmos abordagens filogenéticas que vão além do simples acúmulo de informação evolutiva, mas sim no sentido de identificarmos quais linhagens estão mais suscetíveis aos impactos decorrentes de atividades humanas.

Em uma realidade de orçamento limitado e baixa disponibilidade de áreas para conservação, a escolha do que devemos priorizar é sempre uma questão complicada. Duas caraterísticas importantes do planejamento sistemático são a representatividade e complementariedade das áreas selecionadas. Isso possibilita que se vá além de uma abordagem cumulativa de número de espécies para uma abordagem mais abrangente, englobando ao máximo a árvore filogenética da vida e a diversidade de características funcionais existentes. Mas ao tentarmos maximizar a conservação das dimensões taxonômica, filogenética e funcional, a congruência entre as áreas selecionadas foi baixa. Ainda sim, as áreas de congruência entre dimensões taxonômica, filogenética e funcional mereceriam de especial interesse para investigação e investimentos futuros. A integração dos diferentes componentes da biodiversidade para selecionar áreas mais eficientes para a conservação das espécies ainda é um desafio. Mas o terceiro capítulo representa um passo nesse sentido, apresentando uma maneira biologicamente mais abrangente de se utilizar informação filogenética e funcional em estudos de planejamento sistemático para conservação.

Todos os capítulos desta tese desenvolveram questões de conservação em escala continental ou global. Estimativas de diversidade e identificação de áreas “quentes” para conservação em ampla escala são frequentes. Obviamente, priorizações em escalas amplas não são diretamente aplicáveis, pois decisões políticas relacionadas a conservação são dependentes de governos, e as ações de conservação são tomadas em escala local a regional. Porém, estudos em escalas amplas são importantes como primeiros passos, podendo servir como diretrizes para estudos de aprofundamento e ações de conservação em locais dentro das áreas selecionadas.

Esta tese avança, principalmente, nos aspectos apontados a seguir. Primeiramente, identifiquei associações entre distribuição de linhagens de vertebrados e diferentes impactos advindos do uso antrópico da terra. Além disso, pude selecionar áreas prioritárias para a conservação, não somente avaliando o acúmulo de diversidade de espécies, mas também maximizando a representação da árvore filogenética e a diversidade de características funcionais dos mamíferos. Essas abordagens podem ser utilizadas para outros grupos de organismos, incluindo animais e plantas. Dessa forma, em breve teremos mapas ainda mais propositivos de quais as áreas do planeta mais urgem iniciativas legais de conservação.