UNIVERSIDADE FEDERAL DE ALAGOAS
INSTITUTO DE CIÊNCIAS BIOLÓGICAS E DA SAÚDE
PROGRAMA DE PÓS-GRADUAÇÃO EM DIVERSIDADE BIOLÓGICA E
CONSERVAÇÃO NOS TRÓPICOS
MESTRADO EM DIVERSIDADE BIOLÓGICA E CONSERVAÇÃO NOS
TRÓPICOS

GRACIELLE TEIXEIRA HIGINO

ANÁLISE CIENCIOMÉTRICA E MACROECOLÓGICA SOBRE
PADRÕES DE DIVERSIDADE

MACEIÓ - ALAGOAS
Abril - 2016

GRACIELLE TEIXEIRA HIGINO

ANÁLISE CIENCIOMÉTRICA E MACROECOLÓGICA SOBRE PADRÕES DE DIVERSIDADE

Dissertação apresentada ao Programa de Pós-Graduação em Diversidade Biológica e Conservação nos Trópicos, Instituto de Ciências Biológicas e da Saúde. Universidade Federal de Alagoas, como requisito para obtenção do título de Mestre em CIÊNCIAS BIOLÓGICAS, área de concentração em Conservação da Biodiversidade Tropical.

Orientador: Prof. Dr. Marcos Vinícius Carneiro Vital

MACEIÓ - ALAGOAS
Abril - 2016

Folha de aprovação

Gracielle Teixeira Higino

ANÁLISE CIENCIOMÉTRICA E MACROECOLÓGICA SOBRE PADRÕES DE DIVERSIDADE

Dissertação apresentada ao Programa de Pós-Graduação em Diversidade Biológica e Conservação nos Trópicos, Instituto de Ciências Biológicas e da Saúde. Universidade Federal de Alagoas, como requisito para obtenção do título de Mestre em CIÊNCIAS BIOLÓGICAS, área de concentração em Conservação da Biodiversidade Tropical.

Dissertação aprovada em 29 de fevereiro de 2016.

Prof. Dr. Marcos Vinícius Carneiro Vital/UFAL
Orientador
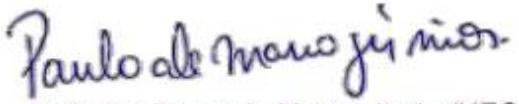
Prof. Dr. Paulo de Marco Junior/UFG
(membro titular)
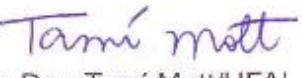
Profa. Dra. Tamí Mott/UFAL
(membro titular)

Prof. Dr. Richard James Ladle/UFAL
(membro titular)

MACEIÓ - AL

Fevereiro / 2016

Quando você percebe que não entende algo, então você está, quase sempre, no caminho certo para entender todo tipo de coisa.

O Dia do Coringa, de Jostein Gaarder

RESUMO

A quantidade de informação sobre biodiversidade reunida pelos naturalistas nos últimos séculos motivou questionamentos sobre a origem e distribuição das espécies. No século XXI, o surgimento dos grandes bancos de dados e novas tecnologias possibilitou a execução de análises estatísticas exaustivas em macroecologia. Esforços recentes em reunir dados globais não têm sido suficientes para diminuir os vieses e lacunas. Esta incompletude tem consequências sérias na conservação e no entendimento da ecologia, e por isso é de suma importância que estas falhas sejam mapeadas, quantificadas e descritas. Os processos por trás da estrutura espacial da biodiversidade têm sido estudados extensivamente ao redor do mundo e por décadas. No entanto, os padrões de biodiversidade ainda não são compreendidos. Neste contexto, este trabalho teve como objetivo mapear e caracterizar os "pontos quentes" da literatura que trata de padrões de biodiversidade, analisar a incompletude do inventário da fauna de vertebrados terrestres da Mata Atlântica, e investigar se algumas variáveis ambientais estão relacionadas com o conhecimento sobre biodiversidade. Além disso, os padrões de riqueza de espécies para vertebrados terrestres foram descritos e a influência de quatro variáveis ambientais nestes padrões foi testada usando correlação de Pearson, modelos lineares e regressão geograficamente ponderada. Os resultados sugerem que existem algumas lacunas na literatura atual, uma vez que apenas alguns países e biomas têm sido largamente explorados e usados como referência. Adicionalmente, a fauna da Mata Atlântica provavelmente não é bem conhecida, pois existem agrupamentos de dados de ocorrência de boa qualidade perto de grandes centros de conservação. Variáveis ambientais comumente utilizadas como indicadores de riqueza de espécies não estavam correlacionadas à completude do inventário nem à riqueza de espécies. Os padrões de riqueza de espécies nesta região são semelhantes entre si. As análises de regressão geograficamente ponderada mostraram que a congruência entre as riquezas das espécies entre grupos não é espacialmente uniforme. Pode-se concluir que o padrão latitudinal de riqueza de espécies não é uma tendência global independente da escala e que temperatura, evapotranspiração potencial, índice normalizado de diversidade vegetal e topografia não determinam a riqueza de espécies ou o tamanho das lacunas de conhecimento nesta ecorregião.

Palavras-chave: Padrões de biodiversidade. Cienciometria. Lacunas de conhecimento.

ABSTRACT

The amount of biodiversity information gathered by naturalists for centuries has motivated questions about species' origin and distribution. In the 21th century, the rise of big data and new technologies have made possible to execute exhaustive statistical analyses on Macroecology. Recent efforts on gathering global data have not been sufficient to surpass biases and gaps. This incompleteness has serious consequences on conservation and ecological understanding, therefore it is of major importance to map, quantify and describe these flaws. The processes underlying the global biodiversity structure have been extensively investigated throughout the world and for decades. However, the biodiversity patterns are still not well understood. In the last few years some hypotheses explored different biological resolutions and tried to resume the processes that results in biodiversity patterns in some few or even only one variable. In this context, this work aimed to map and characterize the literature hotspots concerning biodiversity patterns, to assess inventory incompleteness for the Atlantic Rainforest – concerning amphibians, birds, mammals and reptiles –, and investigate if some environmental variables are correlated to biodiversity knowledge. Moreover, the richness patterns for terrestrial vertebrates of the Atlantic Forest were described and the influence of four environmental variables in their distribution were tested using Pearson's correlation, linear models and Geographically Weighted Regression (GWR). The results suggest that there are a few gaps in the current literature about biodiversity patterns, once only a few countries and biomes have been largely explored and used as reference. Also, the Atlantic Forest fauna is not well known, with clusters of quality information near big conservation centres. Environmental variables commonly referred to as indicators of species richness were not correlated to inventory completeness. Richness patterns in this region are similarly arranged in space and the environmental variables were not correlated to species richness. GWR analyses showed that congruency between groups' species richness are not uniform. We conclude that the latitudinal biodiversity pattern is not a multi-scale global tendency and that temperature, PET, NDVI and topography are not determinants of species richness or inventory completeness in this biome.

Keywords: Biodiversity patterns. Scientometry. Knowledge shortfall.

LISTA DE FIGURAS

Seção 1

Seção 2

Seção 3

Seção 4

LISTA DE TABELAS

Seção 2

Seção 3

Seção 4

SUMÁRIO

1   APRESENTAÇÃO

As próximas páginas tratam de uma área da Ecologia que chamamos de Macroecologia. Pode parecer estranho, mas a Macroecologia tem tudo a ver com um fenômeno "viral" que intrigou muita gente no começo de 2015: o caso do vestido azul/branco/preto/dourado. Se no começo de 2015 você estava sem acesso à televisão ou à internet, ou mesmo se você está lendo isso muito no futuro e não tinha nascido ainda (tem internet no futuro?), acompanhe a seguir uma breve descrição do acontecimento.

Uma moça estava prestes a se casar quando a mãe dela enviou uma foto do vestido que iria usar na cerimônia (Fig. 01). Os noivos então entraram em uma discussão sobre a verdadeira cor do vestido: um o via branco e dourado, outro o via azul e preto. Eles colocaram a foto na internet em busca de ajuda para a resolução do caso e até a Kim Kardashian (quem?) ficou confusa.

Figura 1 - Imagem original que causou a polêmica

Fonte: 2016 BuzzFeed, Inc.

Pois bem, existe um padrão de cores real (afinal, os tecidos que compõem o vestido não podem ser de duas cores no mesmo lugar, ao mesmo tempo) que pode ser detectado com softwares de manipulação de imagens. Existe também o padrão resultante das medições feitas pelo cérebro de cada pessoa. E, além disso, existem os processos evolutivos e neurológicos que levam uma pessoa a decidir qual a cor do vestido. Nosso cérebro tenta decifrar a cor real das coisas descontando a influência das outras frequências de luz do contexto, em especial a luz do dia, que influencia de formas diferentes de acordo com a posição do Sol. No caso desta foto, o que aparece atrás do vestido influencia na resposta que seu cérebro dá (ROGERS, 2015).

A Macroecologia é uma forma de estudar a natureza que faz exatamente o que a Kim Kardashian, os softwares de edição de imagens e, neste caso, alguns neurocientistas fizeram. Na Macroecologia, tentamos entender o padrão real da biodiversidade (e se existe um), levando em consideração os processos que podem nos fazer ver a distribuição das espécies como é hoje (BROWN, J. H., 1995; KEITH et al., 2012).

A matéria prima para os estudos em Macroecologia são os dados espacializados. Isto inclui os registros de ocorrência das espécies ou seus contornos de distribuição, as medidas de variáveis ambientais, as localizações das variações morfológicas, moleculares ou funcionais das espécies, entre outros. Todos estes dados (que correspondem às frequências de luz no caso do vestido) são coletados por pessoas e medidos por aparelhos, ambos com suas margens de erro.

O trabalho dos pesquisadores de campo que resultam nestes dados espacializados depende de várias coisas. Por exemplo, nem todo pesquisador tem financiamento (ou tempo de vida restante) suficiente para verificar a ocorrência da espécie de interesse em todos os lugares, o que garantiria, até certo ponto, uma padronização desta medida. Os pesquisadores procuram pelas espécies que estão estudando quando vão a campo e pode acontecer de vários cientistas se interessarem pela mesma espécie em um mesmo local. Isto faz com que as espécies que não estão sendo estudadas não apareçam no mapa, o que não quer dizer que elas não existam ali. Mesmo que o cientista esteja procurando por uma espécie que ninguém mais quer estudar, estes organismos podem ser muito difíceis de encontrar, o que também faz com que ele não apareça no mapa tantas vezes. Em resumo, os dados disponíveis sobre a biodiversidade do planeta dependem de onde os cientistas estão, de quanto dinheiro eles têm e para onde eles podem ir. Como na foto do vestido, o padrão percebido é influenciado por variáveis que compõem o contexto.

Nos últimos anos, estes problemas têm sido parcialmente resolvidos com a possibilidade de todas as pessoas ajudarem a mapear a biodiversidade (e identificar estrelas, também). O que hoje chamamos de "citizen science" diminuiu as barreiras de financiamento e localização geográfica. Uma pessoa com acesso à internet pode ajudar a identificar animais registrados por uma armadilha fotográfica instalada em outro país, ou mesmo alimentar um banco de dados com fotos georreferenciadas de um organismo encontrado no próprio quintal.

A digitalização e disponibilização dos dados de biodiversidade permite que identifiquemos com muito mais precisão o que sabemos, o que precisamos conhecer, e o que já conhecemos, mas ainda não contamos que sabemos (HORTAL et al., 2015), e isso se reflete diretamente no que entendemos como padrões e processos macroecológicos.

Porém, talvez estejamos fazendo tudo errado! Um estudo de 2012 descreveu onde os ecólogos que estudam organismos terrestres estão trabalhando (Fig. 02), ao coletar dados das revistas com maior impacto na área. Os autores descobriram que a maior parte dos estudos se concentra nas regiões temperadas, em áreas protegidas e em países mais ricos, resultado diferente do esperado pela caracterização do ambiente terrestre global (MARTIN et al., 2012). É como se estivéssemos tentando descobrir qual a cor do vestido supracitado a partir de descrições verbais feitas por pessoas que só enxergam o vestido como sendo branco e dourado.

Figura 2 - O enviesamento da escolha dos locais de estudo pode influenciar o que entendemos como padrões e processos macroecológicos
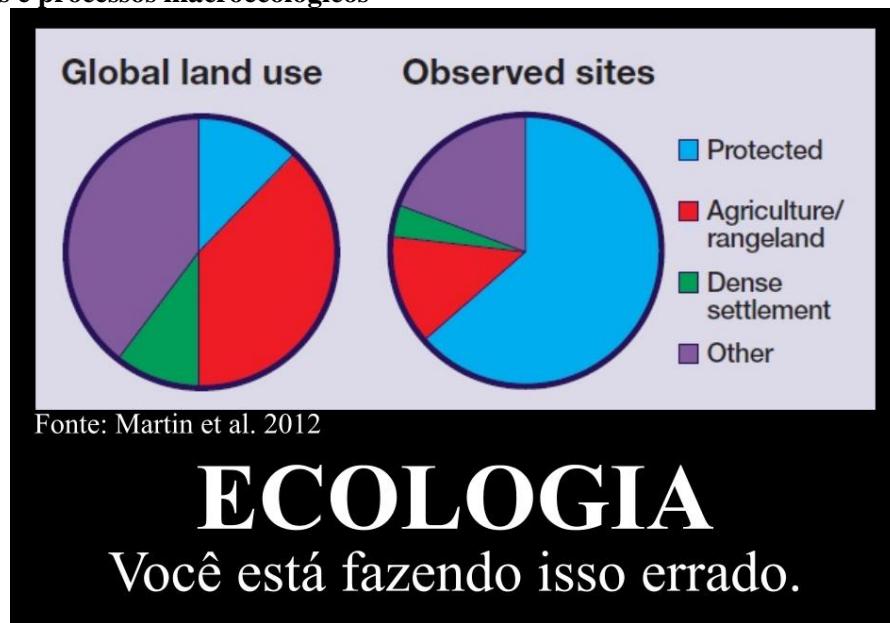
Fonte: Elaborada pela autora.

Todas estas peculiaridades fazem da Macroecologia uma disciplina que ainda pode ser muito explorada e que tem o potencial de responder perguntas que intrigam alguns de nós desde criança. Afinal, não tem sapo na praia. Não tem beija-flor fora das Américas. Tem mais bichos no sítio da vózinha que no meio da cidade. Por quê?

Esta dissertação explorará as facetas da Macroecologia. Primeiro será feita uma caracterização cienciométrica do estado da arte (também identificando os vieses dos estudos sobre padrões de biodiversidade). Em seguida alguns dados de diversidade serão analisados de modo a mapear o conhecimento sobre a biodiversidade na Mata Atlântica. Por fim, estes dados serão utilizados na busca por respostas sobre os padrões de biodiversidade e os processos que podem moldá-los.

A primeira seção trata do que a maior parte dos cientistas conhece sobre padrões de diversidade. Os artigos em inglês de um dos maiores indexadores de revistas científicas foram analisados a partir de dados como locais dos estudos, países de origem dos autores, ano de publicação de cada um e palavras-chave (que serviram como indicadores dos principais interesses de pesquisa nesta área).

Em Macroecologia fala-se muito sobre padrões globais de biodiversidade: existem mais espécies nos trópicos, em locais com maior variação de altitude, em locais com clima mais estável; as espécies tendem a serem maiores em certos locais que em outros; alguns poucos fatores ambientais são capazes de determinar a distribuição das espécies em qualquer lugar do planeta. Sabendo que os cientistas tendem a explorar mais alguns lugares que outros, será que estes padrões globais são mesmo globais? Mesmo que sejam feitos estudos locais em diferentes regiões do mundo, os resultados destes devem ser comparáveis e complementares. Além da caracterização histórica do avanço da teoria sobre padrões de diversidade, também é feita uma discussão sobre a relação entre o investimento em pesquisa e desenvolvimento com a produção científica e o impacto da pesquisa de alguns países.

A segunda parte deste trabalho tem como foco os dados de biodiversidade da Mata Atlântica, um dos biomas mais diversos e ameaçados do mundo. Além disso, esta floresta tropical é um ótimo modelo para estudos macroecológicos devido às grandes variações na sua fitofisionomia, altitude, extensão latitudinal e precipitação. Conhecer todo o seu potencial biológico e como a biodiversidade se relaciona com variáveis ambientais em toda a sua extensão pode ajudar a preservá-la e a preencher importantes lacunas de conhecimento. No entanto, é

importante conhecer os erros e tendências dos dados que caracterizam sua biodiversidade, uma vez que dados enviesados podem até inverter os padrões ecogeográficos que percebemos (FICETOLA et al., 2014). Para investigar isso, as informações de uma das plataformas mais utilizadas pelos cientistas foram utilizadas na descrição do estado atual de conhecimento sobre a fauna deste bioma e na investigação de fatores que podem ter influenciado este cenário.

A terceira seção trata ainda da Mata Atlântica e sua fauna, desta vez em uma tentativa de entender os padrões reais de diversidade e os processos que os determinam. Os mesmos dados da seção anterior são utilizados para responder perguntas como: será que os locais com grande riqueza de espécies de um grupo taxonômico também são locais de grande riqueza para outros grupos? A riqueza de espécies está concentrada em algum lugar na Mata Atlântica? Podemos perceber o padrão latitudinal de riqueza de espécies, dito como global, também na Mata Atlântica? Será que variáveis ambientais como temperatura, relevo e cobertura vegetal estão relacionadas à quantidade de espécies ao longo do bioma?

Nesta seção e na anterior foram utilizadas técnicas de análises espaciais. Este tipo de método leva em conta a localização geográfica e o tipo de padrão que estamos analisando. Um dos pontos importantes a serem levados em consideração é a tendência que as amostras têm de serem mais parecidas quando estão mais próximas umas das outras. Em geral, na Macroecologia utilizamos mapas divididos em unidades ou células (que podem ser retangulares, hexagonais, triangulares etc.). As unidades mais próximas no espaço tendem a ser mais parecidas, o que chamamos de autocorrelação espacial. Às vezes isto pode ser um problema quando precisamos testar hipóteses e estes testes têm como pressuposto a independência das unidades amostrais. Existem diversas formas de lidar com esta característica dos dados e aqui foram utilizados os filtros espaciais (DINIZ-FILHO; BINI, 2005). Este método consegue separar a quantidade de informação que é resultante da proximidade das amostras da variação independente de cada uma.

Na terceira seção também foi utilizado um método de regressão linear que leva em consideração a localização de cada amostra e os valores que as células vizinhas têm para as variáveis em questão (FOTHERINGHAM et al., 2002). O bacana deste método é que ele permite visualizar no mapa se as relações entre as variáveis mudam ao longo do espaço. Isso é muito importante porque um mesmo padrão em locais diferentes pode ser causado por processos diferentes. A esta seção, segue-se uma discussão sobre todos os resultados obtidos e uma conclusão geral.

1.1   Entendendo um pouco melhor a teoria

Ao longo da história, os cientistas notaram que as espécies ou algumas características delas se distribuíam de maneira similar no espaço e descreveram os padrões biogeográficos. Notaram, por exemplo, que áreas maiores comportam mais organismos e, portanto, mais espécies (ARRHENIUS, 1921). Esta observação faz parte da teoria de biogeografia de ilhas, onde parte da explicação sobre o número de espécies presentes em uma "ilha" é justamente o tamanho desta (LOSOS; JONATHAN B.; RICKLEFS, 2009).

A distribuição heterogênea da biodiversidade na natureza é facilmente constatada em viagens por terra, quando percebemos mudanças na fitofisionomia da paisagem ao longo da estrada. Estas mudanças, originadas por diferenças na riqueza de espécies e na abundância dos organismos, podem se repetir no tempo e/ou no espaço e entre diferentes grupos taxonômicos. A estas repetições chamamos de padrões de diversidade, que podem ser percebidos em diferentes escalas, como quando observamos invertebrados bentônicos distribuídos de forma irregular em uma esponja ou espécies "organizadas" em gradientes em uma montanha ou ao longo de um continente. O gradiente latitudinal de diversidade tem sido facilmente percebido (e exaustivamente discutido) há muitos anos: quanto menor a latitude, maior a biodiversidade, com dois picos um pouco afastados do Equador (DARWIN, 1859; FISCHER, 1960; GASTON, 2000; HAWKINS, 2001; HILLEBRAND, 2004; VON HUMBOLDT et al., 1850; ROHDE, 1992; WALLACE, 1878). Intrigante! Mas por que será que existem estes padrões?

Localmente, a diversidade está atrelada a fatores intra e interpopulacionais (como predação, competição, mutualismo e taxas de recrutamento), enquanto fatores evolutivos moldam as comunidades em escalas maiores (especiação, migração e extinção). No entanto, é possível ligar estas perspectivas por processos intermediários, como a habilidade de dispersão das espécies, fidelidade de hábitat, taxas de reprodução e evolução molecular, e respostas fisiológicas a mudanças climáticas. Desta forma, a riqueza local pode influenciar a riqueza regional e vice-versa (WHITTAKER et al., 2001).

Uma vez conhecido o padrão e o possível processo explicativo, um desafio importante a ser enfrentado é o esclarecimento dos limites de resolução em que este processo opera. Aparentemente é neste ponto que reside a falta de consenso sobre quais os fatores que moldam a distribuição dos organismos no planeta (BROWN; MAURER, 1989; WHITTAKER et al., 2001). Além disso, os processos que moldaram a distribuição da biodiversidade como padrões

sobrepostos de riqueza entre diferentes *taxa* podem ser de natureza aleatória (efeito dos domínios médios, respostas similares a fatores em comum, respostas a variáveis diferentes e correlacionadas) ou interativa (interação entre espécies). No entanto, os processos interativos devem ocorrer entre vários grupos para resultar em variação espacial notória e comumente estão relacionados à história evolutiva dos *taxa* (GASTON, 2000; TORANZA; ARIM, 2010).

Uma das hipóteses mais discutidas atualmente é a de que a energia disponível em um sistema determina o número de espécies (ANDERSON; JETZ, 2005; CURRIE, 1991; HAMILTON; WRIGHT, 1983; JETZ; FINE, 2012; WHITTAKER et al., 2001). As variáveis ambientais que podem representar a energia podem ser, por exemplo, a temperatura, a precipitação ou a produtividade primária. Esta última, por sua vez, pode ser representada por medidas de cobertura vegetal, como o índice de vegetação por diferença normalizada (NDVI), ou por medidas de balanço hídrico que combinam temperatura e disponibilidade de água, como a evapotranspiração potencial (PET) e a evapotranspiração real (AET).

Outras hipóteses levam em consideração processos evolutivos, como a especiação. Neste contexto, a disponibilidade de habitats e o tempo de estabelecimento das comunidades podem ser variáveis importantes. Regiões com relevos ou vegetações heterogêneos, por exemplo, favorecem a diversificação tanto por isolamento quanto por especiação simpátrica (aquela que ocorre na ausência de barreira geográfica, geralmente causada por variações comportamentais ou morfológicas nas populações). Portanto, é esperado que estes locais abriguem mais espécies (PIANKA, 1966; WHITTAKER et al., 2001). Adicionalmente, as comunidades podem ter a tendência de se diversificar com o tempo. Por isso, alguns pesquisadores esperam que regiões estáveis há muito tempo (em contraste, por exemplo, com ilhas vulcânicas formadas recentemente) sejam mais biodiversas (JABLONSKI et al., 2006; LEIGHTON, 2005; PIANKA, 1966; WHITTAKER et al., 2001; WIENS; DONOGHUE, 2004).

Estas hipóteses parecem fazer bastante sentido, mas como podemos saber que os padrões que percebemos não são só artefatos da nossa forma de explorar a natureza? E se os locais que consideramos mais diversos são mais estudados e por isso tem mais registros de espécies? E se consideramos uma relação causal entre uma variável ambiental e a riqueza de espécies quando na verdade existe só uma coincidência aleatória, associada ou não às nossas preferências de estudo? Para diminuir estas dúvidas estudamos o viés amostral dos dados espacializados antes de testar as hipóteses supracitadas. Podemos fazer isso com as curvas de rarefação, que nos permite comparar

unidades amostrais bem conhecidas com aquelas aparentemente pouco exploradas (COLWELL et al., 2012).

Imagine um pesquisador que decide conhecer uma ilha que ninguém conhece. No primeiro dia, todas as espécies que ele encontra lá são registros novos para aquela ilha. No segundo dia, ele pode encontrar todas as espécies do dia anterior, mas também encontra algumas novidades. E assim sucessivamente, mas as novidades são cada vez menos frequentes até que um dia ele não encontra mais espécies novas. Nosso pesquisador imaginário agora sabe quantas amostras ele precisa fazer para conhecer a riqueza total daquela ilha. Agora imagine que isto aconteça N vezes, com N pesquisadores diferentes que não se conhecem e estudam a biodiversidade da ilha independentemente. Quando juntarmos os dados de todos estes pesquisadores, teremos uma curva média onde cada ponto nos indica a riqueza esperada para um determinado número de registros. Se esta ilha faz parte de um arquipélago, podemos comparar as curvas de cada ilha e inferir quais são mais conhecidas porque as ilhas menos exploradas terão curvas mais parecidas com retas e um número de espécies menor que a riqueza esperada (Fig. 03).

Figura 3 - Curvas de acúmulo de espécies de um local bem conhecido (A) e de um local subamostrado (B).
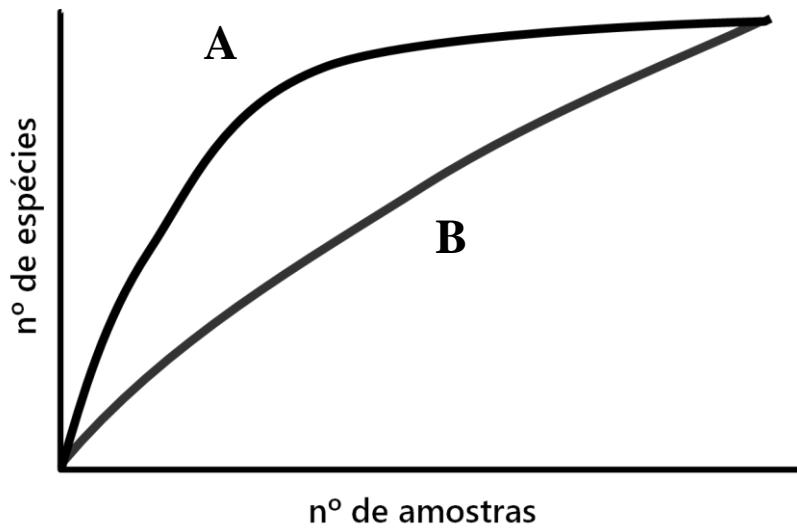
Fonte: Elaborada pela autora.

Vários fatores podem fazer com que alguns locais sejam mais conhecidos que outros, ou que a distribuição de algumas espécies seja mais conhecida que de outras. Entre elas estão variáveis sociais, como acessibilidade, número de pessoas que habitam a região, proximidade de

centros de pesquisa, a situação econômica do local ou mesmo seus índices de violência. A história de vida das espécies, a capacidade de se camuflar e os hábitos dos indivíduos podem tornar mais difícil o registro das ocorrências. Até mesmo fatores mais subjetivos, como a preferência do pesquisador por determinadas espécies ou regiões, pode deixar incompleto o cenário da biodiversidade. Além disso, baseados nas hipóteses descritas acima sobre processos que determinam a biodiversidade, os pesquisadores podem usar as variáveis ambientais para decidir quais locais seriam melhores de estudar por abrigarem mais espécies (BROWN; LOMOLINO, 1998; FICETOLA et al., 2014; WHITTAKER et al., 2005).

Esta dissertação conecta todos estes pontos. Ao investigar os vieses na literatura, podemos imaginar se variáveis sociais estão influenciando nosso conhecimento teórico sobre padrões de diversidade. Em seguida investigamos a completude dos dados de ocorrência, os produtos da maioria dos estudos em ecologia, e nos perguntamos se variáveis ambientais estão relacionadas com a quantidade de conhecimento digital disponível. Por fim, levando em consideração os resultados destas duas partes, tentamos testar as hipóteses de que a biodiversidade da Mata Atlântica está relacionada à disponibilidade de energia e habitat.

REFERÊNCIAS

ANDERSON, K. J.; JETZ, W. The broad-scale ecology of energy expenditure of endotherms. **Ecology Letters**, v. 8, n. 3, p. 310–318, 25 fev. 2005.

ARRHENIUS, O. Species and area. **Journal of Ecology**, v. 9, n. 1, p. 95–99, 1921.

BROWN, J. H.; MAURER, B. A. Macroecology: the division of food and space among species on continents. **Science**, v. 243, n. 4895, p. 1145–50, 3 mar. 1989.

BROWN, J. H. **Macroecology**. 1. ed. Chicago and London: The University of Chicago Press, 1995. v. 6

BROWN, J. H.; LOMOLINO, M. V. **Biogeography**. 2. ed. Massachusetts: Sinauer Associates, Inc. Publishers, 1998.

COLWELL, R. K. et al. Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. **Journal of Plant Ecology**, v. 5, n. 1, p. 3–21, 2012.

CURRIE, D. J. Energy and large-scale patterns of animal - and plant - species richness. **The American Naturalist**, v. 137, n. 1, p. 27–49, 1991.

DARWIN, C. R. **On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life.** 1. ed. London: John Murray, 1859.

DINIZ-FILHO, J. A. F.; BINI, L. M. Modelling geographical patterns in species richness using eigenvector-based spatial filters. **Global Ecology and Biogeography**, v. 14, n. 2, p. 177–185, mar. 2005.

FICETOLA, G. F. et al. Sampling bias inverts ecogeographical relationships in island reptiles. **Global Ecology and Biogeography**, p. 1303–1313, 2014.

FISCHER, A. Latitudinal variations in organic diversity. **Evolution**, v. 14, n. 1, p. 64–81, 1960.

FOTHERINGHAM, A. S. S.; BRUNSDON, C.; CHARLTON, M. **Geographically Weighted Regression: The Analysis of Spatially Varying Relationships**. [s.l.] John Wiley and Sons, 2002.

GASTON, K. J. Global patterns in biodiversity. **Nature**, v. 405, n. 6783, p. 220–7, 11 maio 2000.

HAMILTON, D.; WRIGHT, D. H. Species-Energy Theory: An Extension of Species-Area Theory. **Oikos**, v. 41, n. 3, p. 496–506, 1983.

HAWKINS, B. A. Ecology's oldest pattern? **Trends in Ecology & Evolution**, v. 16, n. 8, p. 470, 8 ago. 2001.

HILLEBRAND, H. On the Generality of the Latitudinal Diversity Gradient. **The American Naturalist**, v. 163, n. 2, p. 192–211, 2004.

HORTAL, J. et al. Seven Shortfalls that Beset Large-Scale Knowledge of Biodiversity. **Annual Review of Ecology, Evolution, and Systematics**, v. 46, n. 1, p. 523–49, 2015.

VON HUMBOLDT, A.; OTTÉ, E. C.; BOHN, H. G. **Views of Nature: Or Contemplations on the Sublime Phenomena of Creation**. [s.l.] Cambridge University Press, 1850.

JABLONSKI, D.; ROY, K.; VALENTINE, J. W. Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. **Science (New York, N.Y.)**, v. 314, n. 5796, p. 102–106, 2006.

JETZ, W.; FINE, P. V. A. Global gradients in vertebrate diversity predicted by historical area-productivity dynamics and contemporary environment. **PLoS Biology**, v. 10, n. 3, p. 1–11, 2012.

KEITH, S. A. et al. What is macroecology? **Biology letters**, v. 8, n. 6, p. 904–6, 23 dez. 2012.

LEIGHTON, L. R. The latitudinal diversity gradient through deep time: Testing the "Age of the Tropics" hypothesis using carboniferous productidine brachiopods. **Evolutionary Ecology**, v. 19, n. 6, p. 563–581, 2005.

LOSOS, JONATHAN B.; RICKLEFS, R. E. **The Theory of Island Biogeography Revisited**. [s.l: s.n.].

MARTIN, L. J.; BLOSSEY, B.; ELLIS, E. Mapping where ecologists work: Biases in the global distribution of terrestrial ecological observations. **Frontiers in Ecology and the Environment**, v. 10, n. 4, p. 195–201, 2012.

PIANKA, E. R. Latitudinal Gradients in Species Diversity : A Review of Concepts. **The American Naturalist**, v. 100, n. 910, p. 33–46, 1966.

ROGERS, A. **The Science of Why No One Agrees on the Color of This Dress**. Disponível em: <http://www.wired.com/2015/02/science-one-agrees-color-dress/>. Acesso em: 25 jan. 2016.

ROHDE, K. Latitudinal Gradients in Species Diversity: The Search for the Primary Cause. **Oikos**, v. 65, n. 3, p. 514–527, 1992.

TORANZA, C.; ARIM, M. Cross-taxon congruence and environmental conditions. **BMC ecology**, v. 10, p. 18, jan. 2010.

WALLACE, A. R. **Tropical nature, and other essays**. London & New York: Macmillan & Co., 1878.

WHITTAKER, R. J.; WILLIS, K. J.; FIELD, R. Scale and species richness: Towards a general, hierarchical theory of species diversity. **Journal of Biogeography**, v. 28, n. 4, p. 453–470, 2001.

WHITTAKER et al. Conservation biogeography: asessment and prospect. **Diversity and Distributions**, v. 11, p. 3–23, 2005.

WIENS, J. J.; DONOGHUE, M. J. Historical biogeography, ecology and species richness. **Trends in ecology & evolution**, v. 19, n. 12, p. 639–44, 2004.

2   LITERATURE HOTSPOTS ON BIODIVERSITY PATTERNS

Abstract

The amount of biodiversity information gathered by naturalists for centuries has motivated questions about species' origin and distribution. In the 21th century, the rise of big data and new technologies have made possible to execute exhaustive statistical analyses on Macroecology. However, the biodiversity patterns are still not well understood, and this may be because of the narrow range of environments where scientists conduct their studies. In this paper, we aim to map and characterize the literature hotspots concerning this subject. We collected Web of Science records using the string "biodiversity pattern*" in the topic field. We analysed frequencies of keywords, authors, journals, publications per year, geographic locations of authors, study sites and citation. The most prolific year was 2015, and the most frequent journals were "PLoS One" and "Biodiversity and Conservation". There is a growing interest on conservation, especially in studies conducted in South Africa. The United States was the most studied and the most cited country. Global studies and theoretical analyses represented almost 20% of all records. The expenditure on R&D was found to be a good proxy for scientific production on this topic. Our results demonstrates that there are a few gaps in the current literature about biodiversity patterns, once only a few countries and biomes have been largely explored and used as reference. It is necessary to map these gaps and address more research effort towards understudied places.

Keywords: scientific literature, wallacean shortfall, macroecology, biodiversity patterns

2.1 Introduction

During the 19th century, naturalists such as Alfred Wallace, Henry Bates, Charles Darwin and Alexander von Humboldt were responsible for a great volume of global biodiversity information, which raised important questions about species origins and the distribution of species on the planet (Willig et al. 2003; Chase 2012), but also about biodiversity gradients (Von Humboldt et al. 1850; Hawkins 2001). The first papers about biodiversity patterns are from the early 20th century, with models of the species-area correlation and the rise of diversity indexes (Arrhenius 1921; Shannon 1948; Pianka 1966). However, researches were focused on communities' structures and small scale patterns.

In 1989, Brown and Maurer introduced the field of research called "macroecology", which explores ecological patterns at large scales and statistical relationships between variables that could influence biodiversity distribution (Brown and Maurer 1989; Keith et al. 2012). The macroecological approach tries to identify processes behind biodiversity patterns by statistically associating interacting ecosystems' components (Brown 1999).

Complex statistical analyses and hypotheses tests using large datasets were made possible owing to the amount of global data available and new technologies of the early 21th century. Since then the number of papers concerning biodiversity patterns has been increasing. In the last few years, ecological niche modelling has improved the search for underlying factors that determine species' distribution and helped elucidate questions about the consequences of climate change (Margules and Pressey 2000; Araújo and Guisan 2006; Rocchini et al. 2011; Beck et al. 2013; Loyola et al. 2014)

Biodiversity research has improved towards international integration, which is important to diminish the difference between local research effort and biodiversity richness (Hendriks and Duarte 2008). However, in the long history of research on biodiversity patterns and the effects of biotic or abiotic variables on it, the methods used are often not comparable, leading to a lack of consensus in literature (Brown and Maurer 1989; Whittaker et al. 2001). The scale of the pattern (its range and resolution) should be compatible with the scale of the explicative variables, i.e., the factors behind species distribution should be relevant at the same scale as the presence/absence observations. Alternatively, the relation between variables should not be scale dependent (Whittaker et al. 2001).

Another problem occurs when global patterns experiments are held in narrow geographic regions and their results are not concisely combined to outline a worldwide framework (Brown and Maurer 1989; Whittaker et al. 2001). As in any other field of research, there may be a bias on study locations towards well developed countries (Holmgren and Schnitzer 2004). Therefore, there is the possibility that the amount of literature testing global biodiversity patterns and explanations may not be solid references on this matter.

Scientometric analysis applies quantitative methods in order to assess science as an information process. This method allows identifying temporal and spatial patterns of publications and evaluating the development of disciplines (Pritchard 1969; Liu et al. 2011; Stork and Astrin 2014). For that reason, scientometry is a good tool to understand gaps in current knowledge of biodiversity patterns, identifying underexplored regions and subjects.

In this paper we aimed to describe the history and the current state of literature on biodiversity patterns. We also investigate the geographic and temporal distribution of publications and study sites in this field of research. We expect that the most studied and most productive countries are located in Europe and North America.

2.2   Methods

A search in the Web of Science (WoS) database was conducted in October 10th 2015 using the search string "biodiversity pattern*" in the WoS topic field (which includes title, abstract, author keywords, and keywords plus). After deletion of 239 duplicate entries, we obtained 739 records. From this database, we obtained total and relative frequencies of authors, journals, countries or territories, years, keywords, citations and study sites (which were classified as global – when several continents or oceans were assessed –, NA – for theoretical analyses and hypothetical models – or by countries' names). Statistical analyses were performed using the statistical programming language R (www.cran.r-project.org) and the "tm" package for keyword analyses (Feinerer et al. 2008; Feinerer and Hornik 2015).

Keywords and keywords plus were treated as a single dataset. Although some of them are duplicated in the same record, overall tendencies could still be noted. Frequencies of each word were obtained using "tm" package in R environment. Plurals were excluded, but their frequencies were added to their correspondent singular, except when the word occupied more than one grammatical class. Spelling was standardized to British English and misspellings were corrected.

Finally, keywords were analysed according to year of publications, authors' addresses and study locations. A principal components analysis (PCA) was made to evaluate interests (keywords) groups using years as sampling units. For that purpose were calculated relative frequencies of keywords per number of publications in each year.

Publication types that typically do not contain study sites as part of the subject (such as book reviews) were not included in the analysis of geographical variation in research interest. Reviews and book chapters were also excluded since they rarely have new information about scientific findings. We assessed geographical variation both in scientific production and study sites. The number of countries studied per year were also analysed in order to investigate international integration and expansion of geographical interests through time. We used a correlation test between the number of studies performed in each country and the number of citations from these studies to evaluate whether the most studied countries were also the ones used as reference in new research papers.

An additional search in the WoS database was made in order to obtain a broader scenario of scientific production in Ecology. All publications from 1991 to 2015 were filtered only by research area, using only values that occurred in the previous dataset, resulting in 1056819 records. This second dataset was used to calculate relative frequencies of publications per year and publications per journal.

2.3 Results

There was an exponential increase in number of publications about biodiversity patterns over the last 24 years. The last three years were especially productive, with 2015's publications overcoming those of 2014 before the end of the year (Fig. 1). The number of publications of these two years together is equivalent to more than 53% of the other 22 years. Publications were made in 266 journals, 30 (11.3%) of which comprise 50% of records. "PLoS One" and "Biodiversity and Conservation" are the two most popular journals, with 35 entries each, followed by "Biological Conservation", with 30 (Fig. 2).
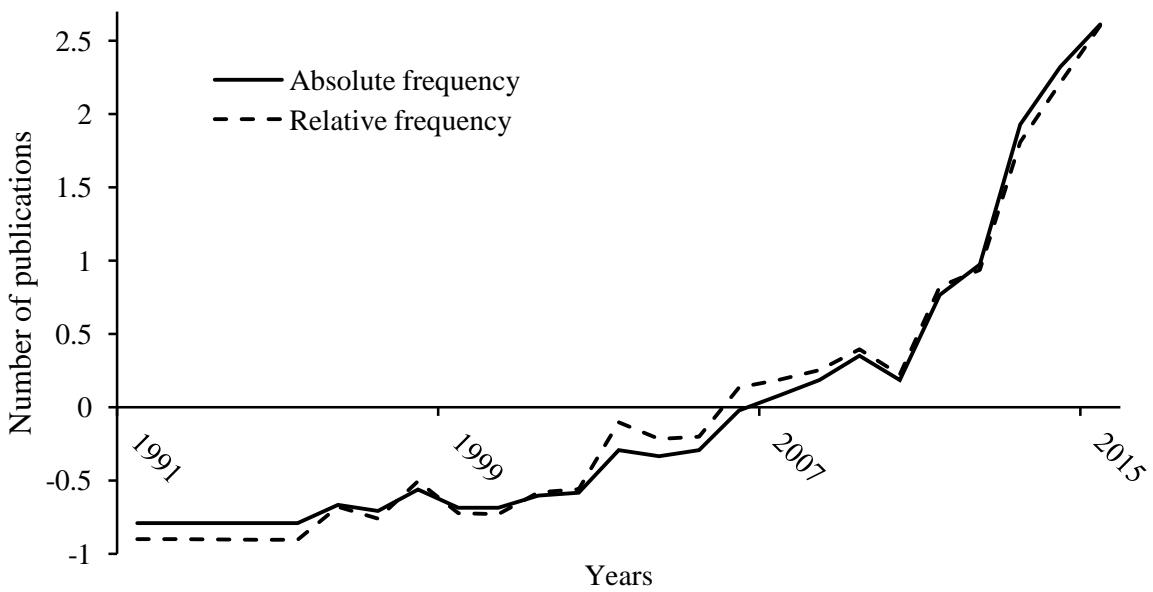
Fig. 1 – Frequency of publications on biodiversity patterns over the last 25 years.
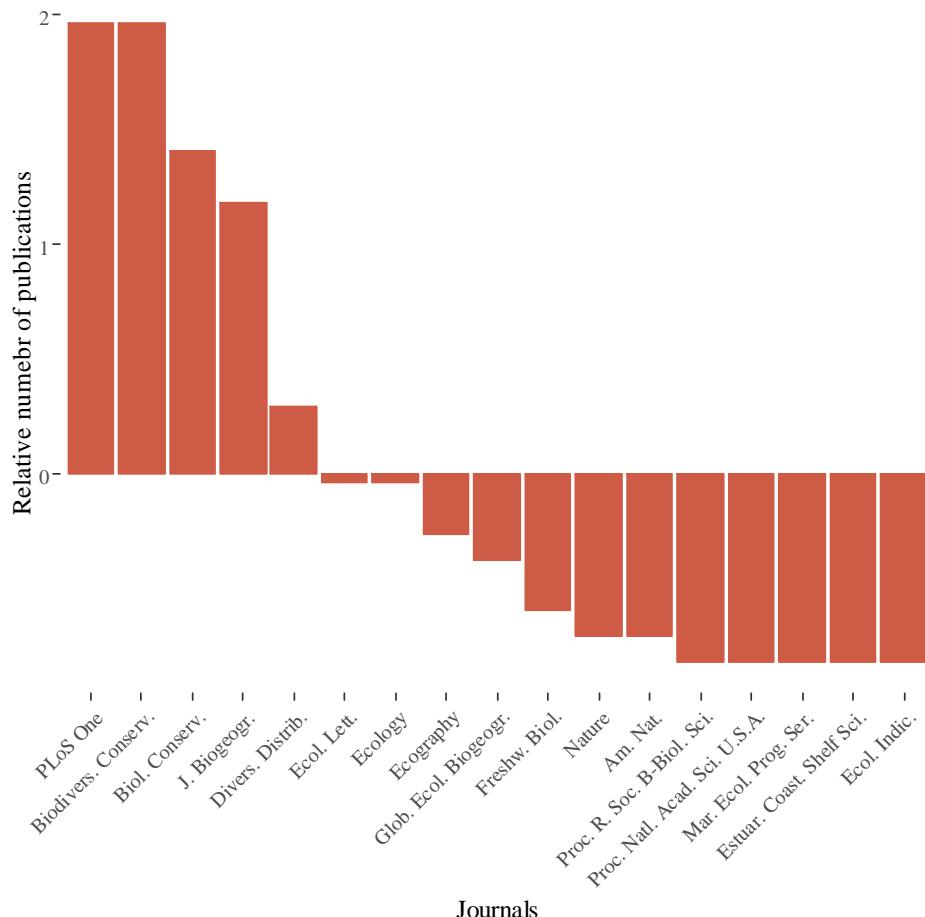
Fig. 2 – Scientific journals with more than 10 records.

The oldest article retrieved was "Coastal-zone biodiversity patterns", published by Biosciences in 1991, which was cited 40 times. In this study, the author explains how biogeography and geomorphology can determine biodiversity patterns in coastal ecosystems. He also tries to predict the consequences of climate change on continental margins, highlighting its importance to oceans and human activities (Ray 1991). The most cited article was "Landscape perspectives on agricultural intensification and biodiversity-ecosystem service management", published by Ecology Letters in 2005. This article delineates the influence of agricultural activities in ecosystems and emphasizes the human role on shaping biodiversity distribution (Tscharntke et al. 2005) and was cited 1001 times.

The geographical extent of experiments has been changing especially in the last four years. From 1991 to 2002, researches took place in no more than 10 different locations (including global studies), except for 1998 with 29 different countries explored and two global studies. In 2003 there was the first occurrence of a theoretical experiment. Since then the number of different locations explored in studies, including at least one theoretical analysis (with 10 records in 2014) and one global study (with 12 records in 2015), has increased, with a peak in 2011 (with 46 different locations) and another one in 2014 (with 53 different locations). Records from 2015 are already ahead of those from 2011, with 49 different locations assessed in the papers (Fig. 3 and 4).
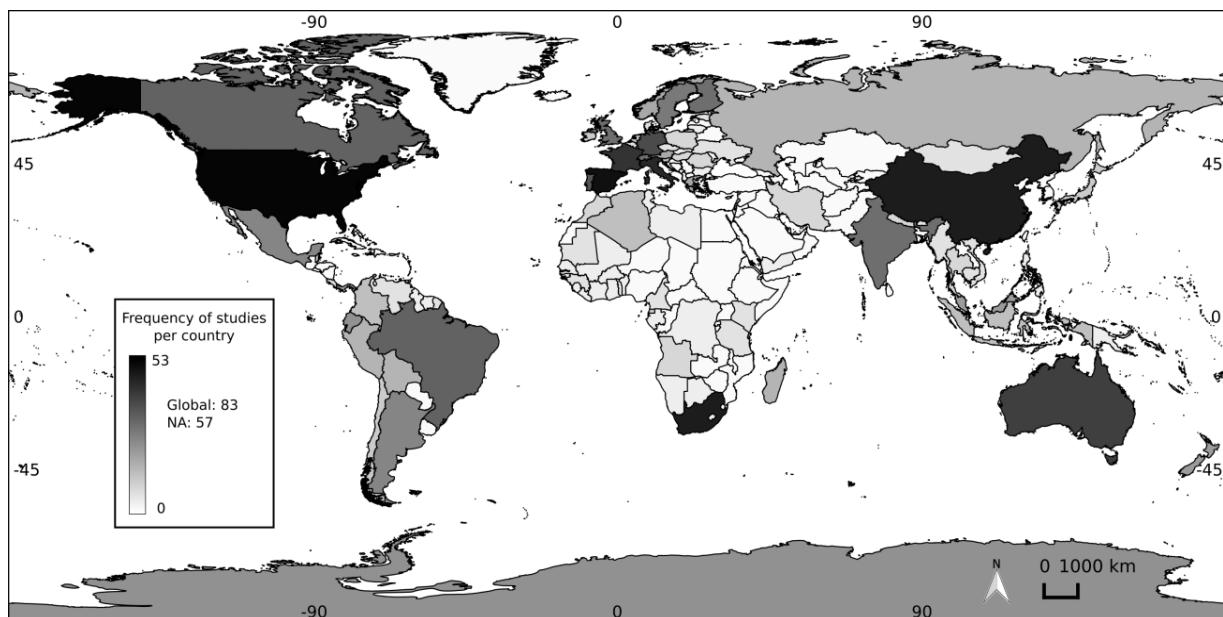
Fig. 3 – Countries where studies were conducted. Records referring to continents or politically undefined areas are not represented. Frequency of "NA" represents theoretical analyses (reviews or models).
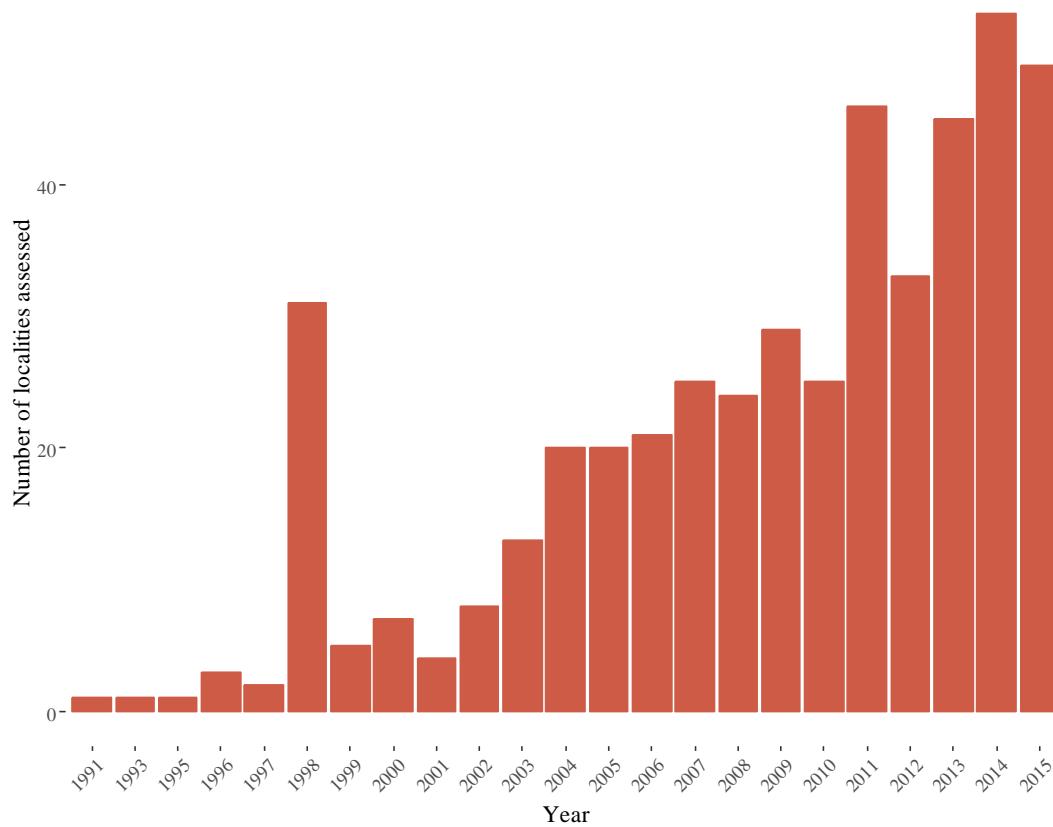
Fig. 4 – Number of different study sites per year.

From all records, 83 referred to global biodiversity, followed by 57 theoretical analyses and 53 studies in the United States of America. All other locations were explored by less than 40 papers. Global studies were the most cited, followed by researches placed in USA and South Africa (Fig. 5). Theoretical analyses were the fourth most cited class. This does not reflect exactly the number of studies in each location: global studies are also the most frequent, but are followed by models and simulations, researches in USA, Spain and South Africa. However, there is a correlation between the number of studies in each location and the number of times these studies are used as reference (R=0.902, p<0.001). Some underexplored localities were object for representative works, such as Papua New Guinea, with only one paper investigating its biodiversity which was cited 117 times.

From all the 2776 authors, the most prolific are Richard Cawling and Robert Pressey, with 11 and 10 articles respectively, and they share the authorship in seven of these papers (Fig. 6). This means that they are responsible for almost 3% of all publications related to biodiversity patterns. Their contributions concern the Cape Floristic Region and conservation of plants. The

majority of authors, however, are from the United States of America, who produces 28% of all researches. Germany, England, Spain and France together produce 47.9% of all papers.
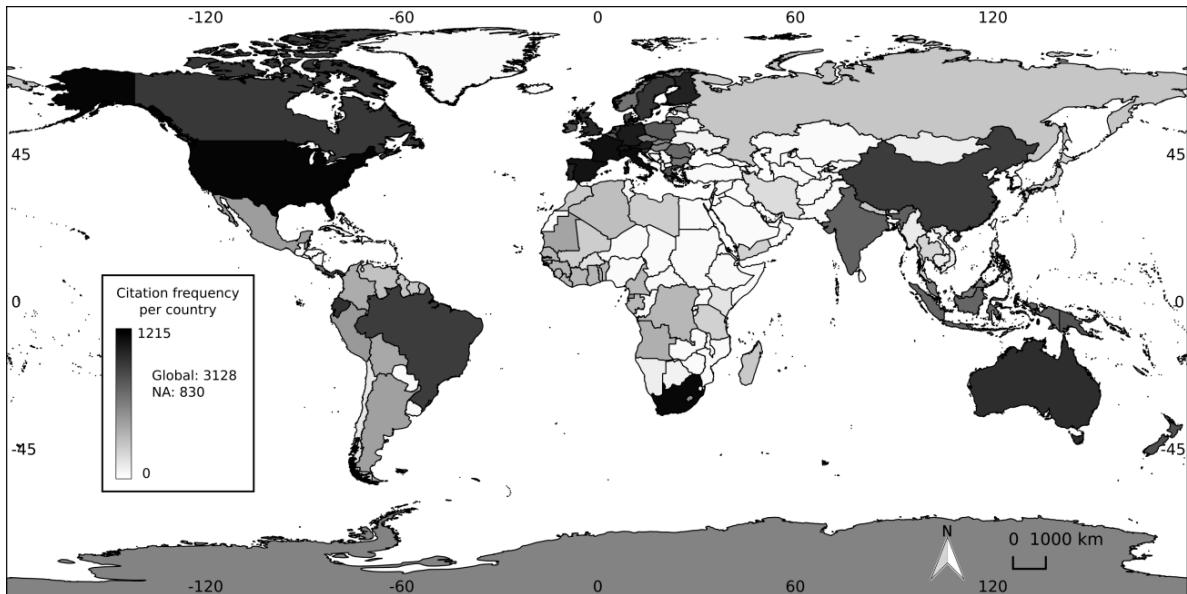
Fig. 5 – Number of citations referring to studies conducted in each country. Records referring to continents or politically undefined areas are not represented. Frequency of "NA" represents theoretical analyses (reviews or models).
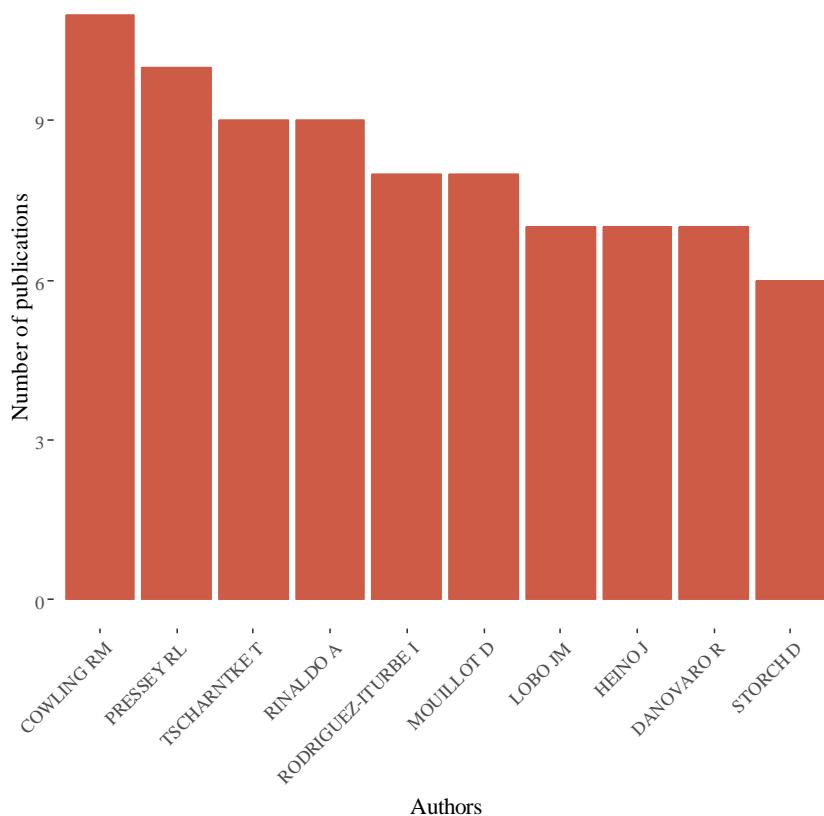
Fig. 6 – The 10 most prolific authors.

The expenditure on research and development (R&D) in the world is still leaded by the United States of America, which also is the country with more R&D professionals (Grueber and Studt 2014; OECD 2015; The World Bank 2016; UNESCO Institute for Statistics). In fact, the amount of financial support on R&D (as a percentage of gross domestic product) can be a proxy for scientific production on biodiversity patterns (Spearman's Rank Correlation = 0.591, p < 0.001). However, the gross expenditure in R&D is not a good predictor of scientific production (Spearman's Rank Correlation = 0.157, p = 0.187).

Words related to diversity (including biodiversity and correlates) were the most common in the keywords dataset. "Species richness" was the next most common keyword, followed by words related to conservation, patterns and community ecology (such as beta-diversity, community structure, community composition, metacommunities and so on) (Fig. 7).
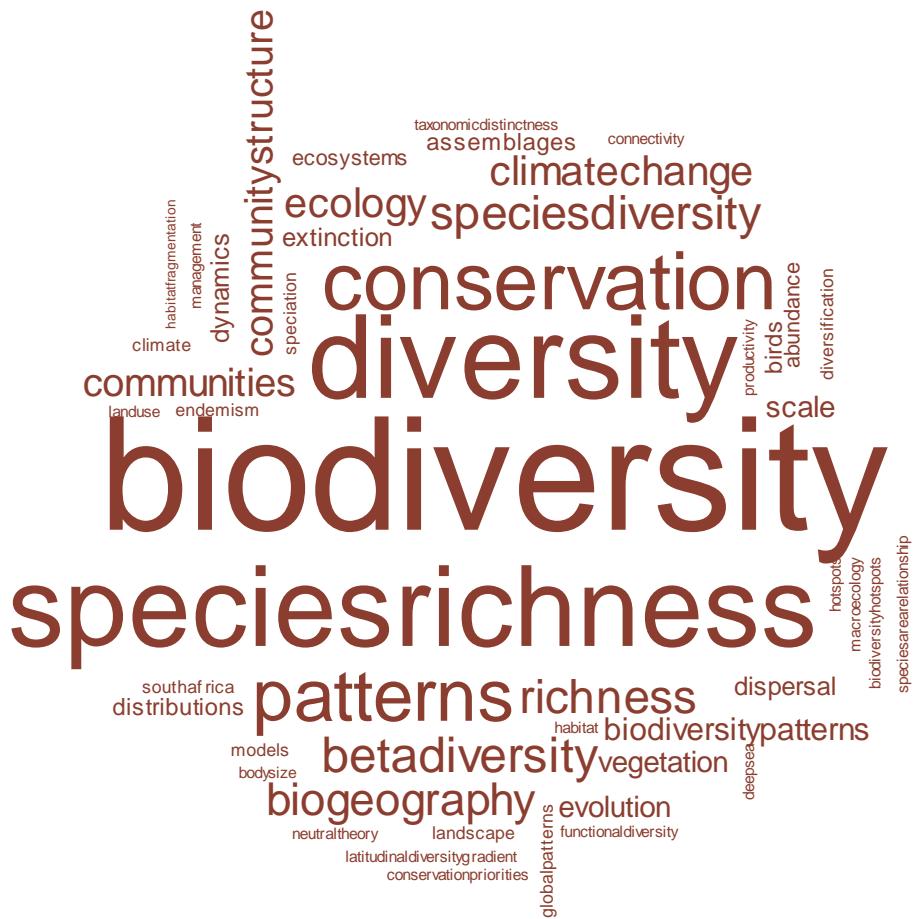
Fig. 7 – The 50 most cited keywords.

There was little temporal fluctuation of keywords and general interests. Words related to biodiversity appeared as the most frequent since 1996 and conservation has been more explored

since 2002. Climate change has been a recurrent theme since 1993, but only appears among the 10 most frequent subjects in few years (2004, 2009, 2012, 2013 and 2015). The PCA analysis suggests that some subjects are frequently co-occurring. Two main groups can be observed: one related to biogeography and vegetation, and other broader group comprising subjects such as ecology, ecosystem, community and species (Fig. 8). Within this second group, we can observe that climate change, dispersal and model are co-occurring keywords that rarely relate to ecosystem, evolution, biodiversity pattern and extinction.

The word "modelling" appeared for the first time in 1993, but the theme became recurrent only in the 2000's, as well as geography-related words. At this time, macroecology becomes a common theme: although the keyword "macroecology" only appears a few times a year since 2003, related themes are frequent (such as spatial patterns, biological, ecological and evolutionary processes, scales and spatial autocorrelation).
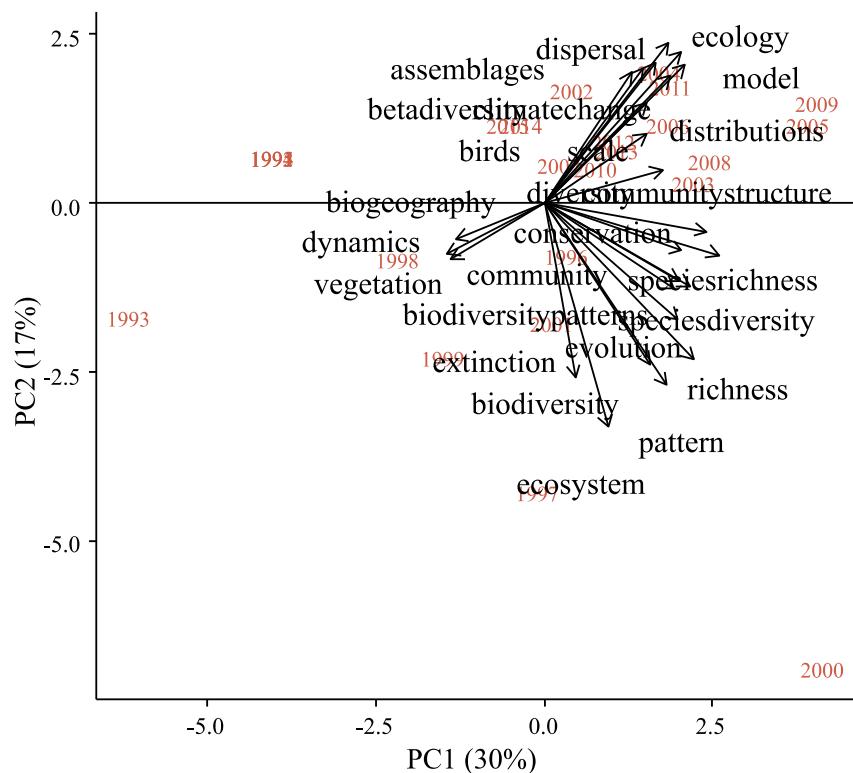
Fig. 8 – Principal Components Analysis of keywords with more than 50 records per year.

Amongst the most productive countries, authors are more interested in biodiversity, richness, gradients and patterns, and communities (Table 1). German authors are distinguished by their interest in models, while French authors are more interested in community ecology. Spanish

authors are the more concerned about conservation: they use this keyword twice as much as authors from the United States of America, while this word does not appear in the "top ten" list of the other three countries.

Table 1 - Frequency (f) of the 10 most frequent keywords used by authors from the five most productive countries.

USA	f	Germany	f	UK	f	Spain	f	France	f
biodivers	34	divers	12	divers	20	divers	58	divers	60
divers	32	model	8	biodivers	16	biodivers	52	biodivers	42
pattern	24	biodivers	6	pattern	16	pattern	49	communiti	36
rich	24	distribut	5	rich	14	rich	43	pattern	33
gradient	17	pattern	5	gradient	10	communiti	25	ecolog	28
speci	14	speci	5	biogeographi	7	conservation	23	rich	27
extinct	12	determin	4	evolution	7	model	22	river	20
latitud	12	echinodermata	4	extinct	7	speci	22	species	19
conservation	11	function	4	latitud	7	species	22	evolut	16
species	11	rich	4	species	7	forest	20	analys	15
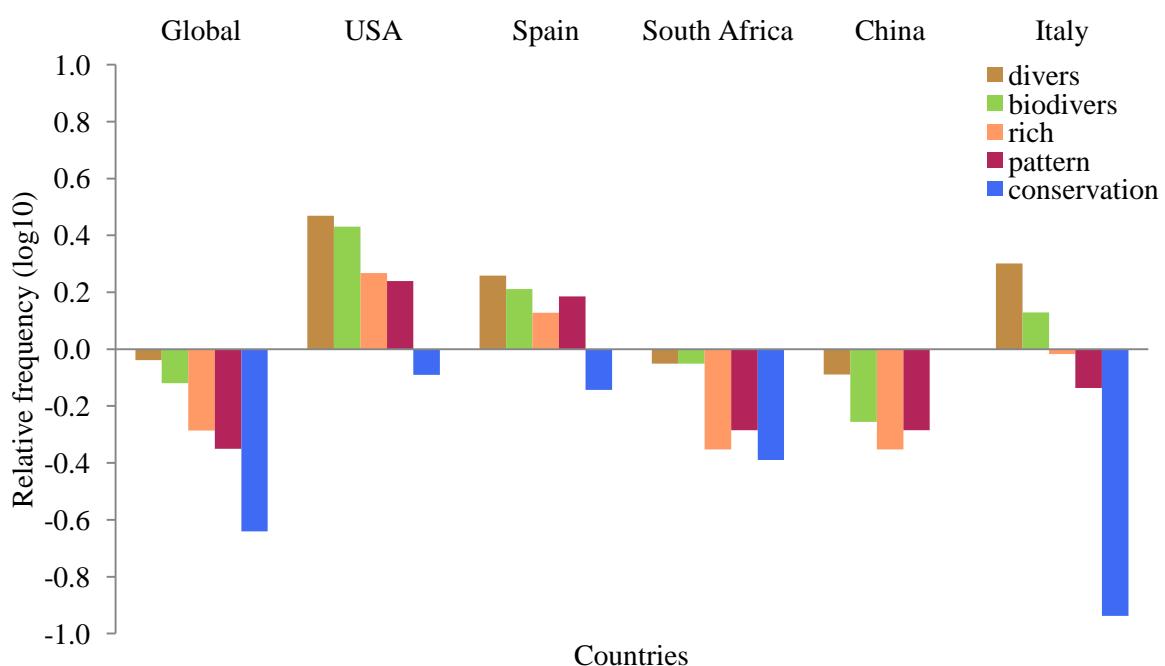
Fig. 9 – Relative frequency of keywords in publications referring to each of the five most studied countries and the globe. The word "conservation" does not occur in studies developed in China.

When experiments were conducted in European countries, the most frequent keywords used were related to biodiversity, richness, patterns, species/speciation and habitats; researches in Africa are associated with biodiversity, conservation and Africa itself. The keyword "patterns" is majorly used in researches executed in Europe, but is also well represented in America and is the third most frequent word in global studies.

2.4 Discussion

The research in biodiversity patterns has been expanding geographically, with most studies focusing on global biodiversity. However, there are great gaps in biodiversity research, with many countries being underexplored. Biodiverse countries tend to be less explored (Wilson et al. 2016), which might have been the case in this study.

Biodiversity patterns can be assessed in all levels (genes, species and ecosystems) (Whittaker et al. 2001), which was reflected in our database: there are keywords for biogeography, community ecology and molecular diversity. We did not classified researches according to types of organisms or ecosystems addressed in the literature, but only 1.38% of keywords' frequencies referred to marine or fish biodiversity, for instance. This reflects the results of Hendriks and Duarte, 2008 (Hendriks and Duarte 2008), who noticed an asymmetry among fields of research when comparing the amount of literature and ecosystem's area. These authors also highlight that the greater part of research on biodiversity is empirical, with no more than 13% of modelling and synthesis studies. Our results support that, with 7.15% of papers in this category. Our results also indicated that there is a great part of the literature testing biodiversity pattern as a global phenomenon. Nevertheless, 82.4% of the studies focused in local or regional biodiversity. This indicates that the global biodiversity patterns may not be so well known.

There is a tendency for global and theoretical/modelling studies to become less frequent (despite the growing technology), as local conservation efforts are necessary. Another reason for this tendency may be the massive cuts in science budgets in the last few years (Chinn 2010) for local conservation research may be cheaper and easy to be funded than pure science (Courchamp et al. 2015). The United States of America leads the rank of gross expenditure on R&D and of R&D professionals (OECD 2015; UNESCO Institute for Statistics). This is reflected in their

leadership on scientific production on biodiversity research (Liu et al. 2011) and is illustrated by our results.

It is important to highlight that the string chosen to retrieve information from the Web of Science database, and the fact that only the principal collection of the WoS was analysed may have resulted in underrepresentation of China and Latin-American countries. Nevertheless, our data still represents the core of biodiversity patterns' theory.

2.5   Conclusion

Biodiversity patterns are being studied locally, which can be good for assessing validity of global patterns at different levels. However, the connection of these results in order to delineate a broader framework must be done carefully. Macroecology is a field of research that might help in these tasks, but it must be better explored so its theoretical background can be solidified.

The study of biodiversity patterns can help in conservation planning, especially in the climate changing scenario. In fact, scientists who study biodiversity patterns are very much interested in conservation, particularly in the last few years, but this interest is better expressed in biodiverse developing countries. Despite the growing technology, study localities are still biased by local financial income. This may be bypassed with investment in citizen science and international collaborations, which should be intensively encouraged.

References

Araújo MB, Guisan A (2006) Five (or so) challenges for species distribution modelling. J Biogeogr 33:1677–1688. doi: 10.1111/j.1365-2699.2006.01584.x

Arrhenius O (1921) Species and area. J Ecol 9:95–99. doi: 10.2307/2255763

Beck J, Ballesteros-Mejia L, Nagel P, Kitching IJ (2013) Online solutions and the 'Wallacean shortfall': What does GBIF contribute to our knowledge of species' ranges? Divers Distrib 19:1043–1050. doi: 10.1111/ddi.12083

Brown JH (1999) Macroecology: progress and prospect. Oikos 87:3–14. doi: 10.2307/3546991

Brown JH, Maurer BA (1989) Macroecology: the division of food and space among species on continents. Science 243:1145–50. doi: 10.1126/science.243.4895.1145

Chase J (2012) Historical and Contemporary Factors Govern Global Biodiversity Patterns. PLoS Biol 10:e1001294. doi: 10.1371/journal.pbio.1001294

Chinn LW (2010) The Global State of Science Funding. ASBMB Today 18–19.

Courchamp F, Dunne JA, Le Maho Y, et al (2015) Fundamental ecology is fundamental. Trends Ecol Evol 30:9–16. doi: 10.1016/j.tree.2014.11.005

Feinerer I, Hornik K (2015) tm: Text Mining Package.

Feinerer I, Hornik K, Meyer D (2008) Text Mining Infrastructure in R. J Stat Softw 25:1–54.

Grueber M, Studt T (2014) 2014 Global R&D funding forecast.

Hawkins BA (2001) Ecology's oldest pattern? Trends Ecol Evol 16:470. doi: 10.1016/S0169-5347(01)02197-8

Hendriks IE, Duarte CM (2008) Allocation of effort and imbalances in biodiversity research. J Exp Mar Bio Ecol 360:15–20. doi: 10.1016/j.jembe.2008.03.004

Holmgren M, Schnitzer SA (2004) Science on the rise in developing countries. PLoS Biol 2:10–13. doi: 10.1371/journal.pbio.0020001

Von Humboldt A, Otté EC, Bohn HG (1850) Views of Nature: Or Contemplations on the Sublime Phenomena of Creation. Cambridge University Press

Keith SA, Webb TJ, Böhning-Gaese K, et al (2012) What is macroecology? Biol Lett 8:904–6. doi: 10.1098/rsbl.2012.0672

Liu X, Zhang L, Hong S (2011) Global biodiversity research during 1900-2009: A bibliometric analysis. Biodivers Conserv 20:807–826. doi: 10.1007/s10531-010-9981-z

Loyola RD, Lemes P, Brum FT, et al (2014) Clade-specific consequences of climate change to amphibians in Atlantic Forest protected areas. Ecography (Cop) 37:65–72. doi: 10.1111/j.1600-0587.2013.00396.x

Margules CR, Pressey RL (2000) Systematic conservation planning. Nature 405:243–53. doi: 10.1038/35012251

OECD (2015) Main Science and Technology Indicators.

Pianka ER (1966) Latitudinal Gradients in Species Diversity : A Review of Concepts. Am Nat 100:33–46.

Pritchard A (1969) Statistical Bibliography or Bibliometrics? J Doc 25:348–349.

Ray GC (1991) Coastal-Zone Patterns Biodiversity. Bioscience 41:490–498.

Rocchini D, Hortal J, Lengyel S, et al (2011) Accounting for uncertainty when mapping species distributions: The need for maps of ignorance. Prog Phys Geogr 35:211–226. doi: 10.1177/0309133311399491

Shannon CE (1948) A Mathematical Theory of Communication.

Stork H, Astrin JJ (2014) Trends in Biodiversity Research — A Bibliometric Assessment. Open J Ecol 04:354–370. doi: 10.4236/oje.2014.47033

The World Bank (2016) World Development Indicators

Tscharntke T, Klein AM, Kruess A, et al (2005) Landscape perspectives on agricultural intensification and biodiversity on ecosystem service management. Ecol Lett 8:857–874. doi: 10.1111/j.1461-0248.2005.00782.x

UNESCO Institute for Statistics (UIS). http://data.uis.unesco.org/Index.aspx.

Whittaker RJ, Willis KJ, Field R (2001) Scale and species richness: Towards a general, hierarchical theory of species diversity. J Biogeogr 28:453–470. doi: 10.1046/j.1365-2699.2001.00563.x

Willig MR, Kaufman DM, Stevens RD (2003) Latitudinal Gradients of Biodiversity: Pattern, Process, Scale, and Synthesis. Annu Rev Ecol Evol Syst 34:273–309. doi: 10.1146/annurev.ecolsys.34.012103.144032

Wilson KA, Auerbach NA, Sam K, et al (2016) Conservation Research Is Not Happening Where It Is Most Needed. PLOS Biol 14:e1002413. doi: 10.1371/journal.pbio.1002413

References formatted following "Biodiversity and Conservation" author guidelines.

APÊNDICE A

Tabela 1 - Dados por países utilizados na seção 2. RDE%GDP refere-se ao investimento em pesquisa e desenvolvimento expresso como porcentagem do produto interno bruto. GERD(PPP) refere-se ao investimento bruto em pesquisa e desenvolvimento em paridade de poder aquisitivo, em dólar americano.

Country	Continent	Studies in this country	Studies by this country	Citations	RDE %GDP	GERD(PPP)
United States	North America	53	209	1215	2.610	322318408.20
Spain	Europe	32	86	541	1.079	13380232.61
South Africa	Africa	27	39	1025	0.787	4031387.67
China	Asia	27	36	170	1.253	114361730.10
Italy	Europe	26	60	797	1.099	18384.58
France	Europe	25	79	608	2.128	38557.94
Australia	Oceania	24	73	287	1.953	12748.75
Germany	Europe	21	100	475	2.493	63606.62
Portugal	Europe	19	28	332	0.981	2384797.28
Brazil	South America	16	29	170	1.057	24125591.69
Canada	North America	16	48	191	1.846	18748.08742
United Kingdom	Europe	12	114	288	1.685	32821952.89
India	Asia	12	6	99	0.751	24553304.13
Switzerland	Europe	12	35	493	2.629	8433600.20
Finland	Europe	12	24	469	3.258	4875.84
Sweden	Europe	11	24	193	3.410	11503441.21
Argentina	South America	10	16	48	0.435	4471994.00
Mexico	North America	10	17	52	0.379	5135.66
Antarctica	Antartica	9	0	62	-	-
Ecuador	South America	9	4	208	0.166	204460.83
Malaysia	Asia	8	4	65	0.728	3561496.36
New Zealand	Oceania	8	19	118	1.132	1204339.00
Panama	North America	8	6	127	0.266	81445.56
Norway	Europe	7	14	71	1.597	3795606.80
Austria	Europe	7	15	470	2.285	6965976.53
Greece	Europe	7	10	117	0.599	1565.06
Russia	Europe	6	10	24	1.106	21388389.28
Peru	South America	6	1	53	0.111	156800.63
Bolivia	South	6	4	46	0.281	82653.25

	America					
Madagascar	Africa	6	4	20	0.170	36595.07
Indonesia	Asia	5	4	91	0.071	1208666.00
Colombia	South America	5	3	35	0.194	769910.25
Algeria	Africa	5	2	26	0.205	611300.20
Belize	North America	4	0	48	-	-
Chile	South America	4	9	7	0.348	-
Equatorial Guinea	Africa	4	0	58	-	-
Japan	Asia	4	13	18	3.192	122043159.30
Slovenia	Europe	4	5	145	1.639	790448.72
Netherlands	Europe	4	29	140	1.810	10105.77
Ireland	Europe	4	3	107	1.283	1824.89
Angola	Africa	3	0	31	-	-
Iran	Asia	3	7	10	0.564	5112838.89
Poland	Europe	3	6	104	0.653	3828869.33
Thailand	Asia	3	0	14	0.238	1421339.85
Romania	Europe	3	4	86	0.464	1052005.44
Morocco	Africa	3	2	20	0.583	832820.33
Costa Rica	North America	3	2	73	0.384	162703.31
Nepal	Asia	3	0	20	0.205	104325.67
Hungary	Europe	3	5	61	0.956	1583.99
Bhutan	Asia	2	0	6	-	-
Cameroon	Africa	2	3	28	-	-
French Guiana	South America	2	0	27	-	-
Guinea	Africa	2	0	30	-	-
Mauritania	Africa	2	0	47	-	-
Myanmar	Asia	2	0	6	-	-
Tanzania	Africa	2	0	18	0.360	-
Venezuela	South America	2	4	25	-	-
Israel	Asia	2	6	14	3.876	7109654.33
Ukraine	Europe	2	2	1	0.951	2666705.82
Vietnam	Asia	2	0	6	0.184	564749
Kenya	Africa	2	3	8	0.571	546710.00
Estonia	Europe	2	4	59	1.155	300112.25
Mongolia	Asia	2	2	4	0.233	37575.00
Cambodia	Asia	2	0	6	0.050	7901.00
Belgium	Europe	2	13	103	1.933	6557.56

Denmark	Europe	2	27	130	2.510	4515.23
Czech Republic	Europe	2	18	63	1.249	3055.61
Benin	Africa	1	1	28	-	-
Côte d'Ivoire	Africa	1	0	28	-	-
Democratic Republic of the Congo	Africa	1	0	28	0.115	-
French Polynesia	Oceania	1	0	9	-	-
Guinea-Bissau	Africa	1	0	28	-	-
Guyana	South America	1	0	24	-	-
Liberia	Africa	1	0	28	-	-
Libya	Africa	1	0	19	-	-
Liechtenstein	Europe	1	0	0	-	-
Papua New Guinea	Oceania	1	0	117	-	-
Sao Tome and Principe	Africa	1	0	6	-	-
Sierra Leone	Africa	1	0	28	-	-
Suriname	South America	1	0	24	-	-
Yemen	Asia	1	0	18	-	-
Tunisia	Africa	1	0	0	0.575	608914.45
Slovakia	Europe	1	5	60	0.641	582933.00
Puerto Rico	North America	1	2	13	0.444	561249.50
Philippines	Asia	1	1	6	0.122	421680.25
Bulgaria	Europe	1	2	66	0.504	405636.44
Lithuania	Europe	1	0	76	0.717	365893.72
Ghana	Africa	1	0	28	0.304	205931.00
Senegal	Africa	1	0	28	0.455	121670.50
Gabon	Africa	1	0	28	0.501	112876.00
Mali	Africa	1	2	19	0.455	98925.50
Botswana	Africa	1	1	1	0.393	89349.50
Burkina Faso	Africa	1	1	8	0.205	26794.40
Namibia	Africa	1	1	4	0.142	25521.00
Togo	Africa	1	0	28	0.237	19568.00
Gambia	Africa	1	0	28	0.057	1491.00
Lesotho	Africa	1	0	55	0.042	1298.40
New Caledonia	Oceania	0	3	0	-	-
Saudi Arabia	Asia	0	3	0	0.051	492500.57
Uruguay	South America	0	4	0	-	140501.38

3   GAPS, GAPS EVERYWHERE: MAPPING BIODIVERSITY KNOWLEDGE IN THE ATLANTIC RAINFOREST.

Abstract

Biodiversity data are fundamental for macroecological studies. Recent efforts on gathering global data have not been sufficient to surpass biases and gaps. This incompleteness has serious consequences on conservation and ecological understanding, therefore it is of major importance to map, quantify and describe these flaws. In this paper we aimed to assess inventory incompleteness for the Atlantic Rainforest, concerning amphibians, birds, mammals and reptiles. We also investigate if some environmental variables are correlated to biodiversity knowledge. Our results suggest that this biome is not well known, with clusters of quality information near big conservation centres. Environmental variables commonly referred to as indicators of species richness were not correlated to inventory completeness, but when only well-sampled units were analysed, mammals' rarefaction slopes could be considered correlated with potential evapotranspiration. Underexplored and impacted regions need investments in sampling efforts so we can know the real biodiversity of this biome and efficiently measure environmental impacts.

Keywords: Inventory completeness. Rarefaction curves. Data bias. Atlantic Rainforest.

3.1   Introduction

Information about life diversity and distribution is a fundamental tool for understanding evolutionary and ecological processes (Graham et al. 2004; Rocchini et al. 2011; Jetz et al. 2012; Ladle and Hortal 2013; Meyer et al. 2015). Since the 19th century, naturalists, taxonomists and, more recently, citizen scientists have been collecting global biodiversity information, resulting in the current knowledge of species' distribution on the planet (Von Humboldt et al. 1850; Hawkins 2001; Willig et al. 2003; Chase 2012).

Museum data served as a primary source of information for research in ecology and evolution for many years and since the 1970's it has been stored in electronic catalogues at slow pace (Graham et al. 2004). Recent web-based initiatives have connected museum catalogues and improved biodiversity data gathering, maybe inspired by the urge (due to extinction) to track variations in species' richness and ranges (Graham et al. 2004; Jetz et al. 2012). Databases such as Global Biodiversity Information Facility (GBIF; http://www.gbif.org/) and Map of Life (https://mol.org/) provide accessible and extensive information on biodiversity, compiling museum, survey and observation data (Graham et al. 2004; Jetz et al. 2012; Beck et al. 2013; Ladle and Hortal 2013).

Despite the recent efforts in gathering global biodiversity data, our knowledge on species diversity and distribution is still biased and full of gaps due to the complex nature of these information (Brown and Lomolino 1998; Whittaker et al. 2005). A myriad of factors can influence the completeness of biodiversity surveys and the quality of global data (such as cryptic species, species' natural history, political borders and topography), leading to underestimation of species richness and distribution. The variation between real and surveyed richness can reach 30% or more, depending on region and taxon (Ficetola et al. 2014). Furthermore, the underestimation of species distribution can have consequences in conservation planning, since range restriction is a classification criterion of species in risk of extinction (IUCN 2012; Ladle and Hortal 2013; Ficetola et al. 2014; Hortal et al. 2015).

The wallacean shortfall (the lack of information about species real distribution (Whittaker et al. 2005) is present in every spatial and temporal scales (Whittaker et al. 2005; Hortal 2008; Hortal et al. 2015). Biases in biodiversity surveys lead to gaps in information, but clustered information also can lead to biased surveys, once researches may prefer assess places knowingly rich or threatened (Boakes et al. 2010; Ahrends et al. 2011; Rocchini et al. 2011; Yang et al.

2014). Moreover, data quality can deteriorate in space (since the certainty of presence of a species decays with distance from a occurrence point) and time (due to taxonomic reviews, climate change, land use, habitat loss, extinction and migration) (Ladle and Hortal 2013). Therefore, the measurement of geographical variation of biodiversity on the planet (represented by distribution maps) has an error associated that must be assessed (Hortal 2008; Rocchini et al. 2011; Ladle and Hortal 2013; Yang et al. 2013).

The acknowledgement of error in biodiversity information is of major importance, since bias can influence and even reverse ecogeographical patterns (Ficetola et al. 2014). Once researchers are aware of the error in their data sets, they can try to correct or diminish it and better analyse the results. It has been recommended to include maps of ignorance in the results or to map data quality and use only well sampled locations on analyses (Hortal 2008; Ladle and Hortal 2013; Ficetola et al. 2014; Yang et al. 2014). This can guide future research and produce more reliable results, since the exact measure of uncertainty clarifies how explicative an inference can be.

There is a growing interest in biodiversity data biases in literature (see Boakes et al. 2010; Yang et al. 2013; Sousa-Baena et al. 2014). Nevertheless, studies mapping South American under-sampled sites are relatively few. This is worrying especially for the Atlantic Forest since it is an important biodiversity and socio-climatic hotspot (Scarano and Ceotto 2015). Human activities and the growth of urban centres have reduced its original area to only 8%, (Galindo-Leal and Câmara 2003; Scarano and Ceotto 2015). Nevertheless, its natural resilience allows the persistence of biodiversity (Scarano and Ceotto 2015) and it hosts 1-8% of the world's total species (Silva and Casteleti 2003; Ribeiro et al. 2009).

Assessing Atlantic Forest's knowledge gaps is important for several reasons. Loss of habitat can lead to extinction before the real biodiversity is described, quantified and mapped. Conservation units can decelerate this process, but their implementation need good biodiversity data. Furthermore, the Atlantic Rainforest is a good model for ecological and evolutionary research because of its large latitudinal and altitudinal range, high endemicity, variation in temperature and precipitation, and historical connexion with other biomes (Silva and Casteleti 2003; Ribeiro et al. 2009; Batalha-Filho et al. 2013). Therefore, biodiversity data biases must be studied in the Atlantic Forest in order to provide good quality inputs for all of these applications and guide new surveys.

Occurrence records from GBIF of the fauna inhabiting the Atlantic Rainforest biome comprise a large temporal period and a variety of datasets. This study aims to use GBIF records to map, describe and quantify digital accessible knowledge relative to Atlantic Rainforest's fauna, focusing on amphibians, birds, mammals and reptiles.

3.2   Methods

The inventory completeness of Atlantic Rainforest fauna was analyzed for amphibians, birds, mammals and reptiles. Occurrence data were downloaded from Global Biodiversity Information Facility (on 20 June 2015) by classes' names, using geometric filtering and excluding fossil records.

Records dated before 1900 and marine animals were excluded. Incomplete taxonomic identifications were either excluded or completed (when the taxon was monospecific) and infraspecific taxa were merged to species level. After that, localities and scientific names were checked for validity, either manually or using "taxize" R package (Chamberlain and Szöcs 2013; Chamberlain et al. 2014), assessing Catalogue of Life (http://www.catalogueoflife.org/), National Center for Biotechnology Information Taxonomy Database (http://www.ncbi.nlm.nih.gov/taxonomy), AmphibiaWeb (http://amphibiaweb.org/), Avibase (http://avibase.bsc-eoc.org/), Handbook of the Birds of the World Alive (http://www.hbw.com/), Mammal Species of the World (3rd edition, http://vertebrates.si.edu/msw/mswcfapp/msw/index.cfm) and The Reptile Database (http://reptile-database.reptarium.cz/). Occurrence points were filtered by the Atlantic Rainforest domain *sensu* Olson et al., 2001 (Olson et al. 2001) (Fig. 01). Species richness and number of occurrences were obtained for grid cells of 60 arc-minutes (100km at Ecuador) (Fig. 2), which were used for calculating inventory completeness.

Two approaches were used to evaluate inventory completeness on Atlantic Forest: the species accumulation curve for the whole region and the analysis of its final 10% slope (Yang et al. 2013), and a rarefaction method for each sampling unit (SU), also assessing the sample slope. The species accumulation curves (SAC hereafter) is a sample-based method for assessing sampling effort and estimate species richness (Colwell and Coddington 1994; Gotelli and Colwell 2001). This approach was performed with the method 'exact' of the function 'specaccum' and the final 10% slopes were extracted with function 'specslope' in the R package VEGAN (Oksanen et

al. 2015). The output of this function was analysed according to Yang et al. (Yang et al. 2013) and slopes > 0.05 were considered as indicators of inventory incompleteness (Fig. 3). Rarefaction curve is an individual-based method that represents the sampling effort needed to reach total estimated richness within an area (Gotelli and Colwell 2001). The 'rarefy' and 'rareslope' functions calculate the rarefaction and slopes of each SU, both operating in the same package abovementioned.

Figure 1 – The Atlantic Rainforest *sensu* Olson et al. 2001 and its main conserved areas (Serra do Mar and Iguazu).

Additionally, we investigated if four environmental variables were correlated with inventory completeness. These variables were chosen based on previous studies indicating their influence on data bias or if they are commonly mentioned as proxies for species richness (Currie 1991; Sánchez-Fernández et al. 2008; Toranza and Arim 2010; Martin et al. 2012; Ficetola et al. 2014; Vasconcelos et al. 2014; Yang et al. 2014). We used annual mean temperature and altitudinal range downloaded from WorldClim (Hijmans et al. 2005; http://www.worldclim.org/;

resolution 10'), potential evapotranspiration (PET) data from the Consortium for Spatial Information of the Consultative Group for International Agricultural Research (Trabucco and Zomer 2009; http://www.cgiar-csi.org/; resolution 30"), and Normalized Difference Vegetation Index (NDVI) from NASA's Earth Observatory Group (Stockli 2015). These last two variables and temperature represent ecosystems' energy income, while altitudinal range represents topographical and, therefore, habitat homogeneity. All variables were also rescaled to 60 arc-minutes resolution grids.

Because spatial autocorrelation can inflate type I errors, Moran's I index were calculated for target variables (using 'spdep' package; Bivand et al. 2013; Bivand and Piras 2015) and corrected by spatial filtering method when needed (Fortin and Dale 2005; Diniz-Filho and Bini 2005). Afterwards, Pearson's correlation tests were performed between each class's slopes, total of records (raw number and slope extracted from the 'rareslope' function) and environmental variables. Statistical analyses were performed using the computing environment R 3.2.3 (R Development Core Team 2015).

3.3 Results

The terrestrial vertebrate biodiversity of the Atlantic Rainforest is not well known, according to our results. All the species accumulation curves had a final slope higher than 0.9 (Table 1), indicating that the biome is still sub-sampled according to GBIF. After data processing and cleaning, the database comprised 170 sampling units and 220496 records, 84.5% of which was from bird occurrences. Mammalian, amphibian and reptile classes represented 8.1%, 5.9% and 1.4% of the records. The same pattern was identified for species richness: from 22024 species, 81.2% were birds, 7.2% were mammals, 7% were amphibians and 4.6% were reptiles. Both total occurrences (Fig. 2A) and total species richness (Fig. 2B) were clustered in southeastern Brazil (Serra do Mar) and northeastern Argentina (Iguazu).

Environmental variables, number of records and rarefaction slopes (both for each class and for total observation) were significantly spatially structured, except mammals' and reptiles' records (Table 2). Moran's I was predominantly low, especially for number of records (although this index was not significant for mammals and reptiles). However, both potential evapotranspiration and temperature are strongly autocorrelated; the distribution of biodiversity knowledge for amphibians can also be considered spatially structured.

Table 1- Inventory completeness for all the Atlantic Rainforest. Slopes close to 1 characterizes a growing curve, which indicates that much sampling effort is still needed to reach the actual richness. Slopes close to 0 indicate that the species accumulation curve reached its asymptote and the probability of finding new species is low (Yang et al. 2013).

Richness	Slopes of the last 10% of the rarefaction curves
Total	0.989
Amphibians	0.978
Birds	0.992
Mammalians	0.983
Reptiles	0.985
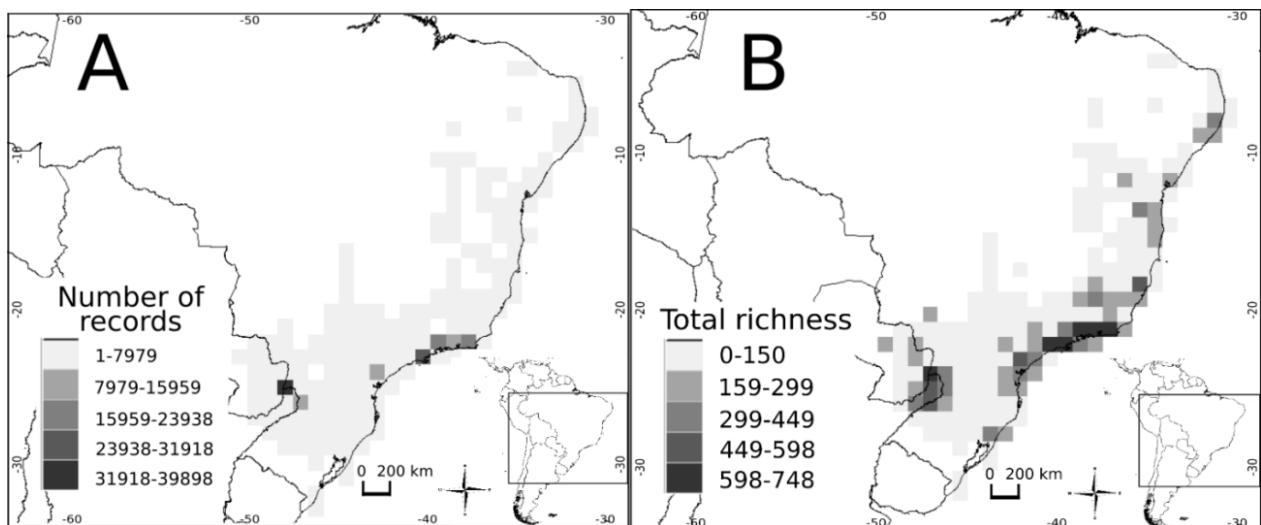
Figure 2 – Distribution of sampling effort (A) and total species richness (B) for the four groups.

Rarefaction slopes for each SU corresponding to total records varied from 0 to 0.99, with a mean of 0.39. Only 25.9% of the Atlantic Rainforest could be considered as well sampled according to the threshold applied by Yang et al. (Yang et al. 2013) (Fig. 3). When each class was assessed separately, the amount of well sampled SU varied from 25.9% for birds to 0.6% for reptiles.
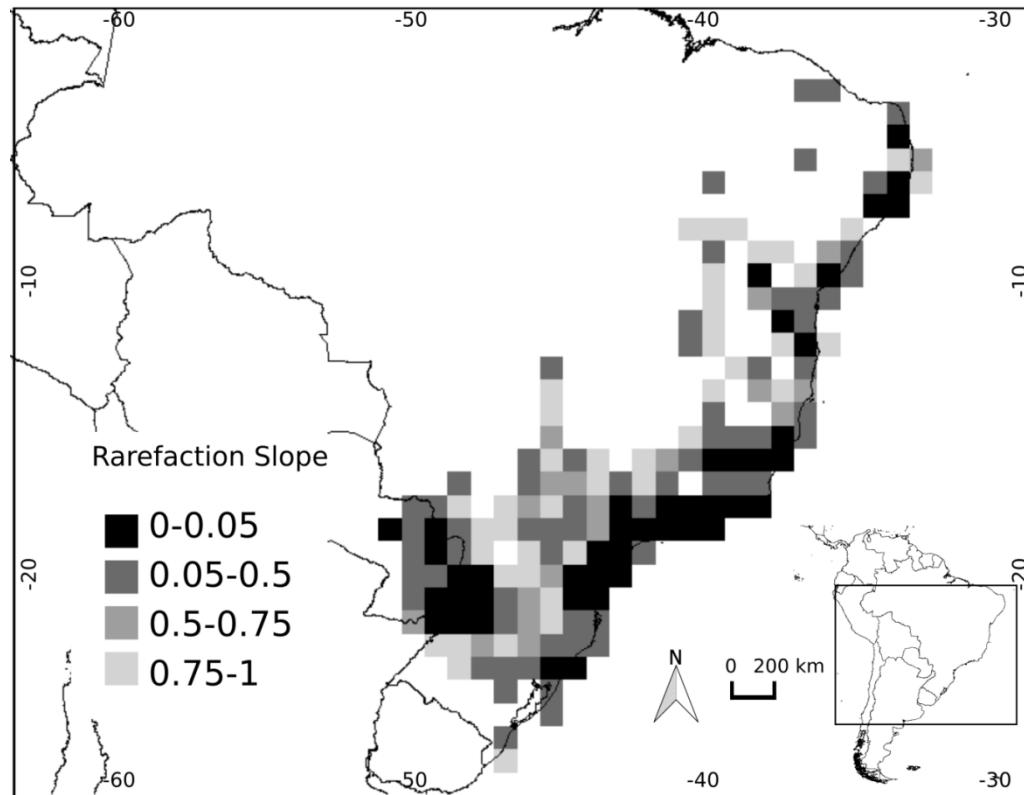
Figure 3 – Map of inventory completeness for the Atlantic Rainforest. Only sampling units with slopes between 0 and 0.5 are considered well sampled.

There was no significant association between corrected variables either using all the knowledge of the whole biome or only the well known regions. However, the mammalian inventory completeness was significantly correlated to potential evapotranspiration (R = -0.3, p=0.048) (Table 3). There was little difference in the environmental characteristics of the SU when only the well sampled cells were analysed, but all variables means were lower in these regions.

Table 2 - Moran's I statistics and respective p value for each variable.

Variable	Moran's I	*p*
NDVI	0.23	<0.01
PET	0.88	<0.01
Temperature	0.88	<0.01
Altitudinal range	0.2	<0.01
Total observations	0.19	<0.01
Amphibian observations	0.34	<0.01
Bird observations	0.2	<0.01
Mammalian observations	0.07	0.12
Reptile observations	0.09	0.09
Total richness slope	0.32	<0.01
Amphibian slope	0.41	<0.01
Bird slope	0.32	<0.01
Mammalian slope	0.36	<0.01
Reptile slope	0.28	<0.01

Table 3 – Pearson's correlation coefficient and p value for each variable combination.

	All cells											
	Total observations		Slopes									
			Total richness		Amphibians		Birds		Mammals		Reptiles	
	R	p	R	p	R	p	R	p	R	p	R	p
PET	0.03	0.70	0.14	0.07	0.05	0.49	0.14	0.07	-0.04	0.60	-0.06	0.40
NDVI	0.08	0.28	0.04	0.60	-0.11	0.15	0.11	0.16	-0.04	0.11	-0.11	0.15
Temp.	-0.07	0.33	-0.10	0.19	-0.05	0.47	-0.09	0.23	-0.13	0.08	0.03	0.74
Altit. range	-0.11	0.15	-0.07	0.36	-0.02	0.82	0	0.99	0.07	0.39	0.05	0.50
	Only well-sampled cells											
	R	p	R	p	R	p	R	p	R	p	R	p
PET	-0.12	0.43	0.11	0.46	0.14	0.36	0.14	0.35	**-0.30**	**0.05**	-0.01	0.97
NDVI	0.12	0.45	-0.09	0.58	-0.18	0.25	-0.17	0.26	-0.15	0.32	-0.27	0.07
Temp.	-0.23	0.12	0.28	0.06	0.12	0.44	0.11	0.49	-0.17	0.27	0.14	0.36
Altit. range	-0.22	0.16	0.22	0.15	0.04	0.79	0.12	0.44	0.16	0.29	0.13	0.40

3.4 Discussion

There is a practical paradox when it comes to biodiversity data sampling. A well studied site may highlight a certain area if it is recognized as biodiverse. Subsequently, protected areas typically attract more research while undersampled sites are ignored by funding projects (Ahrends et al. 2011; Boakes et al. 2016). Some protected areas achieved that status because of

other several reasons to protect a site, such as its natural beauty, its cultural value, its geological conformation or its importance to the ecosystem (Margules and Pressey 2000; Yang et al. 2014). However, even when reserves aim to protect things other than species, they may create an opportune place for biodiversity research.

Sampling bias can have serious consequences in conservation and ecological understanding. For instance, a study with the diverse Chinese flora tried to quantify inventory incompleteness and evaluate the influence of database biases in ecological analyses. They found that 91% of Chinese counties do not have complete inventories and this affected the explicative power of predictive environmental variables (Yang et al. 2013).

A similar study with Brazilian flora aimed to identify sites with insufficient sampling in order to guide future survey efforts. They used a Brazilian database, speciesLink (http://www.splink.org.br/) and metrics of inventory completeness as described by Colwell & Coddington (Colwell and Coddington 1994). Well preserved sites close to important research centres were pointed as well-sampled: three of the highest scores in inventory completeness are located in the Atlantic Rainforest (Sousa-Baena et al. 2014).

This may be the case of our data. Well-known SU are located in areas with a few large or several small protected areas, such as the Iguazu (Argentina-Brazil) and Serra do Mar region (Brazil) (Fig. 1). Additionally, other social variables can enhance biodiversity sampling which also characterize these mentioned regions, such as the number of research centres, accessibility and infrastructure (Ficetola et al. 2014; Yang et al. 2014).

Our analyses did not indicate possible factors that could influence the data bias identified here. The typical environmental variables associated with species richness and attractiveness for collectors were not correlated to inventory completeness nor varied significantly among well-sampled subset and the whole biome. Variables that translate more precisely the social context of the sampling units may have a higher explanatory power on the records number variation.

Local or private data sources could add important information and allow a more precise representation for this biome. There are important independent national databases in Brazil that could add substantial information to the global biodiversity knowledge, such as speciesLink and "Portal da Biodiversidade" (https://portaldabiodiversidade.icmbio.gov.br). The process of transferring data from natural history collections to online databases is naturally slow and is not a

solidified activity yet because it requires trained technicians and infrastructure (Sousa-Baena et al. 2014).

There is a major need for sampling effort in non-protected sites, with intense human activities. The inventory completeness tended to be lower in sites knowingly fragmented. The assessment of biodiversity in those places is important in order to accurately measure human impact on nature. As highlighted by Martin et al., a great amount of ecological knowledge is based on a narrow variety of ecosystems, since researchers tend to study only well preserved sites (Martin et al. 2012; Boakes et al. 2016). These biases surely difficult our perception of patterns and real impacts (Ficetola et al. 2014).

3.5   Conclusion

The Atlantic Rainforest fauna is not well known by the scientific community. Our analyses suggest that the current digital accessible knowledge is insufficient about its biodiversity and there is a bias towards two remarkable areas: Iguazu and Serra do Mar, which are known for their protected areas. We could not indicate an environmental variable that would be related to this bias. Social variables might explain better this trend, once well sampled sites are located close to populated areas and research centres, in addition to the conservation actions forementioned.

Despite the flaws of GBIF data, it still is one of the best tools available for macroecological studies. A reasonable practice would be use more than one data source when feasible. The user must be aware of its incompleteness and profoundly analyse its errors, especially when dealing with species distribution modelling. On the other hand, users are also responsible for furnishing good quality, open access data. The expectation is that this incompleteness will be soon bypassed.

References

Ahrends A, Burgess ND, Gereau RE, et al (2011) Funding begets biodiversity. Divers Distrib 17:191–200. doi: 10.1111/j.1472-4642.2010.00737.x

Batalha-Filho H, Fjeldså J, Fabre PH, Miyaki CY (2013) Connections between the Atlantic and the Amazonian forest avifaunas represent distinct historical events. J Ornithol 154:41–50. doi: 10.1007/s10336-012-0866-7

Beck J, Ballesteros-Mejia L, Nagel P, Kitching IJ (2013) Online solutions and the 'Wallacean shortfall': What does GBIF contribute to our knowledge of species' ranges? Divers Distrib 19:1043–1050. doi: 10.1111/ddi.12083

Bivand R, Hauke J, Kossowski T (2013) Computing the jacobian in gaussian spatial autoregressive models: An illustrated comparison of available methods. Geogr Anal 45:150–179. doi: 10.1111/gean.12008

Bivand R, Piras G (2015) Comparing Implementations of Estimation Methods for Spatial Econometrics. J Stat Softw 63:1–36.

Boakes EH, Fuller RA, Mcgowan PJK, et al (2016) Uncertainty in identifying local extinctions: the distribution of missing data and its effects on biodiversity measures. Biol Lett 0–3.

Boakes EH, McGowan PJ, Fuller RA, et al (2010) Distorted views of biodiversity: spatial and temporal bias in species occurrence data. PLoS Biol 8:e1000385. doi: 10.1371/journal.pbio.1000385

Brown JH, Lomolino M V. (1998) Biogeography, 2nd edn. Sinauer Associates, Inc. Publishers, Massachusetts

Chamberlain S a, Szöcs E (2013) taxize: taxonomic search and retrieval in R. F1000Research 2:191. doi: 10.12688/f1000research.2-191.v2

Chamberlain S, Szocs E, Boettiger C, et al (2014) taxize: Taxonomic information from around the web.

Chase J (2012) Historical and Contemporary Factors Govern Global Biodiversity Patterns. PLoS Biol 10:e1001294. doi: 10.1371/journal.pbio.1001294

Colwell RK, Coddington JA (1994) Estimating Terrestrial Biodiversity through Extrapolation. Philos Trans Biol Sci 345:101–118.

Currie DJ (1991) Energy and Large-Scale Patterns of Animal - and Plant - Species Richness. Am Nat 137:27–49. doi: 10.2307/2462155

Diniz-Filho JAF, Bini LM (2005) Modelling geographical patterns in species richness using eigenvector-based spatial filters. Glob Ecol Biogeogr 14:177–185. doi: 10.1111/j.1466-822X.2005.00147.x

Ficetola GF, Cagnetta M, Padoa-Schioppa E, et al (2014) Sampling bias inverts ecogeographical relationships in island reptiles. Glob Ecol Biogeogr 1303–1313. doi: 10.1111/geb.12201

Fortin M-J, Dale M (2005) Spatial Analysis: A Guide for Ecologists, 1º edn. Cambridge University Press, New York

Galindo-Leal C, Câmara IG (2003) Atlantic Forest hotspots status: an overview. In: Galind-Leal C, Câmara IG (eds) The Atlantic Forest of south america: biodiversity status, threats, and outlook. Conservation International, pp 3–11

Gotelli NJ, Colwell RK (2001) Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. Ecol Lett 4:379–391. doi: 10.1046/j.1461-0248.2001.00230.x

Graham CH, Ferrier S, Huettman F, et al (2004) New developments in museum-based informatics and applications in biodiversity analysis. Trends Ecol Evol 19:497–503. doi: 10.1016/j.tree.2004.07.006

Hawkins BA (2001) Ecology's oldest pattern? Trends Ecol Evol 16:470. doi: 10.1016/S0169-5347(01)02197-8

Hijmans RJ, Cameron SE, Parra JL, et al (2005) Very high resolution interpolated climate surfaces for global land areas. Int J Climatol 25:1965–1978. doi: 10.1002/joc.1276

Hortal J (2008) Uncertainty and the measurement of terrestrial biodiversity gradients. J Biogeogr 35:1335–1336. doi: 10.1111/j.1365-2699.2008.01955.x

Hortal J, de Bello F, Diniz-Filho JAF, et al (2015) Seven Shortfalls that Beset Large-Scale Knowledge of Biodiversity. Annu Rev Ecol Evol Syst 46:523–49. doi: 10.1146/annurev-ecolsys-112414-054400

IUCN (2012) IUCN Red List Categories and Criteria Version 3.1 Second Edition. Switzerland and Cambridge, UK

Jetz W, McPherson JM, Guralnick RP (2012) Integrating biodiversity distribution knowledge: Toward a global map of life. Trends Ecol Evol 27:151–159. doi: 10.1016/j.tree.2011.09.007

Ladle R, Hortal J (2013) Mapping species distributions: living with uncertainty. Front Biogeogr 5:4–6.

Margules CR, Pressey RL (2000) Systematic conservation planning. Nature 405:243–53. doi: 10.1038/35012251

Martin LJ, Blossey B, Ellis E (2012) Mapping where ecologists work: Biases in the global distribution of terrestrial ecological observations. Front Ecol Environ 10:195–201. doi: 10.1890/110154

Meyer C, Kreft H, Guralnick R, Jetz W (2015) Global priorities for an effective information basis of biodiversity distributions. Nat Commun 6:8221. doi: 10.1038/ncomms9221

Oksanen J, Blanchet FG, Kindt R, et al (2015) vegan: Community Ecology Package.

Olson DM, Dinerstein E, Wikramanayake ED, et al (2001) Terrestrial Ecoregions of the World: A New Map of Life on Earth. Bioscience 51:933. doi: 10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2

R Development Core Team (2015) R: A Language and Environment for Statistical Computing. R Found. Stat. Comput. 1:409.

Ribeiro MC, Metzger JP, Martensen AC, et al (2009) The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. Biol Conserv 142:1141–1153. doi: 10.1016/j.biocon.2009.02.021

Rocchini D, Hortal J, Lengyel S, et al (2011) Accounting for uncertainty when mapping species distributions: The need for maps of ignorance. Prog Phys Geogr 35:211–226. doi: 10.1177/0309133311399491

Sánchez-Fernández D, Lobo JM, Abellán P, et al (2008) Bias in freshwater biodiversity sampling: The case of Iberian water beetles. Divers Distrib 14:754–762. doi: 10.1111/j.1472-4642.2008.00474.x

Scarano FR, Ceotto P (2015) Brazilian Atlantic forest: impact, vulnerability, and adaptation to climate change. Biodivers Conserv 24:2319–2331. doi: 10.1007/s10531-015-0972-y

Silva JMC, Casteleti CHM (2003) Status of the biodiversity of the Atlantic Forest of Brazil. In: Galindo-Leal C, Câmara I de G (eds) The Atlantic Forest of South America: biodiversity, status, trends, and outlook. Center for Applied Biodiversity Science and Island Press, pp 43–59

Sousa-Baena MS, Garcia LC, Peterson AT (2014) Completeness of digital accessible knowledge of the plants of Brazil and priorities for survey and inventory. Divers Distrib 20:369–381. doi: 10.1111/ddi.12136

Stockli R (2015) Vegetation Index [NDVI] (1 month - Terra/MODIS).

Toranza C, Arim M (2010) Cross-taxon congruence and environmental conditions. BMC Ecol 10:18. doi: 10.1186/1472-6785-10-18

Trabucco A, Zomer RJ (2009) Global Potential Evapo-Transpiration (Global-PET) and Global Aridity Index (Global-Aridity) Geo-Database. In: CGIAR Consort. Spat. Inf. http://www.csi.cgiar.org.

Vasconcelos TS, Prado VHM, da Silva FR, Haddad CFB (2014) Biogeographic distribution patterns and their correlates in the diverse frog fauna of the Atlantic Forest hotspot. PLoS One 9:e104130. doi: 10.1371/journal.pone.0104130

Von Humboldt A, Otté EC, Bohn HG (1850) Views of Nature: Or Contemplations on the Sublime Phenomena of Creation. Cambridge University Press

Whittaker, Araujo MB, Jepson P, et al (2005) Conservation biogeography: asessment and prospect. Divers Distrib 11:3–23.

Willig MR, Kaufman DM, Stevens RD (2003) Latitudinal Gradients of Biodiversity: Pattern, Process, Scale, and Synthesis. Annu Rev Ecol Evol Syst 34:273–309. doi: 10.1146/annurev.ecolsys.34.012103.144032

Yang W, Ma K, Kreft H (2014) Environmental and socio-economic factors shaping the geography of floristic collections in China. Glob Ecol Biogeogr n/a–n/a. doi: 10.1111/geb.12225

Yang W, Ma K, Kreft H (2013) Geographical sampling bias in a large distributional database and its effects on species richness-environment models. J Biogeogr 40:1415–1426. doi: 10.1111/jbi.12108

References formatted according to the "Biodiversity and Conservation" author guidelines.

4   WHERE IS RICHNESS IN THE HOTSPOT? MAPPING NON-STATIONARITY IN ATLANTIC FOREST BIODIVERSITY CONGRUENCE

Abstract

The processes underlying the global biodiversity structure have been extensively investigated throughout the world and for decades. In the last few years some hypotheses explored different biological resolutions and tried to resume the processes that results in biodiversity patterns in some few or even only one variable. However, the assumption that one factor might explain biodiversity in biomes as distinct as African Savanas and the Atlantic Forest is doubtful. Here we describe the richness patterns for terrestrial vertebrates of the Atlantic Forest and test the influence of four environmental variables in their distribution using Pearson's correlation, linear models and Geographically Weighted Regression (GWR). Richness patterns are similarly arranged in space, but there is no considerable correlation between vertebrates groups, except for amphibians and reptiles. The environmental variables were not correlated to species richness. GWR analyses showed that congruency between groups' species richness are not uniform. Birds and amphibians respond to other groups' biodiversity in the southeastern Brazil, while mammals correlate more with other groups between -19° and -11°. We conclude that the latitudinal biodiversity pattern is not a multi-scale global tendency and that temperature, PET, NDVI and topography are not determinants of species richness in this biome.

4.1   Background

In his groundbreaking book "On the origin of species by means of natural selection", Charles Darwin makes a short review about the geographical distribution of life. He emphasized especially the differences in biodiversity even between similar environments and the importance of geographical barriers, which helped him elaborate his hypotheses of biological diversification (Darwin, 1859). This illustrates how the spatial conformation of biodiversity has been extensively debated in literature, as well as the processes underlying it (Gaston, 2000; Willig et al., 2003; Brown, 2014).

In particular, many hypotheses were elaborated towards an explanation for the high number of species in the tropics (Pianka, 1966; Currie, 1991). For instance, the climate stability hypothesis suggests that adaptations and specializations are more likely to occur in stable conditions (Pianka, 1966); this is part of niche conservatism hypothesis, where clades tend to diversify in similar environments where their ancestors lived (Wiens & Donoghue, 2004). Once the pattern and the possible process are known, an important challenge is to clarify in which scale (i.e., the range and resolution in space and time) this process operates. Apparently, this is the reason of disagreement in the literature about which variables shape the distribution of organisms on Earth (Whittaker et al., 2001; Rahbek, 2005).

In the last few years, researchers have been trying to connect processes that act in different biological resolutions. In this context are the metabolic "theory" of ecology, molecular evolution rates and niche evolution and conservatism (Bromham et al., 1996; Allen et al., 2002; Brown et al., 2004; Jablonski et al., 2006; Dowle et al., 2013). Some of these hypotheses try to resume the complexity of biodiversity patterns in some few or even only one variable. However, the assumption that one factor might explain biodiversity in biomes as distinct as African Savanas and the Atlantic Forest is doubtful. Conversely, a more realistic approach would be to identify the combination of variables that better explain those patterns.

A particular complication in macroecological studies is data bias and knowledge gaps (Brown & Lomolino, 1998; Whittaker et al., 2005). The lack of information about species real distribution (wallacean shortfall) is present in every spatial and temporal scales (Whittaker et al., 2005; Hortal, 2008; Hortal et al., 2015) and can lead to distortions in perceived biogeographical patterns (Yang et al., 2013; Ficetola et al., 2014). Therefore, it is important to assess the errors

associated to biodiversity data (Hortal, 2008; Rocchini et al., 2011; Ladle & Hortal, 2013; Yang et al., 2013).

In order to control natural variation between ecorregions, latitudinal patterns may be better explored in biomes with large latitudinal range, such as the Atlantic Rainforest. The original Atlantic Forest ranged from near Equator to subtropical regions (3ºS to 31°S), with approximately 148 million ha of diverse phyto-physiognomies. This ecoregion was repeatedly connected and disconnected from other biomes, such as Amazon, with consequences in species composition on both (Silva & Casteleti, 2003; Batalha-Filho et al., 2013). The variation in altitude, temperature and precipitation favoured high endemism and diversity in a way that this biome may be home of 1-8% of the world's total species (Silva & Casteleti, 2003; Ribeiro et al., 2009).

The Atlantic Forest is an important biodiversity hotspot. Only 8% of the original forest remains and its territory hosts big urban centres and horticulture plantations (Galindo-Leal & Câmara, 2003; Scarano & Ceotto, 2015). It is also a socio-climatic hotspot (Scarano & Ceotto, 2015) because poverty and loss of habitat interact with climate change leading to even more poverty and environmental accidents. Although extinction is a constant threat, the persistence of biodiversity in such a fragmented ecoregion due to its natural resilience is remarkable (Scarano & Ceotto, 2015). The Atlantic Forest is a good model for testing biodiversity processes and patterns because its large latitudinal range enables the study of the classic latitudinal pattern of biodiversity and its socio-climate hotspot status spotlights the urgency for a better comprehension of this ecoregion.

Here we describe the richness patterns for terrestrial vertebrates of the Atlantic Forest and test the influence of four environmental variables in their distribution. The environmental variables chosen account for availability of energy and habitat, and one of them also represents geographic isolation. We hypothesize that species are arranged similarly across the biome (owing to evolutionary and cross-taxa relationships) and that biodiversity will be related to vegetation and topographical variation.

4.2   Methods

Occurrence data of birds, amphibians, mammals and reptiles were downloaded from Global Biodiversity Information Facility by classes' names, using geometric filtering and

excluding fossil records. Mean temperature and altitudinal range data were downloaded from WorldClim (Hijmans et al., 2005; http://www.worldclim.org/; resolution 10'). Potential evapotranspiration (PET) was obtained from the Consortium for Spatial Information of the Consultative Group for International Agricultural Research (Trabucco & Zomer, 2009; http://www.cgiar-csi.org/; resolution 30"), while Normalized Difference Vegetation Index (NDVI) was downloaded from NASA's Earth Observatory Group (Stockli, 2015). All variables were rescaled to 60 arc-minutes resolution grids (approximately 100km at the Equator).

Records dated before 1900, incomplete taxonomic identification and marine animals were then excluded. After that, scientific names were checked for validity, using "taxize" package in R programming environment (Chamberlain & Szöcs, 2013; Chamberlain et al., 2014; R Development Core Team, 2015) or by manual searches in online catalogues (such as Catalogue of Life, Avibase, Handbook of the Birds of the World Alive, National Center for Biotechnology Information Taxonomy Database, AmphibiaWeb, Mammal Species of the World and The Reptile Database). Coordinates and localities were also verified using Google Maps and visual inspection in the database. Subsequently, occurrence points were filtered by the Atlantic Rainforest domain *sensu* Olson et al., 2001 (Fig. 01; Olson et al., 2001). All data were standardized to 60 arc-minutes raster files and the species richness and number of records were obtained from these grids. To account for data bias, we obtained expected species richness with the "rarefy" function in the R package "vegan" (Oksanen et al., 2015).

All variables were checked for spatial autocorrelation and corrected by spatial filtering method when needed (Diniz-Filho & Bini, 2005; Fortin & Dale, 2005), using "spdep" package (Bivand et al., 2013; Bivand & Piras, 2015). In order to explore species richness patterns, each taxa richness was correlated with each other using Pearson's method. The relationship between richness and environmental variables was investigated by linear regression. Finally, the stationarity of these relations was explored by geographically weighted regressions (GWRs; Fotheringham et al., 2002) with bandwidths selected by golden section search and an adaptive Gaussian Kernel function. These analyses were performed in the software GWR4 (Nakaya, 2014).

Figure 1 - The Atlantic Rainforest and its especially conserved areas: Serra do Mar and Iguazu.

4.3   Results

Richness patterns

Species richness per grid cell varied from one to 748 (Fig. 02). The maximum numbers of species for each class were 561 for Aves, 316 for Mammalia, 102 for Amphibia and 97 for Reptilia, and there were grid cells with zero occurrences for all classes. The most diverse regions for birds, reptiles and amphibians were the southeastern Brazil near the coast and the Misiones province, in Argentina, which is also a hotspot for mammals. The traditional latitudinal pattern was not observed, since the number of species tended to increase towards south, peak between -20° and -25°, and then decrease. This variable is structured in space in a very similar manner for all groups, with significant autocorrelation for samples separated by 1000km or less. Mammals species richness had one outlier (both in the observed and expected species richness) that had to

be removed from subsequent analyses because it biased the results. However, this was not a problem for GWR analyses since there were no prominent residuals indicating local disparity in this variable (Fotheringham et al., 2002).
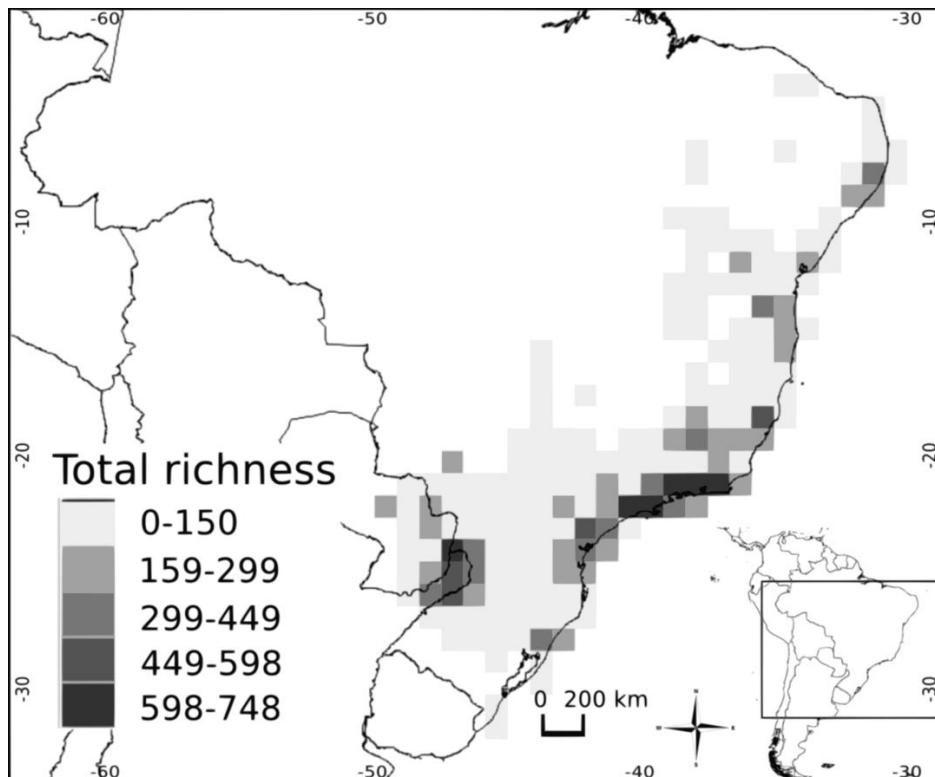
Figure 2 - Total richness in the study area.

All correlations were significant, but suggested that a group's species richness explains only approximately 50% of the diversity variation of another group. However, amphibians could be considered a reasonable good proxy for reptile richness because the coefficient of this correlation were higher than 0.7 (Table 1).

Table 1 - R coefficients for correlations between classes using observed (bottom left) and expected (upper right) richness. All p values were lower than 0.01.

	Aves	Amphibia	Mammalia	Reptilia
Aves	-	0.67	0.61	0.45
Amphibia	0.67	-	0.53	0.71
Mammalia	0.62	0.54	-	0.52
Reptilia	0.45	0.71	0.53	-

The GWR analyses showed similar variation in congruence when birds or amphibians were dependent variables, suggesting that these groups are more representative when the others groups are also diverse in the Brazilian southeastern and Argentine northeastern regions. Mammals were weakly correlated to all other groups throughout the map, but the strongest correlations were located between -11° and -18° for observed richness and between -15° and -23° for expected richness. Reptile observed richness did not display any spatial pattern in its response to other variables, with all correlations varying between 0.56 and 0.57 (Fig. 3). When GWRs were performed with expected richness (Fig. 4), the response of reptiles' species richness to the other groups' diversity changed, becoming similar to that of birds and amphibians.
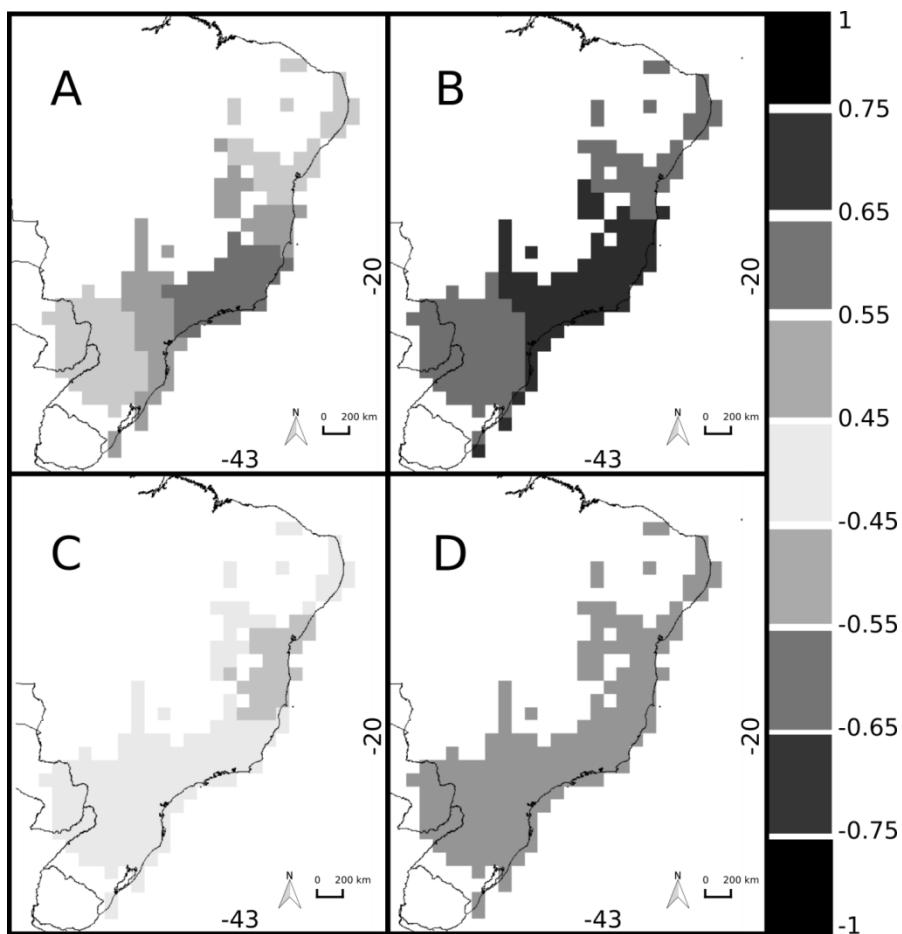

Figure 3 - Maps of the local geographically weighted regressions coefficients of the relationships between observed species richness. Model's independent variables are, respectively, amphibians (A), birds (B), mammals (C) and reptiles (D).
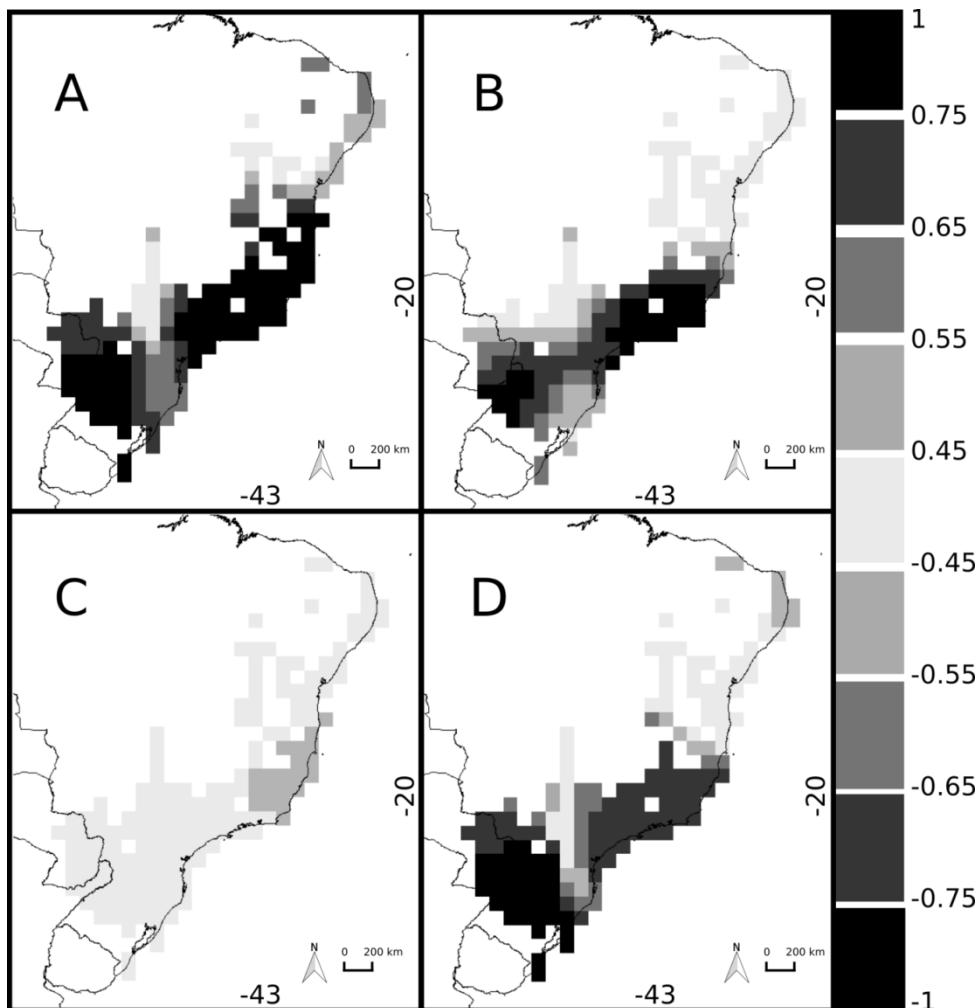
Figure 4 - Maps of the local geographically weighted regressions coefficients of the relationships between expected species richness. Model's independent variables are, respectively, amphibians (A), birds (B), mammals (C) and reptiles (D).

Environmental variables and species richness

Models with total richness and environmental variables returned spatial structured residuals even after spatial filters treatment and therefore are not discussed in this paper (Fortin & Dale, 2005). The variation in temperature, corrected by spatial filtering, was higher between -20º and -30º whilst PET varied the most between -5º and -15º. The topography of the Atlantic Rainforest is highly variable, with greater altitudes near the coast of Brazilian southeast. The NDVI was higher in the Iguazu region and becomes lower towards north. The spatial structure of temperature variation was similar to that of the total sum of species, but there was no correlation between them. There was also no significant effect of any environmental variable on species richness (both observed and expected) in the linear regression models (Table 2).

Table 2 - p values for each regression between environmental variable and classes or total richness.

Observed Richness

	Temperature		PET		NDVI		Topography	
	R²	p	R²	p	R²	p	R²	p
Aves	-0.01	0.74	0	0.19	-0.01	0.78	-0.01	0.59
Amphibia	-0.01	0.98	-0.01	0.82	-0.01	0.43	-0.01	0.80
Mammalia	-0.01	0.58	0	0.26	-0.01	0.59	0	0.13
Reptilia	-0.01	0.95	-0.01	0.83	0	0.29	-0.01	0.61
Total Richness	-0.01	0.82	-0.01	0.33	-0.01	1	-0.01	0.51

Expected Richness

	Temperature		PET		NDVI		Altitude	
	R²	p	R²	p	R²	p	R²	p
Aves	-0.01	0.75	0	0.22	-0.01	0.80	-0.01	0.56
Amphibia	-0.01	0.98	-0.01	0.84	-0.01	0.42	-0.01	0.79
Mammalia	-0.01	0.72	-0.01	0.13	-0.01	0.54	0.01	0.18
Reptilia	-0.01	0.95	-0.01	0.81	0	0.23	-0.01	0.60
Total Richness	-0.01	0.84	-0.01	0.48	-0.01	0.94	-0.01	0.44

4.4 Discussion

Temperature is expected to influence the distribution of ectotherms, with warmer places being also the richest (Allen et al., 2002; Powney et al., 2010; Gerick et al., 2014), but our results do not support that for the Atlantic Forest ecorregion. The richest cell for reptiles corresponded to an 18.2°C temperature, whereas the mean for the biome was 21.39°C. Amphibians had a similar pattern, with the richest cells occupying areas with temperatures between 18°C and 21°C. Other tropical biomes may not have the same pattern: for instance, species richness of Australian lizards is positively correlated with temperature, whereas those of birds, amphibians and mammals in the same region are not (Powney et al., 2010). This suggests that tropical regions should not be

treated as a unity in biodiversity patterns and maybe the latitudinal pattern is not so universal. Instead, ecorregions must be considered separately.

All groups had their richest cells within the mean PET range (1510.2±171.6mm/year), except for reptiles: in this class, the richest cell had a corresponding PET of 1286 mm/year. It is possible that PET is not a limiting factor for reptiles species considered here, since they can become inactive when environmental variables reach stressful levels and can explore low energy areas because of their low metabolic rates (Powney et al., 2010). For this group in tropical rainforests it is possible that the limiting factor is fragmentation.

Low temperatures, irregular topography, actual evapotranspiration and precipitation seasonality are important characteristics of the south-eastern region cluster of anurans species (Vasconcelos et al., 2014), where we have found the richest cells for amphibians. Perhaps potential evapotranspiration is not a good energy measure for this group because in this same region, the richest cells have some of the lowest PET for all Atlantic Forest.

Observed and expected species richness of amphibians and birds, and expected richness of reptiles were more correlated with all the other groups in the Serra do Mar region. This area preserved only small and medium-sized habitats for forest-dependent species in the last glaciations (Carnaval & Moritz, 2008). This may suggest that evolutionary processes for amphibians and birds could have occurred in similar ways through their histories and, perhaps, interactive processes are more important in these groups for shaping their spatial biodiversity structure.

4.5 Conclusions

Our results suggest that variation in species richness in Atlantic Forest and possibly in other tropical rainforests cannot be explained by a single variable, and that temperature should not be treated as a multi-scale determinant of biodiversity distribution. Instead, approaches that explore shared contribution of variables could be more efficient (Moura et al., 2016). Moreover, because the Atlantic Rainforest is highly impacted, future researches should consider social variables and environmental impacts. The change of pattern when only the expected richness was assessed indicates that data bias may be influencing the study of ecological patterns in this biome.

On the other hand, cross-taxon congruence can adequately explain variation in biodiversity distribution in the Atlantic Forest. It would be very interesting to investigate relationships between groups and the environment using spatial and taxonomic finer scales in order to detect which factors are more important locally and regionally. The scale used here may be halfway between these ends, making it possible to detect biodiversity pattern and some influence of environmental variables in some groups, but impossible to infer how and if those variables are determinants in shaping species distributions for all four classes.

References

Allen, A.P., Brown, J.H. & Gillooly, J.F. (2002) Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. Science (New York, N.Y.), 297, 1545–1548.

Batalha-Filho, H., Fjeldså, J., Fabre, P.H. & Miyaki, C.Y. (2013) Connections between the Atlantic and the Amazonian forest avifaunas represent distinct historical events. Journal of Ornithology, 154, 41–50.

Bromham, L., Rambaut, A. & Harvey, P.H. (1996) Determinants of rate variation in mammalian DNA sequence evolution. Journal of Molecular Evolution, 43, 610–621.

Brown, J.H. (2014) Why are there so many species in the tropics? Journal of biogeography, 41, 8–22.

Brown, J.H. & Lomolino, M. V. (1998) Biogeography, 2nd edn. Sinauer Associates, Inc. Publishers, Massachusetts.

Brown, J.J.H., Gillooly, J.J.F., Allen, A.P.A., Savage, V.V.M. & West, G.G.B. (2004) Toward a metabolic theory of ecology. Ecology, 85, 1771–1789.

Carnaval, A.C. & Moritz, C. (2008) Historical climate modelling predicts patterns of current biodiversity in the Brazilian Atlantic forest. Journal of Biogeography, 35, 1187–1201.

Chamberlain, S. a & Szöcs, E. (2013) taxize: taxonomic search and retrieval in R. F1000Research, 2, 191.

Chamberlain, S., Szocs, E., Boettiger, C., Ram, K., Bartomeus, I. & Baumgartner, J. (2014) taxize: Taxonomic information from around the web.

Currie, D.J. (1991) Energy and Large-Scale Patterns of Animal - and Plant - Species Richness. The American Naturalist, 137, 27–49.

Darwin, C.R. (1859) On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life., 1st edn. John Murray, London.

Diniz-Filho, J.A.F. & Bini, L.M. (2005) Modelling geographical patterns in species richness using eigenvector-based spatial filters. Global Ecology and Biogeography, 14, 177–185.

Dowle, E.J., Morgan-Richards, M. & Trewick, S. a (2013) Molecular evolution and the latitudinal biodiversity gradient. Heredity, 110, 501–10.

Ficetola, G.F., Cagnetta, M., Padoa-Schioppa, E., Quas, A., Razzetti, E., Sindaco, R. & Bonardi, A. (2014) Sampling bias inverts ecogeographical relationships in island reptiles. Global Ecology and Biogeography, 1303–1313.

Fortin M-J, Dale M (2005) Spatial Analysis: A Guide for Ecologists, 1o edn. Cambridge University Press, New York

Fotheringham, A.S.S., Brunsdon, C. & Charlton, M. (2002) Geographically Weighted Regression: The Analysis of Spatially Varying Relationships, John Wiley and Sons.

Galindo-Leal, C. & Câmara, I.G. (2003) Atlantic Forest hotspots status: an overview. The Atlantic Forest of south america: biodiversity status, threats, and outlook (ed. by C. Galind-Leal) and I.G. Câmara), pp. 3–11. Conservation International.

Gaston, K.J. (2000) Global patterns in biodiversity. Nature, 405, 220–7.

Gerick, A.A., Munshaw, R.G., Palen, W.J., Combes, S.A. & Regan, S.M.O. (2014) Thermal physiology and species distribution models reveal climate vulnerability of temperate amphibians. 713–723.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology, 25, 1965–1978.

Hortal, J. (2008) Uncertainty and the measurement of terrestrial biodiversity gradients. Journal of Biogeography, 35, 1335–1336.

Hortal, J., de Bello, F., Diniz-Filho, J.A.F., Lewinsohn, T.M., Lobo, J.M. & Ladle, R.J. (2015) Seven Shortfalls that Beset Large-Scale Knowledge of Biodiversity. Annual Review of Ecology, Evolution, and Systematics, 46, 523–49.

Jablonski, D., Roy, K. & Valentine, J.W. (2006) Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. Science (New York, N.Y.), 314, 102–106.

Ladle, R. & Hortal, J. (2013) Mapping species distributions: living with uncertainty. Frontiers of Biogeography, 5, 4–6.

Moura, M.R., Villalobos, F., Costa, G.C. & Garcia, P.C.A. (2016) Disentangling the Role of Climate, Topography and Vegetation in Species Richness Gradients. PLoS One, n–a/n–a.

Nakaya, T. (2014) GWR4.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Wagner, M., Stevens, H.H. & Wagner, H. (2015) vegan: Community Ecology Package.

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'amico, J. a., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P. & Kassem, K.R. (2001) Terrestrial Ecoregions of the World: A New Map of Life on Earth. BioScience, 51, 933.

Pianka, E.R. (1966) Latitudinal Gradients in Species Diversity : A Review of Concepts. The American Naturalist, 100, 33–46.

Powney, G.D., Grenyer, R., Orme, C.D.L., Owens, I.P.F. & Meiri, S. (2010) Hot, dry and different: Australian lizard richness is unlike that of mammals, amphibians and birds. Global Ecology and Biogeography, 19, 386–396.

R Development Core Team (2015) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, 1, 409.

Rahbek, C. (2005) The role of spatial scale and the perception of large-scale species-richness patterns. Ecology Letters, 8, 224–239.

Ribeiro, M.C., Metzger, J.P., Martensen, A.C., Ponzoni, F.J. & Hirota, M.M. (2009) The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. Biological Conservation, 142, 1141–1153.

Rocchini, D., Hortal, J., Lengyel, S., Lobo, J.M., Jimenez-Valverde, A., Ricotta, C., Bacaro, G. & Chiarucci, A. (2011) Accounting for uncertainty when mapping species distributions: The need for maps of ignorance. Progress in Physical Geography, 35, 211–226.

Scarano, F.R. & Ceotto, P. (2015) Brazilian Atlantic forest: impact, vulnerability, and adaptation to climate change. Biodiversity and Conservation, 24, 2319–2331.

Silva, J.M.C. & Casteleti, C.H.M. (2003) Status of the biodiversity of the Atlantic Forest of Brazil. The Atlantic Forest of South America: biodiversity, status, trends, and outlook. (ed. by C. Galindo-Leal) and I. de G. Câmara), pp. 43–59. Center for Applied Biodiversity Science and Island Press.

Stockli, R. (2015) Vegetation Index [NDVI] (1 month - Terra/MODIS).

Trabucco, A. & Zomer, R.J. (2009) Global Potential Evapo-Transpiration (Global-PET) and Global Aridity Index (Global-Aridity) Geo-Database. CGIAR Consortium for Spatial Information.

Vasconcelos, T.S., Prado, V.H.M., da Silva, F.R. & Haddad, C.F.B. (2014) Biogeographic distribution patterns and their correlates in the diverse frog fauna of the Atlantic Forest hotspot. PloS one, 9, e104130.

Whittaker, Araujo, M.B., Jepson, P., Ladle, R.J., Watson, J.E.M. & Willis, K. J., R.J. (2005) Conservation biogeography: asessment and prospect. Diversity and Distributions, 11, 3–23.

Whittaker, R.J., Willis, K.J. & Field, R. (2001) Scale and species richness: Towards a general, hierarchical theory of species diversity. Journal of Biogeography, 28, 453–470.

Wiens, J.J. & Donoghue, M.J. (2004) Historical biogeography, ecology and species richness. Trends in ecology & evolution, 19, 639–44.

Willig, M.R., Kaufman, D.M. & Stevens, R.D. (2003) Latitudinal Gradients of Biodiversity: Pattern, Process, Scale, and Synthesis. Annual Review of Ecology, Evolution, and Systematics, 34, 273–309.

Yang, W., Ma, K. & Kreft, H. (2013) Geographical sampling bias in a large distributional database and its effects on species richness-environment models. Journal of Biogeography, 40, 1415–1426.

References formatted according to the "Global Ecology and Biogeography" authors guidelines.

5   DISCUSSÃO GERAL

Os resultados apresentados nas seções anteriores descrevem parte do cenário da pesquisa em Macroecologia, em especial para a Mata Atlântica. A produção científica sobre padrões de diversidade tem aumentado exponencialmente, mas com pouca variedade nos tipos de ecossistemas estudados e refletindo as variações do investimento econômico em ciência. Algo parecido tem acontecido com os registros de fauna disponíveis para a Mata Atlântica: atualmente, muitos dados estão disponíveis, mas muitos estão geograficamente concentrados.

Em geral, os ecólogos de campo têm dado preferência às regiões temperadas, áreas protegidas e países mais ricos (MARTIN et al., 2012). Os autores que estudam padrões de diversidade têm uma tendência similar: os resultados da primeira seção mostram que a maioria dos experimentos é feita em países com um bom investimento em pesquisa e inovação. Porém, a localização destes estudos é um pouco mais variada. A utilização de dados de biodiversidade que cobrem grande parte do planeta, ou pelo menos vários continentes, é bastante comum. A África do Sul, por exemplo, cujo investimento em ciência é pouco mais que 1% do orçamento dos Estados Unidos para pesquisa, foi o 10º país mais estudado, seguindo países da Europa, Canadá e Estados Unidos.

Os padrões de diversidade podem e devem ser estudados localmente. Porém, os resultados destes estudos devem ser comparáveis, de modo a formarem um cenário global coeso. Esta unificação de resultados pode ser feita em estudos teóricos e com modelagem computacional, mas a frequência destes estudos vem caindo. Isto pode ser um reflexo dos cortes mundiais nos orçamentos destinados à pesquisa e desenvolvimento. Estudos sobre conservação com foco na biodiversidade local são características de pesquisa aplicada, que são mais facilmente financiadas (COURCHAMP et al., 2015).

Não é à toa que a maioria das pesquisas que tratam de padrões de diversidade trata também de conservação. Este assunto tem especial representatividade em estudos conduzidos na África do Sul, um dos países mais biodiversos do mundo. No extremo sul deste país existe um domínio florístico bastante interessante, a região floral do Cabo, apontado como muito vulnerável às mudanças climáticas (MALCOM et al., 2006).

Os padrões de diversidade têm sido estudados em diferentes níveis de organização biológica, investigando assuntos como biogeografia, ecologia de comunidades e diversidade genética. Isto é muito importante porque a compreensão da biodiversidade em diferentes

resoluções poderá fornecer fundamentações mais robustas para futuras hipóteses. Por outro lado, pouca atenção tem sido destinada aos padrões de diversidade em ambientes aquáticos e a maioria dos estudos nesta área é teórica (revisões ou inferências de modelos matemáticos). Em especial em ambientes marinhos, o esforço destinado à pesquisa é desproporcional à área ocupada por este ecossistema no planeta (HENDRIKS; DUARTE, 2008).

A urgência requerida por ambientes muito vulneráveis às mudanças climáticas e impactos provenientes de atividades humanas deve ser atendida. Porém, também é importante preencher as lacunas de conhecimento em ambientes não tão bem explorados. A tecnologia atual permite que os limites geográficos não sejam problema, e que pesquisadores bem financiados estudem padrões de diversidade em países com pouco investimento em ciência.

Este cenário de pesquisas em padrões de biodiversidade têm consequências na quantidade e qualidade de informações disponíveis para estes estudos. Ao indicar locais que podem ter maior riqueza de espécies, estes estudos atraem outros cientistas em busca de novos registros, que por sua vez reforçam a categorização do local como biodiverso (AHRENDS et al., 2011). Isso gera um viés nos dados de diversidade disponíveis.

Com os dados de fauna da Mata Atlântica não é diferente. A maior parte do bioma está subamostrado, mas alguns locais com unidades de conservação estão sobreamostrados. Além da presença destas unidades, algumas outras variáveis sociais podem influenciar ainda mais este viés, como infraestrutura, proximidade de centros de pesquisa e acessibilidade (FICETOLA et al., 2014; YANG et al., 2014). Variáveis ambientais que geralmente estão associadas à riqueza de espécies não estavam relacionadas ao grau de conhecimento das unidades amostrais no bioma, o que reforça que provavelmente as amostragens de fauna estejam sendo bastante influenciadas por particularidades sociais dos locais. Os resultados da segunda seção mostram que é preciso melhorar o esforço amostral na Mata Atlântica, especialmente em ambientes impactados. Como o bioma sofre constantes alterações, é provável que muita diversidade se perca antes mesmo de ser conhecida.

Curiosamente, os padrões de diversidade da Mata Atlântica variam no espaço de forma parecida com o esforço amostral. Na terceira seção vimos que, apesar disso, a riqueza de espécies parece mesmo ser maior nas regiões mais preservadas do sudeste do Brasil e nordeste da Argentina. Mais que isso, vimos que se medirmos a riqueza de espécies de aves, mamíferos ou répteis, podemos esperar que os outros grupos de vertebrados terrestres tenham riqueza parecida.

Assim como nas análises de relação entre esforço amostral e variáveis ambientais, a riqueza de espécies não pôde ser explicada pela quantidade de energia ou relevo da resolução utilizada aqui. É possível que estas variáveis estejam relacionadas com a riqueza, mas talvez precisemos analisar as coisas um pouco mais de perto (ou mais de longe) para enxergar isso. Como anteriormente descobrimos que ainda há muito a se descobrir sobre a fauna da Mata Atlântica, podemos esperar que estes processos macroecológicos sejam melhor esclarecidos no futuro, ou com a combinação de bases de dados que sejam complementares.

REFERÊNCIAS

AHRENDS, A. et al. Funding begets biodiversity. **Diversity and Distributions**, v. 17, n. 2, p. 191–200, 2011.

COURCHAMP, F. et al. Fundamental ecology is fundamental. **Trends in Ecology & Evolution**, v. 30, n. 1, p. 9–16, 2015.

FICETOLA, G. F. et al. Sampling bias inverts ecogeographical relationships in island reptiles. **Global Ecology and Biogeography**, p. 1303–1313, 2014.

HENDRIKS, I. E.; DUARTE, C. M. Allocation of effort and imbalances in biodiversity research. **Journal of Experimental Marine Biology and Ecology**, v. 360, n. 1, p. 15–20, 2008.

MALCOM, J. R. et al. Global Warming and Extinctions of Endemic Species from Biodiversity Hotspots. **Conservation Biology**, v. 20, n. 2, p. 538–548, abr. 2006.

YANG, W.; MA, K.; KREFT, H. Environmental and socio-economic factors shaping the geography of floristic collections in China. **Global Ecology and Biogeography**, p. n/a–n/a, 2014.

6 CONCLUSÃO

Os padrões de diversidade continuam sendo estudados localmente, talvez por ser um assunto bastante relacionado com registros de ocorrências de espécies. Estes dois aspectos da pesquisa em Macroecologia estão enviesados, mas existem tecnologias capazes de minimizar isso. Porém, o investimento em ciência é um fator muito importante para que estas tecnologias se desenvolvam e se disseminem.

As lacunas de conhecimento se tornam mais graves com o aumento das taxas de extinção e são notáveis na Mata Atlântica. A variação no esforço amostral não parece ser causada por fatores ambientais, mas é possível que variáveis como acessibilidade, quantidade de centros de pesquisa e unidades de conservação sejam determinantes neste aspecto. Conhecer as lacunas de conhecimento e de esforço amostral enriqueceu o escopo teórico das análises dos padrões e processos macroecológicos da Mata Atlântica. É importante que a ciência seja analisada periodicamente a fim de identificar seus vieses e novas descobertas sejam incentivadas.

O estudo dos padrões de diversidade depende diretamente da qualidade das informações disponíveis. Na Mata Atlântica, a relativa falta de informação parece ter afetado um pouco o que podemos perceber como a distribuição da fauna de vertebrados. Ao contrário do que acontece na maioria dos ambientes tropicais, as variáveis ambientais não têm qualquer influência na riqueza específica dos grupos, pelo menos na resolução espacial utilizada aqui.

Apesar do gradiente latitudinal de biodiversidade ser notável, as variáveis que podem explicá-lo provavelmente flutuam de formas diferentes em todas as direções. Devido à complexidade das interações biológicas, a elaboração de um modelo ao mesmo tempo geral (válido para todas as escalas, ambientes e organismos) e preciso parece quase impossível. Porém, as ferramentas modernas de modelagem e a quantidade de dados globais disponíveis tem facilitado a busca pelas variáveis corretas (embora uma grande quantidade de dados de ocorrência de espécies ainda não seja de boa qualidade).

A busca dos processos por trás dos padrões geográficos exigirá criatividade, desprendimento da tradição ecológica e exaustivos testes. Porém, uma vez esclarecidos, a aplicação deste conhecimento tem o potencial de ajudar no entendimento da história da vida na Terra, nas previsões mais precisas do destino da diversidade biológica frente às mudanças climáticas e no planejamento de unidades de conservação. O caminho ainda é muito longo, mas cada dia mais curto.

REFERÊNCIAS GERAIS

AHRENDS, A. et al. Funding begets biodiversity. **Diversity and Distributions**, v. 17, n. 2, p. 191–200, 2011.

ALLEN, A. P.; BROWN, J. H.; GILLOOLY, J. F. Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. **Science (New York, N.Y.)**, v. 297, n. 5586, p. 1545–1548, 2002.

ANDERSON, K. J.; JETZ, W. The broad-scale ecology of energy expenditure of endotherms. **Ecology Letters**, v. 8, n. 3, p. 310–318, 25 fev. 2005.

ARAÚJO, M. B.; GUISAN, A.; ARAU, M. B. Five (or so) challenges for species distribution modelling. **Journal of Biogeography**, v. 33, n. 10, p. 1677–1688, 2006.

ARRHENIUS, O. Species and area. **Journal of Ecology**, v. 9, n. 1, p. 95–99, 1921.

BATALHA-FILHO, H. et al. Connections between the Atlantic and the Amazonian forest avifaunas represent distinct historical events. **Journal of Ornithology**, v. 154, n. 1, p. 41–50, 2013.

BECK, J. et al. Online solutions and the "Wallacean shortfall": What does GBIF contribute to our knowledge of species' ranges? **Diversity and Distributions**, v. 19, n. 8, p. 1043–1050, 2013.

BIVAND, R.; HAUKE, J.; KOSSOWSKI, T. Computing the jacobian in gaussian spatial autoregressive models: An illustrated comparison of available methods. **Geographical Analysis**, v. 45, n. 2, p. 150–179, 2013.

BIVAND, R.; PIRAS, G. Comparing Implementations of Estimation Methods for Spatial Econometrics. **Journal of Statistical Software**, v. 63, n. 18, p. 1–36, 2015.

BOAKES, E. H. et al. Distorted views of biodiversity: spatial and temporal bias in species occurrence data. **PLoS Biol**, v. 8, n. 6, p. e1000385, 2010.

BOAKES, E. H. et al. Uncertainty in identifying local extinctions: the distribution of missing data and its effects on biodiversity measures. **Biology Letters**, p. 0–3, 2016.

BROMHAM, L.; RAMBAUT, A.; HARVEY, P. H. Determinants of rate variation in mammalian DNA sequence evolution. **Journal of Molecular Evolution**, v. 43, n. 6, p. 610–621, 1996.

BROWN, J. H.; MAURER, B. A. Macroecology: the division of food and space among species on continents. **Science**, v. 243, n. 4895, p. 1145–50, 3 mar. 1989.

BROWN, J. H. Why are there so many species in the tropics? **Journal of biogeography**, v. 41, n. 1, p. 8–22, jan. 2014.

BROWN, J. H. **Macroecology**. 1. ed. Chicago and London: The University of Chicago Press, 1995. v. 6.

BROWN, J. H. Macroecology: progress and prospect. **Oikos**, v. 87, n. 1, p. 3–14, 1999.

BROWN, J. H. et al. Toward a metabolic theory of ecology. **Ecology**, v. 85, n. 7, p. 1771–1789, 2004.

BROWN, J. H.; LOMOLINO, M. V. **Biogeography**. 2. ed. Massachusetts: Sinauer Associates, Inc. Publishers, 1998.

CARNAVAL, A. C.; MORITZ, C. Historical climate modelling predicts patterns of current biodiversity in the Brazilian Atlantic forest. **Journal of Biogeography**, v. 35, n. 7, p. 1187–1201, jul. 2008.

CHAMBERLAIN, S. A; SZÖCS, E. taxize: taxonomic search and retrieval in R. **F1000Research**, v. 2, p. 191, 2013.

CHAMBERLAIN, S. et al. **taxize: Taxonomic information from around the web**, 2014. Disponível em: <https://github.com/ropensci/taxize>

CHASE, J. Historical and Contemporary Factors Govern Global Biodiversity Patterns. **PLoS Biol**, v. 10, n. 3, p. e1001294, 2012.

CHINN, L. W. The Global State of Science Funding. **ASBMB Today**, p. 18–19, 2010.

COLWELL, R. K. et al. Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. **Journal of Plant Ecology**, v. 5, n. 1, p. 3–21, 2012.

COLWELL, R. K.; CODDINGTON, J. A. Estimating Terrestrial Biodiversity through Extrapolation. **Philosophical Transactions: Biological Sciences**, v. 345, n. 1311, p. 101–118, 1994.

COURCHAMP, F. et al. Fundamental ecology is fundamental. **Trends in Ecology & Evolution**, v. 30, n. 1, p. 9–16, 2015.

CURRIE, D. J. Energy and large-scale patterns of animal - and plant - species richness. **The American Naturalist**, v. 137, n. 1, p. 27–49, 1991.

DARWIN, C. R. **On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life.** 1. ed. London: John Murray, 1859.

DINIZ-FILHO, J. A. F.; BINI, L. M. Modelling geographical patterns in species richness using eigenvector-based spatial filters. **Global Ecology and Biogeography**, v. 14, n. 2, p. 177–185, mar. 2005.

DOWLE, E. J.; MORGAN-RICHARDS, M.; TREWICK, S. A. Molecular evolution and the latitudinal biodiversity gradient. **Heredity**, v. 110, n. 6, p. 501–10, 2013.

FEINERER, I.; HORNIK, K. **tm: Text Mining Package**, 2015. Disponível em: <https://cran.r-project.org/package=tm>

FEINERER, I.; HORNIK, K.; MEYER, D. Text Mining Infrastructure in R. **Journal of Statistical Software**, v. 25, n. 5, p. 1–54, 2008.

FICETOLA, G. F. et al. Sampling bias inverts ecogeographical relationships in island reptiles. **Global Ecology and Biogeography**, p. 1303–1313, 2014.

FISCHER, A. Latitudinal variations in organic diversity. **Evolution**, v. 14, n. 1, p. 64–81, 1960.

FORTIN, M.-J.; DALE, M. R. T. **Spatial Analysis: A guide for ecologists**. 1. ed. New York: Cambridge University Press, 2005.

FOTHERINGHAM, A. S. S.; BRUNSDON, C.; CHARLTON, M. **Geographically Weighted Regression: The Analysis of Spatially Varying Relationships**. [s.l.] John Wiley and Sons, 2002.

GALINDO-LEAL, C.; CÂMARA, I. G. Atlantic Forest hotspots status: an overview. In: GALIND-LEAL, C.; CÂMARA, I. G. (Eds.). . **The Atlantic Forest of south america: biodiversity status, threats, and outlook**. [s.l.] Conservation International, 2003. p. 3–11.

GASTON, K. J. Global patterns in biodiversity. **Nature**, v. 405, n. 6783, p. 220–7, 11 maio 2000.

GERICK, A. A. et al. Thermal physiology and species distribution models reveal climate vulnerability of temperate amphibians. **Journal of Biogeography**, v. 41, n. 4, p. 713–723, 2014.

GOTELLI, N. J.; COLWELL, R. K. Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. **Ecology Letters**, v. 4, n. 4, p. 379–391, 2001.

GRAHAM, C. H. et al. New developments in museum-based informatics and applications in biodiversity analysis. **Trends in Ecology and Evolution**, v. 19, n. 9, p. 497–503, 2004.

GRUEBER, M.; STUDT, T. **2014 Global R&D funding forecast**. [s.l: s.n.]. Disponível em: <https://www.battelle.org/docs/tpp/2014_global_rd_funding_forecast.pdf>. Acesso em: 30 dez. 2015.

HAMILTON, D.; WRIGHT, D. H. Species-Energy Theory: An Extension of Species-Area Theory. **Oikos**, v. 41, n. 3, p. 496–506, 1983.

HAWKINS, B. A. Ecology's oldest pattern? **Trends in Ecology & Evolution**, v. 16, n. 8, p. 470, 8 ago. 2001.

HENDRIKS, I. E.; DUARTE, C. M. Allocation of effort and imbalances in biodiversity research. **Journal of Experimental Marine Biology and Ecology**, v. 360, n. 1, p. 15–20, 2008.

HIJMANS, R. J. et al. Very high resolution interpolated climate surfaces for global land areas. **International Journal of Climatology**, v. 25, n. 15, p. 1965–1978, 2005.

HILLEBRAND, H. On the Generality of the Latitudinal Diversity Gradient. **The American Naturalist**, v. 163, n. 2, p. 192–211, 2004.

HOLMGREN, M.; SCHNITZER, S. A. Science on the rise in developing countries. **PLoS Biology**, v. 2, n. 1, p. 10–13, 2004.

HORTAL, J. Uncertainty and the measurement of terrestrial biodiversity gradients. **Journal of Biogeography**, v. 35, n. 8, p. 1335–1336, 2008.

HORTAL, J. et al. Seven Shortfalls that Beset Large-Scale Knowledge of Biodiversity. **Annual Review of Ecology, Evolution, and Systematics**, v. 46, n. 1, p. 523–49, 2015.

IUCN. **IUCN Red List Categories and Criteria Version 3.1 Second EditionGland**. Switzerland and Cambridge, UK: [s.n.].

JABLONSKI, D.; ROY, K.; VALENTINE, J. W. Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. **Science (New York, N.Y.)**, v. 314, n. 5796, p. 102–106, 2006.

JETZ, W.; FINE, P. V. A. Global gradients in vertebrate diversity predicted by historical area-productivity dynamics and contemporary environment. **PLoS Biology**, v. 10, n. 3, p. 1–11, 2012.

JETZ, W.; MCPHERSON, J. M.; GURALNICK, R. P. Integrating biodiversity distribution knowledge: Toward a global map of life. **Trends in Ecology and Evolution**, v. 27, n. 3, p. 151–159, 2012.

KEITH, S. A. et al. What is macroecology? **Biology letters**, v. 8, n. 6, p. 904–6, 23 dez. 2012.

LADLE, R.; HORTAL, J. Mapping species distributions: living with uncertainty. **Frontiers of Biogeography**, v. 5, n. 1, p. 4–6, 2013.

LEIGHTON, L. R. The latitudinal diversity gradient through deep time: Testing the "Age of the Tropics" hypothesis using carboniferous productidine brachiopods. **Evolutionary Ecology**, v. 19, n. 6, p. 563–581, 2005.

LIU, X.; ZHANG, L.; HONG, S. Global biodiversity research during 1900-2009: A bibliometric analysis. **Biodiversity and Conservation**, v. 20, n. 4, p. 807–826, 2011.

LOSOS, J. B.; RICKLEFS, R. E. **The Theory of Island Biogeography Revisited**. [s.l: s.n.].

LOYOLA, R. D. et al. Clade-specific consequences of climate change to amphibians in Atlantic Forest protected areas. **Ecography**, v. 37, n. 1, p. 65–72, 2014.

MALCOM, J. R. et al. Global Warming and Extinctions of Endemic Species from Biodiversity Hotspots. **Conservation Biology**, v. 20, n. 2, p. 538–548, abr. 2006.

MARGULES, C. R.; PRESSEY, R. L. Systematic conservation planning. **Nature**, v. 405, n. 6783, p. 243–53, 11 maio 2000.

MARTIN, L. J.; BLOSSEY, B.; ELLIS, E. Mapping where ecologists work: Biases in the global distribution of terrestrial ecological observations. **Frontiers in Ecology and the Environment**, v. 10, n. 4, p. 195–201, 2012.

MEYER, C. et al. Global priorities for an effective information basis of biodiversity distributions. **Nature Communications**, v. 6, p. 8221, 2015.

MOURA, M. R. et al. Disentangling the Role of Climate, Topography and Vegetation in Species Richness Gradients. **PLoS One**, p. n–a/n–a, 2016.

NAKAYA, T. **GWR4**, 2014. Disponível em: <https://geodacenter.asu.edu/gwr_software>

OECD. **Main Science and Technology Indicators**. [s.l: s.n.]. Disponível em: <http://www.oecd-ilibrary.org/science-and-technology/main-science-and-technology-indicators_2304277x>. Acesso em: 30 dez. 2015.

OKSANEN, J. et al. **vegan: Community Ecology Package**, 2015. Disponível em: <https://cran.r-project.org/package=vegan>

OLSON, D. M. et al. Terrestrial Ecoregions of the World: A New Map of Life on Earth. **BioScience**, v. 51, n. 11, p. 933, 2001.

PIANKA, E. R. Latitudinal Gradients in Species Diversity : A Review of Concepts. **The American Naturalist**, v. 100, n. 910, p. 33–46, 1966.

POWNEY, G. D. et al. Hot, dry and different: Australian lizard richness is unlike that of mammals, amphibians and birds. **Global Ecology and Biogeography**, v. 19, n. 3, p. 386–396, 2010.

PRITCHARD, A. Statistical Bibliography or Bibliometrics? **Journal of Documentation**, v. 25, n. 4, p. 348–349, 1 jan. 1969.

R DEVELOPMENT CORE TEAM. **R: A Language and Environment for Statistical Computing** (R. D. C. Team, Ed.)**R Foundation for Statistical Computing**: R Foundation for Statistical Computing.R Foundation for Statistical Computing, , 2015. Disponível em: <http://www.r-project.org>

RAHBEK, C. The role of spatial scale and the perception of large-scale species-richness patterns. **Ecology Letters**, v. 8, n. 2, p. 224–239, 17 dez. 2005.

RAY, G. C. Coastal-Zone Patterns Biodiversity. **BioScience**, v. 41, n. 7, p. 490–498, 1991.

RIBEIRO, M. C. et al. The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. **Biological Conservation**, v. 142, n. 6, p. 1141–1153, 2009.

ROCCHINI, D. et al. Accounting for uncertainty when mapping species distributions: The need for maps of ignorance. **Progress in Physical Geography**, v. 35, n. 2, p. 211–226, 2011.

ROGERS, A. **The Science of Why No One Agrees on the Color of This Dress**. Disponível em: <http://www.wired.com/2015/02/science-one-agrees-color-dress/>. Acesso em: 25 jan. 2016.

ROHDE, K. Latitudinal Gradients in Species Diversity: The Search for the Primary Cause. **Oikos**, v. 65, n. 3, p. 514–527, 1992.

SÁNCHEZ-FERNÁNDEZ, D. et al. Bias in freshwater biodiversity sampling: The case of Iberian water beetles. **Diversity and Distributions**, v. 14, n. 5, p. 754–762, 2008.

SCARANO, F. R.; CEOTTO, P. Brazilian Atlantic forest: impact, vulnerability, and adaptation to climate change. **Biodiversity and Conservation**, v. 24, n. 9, p. 2319–2331, 2015.

SHANNON, C. E. A Mathematical Theory of Communication. 1948.

SILVA, J. M. C.; CASTELETI, C. H. M. Status of the biodiversity of the Atlantic Forest of Brazil. In: GALINDO-LEAL, C.; CÂMARA, I. DE G. (Eds.). . **The Atlantic Forest of South America: biodiversity, status, trends, and outlook.** [s.l.] Center for Applied Biodiversity Science and Island Press, 2003. p. 43–59.

SOUSA-BAENA, M. S.; GARCIA, L. C.; PETERSON, A. T. Completeness of digital accessible knowledge of the plants of Brazil and priorities for survey and inventory. **Diversity and Distributions**, v. 20, n. June 2015, p. 369–381, 2014.

STOCKLI, R. **Vegetation Index [NDVI] (1 month - Terra/MODIS).** NASA's Earth Observatory Group, using data provided by the MODIS Land Science Team., 2015.

STORK, H.; ASTRIN, J. J. Trends in Biodiversity Research — A Bibliometric Assessment. **Open Journal of Ecology**, v. 04, n. 07, p. 354–370, 2014.

THE WORLD BANK. **World Development Indicators**. Disponível em: <http://data.worldbank.org/topic/science-and-technology>.

TORANZA, C.; ARIM, M. Cross-taxon congruence and environmental conditions. **BMC ecology**, v. 10, p. 18, jan. 2010.

TRABUCCO, A.; ZOMER, R. J. **Global Potential Evapo-Transpiration (Global-PET) and Global Aridity Index (Global-Aridity) Geo-Database**. Disponível em: <http://www.csi.cgiar.org>.

TSCHARNTKE, T. et al. Landscape perspectives on agricultural intensification and biodiversity on ecosystem service management. **Ecology Letters**, v. 8, n. 8, p. 857–874, 2005.

VASCONCELOS, T. S. et al. Biogeographic distribution patterns and their correlates in the diverse frog fauna of the Atlantic Forest hotspot. **PloS one**, v. 9, n. 8, p. e104130, 2014.

VON HUMBOLDT, A.; OTTÉ, E. C.; BOHN, H. G. **Views of Nature: Or Contemplations on the Sublime Phenomena of Creation**. [s.l.] Cambridge University Press, 1850.

WALLACE, A. R. **Tropical nature, and other essays**. London & New York: Macmillan & Co., 1878.

WHITTAKER, R. J.; WILLIS, K. J.; FIELD, R. Scale and species richness: Towards a general, hierarchical theory of species diversity. **Journal of Biogeography**, v. 28, n. 4, p. 453–470, 2001.

WHITTAKER et al. Conservation biogeography: asessment and prospect. **Diversity and Distributions**, v. 11, p. 3–23, 2005.

WIENS, J. J.; DONOGHUE, M. J. Historical biogeography, ecology and species richness. **Trends in ecology & evolution**, v. 19, n. 12, p. 639–44, 2004.

WILLIG, M. R.; KAUFMAN, D. M.; STEVENS, R. D. Latitudinal Gradients of Biodiversity: Pattern, Process, Scale, and Synthesis. **Annual Review of Ecology, Evolution, and Systematics**, v. 34, n. 1, p. 273–309, 2003.

WILSON, K. A. et al. Conservation Research Is Not Happening Where It Is Most Needed. **PLOS Biology**, v. 14, n. 3, p. e1002413, 2016.

YANG, W.; MA, K.; KREFT, H. Geographical sampling bias in a large distributional database and its effects on species richness-environment models. **Journal of Biogeography**, v. 40, n. 8, p. 1415–1426, 2013.

YANG, W.; MA, K.; KREFT, H. Environmental and socio-economic factors shaping the geography of floristic collections in China. **Global Ecology and Biogeography**, p. n/a–n/a, 2014.

UNESCO Institute for Statistics (UIS). Disponível em: <http://data.uis.unesco.org/Index.aspx>. Acesso em: 1 jan. 2016.