



UNIVERSIDADE FEDERAL DE GOIÁS
DEPARTAMENTO DE ECOLOGIA
PROGRAMA DE PÓS GRADUAÇÃO EM ECOLOGIA E EVOLUÇÃO



Marco Túlio Pacheco Coelho

**PROCESSOS ECOLÓGICOS E EVOLUTIVOS NO SURGIMENTO E
MANUTENÇÃO DA DIVERSIDADE BIOCULTURAL**

Orientador: Dr. Thiago Fernando L.V.B. Rangel

**Goiânia
Fevereiro 2020**

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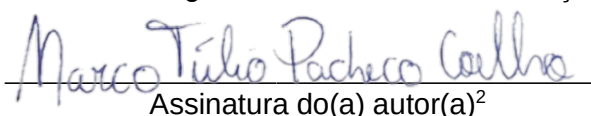
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Orientador: Dr. Thiago Fernando L.V.B. Rangel

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

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Fevereiro 2020**

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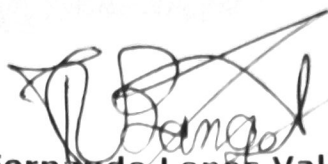


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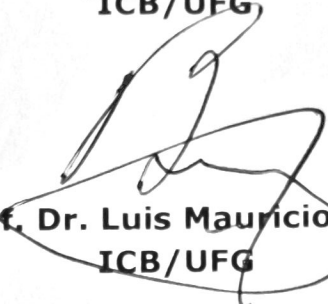
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Aos vinte dias do mês de fevereiro de 2020 (20/02/2020), às treze horas e trinta minutos (13h30min), no Auditório do ICB V, UFG, reuniram-se os componentes da banca examinadora: **Prof. Dr. Thiago Fernando Lopes Valle de Britto Rangel, ICB/UFG; Prof. Dr. Luis Mauricio Bini, ICB/UFG; Prof. Dr. Matheus de Souza Lima Ribeiro, Universidade Federal de Jataí; Dr. Lucas Lacerda Caldas Zanini Jardim, ICB/UFG; Prof. Dr. Robert Knight Colwell, University of Connecticut;** para em sessão pública presidida pelo (a) primeiro(a) examinador(a) citado(a), procederem à avaliação da defesa de tese intitulada: **"Processos Ecológicos e Evolutivos no Surgimento e Manutenção da Diversidade Biocultural"**, em nível de doutorado, área de concentração em Ecologia e Evolução, de autoria de **Marco Túlio Pacheco Coelho**, discente do Programa de Pós-Graduação em Ecologia e Evolução da Universidade Federal de Goiás. A sessão foi aberta pelo(a) presidente(a), que fez a apresentação formal dos membros da banca. A palavra, a seguir, foi concedida a(o) autor(a) da tese que, em cerca de 45 minutos, procedeu à apresentação de seu trabalho. Terminada a apresentação, cada membro da banca arguiu a(o) examinada(o), tendo-se adotado o sistema de diálogo sequencial. Terminada a fase de arguição, procedeu-se à avaliação da tese. Tendo-se em vista o que consta na Resolução nº 1127 de dezembro de 2012 do Conselho de Ensino, Pesquisa, Extensão e Cultura (CEPEC), que regulamenta o Programa de Pós-Graduação em Ecologia e Evolução, a tese foi aprovado, considerando-se integralmente cumprido este requisito para fins de obtenção do título de Doutor(a) em Ecologia e Evolução pela Universidade Federal de Goiás. A conclusão do curso dar-se-á quando da entrega da versão definitiva da tese na secretaria do programa, com as devidas correções sugeridas pela banca examinadora, no prazo de trinta dias a contar da data da defesa. Cumpridas as formalidades de pauta, às 17 h e 00 min.,

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Prof. Dr. Luis Mauricio Bini
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Prof. Dr. Matheus de Souza Lima Ribeiro
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Prof. Dr. Robert Knight Colwell
University of Connecticut

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Ser brilhante, então, não é suficiente por si só para aqueles que sonham com o sucesso na pesquisa científica. A fluência matemática não é o suficiente. Para chegar à fronteira e permanecer nela, é absolutamente essencial uma forte ética de trabalho. É preciso haver uma capacidade de passar longas horas estudando e pesquisando com prazer, mesmo que parte do esforço inevitavelmente leve a becos sem saída. Esse é o preço da admissão no primeiro nível da pesquisa científica.

Edward O. Wilson, Cartas a um jovem cientista

Deixe tudo acontecer com você. Beleza e terror. Apenas continue. Nenhum sentimento é final.

Rainer Maria Rilke

Agradecimentos

Assumir a responsabilidade de fazer um doutorado representa o início de uma jornada longa, cheia de desafios e repleta de altos e baixos emocionais. Não poderia ser diferente, afinal toda jornada desafiadora chega a um fim, com aquele que a experienciou muito mais maduro e preparado para desafios futuros. Para mim, a jornada não poderia ser mais divertida e empolgante, já que eu estava fazendo algo que as vezes me tirava o sono de tanta empolgação.

Ao longo do meu doutorado tentei sair o máximo que consegui de minha zona de conforto. Primeiramente, não dei uma continuação direta do que havia feito no mestrado. No mestrado, estudei padrões estruturais de redes complexas de interação. A ideia consistia em investigar se modelos ecológicos neutros poderiam reproduzir padrões estruturais de redes de interação. Já no doutorado, apesar de existir uma possibilidade de apenas continuar com interações e modelos neutros, resolvi utilizar minha experiência com modelos neutros e aplicá-los em outros contextos dos quais eu não tinha nenhum domínio da literatura, como gradientes de diversidade e padrões de conservação de nicho. Escrevi três capítulos nesse contexto e poderia dar uma continuidade para vários outros com pequenas modificações, trocas de grupos taxonômicos ou localidades. No entanto, percebi, ao longo das tentativas de publicação desses capítulos e de artigos do meu mestrado, que revisores e editores utilizavam arbitrariamente o critério filosófico de parcimônia para julgar os modelos que eu estava usando. Ou os modelos eram simples demais, e por isso inválidos, ou eram complexos demais, e por isso, também inválidos. Resolvi estudar as justificativas epistêmicas para utilizar o critério de parcimônia em modelos ecológicos e me desafiei a escrever um capítulo sobre isso. De fato, foi uma escolha certa. Considero que esse capítulo/artigo foi um dos ápices do meu aprendizado. Pude entender vários conceitos de inferência estatística que me eram absolutamente rasos. Nesse caso, a opção de sair da zona de conforto não poderia ter sido mais produtiva.

Da mesma maneira, vi oportunidades de sair da zona de conforto mais uma vez. Comecei a colaborar com pesquisadores que estavam interessados em padrões de diversidade humana. Percebi ali uma oportunidade que poderia ser explorada por ecólogos e biólogos evolucionistas no mesmo contexto de macroecologia e macroevolução que a minha tese se encaixava. Acabei escrevendo mais dois artigos sobre isso, um deles apontando para ecólogos uma área interdisciplinar que existe e ainda é pouco explorada, e em outro aplicando métodos utilizados para estudar

diversidade de espécies no estudo de diversidade de línguas. Essa decisão não apenas me desafiou a mergulhar em outra literatura, mas também me deu a oportunidade de trabalhar com pesquisadores do mundo todo.

Essa longa jornada, descrita aqui em poucas palavras, não teria acontecido se não fosse pelas inúmeras pessoas que me ajudaram de alguma maneira ao longo do caminho. Não gostaria de correr o risco de esquecer algum nome e por isso vou me abster de fazer uma longa lista de nomes. À minha família, à minha namorada Josiane Pires, amigos (em especial Milena, Elisa, Alice, André e Bruno), colegas, professores, coautores, editores e revisores anônimos, vocês foram essenciais para que eu chegasse ao fim da jornada. Não seria possível terminar o doutorado sem o papel crucial da arte em minha vida. Inúmeros músicos, cineastas e escritores tornaram essa jornada divertida, empolgante e inspiradora.

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Por fim, não se faz ciência sem estrutura e sem dinheiro. Agradeço à CAPES pela minha bolsa de doutorado e por investir grande parte do seu orçamento nos dando acesso aos periódicos científicos. Agradeço à Universidade Federal de Goiás pela estrutura física e por todas as pessoas que a mantém em pleno funcionamento. Nem a CAPES e nem a Universidade pública seriam mantidas se não fosse pela população brasileira por meio de seu trabalho e contribuição.

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Resumo

Um desafio recorrente em ecologia e evolução é entender os efeitos diretos e indiretos de processos ecológicos e evolutivos na estruturação espacial da biodiversidade. Para isso, ecólogos e biólogos evolucionistas utilizam dois tipos principais de modelos: modelos que descrevem a natureza (*i.e.* modelos correlativos) e modelos que explicam a natureza (*i.e.* modelos mecanísticos). Três lacunas principais envolvendo a aplicação de modelos correlativos e mecanísticos para investigar padrões espaciais de diversidade são exploradas em minha tese: (i) critérios heurísticos (*i.e.*, método carente de justificativa racional ou embasamento teórico, mas aceito como suficiente bom para um propósito) herdados desde o início da ciência são utilizados para julgar a credibilidade de modelos correlativos e mecanísticos que visam entender padrões complexos da biodiversidade, porém discussões críticas sobre a validade desses critérios são raros em ecologia e evolução; (ii) Poucos modelos mecanísticos incorporam a interação de processos ecológicos e evolutivos a nível de indivíduos em grandes escalas espaciais e temporais para melhor entender padrões espaciais de diversidade de espécies; (iii) poucos estudos exploraram o efeito de fatores ecológicos e evolutivos utilizando os avanços metodológicos no uso de modelos correlativos e mecanísticos para melhor entender padrões de diversidade humana. Todos os três pontos apresentados acima são explorados nesta tese que está dividida em três partes e seis capítulos. No primeiro capítulo, discuti as bases filosóficas e estatísticas utilizadas para justificar o uso de simplicidade no julgamento da credibilidade de teorias, hipóteses, modelos correlativos e mecanísticos em ecologia e evolução e demonstrei que invocar o princípio de parcimônia em ecologia e evolução é particularmente importante em modelos que são vistos como ferramentas operacionais para fazer previsões. No segundo e terceiro capítulo desenvolvi um modelo de simulação mecanístico que assume ausência de nicho ecológico e incorpora o efeito da energia disponível no ambiente nos processos básicos que estruturam a biodiversidade, tais como especiação, extinção e dispersão. Esse modelo foi capaz de reproduzir o padrão de riqueza de mamíferos terrestres na Austrália (capítulo 2) e padrões latitudinais de riqueza de aves em diferentes continentes (capítulo 3). Utilizando também um modelo mecanístico, no quarto capítulo testei o efeito de processos biogeográficos na diversificação de nicho climático através de um modelo que desconsidera o efeito de qualquer processo adaptativo na retenção de nicho climático. Esse estudo demonstrou o forte papel de processos biogeográficos na evolução de nicho climático, mesmo quando nenhuma força adaptativa está atuando na diversificação de nicho. Por fim, nos dois últimos capítulos explorei aspectos da diversidade humana chamando a atenção de ecólogos para um aspecto da biodiversidade que é ainda pouco explorado na ecologia. No quinto capítulo revisei aspectos da diversidade humana que se assemelham com padrões descritos em biogeografia e macroecologia, demonstrando que ecólogos e biólogos evolucionistas podem contribuir com debates que surgiram em diversas áreas da ciência através da aplicação de métodos utilizados para estudar padrões de diversidade de espécies. Por fim, no sexto capítulo utilizei uma combinação de análise de caminhos, modelo mecanístico e regressão geográfica ponderada (GWR) para investigar o padrão amplamente descrito, mas pouco compreendido, de diversidade de línguas na América do Norte. Esse estudo demonstrou que os preditores ecológicos e evolutivos de diversidade de línguas não são perfeitamente universais nem inteiramente diretos e que o poder preditivo do modelo varia no espaço com regiões onde cerca de 86% da variação é explicada e regiões onde cerca de 40% da variação é explicada.

Palavras-Chave: Parcimônia; Teoria Neutra; Gradientes de Diversidade; Conservação de Nicho; Macroecologia Humana.

Abstract

A current challenge in ecology and evolution is to understand the direct and indirect effects of ecological and evolutionary processes on the spatial structure of biodiversity. To overcome this challenge, ecologists and evolutionary biologists use two types of models: models that describe nature (i.e. correlative models) and models that explain nature (i.e. mechanistic models). Three knowledge gaps, involving the use of correlative and mechanistic models to investigate spatial patterns of biodiversity, are explored in my thesis: (i) heuristic criteria (i.e., a method lacking rational justification or theoretical basis, but accepted as good enough for a given purpose), inherited from the beginning of science, are used to judge the credibility of correlative and mechanistic models that are widely used to understand complex patterns of biodiversity. However, critical discussions about the validity of these criteria are rare in ecology and evolution; (ii) few mechanistic models assume the interaction of ecological and evolutionary processes at individuals' level in broad spatial and temporal scales, when studying spatial patterns of species diversity; (iii) few studies explore the effect of ecological and evolutionary factors, using the methodological advances on the use of correlative and mechanistic models, to better understand human diversity patterns. All the three points presented earlier are explored in my thesis that is divided into three parts and six chapters. In the first chapter, I discussed the philosophical and statistical bases used to justify the use of simplicity when judging the credibility of theories, hypothesis and models in ecology and evolutionary biology. I showed that invoking the parsimony principle in ecology and evolution is particularly important in models that are used as operational tools to make predictions. In the second and third chapter, I built a mechanistic simulation model that assumes the absence of ecological niche but assumes the effect of energy on processes structuring biodiversity, such as speciation, extinction and dispersion. This model reproduced the richness pattern of terrestrial mammals in Australia (chapter 2) and latitudinal patterns of bird richness in different continents (chapter 3). By also using a mechanistic model, in the fourth chapter I tested the effect of biogeographical processes on climatic niche diversification through a model that purposely disregards the effect of any adaptive process on climatic niche evolution. This study showed the strong role of biogeographical processes on climatic niche evolution, even when no adaptive force is acting on climatic niche diversification. Finally, in the last two chapters, I explored aspects of human diversity drawing the attention of ecologists and evolutionary biologists to aspects of biodiversity that are seldom explored in ecology. In the fifth chapter, I revised aspects of human diversity that are similar to several patterns described in biogeography and macroecology, showing that ecologists and evolutionary biologists can contribute to long-standing debates in many fields of science, using their theoretical and methodological tools to study patterns of human diversity. Lastly, in the sixth chapter I used a combination of path analysis, mechanistic model and geographically weighted regression (GWR) to investigate the broadly described pattern of language diversity in North America. This study showed that the ecological predictors of language diversity are not perfectly universal nor entirely direct and that the predictive power of the model vary through space with regions where almost 86% of the variation in language diversity is explained, to regions where around 40% of variation is explained.

Key-Words: Parsimony; Neutral Theory; Diversity Gradients; Niche Conservatism; Human Macroecology.

INTRODUÇÃO GERAL

Desde o século XIX, a partir de grandes expedições de naturalistas ao redor do mundo, padrões não uniformes de riqueza de espécies em grandes escalas espaciais têm sido descritos ¹. Nas últimas décadas, padrões não uniformes de diversidade também foram observados para outros aspectos da biodiversidade que vão além da diversidade taxonômica, filogenética e funcional de plantas e animais. Por exemplo, sabemos que outros aspectos da biodiversidade como genomas e características humanas (e.g. culturas e línguas), são mais ricos nos trópicos do que em regiões temperadas ²⁻⁵. Embora inúmeras teorias, hipóteses e modelos tenham sido propostos para explicar maior acúmulo de diversidade nos trópicos ⁶⁻⁸, ainda somos confrontados com a nossa ignorância sobre (i) como julgar a credibilidade de diferentes teorias, hipóteses e modelos e (ii) quais mecanismos causam padrões diversidade em grandes escalas espaciais.

Dezenas de mecanismos foram sugeridos para explicar as diferenças em diversidade de espécies ao longo de um gradiente espacial ^{7,9}. Esses inúmeros mecanismos podem ser classificados em quatro principais categorias: (i) mecanismos macroevolutivos, que descrevem heterogeneidade em taxas de diversificação ao longo do espaço geográfico ¹⁰; (ii) processos históricos descrevendo principalmente o maior acúmulo de espécies no espaço (área) e no tempo (idade) ¹¹; (iii) restrições energéticas relacionadas ao acúmulo de espécies, principalmente devido à disponibilidade de recursos ^{12,13}; e (iv) restrições de coexistência associados à oportunidades ecológicas e divergências ecológicas entre espécies ¹⁴. Apesar de numerosos estudos investigando os efeitos desses mecanismos em larga escala ^{7,8}, poucos modelos teóricos englobam a interação de processos ecológicos e evolutivos em grandes escalas espaciais e temporais ¹⁵⁻¹⁷. Além disso, a integração interdisciplinar de teorias, hipóteses e modelos

ecológicos e evolutivos com outras áreas da ciência raramente foram realizadas para entender padrões de diversidade humana ¹⁸.

Se múltiplos aspectos da biodiversidade são mais ricos em regiões similares do planeta (e.g. trópicos), então teorias, hipóteses e métodos utilizados nas últimas décadas em ecologia e evolução, para melhor entender padrões de diversidade de espécies, poderiam ser aplicados e/ou modificados para o melhor entendimento de diversidade humana. Além disso, mecanismos similares podem ser mutuamente responsáveis pela emergência de padrões espaciais biológicos e culturais (i.e., bioculturais). No entanto, apesar de grandes avanços em macroecologia e macroevolução, ainda sabemos pouco sobre os processos causais, não apenas por trás de padrões de diversidade humana ¹⁹, mas também por trás de padrões espaciais de diversidade de espécies ⁷. A ausência de um melhor entendimento de processos causais por trás de padrões espaciais de diversidade se dá principalmente por utilizarmos mais frequentemente modelos que não assumem explicitamente relações causais.

Existem dois tipos principais de modelos utilizados em ecologia e evolução para melhor entendermos fenômenos naturais: (i) modelos correlativos que descrevem a natureza e (ii) modelos mecanísticos que explicam a natureza ²⁰. Modelos correlativos são utilizados para encontrar associações funcionais entre variáveis de interesse. Esse tipo de modelo não incorpora explicitamente nenhum tipo de relação causal e apenas resume os dados do pesquisador ²¹. Modelos correlativos são utilizados para explorar a natureza e deixam a cargo do pesquisador a elaboração de *potenciais* relações causais por trás de uma associação estatística encontrada. Por outro lado, modelos mecanísticos são utilizados como veículos de exploração teórica em que pesquisadores testam explicitamente explicações causais para fenômenos biológicos ²⁰. Nesse caso, teorias são mais importantes para definir a estrutura do modelo, já que os parâmetros que

definem o modelo possuem significado biológico e contribuem para a interpretação de fenômenos biológicos complexos.

Três lacunas principais envolvendo a aplicação de modelos correlativos e mecanísticos para investigar padrões espaciais de diversidade são exploradas em minha tese: (i) critérios heurísticos (i.e. método carente de justificativa racional ou embasamento teórico, mas aceito como suficiente bom para um propósito) herdados desde o início da ciência são utilizados para julgar a credibilidade de modelos correlativos e mecanísticos que visam entender padrões complexos de diversidade (e.g. padrões espaciais de diversidade), mas discussões críticas sobre a validade dessas regras são raras; (ii) Poucos modelos mecanísticos incorporam a interação de processos ecológicos e evolutivos a nível de indivíduos em grandes escalas espaciais e temporais para melhor entender padrões espaciais de diversidade de espécies; (iii) poucos estudos exploraram o efeito de processos ecológicos e evolutivos para melhor entender padrões de diversidade humana. Todos os três pontos apresentados acima são explorados em minha tese que está dividida em três partes e seis capítulos.

No primeiro capítulo (Parte I), discuti as bases filosóficas e estatísticas utilizadas para justificar o uso de simplicidade no julgamento da credibilidade de teorias, hipóteses, modelos correlativos e mecanísticos em ecologia e evolução. No segundo, terceiro e quarto capítulo (Parte II) discuti o efeito de dinâmica neutra biogeográfica na estruturação espacial da biodiversidade. Para isso, desenvolvi um modelo de simulação mecanístico que inclui diferentes efeitos de energia disponível no ambiente nos processos básicos que estruturam a biodiversidade, tais como especiação, extinção e dispersão (Capítulo 2 e 3). No quarto capítulo, testei o efeito de processos biogeográficos na retenção de nicho climático através de um modelo que desconsidera o efeito de processos adaptativos para melhor entender os processos por trás de padrões

de conservação filogenética de nicho climático que são comumente associados com a emergência de padrões espaciais de diversidade em larga escala. Por fim, na parte III explorei aspectos da diversidade humana chamando a atenção de ecólogos para um aspecto da biodiversidade que é ainda pouco explorado nas áreas de ecologia e evolução. No quinto capítulo revisei aspectos da diversidade humana que se assemelham com padrões descritos em biogeografia e macroecologia, evidenciando discussões que surgiram em outras áreas da ciência, das quais ecólogos e biólogos evolucionistas possuem amplo conteúdo teórico e analítico para atuar no avanço dessas discussões. No sexto e último capítulo utilizei uma combinação de análise de caminhos, modelo mecanístico e regressão geográfica ponderada (GWR) para melhor entender os processos ecológicos e evolutivos que podem ser responsáveis por padrões espaciais de diversidade de línguas humanas.

PARTE I – O critério de parcimônia em ecologia e evolução

Entender como a diversidade se estrutura no espaço é assumido por ecólogos e biólogos evolucionistas como um dos maiores desafios da ciência moderna ²². Existem muitas razões para isso. Os padrões espaciais que observamos nos dias de hoje acumulam complexidade no espaço e no tempo desde o nível molecular até o mais alto nível de organização biológica. Portanto, desvendar o porquê de encontrarmos mais espécies em algumas regiões do que outras, do nível de paisagem ao nível continental, é de fato um grande desafio. Para tornar o desafio ainda maior, nós ainda não podemos realizar o desejo de Stephen Jay Gould que sonhava em rebobinar a história da vida e identificar os processos que levaram aos padrões atuais ²³. De maneira geral, ecólogos e biólogos evolucionistas que estudam a estruturação da diversidade no tempo e no espaço estão restritos a estudos observacionais que, na maioria dos casos, ajustam

modelos matemáticos a dados atuais da biodiversidade. Através desse procedimento, tentamos ganhar conhecimento sobre o papel de múltiplos processos na estruturação da biodiversidade. Mesmo assumindo que o fenômeno biológico estudado é de alta complexidade, ecólogos e biólogos evolucionistas dão grande importância à simplicidade para julgar a credibilidade de teorias ²⁴, hipóteses ²⁵ e modelos ²⁶⁻²⁸. No entanto, não existe nenhuma evidência empírica de que simplicidade pode representar credibilidade. Mesmo assim, pouca discussão sobre o uso de simplicidade para julgar teorias, hipóteses e modelos surgiu em ecologia e evolução.

Apesar de discussões sobre o uso de parcimônia não terem surgido com frequência em ecologia e evolução, filósofos e cientistas tentam justificar o uso de parcimônia há séculos ²⁹. Mesmo sendo uma discussão antiga, não existe nenhum consenso em ecologia e evolução sobre como justificar o critério de parcimônia, como medir o balanço de complexidade e simplicidade de um modelo e nem mesmo em como deveríamos medir simplicidade de teorias, hipóteses e modelos. Apesar de parcimônia ter sido defendida inicialmente por filósofos e cientistas como uma maneira de entender a natureza assumida com simples ³⁰, é difícil aplicar a mesma justificativa com as evidências que temos hoje sobre a complexidade da natureza. Além disso, a justificativa de que teorias, hipóteses e modelos simples são mais fáceis de compreender e lembrar (i.e., conforto psicológico) também não é um argumento válido, do ponto de vista epistêmico, para atribuir maior credibilidade para explicações simples.

Com o surgimento da estatística moderna, várias estratégias alternativas de inferência surgiram ³¹ e com elas diferentes justificativas para o uso de parcimônia. O que os diferentes métodos estatísticos mostram sobre parcimônia é que não existe nenhuma justificativa universal para o critério, uma vez que alguns tipos de inferência apresentam algum tipo de justificativa para usarem parcimônia (estatística frequentista e

seleção de modelos), enquanto outras não atribuem nenhum papel relevante para o critério (Bayesiana e Likelihood). Da mesma maneira, precisamos entender melhor em quais situações o critério de parcimônia deveria ser invocado em ecologia e evolução e em quais situações deveríamos relaxar o critério. Diante disso, no primeiro capítulo da minha tese de doutorado eu explorei as discussões filosóficas e estatísticas que surgiram para justificar o critério de parcimônia e apresento as ocasiões em que existem razões epistêmicas para invocar o critério de parcimônia e outras em que não existem razões epistêmicas. Como já reconhecido em ecologia, sofremos uma espécie de patologia de evitar modelos complexos, o que tem gerado grande dificuldade de publicar trabalhos que visem a integração de múltiplos processos ecológicos e evolutivos. Portanto, o primeiro capítulo traz à tona uma discussão crítica sobre o critério de parcimônia, suas origens, utilidades e o possível impedimento do desenvolvimento de ciências ecológicas e evolutivas se o critério for aplicado sem nenhuma razão epistêmica.

PARTE II - Dinâmica neutra biogeográfica na estruturação espacial da biodiversidade

Modelos que se concentrem em níveis fundamentais de organização e que incluem processos macroevolutivos são raramente estudados em grandes escalas temporais e espaciais, devido sua alta complexidade ³². Usualmente, modelos teóricos desenvolvidos para estudar padrões de diversidade em largas escalas temporais e espaciais modelam processos evolutivos considerando espécie como nível de organização fundamental ^{15, 33}. Esses modelos, portanto, desconsideram uma série de eventos que ocorrem em níveis inferiores de organização e que afetem processos fundamentais de biodiversidade (e.g. extinção, especiação, dispersão). Uma abordagem promissora seria desenvolver modelos que integrem diferentes campos da ecologia em

escalas basais de organização e que possam ser utilizados para discutir processos que contribuem para a emergência de padrões espaciais em larga escala.

Um bom ponto inicial, seria um modelo teórico baseado na Teoria Neutra de Biodiversidade e Biogeografia ³⁴. Modelos neutros simulam processos evolutivos considerando indivíduos como o nível de organização a ser manipulado e assumem que indivíduos são ecologicamente equivalentes em taxas de dispersão, especiação, morte e reprodução ³⁵. Esses modelos têm como principal objetivo testar a importância de alguns processos na emergência de padrões ecológicos, como limite de dispersão, especiação e estocasticidade demográfica, na ausência de outros (e.g. competição, seleção natural e nicho de espécies). Além disso, novos processos, originalmente ausentes de modelos neutros, podem ser adicionados ampliando suas aplicações para o entendimento de diferentes padrões ³². Modelos neutros podem incluir estrutura de nicho ³⁶⁻³⁸, interações ecológicas ^{35, 39}, seleção natural ³² e teoria metabólica ⁴⁰. No entanto, modelos neutros raramente foram utilizados para entender a emergência de padrões latitudinais de diversidade e a emergência de conservação de nicho climático entre espécies filogeneticamente próximas. Nos trabalhos que constituem a segunda parte dessa tese, testei o efeito de hipóteses energéticas na estruturação espacial de diversidade e testei o efeito de processos biogeográficos na retenção de nicho climático entre espécies relacionadas através de simulações estocásticas neutras.

No segundo e terceiro capítulo, desenvolvi um modelo de simulação estocástico e neutro que assume o efeito da energia disponível no ambiente em processos fundamentais da biodiversidade (e.g. extinção, especiação e dispersão). Entre as diversas hipóteses propostas para explicar gradientes de diversidade, a hipótese de energia se destaca entre as principais ^{7, 27, 41}. Análises correlativas mostrando uma relação positiva entre diversidade de espécies e proxies de disponibilidade energética no

ambiente (e.g. temperatura, precipitação, produtividade, evapotranspiração potencial, evapotranspiração real) levaram à proposição de dois mecanismos principais para explicar a presença de maior número de espécies em locais com maior disponibilidade energética ⁴². O primeiro deles, proposto originalmente por Hutchinson ⁴³, é de que a quantidade de energia disponível no ambiente afeta o número de indivíduos que ocorrem em um determinado local ^{12, 43}. Dessa maneira, se um local possui mais indivíduos, isso acarretaria maior acúmulo de espécies ao longo do tempo ^{7; 12}. O segundo mecanismo assume que temperatura possui um efeito direto no metabolismo e afeta a taxa de especiação ^{44 - 46}, o que explicaria maior acúmulo de espécies em locais mais quentes ^{47, 48}. No segundo capítulo da tese, testei se a simples mudança no número de indivíduos ao longo do espaço, acompanhando um gradiente espacial de produtividade, seria capaz de reproduzir um padrão espacial de diversidade taxonômica e filogenética no continente australiano. Já no segundo capítulo, testei se tanto a mudança do número de indivíduos quanto o efeito metabólico de temperatura em taxas de especiação explicariam a estruturação de gradientes latitudinais de diversidade de aves. Surpreendentemente, modelos neutros que assumem efeito de energia em processos fundamentais da biodiversidade são capazes de reproduzir padrões espaciais de riqueza de mamíferos terrestres na Austrália (capítulo 2), assim como gradientes latitudinais de diversidade de aves em diferentes regiões do globo (capítulo 3).

Por fim, testei o efeito de processos biogeográficos na evolução de nicho climático através de um modelo de simulação neutro. A conservação de nicho climático tem sido atribuída como um dos principais fatores que influenciam a emergência de padrões latitudinais de espécies ^{49 - 50}. No entanto, pouco se sabe sobre os processos que aceleram, ou retardam a evolução de nicho climático entre espécies. Além disso, ainda não é certo se conservação de nicho é um processo, um padrão, ou ambos ^{50 - 52}. No

quarto capítulo testei se conservação de nicho climático poderia emergir através de um modelo que propositadamente assume ausência de processos adaptativos.

Surpreendentemente, a dinâmica neutra de comunidades é capaz de causar conservação de nicho climático, demonstrando que processos biogeográficos podem afetar a retenção de nicho climático entre espécies. Nessa perspectiva, conservação de nicho climático pode ser visto como um padrão, já que pode ser parcialmente atribuído a eventos biogeográficos.

PARTE III – Preditores ecológicos de padrões espaciais de diversidade humana

Ao avaliar as diversas subáreas da ecologia, poderíamos concluir facilmente que os ecólogos estão interessados na relação entre a espécie humana e seu ambiente. De fato, muitos ecólogos estudam o impacto de atividades humanas passadas e atuais na biodiversidade ⁵³⁻⁵⁷. No entanto, poucos ecólogos estudaram como o clima, geografia e fatores socioculturais moldam qualquer aspecto da diversidade humana em grandes escalas ⁵⁸⁻⁵⁹.

A diversidade humana é expressa de inúmeras maneiras: no tamanho e formato dos nossos corpos, em milhares de línguas diferentes, centenas de práticas religiosas e dezenas de normas matrimoniais, sexuais e de criação de filhos. Por isso, o interesse em padrões de diversidade humana existe em muitas áreas da ciência, incluindo antropologia, arqueologia, economia, história, geografia humana, linguística, medicina, ciências políticas, sociologia e muitas outras ^{2, 60 -75}.

Embora a espécie humana possua uma enorme disponibilidade de dados e variabilidade não aleatória de características no espaço geográfico (e.g. tamanho do corpo, número de línguas faladas), ferramentas metodológicas e teóricas da ecologia para descrever e explicar padrões de características de espécies e diversidade de

espécies raramente foram utilizadas nas muitas disciplinas que exploraram as relações entre diversidade humana, clima, fatores geográficos e sociais. Muitas discussões e abordagens metodológicas que foram exploradas em capítulos anteriores de minha tese poderiam ser facilmente aplicados para o estudo de diversidade humana.

No quinto capítulo explorei diversos debates sobre diversidade humana através de padrões de diversidade morfológica, fisiológica e cultural que podem chamar a atenção de ecólogos, devido suas incontestáveis semelhanças com padrões de diversidade estudados em ecologia. Eu enfatizei principalmente temas que foram amplamente explorados por macroecólogos e biogeógrafos para espécies, tais como variação em um gradiente latitudinal de tamanho e formato do corpo (i.e., efeito de Bergmann e Allen), tolerância termal e diversidade. Ao focar em padrões humanos que se assemelham com padrões de diversidade de espécies elucidei as possíveis ligações entre teorias e métodos ecológicos que poderiam ser aplicados para estudar diversidade humana. Dessa maneira, essa revisão representa um chamado para ecólogos contribuírem em debates que surgiram em outras áreas da ciência, o que poderia gerar uma próspera área de pesquisa interdisciplinar.

Um aspecto explorado nessa revisão deu origem ao último capítulo da tese no qual apliquei ferramentas comumente utilizadas por ecólogos no estudo de diversidade de espécies para entender padrões de diversidade linguística humana. Cerca de 7000 línguas são faladas ao redor do mundo e essas línguas não estão distribuídas de forma aleatória ⁷⁶. Muito mais línguas são encontradas em regiões tropicais do que em regiões temperadas ou árticas ¹⁹. Um dos temas mais desafiadores no estudo de evolução cultural de nossa espécie é entender os processos que geram a enorme diversidade de línguas e sua distribuição espacial.

Apesar de diversas hipóteses terem sido propostas para explicar padrões espaciais de diversidade de línguas ⁷⁷, os fatores que moldaram esses padrões continuam pouco compreendidos ¹⁹. Uma barreira para o nosso conhecimento tem sido os resultados contraditórios encontrados nos raros estudos que testaram a associação entre variáveis ambientais e/ou socioculturais e diversidade de línguas ¹⁹. Por exemplo, isolamento é um fator chave para o surgimento não apenas de novas espécies, mas também de novas línguas ⁷⁸. Antropólogos e linguistas argumentam que mais línguas deveriam ser observadas em regiões montanhosas, já que o esforço para contatar grupos vizinhos é maior em regiões com relevo irregular ⁷⁹. Portanto, regiões montanhosas causariam maior isolamento entre grupos humanos que através do tempo acumulariam mais diferenças nas línguas faladas. Para investigar esse efeito, os pesquisadores testam a associação entre complexidade topográfica e diversidade de línguas ^{70,78,80}. No entanto, os resultados se contradizem dependendo da região em que o estudo é aplicado. A relação entre topografia e diversidade de línguas é negativa para línguas do oeste africano ⁸⁰, mas é nula para diversidade de línguas em escala global ⁷⁰. Por outro lado, um estudo demonstra que a relação entre topografia e diversidade de línguas pode ser importante dependendo do continente em que a relação é avaliada ⁷⁸. Esse tipo de contradição é encontrado quando outras variáveis ambientais e socioculturais são testadas contra diversidade de línguas ¹⁹.

Dois fatores importantes contribuem para o surgimento de resultados contraditórios em estudos que investigam padrões espaciais de diversidade de línguas. O primeiro deles é a tradicional busca por preditores universais de diversidade de língua. De maneira geral estudos testam preditores de maneira isolada sem a inclusão da interação entre múltiplas variáveis ¹⁹. É bastante provável que o melhor preditor de línguas na Austrália (i.e., precipitação ⁸¹) não seja o maior preditor de diversidade de

línguas em outras regiões que não possuem os mesmos extremos climáticos da Austrália (e.g. desertos no centro e costas húmidas). Portanto, é bastante plausível assumir que o melhor preditor de línguas varia no espaço dependendo da região investigada. O segundo motivo que contribui para a emergência de resultados contraditórios é a complexidade do fenômeno que está sendo estudado, que é provavelmente gerado por uma rede de diversos preditores que afetam de maneira direta e indireta o maior acúmulo de línguas em algumas regiões do planeta ⁷⁰.

No quinto capítulo da minha tese lidei com os dois fatores metodológicos que contribuem para a emergência de resultados contraditórios definindo um modelo que inclui o efeito direto e indireto de diversas variáveis que foram propostas ao longo dos anos como possíveis preditoras de padrões espaciais de diversidade de línguas. Além disso essa análise também permite a investigação de quais são os melhores preditores de diversidade de línguas em diferentes regiões do espaço. Para isso, utilizei uma combinação entre análise de caminhos, regressões ponderadas no espaço e um modelo mecanístico. Já que línguas são marcadores de limites sociais entre grupos humanos ⁸¹⁻⁸⁴, nessa análise eu explorei o efeito direto e indireto oito variáveis que foram sugeridas na literatura ao longo das últimas três décadas por contribuírem na formação de limites entre grupos humanos.

Esse modelo foi aplicado para melhor entender o padrão espacial de diversidade de línguas indígenas (pré contato colonial) da América do Norte. Apesar de ter recebido grande atenção ao longo das décadas, pouco se sabe sobre os fatores que afetam o padrão de diversidade linguística Norte Americano. Esse trabalho demonstrou que os preditores de diversidade de línguas na América no Norte envolvem variáveis associadas a hipóteses que propuseram o efeito de clima e densidade populacional em diversidade de línguas. Os preditores de diversidade de línguas não são perfeitamente

universais nem inteiramente diretos. Por fim, a predição do modelo varia no espaço com regiões onde mais de 80% da variação em diversidade de línguas é explicada.

CONCLUSÕES

A presente tese contribuiu para uma maior compreensão dos mecanismos que contribuem para o surgimento e manutenção de padrões espaciais da biodiversidade. Além disso, a tese apresenta pontes entre diferentes áreas do conhecimento (ecologia, evolução, geografia, antropologia e linguística) que precisam ser integradas para a melhor compreensão de padrões de diversidade humana. No primeiro capítulo, discuti as bases filosóficas e estatísticas para justificar o uso do critério de parcimônia para julgar a credibilidade de teorias, hipóteses, modelos correlativos e mecanísticos, utilizados para o melhor entendimento de fenômenos naturais complexos. Nesse trabalho, mostrei que existe um valor instrumental no uso de parcimônia para julgar modelos que são construídos para realizar previsões, mas que aplicação do princípio de parcimônia para avaliar modelos mecanísticos é pouco produtivo já que pode comprometer a elucidação de fenômenos verdadeiramente complexos. No segundo e terceiro capítulo desenvolvi um modelo de simulação mecanístico que inclui diferentes efeitos da energia disponível no ambiente nos processos básicos que estruturam a biodiversidade para melhor entender os processos que contribuem para o surgimento de padrões de diversidade em grandes escalas espaciais. Surpreendentemente, um modelo que não considera nicho ecológico, mas inclui efeitos energéticos, é capaz de reproduzir o padrão de riqueza de mamíferos terrestres na Austrália (capítulo 2) e padrões latitudinais de riqueza de aves (capítulo 3). No quarto capítulo, testei o efeito de processos biogeográficos na conservação filogenética de nicho climático, comumente associado com a emergência de padrões espaciais de diversidade em larga escala, através de um modelo mecanístico que desconsidera o efeito de qualquer processo adaptativo na retenção de nicho climático. Esse estudo demonstrou o forte papel de processos biogeográficos na retenção de nicho climático, mesmo quando nenhuma força

adaptativa está atuando na diversificação de nicho. No quinto capítulo revisei aspectos da diversidade humana que se assemelham com padrões descritos em biogeografia e macroecologia demonstrando que ecólogos e biólogos evolucionistas podem contribuir com debates que surgiram em diversas áreas da ciência através da aplicação de métodos utilizados para estudar padrões de diversidade de espécies. Por fim, no sexto capítulo utilizei uma combinação de análise de caminhos, modelo mecanístico e regressão geográfica ponderada (GWR) para investigar um padrão espacial de diversidade humana, o padrão de diversidade de línguas. Esse estudo demonstrou que os preditores ecológicos e evolutivos de diversidade de línguas não são perfeitamente universais nem inteiramente diretos e que o poder preditivo do modelo varia no espaço com locais onde cerca de 86% da variação é explicada a regiões onde cerca de 40% da variação é explicada. Portanto, minha tese ampliou debates filosóficos sobre modelagem em ecologia e evolução; ampliou a aplicação de modelos neutros para estudar padrões de diversidade, hipóteses energéticas e o efeito de processos biogeográficos na retenção de nicho climático de espécies; e por fim, ampliou os horizontes do estudo da biodiversidade ao explorar padrões de diversidade humana e resolver lacunas que surgiram em outras áreas da ciência sobre o que porquê de falarmos mais línguas em algumas regiões do planeta do que em outras.

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PARTE I. O CRITÉRIO DE PARCIMÔNIA EM ECOLOGIA E EVOLUÇÃO

CAPÍTULO 1

A PARSIMONIOUS VIEW OF THE PARSIMONY PRINCIPLE IN ECOLOGY AND EVOLUTION

A parsimonious view of the parsimony principle in ecology and evolution

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Abstract The idea that simplicity of explanation is important in science is as old as science itself. However, scientists often assume that parsimonious theories, hypothesis and models are more plausible than complex ones, forgetting that there is no empirical evidence to connect parsimony with credibility. The justification for the parsimony principle is strongly dependent on philosophical and statistical inference. Parsimony may have a true epistemic value in the evaluation of correlative and predictive models, as simpler models are less prone to overfitting. However, when natural mechanisms are explicitly modelled to represent the causes of biological phenomena, the application of the parsimony principle to judge the plausibility of mechanistic models would entail an unsupported belief that nature is simple. Here, we discuss the challenges we face in justifying, measuring, and assessing the trade-off between simplicity and complexity in ecological and evolutionary studies. We conclude that invoking the parsimony principle in ecology and evolution is particularly important in modelbuilding programs in which models are viewed primarily as an operational tool to make predictions (an instrumentalist view) and in which data play a prominent role in deciding the structure of the model. However, theoretical advances in ecology and evolutionary biology may be derailed by the use of the parsimony principle to judge explanatory mechanistic models that are designed to understand complex natural phenomena. We advocate a parsimonious use of the parsimony principle.

Keywords Parsimony principle, Statistical inference, Ockham's razor, Correlative models, Mechanistic models

Resumo A ideia de que a simplicidade de uma explicação é importante na ciência é mais velha do que a própria ciência. No entanto, os cientistas frequentemente assumem que teorias, hipóteses e modelos parcimoniosos são mais plausíveis do que versões complexas dos mesmos, esquecendo que não existe nenhuma evidência empírica para conectar parcimônia com credibilidade. A justificativa do princípio de parcimônia é fortemente dependente da inferência filosófica e estatística utilizada. Parcimônia pode ter um valor epistêmico verdadeiro na avaliação de modelos correlativos e preditivos, já que modelos simples estão menos sujeitos a *overfitting*. No entanto, quando mecanismos são explicitamente modelados para representar causas de fenômenos biológicos, o uso do critério de parcimônia para julgar a plausibilidade de modelos mecanísticos implicaria em uma visão pouco aceita de que a natureza é simples. Nesse trabalho, nós discutimos os desafios que nós enfrentamos em justificar, medir e julgar o trade-off entre simplicidade e complexidade em estudos ecológico e evolutivos. Nós concluímos que invocar o princípio de parcimônia em ecologia e evolução é particularmente importante em tipos de modelagem em que os modelos são vistos primariamente como uma ferramenta operacional para fazer previsões (uma visão instrumental) e em que os dados possuem um papel fundamental de decidir a estrutura do modelo. No entanto, avanços teóricos em ecologia e evolução podem ser impedidos pelo uso do princípio de parcimônia para julgar modelos mecanísticos explanatórios que são desenvolvidos para entender fenômenos naturais complexos. Nós defendemos um uso parcimonioso do princípio de parcimônia.

Palavras-chave Princípio de parcimônia, Inferência estatística, Navalha de Ockham, Modelos correlativos, Modelos mecanísticos

Introduction

The idea that simple (parsimonious) theories are important in science is as old as science itself. It is difficult to disagree that simple theories, hypothesis and models are elegant, easy to understand and to remember. However, rooted in the parsimony principle, scientists often assume that simple theories, hypothesis and models are more plausible or reliable, although there is no empirical evidence to connect simplicity with credibility (Quine 1963). For example, in the quest to understand the causes of complex biodiversity patterns, such as spatial diversity gradients, ecologists and evolutionary biologists study how multiple processes, interacting over space and time, produce complex biological phenomena across all scales (Wiens and Donoghue 2004, Rangel et al. 2007, 2018, Warren 2014, Rosindell et al. 2015, Connolly 2017, Coelho et al. 2018). However, even acknowledging that biodiversity patterns are immensely complex, and that disentangling their causes is an extremely challenging endeavor (Vellend 2010), simplicity has always had a special role in the judgment of ecological and evolutionary theories (Marquet et al. 2014), hypothesis (Hilborn and Stearns 1982) and models (Holling 1966, Evans et al. 2013, Houlahan et al. 2017). Yet, little discussion is found in ecology and evolution about how to justify, measure and trade-off simplicity.

The ecological and biogeographical phenomena (e.g. uneven distribution of species over space) do not provide universal opportunity for experimental research. Thus, ecologists and evolutionary biologists are usually limited to observational studies, in which curve-fitting techniques are employed to measure the statistical correspondence between observed biological patterns and suspected causal factors. In many cases, the main interest is to elect the most plausible model that fits to the data in hand, as the mathematical representation of a theory or hypothesis (Box 1). If goodness-of-fit was the only criterion to judge the plausibility of models, a complex model that

best fits to the data would be assumed as the most plausible. However, parsimony is also viewed as valuable criterion to evaluate the plausibility of alternative models (Box 1). The main question that emerges from our scientific practice is whether/how parsimony can be used to understand natural processes. Although simple theories, hypothesis and models often strike us as beautiful and easier to understand (Quine 1963, Keuzenkamp et al. 2004), our psychological comfort when dealing with simpler explanations for complex phenomena is not a valid epistemic justification for its general use as a criterion to judge reliability (Pearl 1978, Sober 1981, 2015). For centuries scientists and philosophers have been struggling to find epistemic justifications for the parsimony principle, but no consensus has arisen yet. In this paper, we show that ecology and evolutionary biology employ different justifications for the role of parsimony in alternative inferential frameworks, such as frequentist, Bayesian, likelihood and multi-model inference. We also provide a historical perspective to the parsimony principle, discussing its role in predicting versus explaining nature, and its application to evaluate correlative and mechanistic models. We show that 1) there is an instrumental value in the use of parsimony to judge models that are designed for predictive purposes, but 2) the application of the parsimony principle to evaluate explanatory models is counterproductive, as it may prevent the elucidation of truly complex phenomena.

Box 1. The curve-fitting problem.

Since Laplace and Gauss, curve-fitting is one of the most universal methodologies employed in scientific research (Mulaik 2001). Given the observations made during an experimental (or observational) study of the correspondence between a predictor (x) and a response variable (y), an infinite number of hypotheses (curves, Fig 1) can be proposed to summarize and explain the relationship between the variables (Fig 1). However, praxis is the choosing of only one hypothesis, based on an arbitrary balance between the criteria of goodness-of-fit and simplicity. The curve that best describes the data is always the one that comes closest to the largest number of observations, therefore the best-fit curve. Thus, if goodness-of-fit was the only criteria, one would have to choose the curve that connects all data points (dashed curve, Fig 1). However, the geometric irregularity of the best-fitting curve indicates the mathematical complexity of the hypothesis, which is thus considered not parsimonious. Conversely, the simplest hypothesis is a straight line (red line, Fig. 1), which is far more regular but fails to account for all the available information about the relationship between the variables. Thus, the simplicity criterion is used as a counterweight to the goodness-of-fit criterion, and vice-versa. However, there are infinite alternatives between the simplest and best-fit curves (e.g. blue curve, Fig. 1). The use of simplicity as an additional criterion to select the most plausible hypothesis creates the philosophical problem of how to measure and justify the criterion. Because simplicity is so loosely defined and justified, the final choice is based on an arbitrary evaluation of how well the line fits the observation and how simple it personally feels to the scientist.

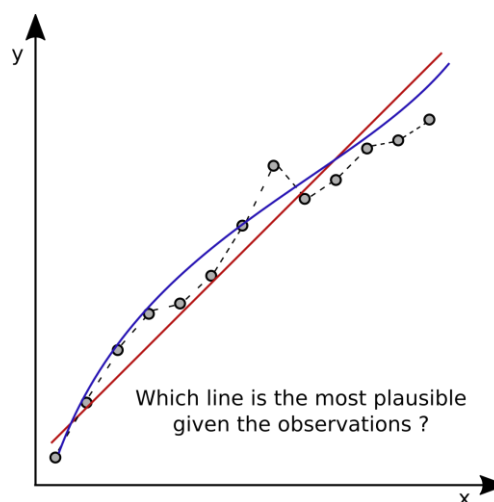


Fig 1. The curve-fitting problem. The choice of the most plausible hypothesis is based on an arbitrary balance between goodness-of-fit and simplicity criteria. The red curve is the simplest, indicating a linear relationship between the two variables, but also the worst-fit. The dashed line is the most complex, but also the best-fit. The blue line is just one of the infinite possible balances between the best-fit and simplest hypotheses.

Historical perspectives of the parsimony principle

Traditionally, most of the slogans used to discuss simplicity are found in William of Ockham's (1285–1348) writings such as 'It is futile to do with more what can be done with fewer', or 'plurality should not be posited without necessity' (Brown 1950, Sober 2015). Not surprisingly, the Ockham's razor criteria for judging competitive theories, hypothesis and models is one of the most popular names for the parsimony principle. However, the origins of the parsimony principle can be traced back at least to Aristotle, whom invoked the principle in many of his writings (Keuzenkamp et al. 2004, Brown 1950). Until the 20th century many philosophers and scientists believed that Ockham's razor was epistemically relevant because simplicity was assumed to be a true feature of nature (e.g. Descartes, Leibniz, Newton and Kant; Sober 2015). Some of them proposed theistic justifications for the parsimony principle (Descartes, Leibniz, Newton), arguing that the Abrahamic God had created a simple world, with simple rules (Sober 1981, 2015), and that understanding nature was equivalent of understanding the mind of God. Thus, the assumption of a simple nature would be a sufficient epistemic justification for the parsimony principle in science. However, other philosophers (e.g. Hume, Mill, Morgan) painted a different picture of parsimony. In their perspective, parsimony is viewed as necessary to make predictions about the world, without any assumption or assurance that nature is indeed simple (Sober 2015). Thus, parsimony would have an operational and methodological justification for scientific research, without any assertion of how nature works.

The rise of modern statistics in the 20th century transformed science into a data-driven investigation of natural phenomena, reducing the emphasis of narrative accounts and description/categorization of observables. However, modern statistics gave rise to many alternative inferential strategies, which differ not only methodologically, but also

epistemologically. The epistemological distinction of alternative inferential strategies of modern statistics unchained the concept of plausibility from parsimony, therefore creating multiple directions in the search for a conceptual justification of the parsimony principle.

The parsimony principle in alternative frameworks of statistical inference

The most common use of Fisher's significance test is the assumption of a parsimonious null hypothesis as a premise (default position). In critical tests of this kind the null hypothesis invokes the least possible complexity by assuming the absence of relationship, association or effect among measured phenomena. Thus, the goal of the analysis is to estimate the degree of compatibility between the observed data and the scenario in which the null hypothesis is assumed to be true (Sokal and Rohlf 1981, Efron and Tibshirani 1994). The null hypothesis may only be rejected if the observed data is substantially (i.e. 'significantly') different from the expectation of the parsimonious null scenario. Because Fisher is also the proponent of the much flexible likelihood theory, it is arguable that he proposed the test of the null hypothesis for its mathematical convenience in analysis of experimental results, in which the experimental manipulation (i.e. treatment) is assumed to produce no effect. In addition, it is easier to derive the probability distribution of the clearly defined null hypothesis, as opposed to the infinite alternative hypotheses in which experimental treatment would promote some undefined degree of effect. Thus, the parsimony of the null hypothesis is a methodological strategy, rather than a statement about the reality of nature.

Parsimony also plays a prominent role in the comparison of models within the framework of model selection and multi-model inference (Burnham and Anderson 2001, 2002). Some information criteria (i.e. Akaike information criterion – AIC,

corrected Akaike information criterion – AICc, kernel-based information criterion – KIC and empirical information criterion – EIC) are designed to asymptotically maximize the expected relative predictive accuracy of models (i.e. the ability to fit future data, Aho et al. 2014). Notably, the AIC have been widely used in ecological and evolutionary research in the last decade (MacNally et al. 2018). The simplicity criterion is mathematically relevant to access the relative predictive accuracy of models because very complex models tend to have poor predictive power (i.e. the curse of dimensionality; Burnham and Anderson 2001, Sober 2002, 2004a, b, Hastie et al. 2009, James et al. 2013). Because complex models tend to over-fit the data, therefore confounding noise with signal, AIC may be used to penalize model complexity to identify the best balance between goodness-of-fit and simplicity. Thus, parsimony has a justifiable epistemic value to gauge the relative predictive accuracy of a model. However, model selection does not downgrade complex models because they are less plausible than simpler models, but because they are often a poor choice for prediction of future data. In addition, model selection does not provide absolute estimates of predictive accuracy, but only a relative measure given the alternative models under consideration. Although model selection with AIC became a popular inferential strategy in ecology and evolutionary biology (MacNally et al. 2018), few models are designed for predictive purposes, as prediction is traditionally not a frequent goal in those sciences (Houlahan et al. 2017).

Some theoretical, simulation and applied studies have shown that AIC is not as parsimonious as once believed. Because AIC is designed to avoid underfitting errors (i.e. potential omissions of processes that do influence the phenomena under study), it becomes prone to overfitting errors (i.e. overrating models that include processes that do not influence the phenomena) (Taper 2004). However, there are more parsimonious

alternative information criteria, which seek to avoid overfitting errors by accepting a higher rate of underfitting errors. For example, consistent AIC (CAIC), Bayesian information criterion (BIC), Hannan–Quinn information criterion (HQC) and many others, can asymptotically identify the model that is closest to the true generating process, given a set of candidate models. As a result, this group of information criteria tend to select compact models, composed mostly of processes with strong influence in the phenomena under study, but potentially missing processes with minor effects.

In contrast with information theoretical approach, Bayesians aim to estimate the probability of different theories, given the available evidence and current knowledge (Ellison 2004), as they equate probability of a theory with its degree of plausibility. Thus, their concept of probability is a measure of credibility, certainty or belief (Horwich 1982, Hilborn and Mangel 1997, Hacking 2001, Ellison 2004). The Bayes theorem is used as a model for the learning process, indicating how scientists should update their knowledge in the light of new evidence. Thus, with the Bayes theorem one can identify the most probable theory, hypothesis or model, given the alternatives. However, parsimony does not play any role in traditional Bayesian estimation of the probability of a theory, as the simplicity of the theory does not increase its probability (Sober 2015).

Although parsimony is not a core principle of Bayesian inference, Jeffrey's postulate of simplicity suggests that when multiple alternative hypotheses are confronted, simple theories should be given higher prior probability (i.e. the degree of justified belief of a researcher in a hypothesis before new evidence of the studied phenomenon is uncovered) (Jeffrey 1965). However, Jeffrey does not provide a valid epistemic justification for his approach, just a heuristic methodological strategy to use the parsimony principle in Bayesian inference. Indeed, Jeffreys' framework is not

commonly applied by Bayesians, and one should search for the most probable hypothesis based only on available knowledge and new evidence (Gelman et al. 2013, Sober 2015). However, there are multiple Bayesian techniques used for model selection that weight models by their goodness-of-fit and simplicity (Hooten and Hobbs 2015). Yet, those methods are seldom employed in ecology, and few discussions about their validity emerged in applied ecological problems. Some Bayesian techniques used in model selection justify the use of parsimony based on predictive accuracy, while others offer heuristic justification similar Jeffrey's postulate of simplicity (Hooten and Hobbs 2015, Sober 2015). Discussions of the correct use of Bayesian model selection emerged in social sciences where it is argued that performing Bayesian model selection is unimportant when the main task is to construct realistic models for complex systems that agree with both theory and data (Gelman and Rubin 1995), which seems to be what ecologists crave. Finally, ecologists frequently use AIC for model selection, instead of alternative Bayesian information criteria (MacNally et al. 2018), which makes the discussion about AIC even more relevant in ecology and evolution.

Likelihoodists and Bayesians share a similar perspective on how to deal with parsimony, but they disagree in the use of prior probabilities. While Bayesians attempt to carry knowledge over time, updating it as new information arises, likelihoodists see no value in the use of prior probabilities. For them, if the model with highest likelihood happens to be the simplest, then parsimony happens to mirror evidential support, but the likelihood of a hypothesis is still proportional to the probability of observing the data if that hypothesis was true (Sober 2004a, b).

Finally, as the parsimony principle started to be unchained from plausibility, it is no longer viewed as a pre-20th century magical argument used by classical philosophers and scientists. However, there is no universal justification for the parsimony principle.

As different frameworks of statistical inference have different epistemic goals, the parsimony principle is invoked, or not, under different epistemic justification.

Simplicity and falsifiability in Ecology and evolution

Karl Popper provided a different epistemic justification for parsimony by arguing that simple theories are more falsifiable (Popper 1959). According to him, because the goal of empirical science should be the refutation of theories, parsimonious theories are desirable because they are in principle easier to be refuted. For example, Popper's 'bold hypotheses' are parsimonious because they use few assumptions to make a myriad of predictions about natural phenomena, being easier to be refuted in case any of the predictions fail. However, according to Popper, if a theory is evaluated repeatedly over time and not refuted, it should not be considered more plausible, but only to have been more corroborated. Although most philosophers of science consider the concept of corroboration too obscure for a useful application in research (Godfrey-Smith 2003), it is frequently assumed that the most plausible theory are those that have been most corroborated (Sober 2004b).

One could argue that ecologists give great importance to parsimony when judging theories, hypothesis and models because of the Popperian argument that simple theories are easier to falsify. However, it is difficult to argue that ecologist and evolutionary biologists are strict Popperians, such that one single critical test that contradicts a model is sufficient to falsify its underlying theory (here not including 'naive falsifications'; Godfrey-Smith 2003). Let's take as an example the latitudinal gradient of species diversity, ecology oldest pattern (Hawkins 2001). It does not seem that we have falsified any hypothesis over time, which can be noticed by analyzing Pianka's (1966) seminal 'Latitudinal gradients in species diversity: a review of

concepts' that still captures currently discussed hypotheses for latitudinal diversity gradients. Ecologists and evolutionary biologists work simultaneously with a plethora of competing theories, hypotheses and models, but rarely discard any, even when conflicting empirical evidence is found. Indeed, ecology and evolutionary biology seems to be best described by Lakatos' competition among multiple scientific programs (Godfrey-Smith 2003), in which scientific progress is associated with gradual improvements of theories that continuously explain the available empirical data. Also, as all scientists, we are deeply attached to our theories (Ginzburg and Jensen 2004). Thus, the importance that a scientist gives to a certain characteristic of a theory, hypothesis or model (e.g. specificity vs generality, simplicity vs complexity) is very much a matter of personal taste (Kuhn 1977).

The parsimony principle in predicting versus explaining nature

Does science truly explain how nature works, or does it identify patterns in natural phenomena? These are two opposite philosophical views about the role of science on understanding nature (Okasha 2002, Godfrey-Smith 2003). On the one hand, the scientific realism argues that the goal of science is to provide a description or explanation of the true underlying reality of nature. On the other hand, scientific instrumentalism holds that scientific theories and models are just instruments to assist researchers to predict natural phenomena. Thus, from an instrumentalist point of view, theories are used to provide predictions of observable data, and there is no contradiction if alternative theories are just as accurate. Conversely, under the realistic perspective, there is only one true theory, which perfectly describes the underlying mechanisms of nature.

From the realistic perspective, invoking parsimony to evaluate a theory is a metaphysical assumption that nature is indeed simple, like many pre 20th century philosophers and scientists defended. However, under an instrumentalist view of science, the Ockham's razor is a methodological criterion to judge among the infinite models that can fit the data (Box 1), as well as choosing the most reliable model to predict new data (higher predictive accuracy). These two different epistemic views of science, which are coupled with alternative uses and justifications of parsimony principle to evaluate theories, are present in discussions of alternative models to reconstruct phylogenetic history within evolutionary biology (Box 2). In fact, the core of that debate was the epistemic value of two alternative model building programs in ecology and evolution: models to describe nature (i.e. correlative) or models to explain nature (i.e. mechanistic) (Gotelli et al. 2009).

Box 2 - The use of parsimony in evolutionary biology

Parsimony principle has been intensely discussed in evolutionary biology within the context of phylogenetic reconstruction (Sober 2015, Sober 1989, Felsenstein 2004). A parsimonious model of trait evolution assumes that the fewest changes in a given trait has occurred over evolutionary history. Thus, one can apply the parsimony criterion as a realistic evolutionary process to estimate the most plausible phylogenetic tree from the observation of traits of a set of species (Felsenstein 2004). The puzzle that tormented evolutionary biologists was how to justify the use of the parsimony principle as an evolutionary model (Sober 2015, Sober 1989). A realistic view of the parsimony principle was invoked by Camin and Sokal (1965) when affirming that the correctness of their method of phylogenetic reconstruction “depends on the assumption that nature is, indeed, parsimonious”. Others provided a methodological justification for parsimony, arguing that parsimony could mirror likelihood (Cavalli-Sforza and Edwards 1967) which was later shown to occur only under specific assumptions (e.g. drift is the process governing trait evolution (Felsenstein 1973, Felsenstein 1978). Popperian arguments were also invoked by suggesting that the most parsimonious tree is easier falsifiable by data (Wiley 1975, Wiley 2001). The problem with the Popperian argument is that data used in phylogenetic reconstruction cannot, in any way, falsify the hypothesis of tree topology (Sober 2015). Later, an instrumentalist view of parsimony was clarified by suggesting that parsimony is not necessarily an assumption about how evolution occurs in nature, but just as a simple and useful methodology for phylogenetic reconstruction (Sober 1989), although not the only methodology available (Felsenstein 2004).

The real weakness of the use of parsimony in evolutionary biology is the impossibility of incorporating knowledge from different processes of evolution to reconstruct a phylogenetic tree (Yang and Rannala 2012). The sophisticated evolutionary models allowed by Bayesian and Likelihood methods began to gradually replace parsimony, especially when molecular data is used in phylogenetic reconstruction. Parsimony remains a controversial issue in evolutionary biology (Yang and Rannala 2012), although it is still used in phylogenetic inference, especially when dealing with discrete characters (i.e. paleontology, behavioral sciences). Today, most phylogenies are reconstructed using statistical procedures that explicitly assume multiple models of evolutionary processes and make no use of parsimony (Sober 2015, Felsenstein 2004).

Correlative models are designed to probe nature and find functional relationships (patterns) among observed phenomena, but no causal story is built into the model. In fact, the data used to fit the model is more important than theory itself, as the statistical methods are used only in summarizing observed data, without explicitly including theories a priori (Gotelli et al. 2009, Pearl and Mackenzie 2018). Because the correlative model-building program is instrumentalist in its essence, the epistemic justification of parsimony is also conceptually tied to an instrumentalist view of science. Thus, parsimony should be invoked by ecologists and evolutionary biologists to judge competing correlative models because predictive accuracy is the main goal of such models. Since reliable predictions of highly complex phenomena and noisy data can be difficult to achieve (Burnham and Anderson 2001, Hastie et al. 2009), applying the parsimony principle to judge between the infinite alternative models reduces the probability of confounding noise with signal. Thus, the parsimony principle within the instrumentalist framework is justifiable only in predictive science, which is not the strong characteristic of ecology (Houlahan et al. 2017).

In contrast, mechanistic models have been used as vehicles for theoretical exploration, proposing causal explanation of a biological phenomenon (Peck 2004, Connolly et al. 2017, Rangel et al. 2018). Contrary to purely correlative models, the parameters of mechanistic models are designed with biological meaning, therefore contributing to the interpretation of the modelled phenomena (Gotelli et al. 2009). Therefore, theory is more important than data for mechanistic modeling, since the final goal is to propose or evaluate the theory behind the ecological and evolutionary processes built into the model (Rangel et al. 2018). Philosophers and modelers argue that those models defy the restrictions found in common correlative models (Winsberg 1999, 2001), because they represent an attempt to realistically describe nature. Thus,

invoking the parsimony principle to judge the plausibility a mechanistic model implies the belief that nature is simple, with few basic processes driving complex observed natural patterns.

Correlative and mechanistic models must not be compared using the parsimony criterion, as they emerge from alternative philosophical approaches, with different scientific goals (Winsberg 1999, 2001). Mechanistic models are in general more complex than correlative models by design, as they attempt to realistically incorporate and integrate complex causal processes. There are, of course, correlative models that are more complex than mechanistical models (e.g. geographically weighted regressions; Fotheringham et al. 2002), assuming that the number of adjustable parameters is a valid measure of complexity (Box 3).

One should not expect simplicity from mechanistic models that attempt to unify different areas of knowledge in ecology and evolution (Cabral et al. 2017), as ecological and evolutionary patterns at high organizational levels e.g. latitudinal diversity gradients) are among the most complex natural phenomena. However, as Hilborn and Stearns (1982) affirmed over thirty years ago, we face a pathology of avoiding complex models, which promotes a major difficulty of publishing conclusions based on integrative mechanistic models (Evans et al. 2013). Neglecting complex models that try to understand and explain causal relationships among ecological and evolutionary processes prevents significant advances in our understanding of nature.

Because mechanistic models are attempts to explain nature as a vehicle for theoretical exploration, these models should be judged by their consistency and consilience (i.e. how well the built-in processes and assumptions of the model capture what is currently accepted by scientific community as valid explanation, or explanations with higher potential to integrate theories from different research fields), accuracy (i.e.

how well the model reproduces empirical patterns) and precision (i.e. the amount of variation in model predictions among replicates of the model) (Gotelli et al. 2009). Conversely, evaluating mechanistic models by contrast against correlative models is analogous to comparing apples with oranges.

Notice that not employing the parsimony principle in the judgment of mechanistic models does not, in any way, neglect or denies the trade-offs between specificity and generality of model building strategies (Levins 1966, Grimm 2005). However, the traditional view that simple models are the safest route towards a general theory is another common misconception, which has been identified as an obstacle for advance of ecological and evolutionary sciences (Evans et al. 2013). Both general and specific models may be complex or simple, as specificity and generality refer to the range of natural phenomena explained by the model, whereas complexity and simplicity refer to the number of assumptions and/or processes that are incorporated by the model. As Dayton (1973) affirm, simple models offer an easier shortcut for generalization, but if they are not based on a deep understanding of natural processes, then they are fated to produce the right predictions for the wrong reasons. Not rarely correlative models have higher predictive accuracy than mechanistic models, but they usually provide poor additional understanding of causal processes (Rangel and Loyola 2012).

Finally, when mechanistic models are used to perform predictions of natural patterns, then they may be compared against alternative models that attempt to predict the same patterns. Thus, parsimony reinserts itself into explanatory modelling as an instrumental criterion to identify competing models with poor predictive accuracy, even under the assumption that nature is complex. Greater evidential support for a model comes from the ability to predict new data than from the ability to match existing data. Echoing many before us, ecology and evolution should be more committed to

predictions (Houlahan et al. 2017). However, one should always consider if the empirical patterns used to validate the model aren't too simple, because, if they are, then they could also be reproduced by some competing model, regardless of complexity. Yet, measuring the complexity or simplicity of models is conceptually and methodologically challenging (Box 3).

Box 3 – Measuring simplicity

Parsimony has a practical value in science but has little support for its epistemic value (Sober 2015), especially when complexity is expected in natural systems. The use of the parsimony principle as a valid criterion in scientific practice raises the problem of how to measure simplicity. The problem begins, first and simply, when using different communication formats. The degree of complexity used to describe reality through theories, models and hypothesis depends of language (Pearl 1978). Thus, our perception of complexity varies greatly according to the language used. Although it is assumed that models and hypotheses are described following a standardized scientific language, valid models and hypotheses can be proposed in a myriad of formats (e.g. verbal, deterministic equation, stochastic equation, computer simulation, etc).

Traditionally, the complexity of a model is measured using two criteria: (i) the number of adjustable parameters or, (ii) the number of assumptions. However, even for very simple models these two criteria may lead to conflicting evaluations. Consider, for example, the linear (A) and parabolic (B) models:

$$(A) \quad y = a + bx$$

$$(B) \quad y = a + bx + cx^2$$

The linear relationship is a special case of the parabolic, where $c = 0$. According to the criterion of simplicity based on the least number of parameters, the linear model is the simplest, as it has two adjustable parameters (a and b) while the parabolic model has three parameters (a , b and c). However, the fewer number of adjustable parameters in the linear model may also be considered as an assumption about a natural process (i.e. x^2 does not affect y , therefore $c = 0$). Thus, one should deem the parabolic model as the simpler regarding the number of assumptions, as it has one less assumption than the linear model. Measuring complexity by counting the number of parameters gained much popularity in inferential criteria. However, model complexity in statistics depend on many factors such as parameter redundancy, parameter stability, random error structure of the model, linearity and nonlinearity of parameters and many others (Bozdogan 2000, Taper 2004).

Although it is common practice in ecology and evolution to evaluate models based on their simplicity, it is important to notice that it is difficult not only to justify the use of simplicity in model building and selection, but it is especially difficult to measure and compare the simplicity of models. While the parsimony of ecological theories is sometimes judged and compared without a clear epistemological justification, completely ignoring parsimony may lead to uninterpretable over-fit models, with hundreds of adjustable parameters (e.g. Phillips et al. 2006, Rangel and Loyola 2012).

The parsimonious view of the parsimony principle

In this paper we discussed the challenge of justifying, measuring and trading-off simplicity/complexity. The parsimony principle can be dangerously used as a silver bullet to solve any argument when contrasting theories, hypothesis and models. Of course, we do not view the instrumental use of simple models as a problem. Indeed, they require less effort to fit and specially to understand. However, the usefulness of simplicity is not a valid justification to judge reliability. Ecologists would benefit from evidential statistics (Taper and Ponciano 2016) when evaluating their theories, models and hypothesis. Evidential statistics has in its core a measure of strength of evidence of a proposition about the studied phenomenon, and is explicit when not enough data is available to reach a conclusion (i.e. indeterminacy). Unfortunately, the framework of evidence statistics is new and has received little attention in ecology and evolution (Taper and Ponciano 2016).

Invoking the parsimony criterion in ecology and evolution is particularly important when building and comparing correlative models, in which theory plays only a modest role, whereas data is critical to decide the structure of the model. Thus, the parsimony principle tends to become even more important with the growing scientific use of big data, deep learning and artificial intelligence techniques, in which scientists use computing power to automate the building of predictive models, without emphasis in understanding or explaining natural phenomena. However, when natural mechanisms are explicitly modelled as representations of causal explanation of biological phenomena, the application of the parsimony principle to judge the plausibility of mechanistic models would imply a realistic belief in a simple nature. Thus, enforcing the parsimony principle in evaluating explanatory mechanistic models could halt the advance of ecology and evolutionary biology. We hope that ecologists and evolutionary

biologists, in their roles as authors, reviewers and editors, use the parsimony principle parsimoniously.

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**PARTE II - DINÂMICA NEUTRA BIOGEOGRÁFICA NA ESTRUTURAÇÃO
ESPACIAL DA BIODIVERSIDADE**

CAPÍTULO 2

EFFECTS OF NEUTRALITY AND PRODUCTIVITY ON MAMMAL RICHNESS AND EVOLUTIONARY HISTORY IN AUSTRALIA

**Effects of neutrality and productivity on mammal richness and evolutionary
history in Australia**

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Abstract Explaining how heterogeneous spatial patterns of species diversity emerge is one of the most fascinating questions of biogeography. One of the great challenges is revealing the mechanistic effect of environmental variables on diversity. Correlative analyses indicate that productivity is associated with taxonomic, phylogenetic, and functional diversity of communities. Surprisingly, no unifying body of theory have been developed to understand the mechanism by which spatial variation of productivity affects the fundamental processes of biodiversity. Based on widely discussed verbal models in ecology about the effect of productivity on species diversity, we developed a spatially explicit neutral model that incorporates the effect of primary productivity on community size and confronted our model's predictions with observed patterns of species richness and evolutionary history of Australian terrestrial mammals. The imposed restrictions on community size create larger populations in areas of high productivity, which increases community turnover and local speciation, and reduces extinction. The effect of productivity on community size modeled in our study causes higher accumulation of species diversity in productive regions even in the absence of niche-based processes. However, such a simple model is not capable of reproducing spatial patterns of mammal evolutionary history in Australia, implying that more complex evolutionary mechanisms are involved. Our study demonstrates that the overall patterns of species richness can be directly explained by changes in community sizes along productivity gradients, supporting a major role of processes associated with energetic constraints in shaping diversity patterns.

Keywords: Neutral theory, community size, phylogenetic diversity, diversity gradients, energetic constraints, neutral biogeography

Resumo Explicar como padrões espaciais heterogêneos de diversidade de espécies emergem é uma das questões mais fascinantes da biogeografia. Um dos maiores desafios é revelar o efeito mecanístico de variáveis ambientais na diversidade de espécies. Análises correlativas indicam que produtividade primária está associada com diversidade taxonômica, filogenética e funcional de comunidades. Surpreendentemente, nenhuma teoria unificadora foi desenvolvida para entender o mecanismo pelo qual a variação espacial de produtividade afeta processos fundamentais da biodiversidade. Baseado em modelos verbais amplamente discutidos em ecologia sobre o efeito de produtividade na diversidade de espécies, nós desenvolvemos um modelo espacialmente explícito que incorpora o efeito de produtividade primária no tamanho de comunidades e confrontamos as previsões do nosso modelo com o padrão observado de riqueza e história evolutiva de mamíferos terrestres na Austrália. As restrições espaciais de tamanho de comunidade criam populações maiores em áreas de maior produtividade e causam o aumento de especiação e turnover na comunidade, e também reduz extinção. O efeito de produtividade nos tamanhos de comunidades modeladas em nosso estudo causa maior acúmulo de diversidade de espécies em regiões produtivas mesmo na ausência de processos baseados em nicho. No entanto, esse modelo simples não é capaz de reproduzir padrões espaciais de história evolutiva de mamíferos na Austrália, o que indica que mecanismos evolutivos mais complexos estão envolvidos. Nosso estudo demonstra que padrões de riqueza de espécies podem ser diretamente explicados por mudanças em tamanhos de comunidades ao longo de gradientes de produtividade dando suporte ao grande papel de processos associados com restrições energéticas na estruturação de padrões de diversidade.

Palavras-chave: Teoria neutra, Tamanho de comunidade, Diversidade filogenética, Gradientes de diversidade, Restrições energéticas, Biogeografia neutra

Introduction

Understanding how heterogeneous spatial patterns in species diversity emerge is one of the oldest and most fascinating objectives in biogeography. The description of these patterns dates back to observations made by early naturalists on long expeditions around the world (Hawkins 2001) and remains the focus of contemporary studies (Brown 2014). Although it is increasingly recognized that general mechanisms can explain spatial patterns of species diversity (Turner 2004), ecologists are far from reaching a consensus (Brown 2014).

Over more than a century, a plethora of ecological and evolutionary hypotheses have been proposed to explain spatial patterns of species diversity (Evans et al. 2005). On the one hand, evolutionary and biogeographical models determine the importance of immigration, speciation, and extinction on species distribution (MacArthur and Wilson 1967, Hubbell 2001, Allen et al. 2007). On the other hand, correlative analyses indicate that environmental factors, mainly productivity and temperature, are associated with the taxonomic, phylogenetic, and functional diversity of communities (Hawkins et al. 2003a, b, Davies et al. 2007, Safi et al. 2011). Although a positive association between productivity and diversity is commonly observed (Evans et al. 2005), the mechanisms by which productivity affects fundamental process of biodiversity are not fully understood (Currie et al. 2004, Storch 2012, Brown 2014).

The mechanism underlying the association between productivity and species richness was first proposed in Hutchinson's 'Homage to Santa Rosalia' (Hutchinson 1959), and later revisited by Brown (1981). The proposed hypothesis suggests that the availability of energy can affect the number of individuals in communities, therefore driving the accumulation of species over space and time. This initial spark culminated in the community size (also referred as community abundance) concept (Wright 1983;

Allen et al. 2007, Hurlbert and Stegen 2014) that states that communities in regions with higher resource availability, mostly represented by primary productivity for animals, have larger number of individuals and are consequently less prone to extinction events.

If community size (i.e. total number of individuals) varies over broad spatial scales, simple stochastic events of dispersal, speciation and extinction could alone cause differences in species accumulation over space. Thus, simple neutral dynamics of individuals (Hubbell 2001) could potentially generate uneven distribution of species diversity over space, because larger communities accumulate more random speciation events over time than smaller communities, supporting more local speciation events and less extinction events. Although it is common in community ecology to contrast neutral expectations to observed data (Rosindell et al. 2012), macroecological studies have seldom employed this approach, frequently relying only on correlative analysis. However, simple correlative analysis can show the strength of statistical association between productivity and diversity, but does not properly model the causes of this association (Peck 2004) and thus should be complemented by different model techniques that explore how productivity affects fundamental processes of biodiversity, such as dispersal, speciation and extinction.

Neutral models incorporate dispersal, speciation, and extinction caused by demographic stochasticity (Hubbell 2001) and generate predictions for several biological patterns (Rosindell et al. 2012). Some neutral models incorporate other biological processes, such as niche structure (Gravel et al. 2006, Chisholm and Pacala 2010, Haegeman and Loreau 2011), random interactions between species (Coelho et al. 2017, Coelho and Rangel 2018), natural selection (Rosindell et al. 2015), and metabolic theory (Tittensor and Worm 2016). However, no previous study has evaluated their

power to explain observed gradients of species diversity without violating the assumption of ecological equivalence between individuals (i.e. neutrality assumption). Here we overcome this limitation by employing a stochastic simulation model to understand the causes of the association between mammal diversity and productivity.

Mammal diversity is strongly associated with productivity and this relationship has been maintained for at least the last 20 million years (Fritz et al. 2016). Moreover, mammal abundance and biomass increase in areas of high productivity over broad spatial scales (Oksanen and Oksanen 2000, Aunapuu et al. 2008, Ripple and Beschta 2012, Letnic and Ripple 2017). A strong association of productivity and mammal diversity is observed in the Australian continent where taxonomic and phylogenetic diversity (PD) of vertebrates in general are strongly associated with water availability and productivity (Hawkins et al. 2005, Powney et al. 2010, Rosauer and Jetz 2015). Although correlated to species taxonomic diversity, PD accounts for species evolutionary history and is more discriminant of niche and neutral process than simple measures of taxonomic diversity (Graham and Fine 2008, Cavender-Bares et al. 2009). Thus, exploring the resemblance between simulated and empirical PD can better disentangle the failing or success of the hypothetical effect of productivity to other aspects of diversity (i.e. evolutionary history). Using a spatially explicit individual based simulation model, we explored the effect of productivity on the spatial pattern of terrestrial mammal diversity in Australia. Based on the proposed effect of productivity on community size (Brown 1981, Wright 1983, Allen et al. 2007), we assumed that community size varies over the Australian continent following the spatial variation of primary productivity and tested the association of species richness and phylogenetic diversity predicted by our model with empirical data for mammals.

We hypothesize that as community size changes from spatially constant, as usually assumed in neutral models (Davies et al. 2011, Coelho et al. 2017), to uneven following a primary productivity gradient, the power of our model to predict the empirical patterns of mammal diversity would increase. With uneven distribution of community size over space, more speciation and less extinction events would occur in larger communities, which could lead to higher accumulation of species diversity over space and time (Brown 1981, Allen et al. 2007). Because species dispersal can be more important than in-situ diversification for vertebrates at global scales (Belmaker and Jetz 2015) we expected that differences in dispersal and in-situ speciation could have imprints in the spatial patterns of diversity. Thus, we tested how the predictive power of our model changes when varying the effect strength of primary productivity on community size, as well as under different scenarios of dispersal and speciation. Finally, we hypothesize that neutral events (i.e. random events independent of species identity) of dispersal and speciation are intensified in areas with high primary productivity and affect the turnover of species composition over space and time. Temporal turnover in species composition is indeed expected for larger communities (Allen et al. 2007, Tittensor and Worm 2016), which under neutral community dynamics could gain more species by immigration and speciation and finally affect the accumulation of species richness and evolutionary history over time. Thus, we explored in greater detail the spatial pattern of the turnover in species composition that emerges from our neutral biogeographical simulation.

Material and methods

Spatialized Biotic and climatic data

Australian terrestrial mammal species richness was mapped in an equal-area grid map with Behrman projection based on expert range maps (IUCN 2010). Equal area grid cells of approximately 110 km resolution (equivalent to 1° at the equator) were used because it is the most appropriate grain for these types of data (Belmaker and Jetz 2011). We characterized each cell in the grid map by its net primary productivity (NPP). NPP ($\text{g C m}^{-2} \text{ year}^{-1}$, 0.5°) was obtained through a dynamic vegetation model, MC1 (Bachelet et al. 2001) because estimates of NPP derived from satellite images in arid areas are unreliable due to problems of image processing (Pettorelli et al. 2005).

The phylogenetic diversity of Australian mammals was also mapped in our gridded map. We used Fritz et al. (2009) mammal super-tree as our source of phylogenetic information. Phylogenetic and spatial data were aligned and pruned to the Australian continent, resulting in a final dataset of 255 species with both phylogenetic and spatial information. To account for phylogenetic uncertainty due to the lack of molecular information (Rangel et al. 2015), 250 trees were randomly drawn from the Bayesian posterior distribution of fully resolved trees generated by Kuhn et al. (2011) to resolve polytomies in the supertree (Fritz et al. 2009), providing more realistic branch length distribution than a single tree (Rosauer and Jetz 2015). Phylogenetic variables were calculated separately for each of the 250 trees and averaged. We computed the phylogenetic diversity (PD) in each cell by summing the branch lengths linking all the taxa occurring in a grid cell to the root of the tree (Faith 1992). Because PD and species richness are strongly correlated, here we disentangled them by comparing the observed PD values in each geographical cell with null models that were randomly drawn species from the regional species pool (i.e. Australian continent). Geographical cells with greater PD than expected by species richness will present positive values of sesPD (standardized effect size of PD) while cells with negative values of sesPD present less

PD than expected by species richness. We calculated the sesPD for the simulated and empirical data as follows:

$$sesPD = \frac{PD_{obs} - \overline{PD_{null\ model}}}{SD_{null\ model}}$$

where $\overline{PD_{null\ model}}$ is the mean PD calculated based on 999 randomizations of species drawn from the regional pool and $SD_{null\ model}$ its standard deviation. For the simulated data, sesPD is calculated for each model replicate and averaged among replicates.

Neutral simulation model

We developed a neutral individual-based simulation model to understand the effect of productivity on fundamental processes of biodiversity. Neutral models purposely disregard niche-based processes to test the importance of missing mechanisms on the emergence of recurrent ecological patterns. Our model follows the basic assumptions of neutral models, in concordance with recent implementations of neutral simulations (Boucher et al. 2014, Tittensor and Worm 2016, Coelho et al. 2017): 1) individuals are ecologically equivalent in probability of death, birth, dispersal and speciation, independent of their species identity (i.e. neutrality assumption) and 2) neutral stochastic events occur in saturated communities. Based on the broadly discussed hypothesis of the effect of productivity on diversity (Hutchinson 1959, Brown 1981), our model assumes that environmental productivity affects the size of communities (i.e. number of individuals in each community) over the geographical domain. Despite the regulatory effect of the environment on the number of individuals in each community, the model is still neutral in the sense that individuals do not differ in their competitive abilities or their adaptation to environmental conditions. Model overview, design concepts, details (ODD, Grimm et al. 2010) and algorithm are available as supplementary material.

The neutral diversification of an artificial biota was simulated on the gridded map of the Australian continent. The geographical domain was initially populated by individuals of an ancestral species. At each time step one individual was randomly chosen to undergo neutral events of death, reproduction, dispersal, or speciation. The randomly chosen individual speciates with probability v (see ‘speciation mode’ in Supplementary material Appendix 1) or dies with probability $1-v$ (Davies et al. 2011, Coelho et al. 2017). If the randomly selected individual dies, the empty spot where it occurred is colonized by an immigrant descended from a randomly chosen individual from the eight neighboring grid cells (with probability m), or by a descendent of an individual of the same cell where the death event occurred (with probability $1-m$). This dynamic is simulated for a given number of generations, considering one generation to be equal to the minimum amount of time required for the replacement of all individuals in the domain (Boucher et al. 2014). To ensure the convergence of model predictions, each simulation was run for 6000 generations.

The neutral simulation dynamic runs over a geographical domain that presents different number of individuals in each community based on the effect of productivity on community size (Fig. 1). We modeled the effect of productivity on the number of individuals in each community assuming that the number of individuals in each community (represented as grid map cells) is linearly associated with NPP in a logit scale (Bolker 2008):

$$J = \frac{N(e^{\alpha+\beta*P})}{1 + e^{\alpha+\beta*P}}$$

where J represents the estimated number of individuals at each grid cell, N the maximum number of individuals that a geographical cell can reach, α the intercept of the curve (average number of individuals), β the slope of the curve (effect of

productivity on community size), and P the productivity represented by the NPP of each grid cell.

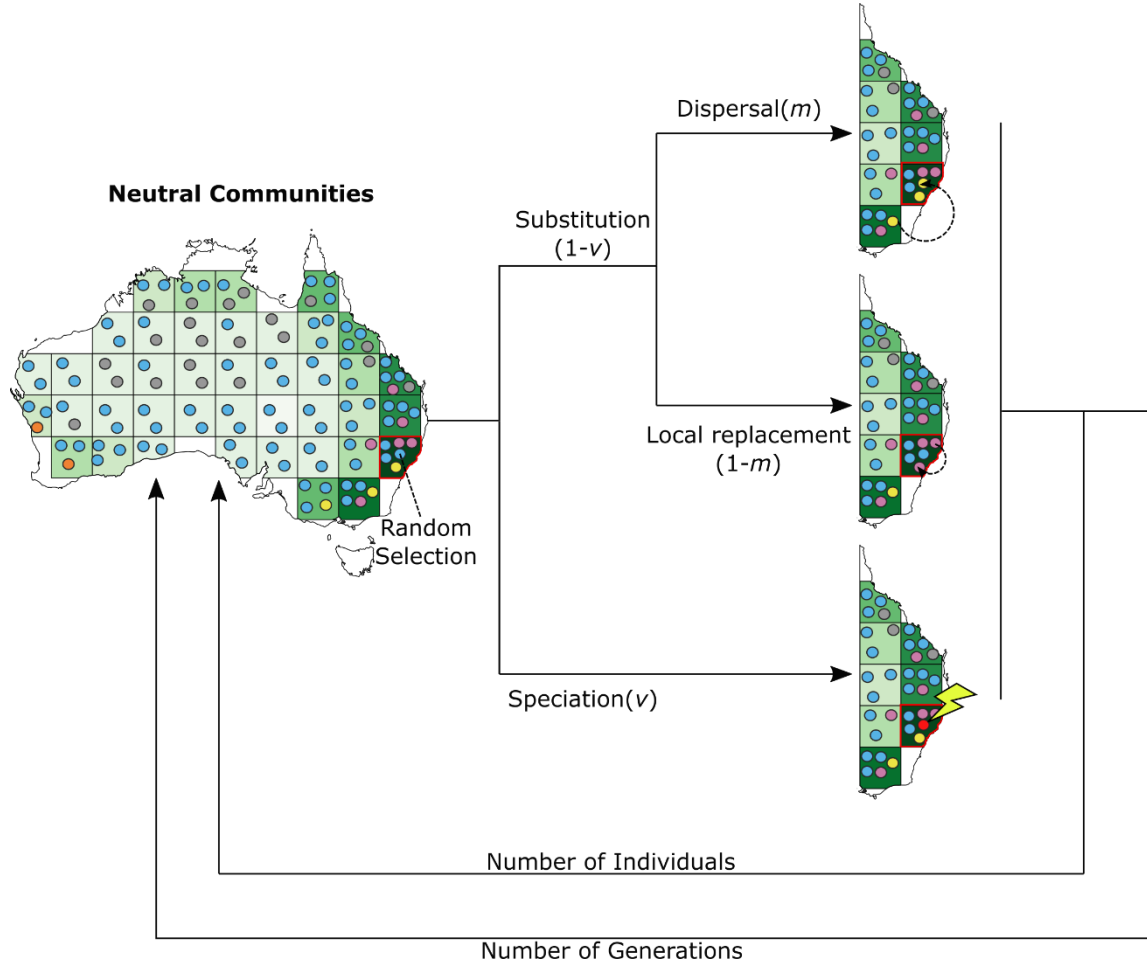


Fig. 1 – Simplified graphical representation of the simulated neutral community dynamics over the Australian continent. Different shades of green define differences in community size over the geographical domain. At each model time step, one individual is randomly chosen and can undergo probabilistic events of speciation or death with subsequent substitution (from the descendants of individuals of the same cell, or by a dispersal event). The model runs for predefined number of generations, one generation being the amount of time necessary for all individuals to die in the simulation and be replaced.

The logit function is used to represent the limitation imposed by space on the maximum number of individuals, alongside with limitation by productivity. In our model, each equal area grid cell represents the geographic delimitation of communities. A maximum number of individuals (N) is defined to represent how many individuals a community can hold when reaching high productivity values. Thus, even if productivity exceeds a saturation limit, space would constraint the maximum number of individuals that a community can support. In our model, the maximum number of individuals, N , was set to 30 for model simplicity and computational tractability. Because the effect of temperature on the diversity of mammals in Australia is much weaker than the effect of productivity ($R^2 = 0.001$ vs $R^2 = 0.56$ Fig. A1 in Supplementary material Appendix1) we did not include temperature in our model.

Parameter sensitivity

We explored the sensitivity of our model to small changes in α and β of the logistic function (effect strength of primary production on community size) as well as changes in dispersal and speciation probability. We also estimated the parameter combination capable of best replicating the spatial pattern of species diversity in the Australian continent. The multi-dimensional ‘parameter landscape’ is defined by the parameters of the logistic function (α and β), dispersal limitation (m) and speciation rate (v), which we explored using a Gibbs sampling Monte Carlo Markov Chain (MCMC) simulation (Gelman et al. 2013). This method can be used to evaluate the effect of parameters on the predictive power of the model (e.g. model goodness-of-fit, f). Instead of maximizing the model predictive power, the sampler provides a complete picture of the parameter landscape, which can be described by the density of sampled parameters within a given parameter region. The density of sampled parameters can be used to

estimate the uncertainty and sensitivity of the analysis. The summary statistic used in the Gibbs sampler (f) is a pseudo-likelihood measure (i.e. probability of data given the model parameters) approximated by a goodness-of-fit measures. Here, f is approximated by the Pearson's coefficient of linear correlation between observed and predicted species richness (see 'parameter estimation' in Supplementary material Appendix 1).

Evaluating the turnover in species composition

We quantified the change of species composition over time for each geographical cell in the geographical domain. We calculated the turnover through Simpson pairwise dissimilarity (Baselga 2010): $\beta_{\text{sim}}(t, t11) = \min(b,c)/a - 1 \min(b,c)$, where 'a' is the number of species that a geographical cell share between times t and $t11$, whereas 'b' and 'c' are the exclusive species of respectively the cell in time t , and in the cell in time $t11$. The Simpson pairwise dissimilarity was calculated for 6000 generations and averaged.

Results

We found that the strength of the effect of primary productivity on community size helps to determine the accumulation of species diversity. As community size moves from constant to uneven with strengthening influence of primary productivity, the power of our model to predict empirical patterns of mammal diversity in Australia increases (Fig. 2) reaching a maximum prediction of approximately 0.77 (Pearson's coefficient of linear correlation). Under the full spectrum of differences on community size across space, the model's prediction is maintained even when different ratios between speciation and dispersal (v/m) are assumed (Fig. 2). Thus, the effect of dispersal and speciation is almost negligible when primary productivity affects

community size. The only situation in which different values of dispersal and speciation probability show an influence (albeit small) on the spatial pattern of species richness, is when the effect strength of primary productivity is held constant and dispersal is highly limited ($m \sim 0$) between communities, or when the probability of speciation is extremely low ($v \sim 0$) (Supplementary material Appendix 1 Fig. A2).

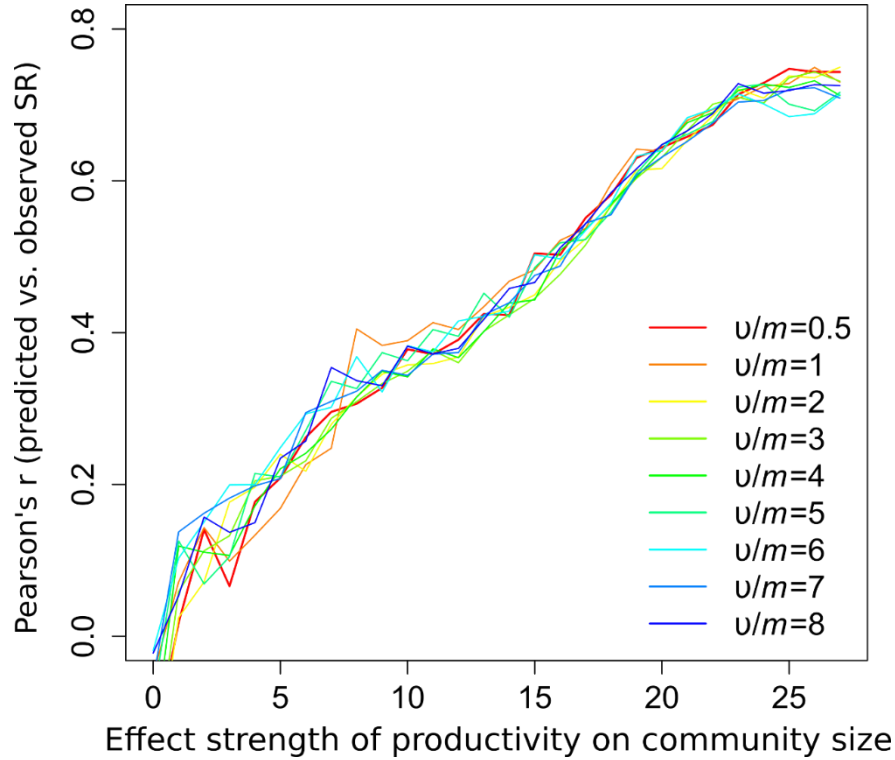


Fig. 2 – Association between predicted and observed species richness under different effect strength of primary productivity on community size in a neutral simulation model. Effect strength of productivity on community size is defined by modifications of the free parameters of the logit relationship between productivity and community size (α and β , Table S1). Different ratios between speciation and dispersal probability (v/m) were tested to explore their effects on model's prediction but have minimal effect on predictions of species richness.

By exploring the parameter space through the Gibbs MCMC (Supplementary material Appendix 1 Fig. A3), a strong association between empirical and simulated species richness emerges ($r = 0.77$, Fig. 3). When primary productivity affects the size

of communities over Australia, empirical and simulated richness are similar in their spatial distribution (Fig. 3a, b), but the model overestimates species richness in the east coastal region and underestimates richness in central Australia (Fig. 3c). On the contrary, by assuming that primary productivity has no effect on community size, as traditional neutral models do, species richness is concentrated in the center of the domain and decreases towards the borders (Fig. 3e) and thus, the relationship between the model's prediction and empirical richness is negative ($r = -0.15$; Fig. 3g.).

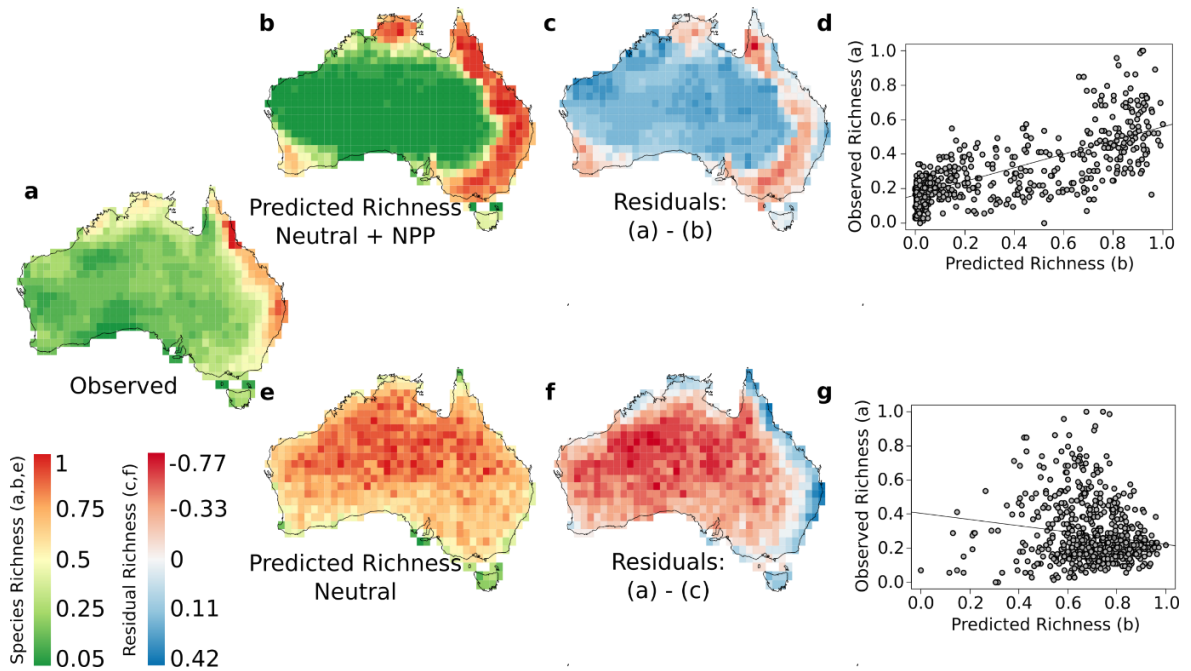


Fig. 3 - Performance of the neutral model with parameters estimated by a Gibbs sampler MCMC. **a**, Observed spatial pattern of mammal richness in Australia. **b**, prediction of mammal richness in Australia of a neutral model that incorporates the effect of productivity on community size. **c**, residuals of the **a** against **b**. **d**, relationship between the patterns on maps **a** and **b** ($r = 0.77$). **e**, prediction of mammal richness in Australia by a basic neutral model (even community sizes across Australia). **f**, residuals of **a** against **e**. **g**, Relationship between the patterns in maps in **a** and **e** ($r = -0.15$). Because the number of individuals of real-world species is unknown and computationally intractable, we cannot produce a simulated absolute value of richness in the same scale

as the empirical richness. Thus, we standardized the observed and predicted richness (ranging from 0 to 1) to calculate the residual maps (*c* and *f*).

All the results described above present the same pattern for Faith's PD because of its strong association with species richness ($r = 0.92$). Thus, as we expected, the turnover in species composition is high in the same areas where empirical richness and PD are also high (Fig. 4). However, when controlling PD for species richness (sesPD), the neutral model fails to predict the accumulation of pure evolutionary history even when productivity affects community size (Fig. 5, Supplementary material Appendix 1 Fig. A4). In fact, the relationship between observed and predicted sesPD is negative for the model that assumes the effect of productivity in community size and for the model that does not. For the empirical data, PD is greater than expected by species richness for the majority of localities in the Australian continent (Fig. 5a). This pattern is due to the highly divergent monotremes which occur throughout the study area. When monotremes are excluded from the analysis, areas where PD is lower than expected by species richness can be observed (Supplementary material Appendix 1 Fig. A4) and the negative relationship between predicted and simulated evolutionary history is maintained (Supplementary material Appendix 1 Fig. A4).

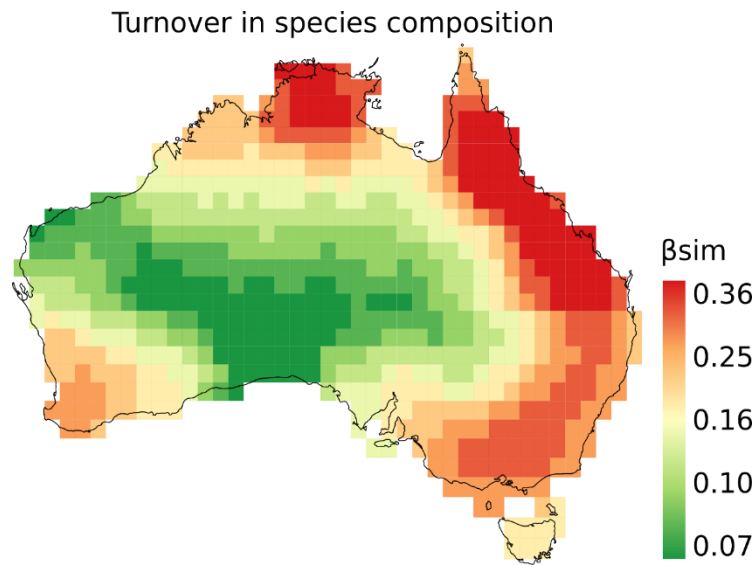


Fig. 4 – Turnover in species composition over time in our neutral model simulation. Turnover was calculated by the Simpson pairwise dissimilarity of species composition over time in each geographical cell (β_{sim}) and averaged for 100 model replicates.

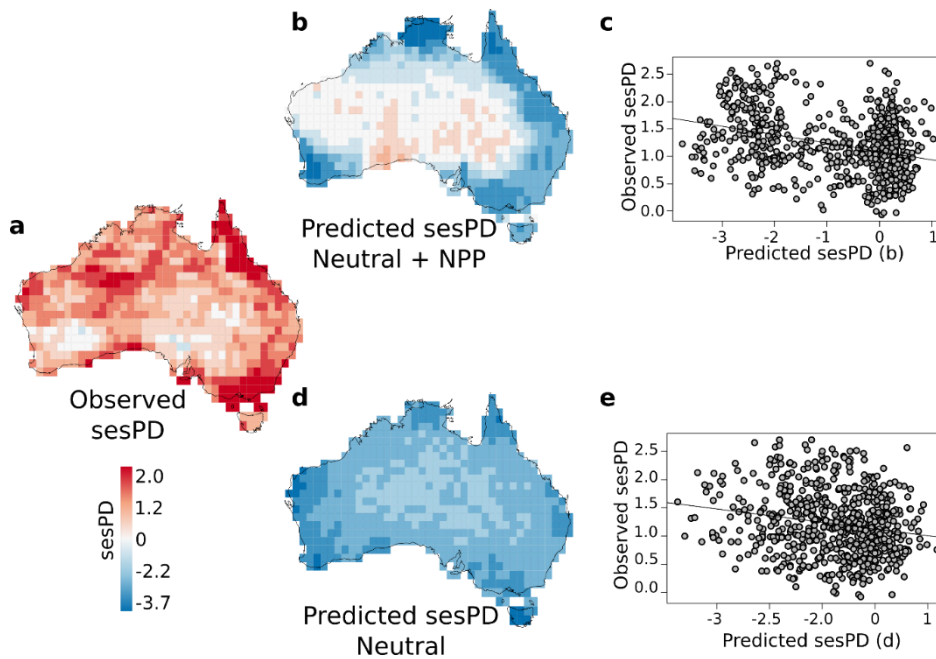


Fig. 5 – Standardized effect size of PD (sesPD) for observed and predicted data. **a**, observed sesPD for terrestrial mammals in Australia; **b**, the sesPD predicted by a neutral model that incorporates the effect of productivity on community size; **c**, relationship between observed **a** and predicted **b**; **d**, the sesPD predicted by a neutral model that assumes no effect of productivity; **e**, the relationship between observed **a** and predicted **d**.

Discussion

Taxonomic and phylogenetic diversity of communities are strongly associated with productivity (Wright 1983, Gaston and Blackburn 2007). However, a debate exists about the mechanisms underlying the associations between diversity and productivity (Evans et al. 2005, Šímová et al. 2011, Belmaker and Jetz 2015). Based on the verbal models proposing the effect of productivity on community size (Hutchinson 1959, Brown 1981, 2014), we designed a simple neutral model in which community size varies over space, as a function of local productivity, to better understand the mechanism underlying the association between diversity and primary productivity. Linking the number of individuals to productivity creates larger populations in areas of high productivity, which increases community turnover and local speciation, and reduces extinction. This simple mechanism leads to higher accumulation of species diversity in productive regions even in the absence of niche differences between individuals. Our process-based model supports the role of mechanisms associated with energetic constraints on population sizes (Wright 1983, Allen et al. 2007). However, our simple model is not capable of reproducing spatial patterns of mammal evolutionary history in Australia and not totally the species richness pattern (Fig. 3, 5).

In Australia, mammal richness is positively associated with productivity (McKenzie et al. 2007). The peaks of diversity in the continent for amphibians, birds, and mammals are in the wetter regions along the east and north coasts (Powney et al. 2010), whereas diversity is low in the arid western and central regions (Hawkins et al. 2005). Previous studies have suggested that complex processes of diversification (Hawkins et al. 2005) and habitat heterogeneity (Williams et al. 2002), associated with the productivity gradient, determine the patterns of vertebrate diversity in Australia.

Here, we showed that with community size varying with primary productivity, spatial patterns of species diversity emerge even under simple neutral community dynamics.

In contrast to predictions of empirical observations of species diversity in Australia, neutral models usually predict higher diversity at the center of a domain (Fig. 3c, Rangel and Diniz-Filho 2005, Economo and Keitt 2010, Dambros et al. 2015).

When carrying capacity is constant across space, as in most neutral models (Economo and Keitt 2010, Davies et al. 2011, Coelho et al. 2017), species diversity is determined only by species dispersal between adjacent communities. For example, islands that are closer to the mainland, and therefore receive more immigrants, have higher diversity than isolated islands (Kalmar and Currie 2006, 2007). In continental areas, communities at the periphery of a domain receive fewer immigrant species than central communities because of the reduced number of neighboring communities at the edges of the domain (Rangel and Diniz-Filho 2005). In contrast to these predictions, we demonstrate that neutral models can create spatial patterns of species richness that better match empirical gradient of species diversity when the environment determines the number of individuals in a community. Thus, instead of predicting higher diversity at the center of the domain (Rangel and Diniz-Filho 2005), the model predicts higher diversity in the productive regions along the east and north coast and low diversity in the arid western and central regions of Australia (Fig. 3b).

Fritz et al. (2016) showed that the relationship between mammal diversity and productivity has been maintained for the last 20 million years. Several studies suggest that biomass and abundance of endothermic predators and herbivores at large spatial scales are well explained by productivity (Oksanen and Oksanen 2000, Aunapuu et al. 2008, Ripple and Beschta 2012, Letnic and Ripple 2017), which supports the hypothesis that productivity could affect community size over space. However, it is important to

note that global relationships of herbivore biomass and abundance with productivity can be weakened by predation (Letnic and Ripple 2017). Thus, although community size could indeed vary over broad spatial scales, the relationship between mammal abundance and productivity could be affected by several niche-based processes that are purposely absent from neutral models.

The large number of individuals in areas of high productivity can lead to increases in diversity due to sampling effects (Gotelli and Graves 1996) and the reduction of extinction rates in large populations (MacArthur and Wilson 1967, Wright 1983). Recent studies suggest that gradients of temperature and productivity are associated with species diversity even when sampling effects are statistically controlled (Currie et al. 2004, Šímová et al. 2011). Diversification processes incorporated into neutral models (i.e. random speciation and extinctions) could explain the emergent association of diversity and productivity (Fig. 3b) in the absence of sampling processes. Neutral models include mechanisms associated with speciation and extinction (Hubbell 2001) and offer an opportunity to integrate multiple processes into a unified framework (Tittensor and Worm 2016). Here, we showed that integrating the effect of productivity on community size into the neutral theory of biodiversity framework can explain overall patterns of species richness.

In addition to sampling effects and extinction, several other processes have been suggested to explain large scale gradients in species diversity (Evans et al. 2005, Allen et al. 2007). Temperature (contemporary, or historical) can affect diversity through several mechanisms (Jetz and Fine 2012), species dispersal can be more important than in situ diversification for birds and mammals at global scales (Belmaker and Jetz 2015) and historical factors could affect mammal evolutionary history. As we found, the hypothesis for the effect of productivity on species taxonomic diversity is not adequate

to predict evolutionary history (Fig. 5). The absence of kinetic effect of temperature (Tittensor and Worm 2016), niche-based processes (e.g. trophic interactions (Letnic and Ripple 2017), climatic niche conservatism (Rangel et al. 2007), adaptation to arid environments (Powney et al. 2010) and historical factors could be a possible reason for the unrealistic evolutionary history that emerges from our model and the residuals of species richness prediction (Fig. 3c). Such a simplistic model is not expected to capture the millions of years of unique evolution of mammals in Australia and thus fails in this attempt.

Several historical factors of the Australian continent could lead to its unique patterns of evolutionary history, but species richness seems strongly explained in their absence. For example, past connections of northern Cape York and New Guinea led to a long history of biotic exchange and have an imprint in regional mammal diversity (Williams et al. 2002). Additionally, the wet eastern biome represents a historically larger biome which has retreated with the drying of the continent, while the arid zone is more recent (Byrne et al. 2011). Our model captures the effect of population sizes and dispersal under contemporary conditions, but not historical factors such as biome history or changes in primary productivity over time. The drying of the Australian continent (Hawkins et al. 2005) is a recent event in mammalian evolutionary history, with imprints on contemporary patterns of species richness and evolutionary history. Thus, past immigration events as well as history could explain differences from predicted and observed patterns of mammalian evolutionary history and the unexplained variation of species richness in our model.

Nevertheless, our results demonstrate that the overall patterns of species richness can be directly explained by changes in community size along productivity gradients, supporting a major role of processes associated with energetic constraints (Hutchinson

1959, Brown 1981, Wright 1983). Additionally, our findings support the neutral theory of biodiversity (Hubbell 2001), offering a simple mechanism to understand the effect of energy availability on fundamental processes of biodiversity in the absence of niche-based processes.

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Appendix 1

Model Overview, Design Concepts, Details and Algorithm

To overcome the difficulty of describing and replicating the results originated from an Individual Based Model (IBM), here we described the IBM developed in our study following the ODD protocol (model overview, design concepts and details, Grimm et al. 2010).

Overview

Purpose

In this study, we developed a neutral simulation individual-based model. In our model, individuals are ecologically equivalents and empirically estimated environmental productivity affects the size of communities (total number of individuals). The model can be used to understand the underlying mechanism behind the statistical association between diversity and productivity in macroecological scales in the absence of niche-based processes. Thus, we employ the model for a mechanistic evaluation of an ecological question (hypothesis) that has been long verbally discussed: does productivity affect the accumulation of diversity over space and time? (Hutchinson 1959, Brown 1981).

State Variables and Scale

Our model consists in a two-dimensional geographical map space. We used the Australian continent, divided into $1^\circ \times 1^\circ$ equal-area grid cells (664 grid cells). Each cell on the grid is characterized by its geographical coordinates, its community size (number of individuals, J) and the observed Net Primary Productivity (NPP).

The temporal resolution of our model is represented by ‘generations’. One generation is represented by the minimum amount of time (i.e., time steps) required for the replacement (by death, recolonization or speciation) of all individuals in the geographical domain, roughly represented by total number of individuals in the geographical domain (Boucher et al. 2014).

Process Overview and Scheduling

Within each model time step, one individual is randomly chosen and may die, disperse, speciate or reproduce according to probabilities implemented as free parameters (see *Algorithm*). The model runs for a predefined number of generations. For example, if the model runs for 6,000 generations and the carrying capacity of all the geographical cells ($n=664$) is defined by 30 individuals ($J=30$), the model will run for 119,520,000 ($664 \times 30 \times 6,000$) individual replacements. A single simulation is finished when the predefined number of generations is reached. The simulation is repeated with the same parameter sets to produce independent model replicates. Variations between model replicates are caused by stochasticity.

Design Concepts

Emergence

A presence absence matrix (PAM) and a phylogeny emerge from the neutral simulated events, as a consequence of random events of speciation, dispersal, birth and death. A unique PAM and a unique phylogeny are produced for each model replicate.

Interaction

Implicit competition occurs among individuals within the same geographical cell because the number of individuals cannot increase beyond the predefined number of individuals that each cell presents. Thus, it is assumed that resources are limited in each geographical cell, and that communities are saturated with individuals competing for space (Hubbel 2001).

Stochasticity

All events in the model are stochastic. Individuals are randomly chosen from the geographical domain and undertake neutral events that are defined according to probabilities.

Model Results

The PAM and phylogeny (outputs) of the IBM generated for each model replicate is used to compare the simulated patterns of diversity against empirical patterns.

Model Details

Initialization

The model starts with all cells populated by an ancestral species. At each time step one individual is randomly chosen to undergo neutral stochastic events (see *Algorithm*).

Input

We studied the effect of productivity on the emergence of spatial patterns of mammal's diversity in the Australian continent. Thus, the inputs for the model are (i) a

gridded map of the geographical domain and (ii) the Mean Net Primary Productivity extracted for each geographical cell.

Algorithm

1. The pairwise distances among all cells of the Australian gridded map is used to represent the geographical arrangement of the continent. In the simulation, each cell is assumed to be connected with all its adjacent neighboring cells (maximum of eight neighboring cells, for non-coastal cells, i.e., Moore neighborhood).
2. All communities (i.e. geographical cells) are saturated and populated by J individuals that compete only for space. At the beginning of the simulation all individuals belong to the same ancestral species.
3. A single individual is randomly selected across the geographical domain to undergo random demographic events.
4. The randomly chosen individual may speciate (v), or die, based on death probability ($1 - v$).
5. If an event of death is the outcome of the stochastic dynamics, a descendent of a randomly chosen individual (parent) will colonize the empty spot. The parent may be from one of the neighboring cells in an event of dispersal (with probability m), or from the same cell in which the death event occurred ($1 - m$).
6. The model is run for a predefined number of generations, enough to reach stability of the patterns in the metacommunity.
7. Each model replicate (i.e., simulation repeated with the same parameter sets) exports a PAM and a phylogeny.

Submodels

Speciation Mode

Many realistic speciation modes have been proposed for neutral models (Rosindell et al. 2010, Desjardins-Proulx & Gravel, 2012). However, we modeled speciation as an instantaneous event, in compatibility with the broad spatial and temporal scales used in our study, as well as for the sake of simplicity and computational tractability (see Davies et al. 2011 and Boucher et al. 2014 for similar assumptions). In this study, speciation events are modeled by *point mutation* (Hubbell 2001), by randomly selecting one individual among all the individuals of the geographical domain, and altering its species identity based on speciation probability (v). In *point mutation* mode, only the randomly selected individual becomes one of the new daughter species (Incipient species abundance = 1). Phylogenies are thus reconstructed based on the history of speciation events. Thus, in our model, time and phylogeny are measured in units of simulation steps. Consequently, the calculated phylogenetic diversity in the model differs in scale from empirical observations. Anyway, differences in scale and units of variables do not affect Pearson's correlation coefficient, as it measures only the association (standardized covariance) between the variables. However, to calculate and map the residuals (difference between observed and predicted PD values), we standardized observed and predicted PD to the same scale (0 to 1). The same procedure was followed for species richness. The neutral model is not designed to replicate the absolute number of species in nature, as the number of individuals of real-world species is unknown and computationally intractable. Thus, to calculate the map of residual richness (difference between observed and predicted richness) we standardized observed and predicted richness to the same scale (0 to 1).

When comparing the simulated and empirical richness (or PD), we want to reproduce the relative variation of richness across space, not the exact absolute number of real-world species in each grid cell.

The same procedure was followed for species richness because the neutral model is not designed to replicate the absolute number of observed species in nature, as the number of individuals of real-world species is unknown and computationally intractable.

Parameter Estimation

In this study, we tested whether our neutral model, with spatially varying community size, is capable of replicating empirical heterogeneous pattern of mammalian diversity in Australia. The multi-dimensional “parameter landscape” is defined by the parameters of the logistic function (α and β), dispersal limitation (m) and speciation rate (v), which we explored using a Gibbs sampling Monte Carlo Markov Chain (MCMC) simulation. This method can be used to evaluate the effect of parameters on the predictive power of the model (e.g. model goodness-of-fit, f). By design, the sampler explores in greater detail (i.e. more frequently) the areas of parameter space of higher goodness-of fit. It also visits areas of the parameter landscape with lower goodness-of-fit, but with lower frequency. Thus, instead of maximizing the model predictive power, the sampler provides a complete picture of the parameter landscape, which can be described by the density of sampled parameters within a given parameter region. This density of sampled parameter values can be used to estimate the uncertainty and sensitivity of the analysis. Here, the summary statistic used in the Gibbs sampler (f) is a pseudo-likelihood measure (i.e. probability of the data, given the model and its parameters) approximated by the goodness-of-fit measure. f is the estimated

Pearson's coefficient of linear correlation (r) between simulated and empirical richness across the Australian continent.

Here we summarize how the Gibbs sampler operates: (i) the sampler defines a particular parameter combination and launches the simulation model using those parameters; (ii) once the simulation is finished, the predictions of the model, given the parameter set, are extracted; (iii) the goodness-of-fit between (Pearson's r) between observed (real-world) and predicted (simulated) data is calculated; (iv) the simulation is replicated 100 times, using the same parameter combination; (v) the pseudo-likelihood of the model and parameter combination (f) is calculated as the average r among all replicates of the parameter combination; (vi) the sampler generates a disturbance (variation) in the model parameters and returns to step i ; (vii) once the sampler explored the parameter space in great detail, it produces the distribution of all the explored parameters; (viii) the distribution of parameters values are averaged and a parameter set defined with the average values is considered as the estimated parameter set. Note that the parameter set that maximized the model prediction is not used, but the parameter set is calculated based on the average of all parameters sets explored by the model (i.e. those with low, medium or high f to empirical data). We ran the sampler during preliminary evaluations of the model and used previous runs as burn-ins. The initial parameters were based on our previous knowledge of model performance under different values of dispersal, speciation, α and β (see Results section). In our analysis, each model run is defined as a unique combination of parameter values, which is replicated 100 times. We ran $\sim 6 \times 10^5$ replicates to explore $\sim 6,000$ parameter combinations (MCMC iterations – total chain length).

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Table A1. The effect of environment on the predictive power of the model (measured as the correlation between observed and predicted PD of mammals in Australia). The predictive power of the model increases as the effect of productivity in community size gets stronger. The same pattern is observed for different ratios between speciation and dispersal (v/m). The parameters used for different v/m ratios are presented on Table S3.

α	θ	Mean Pearson's r for different ratios between speciation and dispersal rate (v/m) based on 100 replicates								
		0.5	1	2	3	4	5	6	7	8
0	0	-0.15	-0.05	-0.19	-0.18	-0.14	-0.08	-0.01	-0.05	-0.02
-17.83	0.02	0.01	0.07	0.02	0.05	0.11	0.12	0.10	0.13	0.05
-17.31	0.020256	0.14	0.14	0.07	0.11	0.11	0.06	0.15	0.16	0.15
-16.80	0.020513	0.06	0.09	0.17	0.13	0.10	0.10	0.19	0.18	0.13
-16.29	0.020769	0.17	0.13	0.19	0.20	0.17	0.21	0.19	0.19	0.14
-15.77	0.021026	0.20	0.16	0.23	0.21	0.22	0.20	0.24	0.20	0.23
-15.26	0.021282	0.26	0.22	0.21	0.23	0.24	0.27	0.29	0.29	0.25
-14.75	0.021538	0.29	0.24	0.27	0.28	0.27	0.33	0.30	0.30	0.35
-14.24	0.021795	0.30	0.40	0.31	0.30	0.31	0.32	0.36	0.32	0.33
-13.72	0.022051	0.32	0.38	0.34	0.33	0.34	0.37	0.32	0.35	0.32
-13.21	0.022308	0.37	0.38	0.35	0.34	0.34	0.36	0.38	0.34	0.38
-12.70	0.022564	0.37	0.41	0.35	0.37	0.37	0.40	0.37	0.37	0.37
-12.18	0.022821	0.39	0.40	0.36	0.36	0.36	0.39	0.41	0.37	0.37
-11.67	0.023077	0.42	0.43	0.42	0.40	0.40	0.45	0.42	0.42	0.41
-11.16	0.023333	0.42	0.46	0.43	0.42	0.43	0.42	0.42	0.43	0.45
-10.65	0.02359	0.50	0.48	0.44	0.44	0.44	0.48	0.50	0.47	0.46
-10.13	0.023846	0.50	0.52	0.49	0.47	0.50	0.51	0.49	0.48	0.51
-9.62	0.024103	0.55	0.53	0.52	0.51	0.53	0.52	0.53	0.54	0.54
-9.11	0.024359	0.58	0.59	0.56	0.56	0.56	0.55	0.57	0.55	0.58
-8.59	0.024615	0.63	0.64	0.61	0.60	0.60	0.60	0.63	0.60	0.61
-8.08	0.024872	0.64	0.63	0.61	0.63	0.64	0.64	0.63	0.63	0.64

-7.57	0.025128	0.65	0.67	0.65	0.66	0.67	0.66	0.68	0.65	0.66
-7.06	0.025385	0.67	0.69	0.68	0.70	0.68	0.67	0.69	0.67	0.68
-6.54	0.025641	0.71	0.70	0.72	0.70	0.71	0.72	0.71	0.70	0.72
-6.03	0.025897	0.72	0.72	0.70	0.70	0.72	0.72	0.70	0.70	0.71
-5.52	0.026154	0.74	0.72	0.73	0.73	0.72	0.70	0.68	0.72	0.71
-5.00	0.02641	0.74	0.74	0.73	0.74	0.73	0.69	0.68	0.72	0.72
-4.49	0.026667	0.74	0.72	0.74	0.73	0.71	0.71	0.71	0.70	0.72

Table A2. Different ratios between speciation and dispersal rate assumed. Different ratios were assumed to test the effect of speciation and dispersal over the predictions of a neutral model under different environmental gradients (Table S1, Fig 2; Fig ,S2).

v/m	Dispersal rate (m)	Speciation rate (v)
0.5	0.1000	0.0500
1.0	0.0004	0.0004
2.0	0.0214	0.0422
3.0	0.0161	0.0474
4.0	0.0109	0.0448
5.0	0.0056	0.0291
6.0	0.0056	0.0343
7.0	0.0056	0.0396
8.0	0.0056	0.0448

Supplementary Figures

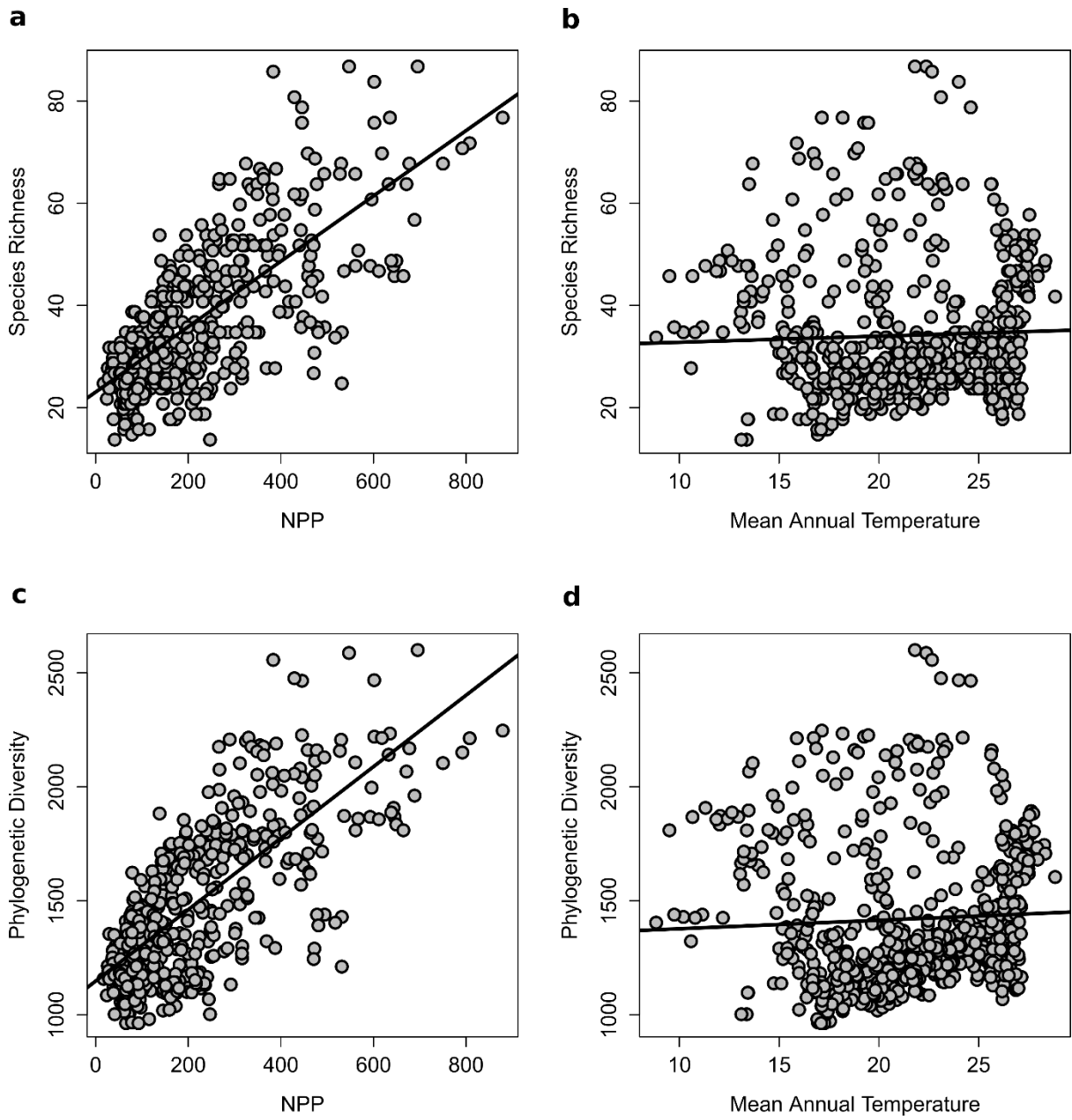


Fig A1. Relationship between observed species richness and phylogenetic diversity with Net primary productivity and Mean Annual Temperature.

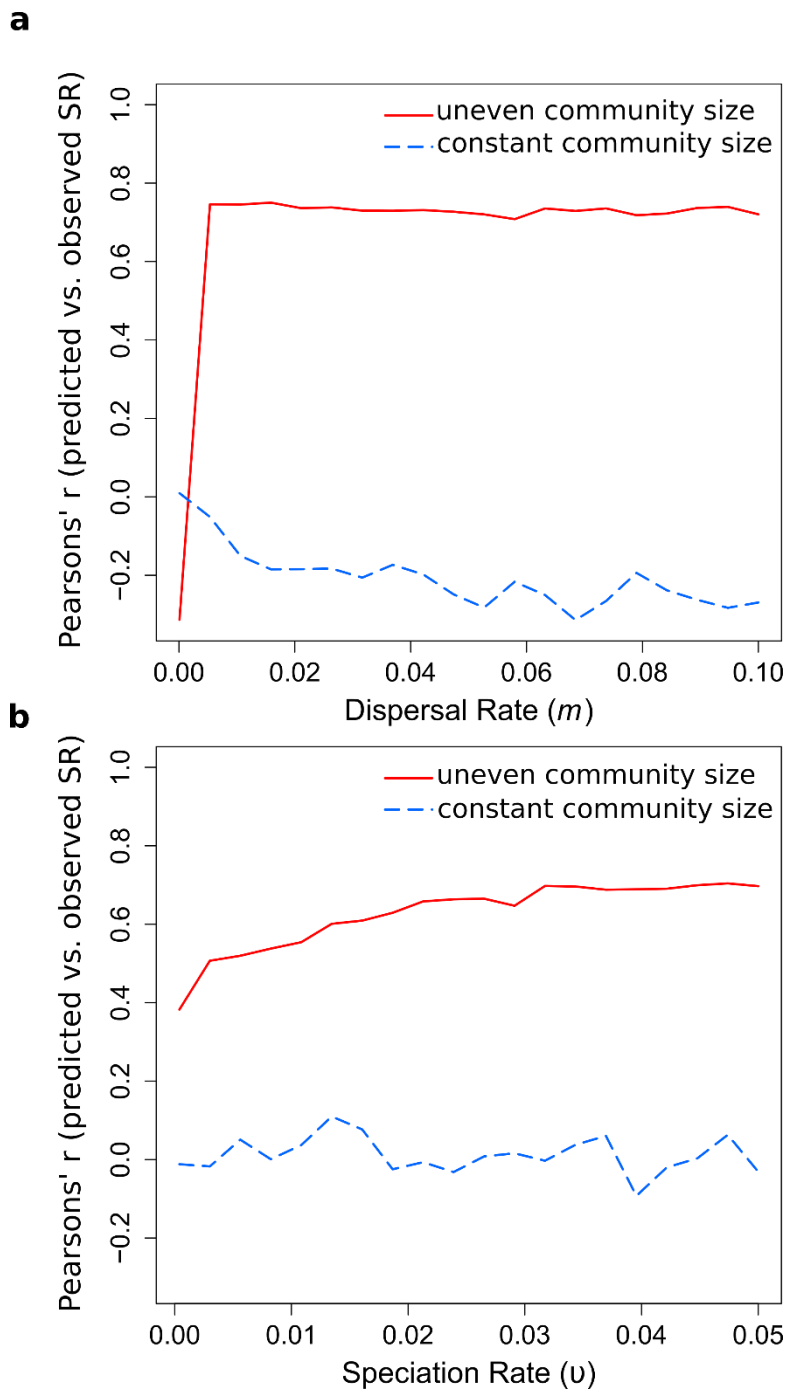


Fig A2 – Effect of dispersal rate (a) and speciation rate (b) on the predictive power of neutral models. The continuous red line illustrates the neutral model that assumes the effect of primary productivity on community size. The dashed blue line illustrates the classical neutral model in which community size is constant over the geographical domain.

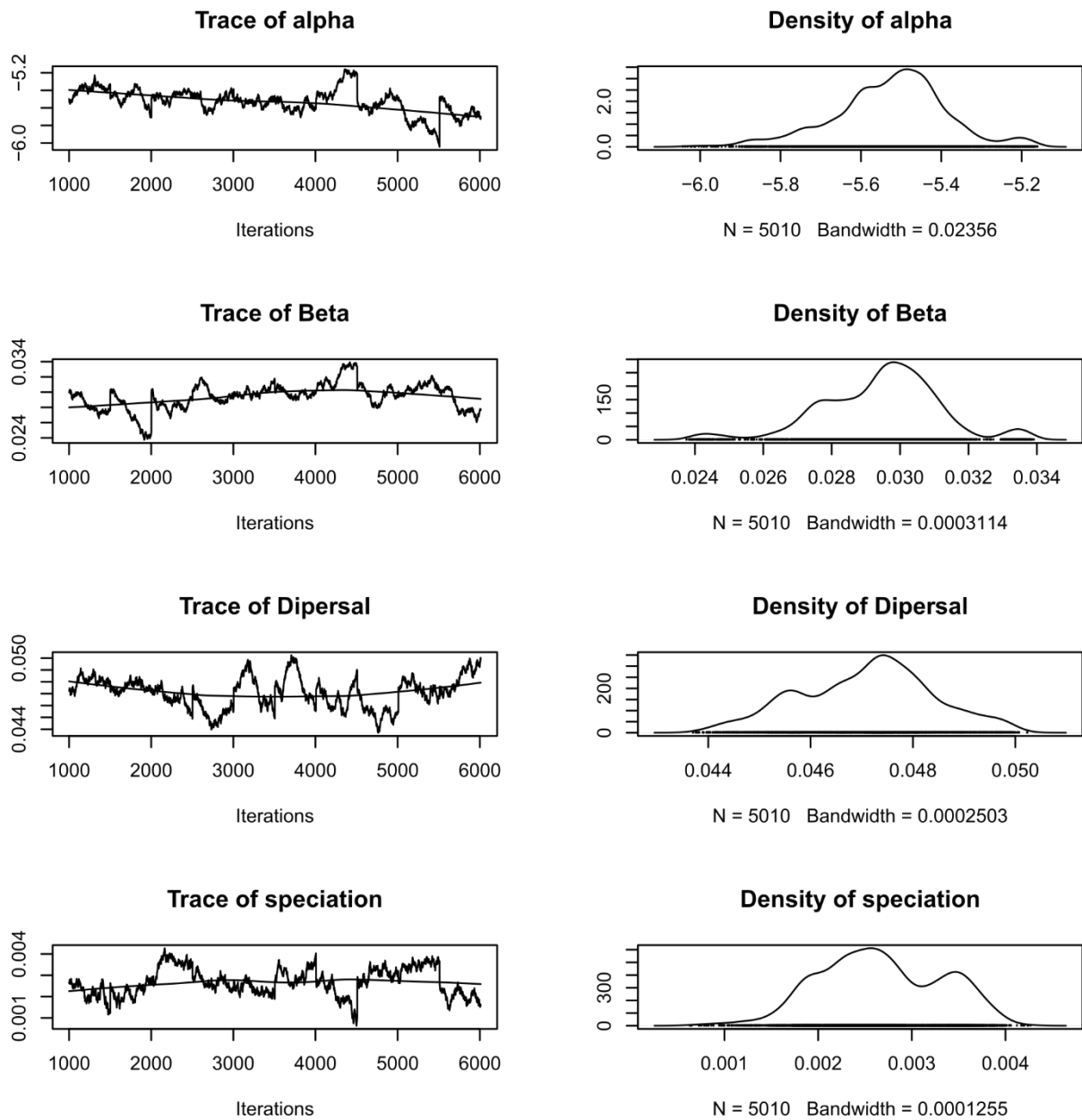


Fig A3. Gibb's MCMC search based on almost 6000 iterations. Parameters were estimated through a mean of their posterior distribution ($\alpha = -5.52774$; $\beta = 0.02942$; $m = 0.04709$; $\nu = 0.00267$).

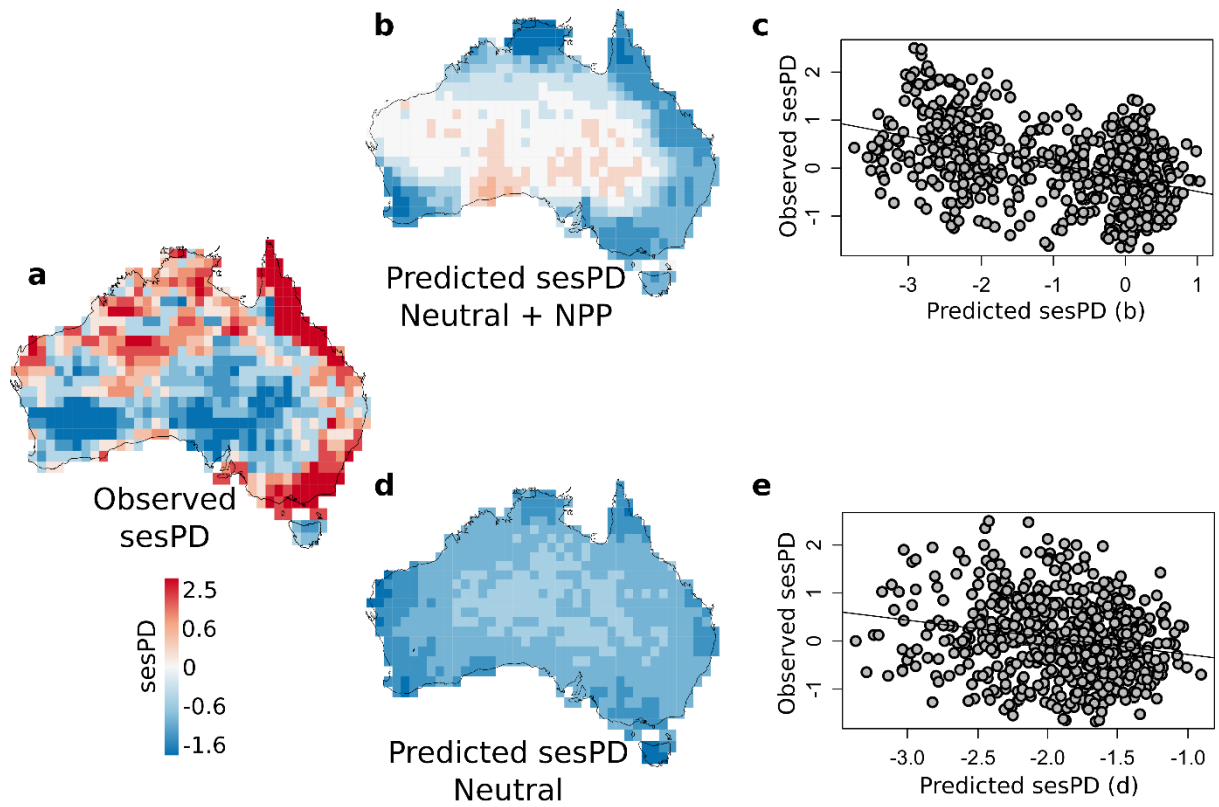


Fig A4. Standardized effect size of PD (sesPD) for observed and predicted data. **a**, observed sesPD for terrestrial mammals in Australia, *excluding monotremes*; **b**, the sesPD predicted by a neutral model that incorporates the effect of productivity on community size; **c**, relationship between observed **a** and predicted **b**; **d**, the sesPD predicted by a neutral model that assumes no effect of productivity; **e**, the relationship between observed **a** and predicted **d**.

CAPÍTULO 3

**LATITUDINAL DIVERSITY GRADIENTS ARE MECHANISTICALLY
PREDICTED BY THE ENERGY HYPOTHESIS UNDER NEUTRAL
COMMUNITY DYNAMICS**

Latitudinal diversity gradients are mechanistically predicted by the energy hypothesis under neutral community dynamics

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Abstract The development of biodiversity theory is generally sustained by qualitative frameworks and correlative analysis, lacking explicit treatments of mechanisms in ecological and evolutionary studies. Here, based on long-debated variants of the energy hypothesis, we developed a neutral stochastic simulation that assumes variation of community size over space according to environmental energy availability (i.e. chemical potential energy effect) and the metabolic effect of temperature on speciation rates (i.e. kinetic energy effect). We confronted our model with empirical latitudinal gradients of bird diversity, and validated it in different regions of the globe, confirming the generality of its predictive power and underlying mechanisms. We show that even in the absence of niche, and assuming simple mechanistic effect of energy on fundamental processes of biodiversity (i.e. dispersal, speciation and extinction), empirical spatial patterns of diversity emerge from neutral metabolic community dynamics.

Key-Words: Chemical potential energy, Energy hypothesis, Kinetic energy, Latitudinal Gradients, Neutral metabolic theory, Neutral Theory, Species Richness.

Resumo O desenvolvimento de teorias da biodiversidade é em geral sustentado por arcabouços qualitativos e análises correlativas, faltando tratamentos explícitos de mecanismos em estudos ecológicos e evolutivos. Nesse trabalho, baseado em variantes amplamente debatidas da hipótese de energia, nós desenvolvemos uma simulação estocástica neutra que assume variações de tamanho de comunidade no espaço de acordo com disponibilidade de energia do ambiente (i.e. efeito potencial químico de energia) e o efeito metabólico da temperatura em taxas de especiação (i.e. efeito de energia cinética). Nós confrontamos o nosso modelo com gradientes latitudinais de diversidade de aves, e validamos o nosso modelo em diferentes regiões do globo, confirmando a generalidade do seu efeito preditivo e dos mecanismos implementados. Nós mostramos que mesmo na ausência de nicho, e assumindo o simples efeito mecanístico de energia em processos fundamentais de biodiversidade (i.e. dispersão, especiação e extinção), padrões empíricos espaciais de diversidade emergem de uma dinâmica neutra e metabólica de comunidades.

Palavras-Chave: Energia potencial química, hipótese de energia, energia cinética, Gradientes latitudinais, Teoria neutra metabólica, Teoria neutra, Riqueza de espécies

Introduction

Descriptions of latitudinal gradients in species richness date back to the XIX century and emerged from observations and data collected during early naturalist's expeditions across the globe (Hawkins 2001). Over the decades, descriptions of latitudinal gradients were expanded beyond plants and animals (e.g. genomes, clades of higher taxa, human cultures and languages), which generalized the increase in diversity in low latitudes beyond species level (Willig et al. 2003, Brown 2014, Fine 2015). However, although ecologists have accumulated more data over the decades, we are still challenged by the outstanding challenge of understanding the drivers of heterogeneous spatial patterns of biodiversity.

Among a plethora of hypotheses, increased attention has been given to a major environmental hypothesis for large scale patterns of species diversity, namely the energy hypothesis (Evans et al. 2005, Currie et al. 2004, Brown 2014). Correlative analyses showing a positive relationship between species diversity and proxies of energy availability in the environment (e.g., temperature, potential evapotranspiration, actual evapotranspiration and precipitation) (e.g., Field et al. 2009), led to the development of two variants of energy effects: (i) chemical potential energy and (ii) thermal kinetic energy (Allen et al. 2007).

The effect of chemical potential energy was explicitly proposed by Hutchinson's seminal "Homage to Santa Rosalia" (Hutchinson 1959), and further developed by Brown (1981) two decades later. The capacity rules (Brown 1981) described the effect of energy availability on the amount of energy flowing through the food webs. Thus, more availability of heat, light, and water would cause higher accumulation of species diversity due to the increase of available energy. This idea was mathematically formulated later by Wright (1983), culminating in the community abundance concept

of the Metabolic Theory of Ecology (Allen et al. 2007, Hurlbert and Stegen 2014). The abundance concept states that communities in areas with more available energy have larger number of individuals and are consequently less prone to extinctions (Hubbell 2001).

The second variant of the energy hypothesis, the thermal kinetic effect, is characterized by the effect of temperature on biochemical reaction rates (Rohde et al. 1962, Allen et al. 2002, Brown et al. 2004). Thus, temperature affects the metabolism of organisms leading to shorter generation times, higher mutation rates, and faster selection rates in warmer regions, which affects the evolutionary speed of organisms (Rohde et al. 1962, Gillooly et al. 2005, Jablonski et al. 2013, Schluter and Pennell 2017). This relationship is represented by the exponential effect of temperature on organismal metabolism that can be mathematically represented as an exponential effect of temperature on speciation probability (Tittensor and Worm 2016). Moreover, these hypotheses must be understood in the overarching concept that richness gradients emerge as a combination of current and historical processes, especially in the context that environmental conditions, or their stability throughout evolutionary time, must drive geographical variation in speciation or extinction rates by affecting demographic processes (Allen et al. 2007, Mittelbach et al. 2007, Schluter and Pennell 2017). Substantial evidences are found to support both the chemical and kinetic energy hypotheses (Hawkins et al. 2003a, Hawkins et al. 2003b, Evans et al. 2005, Davies et al. 2007, Buckley et al. 2012, Field et al. 2009, Currie et al. 2004, Jablonsky et al. 2013, Gillooly et al. 2005). Spatial gradients in temperature (i.e. kinetic energy) and productivity (i.e. chemical potential energy) were identified as primary environmental correlates of diversity for marine biodiversity (Tittensor et al. 2010) and terrestrial vertebrate groups (Jetz and Fine 2012, Rodrigues et al. 2017). However, the

mechanisms behind these correlates are still debated (Dowle et al. 2013, Brown 2014, Tittensor and Worm 2016). There are abundant verbal models in the literature speculating about the potential roles of energy on spatial patterns of diversity (Evans et al. 2005, Brown 2014), which has been the center of recent intense debate in the ecological and evolutionary literature (Rabosky and Hurlbert 2015, Harmon and Harrison 2015). Despite the logical arguments supporting both hypotheses, a mechanistic understanding of the fundamental effects of energy on diversity is still critically needed and would be of great benefit for theoretical advances and synthesis.

The Neutral Theory of Biodiversity (Hubbell 2001) represents an ideal model to test mechanistic effects of the energy hypothesis because it simulates neutral evolutionary dynamics at individual level, allowing the inclusion of thermal and chemical energy effect respectively on speciation probability and community size. Unifying the Neutral Theory of Biodiversity and the Metabolic Theory of Ecology under the same framework was recently proposed (Tittensor and Worm 2016), but it still lacks formal test to empirical patterns of species diversity and the evaluation of different types of energy effect (i.e. chemical and kinetic). By comparing the prediction of mechanistic models against empirical observations of species richness and composition, here we assess the importance of energy on latitudinal patterns of bird diversity. We show that even in the absence of niche, and assuming simple mechanistic effects of energy on fundamental processes of biodiversity (i.e. dispersal, speciation and extinction), empirical spatial patterns of diversity emerge from neutral metabolic community dynamics.

Material and methods

Model assumptions and purpose

We developed a stochastic simulation model to simulate neutral evolutionary dynamics over broad geographical domains. Our model simulates random events of birth, death, dispersal, and speciation for a single trophic group. Simulation approaches for neutral models have been recently used to explore the effect of neutral processes on different patterns of biodiversity (Davies et al. 2011, Boucher et al. 2014, Coelho et al. 2017, Coelho and Rangel 2018). Different from the classical proposal of the Unified Neutral Theory of Biodiversity (Hubbell 2001), our model simulates (i) variations of community size (J) over space according to environmental energy availability and (ii) the metabolic effect of temperature on speciation rates (Tittensor and Worm, 2016). The model is still neutral since individuals of the same community are ecological equivalents in death, birth, dispersal and speciation rates independent of their species identity.

Our model was used to evaluate the importance of ecological limits (i.e. energy effects) on diversity over broad temporal and geographical resolutions, contributing to recent debates in ecology (Brown 2014, Rabosky and Hurlbert 2015, Harmon and Harrison 2015) and filling the gaps of recent implementations of neutral metabolic models (Tittensor and Worm 2016). Here, model's performance is confronted with empirical patterns of bird diversity.

Spatialized Empirical Data

Bird diversity was summarized in an equal area grid map of 110 km of resolution (equivalent to 1° at the equator), the most appropriate grain for this type of data (Belmaker and Jetz 2011). Bird distributional ranges were overlapped to the grid

maps of North America, Europe and South America. Empirical species distributions were obtained from Bird Life (<http://www.birdlife.org>).

To better represent the effect of environmental energy availability (i.e. chemical energy effect) on community size we extracted Potential and Actual Evapotranspiration (PET and AET, <http://www.cgiar-csi.org>) for each grid map cell. These two variables represent all the potential energy available in the environment that could potentially flow through the food webs. However, different from PET, AET considers the effects of water limitation on evapotranspiration. Diversity in the northern hemisphere is less restricted to water availability than southern hemisphere (Hawkins et al. 2003a). Thus, PET and AET association with diversity vary over the continents. Both variables are used in our study to simulate potential energy effect on community size. Mean annual temperature (www.worldclim.org) was also extracted for each cell of the geographical domain and was used to simulate the kinetic effect of energy.

Modeling the effect of chemical energy availability on community size

Empirical evidence suggests that chemical energy availability has a direct effect on the number of individuals in populations and communities (Kaspari et al. 2000, Pautasso and Gaston 2005, Letnic and Ripple 2017). Larger communities have lower extinction rates (Hubbell 2001) which, over time, influence diversity accumulation (Evans et al. 2005). In our model community size varies over space as a function of environmental energy. We assumed that community size varies over an environmental energy gradient (PET, or AET) reaching a maximum number of individuals that is limited by space (Hubbell 2001). Thus, to incorporate the effect of energy availability on number of individuals we assumed that community size is linearly associated with energy availability in a logit scale:

$$J = \frac{N(e^{\alpha+\beta*EE})}{1 + e^{\alpha+\beta*EE}}$$

where J is the estimated number of individuals of each grid map cell (i.e. community size), N the maximum number of individuals in each community that is limited by space (Hubbell 2001), α the intercept of the curve, β the slope of the curve and EE the environmental energy that can be represented by PET, or AET. α and β are unknown parameters and were estimated (see *Parameter estimation*). We assumed a fixed N of 30 because it is not clear how large a community size could be defined to characterize a considerable representation of reality (See Tittensor and Worm 2016). Additionally, if empirical community size over broad resolution were available, the model would not be computationally tractable because of the large number of individuals defined in each geographical cell. Thus, when comparing the simulated and empirical richness we want to reproduce the relative variation of species richness across space, not the exact and absolute number of real-world species in each grid cell.

Thermally mediated speciation rate

The metabolic theory of ecology predicts that rates of metabolic activity increase exponentially as function of temperature and body size (Brown et al. 2004). Differences in body size and mean internal temperature between individuals of different species are disregarded in neutral metabolic models (Tittensor and Worm 2016), because individuals of different species are assumed to be ecologically identical. For simplification and maintenance of the neutrality assumption, our neutral model assumes that environmental temperature equally drives speciation rate for all individuals in a community. Thus, following the Metabolic Neutral Theory (Tittensor and Worm 2016), we assume that speciation is a function of temperature.

$$e^{-E/kT}$$

where E is the empirically derived average activation energy of the respiratory complex (c. ~0.63 eV for respiration limited organisms (e.g. vertebrates); 1 eV = 1.602*10⁻¹⁹ J; Brown et al. 2004), k is the Boltzmann constant (8.617*10⁻⁵ eV K⁻¹) and T is the absolute temperature in Kelvin (K). The Boltzmann-Arrhenius factor describes the temperature dependence of metabolic rates for a series of endotherms and ectotherms with a mean activation energy for a series of taxonomical groups of ~0.63 (Brown et al. 2004). To represent the direct effect of temperature on speciation rate (v), we normalized v as a function of temperature (see Tittensor and Worm 2016):

$$v_i = \frac{v_{base} e^{-E/kt_i}}{\min(e^{-E/kt})}$$

Where V_{base} is the speciation rate assumed in the lowest grid map temperature. This speciation rate is thus multiplied by the metabolic effect of temperature, which is normalized by dividing it by its minimum value. The speciation rate of each grid map cell (v_i) is thus estimated based on the temperature of each grid map cell (T_i) (Fig 1S).

Associations of thermal kinetic effect is commonly linked to ectotherms (Allen et al. 2006, Tittensor and Worm 2016) but do not consider thermoregulation and behavioral habitat choices, which might regulate organismal internal temperature. However, thermal kinetic effect is more strongly linked to ectotherms than endotherms. The expectation for endotherms is that less energy is used for thermoregulation in tropical hot environments and more energy is available for reproduction (Allen et al. 2007), which would maintain a positive effect of temperature on organismal metabolism.

Turnover in species composition over time

Because both chemical and kinetic energy effect are expected to affect the turnover of species composition in communities (Allen et al. 2007, Tittensor and Worm 2016), we quantified the change of species composition over time for each geographical cell in the geographical. We calculated turnover through Simpson pairwise dissimilarity (Baselga 2010) : $\beta_{sim(t,t+1)} = \min(b,c) / a + \min(b,c)$, where a is the number of species that a geographical cell share between times t and $t+1$, whereas b and c are the exclusive species of respectively the cell in time t , and in the cell in time $t+1$. The Simpson pairwise dissimilarity was calculated for all model generations (see *neutral model dynamics*) and averaged.

Neutral model dynamics

The neutral model dynamics followed recent proposals of neutral stochastic simulations (Davies et al. 2011, Boucher et al. 2014, Coelho et al. 2017, Coelho and Rangel 2018) and can be summarized in the following algorithm (Fig. 1).

1. A real-world geographic domain (e.g. continent) is represented by its pairwise distance matrix, representing the distance of all cells to each other. Each cell is assumed to be connected with all its adjacent neighboring cells (maximum of eight neighboring cells for non-edge cells – Moore neighborhood).
2. All communities (i.e. geographical cells) are saturated and populated by J individuals that compete only for space, following a zero-sum game (Hubbell 2001). At the beginning of the simulation all individuals belong to the same ancestral species.
3. An individual is randomly selected across the geographical domain to undergo random demographic events (below).

4. The randomly chosen individual may speciate, according to the speciation probability (v), or die, based on death probability ($1 - v$) (see Davies et al. 2011, Boucher et al. 2014, Coelho et al. 2017).
5. If an event of death is the outcome of the stochastic dynamics, the descendent of a randomly chosen individual will colonize the empty spot. The descendent of the randomly chosen individual might be from the eight neighboring cells (Moore neighborhood) if an event of dispersal occurs (with probability m), or from the same cell where the death event occurred ($1 - m$).
6. Temporal variation is represented by generations. Each generation represents the total number of time steps that is necessary for all individuals to die, roughly represented as the total number of individuals in the geographical domain (see Boucher et al. 2014). The model is run for 6,000 generations, which allows reaching stability of the patterns in the metacommunity.
7. After all generations are run, a presence absence matrix is generated for further analyses.

Based on the chemical and kinetic energy effects, community size (J) and speciation probability (v) varies following respectively environmental energy and temperature. Temporal variations of climatic variables are not assumed because the model reaches stability after 6,000 generations, which can be simulated under current climatic variability. Thus, spatial patterns of biodiversity emerge from current climatic variables in our model.

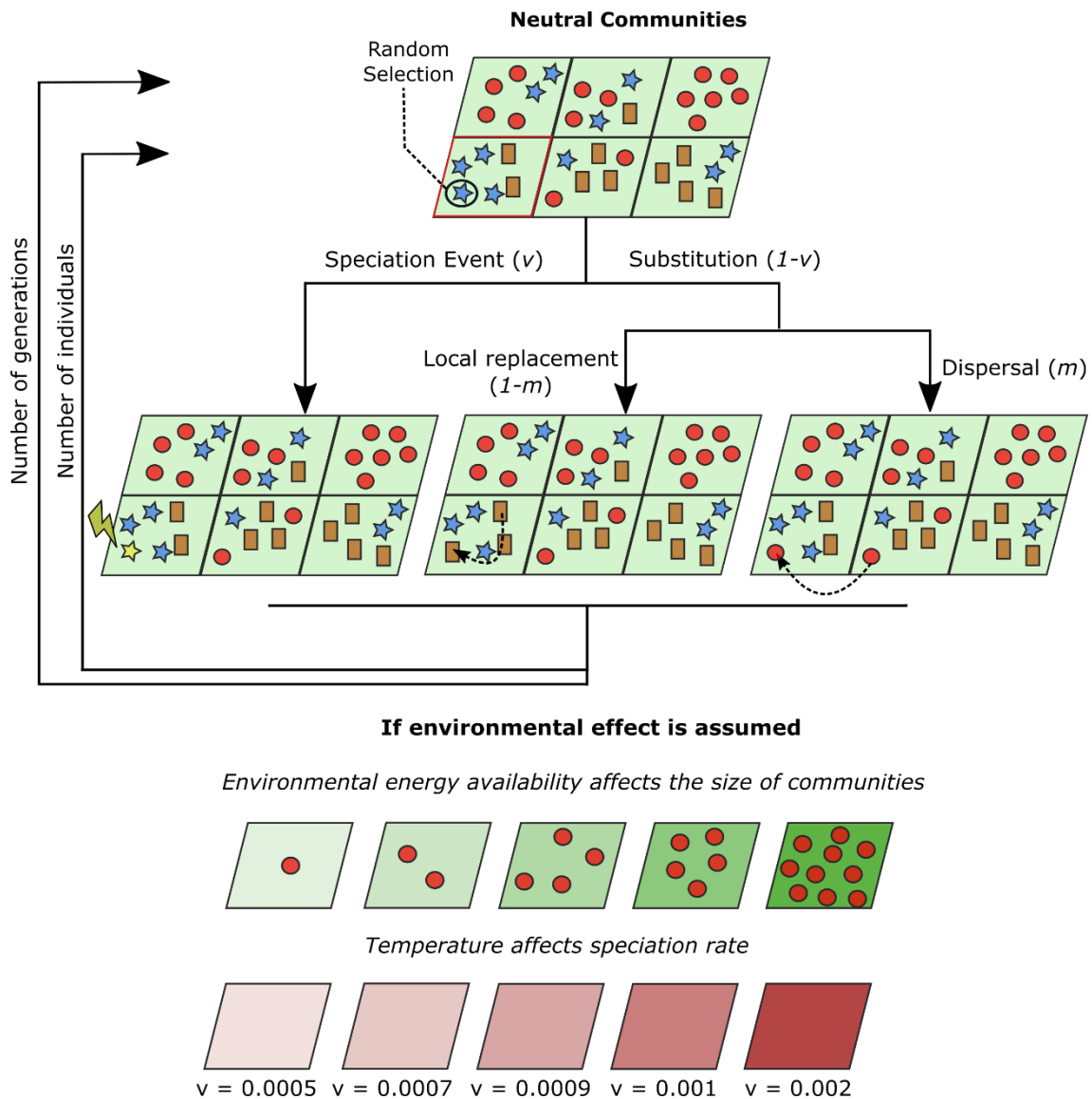


Fig. 1: Visual representation of neutral evolutionary dynamics. Random events of dispersal, speciation, birth and death occurs in an explicit spatial domain. Community size and speciation are respectively affected by environmental energy availability (PET or AET) and temperature if environmental effect is assumed.

Neutral Speciation Modes

More realistic speciation modes have been proposed for neutral models (Rosindell et al. 2010, Desjardins-Proulx and Gravel 2012). However, for the sake of simplicity and computational tractability, we modeled speciation as instantaneous

events (see Boucher et al. 2014, Coelho et al. 2017, Coelho and Rangel 2018). We modeled three types of speciation processes most commonly used in neutral models: Point Mutation, Random Fission, and Equal split (Davies et al. 2011, Coelho and Rangel 2018). These different speciation modes assume different incipient abundance of daughter species (J_s). One individual is randomly selected among all the individuals of the geographical domain and undergoes speciation based on speciation probability (v). In *point mutation* mode, only the randomly selected individual becomes a new species ($J_s=1$). In *random fission* mode, a random number between one and half of individuals of the local population (in the cell where the random individual was chosen) became a new species. *Equal split* mode assumes that the number of individuals of the local population defined as a new species is always half of the population size (in the cell where the random individual was chosen; Davies et al. 2011). Random fission (Hubbell 2001, Etienne et al. 2011) and equal split (Davies et al. 2011) modes were designed to represent allopatric events (Hubbell 2001).

Parameter Estimation

Here we employed the Gibbs MCMC sampling algorithm (Gelman et al. 2013) to explore the multidimensional parameter space and understand the role of each parameter in model predictive power. This modeling procedure is designed to explore parameter space and provide a bigger picture of model's prediction under different parameter sets. To assess the *goodness-of-fit* of the model during the search the Gibbs sampler (1) runs the simulation model using a particular parameter combination, (2) extracts the predictions of the model given the parameter combination, (3) produces multiple goodness-of-fit measures by contrasting each predicted pattern against empirical patterns, and then (4) combines multiple goodness-of-fit measures of each

pattern into a single summary statistics, which describes with a single number the pseudo-likelihood of the model given the parameter set (because our summary statistics does not conform to the precise statistical definition of a conditional probability, the summary statistics is frequently called a pseudo-likelihood).

In our study the *goodness-of-fit* (f) is estimated by the mean coefficient of determination between observed vs. predicted spatial pattern of diversity (R^2) and Kolmogorov-Smirnov similarity of range size distributions (1- Kolmogorov-Smirnov's D):

$$f = \frac{R^2 + (1 - D)}{2}$$

Thus, highest fit is observed when $f = 1$ ($R^2 = 1$ and $D = 0$). By design, the sampler explores in greater detail (i.e. more frequently) the areas of the parameter space of higher goodness-of-fit (f values close to 1). However, the sampler is also designed to explore parameter combinations with lower goodness-of-fit, but less frequently.

Parameters were estimated for four different models: (i) classical neutral model, (ii) neutral model assuming thermal kinetic effect; (iii) neutral model assuming chemical energy effect and (iv) neutral model assuming both energy effects. We ran the Gibbs sampler for 5,000 iterations and assumed 1,000 iterations as burning period. Each iteration replicated the stochastic model 100 times totalizing 6×10^5 replicates.

The MCMC chains were tested for convergence following the Heidelberg and Welch's convergence diagnostic (Plummer et al. 2006) which consists in a two-step convergence diagnostic. First it evaluates if the chain is a stationary distribution by comparisons of multiple subdivisions of the first half of the chain, to the latter 50% portion of the chain. If the chain passes the stationary test, then it calculates a 95% confidence interval of the mean value of the chain. Half of the width of the confidence

interval is compared to the mean value of the chain (i.e. half-width test). If the ratio between the half-width and the mean is lower than a critical value (usually 0.1), then the chain passes the test. One parameter set, assuming the mean values of each parameter after running the MCMC and the convergence statistics, is used for each model (Table S1). A complete visualization of model's pseudo-likelihood distribution is presented to show how models perform assuming multiple parameters combinations and how they vary in prediction power (See results section).

Model comparisons

Assuming the mean parameter values of each model, we compared the four variants of the stochastic simulation model by their Mean Square Errors (MSE). The model presenting the lowest MSE is the best model both in accuracy (i.e. how good is the model to reproduce the empirical spatial pattern of diversity) and precision (i.e. when replicating the stochastic model, how variable are the predictions for multiple replicates). The MSE is represented as the sum of the squared bias and model variance which respectively represents model accuracy and precision (Gotelli et al. 2009):

$$\sum (bias)^2 = \sum_{i=1}^c (O_i + E_i)^2$$

$$\sum (VAR) = \frac{1}{(R-1)} \sum_{k=1}^R \sum_{i=1}^c (U_{ki} - E_i)^2$$

$$\sum (MSE) = \sum (bias)^2 + \sum (VAR)$$

Where O is the vector of observed values of richness for each community i , E is a vector of the mean expected richness in the stochastic simulation for each community i , U_{ki} is the value obtained in the k th simulation for the community i , and R is the number of replicates run for each model.

Model validation

The ultimate test of a model consists in evaluating the generality of the results by fitting the model (parameter estimation) using one dataset (training), and then evaluating its predictive power against an independent dataset (validation). Because there are no true replicates of geological and biological history, no dataset in biogeography is fully independent from another. Still, at the global scale, continents are probably the closest to independent replicates as biogeographers will ever have. To evaluate the generality of our conclusions, for each of the four different models, we used the parameter combination that was estimated for the spatial patterns in North America bird richness to predict the spatial patterns in species richness in Europe and South America. Thus, our conclusions would gain reliability if they hold across three different continents.

Results

Models varied in their performance to reproduce the empirical patterns of bird diversity (Fig. 2). The classical neutral model had the worst prediction, but performance improves when chemical and thermal energy effects were added to the model. The effect of chemical energy is weaker than kinetic thermal effect, but the model with the highest probability to reproduce the empirical pattern of bird diversity in North America is the one that included the effect of both chemical and kinetic effect (Fig. 2). The

inclusion of both effects also generates the model with best predictive accuracy and precision, thus presenting the lowest Mean Square error (MSE; Table 1).

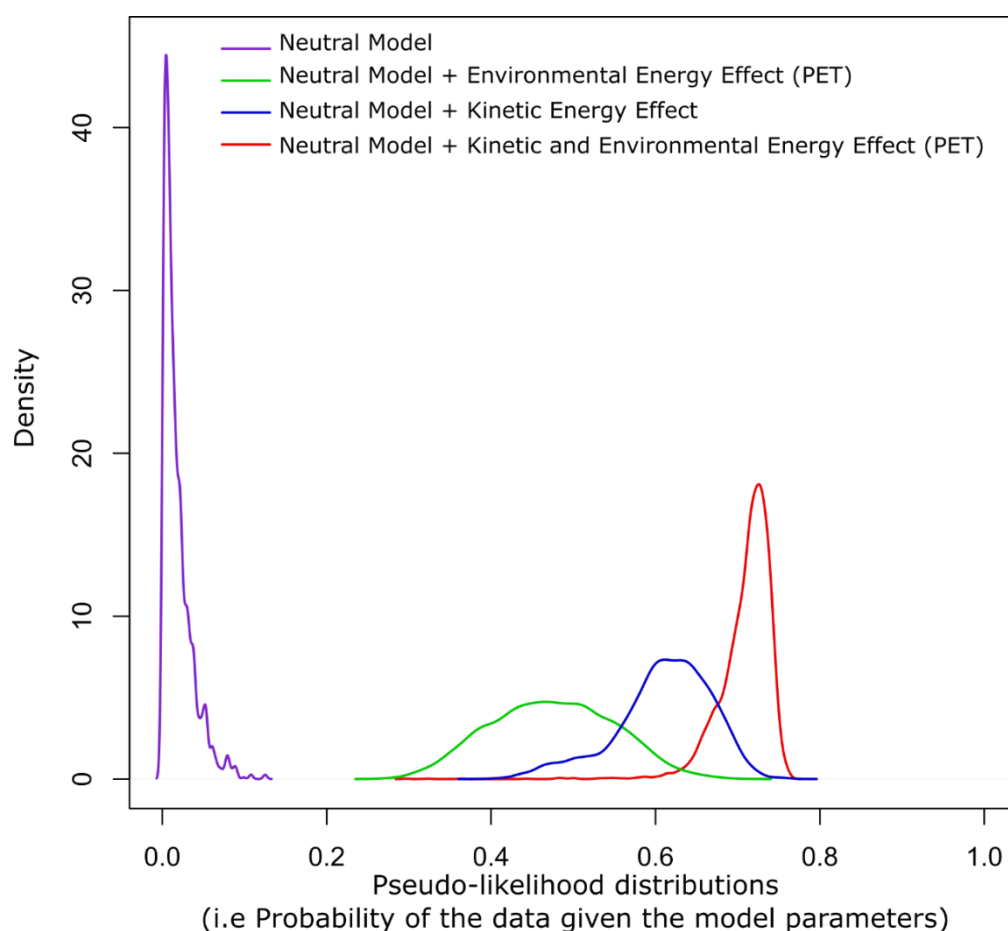


Fig. 2: Pseudo-likelihood (i.e. probability of the data given the model parameters) respectively, from left to right (i) Classical Neutral Model, (ii) Neutral model with the addition of chemical energy effect, (iii) Neutral model with the addition of kinetic energy effect and (iv) Neutral model with the addition of both energy effects. Each distribution represents model predictive power under thousands of parameter combinations.

Table 1: Fit for all the models used in the study. Squared bias (Bias²), model variance (VAR), Mean Squared error (MSE) and the coefficient of determination (R²) are presented for all models. Model with minor MSE represents the model with better accuracy and precision to empirical data.

Models	Bias ²	VAR	MSE	R ²
Neutral + kinetic + chemical energy effect (PET)	75.7621	159.348	235.1101	0.78
Neutral + kinetic + chemical energy effect (AET)	158.3701	78.7400	237.1101	0.37
Neutral + chemical energy effect (AET)	194.1788	186.9551	381.1340	0.23
Neutral + kinetic energy effect	209.4771	259.3928	468.8699	0.74
Neutral model	177.3122	392.8126	570.1248	0.001
Neutral + chemical energy effect (PET)	220.1764	404.7342	624.9106	0.619

Different models generate different spatial patterns of species diversity (Fig. 3). The classical neutral model produces almost a random distribution of diversity over the geographic domain (Fig. 3b). When compared to the empirical spatial gradient, the model fails to predict lower diversity in northern regions and higher diversity in the southern region (Fig. 3c) presenting the lower fit to empirical data (Fig. 3d). The addition of chemical potential energy creates a latitudinal diversity gradient of species diversity by variations of community size. The model approximates the empirical observations specially in northern areas (Fig. 3e, 3f, 3g). A strongest spatial gradient of species diversity is also observed when thermal kinetic effect is included (Fig. 3h). However, there is a tendency of overestimating diversity over the entire geographic domain (Fig. 3i). The combination of both kinetic and chemical effect generates the most similar pattern to species diversity when compared to empirical data (Fig. 3k). The maps of residuals show that northern regions are better predicted by variations of community size, while southern regions of North America seem better predicted by temperature (Fig. 3l). The combination of both energy effects produces the model that is the most precise and accurate to empirical data (Table 1) presenting the highest fit to

empirical data (Fig. 3m). The spatial patterns of diversity and model fitness are not affected by different speciation modes (Fig. S2).

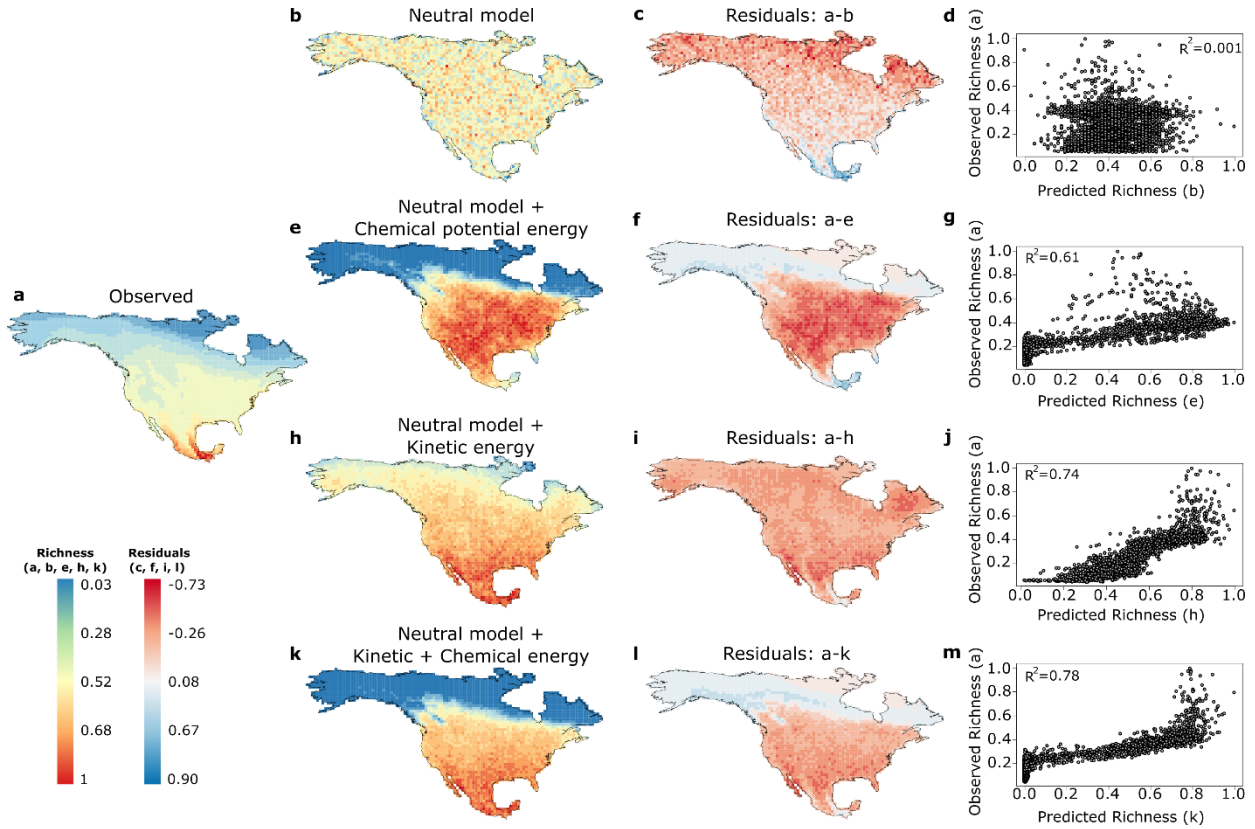


Fig. 3: Contrast between empirical and predicted spatial patterns of species diversity.

The four variants of neutral models were parameterized assuming the mean parameters values estimated through a Gibbs MCMC. **a**, observed spatial pattern of bird diversity in North America; **b**, predicted spatial pattern of species diversity emerging from a classical neutral model; **c**, residuals between observed (**a**) and predicted (**b**) diversity; **d**, relationship between patterns on maps **a** and **b** ($R^2 = 0.001$); **e**, predicted spatial pattern of species diversity emerging from a neutral model that assumed the effect of environmental energy (PET) on community size; **f**, residuals between observed (**a**) and predicted (**e**); **g** relationship between patterns on maps **a** and **e** ($R^2 = 0.61$); **h**, predicted spatial pattern of species diversity emerging from a neutral model that assumed kinetic effect of temperature on speciation probability; **i**, residuals between observed (**a**) and predicted (**h**); **j**, relationship between patterns on maps **a** and **h** ($R^2 = 0.74$). **k**, neutral model assuming the combined effect of kinetic energy on speciation and chemical energy on community size; **l**, residuals between observed (**a**) and predicted (**k**). **m**, relationship between patterns of maps **a** and **k** ($R^2 = 0.78$).

In northern hemisphere, species diversity is less restricted to water availability than in southern hemisphere. This pattern is reproduced by the model when assuming PET instead of AET affecting community size (Fig. 3S). However, independent of the variable used to model variability on community size, the combined effect of chemical and kinetic energy effect presents the higher precision and accuracy (lower MSE), which reinforces the combined effect of kinetic and chemical energy structuring biodiversity (Table 1). Moreover, communities most affected by both energy effects are the ones that present higher turnover in species composition over time (Fig. 4). Thus, larger communities in warmer regions receive more species by immigration and speciation, which affect the accumulation of diversity in those regions.

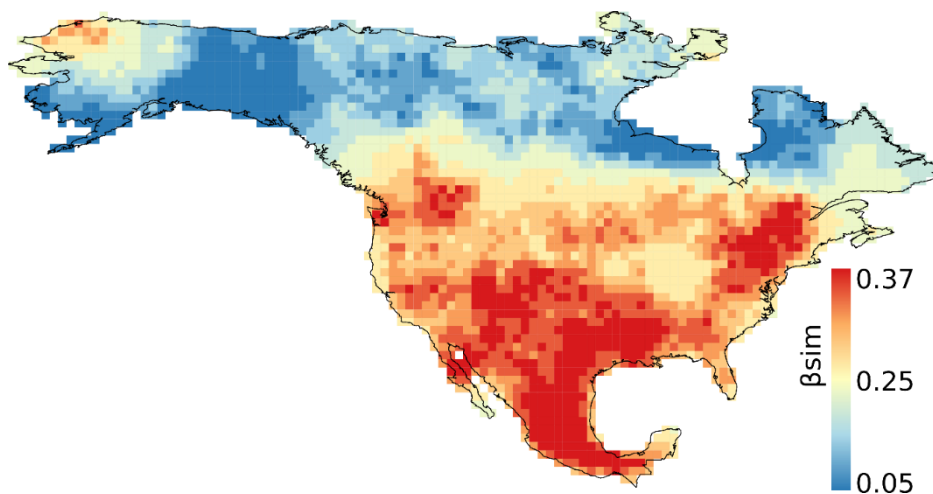


Fig. 4: Temporal turnover in species composition. Turnover was calculated by the average Simpson pairwise dissimilarity of species composition in time for 100 model's replicates that assumed both chemical and kinetic energy effect.

The model with combined effects of kinetic and chemical energy produces the best-fit predictions against empirical patterns of bird diversity not only in North America, but also in Europe and South America (Fig. 5; Table S2). By contrasting the

model estimated using the North American dataset against the European dataset (both in the northern hemisphere), we are able to show that PET is a better proxy for the effect of potential energy availability than AET. In addition, variation on community size assuming AET presents strongest relationships to empirical patterns of birds in South America. Thus, the combined effect of chemical and thermal energy is reinforced even when the model is applied to other regions of the globe. The complete spatial patterns of each model applied to Europe and South America is available as online supporting material (Fig. 4S to Fig. 7S).

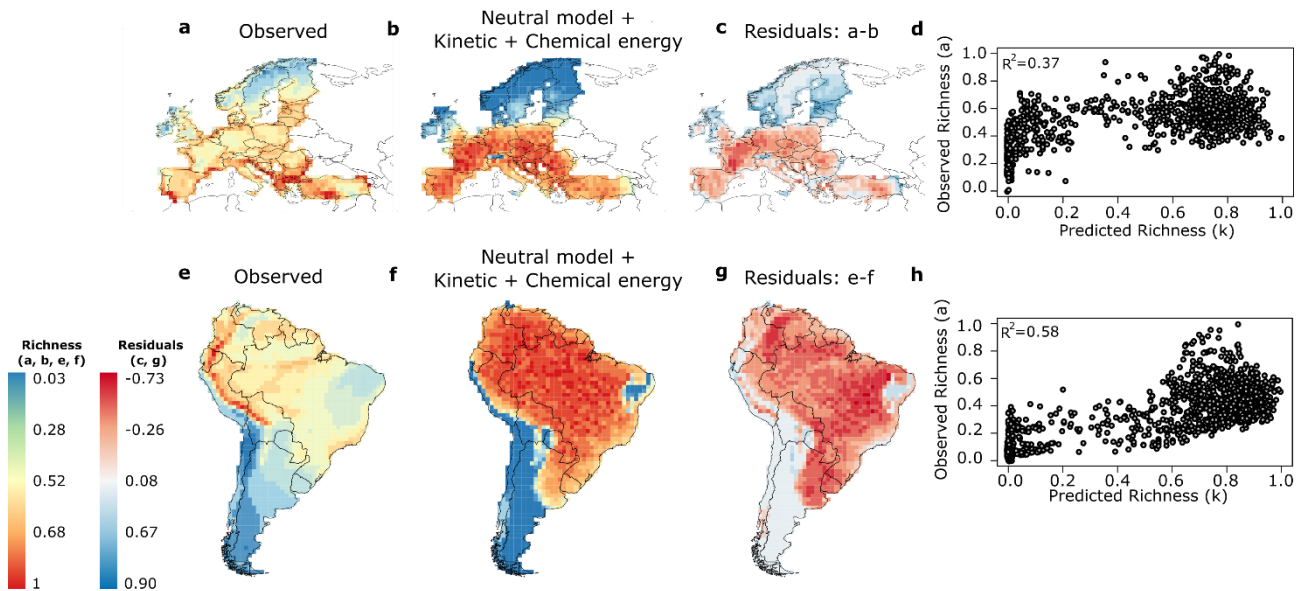


Fig. 5: Contrast between empirical and predicted spatial patterns of species diversity in Europe and South America assuming the model with best accuracy and precision. The combined effect of kinetic and chemical energy remains the most precise and accurate model in different geographical domains. **a**, observed spatial pattern of bird diversity in Europe; **b**, predicted spatial pattern of species diversity emerging from a neutral model that assumed the effect of environmental energy (PET) on community size. **c**, residuals between observed (*a*) and predicted (*b*) richness. **d**, relationship between patterns on maps *a* and *b* ($R^2 = 0.37$). **e**, observed spatial pattern of bird diversity in South America. **f**, predicted spatial pattern of species richness emerging from a neutral model that assumed the effect of environmental energy (PET) on community size. **g**, residuals

between observed (e) and predicted (f) diversity. h , relationship between patterns on maps a and b ($R^2 = 0.58$).

Discussion

The development of biodiversity theory is generally sustained by qualitative frameworks and correlative analysis, urging for explicit treatments of mechanisms in ecological and evolutionary studies (Brown 2014). Here, we simulated the effect of temperature on speciation rates (i.e. kinetic energy effect) and the effect of environmental energy on community size (i.e. chemical potential energy) under neutral community dynamics. The parameterized model of the interaction between both mechanisms produces latitudinal gradients of species diversity that are similar to empirical patterns of bird diversity. We then validated the parameterized model by testing its predictive power in different regions of the globe and confirmed the generality of its predictive power and its underlying mechanisms.

In our neutral metabolic community dynamics, three of the most widely discussed ecological and evolutionary mechanisms are integrated to produce the predicted patterns of species richness: (i) higher diversification rate in warmer regions, (ii) lower extinction rates in communities with larger carrying capacities and (iii) accelerated turnover in larger communities. At broad geographical scales, the balance between these processes over longer periods of time is likely to have driven the current spatial patterns in species richness (Mittelbach et al. 2007, Schluter and Pennell 2017).

Thermal kinetic effect influences probability of speciation. Thus, regions at lower latitude, such as the tropics (Fig. 3), tend to generate more diversity over time. Additionally, highly productive regions, such as warm and wet tropics, tend to harbor more individuals, therefore decreasing probability of extinction (MacArthur and Wilson 1967, Hubbell et al. 2001, Wright 1983). The combined effect of those mechanisms is a

latitudinal gradient in net diversification rate (speciation – extinction), which peaks at lower latitudes (Evans 2005, Davies et al. 2007).

Estimated trends in diversification rates for birds are not consistent across studies. While several studies (Cardillo et al. 2005, Ricklefs 2006, but see Weir and Schluter 2007) report higher diversifications rates of birds in the tropics, Jetz et al. (2012), using data for almost 10,000 bird species, found no spatial patterns of diversification, but a higher accumulation of species in tropical regions of clades with both high and low diversification rates.

The higher accumulation of species in tropical regions can also be explained by the turnover in species composition (Fig. 4). Temporal turnover in species composition is accelerated in larger communities (Tittensor and Worm 2016), because neutral dynamics are intensified in areas with high environmental energy availability. Larger communities receive, over time, more immigrants than small communities, which influence the temporal turnover in species composition and diversity accumulation. This mechanism is described as the energy effect on community's turnover (Brown et al. 2004) and discussed as a possible mechanism to explain patterns of species diversity (Allen et al. 2006, Tittensor and Worm 2016). For diversity patterns of birds and mammals, dispersal can be more important than *in situ* diversification (Belmaker and Jetz 2015), being consistent with the emergent property of our model.

An understanding of the effect of chemical potential energy depends on empirical evidence of variation of community size over broad geographical domain (But see Letnic and Ripple 2017). Over the decades, many ecologists inferred that environmental energy would limit the number of individuals over space as a possible explanation for diversity gradients (Brown 1981, Wright 1983, Currie 1991, Fraser and Currie 1996, Francis and Currie 1998, Kaspari et al. 2000, Brown 2014). More direct

measures of energy availability on experimental and empirical studies found a direct association between energy availability with diversity (Hurlbert and Stegen 2014), but not necessarily with number of individuals (Simova et al. 2011). However, empirical evidence of the constraints of energy availability on the total number of individuals over broad geographical scales is still missing (but see Letnic and Ripple 2017). Although limits on the number of individuals might be partially important in generating diversity gradients (Hurlbert and Stegen 2014), diversity scale faster with kinetic energy (Brown 2014). Here, by simulating both kinetic energy and limitations on the number of individuals over space, we found that kinetic energy effect is stronger in northern hemisphere, but not in southern regions (Fig. 3, Fig. 4S to Fig. 7S).

Our neutral model demonstrates that energy effects on biodiversity are strong even when niche processes are disregarded. The neutrality assumption of our model (i.e. lack of ecological differences between individuals) is not a claim about the reality of natural systems, but helps us to understand the effect of energetic constraints on biodiversity in the absence of niche based processes. Simplifying complex systems with inclusion of general processes is a common procedure of different fields of sciences (Rosindell et al. 2012). The simplified system developed here suggests that the interaction between chemical and kinetic energy effect limits biodiversity by affecting fundamental processes of biodiversity (Vellend 2010), namely dispersal, speciation and extinction. Thus, our model supports a major role of processes associated with energetic constraints (Wright 1983, Rabosky and Hurlbert 2015) by presenting how energy availability affects key ecological processes (see Vellend 2010) and contributes to the emergence of heterogeneous spatial patterns of biodiversity. Integrating the simple energy effects with complex simulation models assuming niche evolutionary dynamics and history (e.g. Rangel et al. 2007) would be of great benefit for theoretical advances

and synthesis, explaining most of the deviation of our model from empirical latitudinal gradients.

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Appendix 1

Table A1 – Convergence of the MCMC chains for each model following the *Heidelberg and Welch's* convergence diagnostic. All chains are stationary distributions. Except for the neutral model, all chains passed in *Halfwidth test*. Since the neutral model has a fit close to zero for all parameters (Fig. 2), the frequency of sampled parameters is high and produce high variability, this relation does not change if the MCMC is run for more iterations. Models assuming chemical potential energy has little variation of the mean parameter values when assuming PET or AET.

Parameters	Stationary Test	Start Iteration	P-Value	Halfwidth test	Mean	Halfwidth
<i>Neutral Model</i>						
Dispersal	Passed	1	0.280	Failed	0.0572	2.25×10^{-2}
Speciation	Passed	1	0.465	Failed	0.0006	8.01×10^{-5}
<i>Neutral Model assuming kinetic energy effect</i>						
Dispersal	Passed	1	0.0805	Passed	0.0478	1.83×10^{-3}
Speciation	Passed	1	0.2641	Passed	0.00014	2.16×10^{-6}
<i>Neutral Model assuming chemical energy effect (PET)</i>						
Alpha	Passed	1	0.528	Passed	-17.8641	0.974
Beta	Passed	1	0.505	Passed	0.02971	9.16×10^{-4}
Dispersal	Passed	1	0.893	Passed	0.04874	2.97×10^{-3}
Speciation	Passed	1003	0.857	Passed	0.00016	1.11×10^{-5}
<i>Neutral Model assuming kinetic energy effect and Chemical energy effect (PET)</i>						
Alpha	Passed	1	0.277	Passed	-18.0632	0.508
Beta	Passed	1504	0.204	Passed	0.0294	7.03×10^{-4}
Dispersal	Passed	1	0.754	Passed	0.0367	1.37×10^{-4}
Speciation	Passed	1	0.710	Passed	0.0001	2.76×10^{-7}
<i>Neutral Model assuming chemical energy effect (AET)</i>						
Alpha	Passed	1	0.6979	Passed	-16.5	0.524
Beta	Passed	1	0.8927	Passed	0.0303	1.02×10^{-3}
Dispersal	Passed	1	0.0627	Passed	0.0497	9.54×10^{-4}
Speciation	Passed	1	0.3169	Passed	0.00015	1.11×10^{-5}
<i>Neutral Model assuming kinetic energy effect and Chemical energy effect (AET)</i>						
Alpha	Passed	1	0.664	Passed	-17.4040	0.646
Beta	Passed	1	0.976	Passed	0.0292	1.39×10^{-3}
Dispersal	Passed	1	0.883	Passed	0.04944	7.77×10^{-4}
Speciation	Passed	1	0.376	Passed	0.00016	9.70×10^{-6}

Table A2: Mean Squared Error and fit for all models applied to Europe and South America. Squared bias (Bias²), model variance (VAR), Mean Squared error (MSE) and the coefficient of determination (R²) are presented for all models. Model with minor MSE represents the model with better accuracy and precision to empirical data.

Models	Bias ²	VAR	MSE	R ²
Europe				
Neutral + kinetic + chemical energy effect (PET)	67.3936	108.8262	176.2198	0.37
Neutral + kinetic energy effect	45.1856	131.6354	176.8211	0.17
Neutral + kinetic + chemical energy effect (AET)	173.3958	38.8504	212.2463	0.06
Neutral + chemical energy effect (AET)	137.5813	81.7348	219.316	0.08
Neutral + chemical energy effect (PET)	59.7189	188.9847	248.7036	0.37
Neutral model	53.5291	212.3045	265.8336	0.001
South America				
Neutral + kinetic + chemical energy effect (AET)	134.7373	275.6038	410.3412	0.58
Neutral + chemical energy effect (AET)	139.1762	273.6960	412.8722	0.44
Neutral + chemical energy effect (PET)	206.2473	288.2344	494.4818	0.05
Neutral + kinetic + chemical energy effect (PET)	232.7885	371.5121	604.3006	0.33
Neutral model	275.2684	395.6761	670.9445	0.08
Neutral + kinetic energy effect	280.1397	401.1901	681.3298	0.32

Supplementary Figures

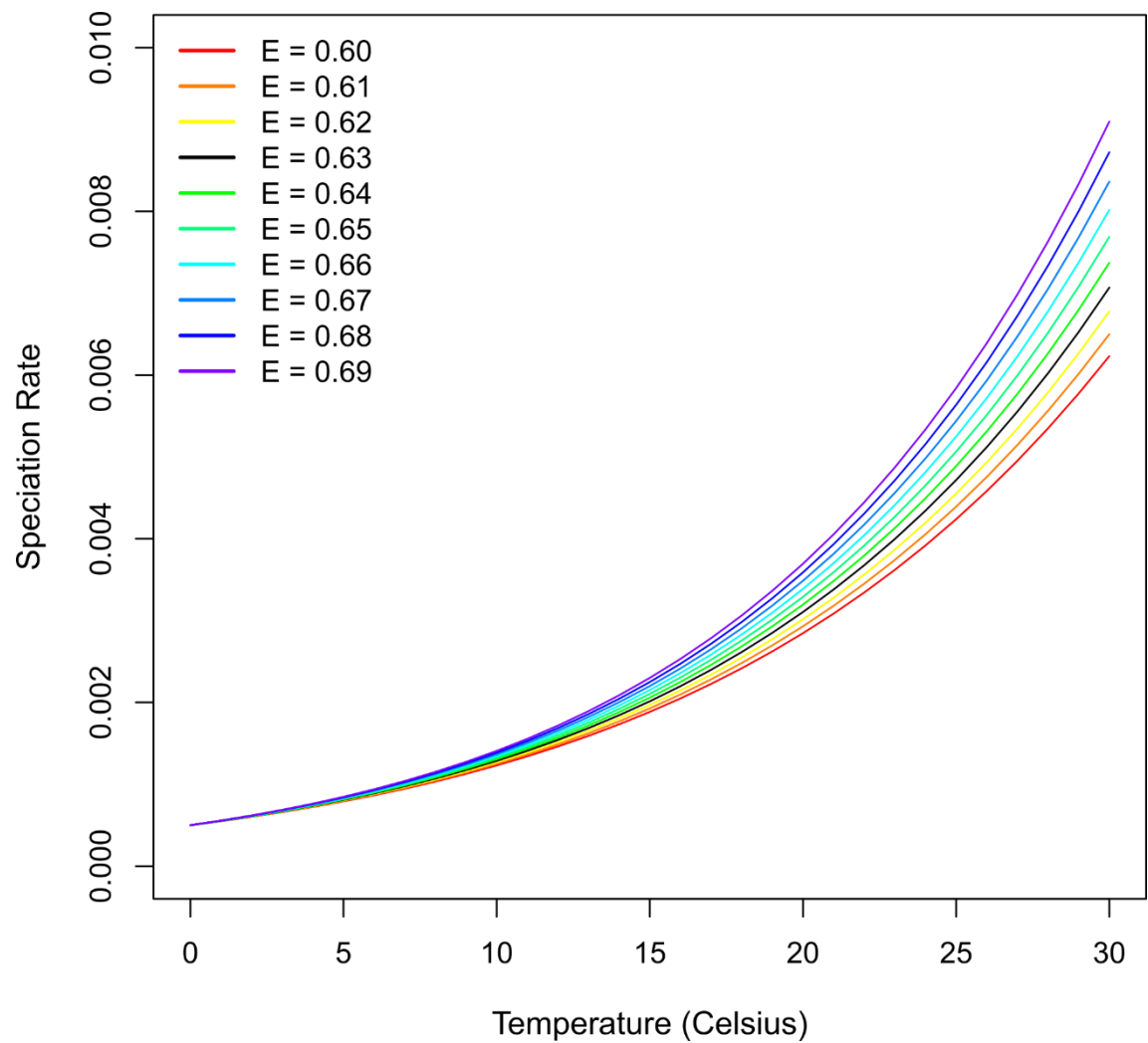


Fig. A1: Exponential increase of speciation rate under different temperatures. Multiple activation energy of the respiratory complex (E) are assumed to illustrate the exponential increase of speciation rate. To exemplify, we assumed that speciation rate in the coldest cell is 0.0005.

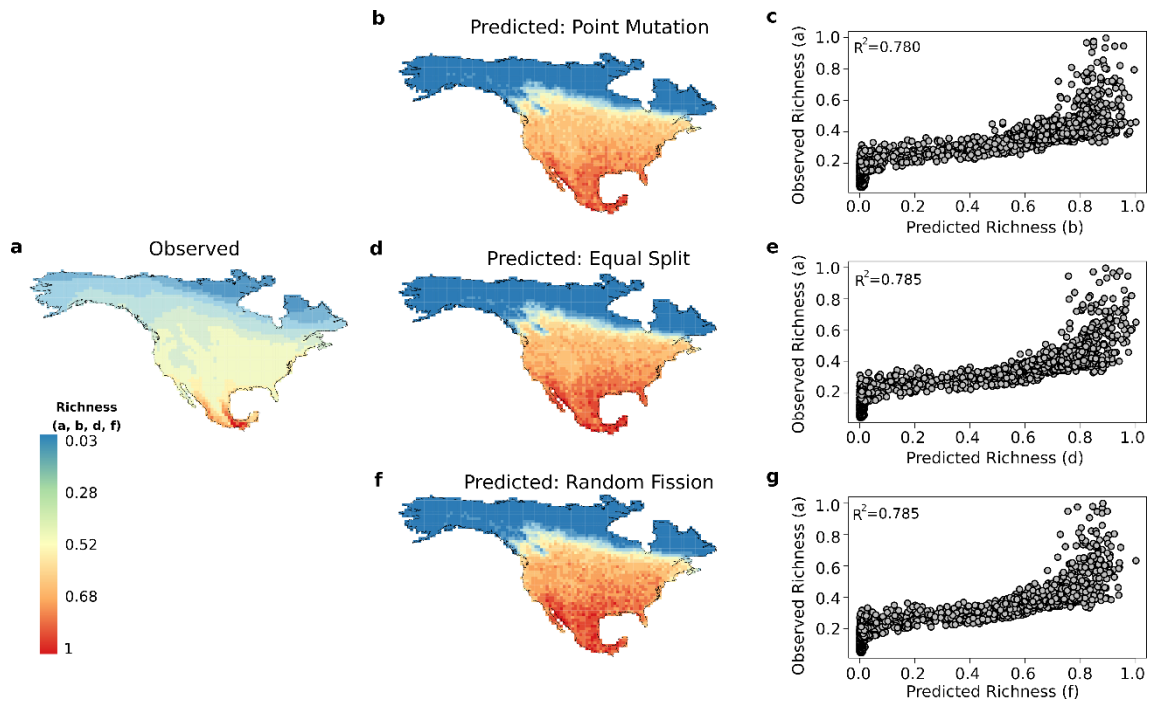


Fig. A2: Spatial patterns of biodiversity generated through neutral metabolic dynamics. The spatial diversity patterns (*b, d, f*) and model fitness (*c, e, g*) do not vary between different speciation modes.

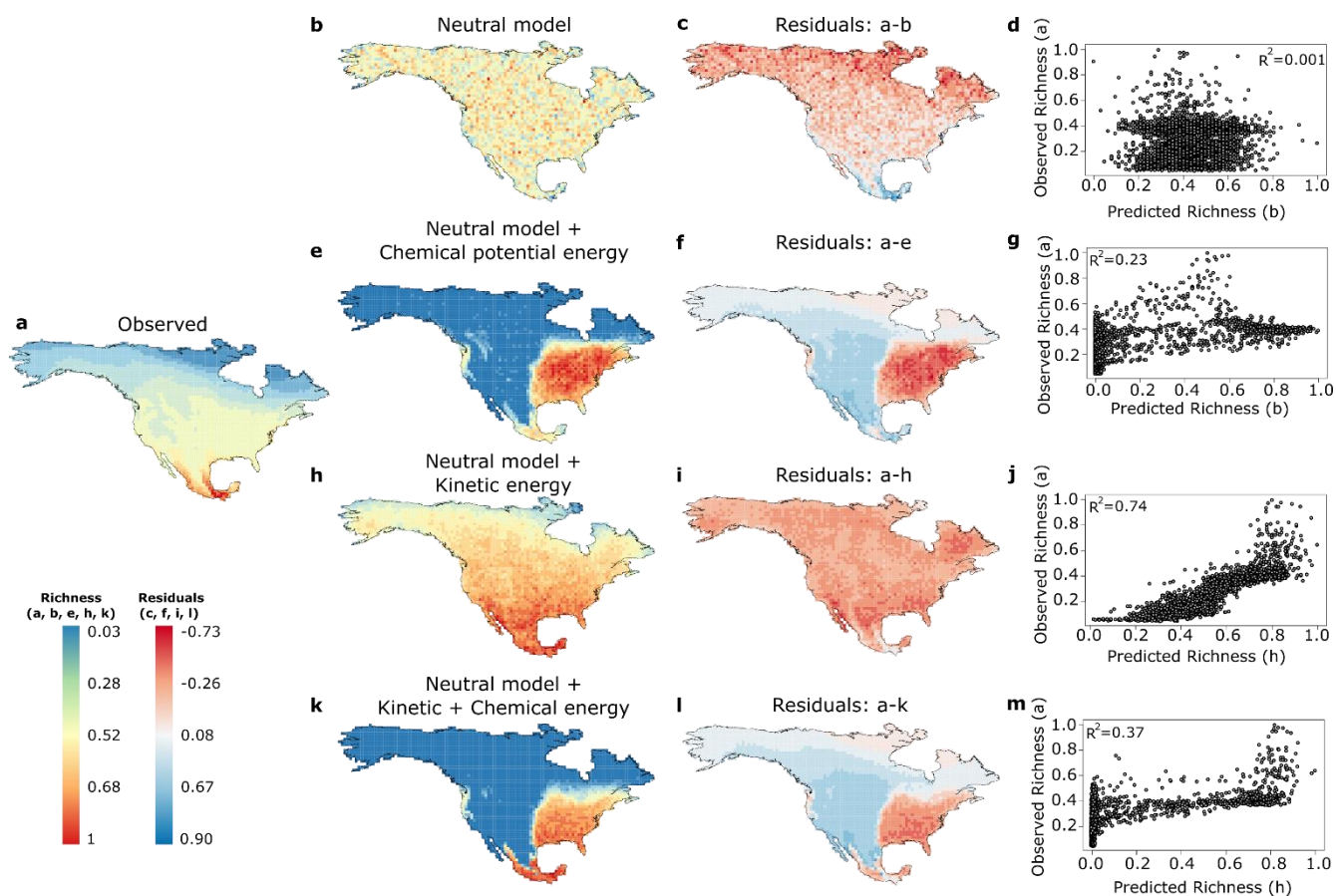


Fig. A3: Contrast between empirical and predicted spatial patterns of species diversity. The four variants of neutral models were parametrized assuming the mean parameters values estimated through a Gibbs MCMC. **a**, observed spatial pattern of bird diversity in North America; **b**, predicted spatial pattern of species diversity emerging from a classical neutral model; **c**, residuals between observed (*a*) and predicted (*b*) diversity; **d**, relationship between patterns on maps *a* and *b* ($R^2 = 0.001$); **e**, predicted spatial pattern of species diversity emerging from a neutral model that assumed an effect of chemical available energy (AET) on community size; **f**, residuals between observed (*a*) and predicted (*f*); **g** relationship between patterns on maps *a* and *e* ($R^2 = 0.61$); **h**, predicted spatial pattern of species diversity emerging from a neutral model that assumed kinetic effect of temperature on speciation probability; **i**, residuals between observed (*a*) and predicted (*h*); **j**, relationship between patterns on maps *a* and *h* ($R^2 = 0.74$). **k**, neutral model assuming the combined effect of kinetic energy on speciation and chemical energy on community size; **l**, residuals between observed (*a*) and predicted (*k*). **m**, relationship between patterns of maps *a* and *k* ($R^2 = 0.78$).

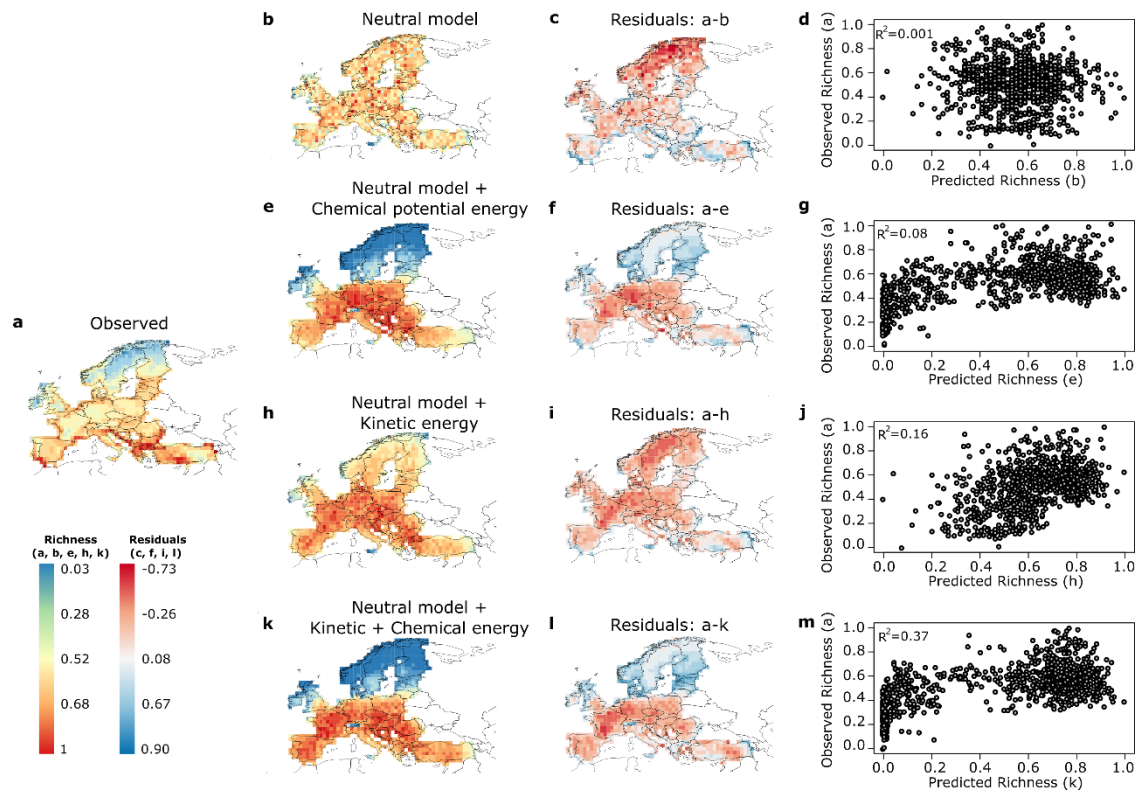


Fig. A4 - Contrast between empirical and predicted spatial patterns of species diversity in Europe. The four variants of neutral models were parametrized assuming the mean parameters values estimated through a Gibbs MCMC. **a**, observed spatial pattern of bird diversity in Europe; **b**, predicted spatial pattern of species diversity emerging from a classical neutral model; **c**, residuals between observed (a) and predicted (b) diversity; **d**, relationship between patterns on maps a and b ($R^2 = 0.001$); **e**, predicted spatial pattern of species diversity emerging from a neutral model that assumed the effect of environmental energy (PET) on community size; **f**, residuals between observed (a) and predicted (f); **g** relationship between patterns on maps a and e ($R^2 = 0.08$); **h**, predicted spatial pattern of species diversity emerging from a neutral model that assumed kinetic effect of temperature on speciation probability; **i**, residuals between observed (a) and predicted (h); **j**, relationship between patterns on maps a and h ($R^2 = 0.16$). **k**, neutral model assuming the combined effect of kinetic energy on speciation and chemical energy on community size; **l**, residuals between observed (a) and predicted (k). **m**, relationship between patterns of maps a and k ($R^2 = 0.37$).

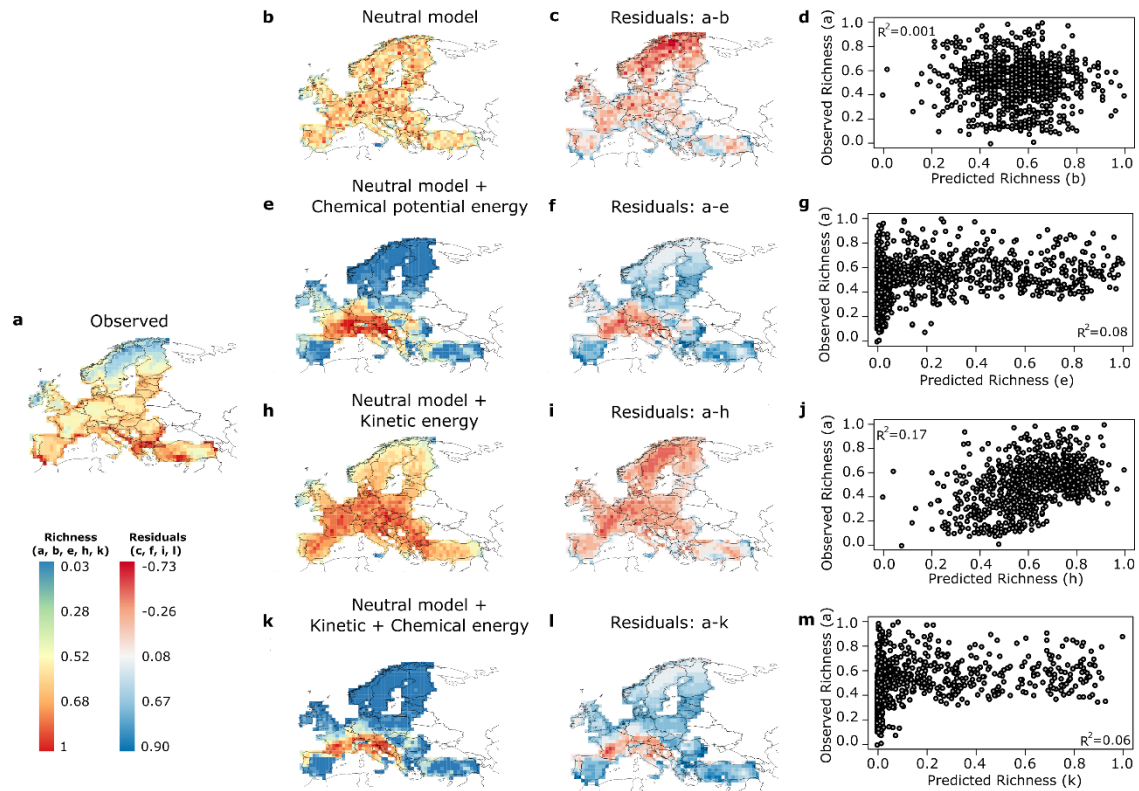


Fig. A5 - Contrast between empirical and predicted spatial patterns of species diversity in Europe. The four variants of neutral models were parametrized assuming the mean parameters values estimated through a Gibbs MCMC. **a**, observed spatial pattern of bird diversity in Europe; **b**, predicted spatial pattern of species diversity emerging from a classical neutral model; **c**, residuals between observed (**a**) and predicted (**b**) diversity; **d**, relationship between patterns on maps **a** and **b** ($R^2 = 0.001$); **e**, predicted spatial pattern of species diversity emerging from a neutral model that assumed the effect of environmental energy (AET) on community size; **f**, residuals between observed (**a**) and predicted (**f**); **g** relationship between patterns on maps **a** and **e** ($R^2 = 0.08$); **h**, predicted spatial pattern of species diversity emerging from a neutral model that assumed kinetic effect of temperature on speciation probability; **i**, residuals between observed (**a**) and predicted (**h**); **j**, relationship between patterns on maps **a** and **h** ($R^2 = 0.17$). **k**, neutral model assuming the combined effect of kinetic energy on speciation and chemical energy on community size; **l**, residuals between observed (**a**) and predicted (**k**). **m**, relationship between patterns of maps **a** and **k** ($R^2 = 0.06$).

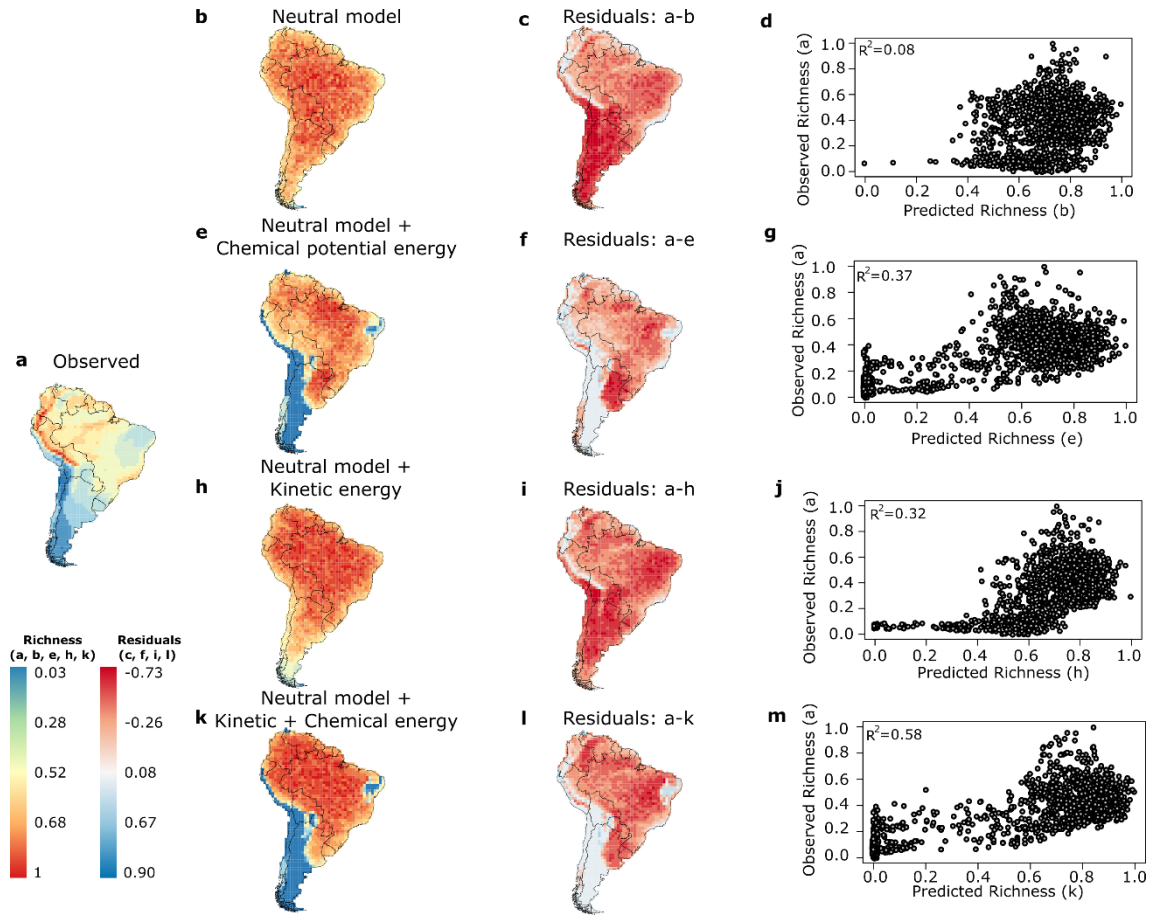


Fig. A6: Contrast between empirical and predicted spatial patterns of species diversity in South America. The four variants of neutral models were parametrized assuming the mean parameters values estimated through a Gibbs MCMC. **a**, observed spatial pattern of bird diversity in South America; **b**, predicted spatial pattern of species diversity emerging from a classical neutral model; **c**, residuals between observed (*a*) and predicted (*b*) diversity; **d**, relationship between patterns on maps *a* and *b* ($R^2 = 0.08$); **e**, predicted spatial pattern of species diversity emerging from a neutral model that assumed the effect of environmental energy (AET) on community size; **f**, residuals between observed (*a*) and predicted (*f*); **g** relationship between patterns on maps *a* and *e* ($R^2 = 0.37$); **h**, predicted spatial pattern of species diversity emerging from a neutral model that assumed kinetic effect of temperature on speciation probability; **i**, residuals between observed (*a*) and predicted (*h*); **j**, relationship between patterns on maps *a* and *h* ($R^2 = 0.32$). **k**, neutral model assuming the combined effect of kinetic energy on speciation and chemical energy on community size; **l**, residuals between observed (*a*) and predicted (*k*). **m**, relationship between patterns of maps *a* and *k* ($R^2 = 0.58$).

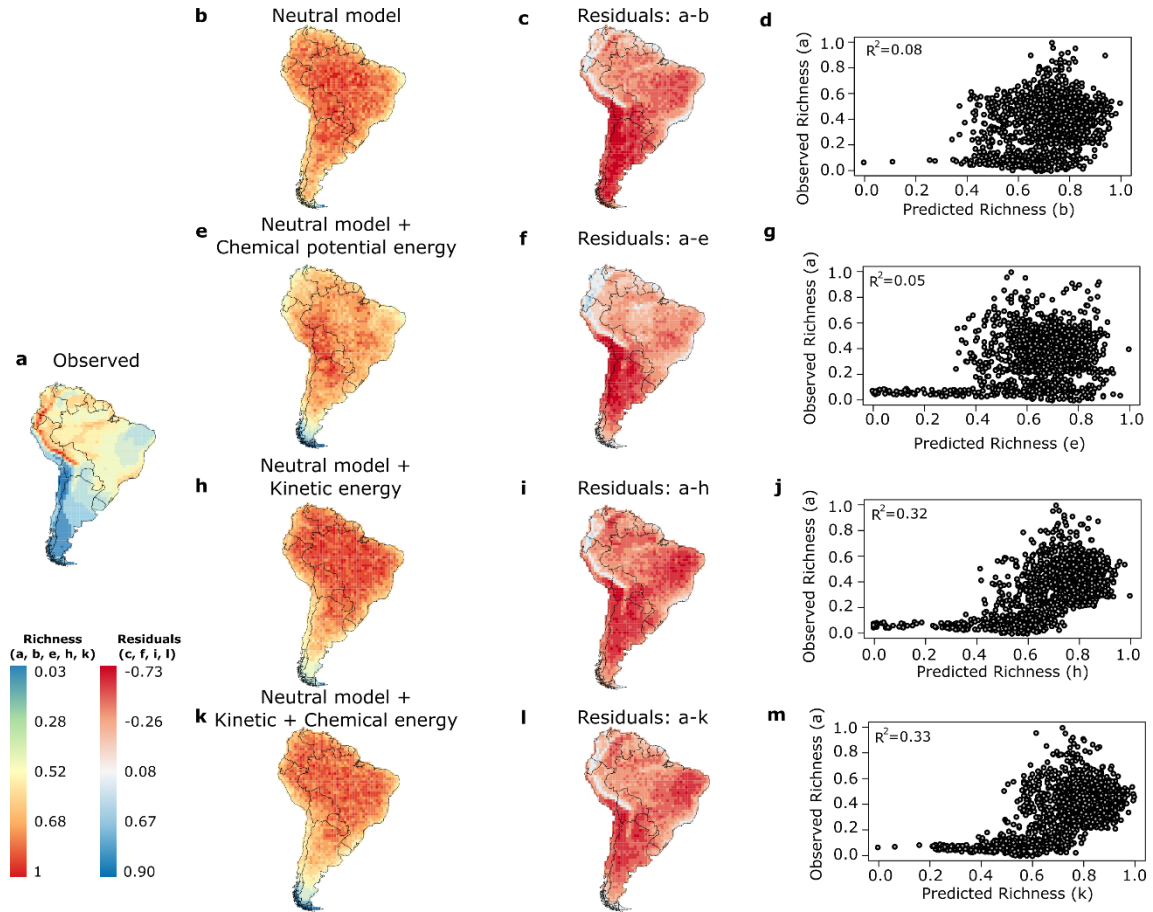


Fig. A7: Contrast between empirical and predicted spatial patterns of species diversity in South America. The four variants of neutral models were parametrized assuming the mean parameters values estimated through a Gibbs MCMC. **a**, observed spatial pattern of bird diversity in South America; **b**, predicted spatial pattern of species diversity emerging from a classical neutral model; **c**, residuals between observed (*a*) and predicted (*b*) diversity; **d**, relationship between patterns on maps *a* and *b* ($R^2 = 0.08$); **e**, predicted spatial pattern of species diversity emerging from a neutral model that assumed the effect of environmental energy (PET) on community size; **f**, residuals between observed (*a*) and predicted (*f*); **g** relationship between patterns on maps *a* and *e* ($R^2 = 0.05$); **h**, predicted spatial pattern of species diversity emerging from a neutral model that assumed kinetic effect of temperature on speciation probability; **i**, residuals between observed (*a*) and predicted (*h*); **j**, relationship between patterns on maps *a* and *h* ($R^2 = 0.32$). **k**, neutral model assuming the combined effect of kinetic energy on speciation and chemical energy on community size; **l**, residuals between observed (*a*) and predicted (*k*). **m**, relationship between patterns of maps *a* and *k* ($R^2 = 0.33$).

CAPÍTULO 4

**BIOGEOGRAPHICAL HISTORY CONSTRAINS CLIMATIC NICHE
DIVERSIFICATION WITHOUT ADAPTIVE FORCES DRIVING EVOLUTION**

Biogeographical history constrains climatic niche diversification without adaptive forces driving evolution

Running title: Biogeographic constraints on climatic niche

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Abstract

Aim: To evaluate the effect of biogeographical history on climatic niche diversification.

Location: Simulated clades evolving in South America.

Methods: We modeled species evolution under neutral community dynamics and purposely assumed that climatic niche is an emergent property of species. This assumption allows us to better understand whether phylogenetic niche conservatism could be observed when climatic niche is only constrained by biogeographical processes of dispersal and speciation. We varied speciation and dispersal probability, calculating phylogenetic signal of niche overlap and distance between niche centroids for each emergent artificial biota. We then compared the phylogenetic signal of our model with the expectation of climatic niche evolution under Brownian Motion.

Results: We found that phylogenetic signal of climatic niche in the spatially explicit neutral model is usually higher than expected by chance, but lower than expected by Brownian Motion evolution. Because simulated climatic niches have lower phylogenetic signal than expected by Brownian Motion evolution, standard ecological and evolutionary interpretation would suggest that climatic niche evolved with little variation over time caused by strong evolutionary constraints. However, our model assumes that climatic niche does not evolve by adaptive forces and is only a consequence of stochastic dispersal and speciation over space and time.

Main conclusions: Our study reinforces the strong imprints of biogeographical processes on climatic niche evolution, even when no adaptive forces are driving niche diversification. Therefore, although testing phylogenetic signal is the most common approach in studies evaluating phylogenetic patterns in climatic niche conservatism, our results reinforce previous claims that these patterns alone are not capable of distinguishing the possible effect of space in the retention of climatic niche. Biogeographical processes alone can leave imprints in patterns of climatic niche overlap between related species. A careful evaluation of macroevolutionary models underlying phylogenetic patterns of niche variation among species is important to avoid pitfalls related to interpretation of mechanisms of niche diversification.

Key-words: Climatic niche; Phylogenetic signal; Neutral Theory; Dispersal; Speciation; Phylogenetic Niche Conservatism.

Resumo

Objetivo: Avaliar o efeito de história biogeográfica na diversificação de nicho climático.

Local: Clados simulados evoluem na América do Sul.

Métodos: Nós modelamos a evolução de espécies sob dinâmica neutra de comunidades e propositalmente assumimos que nicho climático é uma propriedade emergente de espécies. Esse pressuposto nos permite melhor entender se conservação filogenética de nicho poderia ser observada quando nicho climático é apenas restringido por processos biogeográficos de dispersão especiação. Nós variamos a probabilidade de dispersão e especiação, calculando sinal filogenético de sobreposição de nicho e distância entre centroides de nicho para cada biota artificial emergente. Nós então comparamos o sinal filogenético do nosso modelo com a expectativa de evolução de nicho por movimento Browniano.

Resultados: Nós encontramos que sinal filogenético de nicho climático no modelo espacialmente explícito neutro é em geral maior do que esperado pelo acaso, mas menor do que esperado pelo movimento Browniano de evolução. Uma vez que os nichos climáticos possuem menor sinal filogenético do que esperado por movimento Browniano, a interpretação ecológica padrão sugeriria que nicho climático evoluiu com pouca variação através do tempo causada por fortes restrições evolutivas. No entanto, nosso modelo assume que nicho climático não evolui por forças adaptativas e é somente consequência de dispersão e especiação estocástica no espaço e no tempo.

Conclusões principais: Nosso estudo reforça as fortes impressões de processos biogeográficos na evolução de nicho climático, mesmo quando nenhuma força adaptativa está afetando a diversificação de nicho. Portanto, apesar de testar sinal filogenético ser a abordagem mais comum em estudos que avaliem padrões de sinal filogenético em conservação de nicho climático, nossos resultados reforçam reivindicações anteriores de que esses padrões sozinhos não são capazes de distinguir os possíveis efeitos do espaço na retenção de nicho climático. Processos biogeográficos sozinhos podem deixar impressões em padrões de sobreposição de nicho entre espécies filogeneticamente próximas. Uma avaliação cuidadosa de modelos evolutivos por trás de padrões filogenéticos de variação de nicho entre espécies é importante para evitar armadilhas relacionadas a interpretação de mecanismos de diversificação de nicho.

Palavras-chave: Nicho climático; Sinal filogenético; Teoria neutra; Dispersão; Especiação; Conservação filogenética de nicho.

INTRODUCTION

Phylogenetic conservatism of climatic niches, the tendency of species to retain ancestral climatic niche, is commonly associated with the emergence of large scale patterns of species diversity (Buckley et al., 2010; Wiens et al., 2010), driven by species responses to climate change (Bonebrake et al., 2018; Lavergne, Mouquet, Thuiller, & Ronce, 2010; Rangel et al., 2018). In addition, phylogenetic niche conservatism among species is a central assumption of many statistical methods, such as community comparative analysis, community phylogenetics and environmental niche modelling (Pearman, Guisan, Broennimann, & Randin, 2008; Webb, Ackerly, Mcpeck, & Donoghue, 2002). Although phylogenetic niche conservatism is used as a possible explanation for a series of ecological and evolutionary patterns, it is still a controversial issue (Cooper, Jetz, & Freckleton, 2010; Losos, 2008; Wiens, 2008; Wiens et al., 2010). In particular, we are frequently confronted with our ignorance about the conditions that prevent or accelerate the diversification of climatic niche among species in a clade (Losos, 2008; Münkemüller, Boucher, Thuiller, & Lavergne, 2015; Wiens et al., 2010).

Explanations for niche similarity go back at least as far as Darwin, who identified the recent common ancestry of related species as the key reason for their ecological similarity (Darwin, 1859). In addition, biogeographical history can also have an important role in climatic niche evolution (Borcard, Legendre, & Drapeau, 1992; Freckleton & Jetz, 2009), although it is mostly overlooked in studies of niche conservatism (Boucher, Thuiller, Davies, & Lavergne, 2014). As an alternative to Darwin's ancestry explanation, Grafen (1992) proposed that phylogenetically related species tend to be ecologically similar because they share a similar history of adaptive forces, as environmental conditions tend to be spatially autocorrelated and phylogenetically related species tend to occur close to each other in space. Thus,

biogeographical processes (e.g., dispersal limitation and speciation) shape similar spatial distribution of related species (Freckleton & Jetz, 2009; Warren Cardillo, Rosauer, & Bolnick, 2014), affecting the evolution of Grinnellian (i.e., non-interactive environmental variables) and Eltonian niches (i.e., resources consumer dynamics and species' interactions) (Boucher et al., 2014; Coelho & Rangel, 2018; Coelho, Rodrigues, & Rangel, 2017).

The most commonly used method to infer climatic niche conservatism is by testing phylogenetic signal on niche dimensions or surrogates of ecological niches (Buckley et al., 2010; Cooper et al., 2010; Olalla-Tárraga, González-Suárez, Bernardo-Madrid, Revilla, & Villalobos, 2017; Peixoto, Villalobos, & Cianciaruso, 2017). Phylogenetic signal estimates (a) the tendency of species to resemble each other more than would be expected if they were randomly drawn from the phylogenetic tree (Blomberg & Garland, 2002) and (b) the fit of different evolutionary models to the data (Münkemüller et al., 2015). However, a direct association between phylogenetic signal and niche conservatism is sometimes misleading (Losos, 2008), because niche conservatism is an explanation for phylogenetic signal, but the contrary is not necessarily true (Revell, Harmon, Collar, & Oakley, 2008). Even if strong phylogenetic niche conservatism exists, phylogenetic distance may be unrelated to species niches (Revell et al., 2008) and labile niches could lead to a strong association between niche difference and phylogenetic distance (Münkemüller et al., 2015). Cooper et al. (2010) discussed how several macroevolutionary models can be associated with different forms of niche conservatism, revealing that different evolutionary models provide different expectations of phylogenetic signal, ranging from a purely Brownian neutral expectation up to strongly constrained diversification (in the extreme, without any variance and thus low phylogenetic signal).

Here we combined phylogenetic and geographical approaches (Broennimann et al., 2012; Warren, Glor, & Turelli, 2008; Wiens et al., 2010) to test the importance of biogeographical processes on the retention of climatic niche similarities among related species. We evaluated the tendency of higher niche overlap (Broennimann et al., 2012; Cardillo & Warren, 2016; Peixoto et al., 2017) and climatic distance of niche centroids (Hof, Rahbek, & Araújo, 2010; Pyron & Burbrink, 2012) between species that evolved under neutral community dynamics. However, in our simulation, species climatic niches are neither the result of adaptative processes, nor they affect the distribution of simulated species. Indeed, simulated climatic niches are just emergent properties of spatially explicit neutral evolutionary dynamics driving the geographical distribution of species. Although unrealistic, we assumed that climatic niches do not result from adaptative processes to understand how biogeographical processes constrain climatic niche diversification *independent* of adaptation.

In our simulation, the similarity of climatic niche of closely related species (i.e., large niche overlap and/or short distance between niche centroids) indicate that species occupy similar locations in environmental space by pure biogeographical history. Indeed, it is widely known that dispersal limitation and the history of speciation events can cause similar spatial distributions among related species (Grafen, 1992; Kisel & Barraclough, 2010; Warren et al., 2014). After a speciation event, species may remain close to each other in their spatial distribution, either because the speciation event was recent, or by strong dispersal limitation. Thus, observed constraints on climatic niche diversification could be the result of historical speciation and dispersal events even when there is no adaptation constraining niche evolution.

In addition to evaluating the phylogenetic signal in niche overlap and climatic niche centroids, we also contrasted the phylogenetic signal that emerges from our

simulation model against the phylogenetic signal in climatic niches evolving under Brownian motion (BM) (i.e., amount of change in climatic niche is linearly related to the phylogenetic distance, regardless of any other process). The BM model of evolution estimates the value of a trait (e.g., climatic niche) that is not under selection and is evolving purely by a neutral process, sensu Kimura (mutation-drift equilibrium). When a trait is evolving towards a selection optimum, thus strong phylogenetic niche conservatism, little variation is observed for the trait over time resulting in lower phylogenetic signal than expected by BM (Münkemüller et al., 2015). Thus, if phylogenetic signal observed in clades that emerged under neutral biogeographical dynamics is *similar* to the expected under BM evolution, then phylogenetic signal in simulated climatic niches represent the expectation of neutral evolution without biogeographical constraints (Cooper et al., 2010; Wiens et al., 2010). Conversely, if phylogenetic signal observed in neutral simulations is lower than predicted by BM (Münkemüller et al., 2015), then the evolution of climatic niche is under substantial biogeographical constraint, as the neutral simulation does not include any selection or evolution towards optimum.

MATERIAL AND METHODS

Model purpose and assumptions

Here, we used a stochastic simulation model that simulates the evolution of species under neutral community dynamics. In our model, individuals are equivalent in birth, death, speciation and dispersal, independent of their species identity (Hubbell, 2001). Additionally, the climatic niche of species does not evolve from adaptive processes but is an emergent property of each species based on their stochastically

evolving spatial distribution. This assumption allows us to better understand whether phylogenetic niche conservatism could be observed when climatic niche is only constrained by biogeographical processes of dispersal and speciation. In addition, the model can be used to understand whether trait patterns emerging from spatially explicit neutral models are similar to those generated by a neutral BM model of trait evolution.

Geographical and environmental space

The neutral community dynamics was simulated in an equal area gridded map of South America at 1° resolution. Each geographical cell is characterized by four environmental variables obtained from Worldclim (www.worldclim.org; Hijmans, Cameron, Parra, Jones, & Jarvis, 2005): Mean annual temperature (BIO1); Maximum temperature of the warmest month (BIO5); Annual precipitation (BIO12); Precipitation of the driest month (BIO14). Because temperature and precipitation are the main environmental variables constraining species distributions, we choose those variables to represent the variability of mean temperature and precipitation and the variability in two extreme conditions, maximum temperature of the warmest month and precipitation of the driest month. These variables represent the environmental space of the simulation, although they do not affect the evolutionary dynamics of species ranges. Thus, the climatic niche of simulated species emerges from the neutral biogeographical dynamics. The niche is defined according to the environmental conditions of the grid cells occupied by each species.

Neutral community dynamics

Here, we employed recent implementations of neutral simulation models (Coelho, Dambros, Rosauer, Pereira, & Rangel, 2018; Coelho & Rangel, 2018). The

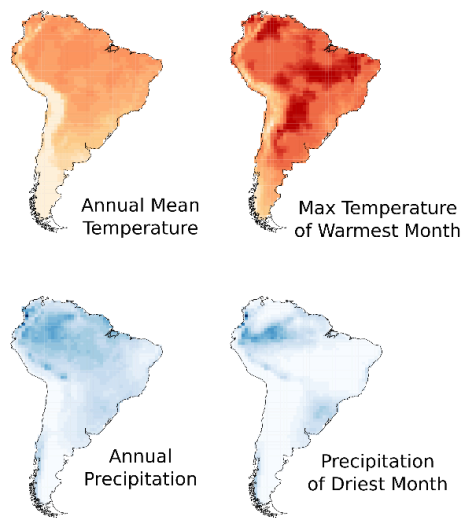
neutral biogeographical processes are simulated in a metacommunity represented by the gridded geographical domain of South America. Each community (i.e., gridded map cells) is constantly populated by thirty individuals (i.e., zero-sum assumption). The model simulates the evolution of species that emerge and colonize the metacommunity by ecological drift. At the beginning of the simulation, all individuals belong to an ancestral species. At each time step of the model, the following sequence of stochastic events occur: (a) one individual of the metacommunity is randomly chosen; (b) the randomly chosen individual can die ($P = 1 - \nu$) or speciate ($P = \nu$); (c) If the individual dies, the descendant of a randomly chosen individual from the same cell ($P = 1 - m$), or from neighboring cells ($P = m$) colonize the empty slot; (d) If speciation is the outcome of the stochastic processes, the speciation event occur for the randomly chosen individual (i.e., Point mutation, Hubbell, 2001) and a new species emerges in the simulation.

The steps described above are repeated for a predefined number of generations, necessary to reach stability of simulated patterns. One generation is defined as the number of iterations equal to the number of individuals in the geographic domain (Coelho & Rangel, 2018). Preliminary sensitivity analyses indicate that 6,000 generations are sufficient to reach stability of three important simulated patterns: (a) number of species, (b) species abundance distribution and (c) spatial patterns in species richness. A presence/absence matrix is constructed based on the occurrence of species at each grid cell. A phylogeny is produced based on the historical record of speciation and extinction events (Coelho et al., 2017).

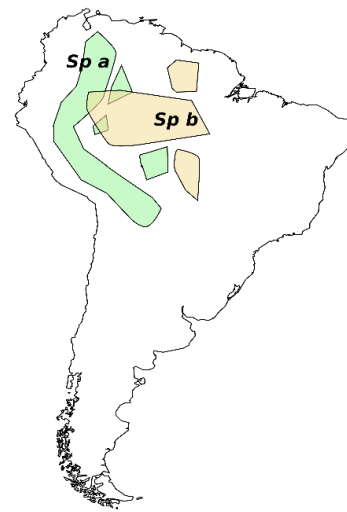
Climatic niche analysis

Here, we followed the method of Broennimann et al. (2012) to calculate the overlap on climatic niche for pairs of species (Figure 1). This method allows the comparison of species climatic niche in environmental space (see Broennimann et al., 2012) and has been recently employed in tests of phylogenetic conservatism of climatic niches (e.g., Hu et al., 2016; Medeiros, Guisan, & Lohmann, 2015; Peixoto et al., 2017). For each pair of species that emerge from the simulation, a reduced multidimensional environmental space (a grid of 100×100 cells) was defined by the first two axes of a principal component analysis (PCA) of the four environmental variables and grid cells where both species co-occur. This reduced multidimensional environmental space is then used to calculate the similarity (i.e., overlap) between the climatic niche of the pair of species through the Schoener's D metric (Broennimann et al., 2012), which varies from zero to one, representing, respectively, no overlap and total overlap between niches. Schoener's D is symmetric, meaning that $D_{a,b} = D_{b,a}$, where a and b are species (Warren et al., 2008). We calculated D for all pairs of species, and then transformed the values into a dissimilarity measure ($1 - D$). In addition, we calculated the median of each axes of the PCA to define the climatic niche centroids of each species, and then calculated pairwise Euclidean distance between niche centroids as an estimate of similarity of climatic niche between species (Figure 1).

1. Environmental layers are used to define the climatic niche of species



2. Species evolve under purely neutral spatial dynamics where climatic niche does not result from adaptive processes



3. For each pair of species the reduced multidimensional environmental space is defined and: niche overlap is calculated (**D**) or, the distance between niche centroids is calculated (**d**). Phylogenetic signal is calculated by a mantel correlation (niche overlap, or distance between centroids vs phylogenetic distance (**PD**)).

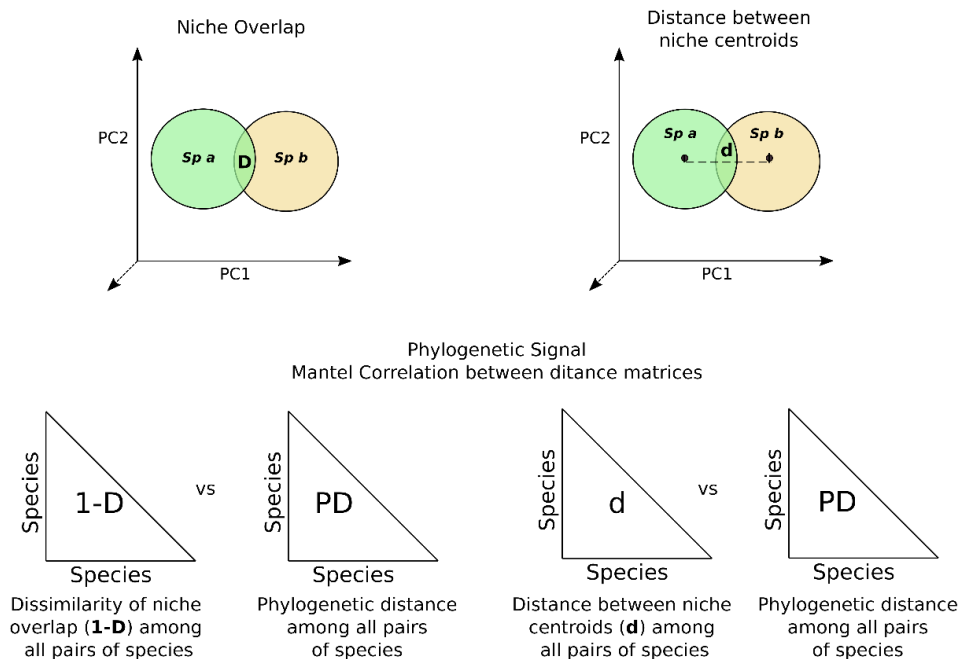


FIGURE 1. Combination of phylogenetic and geographical approach to test whether related species resemble each other in climatic niche overlap and niche centroids. (1) Environmental layers are selected to represent the climatic niche of species. (2) Species emerge under pure neutral biogeographical processes in which climatic niche do not result from adaptive processes, but simply by species distribution over the geographical domain. (3) For each pair of species that emerges from the simulation, a reduced multidimensional environmental space is defined and climatic niche overlap (Schoener's **D**) and niche centroids are calculated. The Schoener's **D** is transformed into a dissimilarity measure (**1-D**) and distance from centroids are calculated and correlated with phylogenetic distance using Mantel correlation.

To estimate phylogenetic signal in climatic niche we used a Mantel correlation between pairwise phylogenetic distance among species and (a) pairwise dissimilarity of species climatic niches and (b) pairwise distance among niche centroids (Cooper et al., 2010) (Figure 1). Statistically significant positive Mantel correlations (estimated after 1,000 randomization) indicate phylogenetic signal in climatic niche. Despite some controversy, phylogenetic signal has been interpreted as one type of niche conservatism (see Cooper et al., 2010; Wiens et al., 2010; but see Losos, 2008).

We compared observed phylogenetic signal emerging from our spatially explicit neutral model with expectations of phylogenetic signal when climatic niche evolved under BM model of evolution, which is not constrained by the biogeographical history of the clade. For each replicate of the neutral biogeographical simulation we used the emerging phylogeny to simulate the independent evolution of two traits under BM (replicated 1,000 times). These two simulated traits represent the evolution of niche centroids in the reduced multidimensional environmental space (Figure 1, PC1 and PC2). Because BM evolution is not a spatially explicit model, it is not possible to simulate the environmental space of species (i.e., environmental information for all the geographical cells that the species occur) and calculate niche overlap. Thus, only niche centroids are simulated by BM evolution.

We investigated the correlation between niche dissimilarity and phylogenetic distance under different combinations of simulation parameters that could affect the spatial distribution of species: dispersal probability and speciation probability. We designed the exploration of parameter space to maximize information, but within the constraints imposed by computational demand required to replicate the biogeographical simulation and niche overlap analysis. Parameters combinations that produced small ranged species (i.e., less than five occurrences) were excluded from analysis (see

Broennimann et al., 2012). Each parameter combination was replicated 100 times and here we report the mean observed phylogenetic signal of climatic niche.

RESULTS

Phylogenetic signal in climatic niche emerges under neutral biogeographical dynamics, as indicated by positive and significant mantel correlations between niche traits and phylogenetic distance (Figures 2 and S1). We found that speciation probability has the strongest effect on phylogenetic signal. As speciation rate increases, the mean phylogenetic signal of niche overlap and distance from climatic niche centroids also increase (Figure 2a,b). Higher speciation promotes higher chances of co-occurrences between related species in the geographical space and generates higher resemblance in environmental space among related species. As speciation decreases, closely related species tend to diverge more in environmental space, showing negative correlations that are close to zero (Figure 2a,b). Lower speciation rates allow more time for species to stochastically disperse over the geographical space, which creates less similarity in climatic niche. Conversely, dispersal probability does not affect the degree of phylogenetic signals when compared to speciation probability (Figure 2a,b).

Although high speciation rates increase phylogenetic signal in climatic niches, the phylogenetic signal is generally weak but statistically significant ($r_{\max} = 0.11$, Figures 1 and 2a,b), indicating that neutral biogeographical dynamics are sufficient to artificially generate phylogenetic signal in non-biological climatic niches (Figures 2a,b and S1). Indeed, the phylogenetic signal of climatic niches that evolved under neutral biogeographical dynamics is always lower than the phylogenetic signal generated by BM model (Figure 2c,d), indicating that biogeographical history imposes a stronger constraint on the evolution of climatic niche than BM model of evolution. However,

although the biogeographical model is neutral with regard to the effect of adaptive forces on niche evolution, the results we observed are usually interpreted as a consequence of stabilizing selection or selection towards a climatic optimum.

When climatic niche centroids are simulated under BM, only the imprints that dispersal and speciation leave in the phylogeny are responsible for the variability of phylogenetic signal (Figure 2c). Phylogenetic signal increases when speciation is low, and dispersal is high, and decreases when speciation is high, and dispersal is low. Thus, the expectation of neutral BM evolution in the phylogeny is different from what is observed in spatially explicit neutral models (Figure 2). The phylogenetic signal observed for climatic niches that emerges under BM is always higher than the prediction of the neutral biogeographical model (Figure 2d).

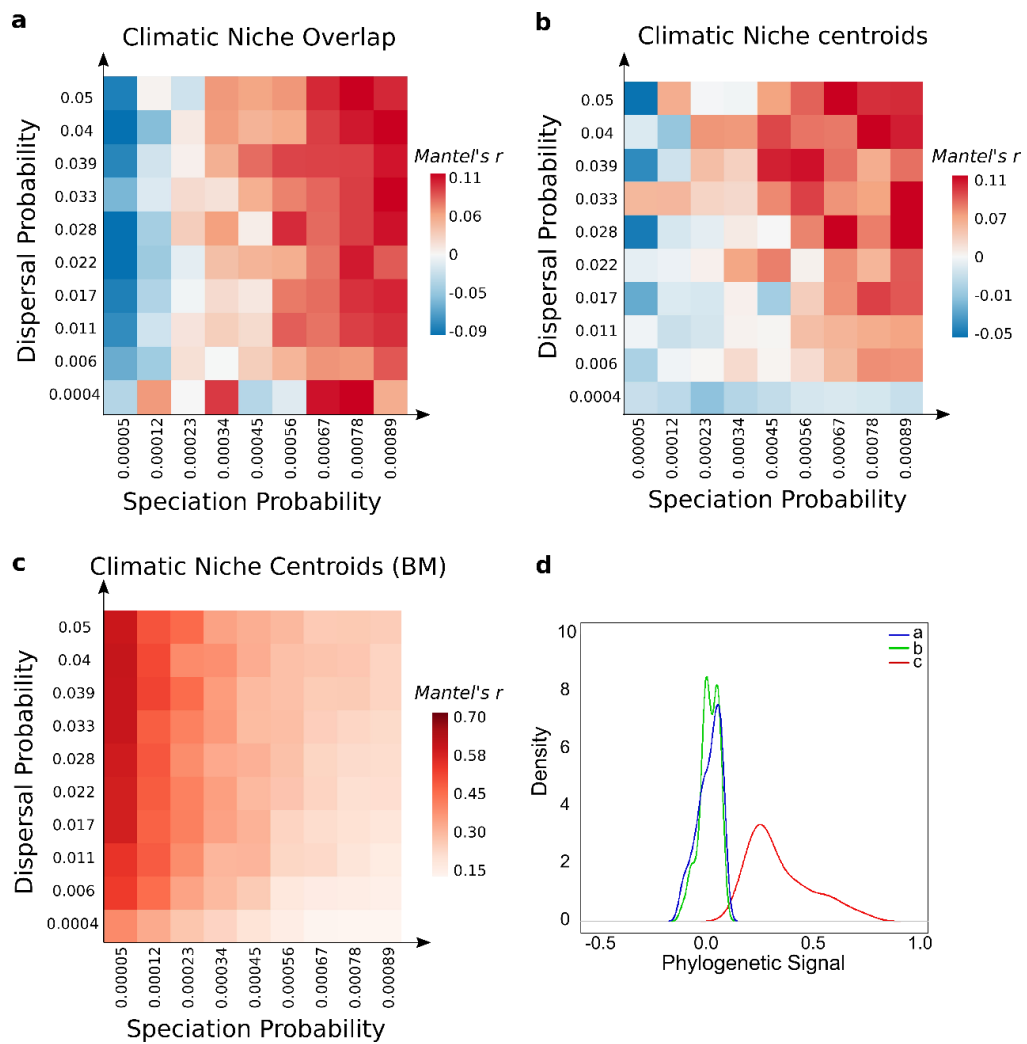


FIGURE 2. Heat maps showing the effect of speciation probability (x) and dispersal probability (y) on the phylogenetic signal (Mantel's r). Each figure represents: **a** – phylogenetic signal of niche overlap; **b** – Phylogenetic signal of niche centroids (distance between centroids); **c** – Phylogenetic signal observed when niche centroids evolve by Brownian Motion (BM); **d** - distribution of phylogenetic signals observed for niche overlap (a), niche centroids (b) and niche centroids simulated under Brownian motion (c).

DISCUSSION

In this study, we developed a simple simulation model to test the effect of biogeographical processes on patterns of climatic niche overlap between related species. We modelled the evolution of species under neutral community dynamics over the geographical domain of South America and purposely assumed that climatic niche is an

emergent property of species. Based on the artificial biota generated under neutral community dynamics, we tested the phylogenetic signal of climatic niches under variations of speciation probability and dispersal probability. We found that a consistent tendency of species to resemble each other in the environmental space under different simulation scenarios. We also found that phylogenetic signal in climatic niche evolving under a spatially explicit neutral model is always lower than expected under a BM model of trait evolution, indicating that biogeographical history is an evolutionary constraint that affect climatic niches. These results emphasize the imprints of biogeographical history on the diversification of climatic niches, a theme that is highly overlooked in ecological literature.

In our simulation, speciation probability is the major force affecting the similarity of climatic niche among related species. As probability of speciation increases, phylogenetically related species tend to co-occur in geographical space, therefore increasing the similarity of their climatic niches. It is widely known that species with overlapping geographical distribution tend to have similar traits (Coelho & Rangel, 2018; Freckleton & Jetz, 2009; Grafen, 1992; Jetz, Freckleton, & McKechnie, 2008; Phillips, Töpfer, Rahbek, Böhning-Gaese, & Fritz, 2018; Warren et al., 2014), but the effect of biogeographical history on phylogenetic signal in climatic niches is seldom studied. Because studies of climatic niche similarities are usually based on empirically estimated realized niches, past biogeographical history of clades must have an important role on the similarity of climatic niche among related species.

Previous studies reported a possible effect of dispersal capacity on phylogenetic signal in climatic niches (Freckleton & Jetz, 2009; Jetz et al., 2008). However, we only found an effect of dispersal on similarity of climatic niche among related species when climatic niche is assumed to evolve by BM. When a spatial explicit model is used,

speciation has a stronger effect on phylogenetic signal in climatic niches than dispersal (Figure 2), probably because our neutral models assumes that new species arise with low abundance and occupy only a small part of the range of the ancestral species (Coelho & Rangel, 2018; Hubbell, 2001).

The definition of phylogenetic niche conservatism as a *pattern* or a *process* is an unresolved and hotly debated topic (Losos, 2008; Münkemüller et al., 2015; Pyron, Costa, Patten, & Burbrink, 2015; Wiens et al., 2010). Climatic niche conservatism has been suggested as a strong driver of contemporary latitudinal gradients in species diversity (Buckley et al., 2010; Wiens & Donoghue, 2004; Wiens et al., 2010). Under the perspective that it drives a pattern, climatic niche conservatism is viewed as a *process*. In fact, mechanistic simulation models in macroecology show the importance of climatic niche conservatism as a process generating species diversity gradients (Rangel, Diniz-Filho, & Colwell, 2007; Rangel et al., 2018). However, our results suggest that phylogenetic conservatism of climatic niches may be an emergent *pattern* driven only by biographical dynamics. This observation has important implications, since a link between tropical niche conservatism (Wiens & Donoghue, 2004) and neutral community dynamics could be realized under neutral and metabolic theory conciliations (Tittensor & Worm, 2016). We would not be surprised if the increased speciation probabilities, caused by higher temperatures in warmer regions (Allen, 2002; Rohde, 1992; Tittensor & Worm, 2016), have generated a stronger pattern of climatic niche conservatism in tropical environments (see Figure 2).

Studies simulating niche evolution under the assumption of a selection optimum, such as Ornstein–Uhlenbeck model, show that phylogenetic signal in climatic niche is weaker than in the absence of selection optimum (e.g., BM, Münkemüller et al., 2015). Thus, under Ornstein–Uhlenbeck a strong stabilizing selection (i.e., the parameter α of

the Ornstein–Uhlenbeck process) (see Martins, Diniz-Filho, & Housworth, 2002) generates little variation in climatic niches over time (strong phylogenetic niche conservatism), resulting in weak phylogenetic signal (Münkemüller et al., 2015). These evolutionary models were designed to describe the emerging pattern when natural selection drives niches towards an optimal niche value (Butler & King, 2004; Hansen, 1997). When traits evolve under OU the phylogenetic signal tends to be lower than BM as under OU the traits are attracted back to the optimum (and both closely related, and distantly related species can have similar traits). Interestingly, the same pattern emerges from our spatial explicit biogeographical model, although no such mechanism to attract climatic niches to an optimal niche value is implemented in the model, and the evolution of niches is neutral. Thus, our results clearly indicate that little variation in climatic niche over time (i.e., strong phylogenetic niche conservatism) may be a consequence of past biogeographical history of clades.

Future studies of climatic niche conservatism will benefit from recent advances in community phylogenetics. Although the most commonly used processes for explaining community phylogenetic patterns were environmental filter and competition (Baraloto et al., 2012; Swenson, Enquist, Thompson, & Zimmerman, 2007), dispersal and past speciation can also have a role on contemporary phylogenetic patterns of communities (Pigot & Etienne, 2015; Vamosi, Heard, Vamosi, & Webb, 2009; Warren et al., 2014). These biogeographical processes were incorporated in more complex null models to evaluate the hypothesized processes shaping community phylogenetics (Pigot & Etienne, 2015). As we showed here, pure biogeographical history can also affect the propensity of higher niche overlap between phylogenetically related species. Since species traits are expected to be the result of evolutionary history (Freckleton & Harvey, 2006; Harvey & Purvis, 1991), as well as their geographical distribution (Borcard et

al.,1992; Freckleton & Jetz, 2009; Grafen, 1992), studies of climatic niche evolution require analytical strategies capable of distinguishing between phylogenetic and spatial components in trait data (e.g., Freckleton & Jetz, 2009), or spatially explicit models of neutral climatic niche evolution.

Testing phylogenetic signal is the most common approach in studies evaluating phylogenetic patterns in climatic niche conservatism. However, our results reinforce previous claims that these patterns alone are not capable of distinguishing between possible causes of phylogenetic niche conservatism, such as selection and biogeographical history (Münkemüller et al., 2015). As shown here, biogeographical processes alone can leave imprints in patterns of climatic niche overlap between related species, even in the complete absence of selection. A careful evaluation of phylogenetic patterns of niche variation among species, as well as their potential causes, is important to avoid pitfalls related to the inference of mechanisms driving niche diversification.

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AUTHORS CONTRIBUTIONS

M.T.P.C., J.F.M.R., J.A.F.D. and TFR designed the study. M.T.P.C programmed the biogeographical simulation model, ran the simulation, created the figures and led

writing with input from all authors. M.T.P.C. and J.F.M.R analysed the data. All authors discussed the results and contributed to the writing.

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BIOSKETCH

Marco Túlio P. Coelho is a PhD student (ecology and evolution). His current work focuses on modelling the processes that shape spatial patterns of species diversity, language diversity and interaction networks.

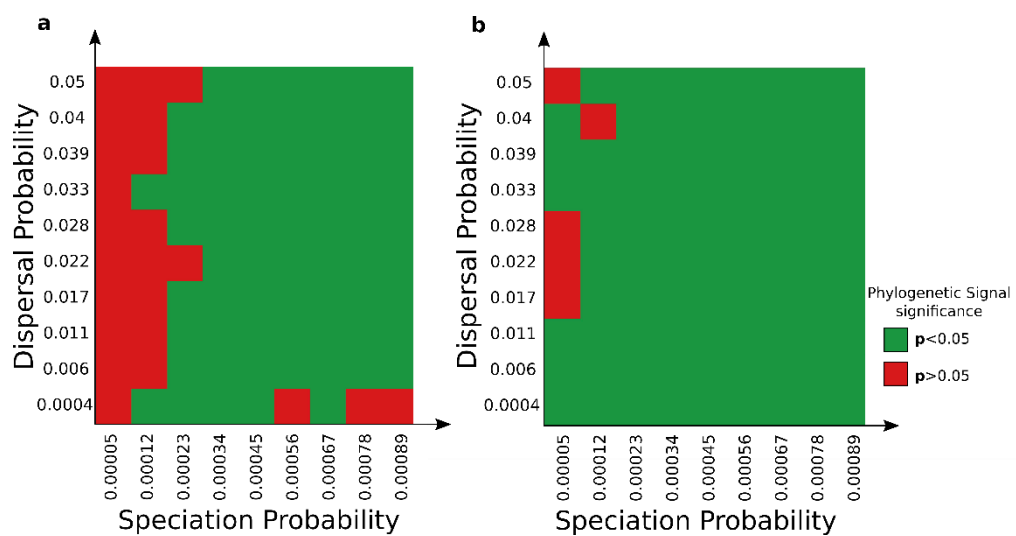
Supporting Information

Biogeographical history constrains climatic niche diversification without adaptive forces driving evolution

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Appendix S1 – Supporting figure illustrating the statistical significance of phylogenetic signal under different parameter combinations

Figure S1 – Significance of phylogenetic signals presented in Figure 2a and Figure 2b. PS significance for niche overlap (a) and niche centroids (distance between centroids) (b).



**PARTE III. PREDITORES ECOLÓGICOS DE PADRÕES ESPACIAIS DE
DIVERSIDADE HUMANA**

CAPÍTULO 5

ADVANCING THE SCIENCE OF HUMAN MACROECOLOGY

Advancing the Science of Human Macroecology

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Abstract

Human diversity is expressed in myriad ways: in the size and shape of our bodies, in thousands of different languages, hundreds of different religious practices and dozens of marital, sexual, and child-rearing norms. Although many large-scale patterns of human diversity resemble species diversity patterns (e.g. latitudinal diversity gradients), human diversity patterns have seldom been studied by ecologists. To date, studies labeled as human macroecology have explored the dependence of resources for population growth, economic development and sustainability, by using theoretical and methodological advances from thermodynamics, allometry, metabolic ecology and macroecology. However, studies of human macroecology are still narrow in terms of using theory and methods from macroecology to study variation in human diversity over space and time. Here, we explore several debates about morphological, physiological and cultural diversity of humans that may call the attention of ecologists, given their resemblance to many patterns of species diversity. We place particular emphasis on themes that have been explored in detail by macroecologists and biogeographers, such as variations in a latitudinal gradient of body size and shape (i.e. Bergmann and Allen effect), thermal tolerance, and diversity accumulation, all of which have been consistently explored for humans in other disciplines. Our review brings together findings across fields to demonstrate how ecological theories and methods do apply to humans even when ecologists have tended not to study humans. Thus, our study not only stands as a call to ecologists to test their ideas on humans, but also to use ecological approaches to contribute to long-standing debates across fields. We hope to call the attention of Ecologists in their roles of authors and editors for a flourishing interdisciplinary field with a lot of potential.

Key-Words: Human Macroecology, Human Diversity, Cultural Diversity, Language Diversity

Resumo

A diversidade humana é expressa de inúmeras maneiras: no tamanho e formato de nossos corpos, em milhares de idiomas diferentes, centenas de práticas religiosas diferentes e dezenas de normas matrimoniais, sexuais e de criação de filhos. Embora existam muitos padrões de diversidade humana em grandes escalas espaciais que se assemelhem aos padrões de diversidade de espécies (por exemplo, gradientes de diversidade latitudinal), os padrões de diversidade humana raramente foram estudados por ecólogos. Até a presente data, estudos rotulados como Macroecologia Humana exploraram a dependência de recursos para crescimento populacional, desenvolvimento econômico e sustentabilidade, usando avanços teóricos e metodológicos da termodinâmica, alometria, ecologia metabólica e macroecologia. No entanto, os estudos da macroecologia humana ainda são limitados em termos de uso de teoria e métodos da macroecologia para estudar a variação da diversidade humana no espaço e no tempo. Aqui, exploramos vários debates sobre a diversidade morfológica, fisiológica e cultural dos seres humanos que podem chamar a atenção de ecólogos, dada sua semelhança com muitos padrões de diversidade de espécies. Colocamos ênfase particular em temas que foram explorados em detalhe por macroecólogos e biogeógrafos, como variações em um gradiente latitudinal de tamanho e forma corporal (isto é, efeito de Bergmann e Allen), tolerância térmica e acúmulo de diversidade. Minha revisão reúne descobertas em vários campos para demonstrar como as teorias e métodos ecológicos se aplicam aos seres humanos, mesmo quando os ecólogos tendem a não estudá-los. Assim, meu estudo não apenas serve como um chamado aos ecólogos testarem suas ideias em seres humanos, mas também para usar abordagens ecológicas para contribuir para debates de longa data que surgiram em diferentes campos da ciência. Esperamos chamar a atenção dos ecólogos em seus papéis de autores e editores para um campo interdisciplinar florescente com muito potencial.

Palavras-chave: Macroecologia Humana, Diversidade Humana, Diversidade Cultural, Diversidade de Línguas.

By evaluating the many subfields of ecology, one might think that ecologists are interested in the relationship between humans and their environment. Indeed, many ecologists study the impacts of past and current human activities on biodiversity (Vitousek et al. 1997; Brooks et al. 2002; Burney & Flannery 2005; Koch & Barnosky 2006; Buchar et al. 2010). However, few ecologists have studied how climate, geography and sociocultural factors shape any aspects of human diversity across the globe (Terrell 1997; Terrell 2006).

Human diversity is expressed in a myriad of ways: in the size and shape of our bodies, in thousands of different languages, hundreds of different religious practices and dozens of marital, sexual, and child-rearing norms. We build different types of houses, exploit different resources for subsistence and we have multiple means of resource management, political institutions and economic organization. Thus, interest in human diversity patterns exists in many fields of science, including anthropology, archaeology, economics, history, geography, linguistics, medicine, political sciences, sociology and many others (Huxley 1863; Carey & Steegmann 1981; Cavalli-Sforza et al. 1988; Binford 2001; Collard & Foley 2002; Ruff 2002; Chaplin 2004; Relethford 2004; Prugnolle et al. 2005; Molnar 2006; Li et al. 2008; Currie & Mace 2009; Scheinfeldt et al. 2010; Betti 2010; Hill et al. 2011; Burger et al. 2012, Botero et al. 2014; Tao et al. 2017; Gavin et al. 2018).

Humans are subject to the same natural laws as millions of other species on earth. However, no other species has had such wide ecological dominance or developed similarly complex socioeconomic systems. Although the human species (*Homo sapiens*) has an outstanding amount of data available and present non-random variability in characteristics over space (e.g. body size, number of spoken languages), ecological theoretical and methodological tools to describe and explain patterns in species traits

and species diversity have barely reached the many disciplines that engaged question about the relationship between human diversity and climatic, geographical and sociocultural factors.

Of course, subjecting humans to our ecological lenses require an interdisciplinary approach, because most of the knowledge about how biology and geography shape human diversity comes from other fields of science. One subfield of ecology that has been continually creating links among disciplines and that could contribute to a more profound understanding of human diversity is Macroecology (Brown & Maurer 1987; Brown & Maurer 1989; Brown 1995). While ecology has been very successful in separating nature into components and studying the behavior of each part in isolation (i.e. reductionist approach), a constant challenge in ecological sciences has been to understand general emergent patterns (McGill 2019) and their underlying processes (Gotelli et al. 2009). Thus, rather than trying to study fine details of nature, Macroecology tries to reveal patterns and processes over large spatial, temporal, or taxonomic scales, aiming to propose generalities (Brown 1995; Gaston & Blackburn 2010; McGill 2019). In order to explore the big picture of nature, macroecology defines a domain in which ecology, biogeography, paleoecology and evolution overlap (Smith et al. 2008).

The idea of studying humans through macroecological lenses is not new (Brown 2004) and the term Human Macroecology has already appeared in the literature (Brown et al. 2011). However, the focus of these prior studies is still narrow given the broad potential of *human macroecology* as recently suggested by Burnside et al. (2012). Even using theoretical and methodological advances from thermodynamics, allometry, metabolic ecology and macroecology, ecologists have tended to focus mostly on the dependence of resources for human population growth, economic development and

environmental sustainability (Brown et al. 2011; Burger et al. 2012; Burnside et al. 2012; Nekola et al. 2013; Brown et al. 2014). In turn, ecologists have not engaged with a vast range of patterns and processes affecting multiple dimensions of human diversity, such as the human-environment interactions that shape human physical and cultural traits over space and time (Molnar 2006; Harcourt 2012). Paradoxically, such patterns, and the processes underlying our own diversity have appeared in the literature of other fields of science (Box 1).

Box 1. Human Macroecology before Macroecology

As science evolves, the increase of knowledge leads to the emergence of scientific specialization which causes the emergence of new science fields (Casadevall & Fang 2015). Larger subdivisions (e.g. Biology) generate finer subdivisions (e.g. Ecology) that subsequently generates even finer subdivisions (e.g. Population Ecology) and so on. In ecology, the emergence of new fields is not a punctuated equilibrium event with a period of stasis followed by a rapid event of branching. It is in fact a gradual process that requires previous developments of one, or several lines of research within a pre-established field. After the new field is labeled by researchers, it is possible to identify previous studies that (i) inspired the definition of a new field and/or (ii) could be classified with the new label, even though being older than the label itself. Macroecology has a detailed documentation of its foundations in different areas of ecology (Smith et al. 2008; Smith et al. 2014). In fact, many of the themes that we focus in this study, such as Bergmann and Allen effect, or the latitudinal diversity gradients, were studied before Macroecology existed as a field and have been currently investigated by macroecologists and other ecologists. The case for Human Macroecology is not different. The description of patterns on human diversity in large spatial and temporal scales and the proposition of their underlying processes emerged in different fields of science. Here, we present some studies that fits the Human Macroecology field, although not being labeled as so.

- i. Variations in human skin color has been intensely studied (Chaplin 2004, Jablonski & Chaplin 2000). Natives from warmer environments tend to be darker than natives from cold environments. Skin color is strongly correlated with latitude and UV (ultraviolet) incidence (Jablonski & Chaplin 2000). Darker skin protects against deleterious effects of UV radiation, such as sunburn, skin cancer and damages to sweat glands which could explain why humans are darker in the tropics and even darker outside of forests (Jablonski & Chaplin 2000).
- ii. Botero et al. (2014) explored the ecology of religious beliefs of 583 societies spread over the world and showed that the belief in moralizing Gods are associated with societies that live in poor environments and are more prone to ecological harshness.
- iii. Recently, Gavin et al. (2018) analyzed data from 818 societies spread over the world and showed that our subsistence strategies (i.e. the way we obtain food) is greatly explained by environmental variables (e.g. environmental stability and productivity), political complexity, and strategies adopted by nearby and closely related groups.
- iv. Kavanagh et al. (2018) showed that the population density of hunters, gatherers and fishers societies spread over the world can be well predicted by a set of environmental and cultural variables such as productivity, topography, precipitation seasonality, distance to coast, resource ownership (i.e. whether resources are owned or not) and residential mobility (i.e. average distance travelled per residential move).

Homo sapiens is the species with the largest amount of data available for macroecological analyses. The enormous amount of data is composed by a diverse array of human characteristics such as genetic, historical, morphological, cultural and medical features (Molnar 2006; Harcourt 2012, See *Future directions section*). An increasing number of molecular markers and genetic samples from hundreds of individuals are a common place for human populations across the globe (Cavalli-Sforza et al. 1994; Binford 2001; Abdulla et al. 2009; Kirby et al. 2016). In addition to data availability, humans from different parts of the globe present great diversity in morphological, genetic and cultural characteristics that have clearly existed for millennia (Molnar 2009). Describing which factors correlate to human variability over space and time, and what processes could be underlying those associations can clearly enter in the scope of macroecological studies and ecological literature since many patterns of human diversity resemble long-standing patterns of species diversity.

Here, we explore several debates about morphological, physiological and cultural diversity of humans that may call the attention of ecologists. We place particular emphasis on themes that have been explored in detail by macroecologists and biogeographers for other species, such as variations in a latitudinal gradient of body size and shape (i.e. Bergmann and Allen effect), thermal tolerance, diversity accumulation and extinction, all of which have been consistently explored for humans in other disciplines. Focusing on human patterns that resemble patterns of species diversity makes it easier to see the possible links between ecological theories and methods that could be applied to study human diversity. We review findings from other fields to demonstrate how ecological theories do apply to humans even when ecologists have tended not to study humans. This review stands as a call to ecologists to test their ideas

on humans, but also to use ecological approaches to contribute to long-standing debates across scientific fields.

We also present the databases in which data for humans are available and offer new directions in which studies investigating human diversity could follow into macroecology. Finally, exploring the big picture of human diversity and proposing generalities also benefit, and call the attention to the protection of our own diversity. Recent estimates of cultural loss rates far exceed the ones from species diversity with at least 50% of world languages being lost until the end of this century (Kraus 1992; Belew et al. 2018). Thus, we also call attention to the need for biocultural conservation and discuss how ecologists can contribute to this growing field.

Bergmann and Allen effects

Humans have the extraordinary ability to regulate their environment by building shelters and escaping the barriers imposed by climate with fire and clothes. However, our intelligence/culture and its consequences (e.g. adaptability, plasticity and technology) did not effectively homogenize the selective pressures of the environment over our biological evolution. Humans have larger bodies and shorter limbs at higher latitude and colder body temperatures than those living in warmer temperatures (Fig 1; Ruff 1994; Ruff 2002; Holliday 1997; Betti et al. 2015). The differences in size of the body and of extremities across different latitudes is common to many organisms and have long been referred to in ecology as Bergmann and Allen effects respectively (Meiri & Dayan 2003; Allen 1877).

Several macroecological studies have described patterns in body size and shape found within and among species. Birds and mammals are the most commonly studied cases for Bergmann and Allen effect as endothermic species have generally larger

bodies and shorter limbs in higher latitudes (Diniz-Filho et al. 2007; Meiri & Dayan 2003; Millien et al. 2006; Olson et al. 2009; Allen 1877; Griffin 1974; Lindsay 1997; Johnston & Selander 1971; Danner & Greenberg 2015). The main hypothesized mechanism underlying the geographic patterns on body size for birds and mammals is the heat conservation hypothesis. This hypothesis proposes that larger body sizes attaining lower body surface area-to-volume ratio, together with shorter limbs, reduce heat loss (Blackburn et al. 1999; Salewski & Watt 2017). Thus, in higher latitudes and colder temperatures larger bodies and shorter limbs are advantageous for maintaining internal temperature. Other complementary hypotheses also emerged to explain geographic patterns in body size in different taxa by proposing the effect of resource availability (i.e. larger bodies in productive regions; Rosenzweig 1968), dispersal capacity (i.e. larger animals with higher probability of recolonizing poleward regions after the ice-sheet melting; Blackburn et al. 1999) and human impact (i.e. higher pressure of hunting on larger individuals causing the reduction of population and species body size in regions with higher human impact; Diniz-Filho et al. 2009, Torres-Romero et al. 2016). However, although a clear Bergmann's effect is well-documented for endotherms, ectotherms do not follow a single pattern (Olalla-Tárraga et al. 2006; Olalla-Tárraga & Rodríguez 2007; Rodríguez et al. 2018). By relying on external heat to maintain internal temperature, smaller-bodied ectotherms gain heat faster in colder regions (Olalla-Tárraga et al. 2006; Olalla-Tárraga 2011).

Like birds and other mammal species, human individuals tend to be larger and have shorter extremities for their body size at higher latitude and colder climates than humans from lower latitude and warmer regions (Roberts 1978; Ruff 1994; Ruff 2002; Holliday 1997; Betti et al. 2015). Thus, Human mass and mass-stature ratio (Mass/Height) increases (Fig 1b), and limb size decreases (Fig 1c), as the mean

temperature of where the person comes from decreases (Harcourt 2012). This pattern is maintained for both male and females, adults and newborns (Ruff 2002). The geographic variation in both size and shape is not only observed for modern humans, but also for earlier *Homo* species (Ruff 2002).

Both Bergmann and Allen effect on humans are also suggested as adaptations to cope with climate (Ruff 1994; Ruff 2002). Indeed, it was experimentally shown that one fifth less body surface area-to-volume correlates with four times less heat loss in humans (Frisancho 1993). Also, individuals with longer legs in a cold room lost more heat than individuals with shorter legs (Tilkens et al. 2007). Losing heat is of extreme importance for performing physical work in the tropics, but retaining heat is crucial to survive in colder climates at high latitudes (Harcourt 2012).

Although experimental studies confirm the thermoregulation hypothesis for modern humans, nutrition and disease are also important factors associated with latitude and that can affect the geographic patterns in body size and shape (Ruff 2002). Higher availability of energy through a richer diet can affect the rate in which the body grows (Ruff 2002, Harcourt 2012). People from the arctic have a diet that tends to be richer in fat than diets in the tropics (Harcourt 2012). Thus, diet is a complementary hypothesis for the thermal regulation effect that could indeed affect the geographic patterns of body size.

The pressure of diseases in the tropics is another complementary hypothesis (Ruff 2002, Harcourt 2012). This hypothesis emerges mainly from observing Pygmies groups. Pygmies have higher probability of dying younger than their non-pygmy neighbors which increased the selective pressure for pigmies populations to reproduce earlier (Migliano et al. 2007, Perry et al. 2009; Walker et al. 2006). By reproducing earlier, the energy that would be available for growth is invested in reproduction

maturation. Because disease pressure and diet are associated with latitude, it is difficult to distinguish their effect independently from the thermal regulation mechanisms.

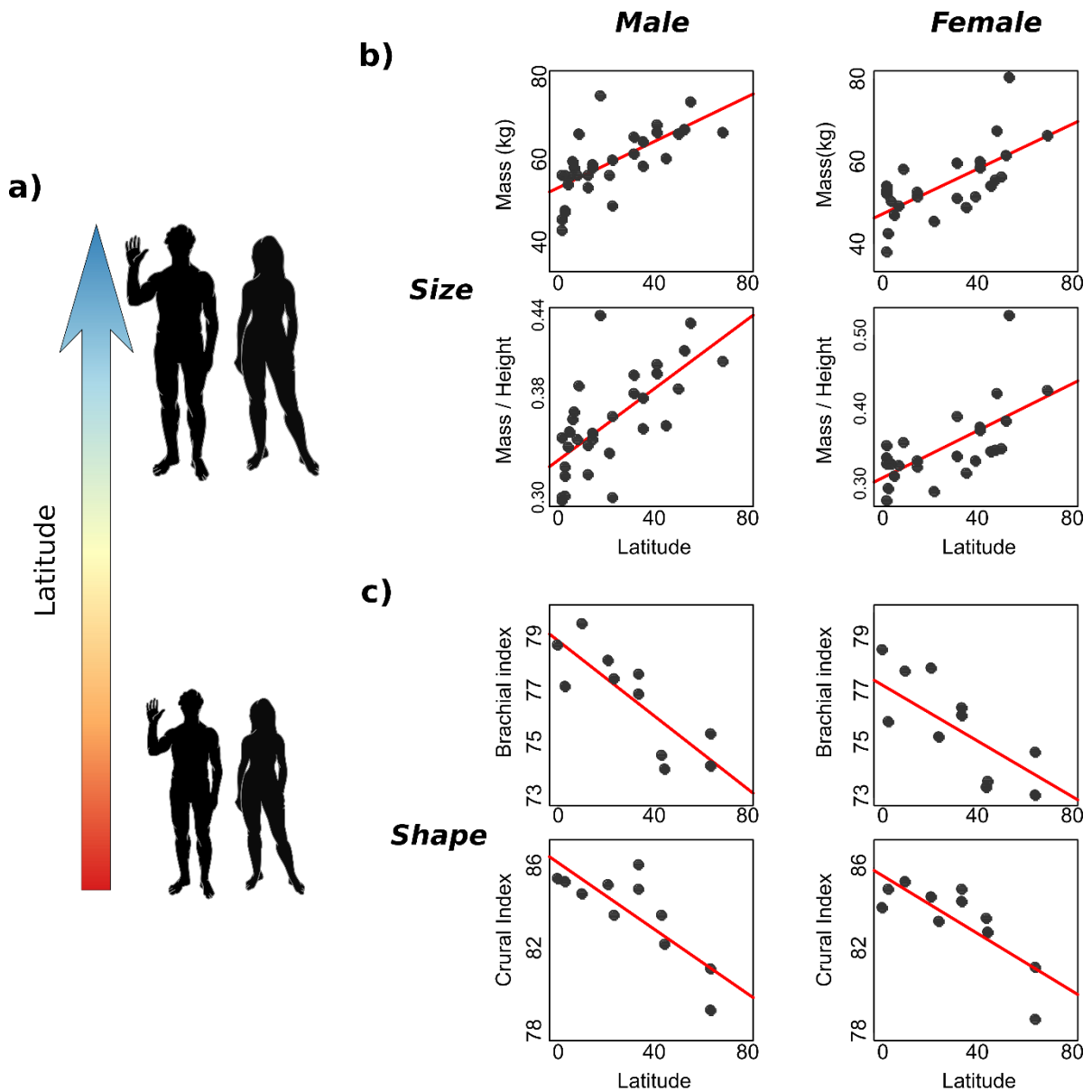


Fig 1. Variations in human shape and size over latitude. Mass and Mass-height ratio (b) increases as latitude increases, while the mean ratio of limb bone length (c), brachial index (radio/humerus) and crural index (tibia/femur), decreases. The pattern is maintained for males and females. The data used to produce this figure comes from Ruff (1994) and Tinkaus (1981). *Homo sapiens silhouettes* (a) are free copyright figures available at <http://phylopic.org/> .

Thermodynamic limits

Over the course of evolution, a diverse array of physiological adaptations has emerged to handle different environmental conditions. For example, mammals and birds from arctic and cold temperate regions have higher Basal Metabolic Rate (BMR) in relation to their body size than do their tropical relatives (Chaffe & Roberts 1971, Wiersma et al. 2007, McNab 2015). Although different strategies exist to handle ambient temperature in different latitudinal and altitudinal conditions, temperature can still impose lethal limits. Thus, species have an upper and lower limit of thermal tolerances defining how much hot and cold they can cope with (i.e. Thermal niche; Porter & Kearney 2009). Physiologically, thermodynamic effects of temperature on metabolic rates (e.g. maintaining ion homeostasis) impose the lower limits of species thermal tolerances (Angilleta 2009; Millian et al. 2012), while destabilizing effects of high temperature on membranes and proteins impose their upper limits (Angilleta 2009).

To describe those limits, a series of physiological studies experimentally subjected individuals from distinct species to different conditions of temperature and detected the maximum and minimum temperature that are lethal to the individuals under study (Pörter 2010; Hoffmann 2013). By defining the thermal tolerances of species, we can better understand the conditions in which species could live and the risks of their extinction given past and future climate changes. While organisms most frequently evolve to cope with cold, we know that hard physiological boundaries constrain evolution of upper thermal limits (Araújo et al. 2013). Thus, tropical ectotherms and endotherms live close to their upper limits in the tropics (Deutsch et al. 2008; Huey et al. 2009; Clusella-Trullas et al. 2011; Cooper et al. 2011). If species are unlikely to alter

upper thermal limits, then the risk of extinctions can be higher for tropical organisms in periods of global warming (Araújo et al. 2013). For humans, the story is similar. Even with the ability to culturally regulate our environment, we present different physiological adaptations to cope with high and low temperatures and ongoing increases in global temperature offer a direct risk to increases in human mortality rate in tropical regions.

Humans present not only physical traits that are adapted to climate (e.g., skin color, Chaplin 2004; body size and shape, Ruff 2002), but also different basal metabolic rates (BMR) to cope with cold. Several experimental studies show that individuals whose ancestors lived in temperate, arctic or near arctic regions and spent their childhood in those environments have higher BMR and skin temperature than individuals from warmer regions (Snodgrass 2005; Galloway et al. 2000; Christin 1993; Leonard et al. 2005; Rode & Shephard 1995; Spurr 1996; Lawrence et al. 1988; Froehle 2008). A meta-analysis of experimental studies with humans estimated a 5kcal/day increase in BMR for every 1 °C drop in mean annual temperature with age, sex and body mass accounted for (Froehle 2008).

Humans also present adaptations to deal with excessive heat. The affinity for salt and the ability to vasoconstrict in response to dehydration are more frequent in tropical populations (Young et al. 2005). The affinity for salt reduces loss of salt in the sweat and vasoconstriction, in response to low blood flow caused by dehydration, inhibits deleterious effects on the circulation. Genes and alleles associated with both loss of salt and vasoconstriction are more frequent in tropical populations independent of how long native populations have been in the tropics (Young et al. 2005; South American Indians have the same frequency of these genes as Africans).

The lethal upper and lower thermal limits for humans may be estimated based on the abundant epidemiological data on mortality across the world (Basu & Samet 2002; Gosling et al. 2009; Ye et al. 2012). Findings from epidemiological studies (Huynen et al. 2001; Rooney et al. 1998) show that mortality increases 12% during cold spells (i.e. period of cold weather that lasts for several days) and 8.9%-12% during heat waves (i.e. hot weather that lasts for several days). More recently, a study showed that 7.71% of mortality in 384 localities across the world is associated with temperature (Gasparrini et al. 2015). The lag period response for heat and cold is different as excess risk by cold is reported to last up to 3 weeks, while the excess risk by heat is immediate and occurs within a few days (Anderson et al. 2009; Analitis et al. 2008). A wide range of cardiovascular and respiratory causes of death have been associated with temperature changes during heat waves and cold spells (Keatinge et al. 1986; Keatinge et al. 1984; Woodhouse et al. 1994).

With the association of mortality and temperature it is possible to estimate the optimum temperature for humans across the world (i.e. average around 75th percentile of ambient temperature in all the countries/regions) as well as the upper and lower thermal limits of our species (Fig 2; Gasparrini et al. 2015). The optimum is represented by the minimum mortality temperature, while the upper and lower limits are represented by the extreme temperature observed in each location in a predefined time frame. By convention, the lower limit is defined as the 2.5th percentile of temperature observed in a given location and the upper limit is defined as the 97.5th percentile of temperature (Fig 2, Gasparrini et al. 2015). Thus, temperature lower than the 2.5th location specific percentile and larger than the 97.5th location specific percentile are considered extreme temperature for humans because these conditions are associated with the increase of mortalities caused by temperature across the world. Knowledge of our tolerance to

climate is urgent because the frequency of heat waves is predicted to increase with the ongoing warming of our planet (Meehl & Tebaldi 2004). Epidemiologists alert that tropical countries are expected to increase heatwave-related excess mortality with global warming in a few years (Guo et al. 2018). Of course, humans are expected to adapt their physiology, behavior, health services and public policies to decrease the impact of ongoing climatic changes in human mortality. However, although macroecology has been advancing in predicting the impact of climate change on species, macroecological studies have seldom included humans into future projections of climate change impact.

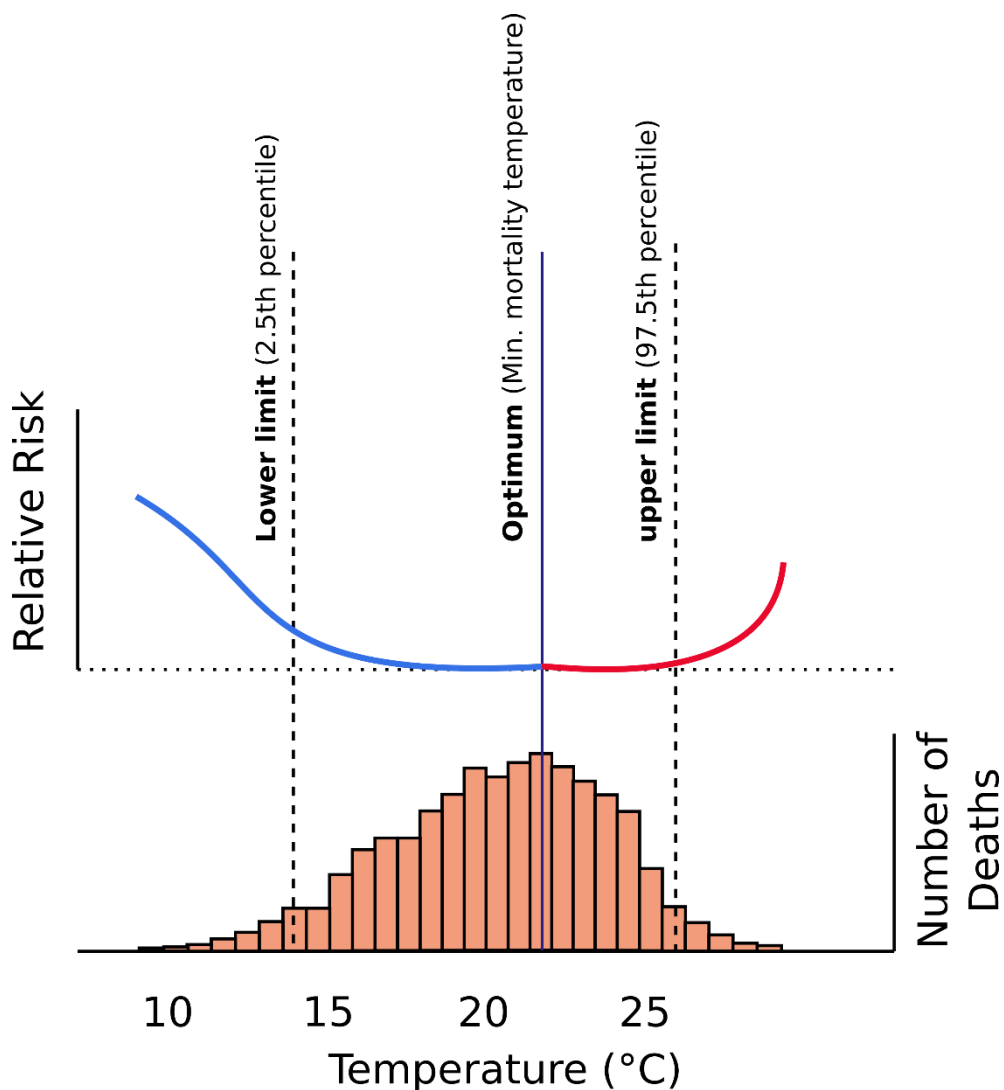


Fig 2. Cumulative exposure response graph. Number of deaths per day is collected for a given period of time and the mean temperature for each day is obtained. The histogram

represents the count of death events for each temperature value. Epidemiological studies use the number of deaths and temperature distribution to estimate the relative risk of death associated with temperature (blue and red lines). For hundreds of cities spread across the world, the relative risk of death increases when exceeding upper or lower thermal limits (see Gasparrini et al. 2015). The value of temperature for optimum, lower and upper limits vary depending on the temperature that humans experience in different regions of the globe.

Latitudinal Diversity Gradient

The latitudinal diversity gradient (LDG), the increase of species diversity from the poles to the equator, is one of the oldest described patterns of species diversity at broad spatial scales (Hawkins 2001). Time has shown for ecologists and evolutionary biologists how complex the LDG is (Pianka 1966, Hilebrand 2004). Over the years, around 30 hypotheses have been proposed to explain the LDG (Currie et al. 2004, Fine et al. 2015, Lomolino et al. 2017). The fact the many of those hypotheses have been supported, shows that a complex interaction among a series of macroevolutionary, historical and energetic mechanisms underlies the spatial patterns of diversity we observe (Pontarp et al. 2019). Spatial variations in *ecological limits*, *diversification rates* and *time for species accumulation* separate the many hypotheses proposed over the years into three categories. Pontarp et al. (2019) showed the *mechanisms* of each hypothesis proposed to explain the LDG in each of these three categories and here we will show that the hypothesis to explain spatial patterns of human linguistic diversity can also be represented in the same categories and resemble many hypotheses formulated to explain species diversity patterns. As humans, not only the shape/size of

our body and our physiology vary over the globe similarly to other species, but also the number of languages we speak follows a LDG.

Linguistic diversity is the best example for a dimension of our culture that could be studied through macroecological lenses because language and species share similar evolutionary mechanisms. There are over 7000 languages in the world (Lewis 2013) and these languages are unevenly distributed over space (Fig 3).

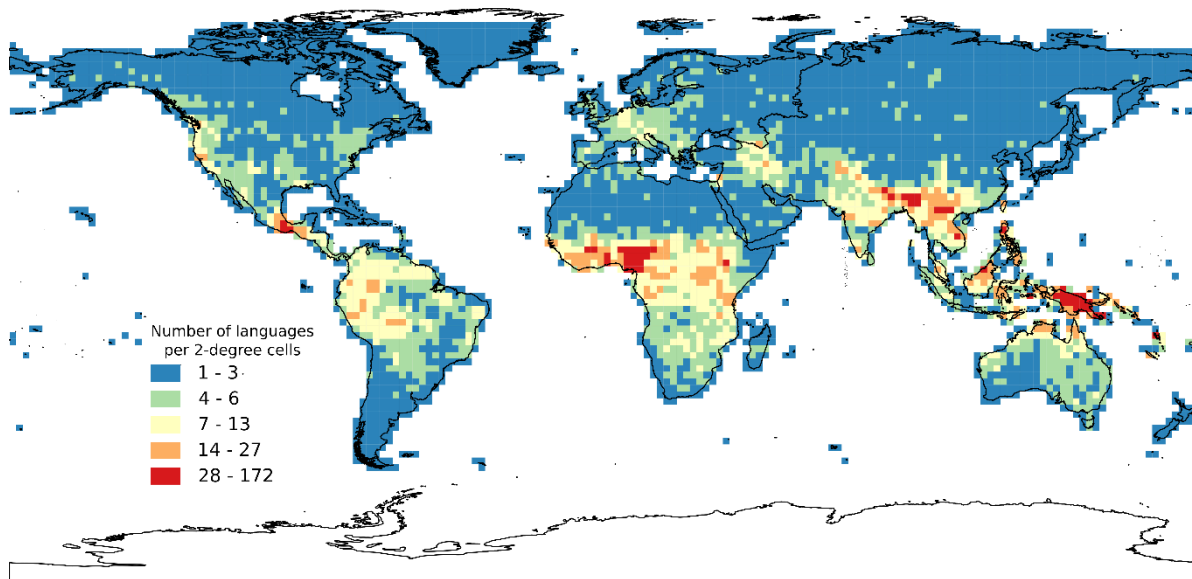


Fig 3. Language diversity across the world. More languages are found within tropical regions than temperate regions. Here, language ranges are counted for each 2-degree cell. The distribution of languages was obtained from the World Language Mapping system (www.worldgeodatasets.com/language). The distribution of language ranges over space differs from those of species because language maps tend not to include range overlap (Gavin et al. 2013).

Language diversity (i.e. number of languages in a given region), phylogenetic diversity (i.e. number of language families) and language disparity (i.e. amount of structural difference between languages) are three distinct types of linguistic diversity commonly used by linguists. Here we focus on the spatial variation of language diversity and its underlying mechanisms. Although cultural diversity has been used in the literature as a synonym of language diversity (Currie & Mace 2009), we use language diversity as one aspect of cultural diversity, and ethnolinguistic groups to refer to human groups that speak different languages. Cultural diversity is a broad term and could represent many other aspects of human culture (e.g. religion).

Mace & Pagel (1995) were the first to show that the diversity of ethnolinguistic groups increases from the poles to the equator. Although the pattern resembles ecology's oldest pattern LDG, only a few hypotheses, applicable to large scale and to a large number of ethnolinguistic groups, emerged. In addition, only a reduced number of empirical studies test the hypotheses proposed and the results from these studies contradict each other (Gavin et al. 2013). Here, we describe the hypotheses used to explain language diversity by separating their underlying mechanisms in three categories of spatial variation in *ecological limits*, *diversification rates* and *time for diversity accumulation*. In each of these categories we show the evidence, contradictory or not, to support each hypothesis and summarize the factors associated with each hypothesis in a theoretical web of causality, assuming the direct and indirect effect of each factor on ethnolinguistic diversity (Fig 4). Because species diversity and ethnolinguistic diversity share a similar pattern, many hypotheses are similar to what has been proposed in ecology, but some hypotheses and methodological approaches used to investigate species diversity gradients have not reached studies of language diversity yet (see future direction section). Thus, the web of causality summarized here might help ecologists and evolutionary biologists to apply their theories and methods to better understand spatial patterns in human cultural/linguistic diversity. In addition, like other aspects of biodiversity, human cultural diversity is threatened, and the human face in global biodiversity loss can be represented by language extinctions (Box 2).

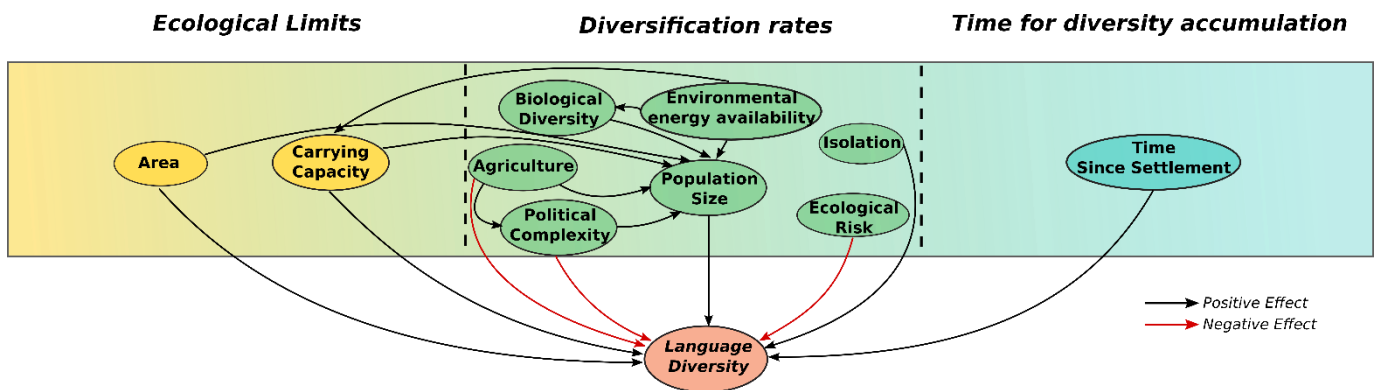


Fig 4. Complex web of factors directly and indirectly affecting language diversity.

Factors were separated in three categories representing variations over space in ecological limits, diversification rates and time for diversity accumulation.

Box 2. The human face of extinctions

The rates of ethnolinguistic extinction far exceed the ones expected from species diversity (Sutherland 2003), with at least 50% of world languages expected to be lost by the end of this century (Kraus 1992; Belew et al. 2018). Many factors are associated with language extinction (Sutherland 2003). Assuming language as a marker of cultural diversity, losing languages also contributes to a loss in the wide-range of variety of cultural aspects that are unique to each ethnolinguistic group.

Many intrinsic, instrumental and relational arguments exist for protecting biological and cultural diversity (Gavin et al. 2015; Gavin et al. 2018). The value for protecting cultural diversity means protecting our variability and rich history across the planet (Rozzi et al. 2008), besides securing the rights of indigenous and local people (Wolverton et al. 2014, Maffi 2005). In addition, different knowledge existent within different cultures were responsible for our adaptability and expansion in all types of habitats of earth and could also be important for future humanity persistence (Davidson-Hunt et al. 2012). Thus, protecting our own diversity is central for a truly sustainable future that conciliates economic development with biocultural conservation.

Protecting our own diversity is a debate that could be reflected into conservation studies that involves large spatial and temporal scales. Although conservation biogeography developed greatly evaluating the effectiveness of protected areas to protect species diversity in current and future times and pointing out locations in large spatial scale with higher potential to represent, species functional, phylogenetic and taxonomic diversity (Ladle & Whittaker 2011), cultural diversity has not yet reached the attention of conservation studies in large spatial scales. Thus, there is a great potential for studies of human macroecology that links the knowledge and methodology of conservation biogeography with biocultural conservation. For instance, Garnett et al. (2018) showed that recognizing indigenous people's rights to land is crucial for global conservation goals as indigenous lands intersects about 40% of global protected areas.

Of course, protecting our own diversity does not solely involve the definition of cultural hotspots, or the effectiveness of protected areas to represent cultural diversity. The protection of cultural and biological diversity in local scales involves serious debates about the power provided to each ethnolinguistic group and their role on protecting biodiversity as a whole (Gavin et al. 2015, 2018). But , our focus is to point out that our diversity is threatened, and that biocultural conservation have seldom been explored in conservation biogeography.

It is important that future macroecological studies see humans not only as the major cause of biodiversity loss worldwide, but also as one species that is exhausting resources (Nekola et al. 2013) and approaching civilization collapses (Diamond 2005). Human macroecology, as an umbrella that involves our activities, our variations and its underlying causes, should also pay attention to how do we achieve a sustainable future with effective biocultural conservation.

Ecological limits and language diversity

Area

Intensely studied in ecology and evolution, larger areas support more individuals, more viable populations and offer different ecological opportunities (i.e. larger niche space) for species (MacArthur & Wilson 1963). The same rationale is applicable for ethnolinguistic diversity (Fig 4). The proposed effect of area and ethnolinguistic diversity is that the number of ethnolinguistic groups in a given a location is proportional to its area (Greenhil 2014). However, this hypothesis is challenged by some clear examples of language diversity that is not restricted by area.

The island of New Guinea has the highest linguistic diversity of the world with around 900 languages on an island of 900,000 Km². Thus, the language diversity in New Guinea is even higher than entire continents (e.g. North America, Australia). Not surprisingly, when area is assumed as a predictor of language diversity, it only shows a modest fit to the data. Gavin and Sibanda (2012) showed that island size explains almost 20 percent of the variation in language diversity when studying 264 islands in the Pacific. Although this example has been pointed out as an exception, it is important to note that scale is crucial for diversity-area relationships. Species-area relationship is clear in fine scale (island biogeography) but when continental scales are analyzed, the relationship disappear (Palmer & White 1994; Turner & Tjorve 2005).

Carrying capacity

Not only area can restrict the number of individuals and viable populations of different species, but also carrying capacity. Carrying capacity limits the number of individuals and populations that a region can support (Brown 1981; Storch et al. 2018). Thus, regions with higher carrying capacity can potentially support more diversity. For

ethnolinguistic groups the same rationale applies, but the mechanism underlying carrying capacity and language diversity also involves the effect of carrying capacity on language range size (Gavin et al. 2017).

Because carrying capacity is mostly defined by resource availability, it is expected that in a productive location with higher carrying capacity (e.g. tropical forest) the individuals of an ethnolinguistic group may obtain enough resources across narrow areas, thus expand less their geographical distribution than populations in less productive locations with low carrying capacity (e.g. deserts). Thus, smaller language ranges would be observed in areas with higher carrying capacity which would cause higher accumulation of language diversity than areas with lower carrying capacity. Gavin et al. (2017) showed that if ethnolinguistic groups with predefined maximum population sizes grow in locations with varying carrying capacity, smaller range sizes accumulate in locations with higher carrying capacity. It is worth noting here that any environmental variable that could affect the carrying capacity for human individuals in one region (net primary productivity, rainfall, etc) should be assumed to affect language diversity indirectly (Fig 4), as these variables affect the variability of carrying capacity over space (Fig 4).

Diversification rates and language diversity

Population size

The number of speakers varies widely across different languages. If the rest of the planet had the same language diversity per capita as the small country of Vanuatu (around 100 languages spoken by 240,000 people), there would be over 4 million

languages on the planet. Thus, population size (i.e. number of speakers) have been considered as one of the factors that might fowl or fuel language diversification.

The spreading of a new mutation within a population not only depends on its increase in individual fitness, but also in the size of the population in which it spreads to (Wright 1931, Kimura 1962). In linguistics, population size is assumed as a key factor defining the rate of spread of new innovations (i.e. new phonemes, or words; Labov 2007, Nettle 1999a). However, contradictory hypotheses have been proposed about how the size of populations affect the spread of new innovations which could lead to more languages as changes accumulate.

Nettle (1999b) argued that new innovations spread rapidly in smaller populations because it takes less time to reach all members of an ethnolinguistic group. However, although there were suggestions that this mechanism could explain language diversity in the Americas, little support for this hypothesis exists. In fact, when the influence of population size on language diversity was empirically tested (Bromham et al. 2015), it showed exactly the contrary as hypothesized by Nettle (1999b). Small populations have higher rates of word loss, while larger populations have higher rates of gain of new words (Bromham et al. 2015). One of the hypotheses is that, because small populations have tighter social networks, they usually tend to be more conservative and restrictive to changes (Bowerman 2010). Thus, population size is expected to positively affect language diversification with higher rates of linguistic innovations in larger populations which could potentially lead to the emergence of new languages.

In addition, discussions about cognitive constraints on human group sizes have emerged in the literature (Dunbar 2008). Larger populations provide benefits for increased mate choice and cooperation in resource acquisition but also increases the cost

of maintaining social ties, including remembering and processing information needed to recognize unrelated individuals (Dunbar 2008). Thus, higher spreading of innovations and limits on group size might be key to explain splitting events and higher accumulation of languages caused by variations in population size. Similar to what has been pointed out when discussing carrying capacity, any environmental variable that can affect population size, should be assumed to have an indirect effect on language diversity (Fig 4). Thus, it is not possible to define a direct mechanism linking temperature, precipitation and net primary productivity with language diversity. Although a diverse array of environmental variables has been confronted with language diversity and explain around 20 percent in diversity variation (Moore et al. 2012, Currie & Mace 2009), the underlying mechanisms linking environmental variables with language diversity assumes that these variables affect population size (and/or carrying capacity), and then language diversification (Fig 4). The same rationale applies to associations between biological diversity and language diversity (Moore et al. 2012), as biological diversity can represent a dimension of resources that is explored by humans and affect population size.

Ecological risk

The ecological risk hypothesis proposes that in locations with lower stability in food production (i.e. higher ecological risk), humans would tend to increase their social networks in order to survive (Nettle 1998). Thus, the cooperation for survival reduces the isolation among human groups in locations with higher ecological risk and potentially decreases language diversification (Fig 4). Originally, Nettle (1998) proposed the ecological risk hypothesis using Mean Growing Season (MGS; i.e. number of months with temperature higher than 6°C and mean precipitation [mm] at least the

double of the mean temperature) as the variable that represents ecological risk for humans. Nettle (1996, 1998) reported a robust association between MGS and language diversity, but latter, other studies found little support for the association between MGS and language diversity (Sutherland 2003, Currie & Mace, Gavin & Sibanda 2012).

There are criticisms for the ecological risk hypothesis arguing that ethnolinguistic groups would not necessarily need to share the same language in order to cooperate with each other (Campbell & Poser 2008). In addition, when thinking about how that MGS is measured, the tropics should be flat in the values of MGS, as almost every tropical region easily achieve the minimum conditions of temperature and precipitation for all months of one year. What defines the growing season of different localities across the world varies from location to location (Walther & Linderholm 2006). Thus, maybe the contradictory results for MGS emerge because the way it is measured do not represent well the ecological risk in different locations of the world.

Isolation affects language diversification

Isolation is another factor expected to affect language diversification. Similar to an allopatric speciation event, when groups of people cross a physical barrier (mountains, rivers or the ocean), the cost of interactions among groups increases. Over time, if the ethnolinguistic groups remain isolated for long periods, it is expected that their languages differentiate and potentially lead to a language splitting event. The evidence for isolation and language diversity is mixed. Positive, negative and weak correlations were reported when altitude and topographic complexity (standard deviation of altitude) were confronted against language diversity (Sutherland 2003, Nettle 1996, Currie & Mace 2009, Axelsen & Manrubia 2014). Recently, Coelho et al. (2019) reported that the effect of topographic complexity on North American language

diversity is weak when it is assumed as a direct effect, but strong and positive indirectly via population density (i.e. topographic complexity affects population density that then affects language diversity). In terms of isolation by distance, Gavin and Sibanda (2012) reported that isolated pacific islands support less languages. Finally, Axelsen and Manrubia (2014), showed that river density is positively associated language diversity in global scale and suggest that river density represents the effect of isolation caused by rivers (but see Coelho et al. 2019).

Not only physical barriers are expected to drive isolation, but also social barriers. Xenophobia is suggested as a type of mechanism that drives the isolation among human groups (Fincher & Thornhill 2008). However, testing the effect of social isolation in large spatial scales is difficult because of the impossibility of summarizing such information in spatially defined sample units (i.e. grid cells).

Sociocultural variables and language diversification

The greater difference in the mechanisms underlying language diversity and species diversity is the effect of human sociocultural aspects on its own diversity. Technological inventions can open new ecological opportunities (new niche dimensions) which increases the rate of language diversification. The invention of canoe is the clearest example of how one single technological advance opened new ecological opportunities, as previously non-accessible areas could be reached by humans, that overtime would spread to new locations and diversify their languages (Greenhil 2014).

Agriculture is another technological innovation that has been assumed as a major driver of language diversity (Diamond & Bellwood 2003), but few evidences for the effect of agriculture on language diversity exist. A coalescent modelling of genetic data shows that farming populations increased in size 5 times faster than hunter and gathers

(Gignoux et al. 2011). Thus, the effect of agriculture on language diversification should be indirect via population size (Fig 4). However, a negative effect of agriculture on language diversity is also assumed in the literature, as the advent of agriculture causes the extinction of hunters and gatherers groups that are conquered by farming populations (Nettle 1999c). Thus, the extinctions caused by farming populations would need to be lower than the number of languages that emerge because of the greater number of innovations in larger populations to cause higher diversification of languages (Fig 4). Finally, increased political complexity is known to emerge in agriculturalist societies (Geenhil 2014). Currie and Mace (2009) showed that political complexity is positive and strongly associated with language area. The greater challenge here is how to test the effect of sociocultural factors and language diversity in large spatial scale as different social and cultural aspects needs to be summarized in variables that can be extracted in different explicit spatial units (e.g. grid cells).

Time for language accumulation

More time for diversification is a central historical factor in ecology and evolution (Fisher 1960; Stephens & Wiens 2003). However, for humans what defines the time to cultural diversity is the time since their settlement in a region (Nichols 1990). If we assume a constant rate of change, locations that were colonized first would have higher language diversity (Fig 4). However, little support for the hypothesis of time exist and time since settlement does not strongly correlate with language diversity (Sutherland 2003, Gavin & Sibanda 2012).

Future directions in human macroecology

Here we discussed how humans vary over large spatial scale in size, shape, physiology, culture, as well as the underlying hypothesis for those variations and the human face in biodiversity loss. In all these themes, biodiversity sciences can extensively contribute to debates on human macroecology that emerged in many fields of science even before macroecology arises. There are thousands of human cultural traits for which global scale data are available and only few of them have been subjected to macroecological investigations (Table 1). Many databases ranging from cultural to medical data are available for humans (Table 1). Here, we give a few examples of how theories and methodologies commonly used in macroecology could build bridges between different areas of science and offer a deep comprehension of human variability over large spatial and temporal scales.

Table 1. Databases with a diverse array of datasets for humans, ranging from cultural to medical data.

Data Sets	Description	Where to find it
<i>Atlas of World languages</i>	Thousands of languages mapped across the world.	Asher, R. E. (2006). <i>Atlas of the world's language</i> . New York: Routledge
<i>Binford Hunter Gatherer</i>	Describes cultural practices and physical characteristics (e.g. height and weight) for 339 hunter, gatherer and fisher societies spread over the world. Contains 40 different traits described for each society	Binford, L. (2001). <i>Constructing Frames of Reference: An Analytical Method for Archaeological Theory Building Using Hunter-gatherer and Environmental Data Sets</i> . University of California Press
<i>Database of Places, Language, Culture and Environment (D-Place)</i>	Include not just cultural features, but also information on the linguistic and ecological environments in which a given cultural feature was documented. Has more than 2000 cultural traits coded for around 2000 societies spread over the world.	https://d-place.org/
<i>Ethnographic Atlas</i>	Describe cultural practices for 1291 societies spread over the world ranging from agriculturalists and hunter gatherers. Contain 94 different traits for each society.	Murdock, G. P., R. Textor, H. Barry, III, D. R. White, J. P. Gray, and W. T. Divale.(1999). <i>Ethnographic Atlas</i> . World Cultures 10:24-136 (codebook)
<i>Global Infectious Diseases and Epidemiology Network (GIDEON)</i>	GIDEON is a medical database that provides continually updated data on the regional presence and the status of pathogens. The database has been used in a variety of recent studies of the consequences and patterns of pathogen richness and prevalence	https://www.gideononline.com/
<i>Glottolog</i>	Database with comprehensive information about dialects, languages and language families spread all over the world	https://glottolog.org/
<i>Human Genome Databases</i>	The human genome databases are a set of 34 databases with genome data for humans and human populations.	http://www1.biologie.uni-hamburg.de/b-online/library/genomeweb/GenomeWeb/human-gen-db-genome.html
<i>Repository of Language Phylogenetic Trees</i>	This repository provides phylogenies for hundreds of language families as a part of D-Place database.	https://github.com/D-PLACE/dplace-data/tree/master/-phylogenies
<i>Seshat: Global History Databank</i>	Continuously code data about social and political organization of societies. It has been used in the literature to test hypothesis about the rise and fall of different societies across the globe	http://seshatdatabank.info/
<i>Standard Cross-cultural sample</i>	Describes cultural traits of 191 societies with over 2000 variables coded.	Murdock GP & White DR. (1969). Standard Cross-Cultural Sample. <i>Ethnology</i> . 9:329–369.
<i>The database of religious history</i>	Codes quantitative information about religion and cultural history across the world.	https://religiondatabase.org/landing/
<i>The western North American Indians</i>	Describes cultural practices for 172 societies in western North America	Jorgensen, JG. (1980). <i>Western Indians: Comparative Environments, Languages, and Cultures of 172 Western American Indian Tribes</i> . San Francisco: W.H. Freeman and Company.
<i>The world language mapping system</i>	Language ranges mapped for over 7000 languages distributed across the world.	http://www.worldgeodatasets.com/language/
<i>World health organization (WHO)</i>	WHO offers a series of data related to health, including causes of deaths at county level.	https://www.who.int/gho/en/

The mountain passes hypothesis and language diversity

The isolating effects of mountains may not be the same in all locations, as Jansen proposed in his seminal paper “Why mountain passes are higher in the tropics” (Janzen 1967). Although the air temperature declines almost linearly with altitude anywhere in the globe (Dillon et al. 2005), Janzen showed that temperature variation is lower in tropical mountains than temperate ones. Because animals are adapted to the environments in which they live, tropical animals experience and tolerate less temperature variation than temperate ones (Janzen 1967; Araújo et al. 2013). A prediction that has emerged from Janzen’s paper is that the physiological barrier imposed by the decrease of temperature in mountain ranges would limit gene flow and dispersal in mountainous regions of the tropics, resulting in higher population isolation and finally leading to higher speciation rates (Ghalambor et al. 2006; Ricklefs 2006; Martin et al. 2009; Pontarp et al. 2019).

Originally, the mountain passes hypothesis was proposed by Janzen while observing a Teaching Assistant (TA), from a mid-elevational region of the tropics, during a course of tropical ecology in Costa Rica (Janzen 1967; Sheldon et al. 2018). Other than the TA, all students in the course were from temperate regions of North America. Janzen observed how the TA struggled with the cold in high elevations and with heat and sweat at sea-level in the tropics, while the North American students appeared more comfortable with any change of temperature due to elevation (Sheldon et al. 2018). Ironically, although Jansen formulated the idea by observing humans, the mountain passes hypothesis has never been applied to our species.

Based on the prior research on variability in physical and physiological differences between temperature and tropical natives, the effect of isolation on language

split and Jansen's original hypothesis regarding tropical mountain passes, higher distance in temperature from one location to another (e.g. base of a mountain to its summit) could be expected to increase isolation between human groups, especially in the tropics. This idea has not been tested and represents one example of a theory that emerged in ecology and that could build bridges between different fields of science.

Modelling human responses to climatic changes

Humans vary in their thermal tolerance across the world and human mortality increases when temperature exceeds our species thermal limits (Gasparrini et al. 2015). Thus, with ongoing climatic changes and the increasing frequency of heatwaves (Meehl & Tebaldi 2004), it is important to invest our resources in predictions of human responses to future scenarios of climatic change in order to better feed discussions about minimizing the direct impact of climate change on human mortality. More importantly, future predictions of human responses need to include our adaptability to future conditions. Until now, studies of mortality responses to climate are based solely on correlative analysis in which mortality data is linked to temperature data (Gasparrini et al. 2015). In order to predict the impacts of climate change on human mortality it is necessary a mechanistic approach that assumes the potential for humans to adapt to future climatic conditions. Recent advances in macroecology (Cotto et al. 2017, Diniz-Filho et al. 2019) enabled the modelling of evolutionary mechanisms at individual and population level to better understand how species would cope with climate change. The same frameworks and rationale could be applied to humans in order to better understand our responses to future climatic conditions. The additional challenge for our species is that our adaptability to future climatic conditions not only depend on our physiology, but also in behavior change, health services and public policies. In addition, temperature

must be modelled daily, as the definition of heat waves specific for humans is “at least two consecutive days of mean temperature exceeding the 95th percentile of the year-round daily temperature” of the location (Guo et al. 2018). Modelling human responses to climate changes is a flourishing area in which macroecology has much to contribute.

Methodological approaches applied to human diversity

Gavin et al. (2013) showed that the reduced amount of empirical studies that tested the relationship between environmental and sociocultural variables and language diversity were based on very simple correlative analysis and that statistical issues of spatial autocorrelation, phylogenetic autocorrelation and multicollinearity were rarely dealt with. Indeed, the literature of human diversity is still slowly evolving, but macroecology can offer a guide for those studies as issues of spatial autocorrelation and multicollinearity have been confronted and solved with species diversity patterns. Not only the field of ecology in general may be a statistical guide for geographical analysis with human diversity, but also as a source for different approaches that could be undertaken to study human diversity in large spatial scales.

Multivariate statistics is one the many methodological frameworks that have been seldom applied to study human diversity in large spatial scales but offers a very simple way forward. When assuming cultural traits for different human societies spread over the world, a simple cultural distance matrix could be obtained by any dissimilarity measure. For example, cultural distance could be defined as $1 - S$, where S is the *Jaccard Index*. Thus, the Jaccard index between a pair of human groups i and j could be calculated as $S_{i,j} = a/(a+b+c)$, where a is the number of cultural characteristics that the pair of groups share, whereas b and c are the exclusive characteristics of groups i and j . When calculated to all pairs of human groups, we can obtain a cultural distance matrix

that can be used as a response variable in a series of multivariate analysis. The procedure highlighted above allows us to investigate if human groups that are similar in many cultural traits live in locations with similar environmental conditions (environmental distance) or speak similar languages (phylogenetic distance of languages). Although these questions are basic in terms of understanding our culture, these types of analysis have not yet been explored.

Similarly, because phylogenies exist for several language families in different regions of the globe community phylogenetic approaches could also be applied to describe spatial patterns of phylogenetic clustering and phylogenetic overdispersal. Mapping phylogenetic language diversity and cultural diversity (via functional diversity in ecology) is also another basic description that is necessary. This approach would allow researchers to answer if language phylogenetic diversity predicts cultural diversity, but also where language phylogenetic diversity is higher than culture and vice-versa.

Finally, better understanding the predictors of diversity and their underlying mechanisms require different frameworks of model building programs. Based on the complex web of factors directly and indirectly affecting language diversity (Fig 4) modelers could follow two different directions to contribute with debates about human cultural diversity. One direction is the design of correlative models that assume the direct and indirect effect of variables with the response variable of interest (e.g. path analysis), a procedure that is still seldom employed in language diversity studies (see Coelho et al. 2019). The other possible direction is the development of macroecological mechanistic simulation models that explicitly incorporates the processes discussed in the literature (Fig 4) and evaluate their importance in the emergence of real-world

patterns. Both strategies have only recently emerged in human diversity studies (See Gavin et al. 2017 and Coelho et al. 2019).

Conclusions

The idea to study how humans vary over large spatial and temporal scales is not new. In fact, all previous studies studying human variability in large spatial scales constitutes what has been recently named as human macroecology (Box 1). However, most of the patterns of human diversity and their underlying processes have not been studied by ecologists. As we show here, ecology in general, and mainly macroecology can contribute with their theoretical and methodological backgrounds with many debates that emerged in different areas of science that study human diversity. We cannot deny that humans call more attention than any other species. Wilson (1975), Diamond (1997) and Pinker (2002) are good representatives of the idea that ecology and biology can help us to understand patterns of human diversity and generate productive discussions across many fields of science. More recently, one of the most successful books of science communication is Hariri's (2015) *Sapiens*, which also offers deep discussions of how different cultural aspects of human society evolved. Thus, addressing human diversity in macroecological studies might attract more attention to ecological sciences.

Finally, it is important to address here that humans are experts in recognizing their differences and perceiving people from other parts of the world as inferior in one, or more traits. However, unfair discrimination does not remove the fact that human differences exists and that it could be studied in large spatial scales. We, as ecologists and evolutionary biologists, should be more involved in describing our differences and their underlying causes, but also in protecting it (Box 2). As we showed here, the

decrease in linguistic diversity is the human face of threatened biodiversity of our planet (Box 2). Although representative studies of human macroecology in the literature are too narrow for the field scope, there are many different directions in which human macroecology could expand and therefore consolidates bridges among different fields of science.

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CAPÍTULO 6

DRIVERS OF GEOGRAPHIC PATTERNS OF NORTH AMERICAN LANGUAGE DIVERSITY

Drivers of geographic patterns of North American language diversity

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Abstract: Although many hypotheses have been proposed to explain why humans speak so many languages and why languages are unevenly distributed across the globe, the factors that shape geographical patterns of cultural and linguistic diversity remain poorly understood. Prior research has tended to focus on identifying universal predictors of language diversity, without accounting for how local factors and multiple predictors interact. Here, we use a unique combination of path analysis, mechanistic simulation modelling, and geographically weighted regression to investigate the broadly described, but poorly understood, spatial pattern of language diversity in North America. We show that the ecological drivers of language diversity are not universal or entirely direct. The strongest associations imply a role for previously developed hypothesized drivers such as population density, resource diversity, and carrying capacity with group size limits. The predictive power of this web of factors varies over space from regions where our model predicts approximately 86% of the variation in diversity, to areas where less than 40% is explained.

Keywords: Language diversity; Path Analysis; Geographically Weighted Regression;

Resumo: Apesar de muitas hipóteses terem sido propostas para explicar por que humanos falam muitas línguas e porque línguas são distribuídas de maneira desigual no mundo, os fatores que moldam padrões geográficos de diversidade cultural e linguística continuam pobremente compreendidos. Pesquisas anteriores tendiam a focar em identificar preditores universais de diversidade de línguas, sem levar em consideração como fatores locais de múltiplos preditores interagem. Neste trabalho nós usamos uma combinação única de análise de caminhos e regressão ponderada no espaço para investigar o padrão amplamente descrito, mas pouco compreendido, de diversidade de línguas na América do Norte. Nós mostramos que os preditores ecológicos de diversidade de línguas não são perfeitamente universais nem inteiramente diretos. As associações mais fortes implicam um papel de preditores previamente hipotetizados como densidade populacional, diversidade de recursos e capacidade de suporte com limites de tamanho de grupo na diversidade de línguas. O poder preditivo dessa rede de preditores varia ao longo do espaço de regiões em que o nosso modelo prediz aproximadamente 86% da variação em diversidade, para áreas em que menos de 40% da variação é explicada.

Palavras-chave: Diversidade de línguas; Análise de caminhos; Regressão geograficamente ponderada.

1. Introduction

Humans collectively speak over 7000 distinct languages, and these languages are unevenly distributed across the globe [1,2]. Surprisingly, we still know little about the complex web of processes that shape these geographical patterns of language diversity (i.e. the number of languages spoken in a given region). Linguists distinguish three types of diversity—the number of languages (language diversity), the number of language families (phylogenetic diversity), and the amount of structural difference between languages (typological diversity or disparity). Here, we focus only on the number of languages, using the term language diversity, which in contrast to the more ambiguous term linguistic diversity indicates that languages are the unit of our diversity measures.

One barrier to our prior understanding has been contradictory results from the limited number of empirical studies that have investigated the relationship between environmental and/or sociocultural variables and language diversity [1,3–8]. Prior studies have found mixed results for the effect of environmental variables, spatial heterogeneity, and isolation on language diversity [8–12]. For example, human populations may expand social networks to cope with higher levels of ecological risk, resulting in larger language ranges and lower levels of language diversity per unit area [13]. Although some prior studies have concluded that the most commonly used measure of ecological risk in linguistics—mean growing season—correlates with language diversity (e.g. [10,11]), others have found little support for this relationship (e.g. [4,8,12]).

Two methodological challenges contribute to the inconsistencies in these results: first, previous studies have tried to identify universal predictors of language diversity, but it is possible that no universal predictor exists. Research in macroecology has shown

that the drivers of observed spatial patterns in biodiversity tend to be spatially variable [14–16]. We might assume that the mechanisms driving language diversification also vary from one location to another, but the methods used to date cannot capture this potential nonstationarity. Second, contradictory results may also reflect the complexity of the pattern being studied, which can be generated by a web of both direct and indirect pathways. For example, environmental drivers of language density vary across subsistence types [17]; the adoption of agriculture, or new boat and fishing technology, may transform the number of people a given ecoregion can support; or political centralization, the product of a particular historical trajectory, may homogenize a previously disparate linguistic mosaic.

Surprisingly, only a limited number of statistical techniques have been used to explore the direct and indirect associations between multiple predictors underlying the heterogeneous spatial patterns of language diversity [1]. To the best of our knowledge, only one previous study briefly explores a simple structural equation modelling approach that considers the direct and indirect effect of three variables on the distributional range size of languages [12]. Here, we overcome prior methodological limitations by designing a path analysis model that assumes direct and indirect effects of environmental and sociocultural variables on language diversity, while exploring spatial variation in the predictors' effects. Our study is the first to use a geographically weighted path analysis (GWPath) to examine possible drivers of human diversity patterns.

(a) Factors contributing to language diversity patterns

Because languages are markers of social boundaries within and between groups [18–20], group boundary formation is a critical step in language diversification. The

formation or dissolution of group boundaries can be influenced by many different environmental and social factors [1]. Variation within a language can lead to new language formation (i.e. cladogenesis) if these group boundaries are stable and socially important, amplifying the degree of linguistic difference between groups to the point that erstwhile dialects become distinct languages. Here, our aim is to demonstrate the importance of complex paths and non-stationarity by examining a subset of variables that have been widely discussed in the literature and may contribute to group boundary formation, thus affecting spatial patterns of language diversity. We do not focus on the internal factors contributing to individual language variation [21–26], rather we focus on a subset of the large-scale processes that may shape language diversity patterns in a broader ecological context.

We examine the direct and indirect effects of eight factors hypothesized to influence group boundary formation and language diversity patterns: river density, topographic complexity, ecoregion richness, climate (i.e. temperature and precipitation constancy, and climate change velocity), population density, and carrying capacity with group size limits. Rivers and topography have recently been proposed as universal predictors of language diversity at a global scale [7]. Movement and isolation are both critical processes for the formation of group boundaries [26,27]. When groups of people move to the other side of physical barriers, the costs of interacting with neighbouring groups can increase, leading to social isolation and group boundary formation [7,28,29]. Rivers and complex topography may act as barriers to contact among groups, promoting isolation and driving diversification, in a mechanism similar to models of allopatric speciation developed in ecology and evolutionary biology to explain biodiversity patterns [29]. This mechanistic link implies that both river density and topographic complexity should be positively correlated with language diversity. Alternatively, rivers

may also improve transportation, which can increase contact among groups and undermine group boundary formation leading to less language diversity in a region [7,30,31]. In addition, in regions such as Southern New Guinea [32,33] complex linguistic differentiation has occurred despite the absence of any complex topography, suggesting linguistic differentiation in circumstances of ethnic intermarriage and multilingualism can sometimes be accelerated by easily traversed terrain.

Many prior studies discuss possible links between language diversity and biological diversity [4,11,34,35]. One possible explanation for the association between biological and language diversity is that biodiversity facilitates group boundary formation through resource partitioning [11]. The development of unique subsistence strategies and technologies may allow different groups to thrive within different ecoregions, each of which represents a distinct assemblage of species [36]. Therefore, ecoregion richness (i.e. number of ecoregions) might be expected to associate positively with language diversity.

Climate may influence group boundary formation and geographical patterns in language diversity via multiple pathways [17]. For example, unstable and extreme climatic conditions of temperature and precipitation contribute to higher ecological risk for human groups, which can lead to the growth of larger social networks that provide a source of alternative resources and manage risk [9,13,32]. Larger social networks limit group boundary formation and promote linguistic homogenization [10,37]. Therefore, we would expect fewer languages in areas that experience greater fluctuation in climatic conditions of temperature and precipitation. We propose that the velocity at which the climate has changed may also be a proxy for longterm ecological risk, because higher velocity of climate change indicates more instability of climate in a region over longer periods of time. In addition, the velocity of climate change over longer periods of time

played an important role in the human colonization of the globe, opening pathways and territories for settlement where climatic conditions were suitable for humans (e.g. warming of northern regions) [38].

Climate may also influence language diversity through its effects on human population densities. When climatic conditions are favourable (i.e. warm and wet) and predictable, human groups can be more assured of rich and stable sources of resources that may support higher population densities [39–41]. Several other environmental and sociocultural variables also shape potential population densities. For example, population densities may increase in coastal regions, given greater access to marine resources; in topographically complex areas due to access to a range of nearby ecosystems and restrictions on available level surfaces for settlement [41,42]; and in areas of higher river density, where rivers provide services such as food and water that directly affect the establishment of human groups [7]. In addition, less mobile groups and those with established land ownership norms tend to have higher population densities [41,43,44].

Multiple possible mechanisms link higher population densities with greater language diversity per unit area. As has been suggested in ecological theory, regions that support more individuals may also accumulate more diversity over time due to stochastic diversification events [44,45]. If more individuals exist in a given location, the probability of high linguistic variation also increases, and therefore we expect higher rates of diversification. Similarly, Bromham et al. [46] found that larger populations have faster rates of innovation, which could lead to more languages as changes accumulate. Another possible link involves the effects of group size on boundary formation. Large groups provide more opportunities to cooperate in resource acquisition, but also increase the costs associated with maintaining social ties

[10,47,48]. Limits on the size of human groups imply that regions that can support higher population densities will tend to have greater language diversity [49]. However, these limits are not fixed—for example, increases in food production per unit area (e.g. as a result of the development of intensive agriculture) as well as the evolution of centralized political institutions have both been associated with increases in maximum group sizes and linguistic homogenization [50,51].

Prior studies seeking to identify factors linked to language diversification have been almost exclusively based on correlative analyses [1], in which no causal story is modelled [52]. Recently, a relatively simple mechanistic simulation model explored causal explanations for language diversity in Australia [49]. The model reproduced the spatial pattern of language diversity in Australia assuming only that carrying capacity varies over space as a function of the environment, and groups have maximum size limits (i.e. carrying capacity with group size limits) [49]. However, the carrying capacity with group size limits mechanism remains untested in other regions of the world.

Here, we test the hypothesized effect of each of the eight factors discussed above (river density, topographic complexity, ecoregion richness, temperature and precipitation constancy, climate change velocity, population density, and carrying capacity with group size limits) using a path analysis that models the multiple paths through which predictors could be associated with language diversity. Each pathway implies a different set of mechanisms that may shape language diversity. River density, number of ecoregions, topographic complexity, and climate may directly shape language diversity, or influence diversity indirectly through effects on population density. Population density can also directly affect language diversity, or influence diversity by contributing to the carrying capacity with group size limits mechanism.

Therefore, large groups of people can occupy small areas if population density is high, which affects the total number of groups in a given region. We designed two types of path analysis models, one assuming that the relationship between predictors is constant over space (i.e. Stationary Path Analysis), and another assuming that the relationship between predictors may vary over space (i.e. GWPath). Our analysis examines the strength of associations between the hypothesized predictors and language diversity, and how these effects vary over space. The only variable that explicitly captures a causal relationship is carrying capacity, which is produced by a mechanistic simulation model (see Methods and [49]).

(b) Geographical domain

We applied our models to understand the spatial pattern of language diversity in North America. We obtained the distribution of languages in North America from Goddard [53], which provides information about the approximate spatial distribution, around the time of colonial contact, of languages north of Mexico, and the Survey of California and Other Indian Languages, which provides additional detail in a particularly diverse region. Using these data, we calculated the number of languages occupying geographical cells on a gridded map at the resolution of 300 x 300 km (figure 1; See Sensitivity analysis in the electronic supplementary material).

North America provides an ideal setting to examine how the relative effects of explanatory factors vary over space, as the continent contains a wide range of environmental and sociocultural conditions and a wide spectrum of language diversity. Prior to European contact, the continent supported hundreds of languages [53,54], unevenly distributed over the continent, with greater richness along the west coast and at lower latitudes [53,55]. Prior research has proposed many factors to explain the

empirical pattern of North American language diversity (e.g. [55]), but no empirical study has tested them. Here, we explore the direct and indirect effects of river density, topographic complexity, ecoregion diversity, climate, population density, and carrying capacity with group size limits on the spatial pattern of North American language diversity. These factors encompass proposed drivers of language richness in North America and are also expected to drive global patterns of language diversity [29].

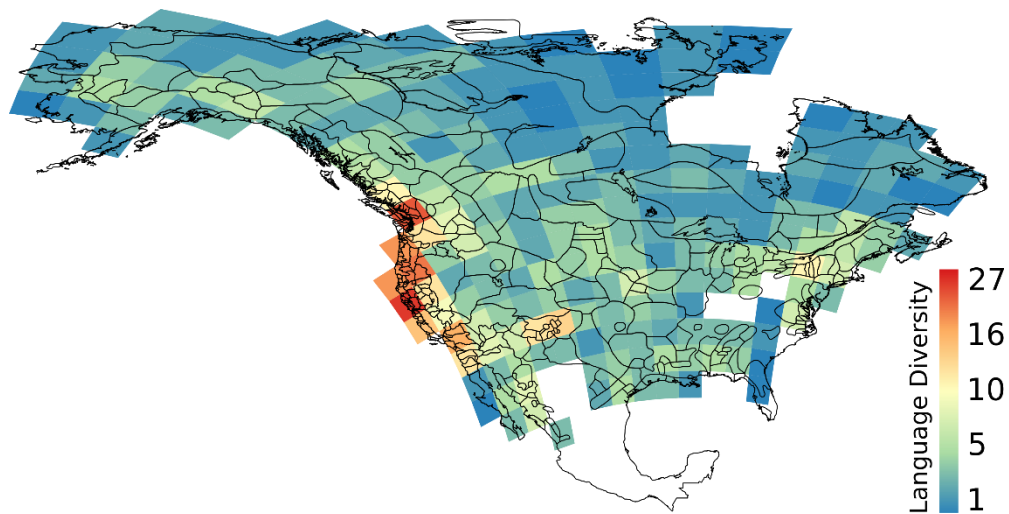


Fig 1. Observed language diversity. Language ranges are shown in the gridded map. Blank spaces on the map indicate regions in which no information about language distribution is available and thus were not compiled in the grid map.

(c) Results and discussion

To explore both indirect and direct effects of each factor, we first conducted a stationary path analysis that assumes the effects of environmental and sociocultural variables are constant over space. The variables included in our model vary in the direction of effect (i.e. negative and positive; figure 2). Population density, carrying capacity with group size limits, and ecoregion richness had the strongest direct effects, suggesting a role for multiple mechanisms in shaping language richness patterns (figure 2).

Population density had the strongest direct effect on language diversity ($\beta = 0.44$; figure 2), supporting the proposed mechanism that a larger number of individuals should lead to a greater accumulation of languages. The simple mechanistic model, simulating the effects of varying carrying capacity with group size limits was also one of the strongest predictors of language diversity ($\beta = 0.25$, figure 2). Therefore, in regions with higher potential carrying capacity, limits on the size of human groups tended to lead to greater language richness [49]. Finally, the strength of the direct effect of ecoregion richness ($\beta = 0.20$, figure 2)¹ implies that resource partitioning may contribute to language diversification [11], as unique subsistence strategies and technologies could allow different human groups to thrive within different ecoregions.

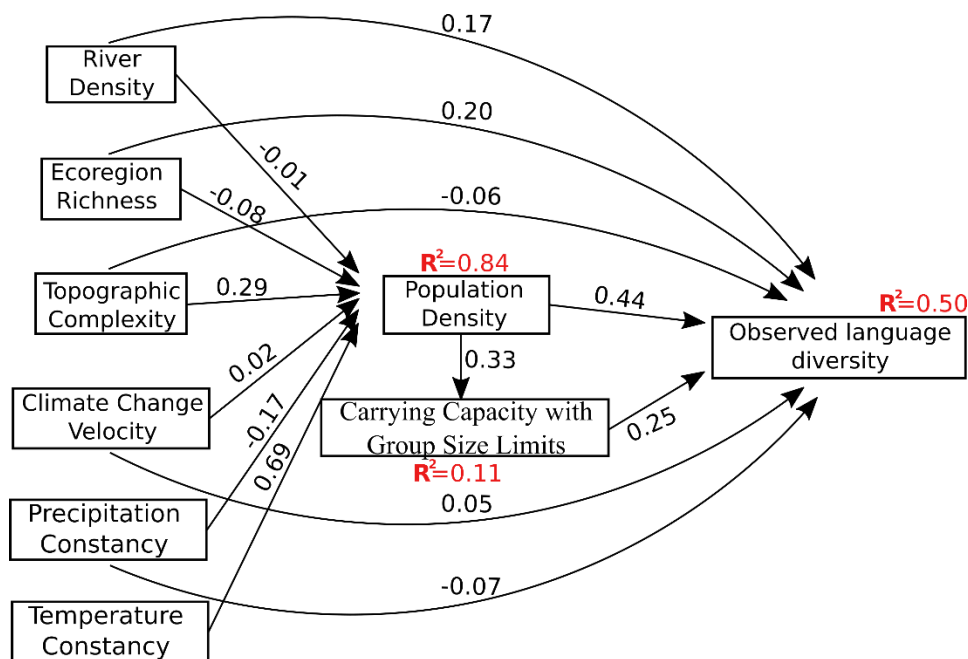


Fig 2. Global path model quantifying direct and indirect effects of environmental and sociocultural factors on North American language richness. The numbers marking each arrow represent the standardized beta coefficients (i.e. path coefficients) for language diversity. Model fits (R^2) are shown for variables directly affected by other factors.

We emphasize here that carrying capacity with group size limits is the only component of our path analysis that is modelled in a mechanistic, explicitly causal

manner. The correlations used to explore all the other components indicate an association with language diversity, but future simulation modelling will be needed to verify the causal mechanisms that link these components with language diversification.

The stationary path analysis approach also demonstrates the indirect roles played by several variables. For example, if we evaluated only the direct effects of variables, as was commonly done in prior language diversity studies [11], we would conclude that topographic complexity has little influence on language diversity. However, each of these variables does have a substantial indirect effect by shaping population density (figure 2). Topographic complexity may indirectly affect population density through its positive association with resource availability [56–58], which, in turn, may influence the number of people that can live in a given location (i.e. population density; [41]).

2. Geographically weighted path analysis

The combination of environmental and demographic variables in our stationary path analysis explains 50% of the variation in the spatial pattern of language richness in North America (figure 2). The stationary path analysis has a large statistical effect (effect-error ratio = 28.430) relative to the magnitude of error given the null expectation (see Comparison to a Null Model in the electronic supplementary material). However, this analysis does not allow us to explore how drivers of linguistic richness vary over space. To overcome this limitation, we conducted a GWPath, which assumes that the effects of hypothesized factors may vary over geographical space. To the best of our knowledge, this is the first study to apply a GWPath to examine human diversity patterns.

The effects of the predictors we tested vary widely over space (figure 3a). The overall model performs well in some regions of North America (e.g. the northwest

region where $R^2 \sim 0.80$, figure 3b), but the model fit varies over space (36–86%), with an average R^2 of 0.61. Our model also has a large statistical effect over space relative to the magnitude of errors given the null expectation (minimum effect-error ratio = 3.7, see Comparison to a Null Model in the electronic supplementary material). In addition, we find no universal predictor of language richness. Instead, the variables that most strongly affect language richness change from one region to another across the continent (figure 3c), implying that the mechanisms of language diversification also vary over space. This result helps to explain why the variables tested in previous global scale studies tend to explain only a limited portion of the variability in language richness, and why different regional analyses point to the importance of distinct sets of variables [1]. Spatial variation in explanatory variables is also found in macroecological analyses of species diversity patterns (e.g. [15,59,60]). For example, although species diversity is strongly limited by water availability in southern regions, in northern regions energy availability is more important [59]. Our results show not only that the most important predictor varies over space, but also that predictors can vary in the direction of their effects in different regions (figure 4). Climate change velocity presents different directions of effect in two different regions of North America: the northern region and eastern region (figure 4d). In the northern region, climate change velocity has a positive direct effect on language richness, while the effect is negative in the eastern region (figure 4d). The high rate of climate change in the northern region reflects rapid warming following the Last Glacial Maximum (LGM) (e.g. ice sheet melting, [61]), which likely opened ecological opportunities for human populations to obtain more resources given the positive effect of past climate change on many aspects of biodiversity in these northern regions [62]. Conversely, in the eastern region (figure 3c), the effect of climate change velocity is negative (figure 4), suggesting that climatic

instability since the LGM prevented or reduced language diversity. The effect of climate change velocity across both regions is consistent with a long-term version of the ecological risk hypothesis [9,13]. Nettle [13] proposed that in areas with high seasonal variation in food availability, humans will experience high levels of ecological risk. An increased probability of food deficiencies may force people to form social bonds across wider areas, to ensure access to sufficient resources. Wider social networks may increase the geographical range of a language and reduce language diversity in areas that pose greater ecological risk. Over thousands of years of human spread in North America, higher climate change velocity likely decreased ecological risk in northern regions, while climatic change may have increased ecological risk farther south. The strong indirect effect of temperature constancy (figure 2; electronic supplementary material, figure S5b) on language diversity is another indication of the importance of ecological risk for shaping population density and language diversity.

Our GWPath also reveals that river density is not the primary predictor of language diversity in any region of North America (figure 3c). River density has been proposed as a global universal predictor of language diversity [7], but it does not show substantial effects in any region of North America when compared to other variables (figure 3c).

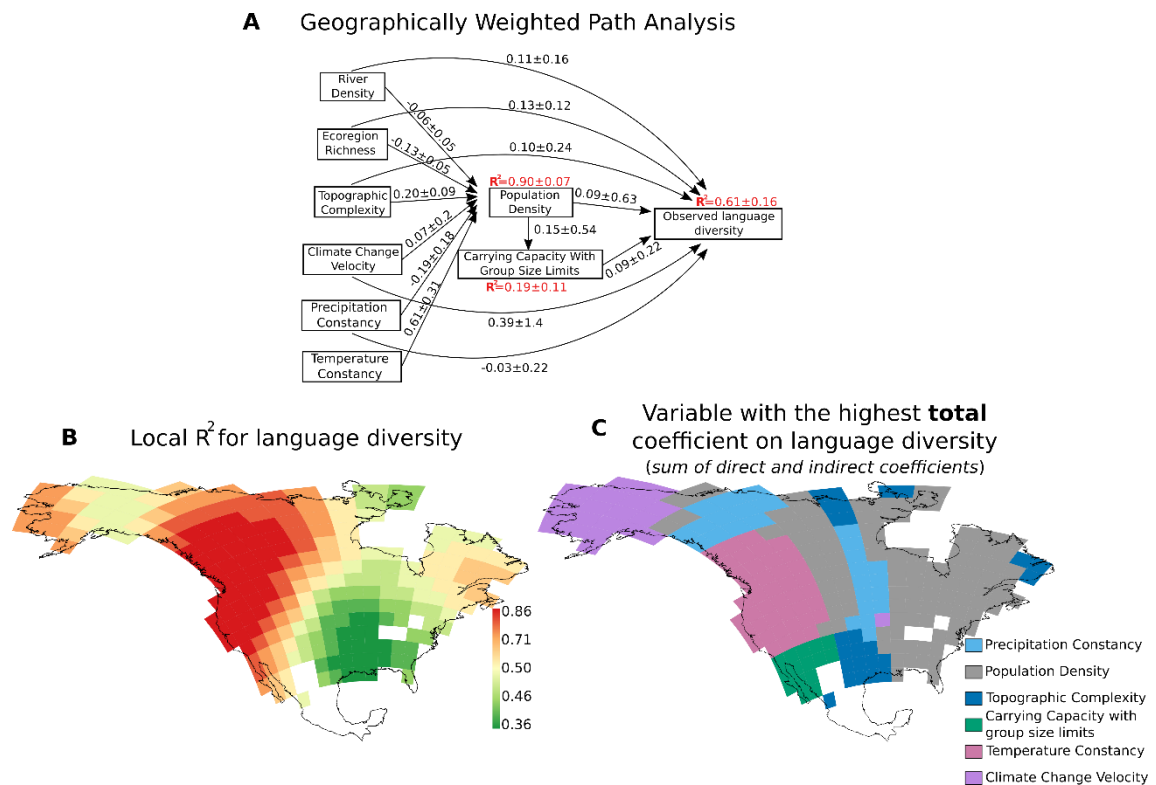


Fig 3. Geographically Weighted Path Analysis (GWPath) applied to North American linguistic diversity. (A) In the GWPath model, the standardized β coefficients of variables, as well as the R^2 for the direct relationships are represented by the average value over the continent, followed by its standard deviation. (B) Model fit varies over the geographic domain of North America. (C) Variables with the highest total coefficient (sum of direct and indirect effects) also vary across the continent.

Where our model performs best ($R^2 > 0.5$; red areas in figure 3b), population density and climate (i.e. temperature or precipitation constancy) are the variables most strongly affecting language diversity (figure 3c). The strong association of these variables in the areas of highest model fit provides support for several of the proposed pathways of language diversification (See factors contributing to language diversity patterns). Therefore, in those regions we can identify the best predictors of language diversity and better understand what is driving the performance of our model. However, in other regions (green in figure 3b), the model explains less than 50% of the variation

in language diversity ($R^2 < 0.5$). One possible reason for the poorer model performance in these regions is that pre-colonial human groups may have used rivers differently in different regions. The observed effect of river density on language diversity in the areas of lower model performance is the opposite (negative effect) to what has been hypothesized in the literature (figure 4a). One potential mechanism that may explain this negative correlation involves the impact of rivers on transportation. Compared to the west, many of the rivers in the central part of the continent flow through plains with fewer rapids, making them more navigable. Therefore, these rivers may have served to connect human groups and reduce language diversity, as opposed to acting as a barrier and means of group boundary formation. Finally, there are multiple sociocultural and historical factors that cannot be summarized in gridded map cells, and thus are absent from our model, including subsistence strategies, agricultural development, trade, and political complexity [12,29,63] that may be part of the unexplained percentage of variation. For example, the spread of politically complex agricultural societies may be a dominant factor in the reduction of language diversity [12].

To the best of our knowledge, this is the first study to investigate the complex web of predictors underlying geographical patterns of language diversity. We show that the strongest effects on North American language diversity involve variables associated with previously developed hypotheses that assume the effect of resource availability, resource diversity, and climate affecting population density, and thus language diversification. The many factors are connected in a complex web of causality, consisting of both direct and indirect effects. Moreover, no single predictor explains the pattern of language diversity in North America, and the best predictors of language diversity vary over space. Thus, our study sheds light on important points that should be taken into consideration in future studies of language diversity, namely that the

ecological drivers of language diversity are neither perfectly universal nor entirely direct. The combination of path analysis techniques with the exploration of non-stationarity in predictors' effects can help us to examine these complexities, and better understand a more complete picture of human biogeography. The methodological approach outlined here may serve as a template for exploring the potential interaction between multiple factors that have shaped geographical patterns of human diversity across the planet.

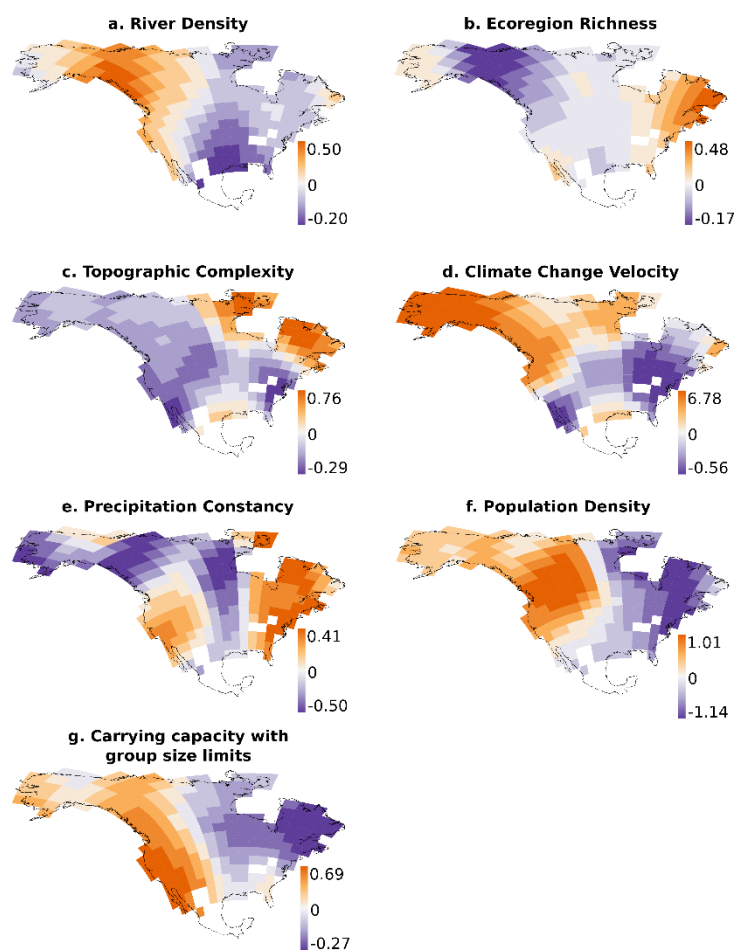


Fig 4. Direct effect of predictors mapped over the North American domain. The standardized β coefficient is mapped for (a) topographic complexity, (b) population density, (c) number of ecoregions, and (d) demographic constraints.

3. Methods

(a) Data

We obtained the approximate distribution of languages in North America immediately prior to European contact from two sources. We used the Survey of California and Other Indian Languages map (<http://linguistics.berkeley.edu/~survey/resources/language-map.php>) for the approximate spatial extents of California language ranges, and we digitized language ranges for other regions from Goddard [53]. The final map consisted of 344 language ranges. The geographical domain of North America was represented by an equal-area, gridded map at the resolution of 300 x 300 km. Our choice of this grid resolution ensured that grid cells were small enough to capture the variation in language diversity across space. We tested the sensitivity of our results to different grid resolutions; and we concluded that the results remained qualitatively insensitive to grid resolution (see Sensitivity Analysis in the electronic supplementary material). We computed the number of languages (i.e. language diversity) and extracted each predictor variable for each grid map cell (electronic supplementary material, figure S6).

High-resolution river maps for North America were obtained from the Global Self-Consistent Hierarchical High-resolution Shoreline dataset ([64], www.soest.hawaii.edu/wessel/gshhg/). Following Axelsen & Manrubia [7], we defined river density as the number of river branches within a geographical cell. We obtained data on ecoregions from the Terrestrials Ecoregions of the World dataset ([36]; www.worldwildlife.org/publications/terrestrial-ecoregions-of-the-world), and we used the number of terrestrial ecoregions within each geographical cell as a measure of ecoregion richness. We measured topographic complexity as the standard deviation of elevation above the sea level (m) within a cell ([65]; www.worldclim.org/). We used climate change velocity since the LGM [62] as a measure of long-term ecological risk.

Climate change velocity measures the rate of displacement of climate over the geographical space by dividing the climatic difference between two periods by climate change over space. We calculated the inter-annual variability (i.e. constancy) of temperature and precipitation following the Colwell index of constancy [66]. Constancy is used to describe the time independent magnitude of variability of temperature and precipitation. We calculated precipitation and temperature constancy using data from ecoClimate [67] for 1900–1949 from the CCSM4 model. We extracted the estimated population density (people per km²) for foraging societies [42] in each grid cell (see Population Density in the electronic supplementary material).

The effect of carrying capacity with group size limits on language diversity was simulated through a recently proposed mechanistic simulation model of language diversity (see Simulation Model section in the electronic supplementary material for additional details) [49]. The model's basic assumption is that the carrying capacity of a region is a function of the environment. Thus, locations that support more humans per unit area can also support more languages. The model accurately predicted the diversity of Australian languages [49], and here we apply it to North America. After running the model, replicated 120 times, we used the simulated geographical distribution of language ranges to summarize the model's prediction in the 300 x 300 km grid of North America. The prediction extracted from the model and used in our path analysis was a ratio between the number of languages predicted in each cell and total number of languages predicted for the geographical domain. We used the average among 120 model replicates as our carrying capacity with group size limits estimation in the path model.

(b) Statistics

Based on the hypothesized roles of the predictors used in our study on language and cultural diversity, we designed a path analysis model including the direct and indirect effects of our predictors on language diversity (figure 1). We evaluated the proposed direct and indirect effect of each variable on language diversity while controlling for the effects of the remaining predictor variables. We used the standardized partial slope coefficient of a multiple regression (i.e. path coefficient) to represent the strength of the effect of each variable on language diversity. This modelling technique allows us to explore direct, indirect (i.e. multiplication of direct coefficients), and total effects (i.e. sum of direct and indirect coefficients) of each predictor.

Path analysis assumes stationarity in the relationship among variables, but no theory would suggest that mechanisms of language diversification must be the same in all locations. In order to explore the potential for non-stationarity in our results, we also employed a GWPath, in which we estimated the coefficients for the predictor variables for each geographical cell following a Geographically Weighted Regression (GWR) [14] with a Gaussian distance function. We estimated a bandwidth for the GWR by visual inspection [14] and Akaike criteria model selection, which considers the likelihood of the model as well as its complexity. The best bandwidth obtained was 88 (approx. 880 km), which avoids overfitting and has a good fit to empirical data. Statistical analysis was conducted in R. GWPath used the ‘gwr’ function of the ‘spgwr’ package ([68]; also see electronic supplementary material for data and code). We also compared the predictions of our model against the expectations of a null model, which randomized language diversity in North America among grid cells, effectively removing the spatial pattern in language diversity (see Contrast Against a Null Model in the electronic supplementary material).

Data accessibility. The data used in this study are available as electronic supplementary material.

Authors' contributions. M.T.P.C. and M.G. jointly conceived the study. M.T.P.C. led the writing and created the figures with input from all authors. E.B.P. performed statistical analysis. H.H., produced the language distribution map. M.T.P.C., E.B.P., K.K., H.H. and P.K. processed the spatial data. T.F.R. programed the mechanistic simulation and M.T.P.C. applied it for North America. All authors contributed conceptually to the design of the study and interpretation of results.

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Endnote

¹In Australia, there are language-origin stories explicitly linking language regions of clans to ecological differentiation through staple foods, such as the tradition of the founding ancestress Warramurrungunji [25], who placed different plant foods (lily roots, yams, etc.) in different parts of the landscape at the same time as she placed people there and instructed them in what their clans would be, what their languages would be, and what they would eat.

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Supplementary Information for

Drivers of geographic patterns of North American language diversity

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Supplementary Methods

Population Density Estimates

Kavanagh et al. [41] used a piecewise structural equation modelling (SEM) that assumes the direct and indirect effects of environmental and cultural variables to estimate the population density of foraging societies. The model assumes the effect of productivity, topography, precipitation seasonality, distance to coast (i.e. access to marine resources), resource ownership (i.e. whether resources are owned or not) and residential mobility (i.e. average distance travelled per residential move). All these variables were previously hypothesized to affect population density of foraging societies due to their influence on the availability of resources or the foraging practices of human groups. Kavanagh et al. [41] fitted a piecewise-SEM to empirical societies of hunters and gatherers, and they showed that the model explained 77% of the variation in population density among observed foraging societies. With the fitted model, the authors estimated population density at 0.5x0.5° cells for the world. In our study we used the estimations of population density for North America in order to explore the effect of population density on language diversity as well as to define the carrying capacity for the simulation model (see *Simulation Model* section).

Simulation Model (Carrying capacity with group size limits)

We estimated the variable “carrying capacity with group size limits” based on a recent simulation model developed to better understand the effects of climate and demography on language diversity [49]. Here we present a detailed description of the simulation model.

Hexagon cell resolution

We defined a hexagon and equal area gridded map of $0.5 \times 0.5^\circ$ for North America, and we extracted population density (people per km^2) [based on 41, see population density section above] for each geographical cell. We used the hexagon cell to simulate the expansion of language ranges over space (see *Model Algorithm* section). Two criteria define the resolution of the hexagon gridded map: (i) cells must be large enough to encompass a group of individuals, but smaller than most observed language ranges in North America, and (ii) population density needs to be extracted without interpolating the data to finer grid resolutions. Population Density is only available in 0.5 degrees of resolution. The use of a finer resolution ($< 0.5^\circ$) would require us to interpolate population density, which would generate uncertainty in the data used as an input to the simulation model (see *Carrying Capacity* section). However, coarser resolutions ($> 0.5^\circ$) would produce fewer total languages because languages with smallest ranges generated by the simulation would have ranges larger than the smallest observed language ranges in North America. Therefore, using a coarsest resolution would generate fewer languages over space because of a spatial constraint in the definition of the grid. As we show latter, this grid resolution can produce a total number of languages that precisely resembles the observed data.

Carrying Capacity

Unlike in Gavin et al. [49], we did not use parameter estimation to define the best mathematical function that describes carrying capacity. Instead of estimating carrying capacity based on different mathematical functions [see 49], we calculated carrying capacity using estimates of population density [41] and the area of each hexagonal cell.

Model Algorithm

Here we summarize the steps of the simulation model, which was implemented following similar procedures as Gavin et al. [49]:

1. Ten individuals of a language group occupy a randomly chosen hexagon cell (i);
2. A maximum group size is defined for the language group by sampling the empirical distribution of hunters, gatherers and fishers group sizes [43].
3. At each algorithm time step (t), a regional carrying capacity is defined ($K_{i,j}$) for each occupied cell (i) by summing the carrying capacity of the cell i (K_i) and the carrying capacity of all its p neighboring cells (i.e. cells that share an edge with the focal cell i).
4. The increase in population size (N) between time step t and the next time step ($t + 1$) is given by:

$$N_{i,t+1} = rN_{i,t} \times \left(1 - \frac{N_{i,t} + \sum_{j=1}^p N_{i,j,t}}{K_i + \sum_{j=1}^p K_{i,j}} \right)$$

where $r = 1.01$ (i.e. per capita intrinsic rate in population growth), $\sum N_{i,j,t}$ is the number of individuals at time t in all p cells, indexed by j , that are adjacent to cell i , and $\sum K_{i,j}$ is the regional carrying capacity. This equation takes into consideration the potential population growth of individuals that are present in the cell i , but also the opportunity for colonization of the adjacent cells. Changes in r do not affect the outcome of the model, only the rates of expansion of each language.

5. The population of the focal language grows until it reaches the maximum group size that was defined based on sampling the empirical HGF distribution (step 2).
6. As soon as the population of the language reaches its maximum population, it stops growing and an empty cell is randomly chosen at the edge of the previous growing language (if it is the first language), or from a randomly selected language (if richness > 1).
7. As the new language emerge in the simulation the same procedures from 1 to 6 are repeated. The new population can colonize any empty cell but do not colonize any occupied geographical cell.
8. The simulation stops when all cells are colonized.

Model prediction

Because we randomly selected the first cell to be colonized by any language group (see steps 1 and 6 of model algorithm), the simulation model is stochastic. Thus, we replicated the model 120 times [49] and recorded the spatial pattern of language diversity (number of languages per 300x300km cells) and the total number of languages. The predictions extracted from the model and used in our path analysis was a ratio between the number of languages predicted in each cell and the total number of languages predicted for the geographic domain (see Fig S7). We used the average among 120 model replicates as our “carrying capacity with group size limits” variable in the path models. The average richness map and the distribution of the total number of languages predicted by the model are represented in Fig S1.

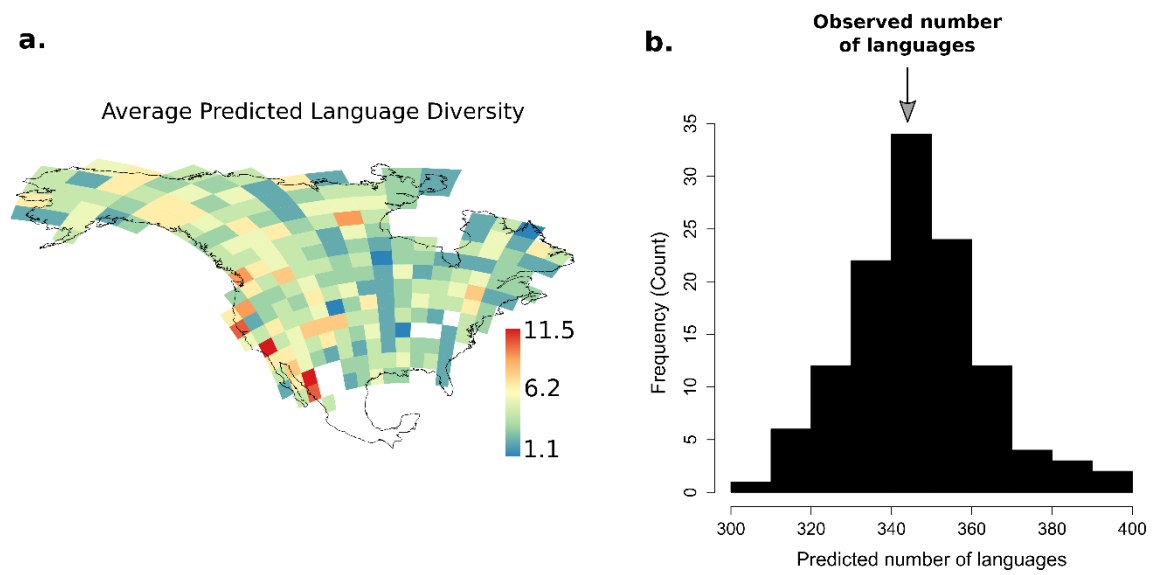


Fig S1. Average predicted language diversity in North America (a) and total predicted language diversity (b) based on 120 model replicates. North America presents 344 aboriginal languages. The simulation predicts and average of 346.49 languages.

Statistical Analysis – Additional details

We Z-transformed all variables to allow for direct comparisons between path coefficients. Therefore, because variables are standardized, we can examine which variable presents the highest or lowest coefficient as in partial regression coefficients. To avoid multicollinearity issues, we tested the association among predictors and followed the standard statistical interpretation that correlations $> |0.70|$ should be avoided between predictors [70]. Because population density and temperature constancy were highly correlated ($r = 0.86$, Table S1) and the direct effect of population density on language diversity already captures the effect of temperature constancy on language diversity, we removed the direct effect of temperature constancy from our analysis. Therefore, the final path model is composed of three linear regressions: (1) population density $\sim$ river density + ecoregion richness + topographic complexity + climate change

velocity + precipitation constancy + temperature constancy, (2) language diversity ~ river density + ecoregion richness + topographic complexity + climate change velocity + precipitation constancy + population density + carrying capacity with group size limits and (3) carrying capacity with group size limits ~ population density (Code and data to perform the analysis are available as supplementary material).

Sensitivity Analysis

To explore the sensitivity of our analysis to grid resolution we defined five different grid resolutions: 200x200km, 250x250km, 300x300km, 350x350km and 400x400km. However, as we show here, our results are qualitatively insensitive to grid resolution. Despite a slight increase in R^2 at coarse resolution grids ($>300 \times 300 \text{ km}$), the spatial pattern in R^2 remains similar across different grid resolutions (Fig S2). Similarly, although the mean coefficient of each variable varies with different resolutions, the coefficients of all variables still vary over space (Fig S3). In our paper we present the results only for the $300 \times 300 \text{ km}^2$ to ensure that grid cells were small enough to capture the variation in language diversity across space and because the same grid resolution has been used to characterize language diversity on other continents [49].

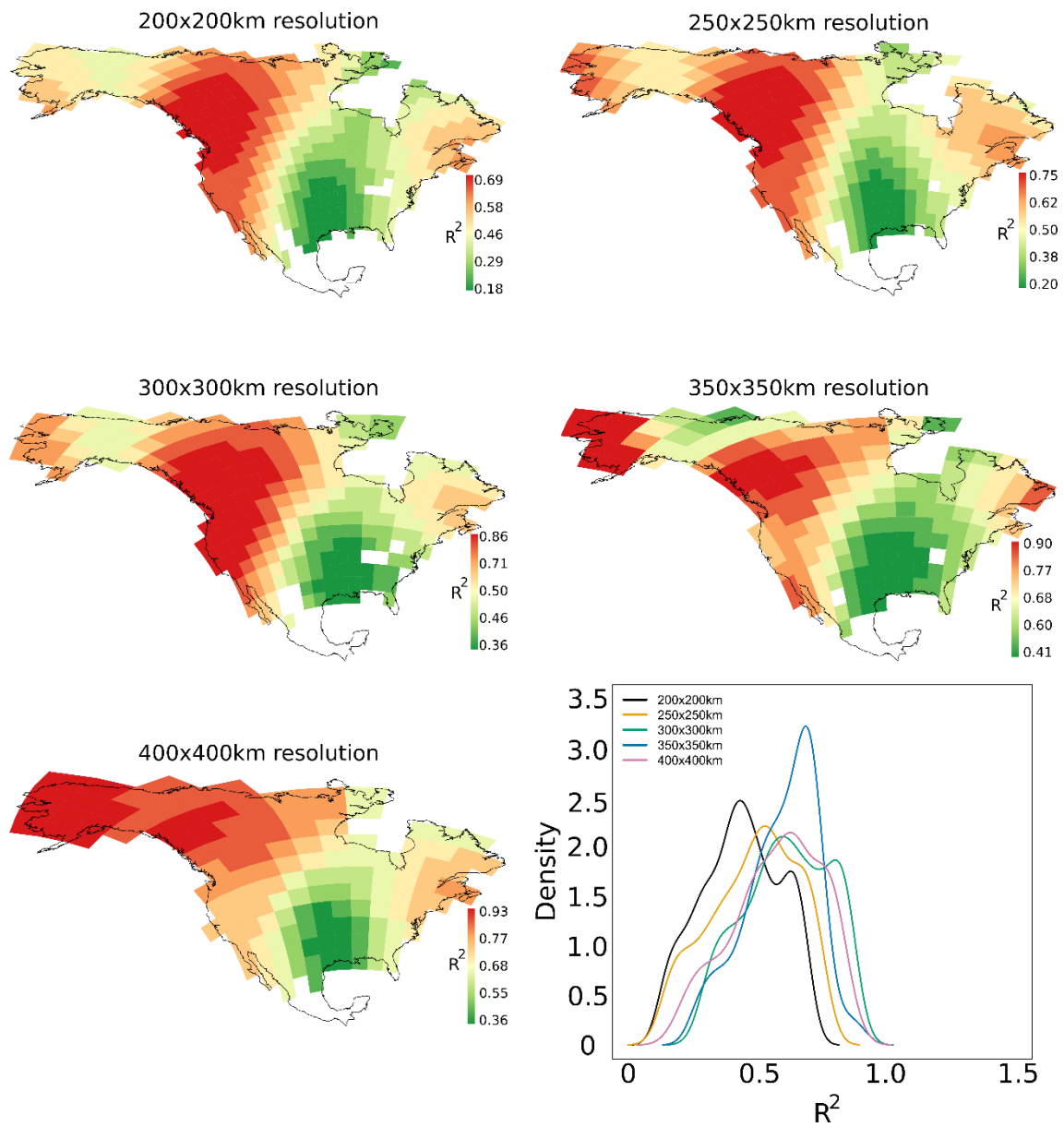


Fig S2. Local R^2 for different grid resolutions and the distribution of R^2 for each resolution.

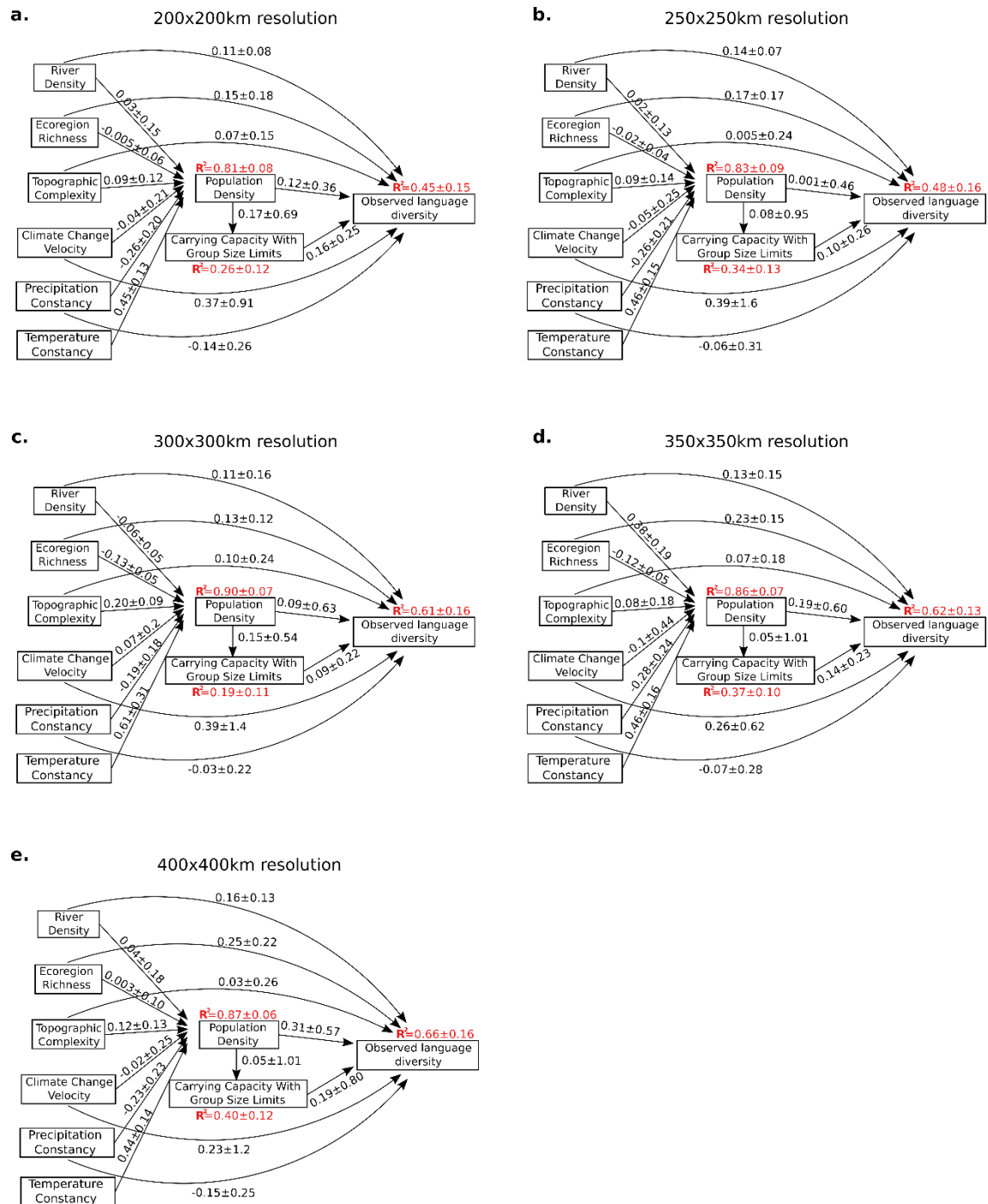


Fig S3. Mean coefficients and their standard deviation in different grid resolution.

Contrast against a null model

We compared the predictions of our model against the expectations of a null model, which randomized language diversity in North America among grid cells, effectively removing the spatial pattern in language diversity. We replicated the null model 1000 times and ran the GWR path analysis for each replicate of randomized language diversity, recording the R^2 for each grid cell (i.e. *local null R^2*). We then calculated a map of the statistical *effect-error* ratio [71], in which the statistical effect is represented by the R^2 for a grid cell (i.e. *local R^2*) obtained by the analysis of empirical language richness, and the statistical error is the standard error of local R^2 , estimated as the standard deviation of local null R^2 for a grid cell [72]. The ratio between the local R^2 (effect) and the standard error of local R^2 (error) follows a z-distribution and is a standardized measure of how much the observed effect is greater than the statistical error. Standard statistical interpretation argues that an effect at least two times larger than the error (i.e., an effect-error ratio of 2) represents substantial evidence that this effect would not have been obtained by sampling error with a 95% confidence level [73]. In our stationary analysis, the effect-error ratio is 28.430. In our geographically weighted model, the minimum *effect-error* ratio is 3.7, indicating that observed R^2 depart substantially from the null expectation. In areas where our model explains more than 50% of the variation in language diversity (Fig 3) we estimate an even larger *effect-error* ratio (7 - 13.9; Fig S4).

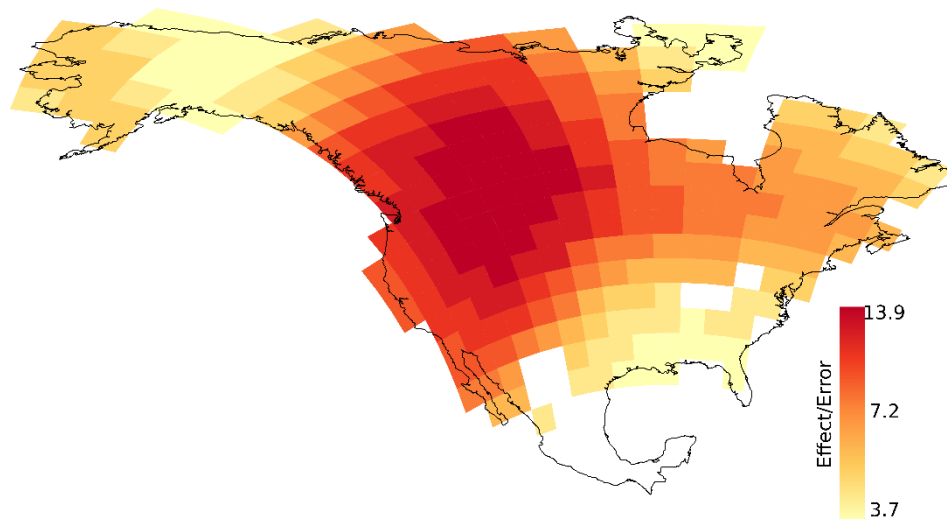


Fig S4. Effect-Error ratio. The effect is represented by the local R^2 obtained by the analysis with the empirical language richness and the error is represented by the standard deviation of the local null R^2 obtained by 1000 randomizations of language diversity in the gridded map of North America.

Supplementary Figures

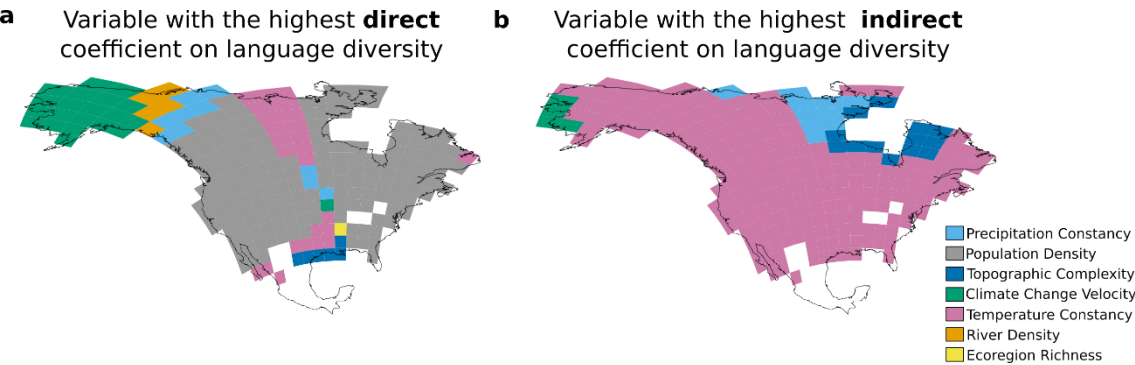


Fig S5. Variables with the highest (a) direct and (b) indirect coefficients.

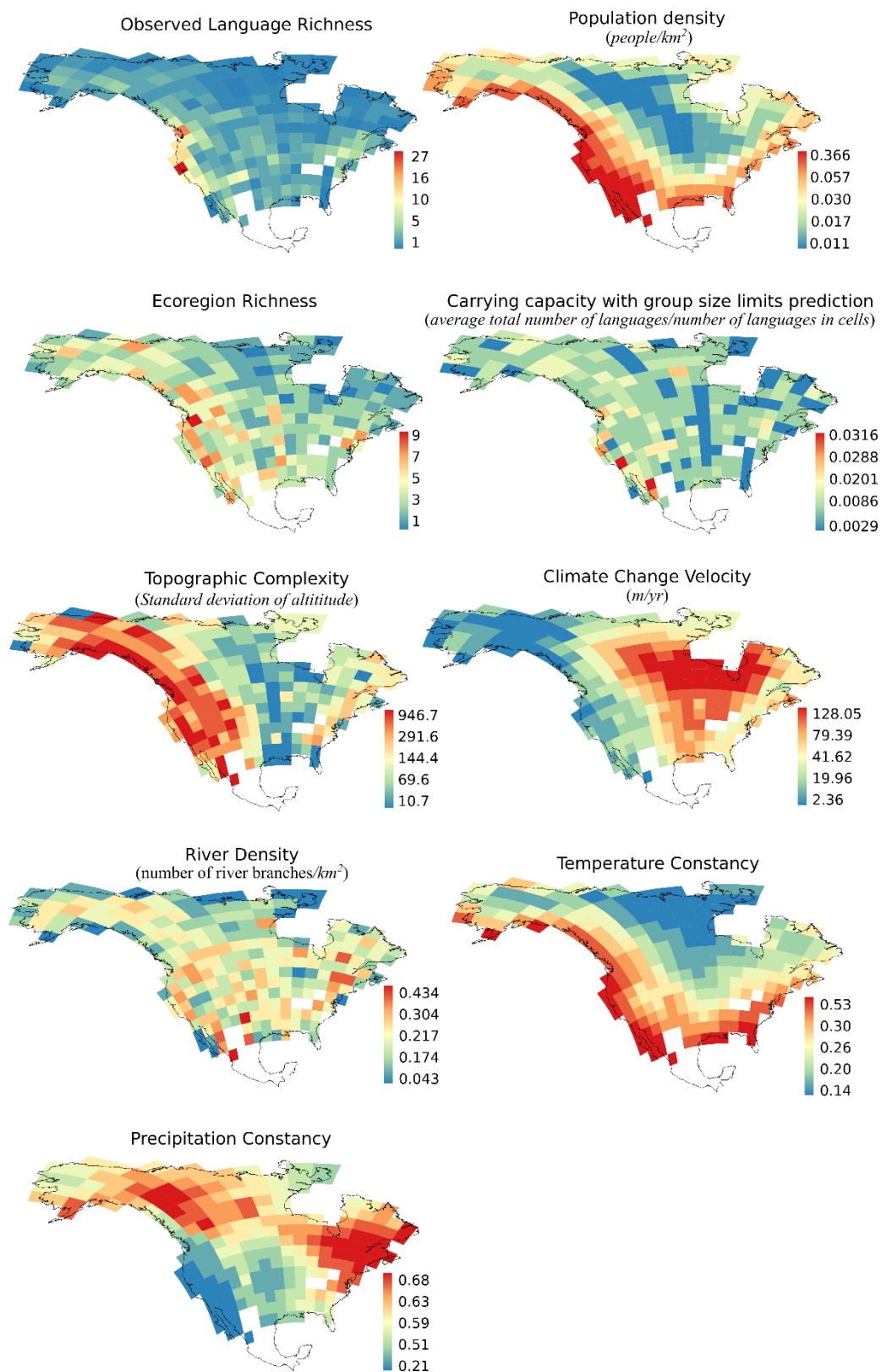


Fig S6. Spatial pattern of language diversity and all predictors tested in this study.

Supplementary Tables

1. Table S1 – Pairwise correlation between predictor variables. Temperature constancy and population density are the only pair of variables that are strongly correlated [see 71]. The direct effect of population density captures the effect of temperature constancy on language diversity. Thus, the direct effect of temperature constancy on language diversity is not assumed in the path models.

	Carrying capacity with group size limits	River Density	Population Density	Topographic Complexity	Ecoregion Richness	Climate Change Velocity	Precipitation Constancy	Temperature Constancy
Carrying capacity with group size limits	1.00	0.07	0.34	0.41	0.26	-0.27	-0.30	0.17
River Density	0.07	1.00	-0.01	0.26	0.26	0.01	-0.10	0.04
Population Density	0.34	-0.01	1.00	0.54	0.37	-0.51	-0.68	0.87
Topographic Complexity	0.41	0.26	0.54	1.00	0.53	-0.68	-0.42	0.38
Ecoregion Richness	0.26	0.26	0.37	0.53	1.00	-0.44	-0.41	0.39
Climate Change Velocity	-0.27	0.01	-0.51	-0.68	-0.44	1.00	0.38	-0.43
Precipitation Constancy	-0.30	-0.10	-0.68	-0.42	-0.41	0.38	1.00	-0.63
Temperature Constancy	0.17	0.04	0.87	0.38	0.39	-0.43	-0.63	1.00

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PARTE IV. APÊNDICES

Apêndice I

Why are so many languages spoken in some places and so few in others?

Artigo de divulgação publicado no portal The Conversation:

<https://theconversation.com/why-are-so-many-languages-spoken-in-some-places-and-so-few-in-others-116573>

Why are so many languages spoken in some places and do few in others?

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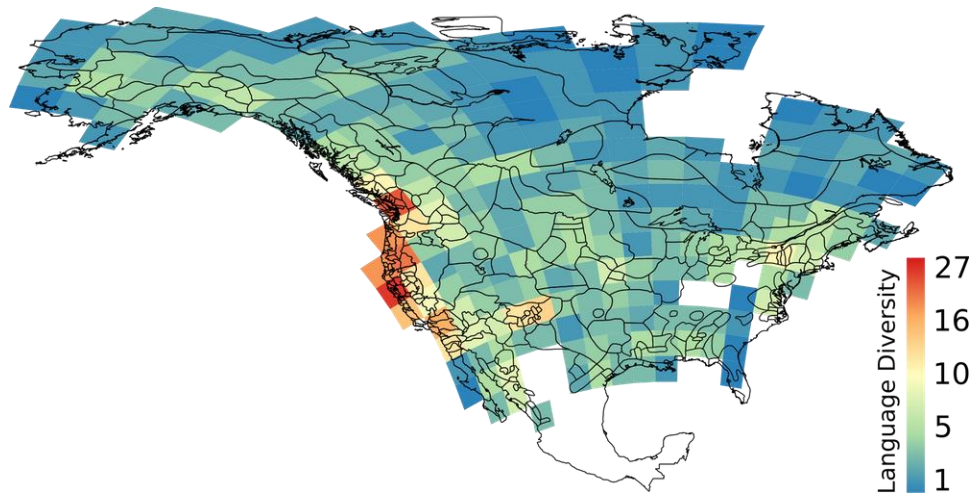
Michael Gavin

Associate Professor of Human Dimensions of Natural Resources, Colorado State University

People across the world describe their thoughts and emotions, share experiences and spread ideas through the use of thousands of distinct languages. These languages form a fundamental part of our humanity. They determine whom we communicate with and how we express ourselves.

Despite continually mapping the distribution of languages across the world, scientists have few clear answers about what caused the emergence of thousands of languages. Collectively, [human beings speak more than 7,000 distinct languages](#), and these languages are not uniformly distributed across the planet. For example, far more languages are spoken [in tropical regions than in temperate areas](#).

But why are there so many languages spoken in some places and so few in others?



A grid map of language ranges in North America prior to European contact. [Coelho et al. RSPB 2019](#). CC BY

Our research team has been tackling this longstanding question by exploring [language diversity patterns on the continent of North America](#). Prior to European contact, North America was home to speakers of around 400 languages, unevenly spread across the landscape. Some places, such as the West Coast from present-day Vancouver to southern California, had far more languages; other areas, such as northern Canada and the Mississippi delta region, appear to have had fewer languages. We drew on methods from ecology originally developed to study [patterns of species diversity](#) to investigate these patterns of language diversity.

Building boundaries

Many theories have outlined [possible ways the world's languages might have diversified](#).

Fundamental to all of these theories is the idea that languages are markers of social boundaries between human groups. People who speak the same language share a common means of communication. And this fact is readily evident both to those who speak the language and those who do not. After just a few words, you can often surmise who is in your group and who is not.

So any factor that might create or weaken the social or physical barriers between groups may also influence the emergence or extinction of languages.

One idea is that physical barriers create boundaries between human groups. When people move to the other side of a large mountain range, for instance, or [the ocean](#), it becomes increasingly hard to interact with previously neighboring groups. Over time, if the groups remain isolated, one might expect their languages to diverge. If physical isolation is a critical factor, then we should find a larger

number of languages in locations that promote more isolation, such as mountainous regions.

Another possible way group boundaries might form involves how much groups must cooperate in order to survive. Some researchers suggest that more extreme or variable climatic conditions [can make food harder to obtain](#). This uncertainty may lead people to build larger social networks in order to share resources in times of need. More frequent contact through the extended social networks could dissolve social boundaries and reduce language diversity. In this case, one would expect [less language diversity](#) in locations with unstable or extreme climatic conditions.

Perhaps how many people can live in a given location also shapes language diversity. Some environmental and social conditions can support higher densities of people. These greater population densities might lead to increases in language diversity in a number of ways. For example, human groups do not increase infinitely. Maintaining social ties may come at a cost, such that when a group gets too big, it will tend to divide. Therefore, you might expect more distinct human groups to accumulate in locations that can support more people. And with more distinct groups, you'd also expect to see [more languages in these locations](#).

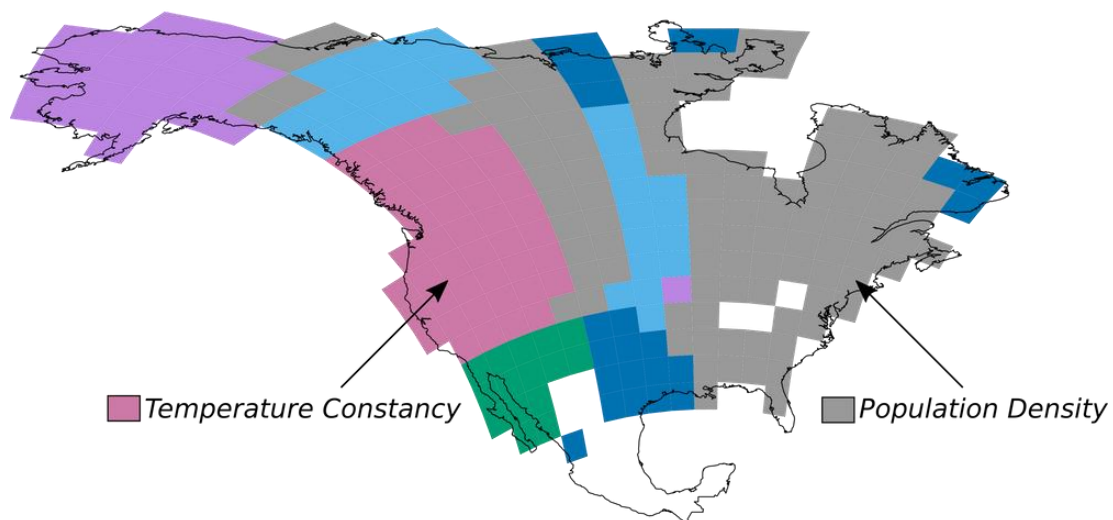
No single explanation

Surprisingly, few of these theories, or many others that researchers have proposed, have been rigorously tested. And the tests that have been done [point to contradictory results](#). For instance, some studies support the idea that less language diversity is found in locations with unstable and extreme climatic conditions, while others found little or no support for that idea.

The problem has been that researchers have tended to search for one silver bullet, a single factor that would explain patterns of language diversity everywhere. But why expect one factor to accurately summarize thousands of years of human history across the entire globe, or even across a continent? What if the story underlying language diversity in northern Canada is totally different from the story underlying language diversity in California?

Recently, our interdisciplinary research group tried to untangle which factors had the most influence on language diversity in different places. Combining ideas from linguists, ecologists, evolutionary biologists and geographers, we took a unique approach. We used statistical techniques to estimate how the effects of [environmental and sociocultural factors on language diversity](#) changed from one location to another. In our study, each location was represented by a 300 km² grid cell, as is visible in all our maps.

We found that the most important variables associated with language diversity varied from one part of North America to another.

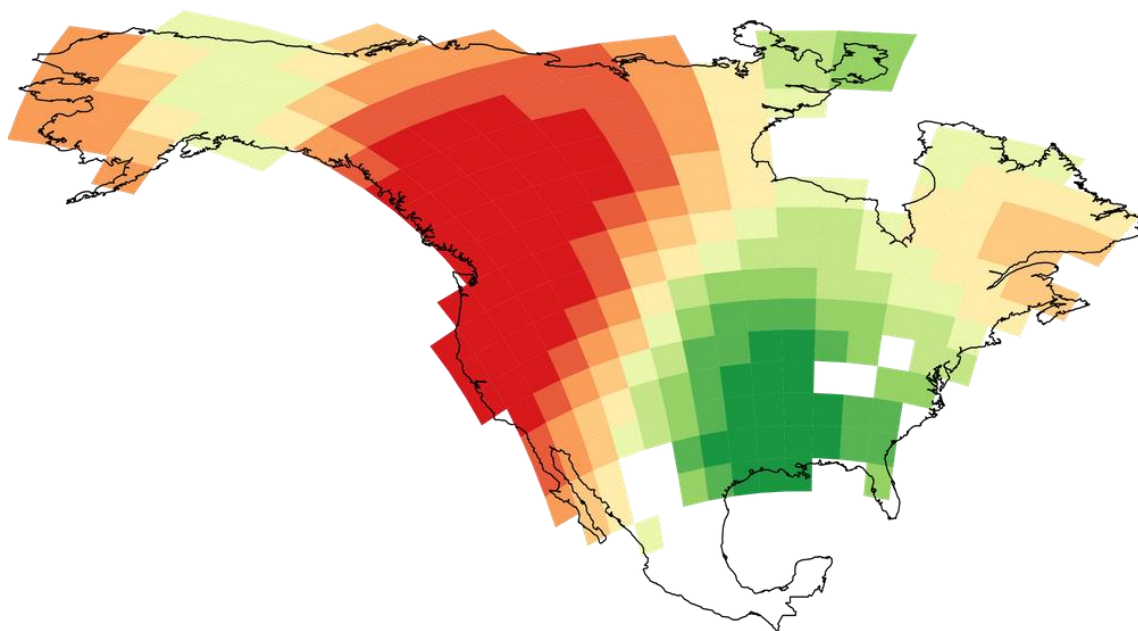


Language diversification in different regions may have been driven by different factors. In some places, like the areas in pink, temperature variability might have been most important. Other possible factors include population density (gray), precipitation constancy (light blue), topographic complexity (dark blue), carrying capacity with group size limits (green) and climate change velocity (purple). [Modified from Coelho et al. RSPB 2019. CC BY](#)

For example, on the West Coast, we found that variability in temperature over time is a key driver linked to language diversity. This result provides some support for the idea that in areas with more stable environmental conditions, human social networks can be smaller and more languages may exist.

However, in the eastern part of the continent, potential population density tends to be the factor most strongly linked to language diversity.

We also found that in some places, such as the high-language-diversity regions on the West Coast, our model could predict the number of languages present very accurately, whereas in other areas, such as the Gulf Coast of the U.S., we have limited understanding of what drove language diversification.



The model's ability to predict the number of languages varied from excellent in some places (red) to poor in others (green). [Modified from Coelho et al. RSPB 2019 CC BY](#)

Our analytical tools were originally developed to study patterns of species diversity; these approaches are now starting to increase scientists' understanding of what factors [shaped human diversity](#). But

our results so far also underscore how much is still unknown about how cultural diversity originated and how it will change into the future.

Disclosure statement

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