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Instituto de Ciências Biológicas

Pós-Graduação em Ecologia e Evolução

Padrões Filogenéticos dos Vertebrados Terrestres: Implicações para Conservação

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Goiânia,

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Tese apresentada ao Programa de Pós-graduação em Ecologia e Evolução, do Instituto de Ciências Biológicas da Universidade Federal de Goiás, como parte dos requisitos para a obtenção do título de Doutor em Ecologia e Evolução.

Orientador: Prof. Dr. Thiago F. Rangel

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Rangel

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UNESP -Rio Claro

Para minha amável mãe, Izabel, meu exemplo de vida e a maior incentivadora de todas as minhas conquistas.

"Por vezes sentimos que aquilo que fazemos não é senão uma gota de água no mar. Mas o mar seria menor se lhe faltasse uma gota".

(Madre Teresa de Calcuta)

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Sumário

Resumo

A acelerada taxa de perda de espécies gerou um crescente número de estudos objetivando o delineamento de estratégias de conservação que sejam eficazes considerando os limitados recursos disponíveis para a preservação da biodiversidade. Nesse contexto, têm sido identificadas prioridades para conservação, investigados possíveis padrões na vulnerabilidade das espécies e elaboradas estimativas de perda da biodiversidade na tentativa de mensurar a magnitude da atual crise de extinção. A história evolutiva (HE) entre os organismos tem sido indicada como uma eficiente ferramenta para as análises citadas uma vez que incorpora a diversidade existente entre as espécies. As diferentes aplicabilidades da HE em estudos voltados para conservação são brevemente revisadas no capítulo 1 desta tese, mostrando ainda possíveis limitações dessas abordagens. As observações realizadas no capítulo 1 demonstram os benefícios de estimativas de perda de HE através de extinções sequenciais (uma espécie de cada vez), que permite simultaneamente a avaliação da eficácia de diferentes estratégias de conservação assim como a identificação de prioridades. Contudo, taxas de perda de HE são, em geral, limitadas a determinados grupos taxonômicos ou regiões geográficas, sendo elaboradas através de diferentes escopos metodológicos e assim restringindo o poder de comparação entre os resultados. Contornando essas limitações, o capítulo 2 apresenta estimativas de perda de HE dos vertebrados terrestres em escala global e regional (células de 1º de longitude por 1º de latitude) através de extinções sequenciais, indicando locais em que a extinção de espécies atualmente ameaçadas seria maior do que o esperado ao acaso. Embora as taxas de perda de HE sejam equivalentes entre os grupos quando analisadas globalmente, nós observamos resultados incongruentes entre os diferentes grupos taxonômicos quando avaliados regionalmente. Porém, a existência de diferentes métricas para mensurar HE tem colocado em dúvida a robustez das estimativas de perda de HE, sendo questionada a possibilidade dos resultados serem distintos caso as estimativas sejam elaboradas através de diferentes métricas, o que foi testado no capítulo 3. Foi observado que de fato há diferença quantitativa na taxa de perda de HE entre diferentes métricas, contudo o resultado não é qualitativamente diferente, ou seja, dentro do nosso escopo metodológico a magnitude de perda de HE é equivalente independente da métrica utilizada.

Abstract

The accelerated rate of species loss has emerged an increasing number of studies to design effective conservation strategies, considering the limited resources available for biodiversity conservation. In this context, it has been identified conservation priorities, patterns in species vulnerability has been investigated and estimates of biodiversity loss has been performed in attempt to measure the magnitude of the current extinction crisis. Amount of evolutionary history (EH) hold by organisms has been indicated as a suitable measure to estimate the potential damage by possible extinctions, since it incorporates diversity among species. The different applications of EH in conservation studies are briefly reviewed in Chapter 1, showing potential limitations of some approaches. Observations made in chapter 1 detail some benefits of EH loss estimates through sequential extinctions, which simultaneously allow an evaluation of the efficiency of different conservation strategies as well as an identification of priorities. However, rates of EH loss are usually limited to specific taxonomic groups or geographic regions, and are estimated through different methodological procedure and thus limit the power of comparison between results. Circumventing these limitations, Chapter 2 presents estimates of EH loss for terrestrial vertebrates on global and regional scales (cells 1 ° longitude by 1 ° latitude) through sequential extinctions, indicating sites where extinction of threatened species would be greater than expected at random. Although rates of EH loss are equivalent between groups when analyzed globally, we observed incongruent results among the distinct taxonomic groups when investigated regionally. However, the existence of distinct EH metrics has created doubt on the robustness of estimates of EH loss. One concern is the possibility that different EH metrics applied to the same group of species could artificially lead to different conservation strategies. In chapter 3 it was observed that there is quantitative difference in the rate of EH loss between distinct metrics, however the result was not qualitatively different, that is, within our methodological procedure the magnitude of EH loss is equivalent independent of the metric used.

Apresentação

Identificar estratégias eficazes para a preservação da biodiversidade é uma tarefa árdua tendo em vista o nosso limitado conhecimento. Além disso, o debate e o desenvolvimento de métricas e metodologias para mensurar a biodiversidade ainda é grande entre a comunidade científica. Por outro lado, já é reconhecida a acelerada taxa de extinção da atualidade, ressaltando a necessidade de implementar políticas que desacelerem essa perda de espécies. Neste sentido, a relação evolutiva entre as espécies tem sido apontada como importante ferramenta no delineamento de políticas de conservação. O presente estudo compreende a integração da história evolutiva (HE) dos organismos com a conservação da biodiversidade. O capítulo 1 apresenta uma breve síntese sobre o histórico da utilização das filogenias em estudos voltados para preservação da biodiversidade. São relatadas as diferentes aplicabilidades das filogenias na geração de informações úteis para o delineamento de estratégias para desacelerar a perda de espécies, assim como vantagens e limitações de cada aplicabilidade.

No Capítulo 2 os padrões de distribuição filogenética das espécies ameaçadas são investigados e comparados à estimativas de intensidade de perda de HE, para os vertebrados terrestres. Adicionalmente, a taxa de perda de HE foi estimada em diferentes cenários, onde a ordem de extinção das espécies é alterada possibilitando investigar de que forma diferentes manejos de espécies (i.e. selecionar qual espécie preservar) pode alterar o montante de HE preservado. Cabe ressaltar ainda que as análises do Capítulo 2 foram realizadas globalmente (i.e. considerando todas as espécies) e regionalmente (i.e. considerando espécies co-ocorrentes em células de 1º de latitude por 1º de longitude ao longo do globo), uma vez que eventos de extinção se iniciam localmente.

No entanto, a taxa de perda de HE é estimada através de extinções sequenciais, cuja ordem na qual as espécies são extintas é definida em função da contribuição de cada espécie para a HE do grupo taxonômico. Assim, a forma utilizada para mensurar a informação filogenética que cada espécie representa pode afetar a ordem de extinção das espécies, podendo gerar resultados contrastantes ao estimar a magnitude de perda de HE. Portanto, no Capítulo 3 a informação filogenética de cada espécie foi mensurada através de diferentes métricas, avaliando assim o impacto de possíveis discrepâncias da ordem de extinção das espécies nas estimativas de perda de HE.

Capítulo 1

FILOGENIA E CONSERVAÇÃO: BREVE HISTÓRICO, APLICAÇÕES E LIMITAÇÕES

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Resumo

A acelerada taxa de perda de espécies em conjunto com os limitados recursos existentes para conservação da biodiversidade requer estratégias urgentes e eficazes. A relação evolutiva das espécies tem sido utilizada de diferentes maneiras para indicar prioridades e investigar determinantes no risco de extinção dos organismos. Nesse contexto, foi observado que o risco de extinção apresenta estrutura filogenética, indicando que a vulnerabilidade das espécies é determinada por atributos intrínsecos das espécies que também possuem sinal filogenético. Assim, identificar atributos que potencialmente conferem vulnerabilidade e avaliar a presença de sinal filogenético foi apontado como uma possível forma de guiar esforços com o intuito de prevenir a extinção de espécies que atualmente não estão listadas como ameaçadas, mas que possuem atributos que as tornam vulneráveis. Outras abordagens também têm sido elaboradas, especialmente com o intuito de priorizar áreas e/ou espécies, porém resultados controversos e imprecisões acerca da relevância da história evolutiva para conservação atuam como limitante para implementação de estratégias baseadas na relação evolutiva das espécies. Limitantes de diferentes aplicabilidades da história evolutiva para conservação são apresentadas, demonstrando que algumas abordagens promissoras ainda são pouco utilizadas. Por fim, é necessário observar que embora existam limitações ou imprecisões na utilização da história evolutiva em estudos voltados para conservação, a relação evolutiva entre as espécies ainda é uma da ferramenta de grande utilidade, especialmente considerando a urgência no delineamento de estratégias para desacelerar as taxas de extinção das espécies.

Palavras-chave: Extinção, filogenia, limitações, conservação, IUCN.

Introdução

Eventos de extinção têm modelado a biodiversidade ainda antes da existência humana, contudo a pressão antrópica é um fator imperativo no acelerado processo de perda de espécies na atualidade. É importante ressaltar que extinções podem resultar em perda de recursos e funções ecossistêmicas, comprometendo a estabilidade de ambientes e até mesmo processos evolutivos (Hooper et al., 2012; Mace & Purvis, 2008; Myers, 1989). Com o intuito de reduzir o impacto antrópico na perda de biodiversidade, tornou-se necessário promover estratégias e ações para a preservação de espécies e/ou áreas. Porém, os recursos destinados a conservação da biodiversidade são escassos mediante tamanha variedade biológica existente, o que implica em eleger prioridades.

Frente à acelerada perda de biodiversidade (Barnosky et al., 2011; Butchart et al., 2010), associada aos limitados recursos para preservação da biodiversidade, diferentes abordagens têm sido empregadas para quantificar a biodiversidade e identificar prioridades de conservação (Avise, 2005). Entre as diferentes métricas para quantificar a biodiversidade em estudos voltados para conservação, é comum a utilização da riqueza de espécies, endemismo, raridade, grau de ameaça, espécie-bandeira e espécie guarda-chuva (Margules & Pressey, 2000; Rodrigues & Brooks, 2007). Entretanto, a utilização destas métricas tem sido criticada por tratar as espécies como equivalentes, ignorando outros aspectos da diversidade como a variação biológica e ecológica, não incorporando assim a ampla diversidade de componentes da biodiversidade (Purvis and Hector, 2000; Vane-Wright et al., 1991).

Há cerca de duas décadas a relação evolutiva entre as espécies é apontada como forma de mensurar a diversidade biológica e ecológica entre as espécies, auxiliando assim a eleger prioridades para conservação (Vane-Wright et al., 1991; Faith, 2013, 1992). Existe, em geral, relação entre a distância evolutiva e similaridade ecológica e biológica dos organismos (Cavender-Bares et al., 2009; Prinzing et al., 2001 but see Kelly et al., 2014), onde um conjunto de espécies filogeneticamente próximas tende a possuir atributos redundantes, enquanto um conjunto de espécies filogeneticamente distantes tende a apresentar maior diversidade biológica e ecológica (e.g. Forest et al., 2007). Assim, é esperado que medidas que incorporem a relação evolutiva, ou seja, a história evolutiva (HE) entre as espécies, sejam efetivas na predição acerca da diversidade de componentes e funções dos organismos e ecossistemas (Faith, 1994, 1992). Nesse contexto, métricas baseadas na HE dos organismos têm sido utilizadas para identificar conjuntos de espécies que incorporem maior diversidade biológica e ecológica, indicando áreas cuja preservação potencialize a persistência da biodiversidade (e.g. Asmyhr et al., 2014; Forest et al., 2007; Rodrigues and Gaston, 2002; Vane-Wright et al., 1991).

De que forma a filogenia tem sido utilizada em estudos voltados para a preservação da biodiversidade?

Diferentes abordagens utilizando a relação evolutiva entre os organismos tem sido empregada nos estudos de conservação. Por um lado, há a possibilidade de avaliar a efetividade de estratégias já estabelecidas na captura da HE. Nesse contexto, é possível, por exemplo, avaliar se a atual rede de áreas protegidas compreende áreas de maior diversidade biológica e ecológica (e.g. de Carvalho et al., 2010; Devictor et al., 2010; Zupan et al., 2014), ou se as áreas protegidas serão eficazes na preservação da HE dos organismos frente a alterações climáticas no futuro (e.g. Loyola et al., 2014; Pio et al., 2014). Adicionalmente, foi avaliado se estratégias de preservação voltadas para as espécies atualmente ameaçadas podem maximizar a biodiversidade, sendo observado que a HE representada pelas espécies ameaçadas é equivalente à de um conjunto aleatório de espécies (Davies et al., 2011; Hidasi-Neto et al., 2013). Portanto, estratégias de conservação baseadas unicamente em avaliações do risco de extinção podem ser ineficazes na maximização da diversidade biológica e ecológica.

Por outro lado, a filogenia tem sido utilizada para analisar possíveis estratégias de conservação a serem estabelecidas. Em uma perspectiva baseada em espécies, o principal objetivo consiste em identificar espécies evolutivamente únicas, especialmente incorporando o risco de extinção (e.g. Isaac et al., 2012, 2007; Pavoine et al., 2005; Steel et al., 2007). Nesse âmbito, o programa EDGE (Evolutionary Distinct and Globally Endangered; Isaac et al., 2007) é amplamente conhecido e estabelece um ranking de espécies prioritárias para conservação, embora tenha recebido críticas acerca do seu cálculo (Faith, 2008). Já em uma perspectiva espacial de conservação, a HE pode ser utilizada, por exemplo, para identificar áreas que maximizam a diversidade biológica e ecológica ou abrigam linhagens endêmicas, por vezes levando em consideração o grau de ameaça das espécies (e.g. Faith et al., 2004; Forest et al., 2007; Rodrigues and Gaston, 2002; Rosauer et al., 2009; Soutullo et al., 2005).

Por fim, as relações evolutivas entre as espécies têm sido utilizadas ainda para investigar possíveis padrões na vulnerabilidade das espécies à extinção, com o intuito de aprimorar o delineamento de estratégias conservacionistas. Nesse sentido, a noção de que alguns grupos apresentam maior risco de extinção do que outros (McKinney, 1997) resultou em estudos investigativos acerca possíveis causas da vulnerabilidade das espécies (Corey, 2010; Cardillo et al., 2004; 2005).

Como a filogenia pode ser utilizada para investigar a vulnerabilidade das espécies?

Existem indícios de que há uma distribuição não aleatória do risco de extinção (i.e. espécies ameaçadas) ao longo da filogenia (Russell et al., 1998; Purvis, 2000; Jones te al., 2003; Vamosi and Wilson, 2008), sugerindo que espécies ameaçadas são filogeneticamente próximas. Considerando a relação entre proximidade filogenética e similaridade de atributos, a concentração do risco de extinção em partes específicas da filogenia indica, portanto, que atributos que conferem vulnerabilidade às espécies também possuem um padrão evolutivo (i.e. sinal filogenético *sensu* Blomberg and Garland, 2002).

Nesse contexto, alguns estudos relativos ao risco de extinção das espécies possuem como principal objetivo identificar atributos (e.g. tamanho do corpo, taxa de fecundidade) que potencialmente conferem vulnerabilidade às espécies. Desta forma, atributos biológicos e ecológicos têm sido correlacionados ao risco de extinção para identificar possíveis características que tornam as espécies vulneráveis (Bennett and Owens, 1997; Bielby et al., 2006; Gaston and Blackburn, 1997; Lips et al., 2003; Meijaard et al., 2008). Assim, identificar clados com concentração de atributos que potencialmente predispõem as espécies ao risco de extinção torna possível guiar esforços de forma a prevenir a extinção de espécies que atualmente não estão listadas como ameaçadas, mas que possuem atributos que as conferem vulnerabilidade (Lockwood et al., 2002). Adicionalmente, a presença de sinal filogenético de ameaças (e.g. poluição, degradação de habitat, declínio enigmático) em clados específicos pode auxiliar em casos onde a biologia e ecologia das espécies é escassa, porém a relação evolutiva é conhecida (Corey, 2010; Corey and Waite, 2008).

Investigando as aves do mundo, Gaston e Blackburn (1995) observaram que as espécies ameaçadas não representam um conjunto aleatório da distribuição de massa corporal, sendo que as espécies ameaçadas possuem, em geral, tamanho corporal maior quando comparadas às espécies não ameaçadas. Após observarem uma estrutura filogenética no risco de extinção dos morcegos, Jones e colaboradores (2003) também analisaram quais atributos podem estar relacionados à vulnerabilidade do grupo, e encontraram que características da asa podem estar correlacionadas ao risco de extinção dos morcegos. Já para primatas e carnívoros foi observado que pequena área de distribuição, populações com baixa densidade e baixa taxa reprodutiva são algumas características que predispõem as espécies ao risco de extinção (Purvis et al., 2000b).

A noção de estrutura filogenética do risco de extinção também implica na perda de clados inteiros, ou seja, em uma acelerada perda de HE, o que pode resultar na perda de funções ecológicas e/ou atributos exclusivos aos clados extintos. Nesse contexto, Nee and May (1997) foram pioneiros ao estimar a taxa perda de HE, encontrando que cerca de 80% da HE poderia permanecer preservada caso aproximadamente 95% das espécies fossem extintas. Contudo, o estudo de Nee e May (1997) recebeu críticas quanto a filogenia simulada que utilizaram e a falta da seletividade filogenética nas simulações de extinção (Heard and Mooers, 2000). Posteriormente foram realizadas outras estimativas de perda de HE, especialmente de forma empírica, quantificando a HE que poderia ser perdida com a extinção de espécies ameaçadas (Mooers and Atkins, 2003; Purvis et al., 2000; Von Euler et al., 2001).

Nesse sentido, Purvis e colaboradores (2000) avaliaram quantos gêneros e gêneros monotípicos poderiam ser perdidos com a extinção de mamíferos e aves ameaçadas, além de quantificar a diversidade filogenética (*Phylogenetic Diversity sensu* Faith, 1992) representada pelos primatas e carnívoros ameaçados de extinção. Para mamíferos, aves e primatas Purvis e colaboradores (2000) encontraram um desvio significativo do modelo nulo, indicando que a perda das espécies ameaçadas pode resultar um incremento de 50% a mais de gêneros perdidos quando comparado ao esperado ao acaso. Posteriormente, A mesma análise de taxa de perda de gêneros e diversidade filogenética foi estimada para as aves da Indonésia (Mooers and Atkins, 2003), onde também foi observado uma perda de HE maior do que o esperado ao acaso. Embora muitos estudos tenham observado um cenário crítico na perda de HE, estudos que traçam prioridades de conservação com base na relação evolutiva entre as espécies são, em geral, pouco aceitos pelos tomadores de decisão, e assim não chegam a serem implementados.

Estudos com base em História Evolutiva: limitações

Dificuldades na implementação de estratégias baseadas em História Evolutiva

Um primeiro fator que dificulta a implementação de estratégias baseadas em HE é a existência de múltiplas métricas (Winter et al., 2013). Concomitante ao crescente número de estudos acerca da integração da HE na conservação, grande variedade de métricas foram desenvolvidas para mensurar a representatividade de espécies. Nesse contexto, existem métricas baseadas unicamente na topologia da filogenia (e.g. Taxonomic distinctness; Vane-Wright et al., 1991), na combinação da topologia da filogenia com os comprimentos de ramos (e.g. Phylogenetic diversity; Faith, 1992; Evolutionary distinctiveness; Isaac et al., 2007), entre outros (veja Veron et al., 2015). Em geral, as métricas se diferem conceitual e matematicamente, capturando diferentes aspectos da HE dos organismos. Porém ainda falta uma comparação robusta entre as diferentes métricas para auxiliar na escolha da mais apropriada a depender dos dados disponíveis e do objetivo do estudo (Kellar et al., 2015 mas veja Vellend et al., 2010).

Adicionalmente, apesar da variedade de estudos sugerindo a HE como componente para conservação da biodiversidade (e.g. Cadotte, 2013; Cadotte et al., 2009; Faith, 2013, 1992; Maherali & Klironomos, 2007), ainda existem controvérsias e lacunas acerca de sua relevância (Venail et al., 2015; Winter et al., 2013). Por um lado, estudos experimentais testaram a eficiência da produtividade primária em comunidades com diferentes composições filogenéticas, observando que, em geral, comunidades com maior HE são mais produtivas (Cadotte, 2013). Por outro lado, estudos teóricos sugerem baixa eficiência da HE como ferramenta para estimar diversidade uma vez que nem sempre funciona como *proxy* de atributos funcionais (Davies, 2015; Venail et al., 2015). Entretanto, a relação evolutiva entre as espécies, quando indicada como ferramenta para conservação, funciona como substituto de uma ampla variedade de atributos morfológicos, fisiológicos, funções ecológicas, dentre outras características que estão representadas na filogenia (Forest et al., 2015). Assim, é preciso ressaltar que a filogenia não ser um bom representante da variação de uma pequena gama de atributos não implica que sua eficácia para conservação seja contestada (Davies et al., 2016).

Incerteza filogenética

Idealmente, todos os estudos acerca de HE devem ser elaborados com base em uma filogenia que foi construída através de métodos estatísticos robustos e abundância de dados sobre a relação evolutiva entre as espécies. Nesse caso, a filogenia em questão será bem resolvida (i.e. sem politomias) (Freckleton et al., 2011; Seger et al., 2013). Entretanto, árvores filogenéticas são hipóteses acerca do parentesco entre organismos que, por definição, incorporam incertezas. Além da falta de conhecimento sobre as espécies, produzindo filogenias incompletas, as incertezas são referentes à existência de filogenias conflitantes, com diferenças no posicionamento entre os organismos, e evidências fracas acerca do posicionamento das espécies, gerando politomias. O efeito da incerteza filogenética deve ser avaliado principalmente nos estudos voltados para conservação uma vez que pode enviesar os resultados (Davies et al., 2012).

Adicionalmente, apesar de pouco aplicado, o efeito de politomias e a falta de conhecimento no posicionamento de espécies faltantes na filogenia devem ser mensurados para avaliar a robustez do resultado (e.g. Batista et al., 2013). Utilizando um método que permite avaliar o efeito da incerteza filogenética quanto ao posicionamento das espécies faltantes (e.g. Rangel et al., 2015), foi observado que estimativas de perda de HE são robustas em relação a incerteza filogenética quando estimada globalmente (Ver Capítulo 2). Assim, é válido afirmar que quando extinções são avaliadas globalmente (i.e. em larga escala taxonômica), a quantidade de HE perdida com a extinção de uma ou poucas espécies é irrelevante frente a HE de todo o grupo, de forma que a incerteza no posicionamento das espécies extintas não altera significativamente o resultado. Contudo, cabe notar que fatores antrópicos de ameaça são estruturados no espaço geográfico e que extinção é um processo que se inicia local ou regionalmente, assim estimativas de perda de HE também foram realizadas de forma espacialmente explícita (Huang et al., 2012), considerando o efeito da incerteza filogenética (Capítulo 2), sendo encontrados resultados discrepantes das análises globais.

A noção de que há uma estrutura filogenética no risco de extinção das espécies desencadeou uma série de estudos na tentativa de identificar atributos que conferem vulnerabilidade às espécies e em estimativas de perda de HE. Esses estudos indicam que as espécies ameaçadas são mais próximas filogeneticamente do que o esperado ao acaso, podendo resultar na extinção de clados inteiros, bem como na perda de características e funções exclusivas à esses clados. Contudo, a escala do estudo ou métodos utilizados parecem interferir no resultado obtido uma vez que novas análises indicam que as espécies classificadas como ameaçadas podem não possuir tendência de serem próximas entre si na filogenia (Capítulo 2). As análises realizadas recentemente são mais inclusivas, considerando os vertebrados do mundo e incorporando o efeito da incerteza na posição filogenética das espécies faltantes na filogenia (Capítulo 2), sendo possível levantar duas possíveis interpretações acerca dos resultados: (1) o efeito da incerteza filogenética não nos permite concluir se há de fato um padrão filogenético no risco de extinção, ou (2) os vertebrados terrestres possuem uma distribuição aleatória ao longo da filogenia.

Além da incerteza no posicionamento de espécies faltantes na filogenia e da existência de politomias, a confiabilidade dos ramos internos, determinando a topologia da filogenia, também é um fator a ser levado em consideração em futuras análises. Para avaliar a confiabilidade dos nós, é indicado que filogenias conflitantes disponíveis para o grupo de estudo sejam levadas em consideração nas análises observando-se a estabilidade dos resultados (e.g. Corey and Waite, 2008; Corey, 2010).

Existe uma análise ideal para delinear estratégias de conservação?

A falta de conhecimento acerca da biodiversidade é o principal limitante na existência de uma análise ideal, assim como no delineamento de estratégias de conservação. Além de conhecer apenas aproximadamente 14% da biodiversidade estimada (Mora et al., 2011), nosso conhecimento acerca da morfologia, fisiologia e ecologia é enviesado (Hortal et al., 2008; Sánchez-Fernández et al., 2008). As lacunas de conhecimento podem gerar resultados contraditórios e enviesar até mesmo avaliações do risco de extinção das espécies (e.g. Vilela et al., 2014). Assim, seria ideal que pudéssemos ter acesso a uma compilação de dados robusta acerca da biodiversidade, incluindo, por exemplo, informações sobre dados funcionais, genéticos e ecológicos, porém o levantamento acerca desses dados é um processo que demanda muito tempo e recurso. Contudo, as estimativas de taxas de extinção sugerem urgência na implementação de estratégias para preservar os organismos e ecossistemas.

Como foi mostrado ao longo do texto, existem formas de lidar com as incertezas acerca da integração da HE em estudos voltados para conservação. Mas ainda precisamos avançar metodológica e conceitualmente para que resultados robustos sejam alcançados e divergências conceituais entre pesquisadores sejam sanadas afim de estratégias baseadas em HE tenham melhor aceitas pelos tomadores de decisão.

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Capítulo 2

PHYLOGENETIC PATTERNS OF EXTINCTION RISK IN TERRESTRIAL VERTEBRATES

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Abstract

The need to decelerate rates of biodiversity loss and better allocate conservation efforts raised a phylogenetic perspective among studies of patterns in extinction risk. A critical scenario has been demonstrated, where the increasing number of imperiled species associated to the observed trends of a non-random phylogenetic distribution of extinction risk might result in a massive loss of Evolutionary History (EH), potentially compromising ecosystem functioning and services. In this context, rates of EH loss has been estimated and used as proxy for conservation planning studies. However, there is a gap of regional assessments of estimated EH loss focused on comparing multiple taxa, at the global level, providing a guide for conservation decision-making integrating results across taxonomic groups. Here we showed a multiple taxonomic and broad geographical estimates of EH loss, identifying concurrence patterns across taxa and providing a comprehensive investigation of spatial patterns of rates of EH loss. We detected that areas with significant rates of EH loss are incongruent between taxa, such as Caribbean region that represents an important region for mammals EH preservation but not for amphibians EH preservation. Combining results among vertebrate groups under analysis, our results suggest that we must concentrate conservation efforts on EH preservation in Mexico, a portion of Greenland, Italy, Sahara Desert, Madagascar, Indonesia, Philippines and Papua New Guinea, in the southeast portion of Australia and New Zeeland. Instead of identifying priority areas based on accumulated amount of EH, we present regions of the world where rates of EH loss might be critical for ecosystem maintenance if threatened terrestrial vertebrates go extinct, deserving attention for conservation efforts on EH preservation.

Introduction

It is recognized that biodiversity is declining fast, potentially compromising ecosystem functioning and services [1–3]. Increasing our understanding about vulnerability of species and accessing the potential impacts of species extinction in biodiversity loss is urgent, as it would enable efficiently use of limited resources for conservation. In this context, a phylogenetic perspective gained attention in conservation studies as it is able to inform about species distinctiveness, helping in estimating the magnitude of diversity that can be lost with species extinction and guiding priorities aimed to maximize diversity preservation [4]. Phylogenetic relationship between species serves as basis to measure biodiversity as a broad set of attributes (feature diversity sensu [4]), which is generally correlated with phylogenetic relatedness [5–7]. Thus, measures of phylogenetic diversity have been used to investigate evolutionary patterns of extinction risk of species using different analytical frameworks [8].

A major finding in studies of extinction risk is the non-random phylogenetic distribution of threatened species, indicating that some clades are more endangered than others [9–13]. Considering that extinction of close related species prune the evolutionary history (EH) of an entire clade, phylogenetic clustering of extinction risk suggests that more EH can be lost than if endangered species were randomly distributed across the phylogeny. Magnitude of EH loss was estimated for new world anurans [14], birds [10,12], mammals [9,15] and other taxonomic groups (plants, corals and fishes; see [16] for a recent review). However, estimates of rates of EH loss on large geographical scale ignore the fact that species extinction occurs at regional and local scales, through reduction in population sizes, therefore underestimating the impacts of extinction on ecosystem processes and function on local spatial scales. Thus, global extinction of a single species may not represent a significant EH loss to a major clade, but the extinction of the same species may represent substantial regional or local EH loss [14].

Regional assessments of estimated EH loss, accounting for idiosyncrasies of regional species assemblages, demonstrated uneven spatial pattern. While some localities might lose larger proportion of EH through extinction of threatened species than if extinctions were random, other localities show opposite pattern [14,17]. Thus, regional assessments are especially important to provide useful comparative background for conservation decision, by identifying regions that are more (or less) susceptible to EH loss [18], such as the estimates of potential EH loss of anurans [14], mammals [17] and corals [19]. However, these published estimates of potential EH loss in regional scales were limited in spatial extent (e.g. New World anurans), therefore not encompassing the whole globe. Furthermore, as evolutionary history is distinct between taxonomic groups, patterns of potential EH loss are also expected to be distinct between both clades and regions, indicating the need of a globally integrated and multi-taxonomic analyses.

A multi-regional and multi-taxonomic approach is important for conservation prioritization by identifying concurrence patterns across taxa, improving use of limited resources for conservation by maximizing diversity preservation across distinct groups at the same time [20,21]. Further, a multi-taxonomic and regional analysis, covering the whole globe, encompasses more species and consequently more EH, which provides a comprehensive investigation of spatial patterns of rates of EH loss. In addition, expanding the spatial scale of analysis offers an opportunity to create a global conservation planning on EH preservation, as all regions of the world can be ranked according to the regional estimates of EH loss rate. Nevertheless, no analyses of regional EH loss focused on comparing multiple taxa, at the global level, has been done so far.

Given the need of a multiple taxonomic and broad geographical estimates of EH loss, here we perform, to our knowledge, the first full assessment of phylogenetic structure of extinction risk and the potential loss of EH of global terrestrial vertebrates. Although phylogenetic patterns of extinction risk have been explored separately for different taxonomic groups, here we provide a comprehensive multi-taxonomic analysis to guide conservation decision-making by standardizing methodological procedure and geographical scale, allowing a robust and direct comparison of patterns across different groups. Then, by integrating results across taxonomic groups, we provide the first unifying spatial estimates of EH loss across distinct groups (i.e. terrestrial vertebrates).

Methods

Our study comprehend all 10.177 birds [22], 7.225 amphibians [23] and 5.509 terrestrial mammals [24]. Reptiles could not be included in the analysis because of large knowledge gaps about phylogenetic relationships and geographic distribution. To investigate the phylogenetic distribution of extinction risk and measure projected EH loss of terrestrial vertebrates we used the phylogenetic hypothesis of [25] for mammals, [26] for birds and [27] for amphibians. However these phylogenies do not encompass all species of their respective clades: bird's phylogeny lacks 184 species, mammal's phylogeny lacks 590 species and amphibian's phylogeny lacks 4.356 species. To include species that are missing from the tree ("Phylogenetic Uncertain Taxa" or PUT) in the analysis we followed [28] methodological procedure (see also [14] for further details), which starts by defining the most derived consensus clade (MDCC) to which each PUT unquestionably belongs. We compiled all the relevant information available in literature to identify the MDCC of each PUT. After all PUT were assigned to their respective

MDCC, a Monte Carlo procedure were employed generating several possible phylogenetic trees that simultaneously include species already present in the published phylogeny and assigning each PUT to a randomly chosen branch within its MDCC. Thus, all analysis were conducted using different phylogenies generated by the Monte Carlo procedure, allowing us to measure the variation in the results produced by phylogenetic uncertainty. In this study we used 100 permutations of phylogenies for each taxonomic group, produced in the software PAM v0.9 (Phylogenetic Analysis in Macroecology, [29]).

To explore the interaction between phylogenetic distribution of extinction risk and rates of EH loss we used the Net Relatedness Index (NRI; [30]) to quantify the phylogenetic structure of species in each IUCN category (Table 1). Higher NRI values indicate that species in the IUCN category are phylogenetically clustered. Conversely, smaller NRI values indicate that species belonging to the IUCN category are scattered (over-dispersed) across the phylogeny. The NRI calculation, for each IUCN category, was replicated 100 times using different phylogenies, therefore allowing the estimation of the effect of phylogenetic uncertainty. To test if level of phylogenetic clustering/over-dispersion is significantly different than random expectation, we performed 100 replicates of NRI under a null model of full shuffle of species identities. Finally, we recorded the frequency of significant NRI (P-value < 0.05) across the permutations of phylogenies (see Figure 1).

Table 1. Number and proportion of species, per taxonomic group, in each IUCN category.

IUCN Category	Amphibians		Birds		Mammals	
	N	(%)	N	(%)	N	(%)
Not Evaluated (NE)	833	11.53	105	1.03	114	2.07
Data Deficient (DD)	1574	21.79	59	0.58	753	13.67
Least Concern (LC)	2425	33.56	7669	75.36	3073	55.78
Near Threatement (NT)	398	5.51	901	8.85	315	5.72
Vulnerable (VU)	645	8.93	705	6.93	496	9.00
Endangered (EN)	795	11.00	399	3.92	472	8.57
Critically Endangered (CR)	520	7.20	202	1.98	210	3.81
Extinct (EX)	35	0.48	137	1.35	76	1.38

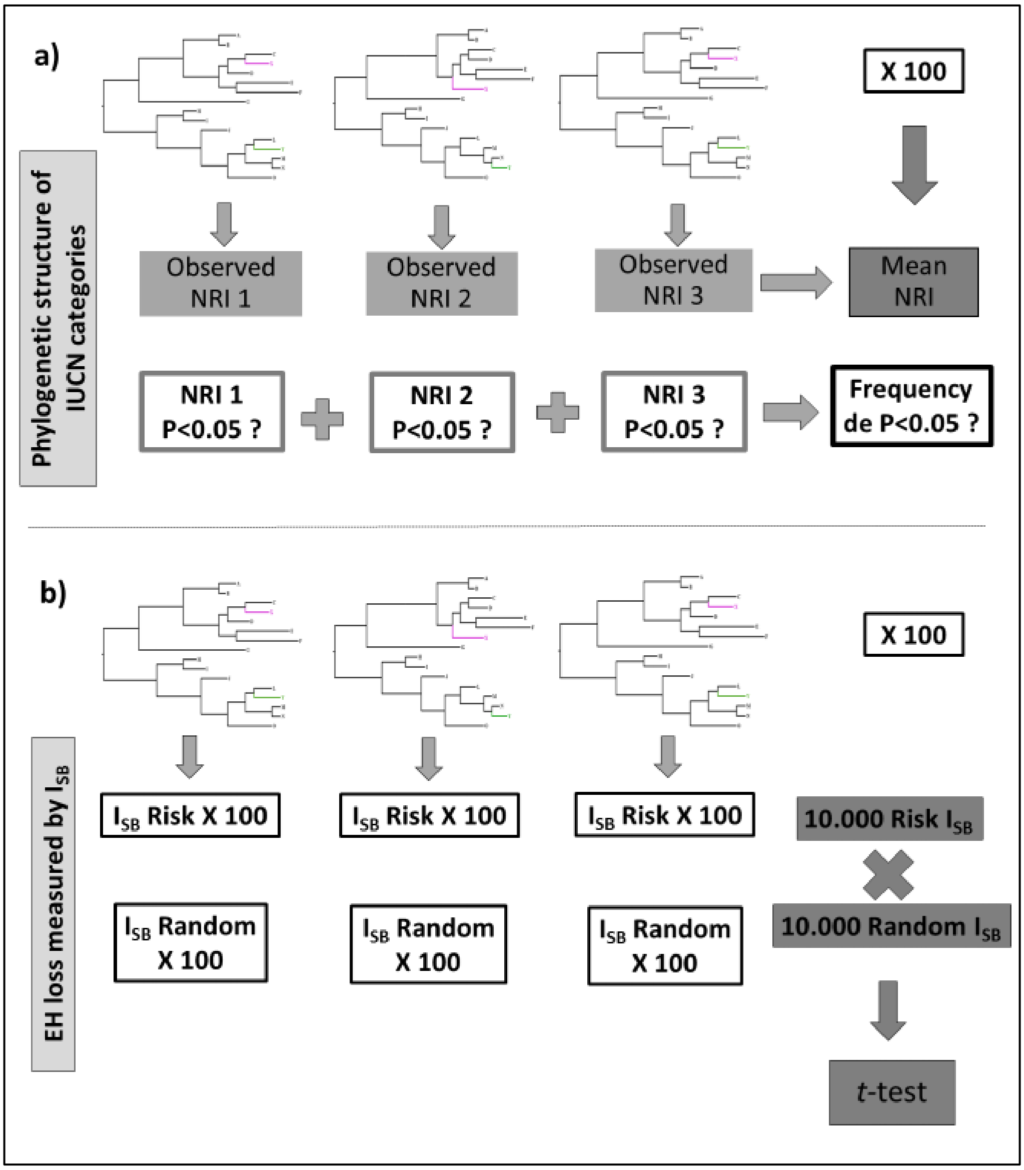


Figure 1. Schematic of permutations employed in our analyses. In this study we used 100 permutations of phylogenies following [28] procedure to account for species that are missing from the tree. For each phylogeny permutation we measured the observed NRI value (panel a) for each IUCN category and tested its significance performing 100 replicates of NRI under a null model of full shuffle of species identities. After, we calculated the mean between observed NRI values and recorded the frequency of significant NRI (P-value < 0.05) across the permutations of phylogenies. EH loss (panel b) were also measured through the 100 permutations of phylogenies and contrasted by the sub-optimality index (I_{SB}). For each phylogeny we replicated 100 times random and risk scenarios as the order in which species go extinct is defined probabilistically, generating different rates of EH loss when the process is repeated, even for the same phylogeny.

Finally, an independent two-sample student’s *t*-test (Welch’s *t*-test) was employed to estimate the magnitude of difference between the 10.000 I_{SB} values for random and 10.000 I_{SB} values for risk scenarios. Note that all methodological procedure were repeated independently for each taxonomic group.

The extinction of a species erases it’s unique EH, which is graphically represented by removing a tip from the phylogeny. However, ancestral EH information is only lost when the last remaining species of the clade goes extinct. For example, given a clade of two sister species, the extinction of one of them leaves the other species as the only remaining representative of the clade, therefore holding additional unique EH (i.e. its ancestral EH information). Thus, at each extinction event, only the tip branch of the extinct species is removed from the phylogeny, resulting in the loss of the species unique EH. Nevertheless, the tip of the remaining species is fused to the ancestor branch, still representing the clade EH. Therefore, rates of EH loss are achieved by measuring the amount of remaining EH after each extinction event, which occur in a stochastically defined sequence (Figure 2).

To investigate how the sequence of species extinctions would affect the rate of EH loss we simulated different extinction scenarios (following methodological procedure of [14]). A “realistic” scenario (risk) predicts that the most likely sequence in which species go extinct is a function of their current extinction risk, estimated by the threat status of the species according to the IUCN Red List (2015). Thus, higher extinction risk increases the chance of a species to go extinct in risk scenario. Conversely, species in non-threatened categories (near threatened, NT; least concern, LC; not evaluated, NE) have the lowest individual chance of going extinct, and therefore are usually the last to go extinct in the risk scenario. Algorithmically, all species in non-threatened categories have, at each step in the sequence of extinction events, the same chance to go extinct (weight: 10^0), whereas species in threatened categories (vulnerable, VU; endangered, EN; critically endangered, CR) have increasingly chance to go extinct according to the severity of the threat status (weights: 10^1, 10^2, 10^3, respectively). Considering the high number of Data Deficient (DD) species that were recently re-evaluated and re-assigned to a threatened category [31,32], here we set the same chance of extinction of DD species as VU species. Under the risk scenario, the relative probability of a single species becoming extinct is measured as function of the weight of its IUCN status and the number of species assigned to each status. For example, if each one of the seven IUCN categories described above had only one species (totaling seven species), the sum of weights would be 1123 ($10^0 + 10^0 + 10^0 + 10^1 + 10^1 + 10^2 + 10^3$). Thus, the relative probability of extinction assigned to each species in non-threatened categories (NE, LC and NT) would be 0.089% (10^0/1123), whereas species in threatened categories (VU, DD, EN and CR) would have a relative extinction probability of 0.89% (VU: 10^1/1123), 0.89% (DD: 10^1/1123), 8.9% (EN: 10^2/1123) and 89% (CR: 10^3/1123). Some species already extinct were also include into analysis, weighting very high (10^9) to guarantee that they are the first to go extinct under the risk scenario.

To establish a baseline comparison we implemented a null scenario (random), which assigns equal probability of extinction to all species, regardless of the threat status of each species. Effectively, this scenario creates a random sequence of extinction events. In addition, we calculated the sequence of extinction events that yields the maximum and minimum rate of EH loss, which we used to measure a standardized index of EH loss rate for both risk and random scenarios. The minimum and maximum rate of EH loss occurs when the sequence of extinction events is defined according to the branch length of the species. Thus, if the species with the shortest branch length is always the next to go extinct, the resulting rate of EH loss is the lowest possible. Conversely, if the species with the longest branch length is always the one going extinct, the maximum possible rate of EH loss is achieved. Notice that minimum and maximum rates of EH loss is an algorithmic procedure that uses only information on the branch length of the species, regardless of their actual risk of extinction.

The order in which species go extinct in the risk and random scenarios is defined probabilistically, generating different rates of EH loss when the process is repeated, even for the same phylogeny. Thus, for each permutation of the phylogeny, we replicated 100 times each probabilistic extinction scenario. In contrast, given a phylogeny, the minimum and maximum rate of EH loss is invariant, as there is a unique and constant order of species extinction that leads to minimum and maximum rate of EH loss. To contrast extinction scenarios, we measured the sub-optimality index (I_{SB}) [14] for each permutation of the phylogeny (100 times), and each replicated of random and risk scenarios (100 times), totaling 10.000 I_{SB} values for each probabilistic scenario (Figure 1). The ISB index is obtained by dividing the area enclosed between the curves defined by minimum and probabilistic EH loss (area A, in Fig.2), by the total area enclosed between the curves of minimum and maximum EH loss (area A+B, in Fig.2), or I_{SB}=A/(A+B). Thus, the index varies between 0, indicating that the probabilistic EH loss curve is close to the minimum EH loss scenario, and 1, indicating that the probabilistic EH loss curve is close to the maximum EH loss scenario.

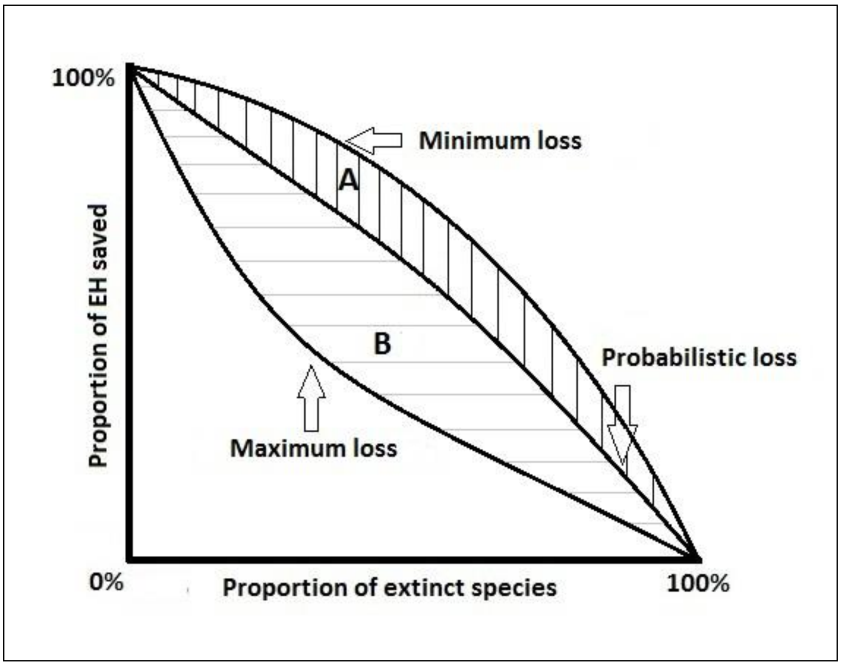


Figure 2. Figure adapted from [14] showing average rate of EH loss as function of species extinction under distinct scenarios. The probabilistic curve represents the random or risk extinction scenarios. The maximum loss curve represents the fastest rate of EH loss (worst-case scenario), whereas the minimum loss curve represents the slowest rate of EH loss (best-case scenario). The area encompassed between minimum and probabilistic loss curves is named (A), whereas the area between maximum and probabilistic loss curves is named (B). A sub-optimality index (I_{SB}) measuring how a given probabilistic scenario approaches the maximum loss curve can be defined as $I_{SB}=A/(A+B)$.

We employed independent two-sample student's *t*-test (Welch's *t*-test) to estimate the magnitude of difference between the 10.000 I_{SB} values for random and 10.000 I_{SB} values for risk scenarios. The *t* statistic is also useful to describe the direction of the average difference between the random and risk scenarios. Positive *t* values indicate that the EH loss in the risk scenario occurs faster than the random scenario (average I_{SB_risk} >

average I_{SB_random}), whereas negative *t* values indicate that the risk scenario shows slower rate of EH loss compared to the random scenario (average I_{SB_risk} < average I_{SB_random}).

To describe rates of EH loss regionally, the geographical distribution of species was compiled from IUCN database (available at http://www.iucnredlist.org/technical-documents/spatial-data). We used SAM v4.0 (Spatial Analysis in Macroecology [33]) to overlay the range polygons in grid cells of 1° X 1° latitude – longitude. A species was considered present in a cell only if it occupied at least 50% of the cell area, except for species whose range was restricted to an area below this threshold. For species missing from database, we compiled distribution maps or point-locality records from specific studies. Therefore, we replicated the entire analytical protocol relative to EH loss for each cell of the grid, redefining the species pool according to the species assemblage that occupy the cell, and used the *t* statistic as a spatial measure of departure of the risk from the random scenario of rate of EH loss for each taxonomic group. Finally, we provided a single spatial EH loss estimate for terrestrial vertebrates by summing the *t*-values across taxonomic groups for each cell. Thus, if a given cell exhibits a *t*-value of 4.56 for amphibians, -2.1 for mammals and 0.5 for birds, the *t*-value for terrestrial vertebrates in that given cell would be 2.96.

Results

Phylogenetic structure of species in IUCN categories have non-random clustering patterns (Figure 3). For amphibians, Not Evaluated (NE), Near Threatened (NT) and Vulnerable (VU) categories are composed by phylogenetic over-dispersed species, while species in Least Concerned (LC), Critically Endangered (CR) and Extinct (EX) are phylogenetically clustered. For birds, most categories are composed of phylogenetically over-dispersed species, except LC and NE. For mammals, species in the Data Deficient (DD) category are phylogenetically clustered, indicating that knowledge gaps are concentrated in specific sub-clades. Further, NT and CR mammals are over-dispersed across phylogeny, whereas NE and LC are clustered. At the global scale, threatened terrestrial vertebrates tend not to be phylogenetically clustered, with exception of CR amphibians.

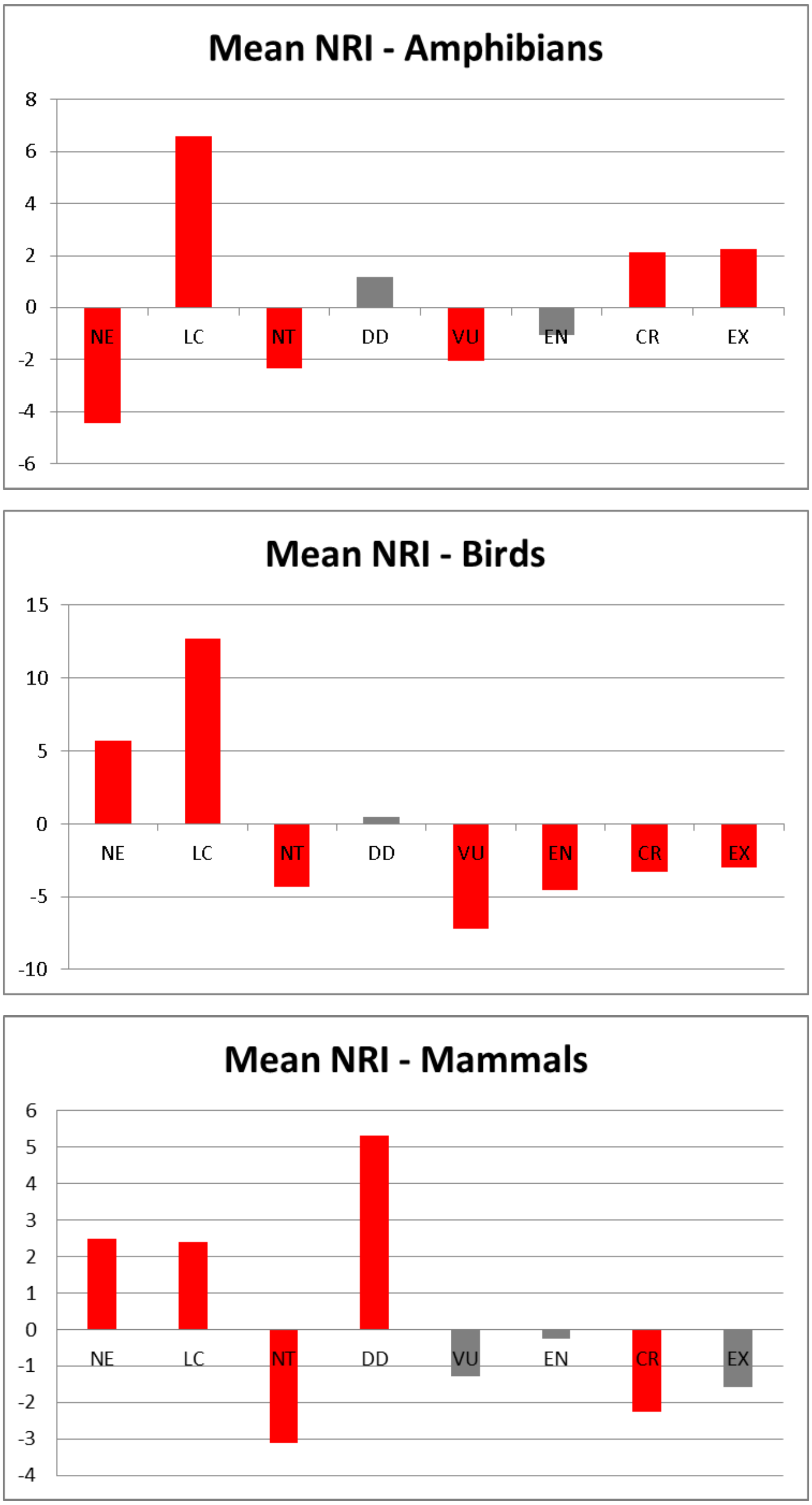


Fig 3. Average net relatedness index (NRI) for each IUCN category. Significant ($P < 0.05$) averages are shown in red. NE = Not Evaluated; LC = Least Concerned; NT = Near Threatened; DD = Data Deficient; VU = Vulnerable; EN = Endangered; CR = Critically Endangered; EX = Extinct.

If threatened terrestrial vertebrates go extinct prior to the non-threatened vertebrates, the global loss of EH would not be substantially faster than the random extinction of the same number of species. Indeed, patterns of rates of EH loss among taxonomic groups (Fig. 4) are similar, with risk and random curves of EH loss overlapping almost entirely. For amphibians, the average I_{SB} index for the random scenario is 0.434, whereas for the risk scenario the average I_{SB} is 0.449. Birds showed average I_{SB} index for the random scenario equal to 0.405 and 0.413 for risk scenario. Finally, for mammals, the average I_{SB} index for the random scenario is 0.424 and for risk scenario is 0.437. Average I_{SB} index for risk scenario is higher than average I_{SB} index for random scenario in all groups, indicating that risk scenario shows faster EH loss than if extinctions were random. However, as showed by the t-test, difference between probabilistic scenarios are not significant (amphibians, $t = 0.1470$, P-value = 0.076; birds, $t = -0.93$; P-value = 0.34; mammals, $t = -1.30$, P-value = 0.19).

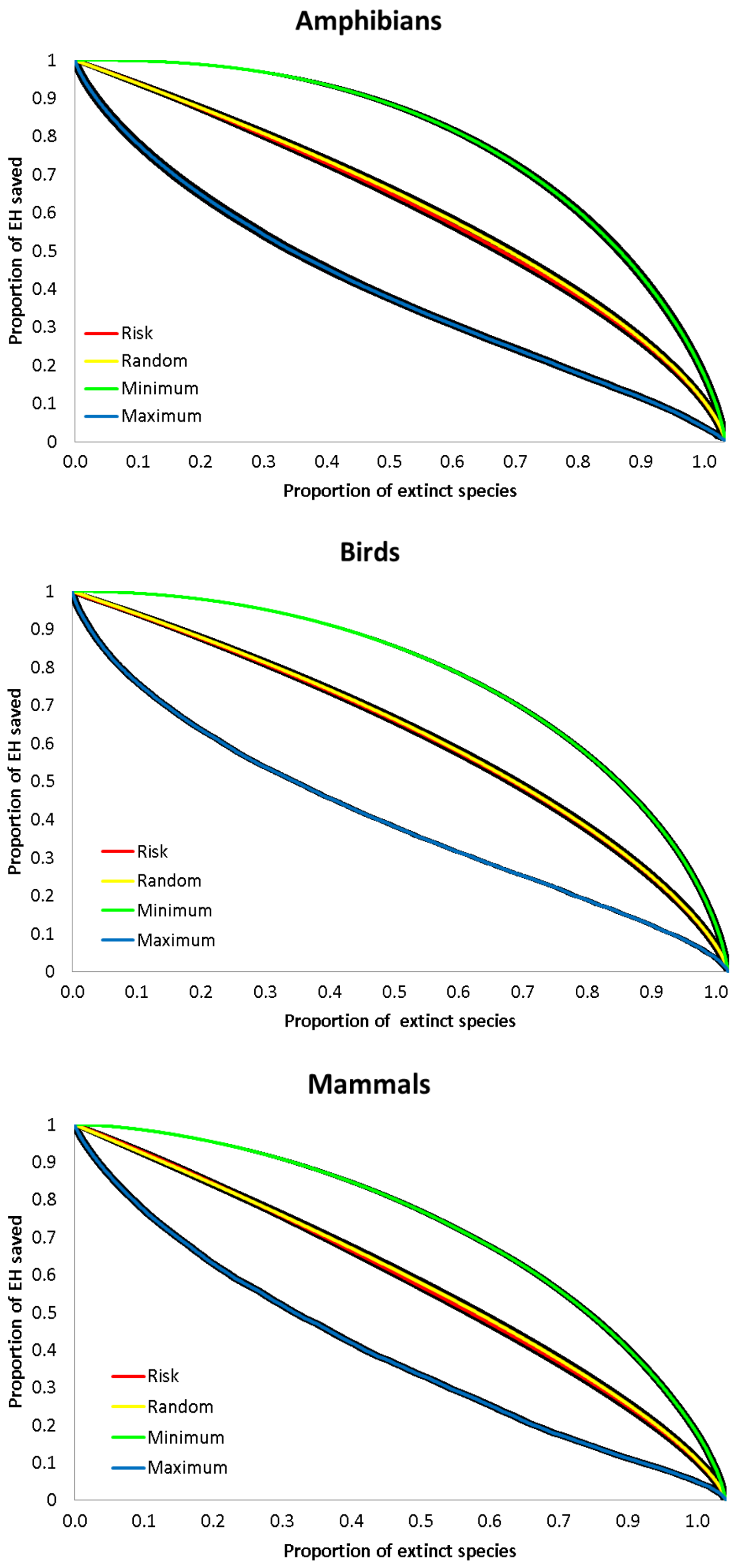


Fig 4. Average remaining EH for Amphibians, Birds and Mammals in four scenarios of extinction. Black lines around the EH loss curves are the 95% confidence interval around average.

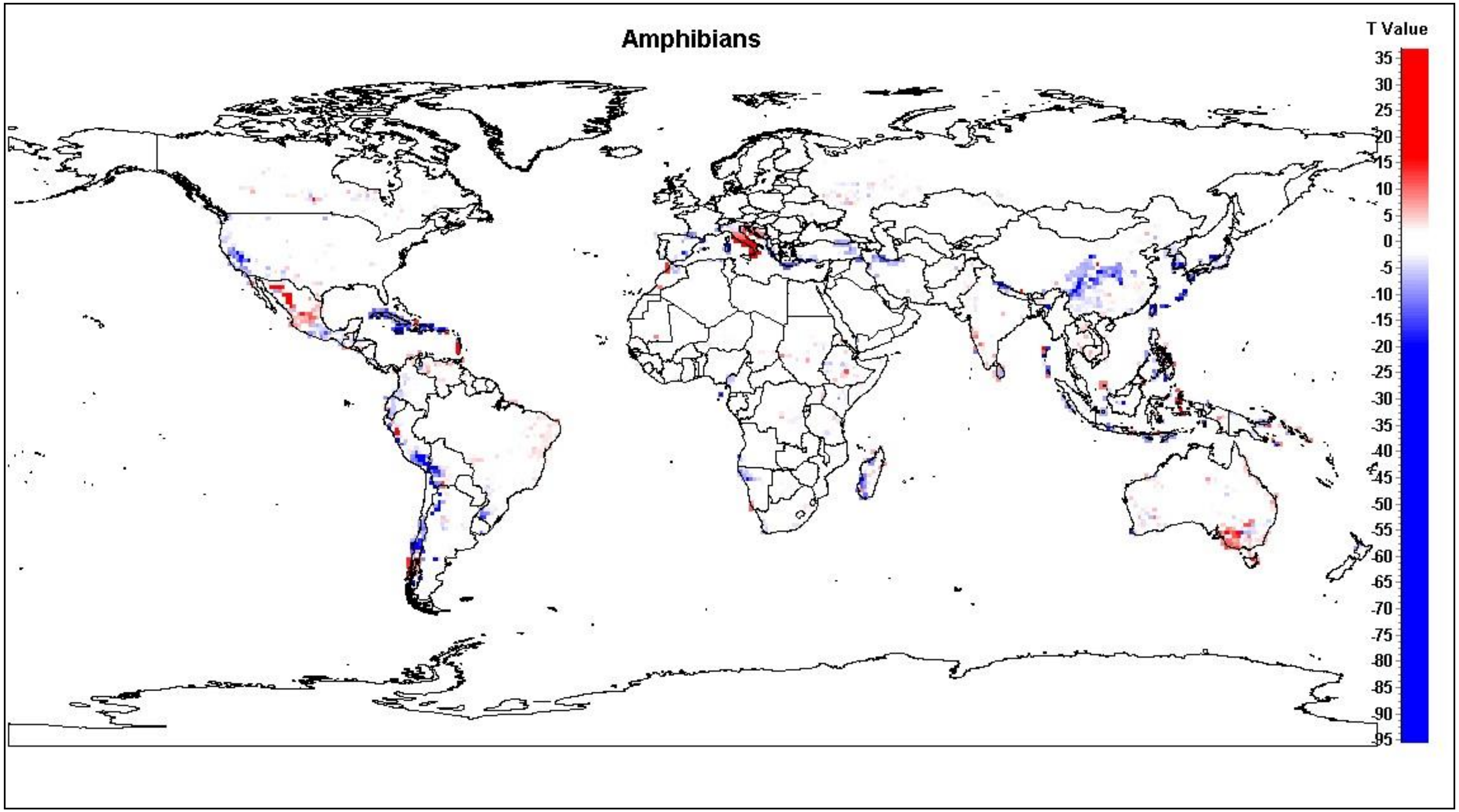
Contrary to the global and non-spatial assessments of EH loss, estimates of regional rates of EH loss show substantial discrepancies among extinction scenarios, caused by differences in assemblage composition and by threat status of species in each taxonomic group (Fig. 5). Departure between risk and random scenarios were measured by *t* statistic, describing the direction and magnitude of difference between I_{sb} values of risk and random scenarios for each cell. The *t* statistic allow us to use a threshold of $t > 1.96$ or $t < -1.96$ to indicate that the difference concerning random and risk scenarios is unlikely due to chance alone, whereas *t*-values between $-1.96<t<1.96$ indicates that the difference between random and risk is small and/or the uncertainty is too large for a reliable conclusion. However, regions of low species richness showing significant *t* values must be interpreted with caution, as results are extremely dependent of the most threatened species. Simulation replicates tend to have zero variance in cases where species richness is small (particularly below 5 species), as the results obtained for cells that are species poor are always trivial, not resulting from a strong pattern of species phylogenetic structure. In addition, we believe that no analysis is necessary to conclude that conservation actions targeted at those regions are urgent, as the loss of one species would mean a significant loss of EH to the regional pool.

Regional estimates of EH loss for amphibians showed large positive *t*-values (shown in red at Fig. 5) concentrated mainly in Mexico, Italy, in the southeast portion of Australia and Tasmania, indicating faster EH loss in the risk compared to random scenario of extinction. Conversely, negative *t*-values (shown in blue) indicate that loss of EH is slower in the risk than in the random scenario, a pattern occurring in a portion of west coast of USA, Caribbean region, Andean region, China and some cells in Madagascar. Southeast Asia and northern of Oceania showed highly uneven patterns of departure between extinction scenarios, although *t*-values estimated at those regions are relatively small, suggesting small differences between risk and random extinction scenarios.

For birds, positive *t*-values were observed in Sahara Desert (specifically in the border between Mauritania, Algeria and Mali; also between Egypt and Libya) and some punctuated islands in Pacific Ocean, Santa Helena in Atlantic Ocean, Mariana Islands and islands around Madagascar (Reunion Island, Seychelles Islands). Conversely, negative *t*-values are observed in some islands of Pacific Ocean such as Hawaii, North of Canada and North of Siberia. Finally, heterogeneous patterns of departure between extinction scenarios were observed for Birds in southwestern Greenland. Notice, however, that *t*-values for birds are not as large as observed for amphibians and mammals, indicating that risk scenario are not so discrepant from random scenario, especially in continents. In addition, regions as North of Canada, Greenland, North of Siberia and Sahara Desert are regions of low species richness (see S1 Fig.), and departure between risk and random scenarios must be determined by the few threatened birds in each cell of those regions (see S2 Fig.).

Finally, we observed many regions with large positive *t*-values for mammals, indicating that the extinction of threatened and DD species (risk scenario) would cause larger EH loss than a random sequence of extinctions (random scenario). Our results suggests that faster rates of EH loss in risk scenario might occur in Caribbean region, Central America, Bolivia, Argentina, New Zeeland, Madagascar, Indonesia, Philippines and Papua New Guinea. In contrast, the Himalayas, Tasmania and Solomon islands showed negative *t*-values, indicating that extinction of threatened and DD species would cause slower EH loss than random extinctions. The patterns observed for mammal extinction in Greenland, Sahara Desert, North Canada and North Siberia are also strongly influenced by the poor species richness in those regions (S1 Fig. and S2 Fig.).

When the three taxonomic groups are evaluated together, rates of EH loss suggests that faster EH loss in the risk compared to random scenario of extinction would occur in in Mexico, a portion of Greenland, Italy, Sahara Desert, Madagascar, Indonesia, Philippines and Papua New Guinea, in the southeast portion of Australia and New Zealand. Conversely, slower loss of EH in the risk than in the random scenario is expected to occur in northeast of Greenland, North of Canada, some cells in a portion of west coast of USA and Caribbean region, Andean region of Peru, Bolivia and Chile, Himalayas and some cells around Japan.


Amphibians
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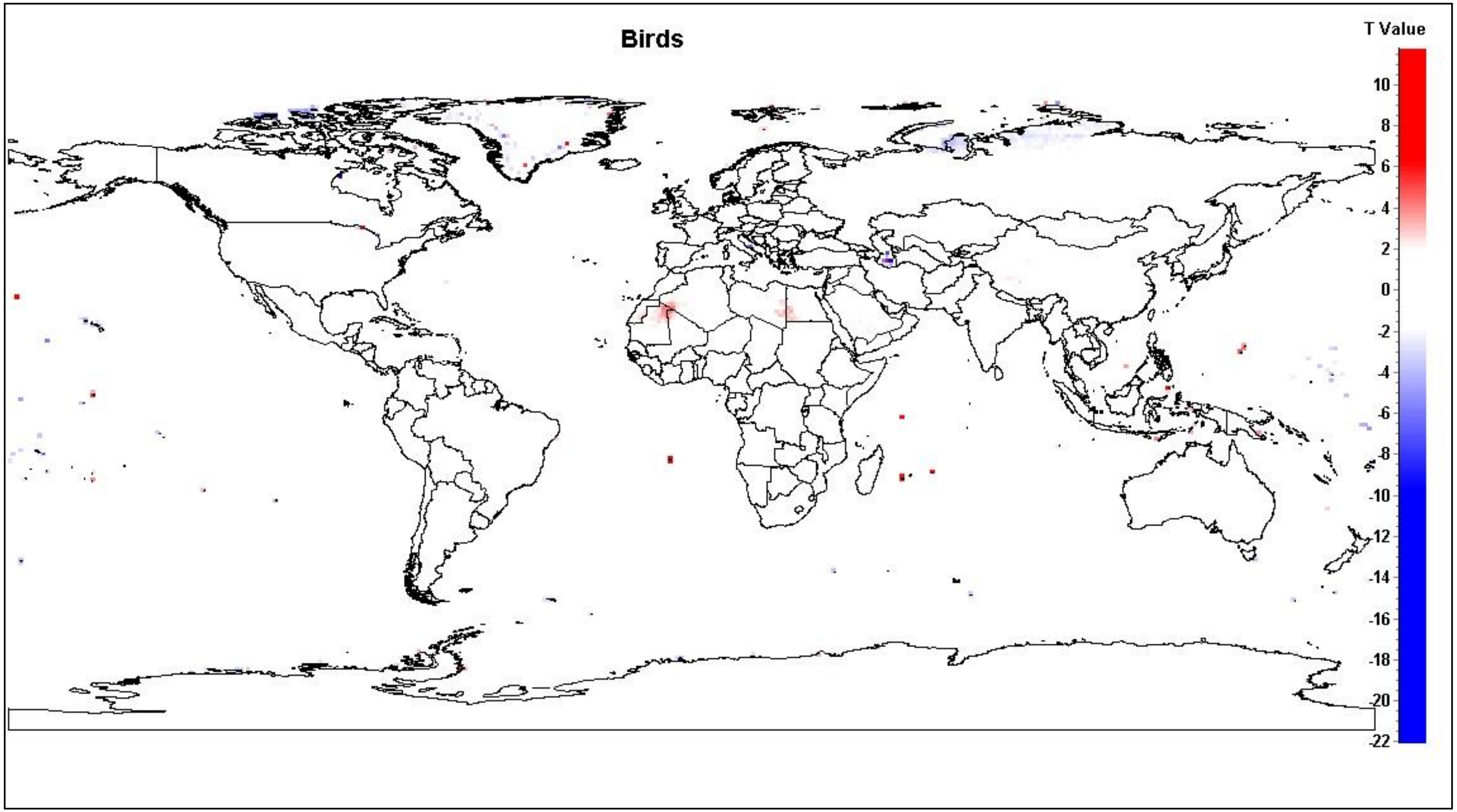
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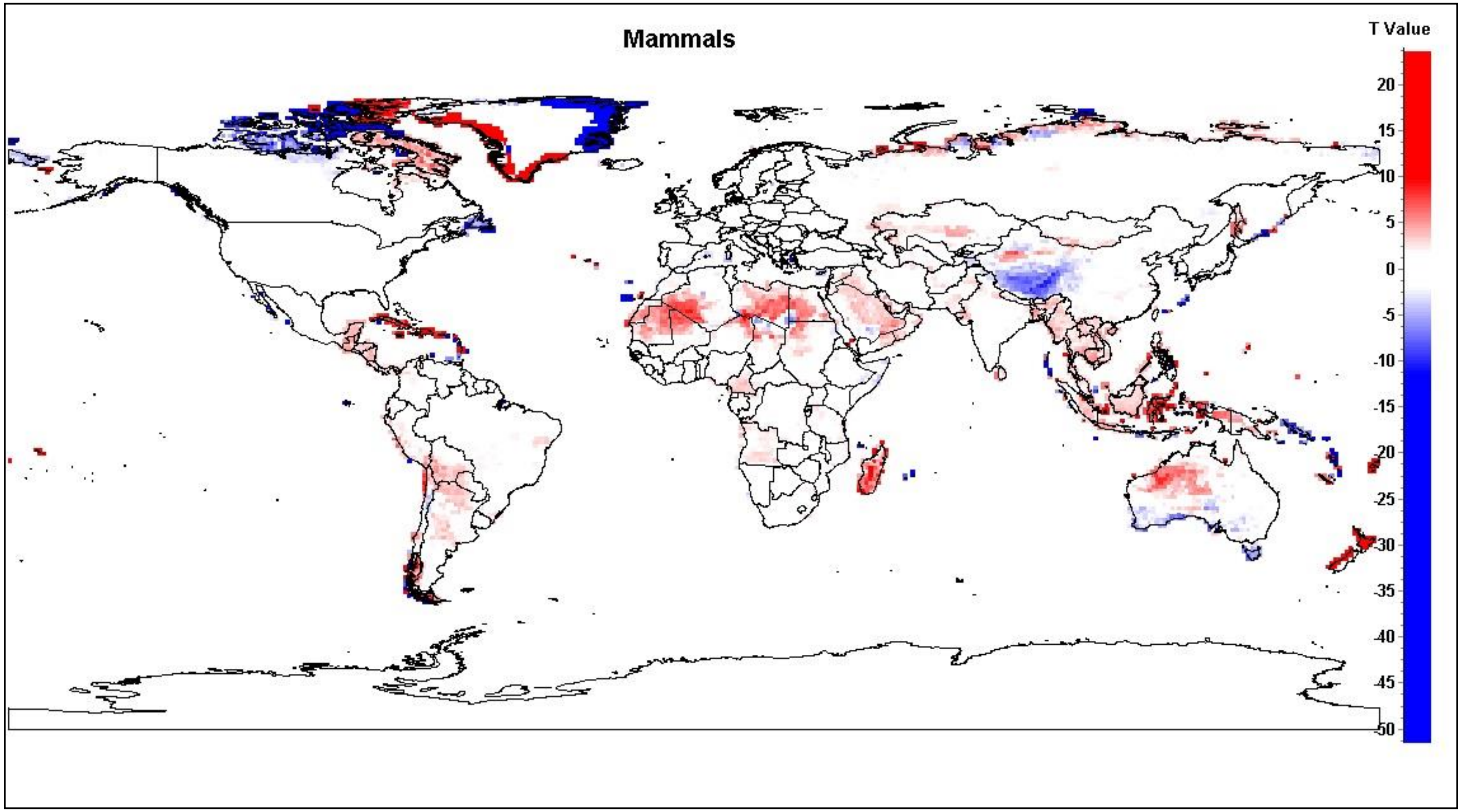
Mammals
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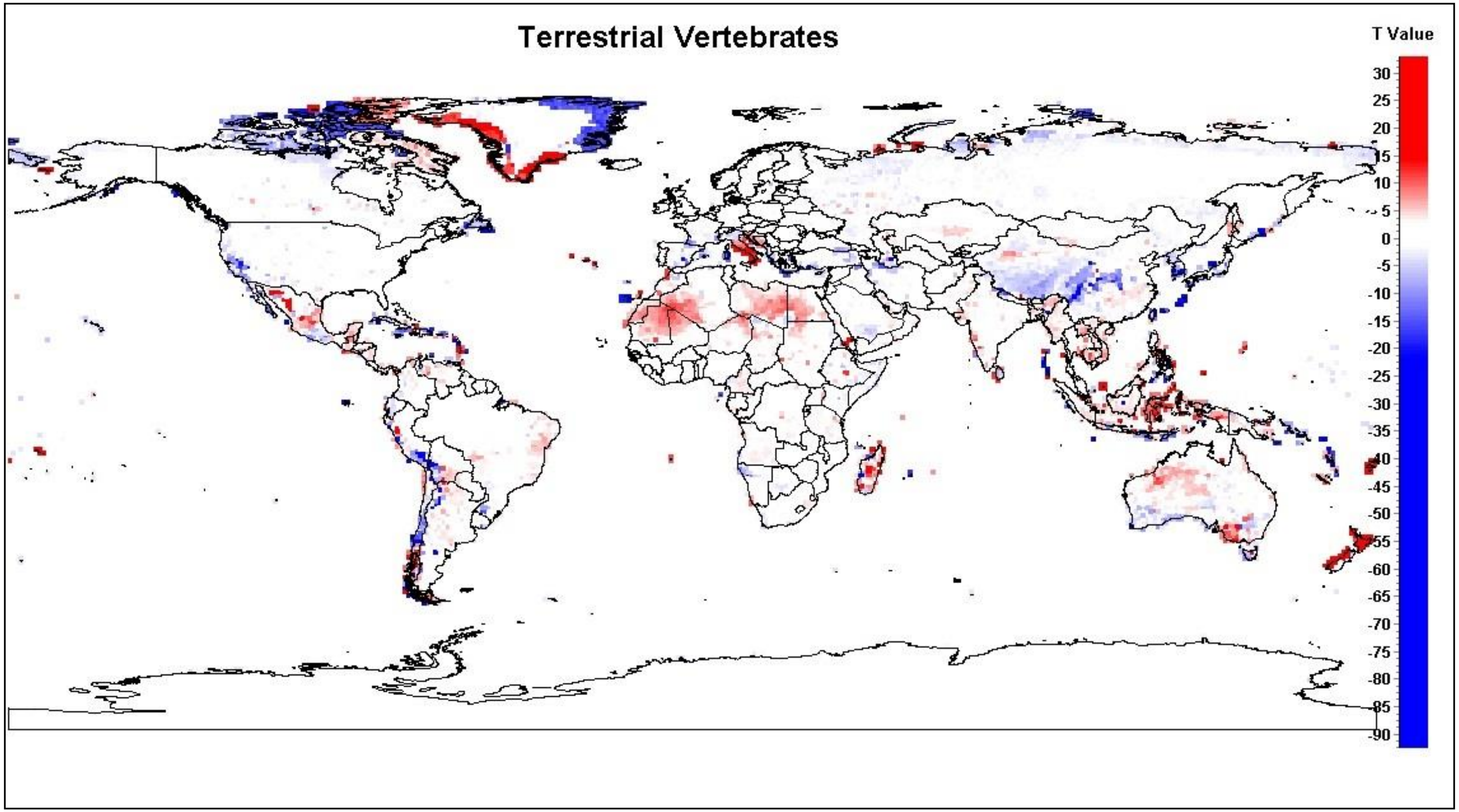


Fig 5. Regional estimates of EH loss for Amphibians, Birds, Mammals and Terrestrial Vertebrates (the three taxonomic groups together) showing departures between scenarios of extinction measured by the *t* statistic. Positive values of *t* (showed in red) indicates regions where the extinction of threatened and Data Deficient (DD) species would result in faster EH loss than random extinctions. Conversely, negative *t* values (showed in blue) indicates regions where random extinctions would cause faster EH loss than extinction of threatened and DD species.

Discussion

In a global context, our results indicates that equivalent rates of EH loss would result from the extinction of currently threatened terrestrial vertebrates or the same number of randomly chosen species. Further, for amphibians, birds and mammals, about 80% of EH would still exist after extinction of nearly 25% of all existing species, whether threatened or not. In other words, conservation efforts designed to preserve threatened species would achieve similar results (as measured by preserved EH) by protecting non-threatened species. Similar results were demonstrated for Brazilian birds [34]. However, a regional analysis showed very uneven patterns across the world and among taxonomic groups, demonstrating the importance to account for regional idiosyncrasies of species vulnerability in estimates of EH loss [14,17]. Indeed, globally the EH loss promoted by the extinction of one or few species is too small compared to the total EH of the entire taxonomic group. However, in regional scale, the extinction of one or few species could represent a considerable reduction in regional EH.

Our spatial analysis of rates of EH loss across the globe showed several regions where extinction of threatened and DD species would result in slower EH loss than random extinctions, as indicated by the negative *t*-values in Figure 5. Amphibians showed strongest spatial patterns of negative *t*-values, especially in the west coast of USA, Caribbean islands, Andean region, China and part of Madagascar. This result indicates that threatened and DD species of those regions might be phylogenetic recent compared to the co-occurring species pool. Trends of correlations between extinction risk and recent speciation were observed for plants [35] and the authors suggested that mode of diversification in plants, through small and reproductively isolated populations, increase the probability of recently diverged species to be classified as threatened, because range size is a key criterion used by IUCN evaluations [36]. Similar hypothesis were raised for New World threatened anurans [14], suggesting a link between recent evolutionary age and small range size related to patterns of diversification in high topographic heterogeneity. In fact, previous analysis showed that most threatened amphibians species tend to have small geographical ranges [37], which is also observed in our data (Figure S4), and tend to be concentrated at topographically heterogeneous regions [38,39]. However, because of substantial phylogenetic uncertainty in amphibian data, the correlation between threat status and taxa age (branch lengths of tips) could not be confirmed.

For mammals, regions indicating slower rates of EH loss as consequence of extinction of threatened and DD species (negative *t*-values) are the Himalayas, Tasmania and Solomon islands. Similarly to observed for amphibians, results for mammals suggests that threatened and DD species at islands and at regions of high topographic heterogeneity tend to be phylogenetic recent [40], and conservation policies for those species would preserve similar amounts of EH than conservation policies targeting any set of species. Interestingly, previous studies observed that loss of range restricted species, which is a pattern that commonly occurs in islands and regions of high altitudes, would result in a relatively small effect on EH loss [41,42]. In general, our results indicate that threatened and DD amphibians and mammals in islands or in high topographic variation regions tend to be phylogenetic recent, not being of relatively urgent concern for conservation strategies designed at EH preservation. In the Caribbean islands, for example, although we observe several threatened *Eleutherodactylus* spp with small range size, our results suggest that extinction of those species would not result in a severe EH loss. Nevertheless we strongly encourage detailed studies, specially focused on phylogenetic patterns of threatened species classified by range size criteria of IUCN evaluation.

Conversely, positive *t*-values indicating that extinction of threatened and DD species would result in faster EH loss than random extinctions, showed stronger patterns for mammals, with concentrations in the Caribbean region, Central America, Bolivia, Argentina, New Zealand, Madagascar, Indonesia, Philippines and Papua New Guinea, similar to previous estimates of Phylogenetic Diversity loss [17]. In general, those regions corresponds to high endemic species richness [43], suggesting that threatened and DD mammals at centers of endemism might be phylogenetically basal. For example, the endangered primate *Daubentonia madagascariensis* is endemic to Madagascar and the only living species of the genus Daubentonia and family Daubentoniidae. Another instance is observed in Caribbean region, where the two extant species of Solenodons (*Solenodon cubanus* and *Solenodon paradoxus*), endemics to Cuba and Hispaniola (Haiti and the Dominican Republic), are highly evolutionarily distinct, with divergence estimated of 25 million years between them [44].

For amphibians, regions of faster EH loss in risk scenario (positive *t*-values) are concentrated mainly in Mexico, Italy, in the southeast portion of Australia and Tasmania. It is interesting to note that these regions listed for amphibians are not rich in number of species or number of endangered species (Figure S1 and S2). Thus, few threatened and DD species are responsible for the faster EH loss in risk scenario, such as in Italy. Regions with large positive *t*-values are of conservation concern because the set of threatened and DD species might be phylogenetic distinct and their extinction could cause serious losses of EH and, consequently, disturbances in assemblage stability and ecosystem function. Still, it is important to note that species poor regions with positive *t*-values are also of conservation concern, as is the case of New Zeeland, where large positive *t*-values observed is due the threatened bats *Mystacina robusta* and *Mystacina tuberculate* that are endemics and the only representatives of the Mystacinidae family.

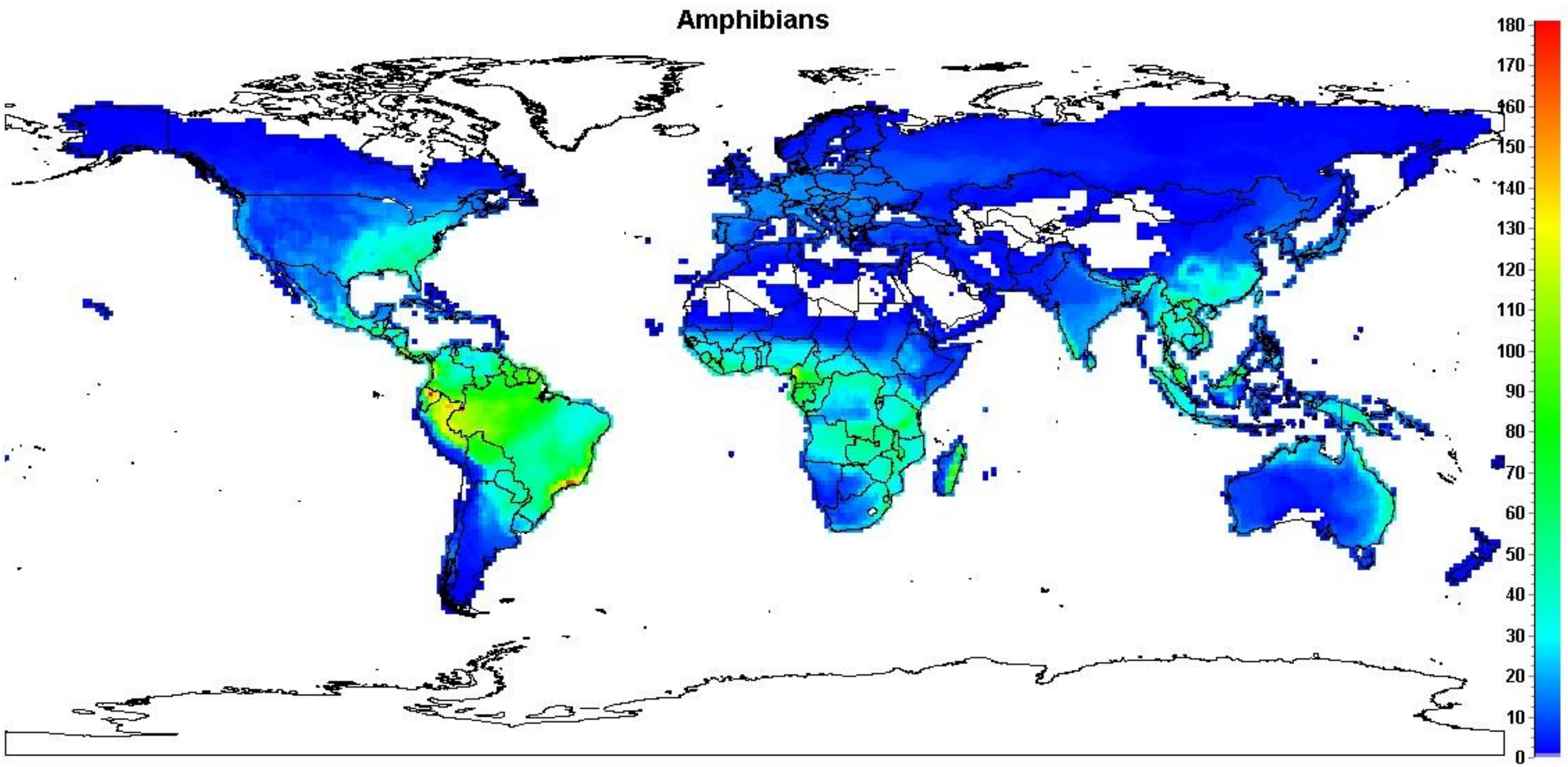
For birds, regional assessments of EH loss did not showed a clear pattern, but departures from random extinctions are concentrated in islands (Figure 5). Areas indicating that extinction of threatened and DD species would result in slower EH loss than random extinctions (negative *t*-values) is more apparent at islands of Pacific Ocean, such as Hawaii and Johnston Atoll. Although islands are of conservation concern [45,46] especially due richness of endangered species (Figure S2), some islands shows a high rate of diversification, particularly on Pacific Ocean [26] and, extinction of threatened species in those islands might not cause worse impacts than random extinctions. Furthermore, species with most of the range in islands are less likely to be evolutionarily distinct [18]. However, opposite patterns (positive *t*-values) were also restricted to islands, more specifically at some punctuated islands in Pacific Ocean, Santa Helena in Atlantic Ocean and islands around Madagascar (Reunion Island, Seychelles Islands). Thus, our results indicate that some islands are of conservation concern in EH preservation and others are not, showing contrasting patterns even for geographically close islands, which might be reflect of a multiple interacting process of bird's vulnerability and diversification.

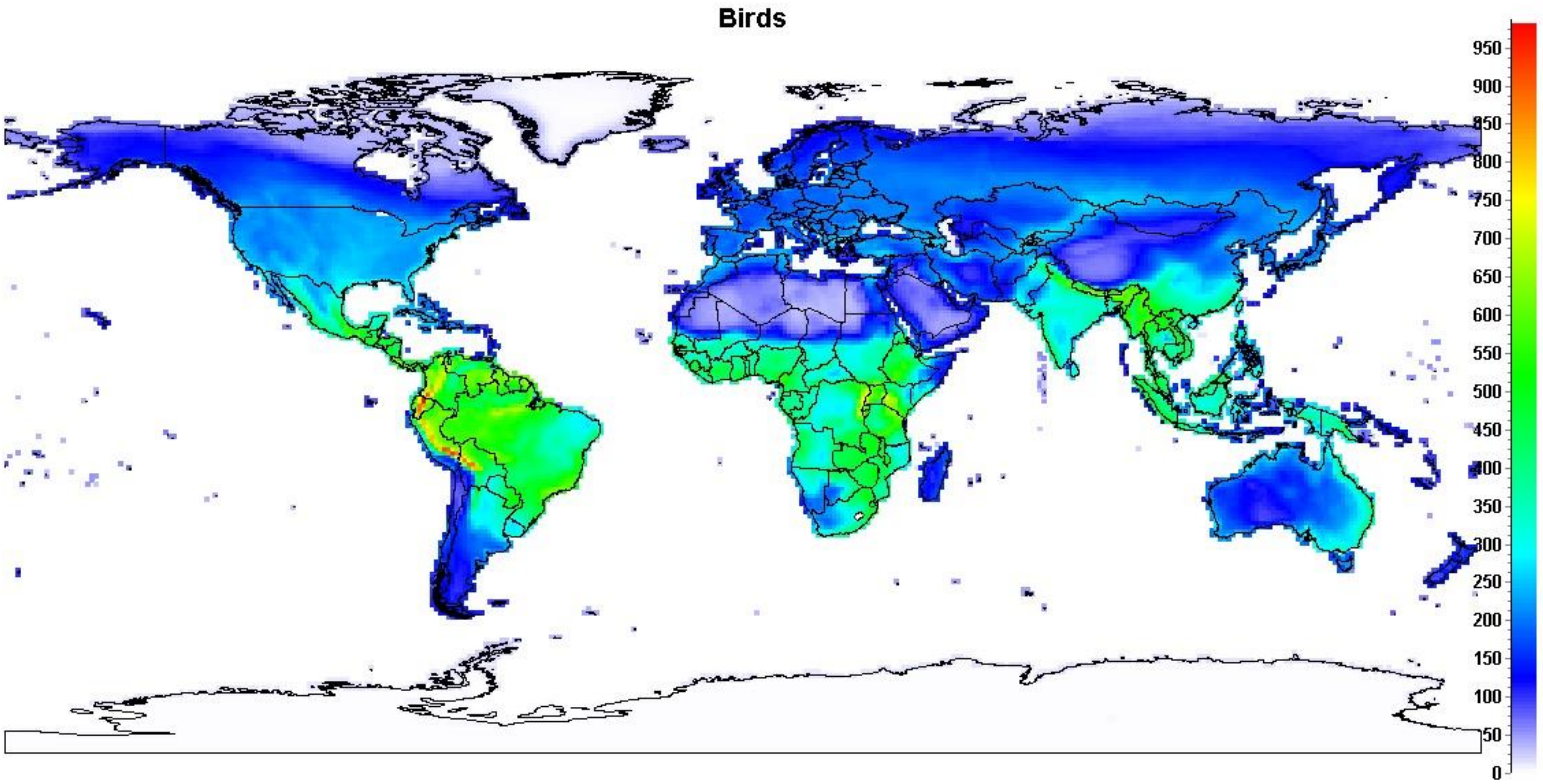
Rates of EH loss for terrestrial vertebrates are mainly a combination of observed results for the three taxonomic groups, as the majority of areas with departures of rates of EH loss from random expectation are incongruent between taxonomic groups (see also [47]), reflecting differences in their biogeographic histories. For example, New Zeeland showed positive *t*-values only for mammals, whereas Italy showed positive *t*-values only for amphibians, resulting in positive *t*-values for both regions when all groups were evaluated together. However, few regions showed opposite patterns, for example, the Caribbean region would experience serious EH loss if threatened and DD mammals go extinct, but extinction of threatened and DD amphibians would result in a slower EH loss than extinction of the same number of random species. Therefore, combining all the three vertebrate groups under analysis, our results suggest that we must concentrate conservation efforts on EH preservation in Mexico, a portion of Greenland, Italy, Sahara Desert, Madagascar, Indonesia, Philippines and Papua New Guinea, in the southeast portion of Australia and New Zeeland.

Here we provided a global guide for conservation of species based on potential rates of EH loss as consequence of species extinction. Our results highlight the importance of measuring the degree of EH loss considering regional idiosyncrasies [14,17,19]. Moreover, instead of identifying priority areas based on accumulated amount of EH (e.g. regions with high concentrations of evolutionarily distinctive and globally endangered species;[47]), our methodological procedure also encompasses the phylogenetic structure of species co-occurring in each cell. Thus, our results cover a multi-taxonomic and multi-regional analysis, indicating regions of the world where rates of EH loss might be critical for ecosystem maintenance if threatened and DD terrestrial vertebrates go extinct.

Supporting Information

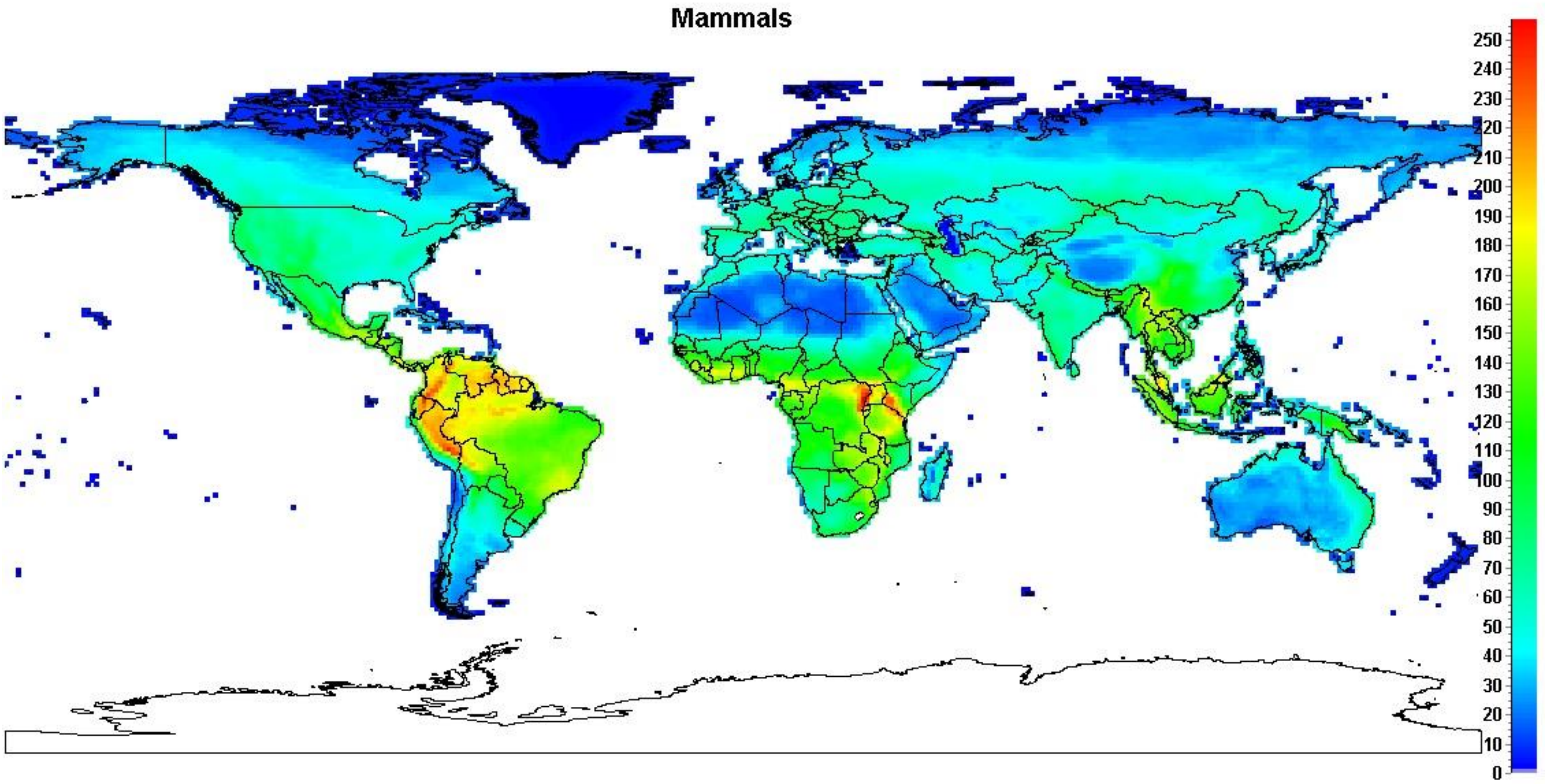
S1 Fig. Geographical distribution of species richness for each taxonomic group.



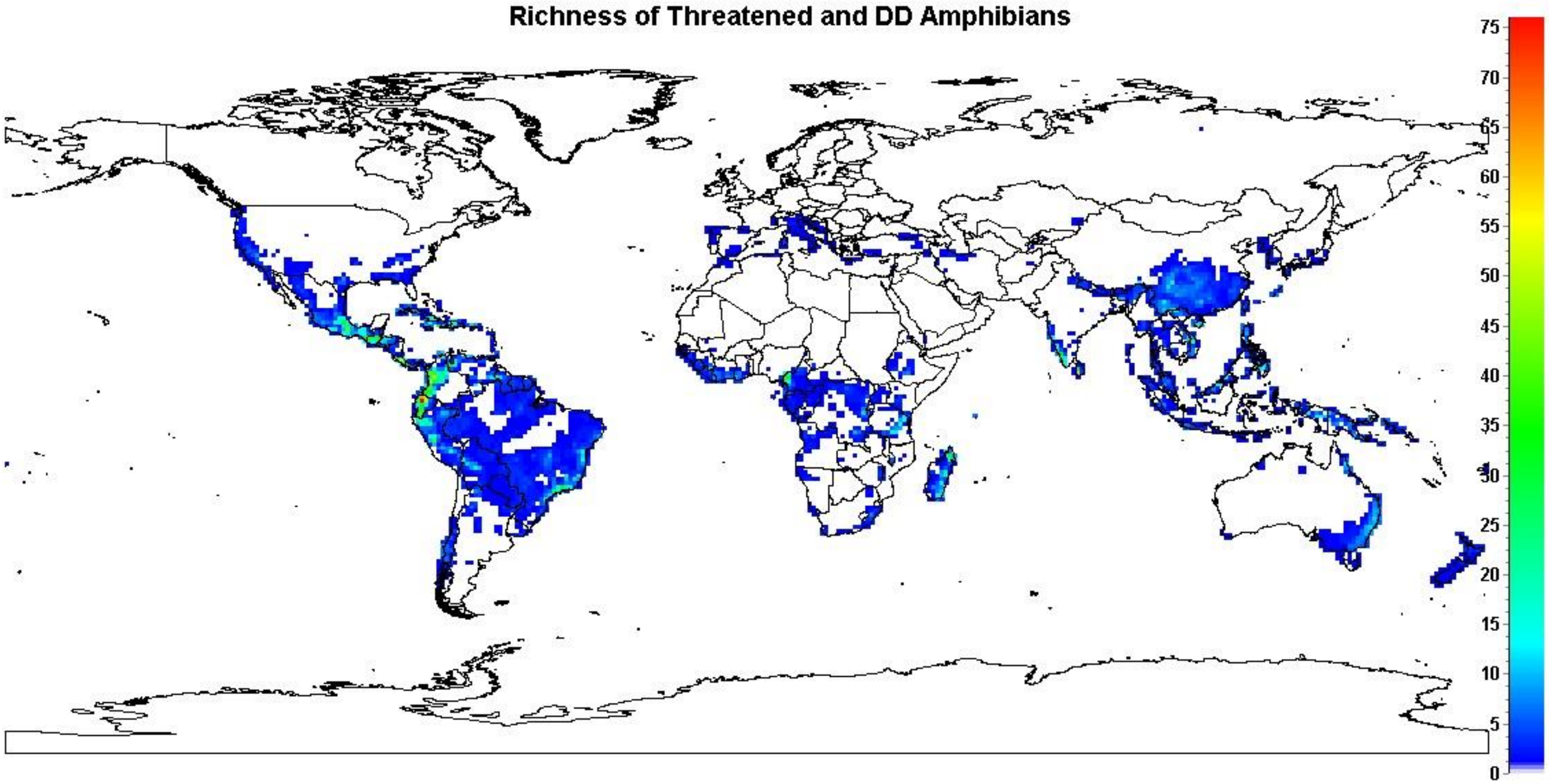


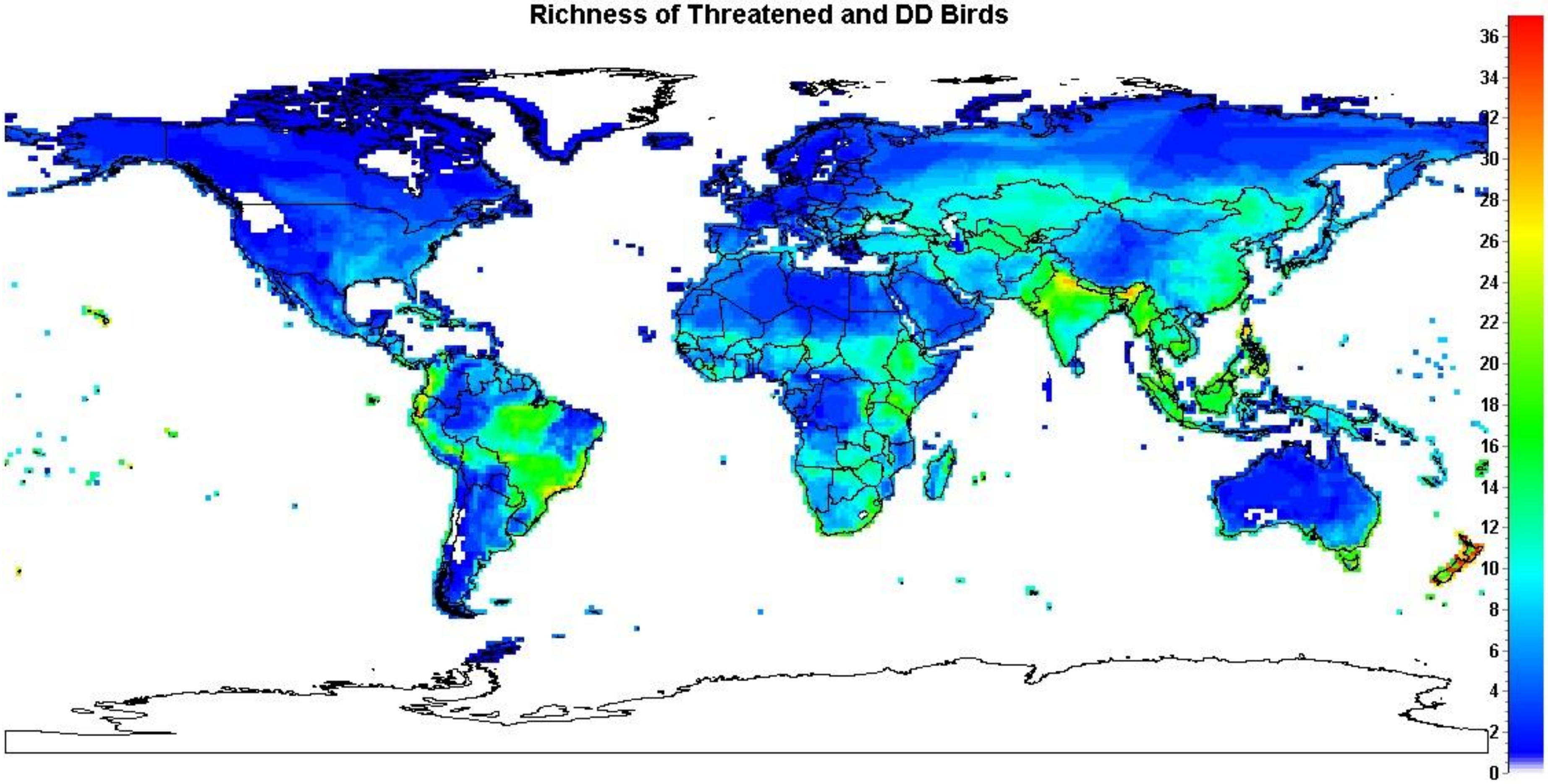
Birds

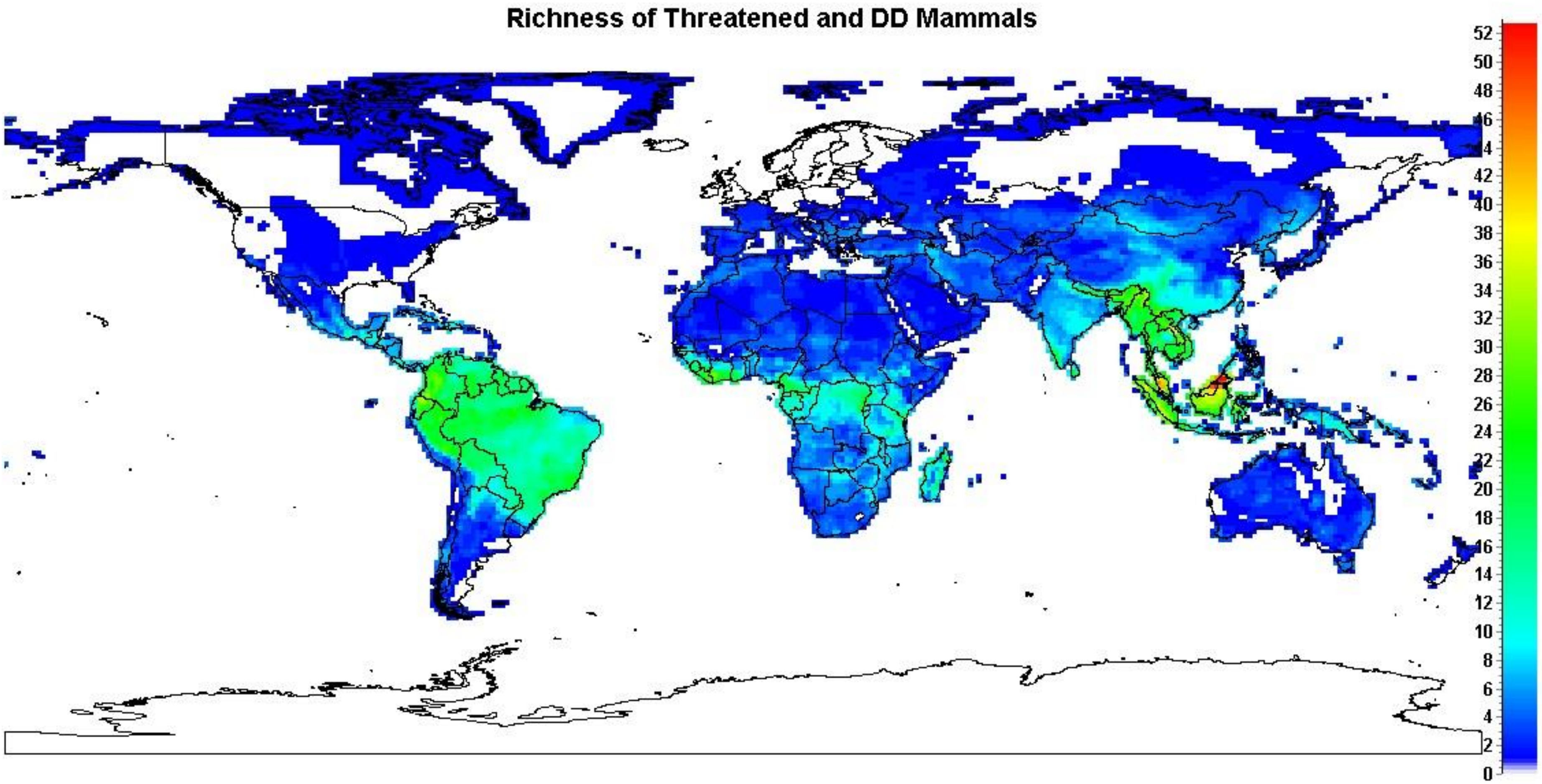
950
900
850
800
750
700
650
600
550
500
450
400
350
300
250
200
150
100
50
0


Mammals
250
240
230
220
210
200
190
180
170
160
150
140
130
120
110
100
90
80
70
60
50
40
30
20
10
0

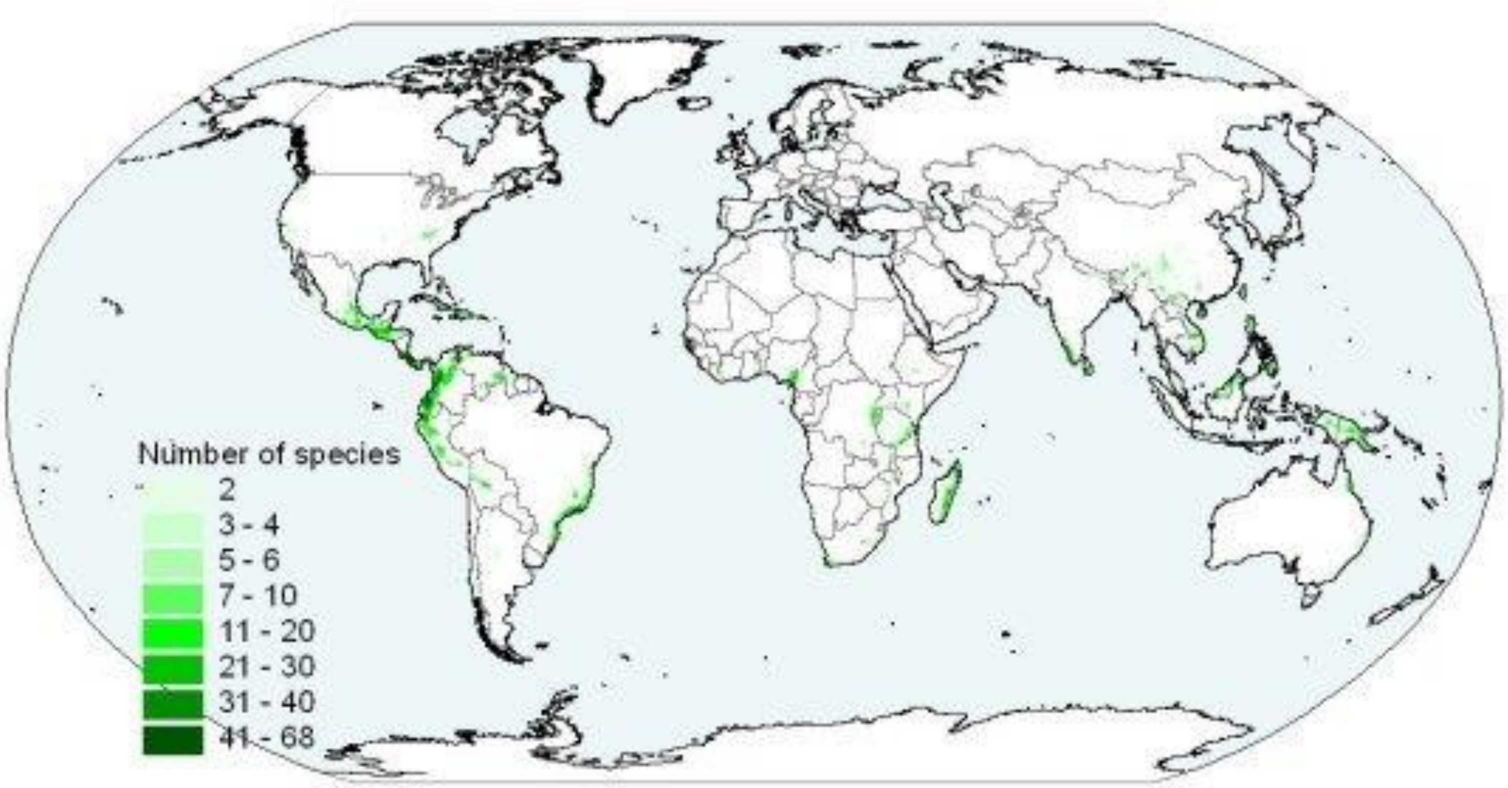
S2 Fig. Richness of threatened and DD species for each taxonomic group.


Richness of Threatened and DD Amphibians

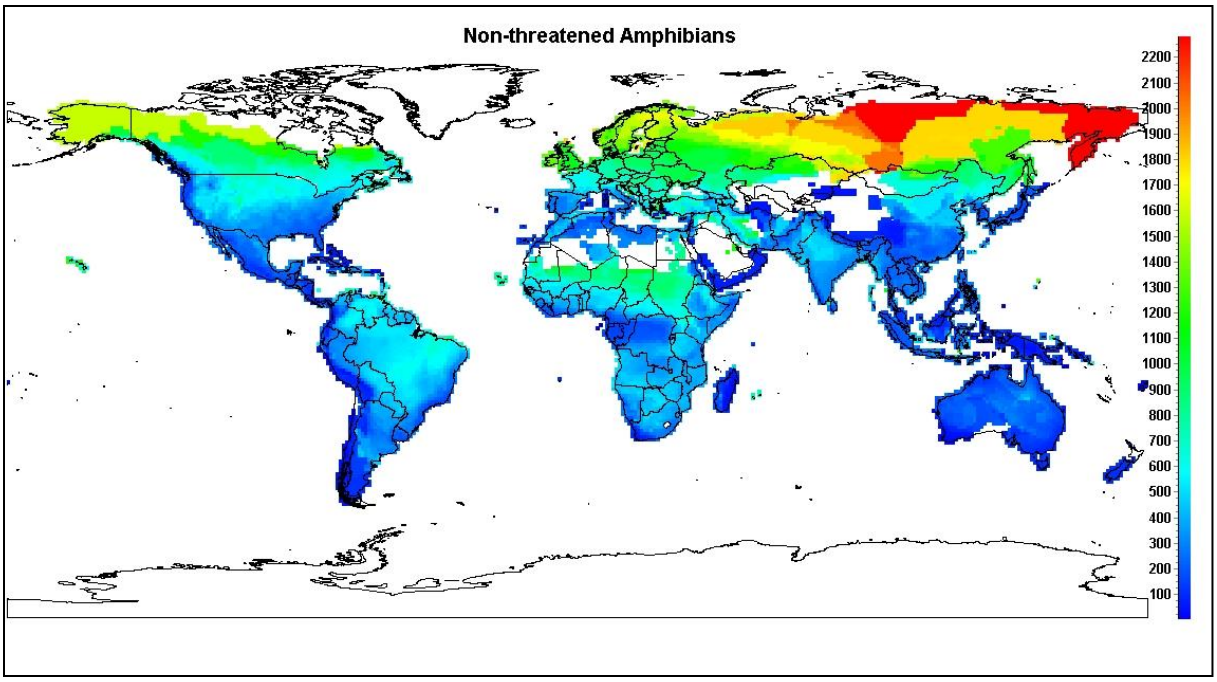

Richness of Threatened and DD Birds
36
34
32
30
28
26
24
22
20
18
16
14
12
10
8
6
4
2
0

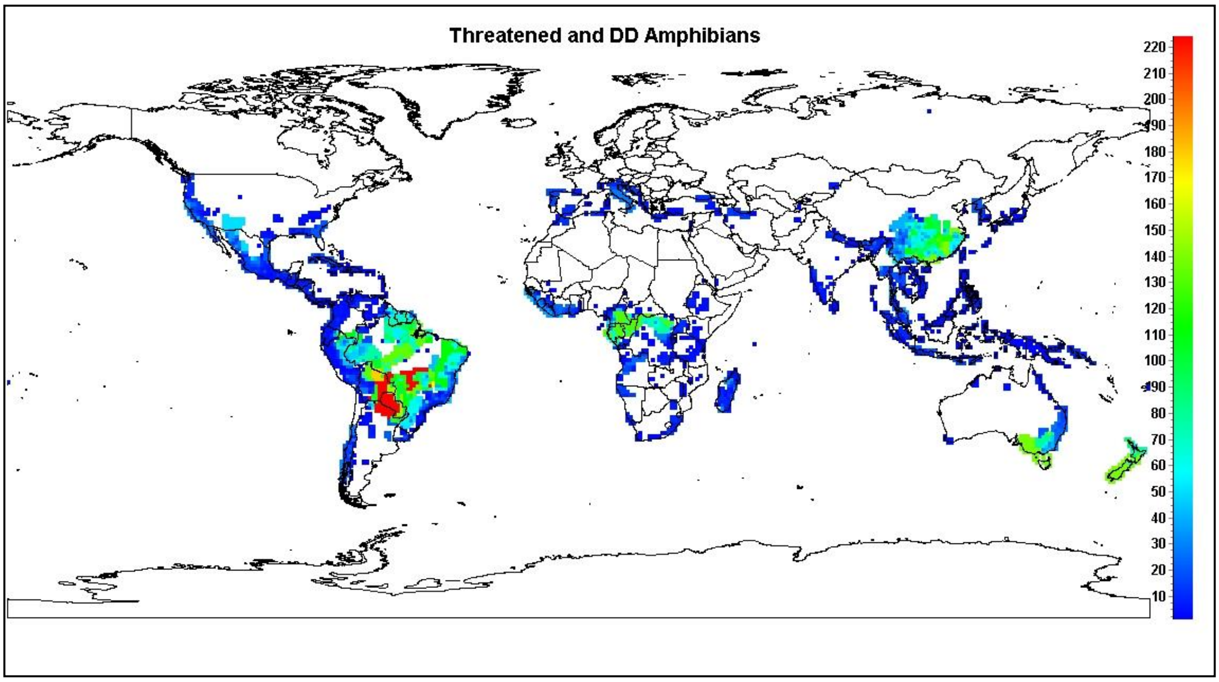

Richness of Threatened and DD Mammals
52
50
48
46
44
42
40
38
36
34
32
30
28
26
24
22
20
18
16
14
12
10
8
6
4
2
0

S3 Fig. Spatial distribution of endemic amphibian species richness extracted from IUCN Red List assessments, available at http://www.iucnredlist.org/initiatives/amphibians/analysis/geographic-patterns.



S4 Fig. Average range size for (i) non-threatened and (ii) threatened and DD species amphibians, measured by the average number of grid cells that the respective pool of species occupies.





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Formal analysis: MB TR

Investigation: MB TR

Methodology: MB TR

Software: TR

Writing – original draft: MB

Writing – review & editing: MB TR

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Capítulo 3

LOSS OF EVOLUTIONARY HISTORY MEASURED BY DISTINCT METRICS

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Abstract

Although there is an increasing effort to set priorities for conservation based on evolutionary relationship between species, the vast number of existing indices to measure evolutionary history (EH) has been pointed as a reason for the difficult in use of EH in applied conservation. Different metrics may lead to distinct conservation decisions, as each metric emphasize different aspect of EH. Conversely, there is also redundancy among metrics. Here we investigated similarities and discrepancies between three EH metrics (Evolutionary Distinctiveness, Expected Phylogenetic Diversity and Pendant edge) by estimating rates of EH loss for South American anurans. By simulating a hypothetical sequential extinction of species, our results showed significant differences of rates of EH loss between the metrics. However, detailed interpretations showed that those differences are mostly due simulation dissimilarities as function of each metric properties. Further, overall amount of EH loss is not substantially distinct among the three metrics, indicating that, general interpretation of effect of species extinctions is similar between the three metrics. However, the choice of which metric to use depends also on the question to be answered and the spatial and taxonomic scale of data, as for analyses encompassing few species the differences among metrics might be relevant.

Palavras-chave: Metrics, Evolutionary History, Extinction, Conservation

Introduction

It is now widely accepted that we are facing an extinction crisis (Butchart et al., 2010; Ceballos et al., 2015). Although extinction is an evolutionary process that has been shaping biodiversity patterns long before the rise of human species, anthropogenic-driven processes are accelerating rates of species extinctions to a level comparable to mass extinction events (Hoffmann et al., 2010; Pimm et al., 2014). As it is not possible to protect all species, conservation biologists face the challenge of designing strategies to preserve the greatest amount of biodiversity with the limited available resource for conservation. In this context, multiple criteria were suggested to set priorities for conservation, such as regions with highest richness or endemism, species with highest risk of extinction, species that are rarest, or umbrella and charismatic species. However, in general those traditional conservation strategies do not incorporate biological and functional differences between species, failing in maximize biological diversity (Arponen, 2012; Purvis and Hector, 2000). For example, choosing one region for conservation based on richness tend to neglect the diversity aspect of species composition, which is responsible for maintaining ecological process.

Thus, over the last two decades there has been a growing consensus about evolutionary history (EH) as a robust measure of biodiversity, and its role as a surrogate for diversity of species' features (e. g. ecological function, trait diversity) (Faith, 1992; Vane-wright et al., 1991). In other words, EH is a proxy for multiple aspects of biological diversity (Faith, 2013). Indeed, a set of more distantly related species tend to represent a larger set of biological features, such as behavior, ecological relationships and morphological traits (Prinzing et al. 2001; Cavender-Bares et al. 2009; Mouquet et al. 2012, but see Kelly et al. 2014). In addition, the ecosystem functions performed by the set of distantly related species tend to be more diversified, compared to a set of closely related species (Cadotte et al., 2009, 2008; Forest et al., 2007; Knapp et al., 2008; Maherali and Klironomos, 2007). Because of evidence supporting EH as a good predictor of biodiversity, many studies have set priorities based on evolutionary relationship between species (Faith, 1992; Forest et al., 2007; Cadotte et al., 2008; Safi et al., 2011, but see Devictor et al., 2010; Kelly et al., 2014).

Several principles and methodological procedures were designed to incorporate EH into conservation planning (Vellend et al., 2010; Veron et al., 2015). On one hand, there are studies that focus on individual species, measuring the distinctiveness or isolation of single species, such as Taxonomic Distinctiveness (TD, Vane-wright et al., 1991), Pedant Edge (PE, Altschuls & Lipman, 1990) and Originality (Pavoine et al., 2005). The evolutionarily distinct and globally endangered (EDGE) also focuses on species as units of conservation, but aims to rank them according to priorities for conservation based on evolutionary distinctiveness and extinction risk (Isaac et al., 2007, 2012). On the other hand, there are studies that focus on identifying areas (or networks of conservation units) that, if conserved, would maximize the protection of EH (Loyola et al., 2008; Polasky et al., 2001; Rodrigues and Gaston, 2002). Finally, there is also an effort to indicate areas with higher concentration of endemic EH (Rosauer et al., 2009; Rosauer and Jetz, 2015). Nevertheless, the integration of EH into conservation studies can be even wider, supporting analysis of the causes of species vulnerability and the extent of EH loss through species extinctions (Bennett and Owens, 1997; Huang et al., 2012).

Despite increasing support for the use of EH, the existence of multiple indices and methodological procedures has been pointed as a reason for neglecting the use of EH in applied conservation (Brooks et al., 2015; Winter et al., 2013). Because different metrics may lead to distinct conservation decisions, as each metric emphasize different aspect of EH (e.g. Huang & Roy, 2015), decision-makers find it hard to justify their choices on EH estimates (Rolland et al., 2012). In contrast, redundancy between the increasing number of metrics is also observed (Redding et al., 2014; Vellend et al., 2010), indicating the need to investigate the causes of mismatches between different metrics to unify the concept and its use in applied conservation. Conceptual advantages and disadvantages of different EH metric have been discussed in the literature (Faith, 2015; Vellend et al., 2010; Veron et al., 2015), but formal and empirical comparison between them is still missing (Kellar et al., 2015), specially for conservation purposes.

As an example, rates of EH loss through species extinctions has been estimated (Huang et al., 2012; Nee and May, 1997), however it has been argued that results might be controversial if estimated by distinct EH metrics (Faith, 2015). Estimates of EH loss are based on the concept that extinction of one species prunes a leave (tip) of the tree, and reduce the EH by erasing the evolutionary uniqueness of the extinct species. In previous simulations, as currently occurs in real world, species go extinct sequentially, but the sequence of species that go extinct is not known. Therefore, scenarios of species-by-species extinction were simulated in function of distinct criteria to define the next species to go extinct (see Batista et al., 2013), evaluating, for example, how different the theoretically slowest rate of EH loss (i.e. species less evolutionarily distinct go extinct first) would be from a random order of species extinction (i.e. all species has the same chance to go extinct). Thus, a scenario of species-by-species extinction provides an opportunity to evaluate how EH loss can be affected by the order of the extinction events and the identity of species that go extinct. However, the effect of the collective and sequential extinction of species can be evaluated by the rate of EH loss measured by different metrics, as each one quantify the contribution of each species for EH, but highlighting different aspects of EH.

In this context, here we investigate the similarities and discrepancies between different measures of EH, focusing on biodiversity conservation. By simulating a hypothetical sequential extinction of species, we estimate the rate of loss of EH as measured by Evolutionary Distinctiveness (ED, Isaac et al., 2007), Expected Phylogenetic Diversity (ExpPD, Faith, 2008) and Pendant edge (PE, Altschuls & Lipman, 1990). Thus, our results show how different indices quantify the loss of EH as the result of species extinctions. Most importantly, our study allows the investigation of the impact of different metrics used in the design of conservation strategies.

Material and methods

Phylogenetic and conservation status data

We focused our analysis on South American amphibians, which is one of the most diverse and threatened groups of terrestrial vertebrates. Measures of EH were based on evolutionary relationship between species derived from phylogenetic hypothesis of Pyron & Wiens (2011). Further, we investigated how ultrametric (time-calibrated, Pyron & Wiens, 2013) and non-ultrametric phylogenies affect the different measures of EH loss. Finally, we compiled the current conservation status for each species from IUCN red list (IUCN, 2015) to proceed scenarios of EH loss explained below.

Metrics

We evaluated three widely used metrics: Evolutionary Distinctiveness (ED, Isaac et al., 2007), Expected Phylogenetic Diversity (ExpPD, Faith, 2008) and Pendant edge (PE, Altschuls & Lipman, 1990). The three metrics are used in conservation studies to give value to each species, guiding priorities based on evolutionary information. However, each one highlight different aspects of species EH. Firstly, the simplest measure to calculate, PE measures the unshared EH of each species or, in other words, the uniqueness of each species. PE is measured as the length of the terminal branch that connects the species to the rest of the tree. For example, in Figure 1(a), PE value for species A is 3 whereas for species C is 1. In contrast, ED quantifies the phylogenetically distinctiveness of a species, as function of how distant and how many species there are. ED is one of the most commonly used EH metric in conservation biology and is measured as the sum of all branch length along the path between a focal species to the root, however dividing each branch length by the number of species subtending it. In our example (Figure 1a), ED value for species A is the sum of the terminal branch (3) with internal branch divided by three species (A, B and C). Thus, total ED value for species A is (3+2/3) = 3,66.

However, species values measured by PE and ED changes if an extinction occurs, and thus must be recalculated after each extinction event, therefore accounting for changes in shared ancestral branches. For example, in Figure 1(a), ED value for species B is (2+4/2+2/3) = 4,66. However, if species C go extinct (see Figure 1(b)), species B becomes the only representative of the ancestral branch and thus its ED value become (2+4+2/2) = 7. For PE, extinction of a species erases the amount of EH that is unique to the single species. For example, if species C goes extinct we loss PE = 1, then it sister species B will be the only remaining of the ancestral branch and thus must be fused with the ancestral branch previously shared by both species (see Figure 1b). Therefore, after each extinction event, we must recalculate the branch length for all species accounting for internal branches.

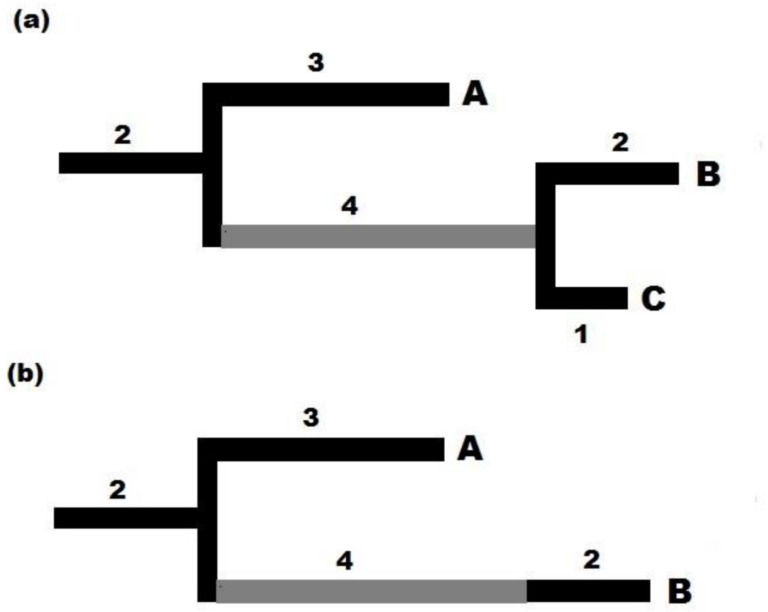

Figure 1. Hypothetical evolutionary relationship between three species (a) highlighting changes of shared ancestry after extinction of species C (b).

Furthermore, ED is used in the EDGE (Evolutionarily Distinct and Globally Endangered) program, which ranks individual species according to conservation priorities by identifying those that are most vulnerable and phylogenetically distinct. However, EDGE rank does not take into account the probability of extinction of closely related species, assigning the same priority for two species that are equally evolutionary distinct and endangered. Hence, EDGE scores are static if the threat status of closely related species is changed. A negative implication of static scores is to not prioritize cases that would increase the risk of losing an entire clade. In this context, a threatened species with an endangered close relative increase the chance of losing higher proportions of EH compared to an equally evolutionary distinct and endangered species with non-threatened close relatives. For example, extinction of species B or E in Figure 2 would result in loss of equal amount of EH and both are endangered (Probability of extinction = 0,9), therefore having the same EDGE value. However, species B has a closely related species that is also threatened (species A), whereas the sister of species E is currently non-threatened. Thus, extinction of species B would increase the chance of losing higher proportions of EH by extinct of an entire clade.

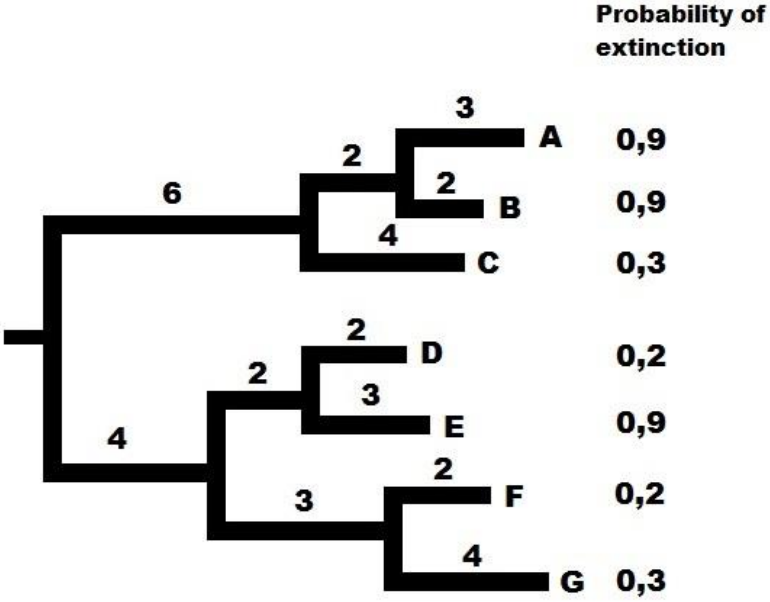

Figure 2. Hypothetical evolutionary relationship between seven species, with respective probabilities of extinction, to illustrate measures of Expected Phylogenetic Diversity and Evolutionary distinctiveness.

In contrast to PE and ED, ExpPD is a clade-based measure of EH that accounts for the degree of extinction risk of all species, avoiding static measures such as EDGE. Also designed to give species values, ExpPD incorporates the principle of complementarity (Faith 2008, 2015) by measuring the species contribution to EH integrating the extinction probabilities of all species in a set. ExpPD is calculated as:

$$ExpPD = \sum_{k} \left[L_k (1 - \prod_{dk} P_{dk}) \right] - \sum_{k} \left[L_k (1 - \prod_{dk} P'_{dk}) \right]$$

where k designates different branches on the tree, L_k is the length of the kth branch and dk indicates the different descendants of branch k. P_{dk} is the original probability of extinction of descendant dk and P'_{dk} is a new probability of extinction of descendant dk in case of a change in extinction risk. Thus, ExpPD may express gain if a species decrease its risk of extinction (i.e. $P_{dk} > P'_{dk}$) or loss if a species increase its risk of extinction (i.e. $P_{dk} < P'_{dk}$). Notice that probability of extinction ranges from 0, when a species is currently persisting, to 1, when a species get extinct. Further, considering that the contribution to EH provided by each species is weighted by the probability of extinction of all species, there is no need to recalculate branch lengths after each extinction event, as the *P'* already designates how internal branches will be computed after changes in species extinction risk.

Theoretically, for ExpPD the threatened species contribute less for preserving the clade EH because of their higher risk of becoming extinct, whereas non-threatened species have more chance to preserving the clade EH. Thus, in contrast to EDGE, two species that are equally evolutionary distinct and endangered have different scores in ExpPD measure, depending on the probability of extinction of their close relatives. In our example of Figure 2, species B and E would have distinct priority (4.878 and 3.1032, respectively), indicating that preserving species B would promote a higher gain of EH (or PD, following Faith) compared to species E.

Mathematically, these metrics can be distinguished by the way they account for deeper branches. In PE, internal branches only become computed when a clade has just one remaining species, as internal branches are fused with the remaining species tip. In ED, however, internal branches are equally distributed for the descendants, and ExpPD distributed internal branches as function of probability of extinction of each descendant tip. In ExpPD, a non-threatened species represents a higher portion of internal branches as it has more chance of maintaining the clade EH, whereas a high-threatened species may not guarantee clade EH persistence and so represents a smaller portion of internal branches.

Measuring EH loss

We implemented two scenarios (algorithms) to perform the sequential extinction of species. In our first scenario (hereafter "risk scenario"), the probability of extinction of a species is a function of its risk degree (here we used IUCN Red List of threatened species, 2015), in which most endangered species have higher probabilities of extinction at each extinction event. Thus, our risk scenario is a probabilistic simulation of the sequence of extinction events, and provide different order of species extinction if replicated.

In contrast to the risk scenario, we create a second scenario in which species go extinct randomly, regardless of its threat status. This “random scenario” may be thought as null in relation to any ecological feature or conservation status of the species. As the order in which species go extinct in both risk and random scenarios is defined probabilistically (although the probability of extinction of species vary between scenarios), repeating the scenarios yield different sequences of extinction, therefore yielding different rates of EH loss for each run of the algorithm. To account for the variation of EH loss predicted by risk and random scenarios, we repeated (replicated) the extinction sequence under each scenario 99 times.

In addition to risk and random scenarios, we calculated the sequence of species-by-species extinction that generates the maximum and minimum possible rates of EH loss. The maximum and minimum rates of EH loss for sequential extinction events is achieved by selecting the individual species that goes extinct based only on its contribution for EH. Thus, maximum scenario is calculated by always removing, among the remaining species, the one with highest contribution to EH, whereas minimum scenario is calculated by always removing, among the remaining species, the one with lowest contribution to EH. Thus, maximum and minimum scenarios are not probabilistic as the order of species extinction is invariant.

By using maximum and minimum rates of EH loss as reference, we were able to compute a standardized index of rate of EH loss for the probabilistic scenarios described above (risk and random). Considering that minimum and maximum rates of EH loss are unique, the sub-optimality index (I_{SB}) (Batista et al. 2013) describes, for each replicated of an extinction sequence in risk or random scenarios, a standardized distance of a given extinction scenario in relation to the minimum rate of EH loss. The I_{SB} is calculated by dividing the area enclosed between the curves defined by minimum and probabilistic EH loss (area A, in Figure 3), by the total area enclosed between the curves of minimum and maximum EH loss (area A+B, in Figure 3), or $I_{SB}=A/(A+B)$. Thus, the index ranges between 0, indicating that the probabilistic EH loss curve is close to the minimum EH loss scenario, and 1, indicating that the probabilistic EH loss curve is close to the maximum EH loss scenario.

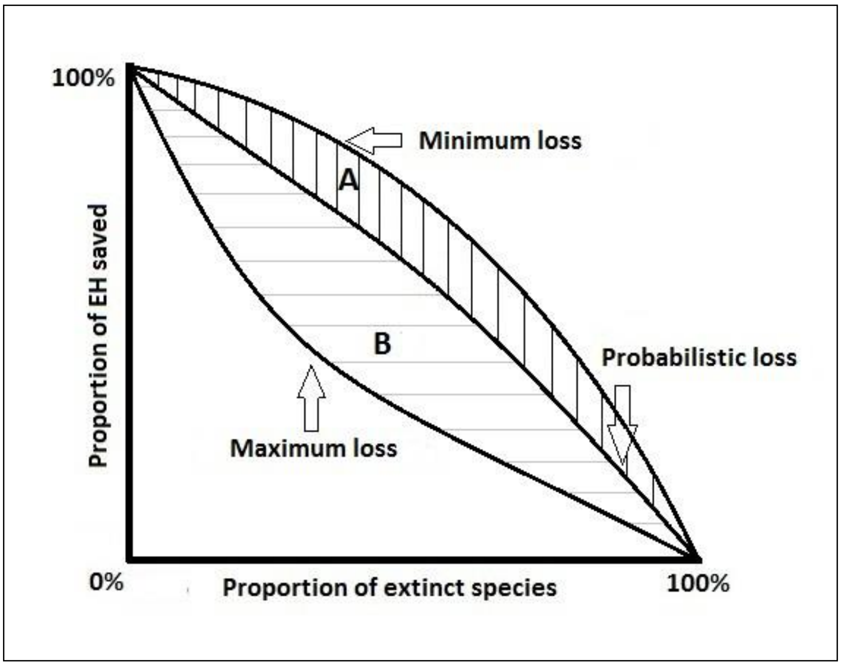

Figure 3. Figure adapted from Batista et al., (2013) showing average rate of EH loss as function of species extinction under distinct scenarios. The probabilistic curve represents the random or risk extinction scenarios. The maximum loss curve represents the fastest rate of EH loss (worst-case scenario), whereas the minimum loss curve represents the slowest rate of EH loss (best-case scenario). The area encompassed between minimum and probabilistic loss curves is named (A), whereas the area between maximum and probabilistic loss curves is named (B). A sub-optimality index (I_{SB}) measuring how a given probabilistic scenario approaches the maximum loss curve can be defined as I_{SB}=A/(A+B).

Finally, we employed a one-way ANOVA to test for difference between the 99 I_{SB} values of each metric in risk scenario. We also implemented an independent two-sample Student's t-test (Welch's t-test) considering the I_{SB} values, to investigate the significance of difference between risk and random scenarios for each metric. In addition, a nested ANOVA concerning I_{SB} values of each metric allowed comparing if there is difference in estimates between a calibrated and uncalibrated phylogeny. See below for further details about metrics and scenarios procedure.

(a) Pedant edge (PE)

To achieve the worst-case scenario (maximum rate of EH loss), the species with higher PE value (i.e. longest terminal branch) is always the next to go extinct, whereas the best-case scenario (minimum rate of EH loss) occurs when species with lowest value of PE (i.e. shortest terminal branch) is always the next to go extinct. In contrast, risk and random scenarios are probabilistic and were replicated 99 times. Still, it is important to note that in all EH loss scenarios PE is recomputed after each successive extinction, ensuring that internal branches will also be accounted into analysis.

For risk scenario we followed Batista et al., (2013) to achieve each species probability of extinction. Therefore, species in non-threatened categories (near threatened, NT; least concern, LC; not evaluated, NE) are weighted equally and assigned the lowest weight: 10^0. Species considered threatened are weighted according to their IUCN status: vulnerable (VU), endangered (EN) and critically endangered (CR) are assigned a weight of 10^1, 10^2 and 10^3, respectively. Further, we assigned to DD (Data Deficient) status the same weight as we did for the VU category: 10^1 (Nori & Loyola, 2015). Lastly, as explained above, in random scenario all species have the same chance to go extinct.

(b) Evolutionary distinctiveness (ED)

To allow direct comparisons between ED and PE, we implemented the same four scenarios of sequential extinction: minimum vs maximum rate of EH loss and random vs risk. Thus, our analysis allows not only comparisons of different scenarios using a given metric, but also the same scenario using different metrics. As in PE, the random scenario for ED is probabilistic, as all species have the same chance to go extinct. Thus, to measure and control for stochasticity, this scenario is replicated 99 times. In contrast, under the risk scenario each species has a probability of extinction defined according to its current conservation status, therefore defining the sequence of extinction events in the simulation. The ED metric was originally created in the context of conservation programs, and designed to be integrated with the species status of conservation. Thus, the EDGE index, combines the degree of evolutionary distinctveness (ED) and globally endangered (GE) of each species, and is calculated as:

$$EDGE = \ln(1 + \mathrm{ED}) + \mathrm{GE} * \ln(2) \qquad (1)$$

Where, GE is the Red List category weight (Least Concern = 0, Near Threatened = 1, Vulnerable and Data Deficient = 2, Endangered = 3, Critically Endangered = 4; further details see Isaac et al., 2007; 2012). Thus, we measured the rate of EH loss in risk scenario of ED using the EDGE value as weight to generate a probabilistic rate of EH loss, in which the species with highest value of EDGE has higher chance to go extinct. However, notice that an extinction event alters the calculated EDGE scores of some of the surviving species because the extinction changes the shared ancestry. Thus, EDGE values must be recalculated for the entire surviving pool of species at each step of the simulation. Finally, to achieve the maximum and minimum rates of EH loss under the ED index the simulation removed the species with the highest and lowest ED values at each time step.

(c) Expected PD loss (ExpPD)

In the simulation of sequential extinction events we calculated the ExpPDloss as:

$$ExpPDloss = \sum_{k}\left[L_k(1-\prod_{dk} P_{dk})\right] - \sum_{k}\left[L_k(1-\prod_{dk} P'_{dk})\right] \qquad (2)$$

where P’ is a species-based probability of extinction that is manipulated in the simulation. First, P’ always set to 1 for all extinct species. In addition, in the algorithmic search for the species that, if extinct, would cause the maximum or minimum reduction of EH, P’ is tentatively set to 1 for each individual species at the time, while P is set to 0 for all other non-extinct species. Thus, in the simulation of sequential extinctions, the next species to go extinct in worst-case scenario (maximum rate of EH loss) is the one that promoted the highest increase in ExpPDloss when its P’ was raised to 1. Conversely, species that promote the lowest increase in ExpPDloss when its P’ is raised to 1 is the next to go extinct in best-case scenario (minimum rate of EH loss).

As implemented for other metrics, random scenario for ExpPDloss is probabilistic (replicated 99 times) and all species has the same chance to go extinct (i.e. P’ = 1). Under the risk scenario, we followed the ExpPD calculation for single species (hereafter ExpPD scores), measured as:

$$ExpPD\ score = \left|P_j - P'_j\right| \sum_{aj}\left(L_{aj}\left(\prod_{daj} P_{daj}\right)\right) \qquad (2.1)$$

where *aj* is the branch ancestral to *j* and *daj* is the species (excluding *j* itself) descendant from branch *aj*. Measures of ExpPD score express the gain in ExpPD when a species gets a reduced extinction risk (e.g. $P'_j = 0$) or loss in ExpPD when a species reach higher risk degree (e.g. $P'_j = 1$). Therefore, ExpPD score could be used to set priorities for conservation by the amount of gained ExpPD with species preservation (i.e. $P'_j = 0$). To compare ExpPD with EDGE simulation, species with higher ExpPD scores when preserved (i.e. $P'_j = 0$) has higher chance to go extinct. Based on IUCN Red List transformation (Mooers et al., 2008), species probability of extinction (i.e. P_j) used in ExpPD scores calculations are: CR: 99,9%, EN: 67%, VU: 10%, NT: 1% and LC: 0,1%. Further, we assigned to DD status the same weight as we did for the VU category: 10%. Finally, we replicated the risk scenario with ExpPD scores 99 times.

Results

In general, all scenarios showed similar rates of EH loss for South American anurans, regardless of the metric that was used to measure each species contribution to EH (Figure 4). Graphically, rates of EH loss between metrics showed higher divergence for risk scenario. Average sub-optimality index (I_{SB}) for risk scenario concerning PE is 0,38, while for ED (EDGE) is 0,42 and for ExpPD is 0,57. Thus, ExpPD indicates a more pessimistic rate of EH loss, compared to PE and ED, if threatened South American anurans go extinct first. Indeed, the one-way ANOVA suggests a significant difference ($F_{2, 294} = 66.757$, $p < 0,001$) between risk scenario for the three metrics. In fact, a Tukey test showed that risk average I_{SB} for ExpPD differs significantly from PE ($p < 0,001$) and ED ($p < 0,001$), whereas PE and ED averages do not differ from each other ($p = 0,059$).

We also observed significant difference when risk and random scenarios were compared (ED, $p < 0,001$; ExpPD, $p < 0,001$), except for PE measure (PE, $p = 0,046$). In contrast, for minimum and maximum rates of EH loss we observed that estimates with ED showed very similar pattern as PE and ExpPD for minimum scenario, whereas for maximum scenario ED estimates showed pessimistic average rate of EH loss than other metrics. Other important observation is that minimum and maximum scenarios exhibited the same result for PE and ExpPD, with curves totally overlapping (Figure 4).

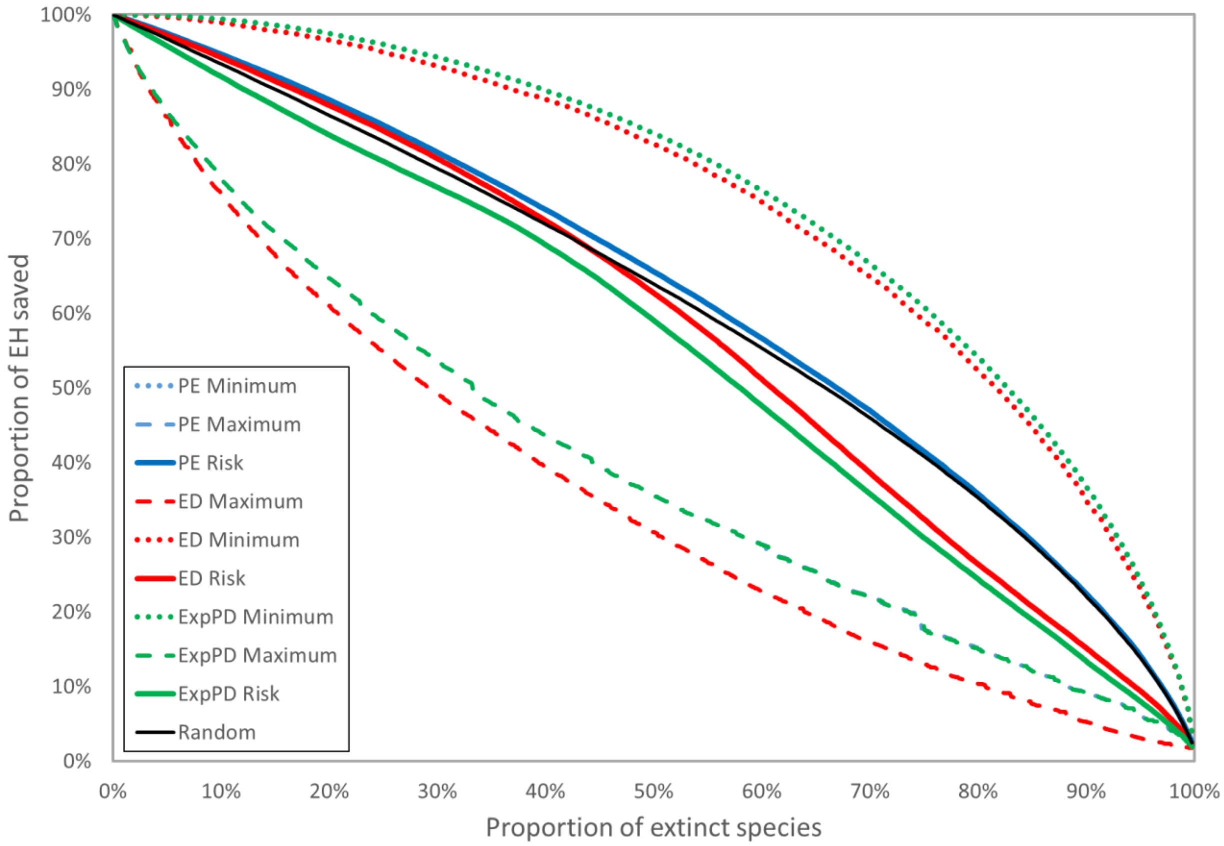

Figure 4. Remaining EH for the 837 South American anurans measured by PE (Pedant edge), ED (Evolutionary distinctiveness) and ExpPD (Expected PD) in four scenarios of extinction concerning the uncalibrated phylogeny. Random scenario is showed only once, as the result is the same for all metrics. Curves of ExpPD minimum and maximum is covered by PE minimum and maximum.

Finally, a nested ANOVA showed a lack of significant difference ($F_{1,588} = 0.1950$, $p = 0.65$) between results of an uncalibrated and time-calibrated phylogeny concerning the same 837 South American anurans. Further, note that average sub-optimality index for risk scenario under calibrated phylogeny (PE = 0,37; ED = 0,37 and ExpPD = 0,61) approaches values under uncalibrated phylogeny.

Discussion

Our analysis showed that distinct metrics (Pedant edge, Evolutionary distinctiveness and Expected PD) produces statistically distinct estimates of EH loss in simulation of sequential species extinction, but this result requires carefully interpretations. Although each metric produces distinct rates of EH loss, results of previous studies (Steel et al., 2007; Vellend et al., 2010; Martyn et al., 2012; Redding et al., 2014) suggest correlation between PE, ED and ExpPD. Comparisons between different evolutionary and ecological metrics underlying EH found redundancy between PE and ED (Vellend et al., 2010; Reeding et al., 2014), although ED is considered more informative about species EH. Furthermore, a metric similar to ExpPD, called Heightened Evolutionary Distinctiveness (HED; Steel et al., 2007), is strongly influenced by PE (Steel et al., 2007; Martyn et al., 2012). Both ExpPD and HED measures species contribution to EH in an equivalent scope, indicating that ExpPD might also be strongly correlated with PE. Apparently, evidences of correlation between the three metrics compared here seems to contrast to our results, but detailed interpretations of the curves of EH loss show other perspectives.

The highest divergence of measured EH by different metrics is in the risk scenario (Figure 4). A careful inspection of the risk curves suggests that they may be split into two sections. First, up until extinction of nearly 40% of species, loss of EH have similar rates, regardless of the metric used. However, after extinction of nearly 40% of species, different metrics start diverging substantially with regard to the remaining EH and rates of loss of EH. This threshold of divergence in EH loss corresponds roughly to the number of threatened species in the dataset (35.6% of all anurans, considering DD species). Because threated species have higher probability of extinction, it is reasonable to assume that the rates of EH loss start to diverge once these species have gone extinct. Indeed, each metric behaves differently after extinction of all threatened species as a consequence of its mathematical properties. For PE, the chance of each species going extinct in risk scenario is function only of the probability of extinction, and for non-threatened species the chance is the same for all species. Thus, because PE does not differentiate between non-threatened species, after extinction of all threatened species the risk scenario becomes similar to a random sequence of extinction events. Conversely, for ExpPD and ED risk scenarios, the chance of species going extinct is a combination of risk of extinction and the amount of EH represented by each species. The mathematical properties of ExpPD and ED and simulation procedure results in higher chance of extinction of distinct species, even between non-threatened one. Thus, after extinction of all threatened species in risk scenario, ExpPD and ED rates of EH loss approach rates of extinction of the maximum scenario. Therefore, the properties of the three metrics with regard to threatened vs non-threatened species might explain the statistical difference of I_{sb} values among simulations.

In addition, notice that minimum and maximum scenarios totally overlap for ExpPD and PE, indicating the exactly same result for the two metrics, whereas ED showed more pessimistic in both scenarios. The similarity of scenarios of minimum and maximum rates of EH loss between PE and ExpPD is caused by their mathematical proprieties, which do not rely on probabilities of extinction of species. Thus, the worst-case scenario can be found only when the remaining most evolutionarily distinct species is always the next to go extinct, whether that species is listed as threatened or not. Conversely, the best-case scenario is achieved when the remaining least evolutionarily distinct species is always the next to go extinct, whether that species is listed as threatened or not. Thus, ExpPD behaves similarly to PE when probabilities of extinction to species are ignored. Furthermore, it is important to note that ignoring probabilities of extinction of species in ExpPD minimum and maximum scenarios allows a direct comparison of scenarios between the three metrics, as the amount of EH was the standard criteria used at these scenarios. However, by design the ExpPD incorporates simultaneously the amount of EH of the clade and the risk of extinction of all species, even in worst and best cases scenarios of EH loss (see Faith, 2008 for examples).

To test for discrepancies between metrics when incorporating extinction probabilities into the scenarios of minimum and maximum rates of EH loss using ExpPD, we performed an additional simulation with an alternative version of ExpPD calculation. This additional simulation employs the same methodological procedure described before, but incorporate the probability of extinction as function of IUCN status in the calculation of ExpPD (see Appendix S1). Results of this alternative calculation of ExpPD showed a distorted pattern for scenario of minimum rate of EH loss. The minimum scenario for ExpPD showed similar pattern to risk scenario until extinction of nearly 30% of species, and then followed a pattern similar to ED and PE minimum scenarios. The similarity to risk scenario in the first portion of the curve is due to extinctions of highly threatened species first, which contribute less for EH persistence because their higher probability of extinction reduces their contribution to EH in ExpPD calculation. In comparison to the risk scenario, the design property that differentiate minimum loss of EH for ExpPD is the requirement that the first species to go extinct must have non-threatened close relatives and small branch lengths in the calculation of the minimum rate of EH loss scenario.

Finally, the maximum scenario is mostly unaffected by the choice of EH metric, especially between PE and ExpPD.

The additional simulation of minimum and maximum scenarios for ExpPD highlights the difficulty in implementing ExpPDloss in our EH loss estimates procedure, which analyze the effect of the collective and sequential extinction of species in EH loss. Divergence in the curve of minimum EH loss between ExpPD and ED, as well as ExpPD and PE, is due the smaller weight assigned to threatened species in ExpPD calculation, therefore leading endangered species to become extinct sooner. However, an endangered species may be also evolutionary distinct and its extinction could result in higher EH loss when compared to extinction of a non-threatened and evolutionary recent species. Therefore, using the probability of extinction based on IUCN status in the calculation of ExpPDloss, the minimum EH loss rate scenario does not reach the lowest possible rate of EH loss. Conversely, calculation of maximum EH loss rate using ExpPDloss causes the early extinction of species that are evolutionary distinct, which is the sole criterion used in ED and PE. Nevertheless, ExpPDloss did not reach the fastest rate of EH loss. Thus, although ExpPDloss apparently optimizes the definition of conservation priorities, it does not allow direct comparison with best-case or worst-case scenarios when considering probabilities of extinction.

Evolutionary History (EH) has been widely suggested as a guide for conservation programs (e.g. EDGE). Hence, we must understand the redundancies and discrepancies in different measures of species contribution to EH. Here we showed that the three most used metrics to measure EH, as well as effects of extinction on EH loss, are not substantially different in the overall amount of EH loss. Although our results indicated significant quantitative difference between rates of EH loss among metrics, a close inspection of the patterns of EH loss show that differences are due to variation in the simulation procedure and mathematical properties inherent to each metric. However, in estimating rates of EH loss across large spatial and/or taxonomic scales, the choice of EH metric is unlikely a major methodological decision, as the qualitative interpretation of patterns of EH loss tend to be robust across different metrics. Nevertheless, we advocate for the use of ED, as it is more informative than PE and more intuitive than (easier to interpret) than ExpPD. However, conservation programs designed to set priorities for protection among few species would likely be affected by the choice of EH metric. For example, ExpPD differentiate species based on the probability of extinction of phylogenetically closely related species, even if the species are equally evolutionary distinct and endangered. Conversely, the EDGE ranking is not designed to draw such distinction. Thus, the choice of which metric to use depends also on the question to be answered and the spatial and taxonomic scale of data. Finally, the similarity of results between uncalibrated and time-calibrated phylogenies suggests that topology is equally important, or even more important, than branch lengths (Cadotte, 2015). So, the correct position of species into the phylogeny must be an issue of attention in future works.

Appendix

S1 – Additional analyses regarding estimates of expect PD loss with IUCN extinction risk in maximum and minimum scenarios.

In previous simulation of sequential extinction events we calculated the ExpPDloss as:

$$ExpPDloss = \sum_{k}\left[L_k(1-\prod_{dk}P_{dk})\right] - \sum_{k}\left[L_k(1-\prod_{dk}P'_{dk})\right]$$

where P’ is a species-based probability of extinction that is manipulated in the simulation. First, P’ always set to 1 for all extinct species. In addition, in the algorithmic search for the species that, if extinct, would cause the maximum or minimum reduction of EH, P’ is tentatively set to 1 for each individual species at the time, while P is set to 0 for all other non-extinct species. Thus, in the simulation of sequential extinctions, the next species to go extinct in worst-case scenario (maximum rate of EH loss) is the one that promoted the highest increase in ExpPDloss when its P’ was raised to 1. Conversely, species that promote the lowest increase in ExpPDloss when its P’ is raised to 1 is the next to go extinct in best-case scenario (minimum rate of EH loss). Note that in this previous simulation we only have extant (i.e. P = 0) and extinct (i.e. P’ = 1) species, ignoring the extinction risk of each species.

In this additional simulation, we only changed the minimum and maximum scenarios for ExpPD by incorporating the probabilities of extinction based on IUCN status for all species. Thus, in the algorithmic search for the species that would cause the maximum or minimum reduction of EH when P' is tentatively set to 1 for each individual species at the time, the value of P of all other non-extinct species is its probability of extinction (rather than P = 0, as in previous simulation). We assigned to each species the same probabilities used in risk scenario for ExpPD: CR: 99,9%, EN: 67%, VU: 10%, DD: 10%, NT: 1% and LC: 0,1%. The result of new simulation is showed below, in Figure 1.

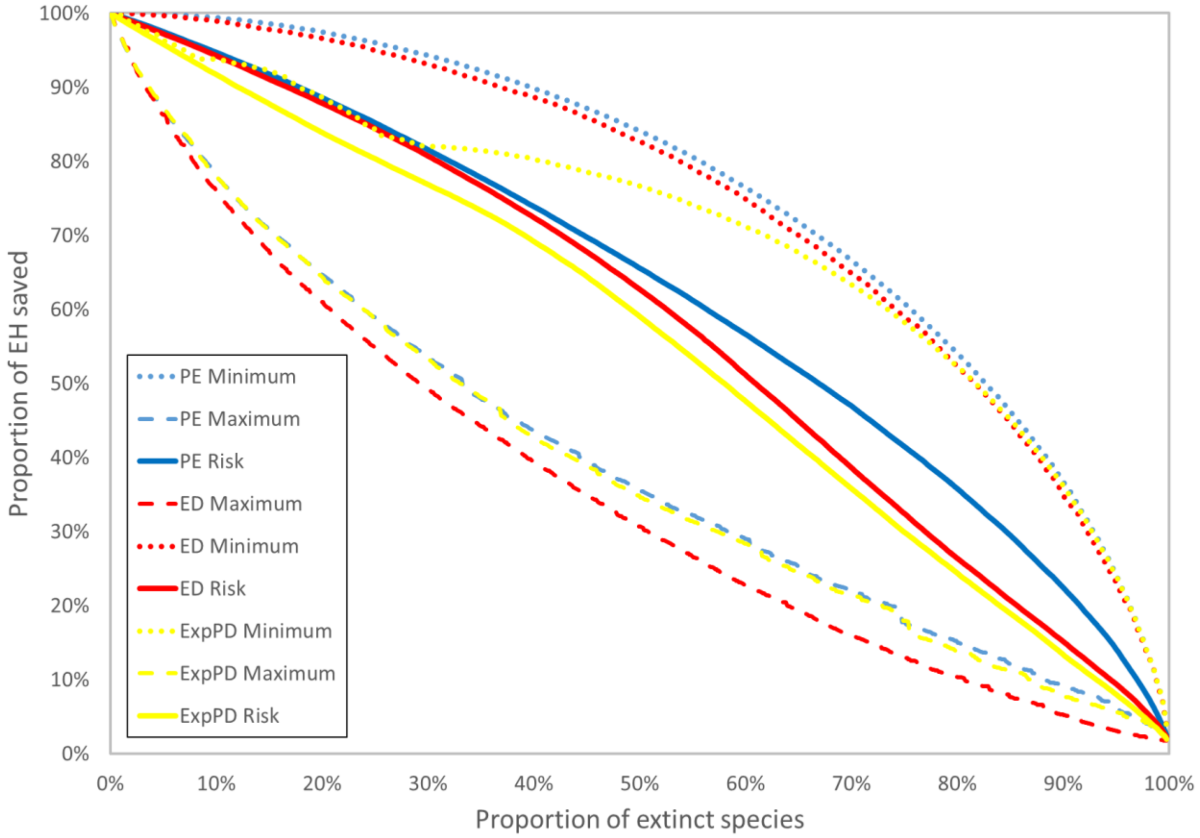

Figure 1. Remaining EH for the 837 South American anurans measured by PE (Pedant edge), ED (Evolutionary distinctiveness) and ExpPD (Expected PD) in four scenarios of extinction concerning the uncalibrated phylogeny. Distinguishing from previous simulations, here the minimum and maximum scenarios for ExpPD encompass risk of extinction (based on IUNC status) of each species.

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Considerações finais

Seria ideal para a biologia da conservação que o conhecimento acerca das interações entre as espécies, suas distribuições geográficas, características morfológicas, fisiológicas, entre tantos outros atributos, fosse robusto. Porém, as lacunas de conhecimento ainda são extensas e os recursos para inventariar e investigar a biodiversidade é escasso. Neste sentido, é importante observar que a história evolutiva (HE) é uma das melhores ferramentas que a comunidade científica possui, no momento, frente a tamanha urgência na preservação da diversidade ainda que haja muito debate acerca da relevância da HE no delineamento de estratégias de conservação. Assim como em outras linhas metodológicas, a HE utilizada em estudos voltados para conservação também apresenta limitações, contudo, o presente estudo demonstrou de forma empírica que é possível lidar com algumas dessas limitações, como no caso a incerteza filogenética. É evidente a importância da continuidade de estudos que aprimorem nosso conhecimento sobre a biodiversidade, assim como estudos sobre a relevância da HE para a conservação, contudo, ignorar a HE na implementação de estratégias significa, por si só, ignorar um importante aspecto da biodiversidade.

Os resultados aqui encontrados reforçam a necessidade de investigar, especialmente estimar a perda, de HE de forma espacialmente explícita. Quando analisamos a HE entre as espécies de forma global, estamos comparando a HE de uma única ou algumas poucas espécies com o restante do grupo, porém a HE que uma única espécie ou poucas espécies representam geralmente será pequena quando comparada a HE de um grupo taxonômico inteiro. Observamos ainda que a incerteza filogenética sobre o posicionamento de espécies faltantes na filogenia é irrelevante em estimativas de perda de HE em escala global. Contudo, vale considerar que as extinções se iniciam localmente, afetando primeiramente a comunidade regional, e diferentes comunidades regionais podem ser afetadas de formas distintas frente à extinção de uma mesma espécie. Assim, realizamos estimativas de perda de HE em escala regional, sendo observados resultados distintos entre os diferentes grupos taxonômicos aqui estudados (i.e. anfíbios, mamíferos e aves), indicando que áreas prioritárias para conservação da HE são diferentes entre os grupos. Cabe ressaltar que as estimativas regionais incorporam padrões históricos de dispersão de cada grupo, bem como a estrutura filogenética da comunidade e padrões de risco de extinção, levando em consideração ainda a incerteza filogenética. Por fim, ressaltamos que a escolha da métrica para mensurar HE não é trivial e depende da questão a ser respondida e da escala taxonômica e espacial do estudo.