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**MODELOS DE NICHOS ECOLÓGICO E O EFEITO DO CLIMA NA
DISTRIBUIÇÃO DAS ESPÉCIES**

LILIAN PATRÍCIA SALES MACEDO

Orientador:
Prof. Dr. Rafael Loyola

Goiânia, GO – Brasil
2018

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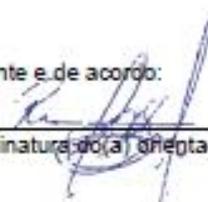
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LILIAN PATRÍCIA SALES MACEDO

**MODELOS DE NICHOS ECOLÓGICOS E O EFEITO DO CLIMA NA
DISTRIBUIÇÃO DAS ESPÉCIES**

Tese apresentada ao Programa de Pós-Graduação em Ecologia e Evolução, da Universidade Federal de Goiás, como requisito parcial à obtenção do título de Doutora em Ecologia e Evolução,

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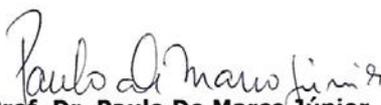
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Aos quinze dias do mês de junho de 2018 (15/06/2018), às quatorze horas (14h), no Auditório do ICB V, UFG, reuniram-se os componentes da banca examinadora: **Prof. Dr. Rafael Dias Loyola, ICB/UFG; Prof. Dr. Paulo De Marco Júnior, ICB/UFG; Prof. Dr. José Alexandre Felizola Diniz Filho, ICB/UFG; Dra. Priscila Lemes de Azevedo Silva, UNESP/Rio Claro; Prof. Dr. Mauro Galetti Rodrigues, UNESP/Rio Claro;** para, em sessão pública presidida pelo (a) primeiro(a) examinador(a) citado(a), procederem à avaliação da defesa de tese intitulada: **"Modelos de nicho ecológico e o efeito do clima na distribuição das espécies"**, em nível de doutorado, área de concentração em Ecologia e Evolução, de autoria **Lilian Patrícia Sales Macedo**, 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 40 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 APROVADA, 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

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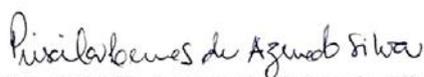
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RESUMO GERAL

As alterações climáticas previstas para o século XXI afetarão a biodiversidade e seus padrões de distribuição. Nesta tese, buscamos antecipar os efeitos do clima e das mudanças climáticas na distribuição geográfica de diferentes espécies de vertebrados. Nossas projeções futuras sugerem uma redistribuição da biodiversidade, devido à realocação das ocorrências espécie-específicas, através de migrações de fauna direcionadas a climas mais favoráveis. Novas comunidades serão assim formadas, como consequência das mudanças climáticas, gerando padrões inéditos de co-ocorrência, incluindo a perda e a substituição de algumas espécies. Tais migrações de fauna devem ser recorrentes em gradientes altitudinais, como os da Cordilheira dos Andes, que pode funcionar como um refúgio climático. Alguns grupos taxonômicos, como os primatas, sofrerão grandes reduções na área climaticamente adequada. Mesmo as espécies com pouca ou nenhuma redução de distribuição parecem não ser capazes de migrar em velocidade suficiente. Além disso, novos integrantes - como o javali - serão adicionados às comunidades locais, pela ação deliberada ou inadvertida do homem. Apesar de haver variação entre as projeções de modelos calibrados com dados e/ou algoritmos diferentes, os padrões acima são evidentes na maioria dos mapas consenso. Além disso, fazemos também um panorama histórico do conceito de nicho, que fornece a base teórica da maior parte da literatura sobre os efeitos do clima na distribuição das espécies.

Palavras-chave: mudanças climáticas, distribuição geográfica, conservação da biodiversidade, espécies invasoras, nicho ecológico.

¹ Orientador: Prof. Dr. Rafael Loyola.

SALES, L.P. Ecological niche models and the effect of climate on species distribution. 2018. 127p. Thesis (PhD on Ecology and Evolution) – Institute of Biological Sciences, Universidade Federal de Goiás, Goiânia, 2018.¹

ABSTRACT

Twenty-first century climate change will have a profound impact on the distribution of global biodiversity. In this thesis, we aim to anticipate the effects of climate and the projected changes on the geographical distribution of several vertebrate species. Our future projections suggest a biodiversity redistribution, due to the relocation of species-specific ranges, via faunal migrations toward suitable climates. Novel communities will be thus formed, creating new co-occurrence patterns, which include species losses and substitutions. Climate-driven faunal migrations might be recurrent on altitudinal gradients, such as the Andes mountain range, which might act as a climate refugia. Some taxonomic groups, primates for example, will experience large shrinks on suitable climate area. Even the species likely to lose little or no area do not seem able to migrate fast enough, to track their climate niche. New community members, like the wild boar, will be added to local species pool, by the intentional or inadvertent human action. Although there is some variation from models calibrated with different datasets and/or modeling algorithms, the patterns above are consistent among projections. In addition, we build a historical panorama of the niche concept, the one which supports most of the literature on the effects of climate on species distribution.

Key words: climate change, geographical distribution, biodiversity conservation, invasive species, ecological niche.

¹ Advisor: Prof. Dr. Rafael Loyola

Introdução Geral

Sales LP & Loyola RD (2018). **Modelos de nicho ecológico e o efeito do clima na distribuição das espécies**

Introdução Geral

Donald Trump, presidente eleito dos Estados Unidos da América, retirou oficialmente o país do Acordo de Paris, em junho de 2017. O acordo propõe metas para reduzir a emissão de gases do efeito estufa e de incentivo a políticas de energia limpa, baseada em fontes renováveis, e havia sido ratificado por 147 países, inclusive pelos EUA. A saída do país, historicamente o maior emissor de gases do efeito estufa no mundo, faz parte da política anti-ambientalista e de enfraquecimento dos tratados internacionais de mitigação das mudanças climáticas, adotada pelo governo Trump. Ainda que o setor de tecnologia em produção de energia limpa seja um dos que mais cresce em geração de emprego e renda nos EUA, alguns políticos mais “conservadores” (muitas vezes financiados por tradicionais companhias petrolíferas, de extração de carvão, etc.) fomentam o discurso de que as mudanças climáticas são uma fraude. Apesar de parecer irracional, a crença de que a ação humana em nada interfere no clima e em seus padrões é ubíqua, principalmente em setores não-acadêmicos.

Mudanças climáticas

O fato em si é incontestável: a influência humana é a causa dominante do aquecimento global observado desde a metade do século XX (IPCC, 2014a, 2014b; Cook et al., 2016; O’Neill et al., 2017). Ainda no ano de 1995, o Painel Intergovernamental sobre Mudanças Climáticas – *Intergovernmental Panel on Climate Change* (IPCC, 1995) – já afirmava que alterações climáticas antropogênicas eram detectáveis. Desde então, diversos artigos independentes tem concluído que ações humanas afetam o clima, numa

meta-conclusão de que há consenso científico sobre isso (Oreskes, 2007; Cook et al., 2014, 2016). A maior parte dos pesquisadores sobre o clima concorda que a ação humana atualmente é uma força direcionadora do clima em escala regional e global (Cook 2015). Os trabalhos que rejeitam o consenso sobre o aquecimento global antropogênico são uma porção extremamente pequena dos artigos científicos revisados pelos pares (Cook 2013). Alguns refutadores provém ainda de grupos não-pertencentes à comunidade científica, com interesses econômicos (Oreskes, 2007).

Clima e distribuição potencial

O clima de um ambiente inclui tanto as médias de temperatura e precipitação quanto outras medidas de sua variação ao longo do ano (Hijmans et al., 2005). Podemos analisar, por exemplo, se a sazonalidade do clima define bem as estações do ano, ou como a precipitação se distribui entre as estações seca e chuvosa (se houver), e ainda o quanto a amplitude climática gera climas extremos e hostis à vida. Pensando em escalas espaciais geográficas, as tolerâncias climáticas e os limites fisiológicos das espécies, em conjunto com as interações bióticas e as limitações de dispersão, definem como as espécies se distribuem (Soberón & Peterson, 2005). Uma espécie apenas ocorrerá apenas onde o clima permitir sua existência –um urso polar, por exemplo, não resistiria ao calor tropical. Mas a interação com outras espécies também restringe a ocupação de territórios, de modo que uma espécie competitivamente inferior ou dependente de recursos alimentares específicos pode não conseguir colonizar certos territórios, ainda que o clima lhes seja favorável (Post, 2013). Por fim, mesmo onde o clima e as interações bióticas permitam a

persistência de uma espécie, a colonização de um território dependerá da história biogeográfica e limitações de dispersão da espécie (Peterson, 2003).

A área que uma espécie ocupa depende, portanto, do clima de uma região, mas é limitada ainda pelas interações com as espécies residentes e por sua capacidade intrínseca de dispersão (Soberón & Peterson, 2005). Na Figura 1, os círculos coloridos representam os principais fatores que determinam a distribuição de uma espécie (A - fatores abióticos; B - fatores bióticos; M - fatores ligados à movimentação). A intersecção entre os três círculos representa a área efetivamente ocupada por uma espécie, ou seja, os locais onde as condições bióticas e abióticas permitem a existência da espécie, e que puderam ser colonizados, dadas as características de dispersão. A região de sobreposição entre A e B, exclusivamente, indica zonas de invasão potencial. Nestas zonas, a espécie teria condições de persistir, caso pudesse alcançá-la geograficamente. A movimentação de espécies, intencionalmente ou não, pelo homem acaba permitindo que algumas barreiras biogeográficas sejam ultrapassadas, levando à introdução de espécies exóticas (Peterson, 1999). Essas espécies encontram condições (bióticas e abióticas) favoráveis à sua sobrevivência e podem se dispersar pelo novo território, muitas vezes causando problemas à biodiversidade e economia locais (p.ex. o javali *Sus scrofa*, Barrios-Garcia & Ballari, 2012; Sales et al., 2017).

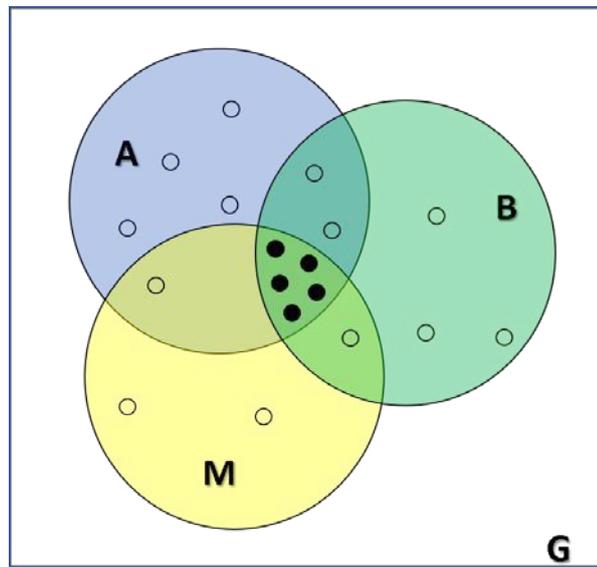


Figura 1 Diagrama de BAM, proposto por Soberón & Peterson (2005). Nesta figura, os círculos representam os principais elementos que determinam a distribuição de uma espécie, no espaço geográfico G. Em A, temos os elementos abióticos e ambientais, como clima, relevo, pH, salinidade do solo, etc. Em B, temos os fatores bióticos, como as interações competitivas que permitem co-existência, disponibilidade de recurso alimentar, tamanho populacional mínimo viável, entre outros. O último círculo, M, indica o elemento de movimentação da espécie, ou seja, as áreas dentro de uma distância de dispersão viável, que não sejam inalcançáveis por alguma barreira biogeográfica.

Modelos nicho ecológico

Como cada espécie tem seu conjunto restrito de condições ambientais que lhes permite sobreviver – seu nicho Grinnelliano ou nicho climático (Grinnell, 1917; Soberón, 2007; Peterson et al., 2011), as espécies respondem individualmente às alterações ambientais (Moritz et al., 2008), com base em suas preferências climáticas (Figura 2). Para prever as alterações em distribuição potencial, o paradigma científico atual tem sido calibrar e avaliar modelos de nicho ecológico (MNE) ao longo da distribuição conhecida da espécie na atualidade (Peterson et al., 2011). Os MNE assim gerados são, então,

transferidos para as condições climáticas projetadas para um futuro próximo, cerca de 30 a 70 anos a partir do presente (Peterson et al., 2018). Os MNE calibram as condições ambientais que ocorrem numa dada região geográfica e projetam essa relação para outro tempo ou outra região. Isso é possível devido à dualidade do nicho de Hutchinson, em que para cada ponto do espaço ambiental possui uma ou mais correspondências no espaço geográfico (Colwell & Rangel, 2009). As projeções climáticas do futuro são baseadas em modelos globais do clima – *general circulation models*, GCM, que antecipam as condições ambientais a partir de cenários de desenvolvimento humano e emissão de gases do efeito estufa (Baker et al., 2016).

As mudanças ambientais geram um “dilema”. Se o clima muda e passa a não mais pertencer ao nicho climático da espécie, as condições abióticas locais passam a ser desfavoráveis à persistência das populações, o que aumenta a probabilidade de extinções locais. Assim, para evitar esses efeitos climáticos deletérios, as espécies precisam encontrar mecanismos comportamentais para evitar o clima desfavorável, como adaptações *in situ*, ou migrar para ambientes mais favoráveis (Thomas, 2010). O registro fóssil mostra que, para muitas espécies, migrações como resposta às mudanças climáticas permitiram que espécies viventes tenham sido encontradas em regiões distantes de suas distribuições atuais (Davis & Shaw, 2001; Gavin et al., 2014). As distribuições das espécies não, portanto, são estáticas. Elas mudam com o tempo, à medida em que o clima se altera. Isso acontece porque as espécies precisam migrar de um lugar a outro para se manter dentro de suas condições ambientais favoráveis (Pechl et al., 2017). Assim, elas precisam correr (no espaço geográfico), para se manter no mesmo lugar (no espaço ambiental).

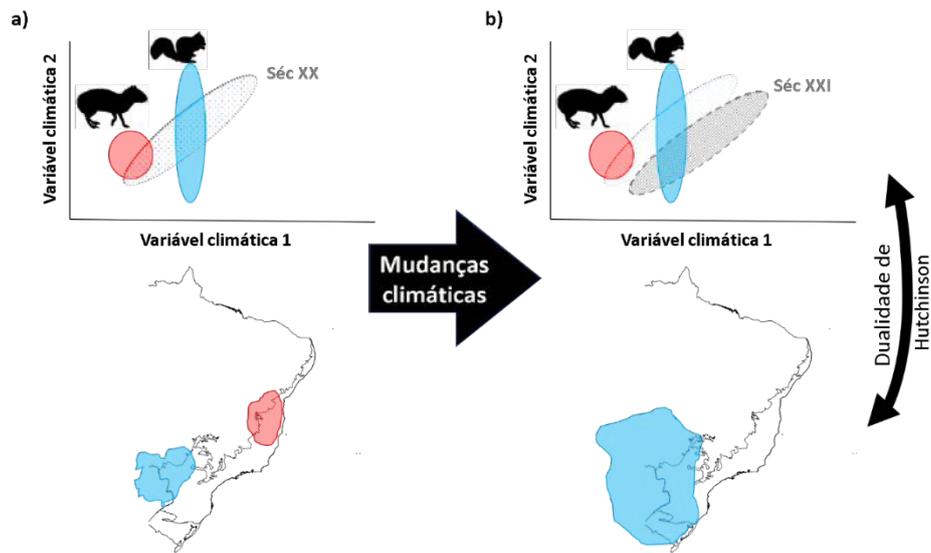


Figura 2 Alteração da distribuição geográfica como resposta às mudanças climáticas. As espécies respondem individualmente às mudanças climáticas, pois as condições que permitem suas existências são espécie-específicas. Nesta figura, as elipses coloridas representam o conjunto de condições ambientais que possibilita a existência das espécies – seu nicho Grinnelliano fundamental, num gráfico de duas variáveis climáticas. A elipse azul mostra, então, o nicho climático do esquilo e a elipse vermelha, o nicho da cutia. As condições ambientais do século XX permitem a existência de ambas as espécies, como pode ser percebido pela distribuição das mesmas no território brasileiro. Devido às mudanças climáticas, o clima do século XXI não incluirá mais as condições presentes no nicho da cutia, que será extinta.

O aquecimento global levará a migrações de fauna em direção às montanhas, que funcionarão como refúgios climáticos, por possuírem condições mais amenas (Keppel et al., 2012; Gavin et al., 2014). Assim, muitas espécies deverão “subir o morro”, ou ainda migrar para latitudes mais altas, nas porções mais frias de suas distribuições. Nas regiões de maior aquecimento, a distribuição das espécies deve se contrair, devido a perdas por

extinção local ou migração das populações remanescentes (Parmesan & Yohe, 2003; Forero-Medina et al., 2011; Gavin et al., 2014). Essa combinação de colonização de ambientes outrora inóspitos e extinção ou migração de locais previamente adequados é o que causará as mudanças na distribuição geográfica das espécies.

O efeito do clima na distribuição das espécies

Os efeitos das mudanças climáticas na distribuição das espécies incluem tanto a variação na quantidade de área climaticamente adequada, quanto o deslocamento dessa área ou ainda a exposição a climas não-análogos. O aumento ou redução da área que contém as condições ambientais adequadas à sobrevivência de uma espécie é a métrica mais utilizada para se verificar como as mudanças climáticas podem vir a afetar sua distribuição (Chen et al., 2011). Extinções locais nas áreas que não possuem mais as condições adequadas para a sobrevivência da espécie podem levar a contrações de distribuição geográfica (Bellard *et al.*, 2012; Cahill *et al.*, 2012). Reduções de distribuição já foram, inclusive, observadas para espécies com alta mobilidade (Forero-Medina *et al.*, 2011) e após eventos climáticos extremos (Smale & Wernberg, 2013).

Essa área climática que permite a sobrevivência da espécie – o elemento “A” no Diagrama de BAM – pode não ter variação em termos de área, mas ser deslocada no espaço geográfico por distâncias variadas, que podem ou não ser alcançadas por dispersão (Carroll et al., 2015). Assim, ainda que a distribuição potencial de uma espécie, com base em seus requerimentos ambientais, não sofra alterações significativas, as mudanças climáticas podem deslocar a área que a espécie pode ocupar para regiões inacessíveis à espécie (Carroll et al., 2017). Portanto, à medida em que o clima muda, o ambiente

favorável a uma espécie pode se mover de um lugar para outro e algumas populações devem ser capazes de realizar tais migrações (Davis & Shaw, 2001). No entanto, barreiras geográficas, como rios e cadeias montanhosas, ou mesmo matrizes de paisagens antrópicas inóspitas ao deslocamento das espécies, podem impedir as movimentações de fauna (Hayes & Sewlal, 2004; Cisneros et al., 2015). Além disso, essas migrações precisam ocorrer acima de uma velocidade mínima, que é a velocidade de mudança do clima (Carroll et al., 2015). Se o clima muda mais rápido do que as espécies conseguem alcançar, devido a limitações de dispersão, a espécie pode não vir a ocupar toda sua distribuição potencial (Hamann et al., 2015).

A ocupação da distribuição potencial de uma espécie no futuro, dadas as mudanças climáticas previstas, vai depender, portanto, de como sua área ambientalmente adequada será afetada e se a dispersão permitirá a colonização dos novos ambientes (Schloss et al., 2012; Gouveia et al., 2016). Tais migrações dependerão, *a priori*, da existência de rotas migratórias permeáveis ao deslocamento das populações. Sabemos, porém, que a perda e fragmentação de habitats criam mosaicos na paisagem, gerando bolsões intransponíveis a diversas espécies, o que acaba confinando muitas populações aos habitats remanescentes (Fahrig, 2013). Se o clima presente nessas regiões se alterar de forma significativa, as populações presentes nestes fragmentos ficarão confinadas às manchas de habitat com condições climáticas desfavoráveis (Schloss et al., 2012; Gouveia et al., 2016). Como consequência, as espécies terão que conviver com condições climáticas diferentes das quais estão acostumadas ou adaptadas, que podem exceder a amplitude, os extremos e os valores de sazonalidade atuais – climas não-análogos (Ribeiro *et al.*, 2016). A exposição a climas não-análogos provavelmente será a regra para

a maioria da biodiversidade global, uma vem que condições climáticas inéditas são previstas para um terço do território do planeta, além do desaparecimento de muitas condições locais (Williams et al., 2007).

Objetivos gerais desta tese

Esta tese teve como objetivo geral projetar os efeitos do clima na distribuição de espécies de vertebrados, usando para isso modelos de nicho ecológico. No primeiro capítulo, discutimos o uso do conceito de nicho em diferentes sub-áreas da Ecologia. Intitulado “*Key components of the niche concept: a historical panorama and theoretical overview*”, o trabalho se inicia com uma revisão histórico-bibliográfica sobre as origens e o desenvolvimento do conceito de nicho. Então, através de uma revisão bibliográfica sobre o uso do conceito de nicho e suas variações de retórica científica, discutimos como áreas distintas referem-se a elementos particulares dos conceitos. Ao invés de sugerir mais um termo e acrescentar outro conceito a uma lista de conceitos, que já é grande por si só, nós particionamos as ideias clássicas em componentes principais e sugerimos que os autores atuais definam explicitamente em seus trabalhos a quais componentes se referem.

No segundo capítulo, intitulado “*Model uncertainties do not affect observed patterns of species richness in the Amazon*” e publicado na revista *PLoS ONE*, analisamos os padrões de resposta de vertebrados endêmicos à Amazônia a mudanças climáticas, ao incluirmos a maioria das fontes de variação conhecidas. Encontramos que a fauna Amazônica é potencialmente ameaçada pelas mudanças climáticas, em especial os primatas. Se as espécies não forem capazes de conviver *in situ* com as novas condições climáticas, seja através de aclimação ou de comportamentos de termoregulação, e não

forem capazes de migrar em busca de condições mais propícias a suas sobrevivências, efeitos deletérios no tamanho populacional e na capacidade reprodutiva podem gerar altas perdas de biodiversidade local. Movimentos de fauna também são esperados em direção às montanhas dos Andes, que provavelmente funcionarão como refúgios climáticos. Além disso, os padrões encontrados não são afetados pelas fontes de incerteza e algumas sugestões metodológicas são discutidas.

O terceiro capítulo, intitulado “*Projected vulnerability of Amazonian primate species to climate change*” e em revisão na revista *Diversity and Distribution*, enfoca os primatas endêmicos à Bacia Amazônica como objeto de estudo. Neste capítulo, nós incluímos diferentes linhas de evidência geralmente tomadas isoladamente em estudos dos potenciais efeitos das mudanças climáticas sobre a biodiversidade. Comparamos uma resposta da biodiversidade (alterações na distribuição geográfica) a mudanças no clima regional, usando para isso as métricas de variação na área de distribuição potencial, velocidade biótica e exposição a climas não análogos. Com isso, buscamos prever os impactos das mudanças climáticas na distribuição geográfica de primatas endêmicos à Bacia Amazônica. Encontramos que os primatas Amazônicos serão expostos a condições climáticas não-análogas às atuais, em grande parte de seus territórios. Mesmo quando a distribuição potencial, com base na adequabilidade climática, parece aumentar em resposta ao clima, as espécies provavelmente não conseguirão migrar na velocidade necessária para manterem-se dentro de seus nichos climáticos.

No quarto capítulo, intitulado “*Niche conservatism and the invasive potential of the wild boar*” e publicado na revista *Journal of Animal Ecology*, analisamos o potencial invasivo do javali *Sus scrofa*, considerada uma das piores espécies invasoras do mundo,

nas regiões onde a espécie é sabidamente invasora. Comparando os requerimentos ambientais de populações nativas e exóticas, as mudanças observadas no nicho realizado foram particionadas em diferentes componentes, que representam expectativas de comportamento do nicho (expansão, estabilidade e não-preenchimento). Apesar de a ampla distribuição nativa do javali já sugerir uma pré-adaptação a diferentes climas, sua invasão em diferentes regiões biogeográficas não exhibe evidência de evolução de nicho. Desta forma, o potencial invasivo do javali provavelmente reside em outros aspectos biológicos da espécie, como reprodução, dieta, morfologia e termoregulação comportamental.

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Capítulo 1

Sales LP, Hayward MW & Loyola RD (2018). **Key components of the niche concept: a historical panorama and theoretical overview.**

1 **Key components of the niche concept: a historical panorama**
2 **and theoretical overview**

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4

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1 **Abstract**

2 Ecologists have long had a “love-hate” relationship with the niche concept. Sometimes
3 referred to as a term best left undefined, the niche concept nonetheless spans ecology.
4 Deeply rooted in Darwinian ideas regarding struggle for survival, “niche” has been a core,
5 though slippery, idea in ecology since the origins of the field. What ecologists have meant
6 by niche has changed semantically over time. In this paper, we review the history of the
7 term, focusing on its uses and disagreements in ecology. Because classic niche concepts
8 are not exclusive and indeed share some similarities, we disentangle them into key
9 theoretical components to create a heuristic classification scheme for niche concepts. Our
10 heuristic scheme provides a way to analyze coherence on rhetoric of ecological literature,
11 by classifying *how* ecologists use niche concepts in their speech, aiming at clarifying
12 communication on *what* is being studied. To demonstrate the usefulness of our
13 classification, we also surveyed a sample of three currently active research areas of
14 ecology: ecological niche modeling, coexistence between species and meta-communities.
15 We found that sub-areas in ecology seem to be segregated when it comes to rhetoric about
16 niches. Ecologists have long tried to achieve a truly unifying biodiversity theory, or at
17 least a universal definition of niche. We move in the opposite direction and suggest that
18 niche concept should be dismembered into its key components, highlighting which
19 elements of the concept are being addressed and analyzed. Explicitly stating to which
20 niche concept a study is referring may enhance communication among researchers from
21 different backgrounds and resolve a century-old dilemma.

22 **Keywords:** analysis of rhetoric; scientific jargon; ecological epistemology

1 **Introduction**

2 Languages are relatively free entities. Words and their meanings come and go through
3 time, by use and disuse, in both colloquial and scientific terminology. Although
4 mandatory attempts have been made to homogenize concepts and terms in ecology (e.g.
5 invasive species, Davis and Thompson 2001, ecosystem, O'Neill 2001, population and
6 community, Magnusson 2013), no language ever truly changes by decree. A word's
7 meaning not only relies on semantics, but also depends on context, and humans are
8 remarkably good at understanding meaning from context (Hodges 2008). Natural
9 semantic transitions are expected in time, and overly constrained definitions early in the
10 history of a scientific word may hamper development of new theories (Hodges 2008,
11 Herrando-Pérez et al. 2014). One would nonetheless expect that a fundamental concept
12 with a hundred year history would have at least a coherent basis across modern theories,
13 as long-lasting uncertainties and lack of consensus can hinder progress in any scientific
14 area (Herrando-Pérez et al. 2014).

15 The niche concept has been a mainstream ecological concept since its origins
16 (Grinnell 1904), although ways of defining, measuring and predicting niches cause
17 persistent controversy among ecologists (McInerny and Etienne 2012a). From the early
18 Linnaean focus on a species' place in the divine balance of nature, the niche concept
19 moved towards the environmental requirements for survival across a species' geographic
20 distribution (Grinnell 1904, 1917, 1924) and the role of interacting species in a
21 community (Elton 1927). Then, it went from this functional concept to a geometric
22 definition of an environmental hypervolume or ecological space occupied by a species
23 (Hutchinson 1957). Finally, niche became a more operational concept based on the
24 distribution of resource utilization by focal species (MacArthur and Levins 1967). The

1 21th century has experienced two major challenges: a supposedly unified and mechanistic
2 theory of niche was proposed (Chase and Leibold 2003), while another unified but neutral
3 theory emerged, claiming the niche concept was not *a priori* required to understand
4 community assembly (Hubbell 2001). In the meantime, the explicit delimitation of factors
5 shaping species geographic distributions and what is estimated by “ecological niche
6 models” (Soberón and Peterson 2005, Soberón 2007), enabled additional clarity in the
7 emerging “distributional ecology” field.

8 Classifying concepts of niche thus requires a thorough understanding of which
9 elements are being measured, the spatial scale of the study, and the particular questions
10 being answered. To create a more objective classification system of niche concepts, we
11 disentangle them into main components, based on relative weights of different features
12 from the classic definitions. Rather than adding a new piece to the puzzle of niche
13 definitions, we hope that this paper will allow researchers to situate themselves within a
14 holistic overview, thus avoiding miscommunication and confusion.

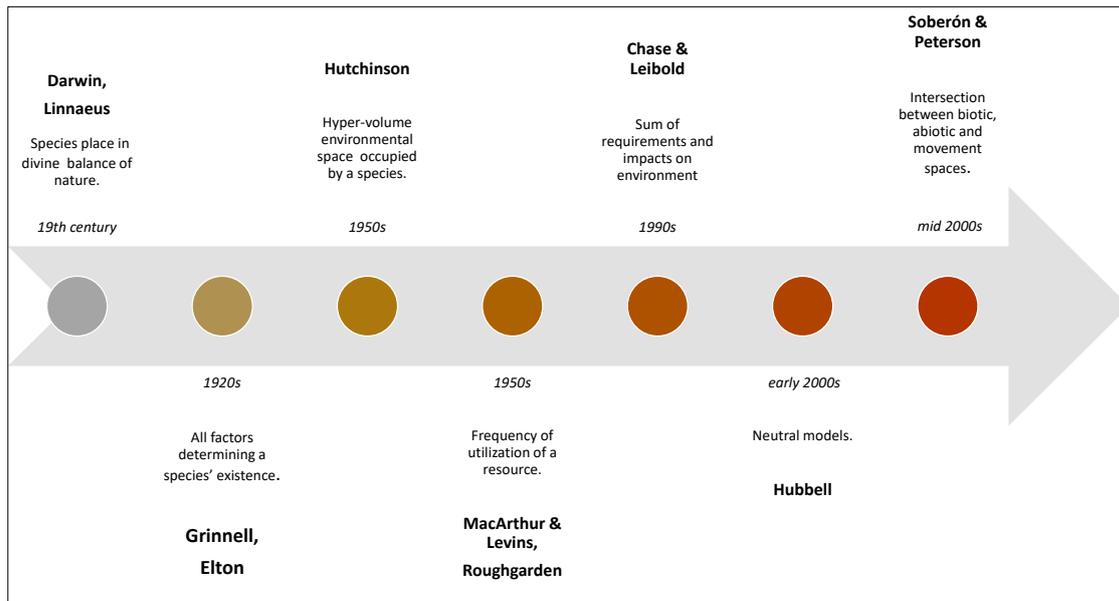
15

16 **The history of the niche concept**

17 **Grinnell.** Although the term “niche” was first used in Johnson’s (1910) paper on the color
18 pattern of lady-beetles, Joseph Grinnell (1924; 1904; 1917) was the first to offer a more
19 comprehensive consideration of the niche concept and to insert it into a research program
20 (Griesemer 1992) (Fig. 1). Grinnell investigated how variations in environmental
21 conditions were linked to species’ distributions, with special interest in vertebrate
22 evolution, for he believed that “the existence [...] of species is vitally bound up with
23 environments” (Grinnell 1924 p. 226). The term niche was defined as all factors
24 determining a species’ existence in a given location, both abiotic (e.g. temperature,

1 humidity, rainfall) and biotic (e.g. food, nest sites, cover), including competitor species
 2 (Pocheville 2015). However, he clearly emphasized the abiotic dimensions, and
 3 considered that the biotic factors would ultimately be controlled by their proportions and
 4 by geographic forces (Grinnell 1924).

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6

7 **Fig. 1** Timeline of main niche concepts and their authors throughout history. The definition of niche has gone
 8 through major changes. From a nineteenth century Darwinian view of a species' place in the economy of nature, to
 9 environmental requirements (Grinnell 1924) and species' roles in trophic webs (Elton 1927), niche concepts moved to
 10 more precise mathematical delimitations of factors determining species' indefinite existence (Hutchinson 1957) and
 11 resource utilization distributions (MacArthur and Levins 1967). After the end of the competition-centered era, niches
 12 were confronted as relationships with the environment (Chase and Leibold 2003), but put in check by neutral models
 13 (Hubbell 2001). Recent heuristic operationalization (Soberón and Peterson 2005) enabled a resurged era on niche
 14 studies.

15 The notion that “nature abhors a vacuum” implied that, if a new ecological niche
 16 arose or if a niche was emptied, a new occupant would fill it (Grinnell 1924 p. 227). The
 17 axiom that “no two species regularly established in a single fauna” would have the same
 18 niche relationships was unquestionable at that time (Grinnell 1917 p. 433). If two species
 19 had identical environmental requirements, one would force out the other, by excluding

1 the least fit (Grinnell 1904). Similar environments would also yield similar niches that
2 could be occupied in one region, but vacant in another, owing to geographic barriers and
3 dispersal limitation. A logical result was that types of animals with similar ecological
4 niches or “ecological equivalents” would evolve to fill these similar niches in widely
5 separated regions. Those “similar ecologic types of animals which are developed in
6 widely separated regions and which are derived from unrelated stocks” (Grinnell 1924 p.
7 227) illustrate an evolutionary pattern known today as convergent evolution.

8

9 ***Elton.*** Another early researcher who studied ecologically equivalent species was Charles
10 Elton, although in a different context (Box 1). Elton’s interest was in what animals *are*
11 *doing* (Griesemer 1992), especially in terms of food relations. Individual species would
12 be interconnected in animal communities, mainly through trophic webs. This focus in
13 trophic relationships led Elton to characterize niches in terms of predators and prey, as
14 the “place in the biotic environment, its relations to food and enemies” (Elton 1927 p.
15 250). As the animal’s place in a community, a species niche would be defined in large
16 part by its body size and food habits. These ideas were developed to account for food
17 chains and cycles in his new concept of “pyramid of numbers”, which related numbers of
18 organisms at a given trophic position to their body sizes. Organisms at the base of the
19 food chains were expected to be more abundant than organisms higher in the chain
20 (Pocheville 2015).

21 While also considering the niche as a property of the environment, Elton
22 explained similarities among widely separated communities using ecological equivalents,
23 in the same context as Grinnell. Species with similar food relations would occupy similar
24 niches (e.g. the Arctic fox feeding on eggs of guillemots; and the spotted hyena, on eggs

1 of ostriches). The same niche could therefore be filled by entirely different species in
2 separated regions of the world. Those “very different animal communities may resemble
3 each other in the essentials of organization” (Elton 1927 p. 250). Elton indeed argued
4 that the niche concept would end up being equivalent to small sub-divisions of old
5 concepts of trophic guilds, such as carnivores, herbivores, and insectivores.

6

7 **Box 1** *Grinnell vs. Elton*

8 Whittaker (1973) first pointed out that Grinnell and Elton’s niche concepts could be
9 broadly classified into “habitat niche” vs. “functional niche” ideas, respectively. Some
10 similarities are indeed evident. The rationale of the two concepts is based on the idea of
11 “ecological equivalents”, i.e. species that occupy similar niches in separate regions of the
12 world. The niche is therefore defined as a property of the environment, independent of
13 the presence or identity of the occupant (Griesemer 1992). Some have speculated that
14 their independent formulation is even unlikely (Schoener 1989 pp. 86–87). However, a
15 thorough examination of the original papers reveals that each has a radically different
16 focus. While Grinnell focused on explaining species’ distributions and speciation with
17 respect to environmental factors, Elton was more interested in animal community
18 structure, especially food webs. Niche-related variables in a Grinnellian view are non-
19 interactive, particularly environmental conditions at coarse spatial scales (Peterson et al.
20 2011), aimed at understanding ecological, geographic, and evolutionary phenomena. The
21 Eltonian niche is described, on the other hand, by interactive predictors, focusing on biotic
22 resource-consumer dynamics, measured at local spatial scale (Soberón 2007).
23 Throughout history, the Grinnellian and Eltonian niche concepts were treated as bionomic
24 and scenopoetic niche predictors (Hutchinson 1957), then as requirements and impacts

1 on environment (Chase and Leibold 2003), and still more recently as non-interactive and
2 interactive niche dimensions (Peterson 2014).

3

4 **Hutchinson.** Competitive exclusion (Box 2) caused by niche overlap was the focus of
5 studies by G. Evelyn Hutchinson (1944, 1957, 1978). This work came with an additional
6 twist: the niche was now considered a property of the species, not of the environment.
7 That shift started a revolution in ecology (Schoener 1989). The niche was then defined as
8 the combined effect of all environmental factors affecting an organism (or population).
9 An n-dimensional hypervolume was delimited, in which an area would be defined, “each
10 point of which corresponds to a possible environmental state permitting the species to
11 exist indefinitely.” (Hutchinson 1957 p. 416). Being a property of the species,
12 Hutchinson’s concept does not allow for the existence of empty niches (Griesemer 1992),
13 differently from Grinnellian and Eltonian counterparts.

14 A distinction between “fundamental” and “realized” niches was the cornerstone
15 of Hutchinson’s ideas. That division also highlighted competition as a major process in
16 defining a species’ niche (Griesemer 1992, Pocheville 2015). Hutchinson (1957) stated
17 that, under constant conditions, two species sharing, and limited by, the same quantities
18 of a resource could not coexist indefinitely, following Gause’s (1934) rationale (Box 2).
19 Overlap regions in niche space would therefore restrict occupancy of competitor species,
20 reducing the fundamental niche to the realized niche, i.e. points of the hypervolume in
21 which a species outlives its competitors (Hutchinson 1957).

22

23 **Box 2** *The competitive exclusion principle*

1 Early niche ideas, especially Elton's concepts on the importance of food web relations
2 for defining a species' niche, led to an age of experiments. Gause (1934), in an extremely
3 influential paper, conducted a series of experiments to test the population predictions of
4 Lotka (1925) and Volterra (1926) – based on the so-called “Lotka-Volterra” differential
5 equations. Gause (1934) concluded that all populations should be subjected to
6 quantitative and perfectly defined laws. Competition intensity should be related to
7 competitor's requirement similarities, or coefficients of “struggle for existence” (depicted
8 as α). Those competition coefficients were related to the degree of influence of one
9 species on growth opportunities to another. Species occupying the same niche would have
10 $\alpha = 1$, which prevents equilibrium in the Lotka-Volterra equations. Therefore, two species
11 could only exist indefinitely if they occupied different niches. After Gause's work, the
12 concept of niche was dominated by population studies, to which competitive exclusion
13 was attributed (Whitaker et al. 1973, Griesemer 1992, Pocheville 2015), often
14 uncritically (Gould and Lewontin 1979).

15
16 **MacArthur and Levins.** The 1960's have been considered as the “golden age” for the
17 niche theory (Pocheville 2015). Workers in this period gathered previous concepts of
18 place and role of species in a community into a competition-centered niche concept. That
19 concept established the logical conditions under which competitive exclusion could be
20 inferred (Griesemer 1992). Ideas of resource utilization distribution then replaced
21 Hutchinson's hypervolume in ecological theory. As an example, Robert MacArthur and
22 Richard Levins (1967) defined niche in terms of a resource probability function, or the
23 frequency of utilization of a resource. For a given resource, the utilization probability by
24 an individual of species i at a particular time unit was defined by its resource probability
25 function. The area under that curve was the “total resource utilization” for species i

1 (MacArthur and Levins 1967). Axes could be as diverse as food, space, and time
2 (Pocheville 2015).

3 That competition-centered niche theory was developed in terms of competition
4 coefficients along environmental gradients (Griesemer 1992). Assuming that niche
5 utilization overlap could be used to calculate competition coefficients, Lotka-Volterra
6 equations were used to estimate the limiting similarity between competitor species
7 (MacArthur and Levins 1967, Schoener 1974). By doing so, the total number of species
8 in a community could also be assessed through integrating the environmental range
9 present and species niche breadth. Furthermore, the competition-centered niche concept
10 encouraged studies on limiting similarity and character displacement, which dominated
11 ecological literature at the time (e.g. MacArthur 1957, MacArthur and Levins 1964, 1967,
12 Abrams 1975, Roughgarden 1976).

13

14 ***Chase and Leibold.*** After the 1980's reflection (see Box 3), niche theory was largely
15 ignored for some time. In an attempt to develop a unified ecological theory, Jonathan
16 Chase and Mathew Leibold (2003) renewed interest in the niche. Their niche concept was
17 based on Tilman (1982)'s mechanistic, resource-based explanation about the structure
18 and functioning of ecological communities. By coupling conventional niche theory with
19 individual-based mechanistic models, they attempted to modernize the niche concept
20 (Leibold 1995). By distinguishing between environmental *requirements* and *impacts* on
21 environment, they highlighted a dichotomy within the ecology of an organism. As such,
22 responses of organisms to the environment (influence of a given ecological factor) and
23 their effects upon it (the organism impacts on the ecological factor) were contrasted
24 (Leibold 1995, Pocheville 2015).

1 Chase & Leibold (2003) also claimed to have unified the historical niche concepts
2 of Grinnell (1924), Elton (1927), Hutchinson (1957), and MacArthur & Levins (1967).
3 They perceived two major views of the niche concept: 1) a biogeographic approach that
4 addresses how environmental conditions restrict species' distribution; and 2) an
5 ecosystem ecology view that addresses how species functional traits affect ecosystems.
6 Grinnell and Hutchinson's concepts would be more related to the biogeographical
7 approach by focusing on environmental requirements; while the ideas of Elton and
8 MacArthur & Levins corresponded to the ecosystem ecology view, focusing on impacts
9 on the environment. Therefore, they unlinked niche theory from a focus on competition
10 and local interactions (Pocheville 2015).

11

12 **Box 3** *The 1980s "cold shower"*

13 Some key elements were, however, missing in the theory of niche. First of all, few niche-
14 based studies had any ability to distinguish among competing hypothesis (Simberloff
15 1978, Strong 1980). Statistical tests were usually omitted or weak. When tests were
16 presented, they did not effectively test a null hypothesis (Simberloff 1978). Back then,
17 competition in ecology had attributes of a paradigm – an idea so dominant that other
18 approaches seemed negligible (Strong 1980), to the point that cause was attributed to
19 pattern uncritically (Gould and Lewontin 1979). Although doubters have always existed,
20 belief in the relevance of interspecific competition was increasingly questioned (Schoener
21 1983). The utility of niche theory was also questioned (Hurlbert 1981), given issues of
22 circularity in the competitive exclusion principle. If two species coexist, then their niches
23 must not overlap – as result of competitive exclusion. Conversely, species do not coexist
24 because their niches overlap. That argument was considered "competitionist story-

1 telling”, for assuming that competition is ubiquitous and can explain all community
2 relations (Griesemer 1992).

3
4 Finally, the relationship between niche overlap and competition coefficients, a crucial
5 assumption of competition theory, was also questioned (Simberloff 1978, Schoener
6 1983). Competition coefficients neglected high-order interactions and were difficult or
7 impossible to measure in the field (Simberloff 1978). In addition, new evidence indicated
8 that high ecological overlap was not linked to competition, rather was the result of
9 interspecific tolerance (Strong 1980). Some authors began explicitly not to mention niche
10 as an explanation for species’ distribution (e.g. Hubbell 1979). “Niche” was then labelled
11 as “a term perhaps best left undefined” (Bell 1982 p. 510).

12
13 **Hubbell.** Although exciting in its unification of disparate ideas, Chase & Leibold’s
14 mechanistic niche still worked by the same niche-based rules. Then, Stephen Hubbell
15 (2001) proposed a ground-breaking novelty in ecology. He argued that niche concepts
16 were not *a priori* needed for understanding species distributions and community
17 assemblage patterns. Ecological communities were assumed to be entirely assembled by
18 ecological drift, dispersal and speciation. Classical neutral theory posits a
19 metacommunity (i.e. a set of communities linked by dispersal) and a local community, in
20 which rates of immigration and local extinction are in dynamic equilibrium. In a neutral
21 metacommunity, all individuals are subject to similar death, birth, dispersal and
22 speciation rates, regardless of their species identity (Rosindell et al. 2011). As neutrality
23 comes from organismal equivalence, it is defined for *individuals*, not species. Differences
24 among species emerge stochastically in neutral models due to variation in abundance,

1 which affects chances of speciation and immigration events. More abundant species will
2 have higher chances of speciation and of colonizing empty spots (Hubbell 2001,
3 Rosindell et al. 2011).

4 Hubble (2001) discerned two main ecological perspectives: the niche-assembly
5 and the dispersal-assembly perspective. The niche-based point of view assumes that
6 communities are groups of interacting species, with identities determined by competition
7 among distinct evolutionary lineages. Those niche-assembled communities supposedly
8 coexist in adaptive equilibrium (or near-equilibrium), maintained by natural selection.
9 Dispersal-assembled entities, on the other hand, are open, non-equilibrium communities,
10 gathered by chance, history and random dispersal (Hubbell 2001). Occurrence dynamics
11 are mediated by stochastic events of dispersal and extinctions in space and time (Rosindell
12 et al. 2011). Neutral models showed intriguing predictive power of neutral models against
13 some empirical datasets (Hubbell 1999, Bell 2000, Condit et al. 2002), which challenged
14 universally accepted neo-Darwinian, competition-based assembly rules. Therefore,
15 besides providing null models against which adaptation and natural selection could be
16 tested (Rosindell et al. 2011), neutral models' apparent success in explaining biodiversity
17 patterns supposedly put the niche concept in check again (Pocheville 2015). However,
18 the predictive success was quickly challenged by the results of many additional studies
19 (e.g. Clark and McLachlan 2003, Wootton 2005, McGill et al. 2006).

20

21 ***Soberón & Peterson.*** Parallel to the discussion on niche vs neutral rules on structuring
22 communities, a renewed field began to emerge and dominate current literature: the
23 “distributional ecology” (Box 4). Species' distributions over geography are depicted as
24 gridded projections, in which each spatial unit (grid cells) has a value of n environmental

1 features at a given time (Colwell and Rangel 2009). If the niche space is defined based
2 on those exact n environmental features, then reciprocal linkages between the species'
3 ecological niche (environmental space) and its distribution (geographic space) are
4 possible, the “Hutchinson duality” (Colwell and Rangel 2009). The fundamental niche
5 reflects physiological constraints and sets an overall potential distribution. Because not
6 all the fundamental niche is represented on relevant landscapes, the “existing” niche was
7 recognized to emphasize that the full fundamental niche may not be always observable.
8 Important sectors of the fundamental niche may remain invisible owing to the masking
9 effects of limited dispersal, incomplete representation of environments, and negative
10 interactions with other species. The realized niche therefore expresses a further reduction
11 of the fundamental niche, as the outcome of the combined effect of species interactions
12 and dispersal limitation (Colwell and Rangel 2009, Guisan et al. 2014).

13 By explicitly disentangling fundamental niche space (*sensu* Hutchinson 1957)
14 into biotic, abiotic and dispersal components, manifested geographically, in the so-called
15 “BAM diagram” (Soberón 2007), Soberón & Peterson (2005) presented a heuristic model
16 of what quantities are indeed estimated in “species distribution models” and/or
17 “ecological niche models” (Peterson et al. 2011). These concepts focus primarily at
18 geographical extents and coarse spatial resolutions, so focus is on non-interactive, coarse-
19 grained, “Grinnellian” niche dimensions (Peterson et al. 2011). Indeed, Peterson *et al.*
20 (2011) posited the “Eltonian Noise Hypothesis”, the idea that at geographic extents and
21 coarse spatial resolutions, biotic interactions will constrain species’ distributions only
22 infrequently. These viewpoints contrast sharply with the niche-neutral, interaction-rich
23 world imagined by others (e.g. Hubbell 2001). In this distributional ecology framework,
24 niche is still a property of species or populations as a direct coarse-grained translation of
25 species’ physiology, with biotic and abiotic components having distinct scales of time

1 and space. Correspondence between niche space and geography (Colwell and Rangel
2 2009, Peterson et al. 2011) allows modelling the “realized distribution” (Soberón 2007),
3 which has profound implications for conservation, invasive species biology, agronomy,
4 and so forth. This general paradigm is presently accounting for hundreds of published
5 studies each year.

6

7 **Box 4 The relationship between niche and distribution**

8 Parallel to the niche *vs* neutral debate, another research agenda, on the relationship
9 between niche and distribution has flourished in the early 21st century. An exponential
10 increase was observed in the last couple of decades in the number of papers employing
11 “ecological niche models” and “species distribution models” (Lobo et al. 2010). The ease
12 of obtaining predictor variables for Grinnellian niches - those regarding distribution on
13 broad geographic extents (e.g. average temperature, humidity, solar radiation, slope) -
14 probably explain that literature increase (Soberón 2007). New developments in
15 geographic information system have been accompanied by digitization of museum and
16 herbarium (Beaman and Cellinese 2012). Modeling species distribution and “ecological
17 niches” is now nearly trivial, given the number of user-friendly tools available for such
18 task, such as the stand-alone software Maxent (Phillips and Dudík 2008) and ModEco
19 (Guo and Liu 2010), and the R packages *dismo* (Hijmans et al. 2013), *BIOMOD* (Thuiller
20 et al. 2009), and *sdm* (Naimi and Araújo 2016). However, placing these models in
21 appropriate ecological and biogeographic contexts is crucial, yet often neglected - see
22 methodological updates and insights presented by Barve *et al.* (2011), Saupe *et al.* (2012)
23 and Owens *et al.* (2013).

24

1 Those approaches correlate species occurrences to environmental features, and are
2 considered *correlative* models (Peterson et al. 2015). Another approach to estimating a
3 species' niche is based calculations of physiological response surfaces in relation to
4 environmental predictors, known as *mechanistic* models (Peterson et al. 2015). Eltonian
5 niche dimensions, which rely on specific and detailed empirical and experimental data on
6 biological interactions and are therefore dynamic and interactive, more difficult to obtain.
7 Particularly at geographical scales, measuring Eltonian niche elements can prove to be an
8 unsuccessful task, which probably explains the lack of such studies (Soberón 2007).

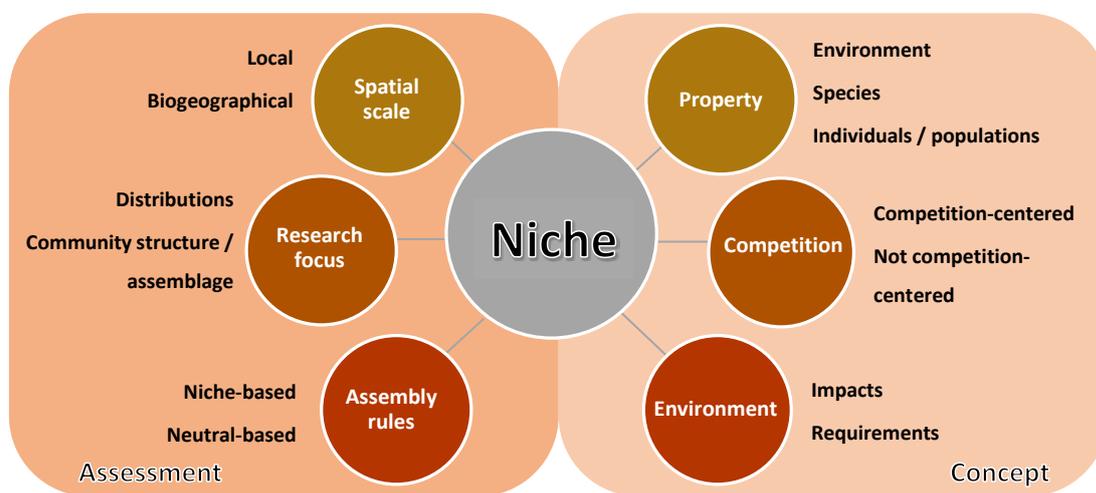
11 **Key components of the niche concept**

12 Throughout history, different fundamental aspects of niche concepts received different
13 levels of emphasis and attention. Disentangling the classical niche concepts into distinct
14 features - key components - thus requires an overview of the classical authors' research
15 agendas. Here, we suggest a new categorization, based on what we believe to be the
16 theoretical roots of each of the classical niche concepts that we have just reviewed. We
17 provide a heuristic scheme in which we classify *how* ecologists use niche concepts in their
18 speech, aiming at clarifying communication about *what* is being studied (Table 1).
19 Deconstructing the niche into its main components has already been suggested as a way
20 to underpin straightforward ecological thinking (McInerney and Etienne 2012b). However,
21 the classification presented here is the first attempt to include niche components other
22 than effect and response.

23 Our classification scheme is based on a few main questions within the text of the
24 paper being analyzed (Fig. 2). Three questions relate to the niche elements that have

1 historically been subjected to debate: 1) To whom the niche belongs (to the environment,
 2 to species, or to populations/individuals)? 2) Is the niche competition-centered? 3) Is the
 3 relationship between niche and environment based on impacts or requirements? The
 4 remaining three questions relate to how the niche is assessed and measured: 1) What is
 5 the spatial scale (local or biogeographical)? 2) What is the author's research goals (to
 6 study geographic distributions or community structure/assemblage)? 3) What rules drive
 7 community assembly (niche-based or neutral rules)?

8



9

10 **Fig. 2** Key components of the niche. Throughout history, niche features were differently weighted and measured.
 11 Niche has been measures in both local and biogeographical spatial scales, aimed at understanding distributions or
 12 community structure and/or assemblage, for which communities were though as governed by niche-based or neutral-
 13 based rules. The niche itself has been considered a property of the environment, the species, the individuals and/or
 14 populations. The niche has also been attributed exclusively to competition, or to different forms of relationship with
 15 the environment (impacts and/or requirements).

16 To demonstrate the usefulness of our classification scheme in clarifying *how*
 17 modern ecologists investigate the niche to understand *what* is meant by niche, we did a
 18 survey on current literature. We surveyed 75 papers in three areas of ecology: ecological
 19 niche modeling, coexistence between species and meta-communities. We selected the

1 most influential papers on each year, from 2011 to 2015. Papers were classified by their
2 number of citations, and only the top 10 most cited papers from each year were included
3 in this review. We assumed that number of citations reflects the degree to which the
4 scientific community perceives appropriate use of terminology in these papers.

5 This search was performed on Web of Science (www.webofknowledge.com)
6 using the keywords: 1) “distribution” AND “niche”; 2) “coexistence” AND “niche”; 3)
7 “metacommunit*” OR “meta-communit*” AND “niche*”. Such a search is superficial so
8 it was not meant to be exhaustive. Rather, the dataset was used to demonstrate how
9 disentangling the niche concept into its main components can enhance communication
10 among researchers from different theoretical backgrounds in the current ecological
11 literature. We include this analysis as a first illustration of the rhetorical trends regarding
12 niche concepts in current ecological studies; a complete synthesis is not within the scope
13 of this paper.

14 By unravelling niche concepts into those key components, we created a more
15 objective classification of niche concepts used in current papers. We note that classifying
16 contemporary papers into more than one niche concept was also possible. Our
17 classification is therefore non-comprehensive, but inclusive. It is non-comprehensive
18 because we did not survey current literature exhaustively and focused only on the most
19 cited papers; however, it is inclusive because more than one possibility of niche concept
20 may be assigned to a given paper.

21 **Uses and misuses of niche concepts: a literature survey**

22 **Ecological niche models**

1 In our sample of the “ecological niche modeling” literature including “species distribution
2 models” (henceforth ENM), most papers focused on understanding species’
3 environmental requirements at geographical scales (resolution and extent) (Fig. A1). By
4 analyzing species’ geographic distributions, ENM researchers focused on explaining
5 large-scale distributional patterns. Species’ niches in ENM papers were usually assessed
6 in terms of coarse-grained environmental variables, such as climate and topography.
7 Considering “environmental niche” as equivalent to “ecological niche” was recurrent
8 (e.g. Beever et al. 2011, Reygondeau and Beaugrand 2011, Schweiger et al. 2012,
9 Alvarado-Serrano and Knowles 2014). Based on climatic conditions under which species
10 occurred, current or future climate maps were used to assess distributional potential.

11 Ecological niche modelers usually aimed at understanding species’ environmental
12 requirements to estimate potential distributional areas. The ENM approach therefore
13 aligns with Soberón & Peterson (2005)’s distributional ecology, coupled with Grinnellian
14 ideas on niche and biogeography. Such classical ideas explicitly incorporate species
15 interactions in their framework. Grinnell (1924) included biotic factors as a driver of
16 species’ persistence (e.g. food, nest sites, cover), and Soberón & Peterson (2005)
17 accounted for constraining factors on a species’ fundamental niche - the “biotic element”
18 of the BAM diagram (Soberón and Peterson 2005, Peterson et al. 2011). Although present
19 in theory, biotic interactions seem to be included in ENMs only infrequently (none of the
20 analyzed papers did so). Biotic interactions usually take place at local spatial scales, not
21 the focus of most ENM studies, and are difficult to assess in field, which may explain
22 their absence in the reviewed papers. Therefore, ENM studies usually predicted potential
23 distributions, on broad geographic scales, exclusively from the climatic dimensions of
24 species’ existing niches.

25

1 **Co-existence between species**

2 In the co-existence literature, understanding how species interact and partition niche
3 space was the main goal of most papers, with consistent focus on biotic processes and
4 ecosystem functions. Researchers typically addressed community assembly and structure,
5 by analyzing species' impacts on environments at local scales. Stabilizing niche
6 differences and fitness variation and/or competitive exclusion outcomes were generally
7 analyzed as regards species' functional traits. A new term, the "functional niche", was
8 recurrent in co-existence studies (e.g. Blüthgen and Klein 2011). Species co-existence is
9 supposedly driven mainly by niche complementarity, non-overlap of niches in a
10 community (HilleRisLambers et al. 2012). The niche concept used in co-existence studies
11 thus resembles the ideas of MacArthur and Levins' (1967) definition, or the competition-
12 centered niche concept, under the assumption that co-occurring species have more
13 dissimilar niches than expected by chance. Competitive exclusion leads to different
14 resource utilization patterns and ultimately drives character displacement (e.g.
15 Zupping-Dingley et al. 2014, Gerhold et al. 2015). Niche overlap is therefore
16 determined by resource utilization distributions and drives local biodiversity patterns.

17 Most of the co-existence literature focused on impacts of species' "functions" on
18 "roles" in the environment. Some Eltonian elements are evident in some co-existence
19 papers, such as testing whether co-existence is driven by "diet niche" separation (Vanak
20 et al. 2013). Features of the competition-centered niche concept have also been
21 incorporated by ENM and co-existence literatures. Niche overlap measures, such as
22 Schoener's D , were modified to include solely environmental predictors (e.g. Zhou et al.
23 2012, Boulangeat et al. 2012, Shcheglovitova and Anderson 2013, Narwani et al. 2013).
24 Exclusive consideration of non-interactive environmental variables probably reflects the
25 ease of measuring them, especially in field. The Schoener's D index, originally developed

1 to compare diet overlap, although microhabitat could be included (Schoener 1968), was
2 created in the 1960s golden era of the competition-centered niche theory. At that time,
3 resource partitioning was considered essential for understanding niche overlap patterns,
4 but the difficulty of creating resource utilization functions from biotic interactions
5 appears to have caused its replacement by abiotic environment variables.

6

7 **Metacommunity**

8 In our sample of the meta-community literature, disentangling effects of niche *vs.* neutral
9 (or environmental *vs.* spatial) processes was the main objective of most papers.
10 Researchers' objectives were mainly to determine community structure and assembly,
11 coupled with assessing patterns of biodiversity distribution in local scales. Predictors
12 measuring niches were typically local environmental variables, but also included species'
13 life-history traits such as dispersal ability and diet or trophic guild. Hubbell (2001)
14 perceived two major ecological points of view in science: the niche-assembly and the
15 dispersal-assembly perspectives. Confrontation of real-world data with neutral models
16 was meant to be a null hypothesis test of absence of niche-assembly effects (Hubbell
17 2005). Testing whether a community assemblage is niche or dispersal-driven was indeed
18 common in meta-community papers (e.g. Beaudrot and Marshall 2011, Diniz-Filho et al.
19 2012, Siqueira et al. 2012, Alahuhta and Heino 2013). In determining niche *vs.* dispersal-
20 assembly, studies usually aimed at partitioning variation related to environment *vs.* space.
21 Stronger influence of environmental elements would thus suggest a closer relatedness to
22 niche-based assembly rules. However, confronting neutral models with models based on
23 niche rules implies measuring some niche element. Yet one question remains from

1 Grinnell's time: how to measure niches? What are the variables that, at least indirectly,
2 refer to a species' niche?

3 Because of that unsolved challenge, a shift from the “niche *vs.* dispersal-
4 assembly” question towards a more operational “environmental *vs.* spatial” seems to have
5 occurred in the meta-community literature. The difficulties in measuring niche elements
6 probably led researchers to adapt Hubbell's original proposal to a more convenient
7 “bioclimatic” or “environmental niche”, which is more easily measured in the field (e.g.
8 Mokany et al. 2011, Özkan et al. 2013, Myers et al. 2013). The original null hypothesis
9 test of factors driving community assembly is apparently not as feasible as suggested by
10 Hubbell (2001). Also, in our sample of the meta-community literature, most authors
11 considered niche differences at the species-level (as in uses of functional traits), but then
12 analyze their causes (niche-assembly processes) using environmental-level variables
13 (such as precipitation, temperature, soil conditions, etc.) (Lekberg et al. 2011, Patrick and
14 Swan 2011, e.g. Beaudrot and Marshall 2011, Mokany et al. 2011, Alahuhta and Heino
15 2013, Özkan et al. 2013, Myers et al. 2013, Stegen et al. 2013, Székely and Langenheder
16 2014). As such, only environmental factors are considered as niche space, although
17 explanations usually refer to species-level traits. However, interpreting environmental
18 and spatial components as direct expressions of the niche has been criticized recently
19 (Algarte et al. 2014).

20 Hubbell (2001) offered a null hypothesis against which niche-based models could
21 be tested. However, we have reasons to believe that niche theory will be blended into
22 meta-community thinking for a while. Although a comprehensive evaluation of neutral-
23 theory empirical validations was not intended here, we could not help noticing that most
24 papers were based on empirical tests, and found evidence for niche-based assembly rules.
25 It is noteworthy, however, that several of the papers were cast at local scales. Supporters

1 of the dispersal-assembly perspective generally are working at large spatial scales
2 (Hubbell 2001), and the importance of niche-assembly rules may be scale-dependent
3 spatially (Götzenberger et al. 2012). Also, niche elements were measured according to
4 researcher's preferences, so "niches" are not comparable among studies. Nonetheless, we
5 believe that niche theory may not be unimportant at all in current literature: from an
6 Eltonian interpretation of trophic niches, or guild-specific effects on meta-community
7 structure (Cisneros et al. 2015), to environment vs. space tests, the niche concept still
8 appears to be an important element driving community assembly.

9

10 **Discussion**

11 The studies that we analyzed often appealed to radically different concepts when dealing
12 with niches. The ecological niche modeling literature usually measures environmental
13 variables to assess species' niches, and focuses on environmental requirements as drivers
14 of species' distribution, thus aligning chiefly with the Grinnellian and Soberón &
15 Peterson's concepts. The co-existence literature, on the other hand, generally uses
16 functional traits to measure niches, focusing on species' roles on communities, thus
17 conciliating with MacArthur and Levins' competition-centered approach and Chase and
18 Leibold's impacts on environment. However, meta-community studies address niches
19 with both environmental predictors and functional traits, using all means to define species
20 in terms of both requirements and impacts on environment, thus aligning with Chase and
21 Leibold's full definition of niche.

22 Pre-Hutchinsonian ideas of environmental niche, or niche as a feature of the
23 environment, still haunt some current literature. A few authors, perhaps inadvertently,
24 still consider niche a property of the environment. When dealing with invasion, for

1 example, interactions with resident species may inhibit “adaptation of nonresident species
2 to new niches” (Urban et al. 2012). Also, variation in nearby community composition
3 “reduces the ability of immigrants to either survive or out-compete inhabitants adapted to
4 available niches” (Zhou et al. 2012). Species diversity has been considered a result of “the
5 number of available niches” (Jeraldo et al. 2012). If a niche is available in a place, it is
6 thus a property of the environment. As such, similar niches can be occupied by different
7 species at widely separated places in the world, ideas that resemble the Grinnellian and
8 Eltonian ecological equivalents. Current debate on whether available niche space can
9 exist in emptied communities (Colwell and Rangel 2009, Heino 2013) is also a hotspot
10 of debate.

11 From our small sample of the current literature, sub-areas in ecology seemed to
12 be segregated when it comes to rhetoric about niches. That segregation is evident in
13 synthesis and reviews on the topic. For example, in a recent essay on the history of niche
14 theory, Pocheville (2015) mentioned the word “competition” more than 50 times but did
15 not include the latest definitions of niche (e.g. Soberón and Peterson 2005). Pocheville’s
16 review focused on opposing neutral and niche theory, but disregarded significant present-
17 day literature, e.g. on the relationships between niches and geographic distributions.
18 Meanwhile, in a volume of *Journal of Biogeography* dedicated to discussions about
19 niches, three theoretical papers (McInerny and Etienne 2012a, b, c) focused on niches
20 related to the Eltonian, Grinnellian and Hutchinsonian concepts, and questioned whether
21 the utility of niche concepts. McInerny and Etienne did not address any of the
22 competition-centered niche concepts that dominated ecological literature for almost 30
23 years (e.g. MacArthur and Levins 1967). Defining the niche in such a way that pleases
24 all ecologists is challenging when researcher’s goals over-compartmentalize and
25 stovepipe research agendas.

1 “Niche” is thus concept with which ecologists have had a long love-hate
2 relationship (Leibold 1995). All this uncertainty around the word “niche” in
3 contemporary ecological literature raises questions of whether the term should be used at
4 all. Some say that if ecologists were to use the term niche only when it could be
5 completely estimated, i.e. using directly relevant variables only, the term would probably
6 disappear (Warren 2012). However, vagueness and lack of consensus in ecological
7 terminology has long led to misunderstandings (Hurlbert 1981). Our classification
8 scheme therefore revealed that different research areas use essentially distinct features to
9 measure, analyze, and predict niches. However, *how* the author uses terminology may
10 allow understanding *what* is meant by “niche”. That clarification improves readability
11 among researchers from different backgrounds for highlighting the main aspects (key
12 components) of the niche concept to which an author is referring. Hence, when a reader
13 intends to understand a paper from another research area, our classification scheme may
14 smooth that task for him or her. If the key components of what is being considered a
15 “niche” (property, community assembly rules, interaction with environment, spatial scale
16 of study, relevance of biotic interactions, and research goals) are highlighted, the niche
17 concept used in the study becomes evident and understandable.

18 Although several attempts have been made to develop a unified theory of
19 biodiversity (e.g. Hubbell 2001, Chase and Leibold 2003, Soberón and Peterson 2005),
20 ecology still lacks consensus even on what is a niche. Rather than adding another
21 definition to that already long list, our classification scheme may provide a simple way
22 to classify niche concepts into operationalized subdivisions and ease communication
23 among researchers. By addressing the main historical concepts of niche, we hope to have
24 provided useful guidance for readers from different scientific backgrounds. Explicitly

1 stating to which niche concept one is referring could avoid overuse of jargon while
2 enhancing readability among general scientific community.

3

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1 **Tables**

2 **Table 1.** Key components of classical niche concepts. Components refer to the niche concept itself or to the way niche was measured/assessed in
 3 classical studies. Classical concepts are classified into one or more features, to highlight their differences and shared attributes.

Niche concept	Niche itself			Measurement of the niche			Main idea
	“Niche” is a property of	Interaction with environment	Competition as main driver	Community assembly rules	Researcher’s agenda	Spatial scale of study	
<i>Grinnelian niche</i>	Environment	Environmental requirements	No	Niche-based rules	Distribution	Biogeographic	“[...] the existence [...] of species is vitally bound up with environments.”(Grinnell 1924)
<i>Trophic or Eltonian niche</i>	Environment	Impacts on environment	Yes	Niche-based rules	Community structure	Local	“By a niche, is meant the animal's place in its community, its relations to food and enemies [...].” (Elton 1927)
<i>Hutchinsonian niche</i>	Species	Environmental requirements	Yes	Niche-based rules	Community structure	Local	“niche [...] is a region of an n-dimensional hyper-space [...]”, “each point [...] permitting the species to exist indefinitely.” (Hutchinson 1957)
<i>Competition-centered niche</i>	Species	Impacts on environment	Yes	Niche-based rules	Community structure	Local	“From resource utilization efficiencies and habitat preferences, [...] niche overlap] can be calculated.” (MacArthur and Levins 1967)
<i>Mechanistic niche</i>	Individual	Environmental requirements and impacts on environment	No	Niche-based rules	Community assembly	Local	“The distinction between the requirement and impact components of the niche [...].” (Chase and Leibold 2003)

<i>Neutral models</i>	Individual	Random	No	Dispersal, drift and mutation	Community assembly	Local and biogeographic	"[...] communities are dispersal assembled, [...] and niche differences are not essential to coexistence." (Hubbell 2001)
<i>Niche related to distributions</i>	Species and/or populations	Environmental requirements	No	Niche-based rules	Distribution	Biogeographic	"[...] the appropriate set of abiotic factors for the species [...] may be regarded as the geographic expression of the fundamental niche [...]." (Soberón and Peterson 2005)

Capítulo 2

Sales LP, Neves OV, De Marco P & Loyola RD (2018). **Model uncertainties do not affect observed patterns of species richness in the Amazon**

RESEARCH ARTICLE

Model uncertainties do not affect observed patterns of species richness in the Amazon

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Abstract

Background

Climate change is arguably a major threat to biodiversity conservation and there are several methods to assess its impacts on species potential distribution. Yet the extent to which different approaches on species distribution modeling affect species richness patterns at biogeographical scale is however unaddressed in literature. In this paper, we verified if the expected responses to climate change in biogeographical scale—patterns of species richness and species vulnerability to climate change—are affected by the inputs used to model and project species distribution.

Methods

We modeled the distribution of 288 vertebrate species (amphibians, birds and mammals), all endemic to the Amazon basin, using different combinations of the following inputs known to affect the outcome of species distribution models (SDMs): 1) biological data type, 2) modeling methods, 3) greenhouse gas emission scenarios and 4) climate forecasts. We calculated uncertainty with a hierarchical ANOVA in which those different inputs were considered factors.

Results

The greatest source of variation was the modeling method. Model performance interacted with data type and modeling method. Absolute values of variation on suitable climate area were not equal among predictions, but some biological patterns were still consistent. All models predicted losses on the area that is climatically suitable for species, especially for amphibians and primates. All models also indicated a current East-western gradient on endemic species richness, from the Andes foot downstream the Amazon river. Again, all models predicted future movements of species upwards the Andes mountains and overall species richness losses.

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Data Availability Statement: Species occurrence data is freely available at IUCN Red List website (<http://www.iucnredlist.org>) and GBIF (gbif.org). Climate data is available at WorldClim (<http://www.worldclim.org>).

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Conclusions

From a methodological perspective, our work highlights that SDMs are a useful tool for assessing impacts of climate change on biodiversity. Uncertainty exists but biological patterns are still evident at large spatial scales. As modeling methods are the greatest source of variation, choosing the appropriate statistics according to the study objective is also essential for estimating the impacts of climate change on species distribution. Yet from a conservation perspective, we show that Amazon endemic fauna is potentially vulnerable to climate change, due to expected reductions on suitable climate area. Climate-driven faunal movements are predicted towards the Andes mountains, which might work as climate refugia for migrating species.

Background

Climate change is arguably a major threat to biodiversity [1–3]. Loss of suitable climatic conditions may potentially lead to expressive contractions on species and ecosystems distribution as we know so far [2,3]. In synergism with other stressors, such as deforestation, climate change may lead to negative feedbacks in ecosystem resilience [4,5] and increase extinction risk for a large number of species, during and beyond the 21st century [6–8].

Traditionally, the most widely used method to assess the effects of climate change on species distribution are the so-called “species distribution models”—SDMs [9–11]. The SDMs appraise how climatic conditions drive species distribution, at broad spatial scales [12,13]. Although established in literature as one of the most useful tools to analyze impacts of climate change on species distribution, SDMs are inherently fraught with uncertainties [9,12,14]. Uncertainties on SDMs emerge as mathematical modeling methods can provide dramatically different responses [12]. Also, the climate forecasts, or coupled Atmosphere-Ocean General Circulation Models—AOGCMs, may lead to distinct results, as well as should distinct greenhouse gas emission scenarios [1,15].

In addition, the two most widely used sources of species distribution data, i.e. occurrence records and maps of extent of occurrence (henceforth range maps; Elith and Leathwick [9]), may lead to potentially different model outcomes. Point-locality records should intuitively have greater reliability than range maps, because the exact location of each species record is known. Data deficiency nevertheless arises for many species, especially those inhabiting remote places [16]. For those species, SDMs fitted with distributional data based on range-maps could supposedly provide an initial understanding of habitat preferences, to be later improved with data refinement [17–19].

Although species-specific responses to climate change may vary with different sources of uncertainty in model predictions, some patterns are emerging globally. Impacts of climate change on biodiversity seem to be trait-mediated and to rely on taxon-related vulnerability [20,21]. Changes not only on population size and reproduction dynamics [22], but also on community composition [23] and species interactions [24] are predicted worldwide. As regards to their geographical distribution, endemic species with small ranges are expected to be the most vulnerable to risks from climate change [25]. Poleward and/or upslope climate-driven faunal migrations are also predicted as temperatures rise [26–28]. If species are unable to keep pace with their suitable climate, or to adapt *in situ*, climate change may lead to global extinction thresholds, at least for some vulnerable taxa [2,29].

Tropical species can be particularly threatened by climate change [30–32]. Species inhabiting equatorial zones experience climate conditions closer to animals upper thermal physiological thresholds [31,33], which are highly preserved among lineages [34]. Even small temperature increases might therefore have negative effects on tropical species' long-term persistence. As temperature raises, climate-driven faunal movements of tropical species towards more suitable areas, i.e. climate refugia, are also constrained by dispersal limitation and restricted to the upslope direction [35,36]. In this work, we assessed the expected effect of climate change on species' suitable climate areas, and on overall species richness. We used a potentially threatened biota—the Amazon basin endemic fauna of amphibians, birds and mammals—as our study case. Uncertainties and knowledge gaps are a major issue on assessing the impacts of climate change on biodiversity [37], especially for species-rich regions such as the Amazonia [32]. Enormous extensions of primary tropical forests and road access constraints create geographic bias on occurrence records of Amazonian biodiversity and also on climate data [38,39].

The main goal of this paper was to test whether the expected responses to climate change, in terms of species geographic distribution, are affected by the most recognized sources of uncertainty on SDMs. Specifically, we tested whether: 1) the patterns of species-specific shifts on suitable climate area vary among ensembles of species distribution models calibrated with different types of inputs; 2) the predicted impacts of climate change are uneven across different taxonomic groups. 3) the species richness patterns at biogeographical scale, which emerge from models of species distribution projected in future climate forecasts, are affected by the different combination of inputs in SDMs.

Methods

Distribution data

We chose to use the basin of the Amazon river as case study because the origin of Amazonian biodiversity is attributed to river dynamics. Also, Andean post-lift drainage patterns [40,41] contributed to create current Amazonian biodiversity scenario, which is biogeographically intricate with the geologic history of the Amazon basin. Furthermore, stream and river ecosystems (“riverscapes”) are suggested as natural units to which conservation efforts should be targeted [42]. Using the Amazon river basin as a conservation unit target could be potentially useful, as the Amazonia spans over nine countries and, therefore, is not delimited by political borders (Fig 1). The choice of modeling endemic vertebrates was due to a trade-off between the conservation value usually attributed to endemics [43], coupled with threat projections [25], and data availability, which is generally greater for flagship groups like the amphibians, birds and mammals [44].

To compare the results obtained with different sources of data on species occurrence, we calibrated SDMs using two of the most widely used data types: IUCN range maps and point-locality records. At first, we downloaded range maps for all terrestrial mammal species in the world from the International Union for Conservation of Nature and Natural Resources (IUCN) database (www.iucnredlist.org). In the absence of an official list of endemics for the Amazon basin, we selected all amphibian, bird and mammal species whose range maps were completely within the Amazon basin territory plus a 200km surrounding buffer. The identification of endemics based on pre-existing range maps allows to surpass shortcomings on biogeographical data, such as incomplete or biased knowledge of a species distribution based on its occurrence records, and is considered useful for large-scale modeling studies [46,47]. Adding a 200km buffer around the Amazon territory also allows incorporating uncertainties on borders of the IUCN range maps.



Fig 1. The Amazon basin. Formed by the Amazon River and its tributaries, the Amazon basin spans over nine countries of South America, from the Eastern foot of the Andean mountains towards the Atlantic Ocean. The extent of our study area is also depicted (in the smaller picture) as the Tropical Southern & Central America. Shapefiles of the Amazon River basin were obtained from the Oak Ridge National Laboratory Distributed Active Archive Center [45].

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The extent of a study area, for species distribution modeling purposes, ideally should only include areas that are accessible for species. Accessible areas, in this case, are those within reach of species dispersal from a biogeographical perspective [48]. To accommodate that restriction, we chose a background representative of all climate conditions that Amazon endemic species probably experienced and/or were restricted to by biogeographical history. Our extent therefore is delimited by a new biogeographical regionalization—the Tropical Southern & Central America (Fig 1)—in which the Neotropical region is splitted into a core tropical and a temperate portion [49]. After defining the study area extent, the species range maps were overlapped into a fishnet-like square grid, in an equal area projection (Albers equal area conic), covering the full extent of the Tropical Southern & Central America (xmn = -85, xmx = -33, ymn = -33, ymx = 22). For each species, all cells with more than 50% of their area overlapped by a range map were attributed as “presences”. Cells outside range maps were considered “absences”, thus creating a presence-absence-like matrix [henceforth PA-matrix]. Only species with more than 30 “presences” in the PA-matrix were considered in this work.

The choice of the grid resolution used here (25 x 25 Km) aimed at maximizing the reliability of climate information, while assuming moderate commission error. Because there are few weather stations in low populated areas such as the Amazonia, the WorldClim interpolated data for those regions is based on small satellite information [39]. Uncertainty is higher and climate predictions are therefore less accurate for those areas compared to other well sampled regions. Although there are very high resolution climate data available for the Amazon region, these data are likely unreliable for fine resolution analysis [39]. Had we chosen to use a finer resolution (10 x 10 Km, for example) would imply assuming higher levels of uncertainty while

falsely giving the impression of a fine resolution. Also, inferences from range maps at very fine resolutions are known to overestimate the area of occupancy of individual species and lead to erroneous patterns of species richness [50]. To allow for quantitative comparisons (please see [Methods](#) sub-section “Uncertainty analysis”) between model results from range-maps vs point-locality data, we also needed that both data were in the same resolution.

We are aware that using a 25 x 25 Km grid to convert range maps to a PA-matrix probably inflates commission error (all cells within a species’ range are converted into “presences”, although the actual species distribution may be uneven across its range [50]), even though the use of such resolution is common practice in SDM literature [18,51–54]. However, upscaling point-locality occurrence information to coarser scales (e.g. 100 x 100 Km) also results in commission error, because regions as far as 100km from where the species was found are likewise included as “presences”. In this study, gridding was necessary for comparison between model outcomes, so that we needed to use the same resolution for models calibrated with both types of distribution data (range maps and point-localities). Because our main goal is comparative, we caution that our results should not be interpreted individually.

After defining the species that are endemic to the Amazon basin, we also downloaded point-locality records for those species to compare results from range-map-based vs point-locality-based SDMs. These records were downloaded from three virtual databases: the Global Biodiversity Information Facility (GBIF; www.gbif.org); the SpeciesLink project (www.splink.cria.org.br); and the VertNet database (www.vertnet.org). All these sources are freely available online. In addition to those records, we had access to a dataset from the Instituto Chico Mendes para Conservação da Biodiversidade (*Chico Mendes Institute for Biodiversity Conservation*–ICMbio); the official national parks agency in Brazil. Whenever possible in each website search, we included only records previously checked by experts. All these records were individually assessed.

For records that were located more than 200km distant from the IUCN range map border, a literature survey was conducted to verify if new distribution limits were recently defined for species. When there was no evidence of new valid records, all occurrences more than 200km apart from IUCN range map border were removed from our dataset. By doing so, we assumed a conservative approach and only relatively reliable records were maintained. At the same time, removing records distant from the known occupied areas prevented highly updated—but possibly inaccurate—information on species distribution. Another fishnet-like grid with the same extent and resolution was created for point-locality records. Grid cells containing at least one record were considered as “presence” and cells without records as “absence”. Only species with more than 30 records in the grid were modeled, which resulted in a sample size of 288 species. Spatial autocorrelation was accounted for by removing duplicate records on each cell (one “presence” is attributed to a cell regardless one or more records are found). Although there are other methods to account for spatial and environmental autocorrelation, these methods usually only refer to point-locality and abundance data, not to data from range maps [55,56]. As our main goal is comparative, we therefore chose to maintain the same structure for all models.

Climate data

Climate data for current conditions were produced by interpolation of weather stations information from years 1960–1990 [39] and are available in the WorldClim database (www.worldclim.org/current). For selecting from all bioclimatic variables available in WorldClim, we created a pairwise correlation matrix. From the least-correlated variables (cutoff = 0.6), we selected those thought to be biologically relevant for our study. Because tropical species

experience relatively constant temperatures—compared to temperate species—which are usually close to animal’s upper safety thresholds [31], we chose variables related to temperature range and heat extremes. Water availability is associated with thermoregulatory behavior, which can alleviate climate effects on organisms [33], so we also selected variables related to precipitation on hostile periods, such as the driest month and the warmest quarter. Variables used for species distribution modeling in this work therefore were: Mean Diurnal Range (Bio 2); Temperature Seasonality (Bio 4), Mean Temperature of Warmest Quarter (Bio 10), Precipitation of Driest Month (Bio 14), Precipitation of Warmest Quarter (Bio18). Prior to variable selection, the WorldClim dataset was clipped to our study extent and re-scaled for our resolution, by averaging neighboring values (function = mean), using the function *lets.presab* in *letsR* package [57]. All variable selection analysis were performed using the *caret* package [58].

We used future climate scenarios developed by the Fifth Assessment Report (AR5) of The Intergovernmental Panel on Climate Change (IPCC), also available from WorldClim (www.worldclim.org/cmip5_30s). We used climate models for year 2070 due to our focus on uncertainty sources, once differences among projections increase from year 2050 on [1]. Future climate projections are based on expectations of greenhouse gas emission rates derived from anthropogenic actions. Predicted values of temperature and precipitation vary with different emission scenarios. In this work, we included two different scenarios (representative concentration pathways *rcp26* and *rcp85*), which represent extreme expectations of greenhouse gas emission rates. The *rcp26* is an “optimistic” stringent mitigation projection, and *rcp85* is a “pessimistic” or baseline scenario without additional efforts to constrain emissions [1]. Within these extreme scenarios, uncertainties also arise because different climate forecasts, or Atmosphere-Ocean General Circulation Models (AOGCMs), can project distinct climatic conditions for certain areas [59]. So we chose five representatives of each climate forecast known to predict divergent changes in temperature and precipitation [60], to include a wide range of different predictions. The chosen AOGCMs were BCC-CSM1.1 (BC), GFDL-CM3 (GF), HadGEM2-ES (HE), CCSM4 (CC), MIROC-ESM (MR).

Species distribution modeling

Species point-localities or range maps data, coupled with climate predictors, were used to model species potential distribution and to assess the effects of climate change on species future distribution. We fitted those data to nine different modeling methods, and performed ensembles exclusively among methods known to be statistically and conceptually similar, according to Rangel and Loyola’s [59] classification scheme. In that classification, distance-based or “envelope” are considered the simplest modelling methods, which assume that species geographic distribution is constrained by climatic tolerances. Regression-based or “statistical” methods can fit a larger number of parameters to different types of relationships between species occurrence and environmental variables. Machine-learning methods, the most complex algorithms in this classification, attempt to maximize the relationship between occurrences and predictors, while minimizing the number of parameters.

Those three main groups of algorithms were used in this work and their representatives were: 1) Envelope methods (bioclimatic models—BIOCLIM, Euclidian distance, ecological niche factor analysis—ENFA); 2) Statistical methods (generalized linear models—GLM, generalized additive models—GAM, multivariate adaptive regression splines—MARS); 3) Machine-learning methods (random forest—RndFor, artificial neural networks—NNet, and maximum entropy—MaxEnt). By fitting models according to this algorithm grouping approach, we maintain interpretability of ensemble model outputs [61]. For a general description of these methods, please see Franklin [62] and Peterson et al. [10]. The same kind of pseudo-absence data

was randomly chosen and used in all models (*sensu* de Oliveira [55]), regardless presence-only or presence-absence methods. (Details on model parameterization can be found as supporting information on [S1 Table](#)).

We randomly partitioned the “presences” in PA-matrix data into two subsets of calibration or train (75% of data), and validation or test (remaining 25%), and this process was repeated 10 times. Training outputs therefore yielded Grinnellian niche projections on the geographic space [56,63], whereas the test dataset evaluated model performance. Continuous predictions of habitat suitability were converted into binary projections. For doing so, we found the threshold in the relative operating characteristic (ROC curve), with maximum sensitivity (proportion of correctly predicted presences) and specificity (proportion of correctly predicted absences) values. Then, model accuracy was evaluated with the True Skills Statistics (TSS), the measure of choice for binary predictions [64], also obtained from sensitivity and specificity ($TSS = \text{Sensitivity} + \text{Specificity} - 1$) [62]. Values of TSS range from -1 to +1, in which values close to +1 indicate good model predictions and values equal or smaller than zero are no better than random predictions [64]. Although presence-only methods do not require pseudo-absences in model calibration, accuracy assessment from TSS-like measures thus depend on “absences”, or pseudo-absences. Therefore, pseudo-absences in presence-only methods, such as BIOCLIM, were used to characterize the study background and enable calculation of TSS metrics.

Ensembles of forecasts

Predictions of species response to climate change are filled with uncertainties [12]. Ensembles of forecasts are expected to produce stronger predictions and are considered a useful framework to account for uncertainties on model projections [12]. We performed model ensembles by weighting each model per TSS performance, to discriminate models in terms of their accuracy. Models with $TSS < 0.5$ were removed from final ensembles. Ensembling procedures included only conceptually similar methods (envelope *vs* statistical *vs* machine-learning methods) and only data from the same source (point-localities *vs* range maps). Consensus maps of potential distribution for current and future time-periods were then created from the frequency at which species appears in each grid cell. The overlay of *per* species consensus layers resulted in the final species richness maps.

A total of 180 models were fitted for each species (2 datasets X 9 methods X 10 random partitions of PA data). For current conditions, 90 projections of distribution (9 modeling methods X 10 random partitions of PA data) were obtained per species per data type. Ensemble models for current conditions resulted in six projected distributions (2 datasets X 3 ensembles) per species. Further, ensemble models generated 60 future projections for each species (2 datasets X 3 ensembles X 2 climate scenarios X 5 climate models). A visual depiction of those combinations is presented in [Fig 2](#).

Uncertainty analysis

We aimed at evaluating the impact of different sources of uncertainty on the expected responses of species distribution to climate change. To quantify the relative contribution of such distinct sources of variation among model projections, we performed a hierarchical Analysis of Variance (ANOVA) without replication for each cell [65]. The difference between current projected richness (C) and future projected richness (F) was considered here a proxy of the impact of climate change on species richness ($C - F$) and was used as response variable.

Data source (range maps and point-locality records), modeling method (BIOCLIM, Euclidian distance, ENFA, RndFor, NNet, MaxEnt, GLM, GAM, MARS), representative concentration

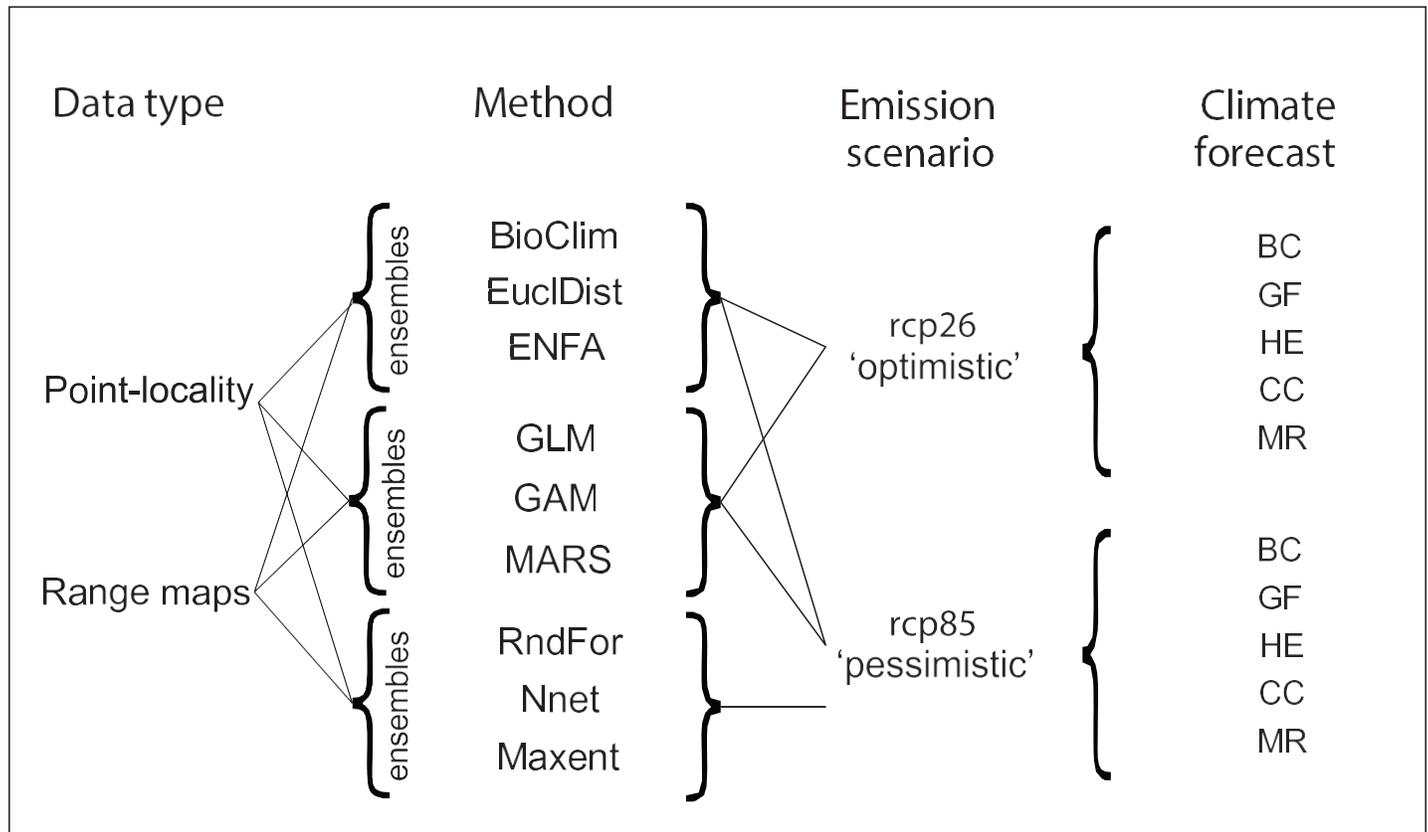


Fig 2. Tree of possibilities. We modeled the distribution of amphibians, birds and mammals that are endemic to the Amazon, using two types of data (point-localities and range maps); three ensembles of envelope (BioClim, EuclidDist, ENFA), statistical (GLM, GAM, MARS) and machine-learning (RndFor, NNet, Maxent) methods. Those models were then projected into five climate forecasts (BC, GF, HE, CC, MR) within two greenhouse gas emission scenarios (*rcp26* and *rcp85*). Acronyms for methods indicate: BioClim = Bioclimate envelope; EuclidDist = Euclidian distance; ENFA = Ecological niche factor analysis; GLM = generalized linear models; GAM = Generalized additive models; MARS = Multivariate adaptive regression splines; RndFor = Random forest, NNet = Artificial neural networks; Maxent = Maximum entropy. Acronyms for climate forecasts indicate: BC = BCC-CSM1.1; GF = GFDL-CM3; HE = HadGEM2-ES; CC = CCSM4; MR = MIROC-ESM. Representative concentration pathways are represented as *rcp*.

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pathways (*rcp26* and *rcp85*) and future climate forecasts (AOGCMs: BC, GF, HE, CC, and MR) were considered factors. Then, we obtained the sum of squares attributed to each factor. Variance components were considered the proportion of the sum of squares compared to the total sum of squares, as suggested by Diniz-Filho et al. [12]. By doing so, we could identify regions of the Amazonia associated to high uncertainty and their respective drivers. Consensus maps were produced in Bioensembles software [66]. All figures shown in this paper are original and were created in R and ArcGIS 10.3.1 (ESRI, Redlands, CA, USA).

Model outcome comparison

To verify if data type and modeling method affected model performance, we compared the TSS values of model ensembles. Finally, we tested whether variation on projected range shifts, i.e. current potential distribution (C) minus future potential distribution (F) = projected range shifts (C-F), could be attributed to species' observed range size. We calculated the standard deviation of the values of range shift estimated by all combinations of the factors cited previously. Our rationale here is that differences among projected range shifts could be a result of the differential sampling of varying range sizes. All differences among model outputs were

tested with linear models, using the appropriate link function and family distribution in each case.

Results

Range shifts

A total of 288 species were modeled (40 amphibian, 225 bird, and 23 mammal species), 18169 point-locality records were used in the modeling, with an average of 63 records per species, though most species had 30–46 records. Seven taxonomic families of amphibians, 35 of birds, and 9 of mammals were represented in this study (S2 Table). One critically endangered (CR), seven endangered (EN), 11 vulnerable (VU), 19 near threatened (NT) and 250 least concern (LC) species, according to IUCN latest classification [67] were modeled in this study (S2 Table).

Though range shift predictions varied between biological data type, overall model predictions were usually consistent within taxonomic groups (Fig 3). All orders are expected to experience range contractions (S3 Table). At the taxonomic level of family, the same pattern is observed. All vertebrate families are expected to experience range shrinks in both *rcp* scenarios. Range contractions are predicted for most species by all combinations of *rcp* scenarios and biological data types. Overall, amphibians are the group expected to lose the larger climate area (mean = -0.70 ± 0.10), followed by mammals (mean = -0.68 ± 0.16) and birds (mean = -0.59 ± 0.14). Primates were the mammal group most likely to be threatened by climate change. Within birds and amphibians, there was not a dominant group in terms of climate change vulnerability.

In the “optimistic” scenario, five species (*Gastrotheca griswoldi*, *Grallaria przewalskii*, *Rhinella poeppigii*, *Scytalopus acutirostris*, *Stefania evansi*) are predicted to lose all of their climatically suitable areas by at least one ensemble model. In the “pessimistic” scenario, that number raises to 12 species, which are likely to have no climatically suitable area in year 2070 (*Alouatta discolor*, *Amazona kawalli*, *Certhiaxis mustelinus*, *Gastrotheca griswoldi*, *Grallaria przewalskii*, *Odontophorus stellatus*, *Poecilatriccus albifacies*, *Rhinella poeppigii*, *Scytalopus acutirostris*, *Stefania evansi*, *Veniliornis sanguineus*, *Xiphorhynchus spixii*), according to predictions of at least one ensemble model. Very few species are predicted to experience some range expansion, i.e. two species in the optimistic greenhouse gas scenario and only one in the pessimistic scenario (S3 Table).

Uncertainty, model fit and species richness patterns

Hierarchical ANOVA showed that the greater source of variation in the effects of climate change on species distribution was the modeling method (median explained variation = 0.50, CI = 0.32–0.66), followed by biological data type (median explained variation = 0.28, CI = 0.07–0.5), climate forecasts (median explained variation = 0.08, CI = 0.05–0.13) and *rcp* scenario (median explained variation = 0.04, CI = 0.002–0.009). Uncertainty patterns varied geographically across the Amazon basin and among the main ANOVA factors (S1 Fig). Total uncertainty seems to be concentrated at Roraima state, in Brazil, and at the Southeastern portion of the Amazon basin, close to the region called the “Arch of Deforestation”. Also, a large amount of variation was depicted to the Andes mountains, especially for climate-related factors (greenhouse gases emission scenarios—*rcp26* and *rcp85*—and climate forecasts—AOGCMs). Uncertainty attributed to biological data type was mainly aggregated at the center of the Amazon basin. Methods uncertainty was less spatially structured than other factors, although a smooth trend towards peripheral zones of the Amazon basin could be observed.

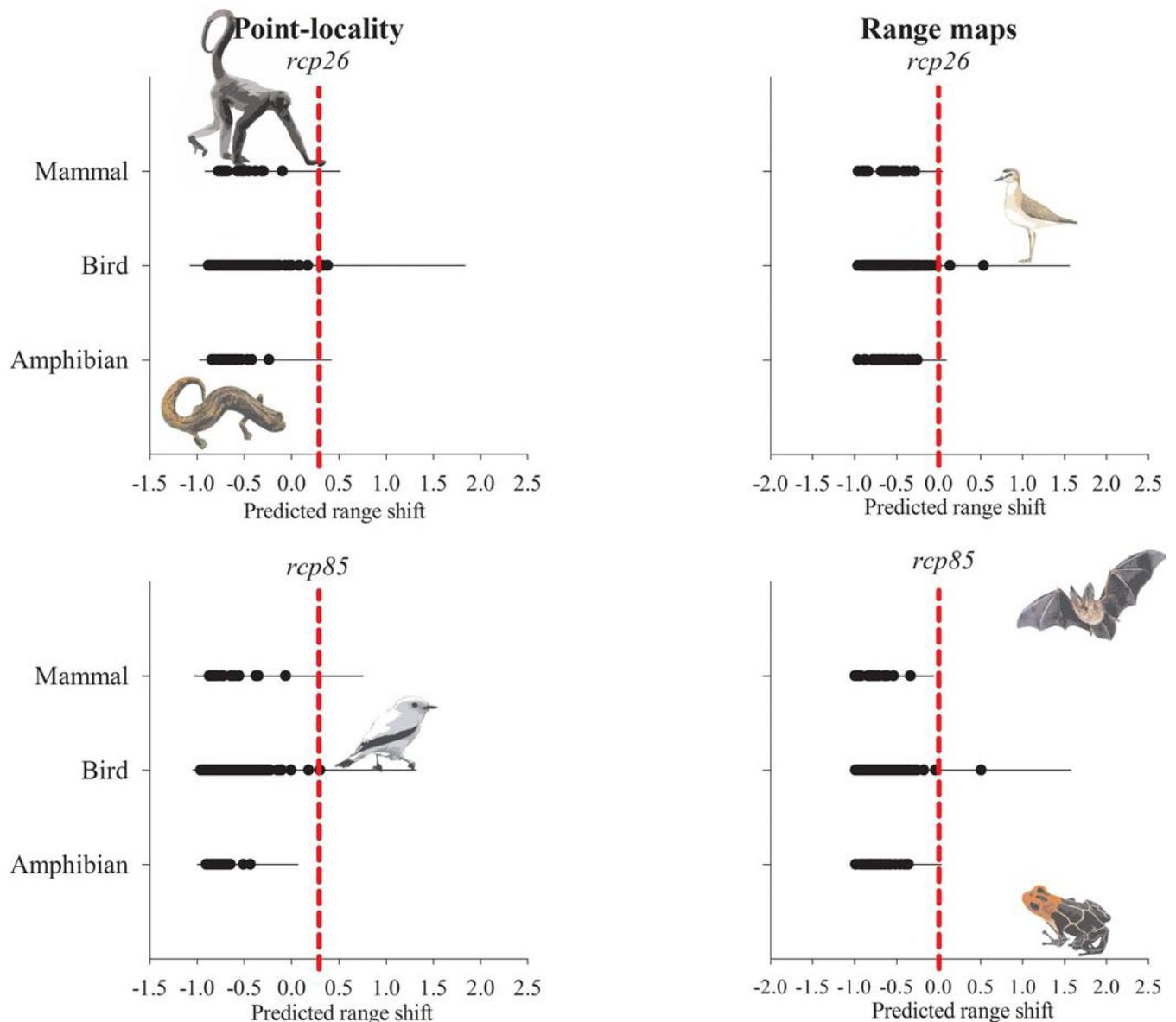


Fig 3. Cumulative variation on predicted climatically suitable areas by taxonomic Family. Horizontal thin bars indicate variation within taxa and black dots are species-specific means on the predicted variation of geographic range (the difference between current and future climatically suitable areas).

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Model outcome comparison

Ensembles of methods had consistently better model fit than their respective isolated methods (Fig 4). Model performance (in terms of TSS) exhibited a relationship between data type and modeling method. Both data types had higher TSS values on ensembles of statistical methods (Point-locality: $TSS_{\text{mean}} = 0.75 \pm 0.06$, Range-maps: $TSS_{\text{mean}} = 0.75 \pm 0.06$) and lower TSS values on ensembles of envelope methods (Point-locality: $TSS_{\text{mean}} = 0.72 \pm 0.05$, Range-maps: $TSS_{\text{mean}} = 0.75 \pm 0.06$). Machine-learning ensembles, however, produced better results on models calibrated with point-locality records (Point-locality: $TSS_{\text{mean}} = 0.60 \pm 0.06$, Range-maps: $TSS_{\text{mean}} = 0.66 \pm 0.06$).

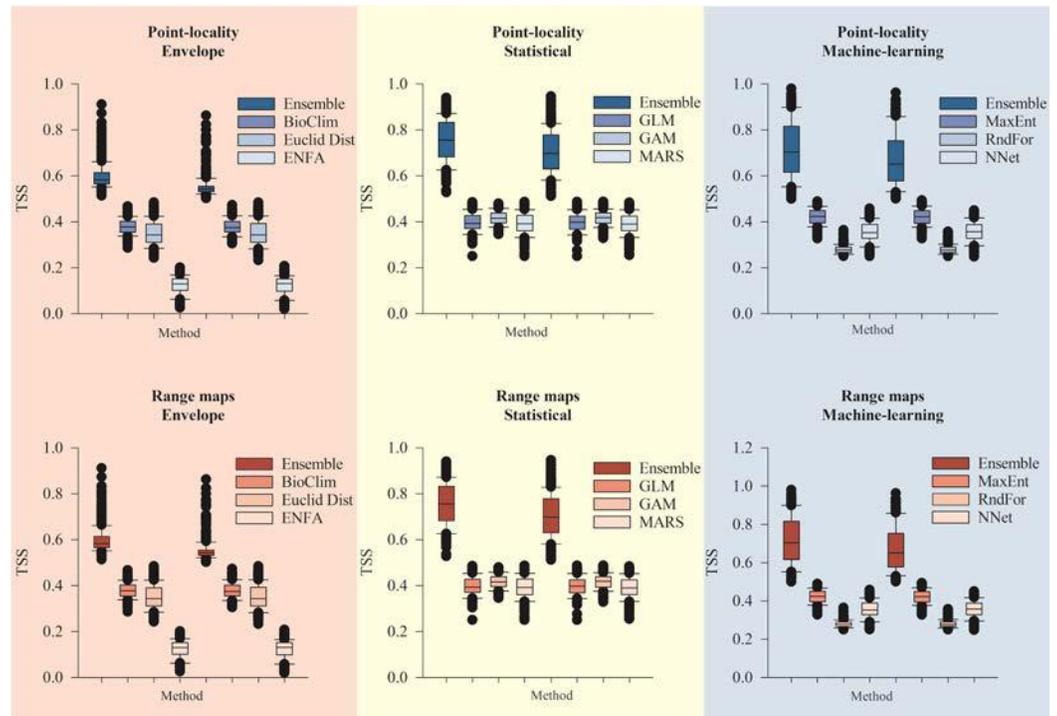


Fig 4. Model fit in relation to biological data and modeling method. Thick bars represent median and 95% confidence interval, dots are outlier values. Ensembles of envelope (bioclimatic models—BIOCLIM, Euclidian distance, ecological niche factor analysis—ENFA); statistical (generalized linear models—GLM, generalized additive models—GAM, multivariate adaptive regression splines—MARS); and machine-learning methods (random forest—RF, artificial neural networks—ANN, and maximum entropy—MaxEnt) were built and their model fit compared to individual methods. True Skills Statistics (TSS) values did not differ neither between biological data source (Point-locality vs Range-map-based models), or ensembles of methods, although they differed among individual modeling methods. Acronyms for methods indicate: BioClim = Bioclimate envelope; EuclidDist = Euclidian distance; ENFA = Ecological niche factor analysis; GLM = Generalized linear models; GAM = Generalized additive models; MARS = Multivariate adaptive regression splines; RndFor = Random forest, NNet = Artificial neural networks; Maxent = Maximum entropy. Acronyms for climate forecasts indicate: BC = BCC-CSM1.1; GF = GFDL-CM3; HE = HadGEM2-ES; CC = CCSM4; MR = MIROC-ESM. Representative concentration pathways are depicted as *rcp*.

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Point-locality-based models predicted slightly smaller contractions on climate area, but variation was larger ($rcp26_{mean} = -0.53 \pm 0.22$; $rcp85_{mean} = -0.64 \pm 0.19$) than range-map-based model outputs ($rcp26_{mean} = -0.59 \pm 0.17$; $rcp85_{mean} = -0.71 \pm 0.15$). We also found a negative relationship between the species' observed range size and difference among model outcomes ($F = 13.886$, $p = 0.0002$, $DF = 286$). In other words, distribution models for species with smaller range size resulted in more divergent outputs than did those for widely distributed species.

Although patterns of species richness varied per data source and ensembles of modeling methods, average species richness was expected to be reduced across the entire Amazon basin. For all models, current richness of endemic species was concentrated on the eastern portion of the Amazon basin, in a gradient downstream the Amazon River. All consensus maps predicted that, on year 2070, climatic suitable areas for most species will be more concentrated in the eastern portion of the Amazon basin, moving upwards the Andes mountains, in a comparison with current location of climatic suitable areas for most species (Fig 5). As for present-day species richness patterns, envelope methods predicted higher climate suitability for a larger number of species outside the Amazon area. Those climate areas predicted by envelope methods

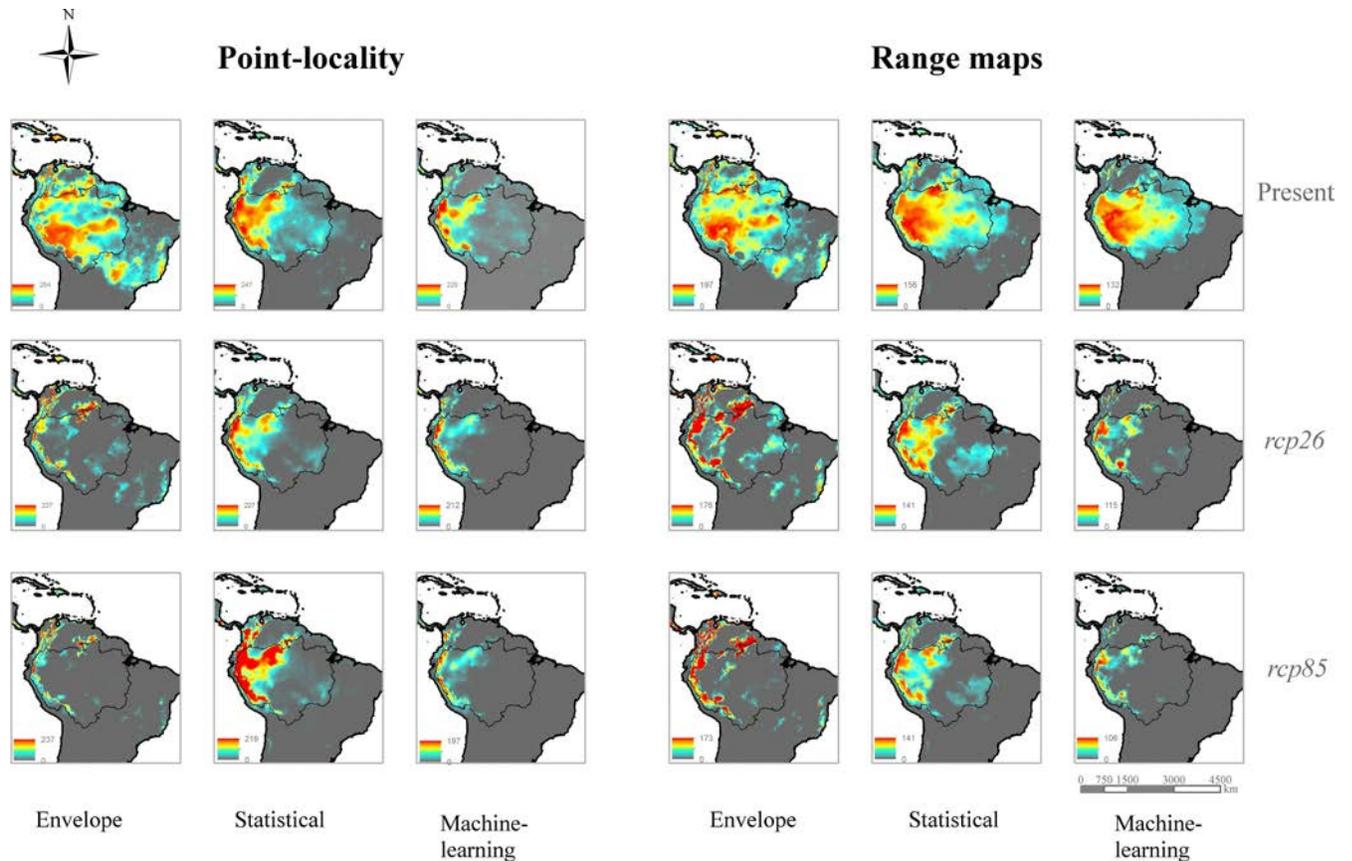


Fig 5. Species richness patterns expected for Amazonia species on year 2070. Based on ensembles of modeling methods (Envelope: BIOCLIM, ENFA, Euclidian distance; Statistical: GLM, GAM, MARS; and Machine-learning: MaxEnt, RF, ANN) projected on two extreme greenhouse gas emission climate scenarios (*rcp26* and *rcp85*), using two sources of biological data (IUCN range maps and point-locality records).

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also include some portions of the Brazilian Atlantic forest. Statistical methods were more “conservative” and predicted smaller range contractions across the Amazon territory in year 2070.

Discussion

Much has been said about model uncertainty regarding the use of species distribution models (SDMs) to assess climate change effects on the geography of biodiversity [12,15,68,69]. Addressing the impacts of yet-to-come threats to biodiversity is a task inherently fraught with uncertainty. No validation can be performed on future climate models and different data sets and/or modeling methods are expected to produce divergent results [13,16]. Yet the impact of model uncertainties on observed ecological patterns is still obscure. In this paper, we modeled the potential distribution of Amazon endemic species and projected those distributions into future climate, while explicitly incorporating the major factors known to affect the outcome of SDMs. Although predictions were not identical among the many sources of uncertainty addressed in this work, especially when comparing individual modeling methods and data sources, some biological patterns were evident in most model outcomes.

We found the same visual patterns of geographic distribution on species richness of Amazon endemic vertebrates (discussed below) using both kinds of data. Point-locality-based maps revealed the same broad biogeographical patterns as those calibrated with range-map based data. Maps calibrated with both types of data were also similar in terms of expected range

shifts. Converting range maps into presence-absence matrices with grid resolutions higher than 1–2 degrees of lat/long supposedly alters biogeographical patterns of species richness [50], although changes in grain size do not seem to affect predictions from SDMs [70]. In this work, we used point-localities and range maps as source of species distribution information for calibrating SDMs at 25 x 25 Km (0.25 degrees of lat/long) and we found the same biogeographical patterns using both data types. Model outcomes of both data types exhibited similar patterns of species richness and range shifts expected as response to climate change.

Here we do not advocate the indiscriminate use of IUCN range maps as distributional data for all species, but we recognize that range maps could provide an initial knowledge about species niche requirements, especially those that are range restricted, data deficient and/or those that occupy remote places [12]. Our small sample size ($n = 288$ species) and particularities regarding endemics' restricted distribution prevent us from making wider generalizations. We do however acknowledge that data deficiency may lead to underestimated conservation efforts and that some biogeographical patterns may be consistent and detectable enough to justify the use of IUCN range maps as distributional data in some cases. However, we also found a negative relationship between the variation on predicted range size and the size of the species' known distribution. Therefore, predictions are less convergent for geographically restricted species, so our results should be interpreted with caution in those cases.

Methods used to model species distribution can provide such variable outcomes, that simply assessing whether a species' range may reduce or expand can prove unsuccessful in some cases [71]. In this work, the greatest source of variation on predictions was the modeling method, which has been shown to severely affect the outcome of SDMs [12]. Ensembling among models however improved our predictions and reduced output variation, which was already expected because ensembles of forecast are known to reduce uncertainty related to modeling methods [12]. Differences among outputs of ensemble models were much smaller than those from individual models. Surprisingly, ensembles of statistical methods had better performance than machine-learning and envelope methods. Machine-learning methods are more complex and usually related to more explanatory power [61], in which predictions are best fit to the original data [9]. Machine-learning methods had better performance only for point-locality data, but not for models calibrated with range maps. Once machine-learning methods usually benefits precision but penalizes generality and ability to extrapolate [10,61], we suggest that machine-learning predictions for point-locality data should give more precise but less extrapolatable projections. Envelope methods had the worst performance, probably because they sacrifice predictive power for the sake of generality, contrary to machine-learning methods [61].

The first biogeographical pattern consistent in all consensus maps of species richness was an East-western gradient from the Andes foot downstream the Amazon River. That pattern was already expected because, as mentioned before, the Amazon biodiversity is biogeographically linked to the Amazon River geologic history. The uplift of Andean mountains in the pre-Quaternary reconfigured the previously deltaic Amazon basin drainage patterns, by creating an influx of nutrients and sediments into the basin, and an edaphic mosaic extremely rich in species [41]. The Amazon basin biodiversity therefore results from complex interactions between paleoclimatic and vegetational shifts, in addition to spatial variability on precipitation, especially in East-west but also North-south direction [72]. Our findings highlight that the Western portion of the Andes mountains contains an expressive richness of endemic species, which smoothly diminishes downstream the Amazon River towards the Atlantic Ocean. That East-western pattern on current species richness was consistent across all types of data source and ensembles of methods.

A second pattern we found in this work was species migration upwards the Andes lift. All model projections for year 2070 predict an increase of species richness for the Andean region of the Amazon, followed by reductions across the Amazon basin. As climate changes, species have historically moved towards more suitable climates [35]. Climate-driven faunal movements are successful when directed to environmental habitats that enhance biota survival at spatio-evolutionary timescales [35,73]. Those environments offer the best chances of survival on climate change and are therefore called “climate refugia” [26,73]. Poleward and/or upslope faunal movements as response to recent climate are a trend across the globe [28]. As temperature raises, poleward movements are restricted for tropical species but upslope migrations are expected and have been observed for some groups [27]. Some regions, such as the Amazon basin, are predicted to concentrate high density of faunal movements towards higher altitudes [35]. Our results indicate that Andean slopes may work as climate refugia for Amazon endemic species as upwards climate-driven movements may allow species to track their suitable climate, which has strong applications for Amazon conservation. That uplift movement pattern was also consistent and detectable for all data source types, modeling methods, greenhouse gas emission scenarios and climate forecasts.

Predictions of species’ expected contractions on suitable climate area were also consistent and similar in most model outcomes. Most species are expected to lose some climatic area in the future, a consistent pattern across all data source types, modeling methods, climate scenarios and climate models. Losses are congruent among taxonomic levels and all orders and families are likely to lose expressive amounts of suitable climate for most species. If such species are not able to keep pace with climate change and track their suitable areas or adapt *in situ*, they will probably be highly threatened in the wild [29]. Our results suggest that some groups may lose larger areas of suitable climate and could be more exposed to non-analogue climates.

Amphibians in special were highlighted in this work as more threatened than birds and mammals. The Amazon basin has also been considered a hotspot of endemism of amphibians that are highly vulnerable to climate change [20]. Ectotherms are dependent on the surrounding temperature and most amphibians have a highly permeable skin, in both terrestrial and aquatic life stages. Those eco-morphological features explain amphibians’ sensitivity to environmental change and are probably related to their decline worldwide [74]. Among mammals, our work suggests that climate change impacts will be more deleterious to primates than to any other mammal group, in terms of average predicted losses in suitable climate area. Neotropical primates are essentially poor dispersers for their arboreal habits and canopy-dependence [75], which will probably prevent them to keep pace with climate change [36]. Species that occupy lowland human-modified landscapes may require long migrations in order to access suitable climates and severe reductions in range size have already been predicted for other primates [36].

Although we found some variation on species distribution model outputs, our work suggests that some biogeographical patterns may be detectable and consistent on model outcomes from the traditionally used methods in SDM. Congruence among predictions of different model outcomes and alarming consequences for biodiversity as response to climate change have already been observed for a myriad of taxa and biodiversity levels [2]. Coherence on expected outcomes of models including the major sources of known uncertainties reinforces the usefulness of SDM approaches on assessing biodiversity responses to climate change, meanwhile highlights the need for substantial conservation actions.

Supporting information

S1 Fig. Uncertainty on species richness pattern for Amazonia mammals. Species distribution models projected for year 2070, derived from the hierarchical ANOVA factors: biological

data source (IUCN range maps and point-locality records), modeling method (BIOCLIM, ENFA, Euclidian distance, GLM, GAM, MARS, MaxEnt, RF, and ANN), greenhouse gases emission scenarios (rcp26 and rcp85) and future climate simulation models (AOGCs: BC, GF, HE, CC, and MR). Acronyms for methods indicate: BioClim = Bioclimate envelope; EuclidDist = Euclidian distance; ENFA = Ecological niche factor analysis; GLM = generalized linear models; GAM = Generalized additive models; MARS = Multivariate adaptive regression splines; RndFor = Random forest, NNet = Artificial neural networks; Maxent = Maximum entropy. Acronyms for climate forecasts indicate: BC = BCC-CSM1.1; GF = GFDL-CM3; HE = HadGEM2-ES; CC = CCSM4; MR = MIROC-ESM. Representative concentration pathways are represented as rcp.

(TIF)

S1 Table. Details on model parameterization. Model parametrization of the nine methods used to model species distribution and evaluate the impacts of climate change on Amazon biodiversity. All methods included the automatic search using ROC as probability cutoff, permutation with 10 cross-validation replicates and 75% replicate training.

(DOCX)

S2 Table. Taxonomic information and conservation status of the species used in this work. Acronyms are indicated, as follows: LC: least concern, NT: near threatened, VU: vulnerable, EN: endangered; Decr: decreasing, Sta: stable, Unkn: unknown.

(DOCX)

S3 Table. Summary statistics of Amazon endemic amphibians, birds and mammals. Taxonomic information of species for which we estimated vulnerability to climate change is included. The mean range shift is the variation in the number of suitable climate cells in species potential distribution (current potential distribution—future potential distribution) and was calculated for two scenarios of climate change (*rcp26* and *rcp85*), using IUCN range-maps and point-locality records as input data.

(DOCX)

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Capítulo 3

Sales LP, Ribeiro BR, Chapman C & Loyola RD (2018). Projected vulnerability of Amazonian primate species to climate change

1 **Projected vulnerability of Amazonian primate species to**
2 **climate change**

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19 **Short title:**

20 Climate change effects on Amazon primates

21

22

1 **Abstract**

2 Owing to climate change, species' geographical distribution may be extended, reduced or
3 displaced in the future. Across species' ranges, novel climate conditions might also
4 expose species to thermal conditions they are not adapted to. Migration towards more
5 suitable climates will also only be possible if species are able to keep pace with climate
6 change. Here, we analyze different lines of evidence to assess the predicted impacts of
7 climate change on a potentially threatened fauna. We found that endemic Amazonian
8 primates may face a future harsher than expected so far. Primate species will be exposed
9 to novel climate conditions in a large portion of their territories and are not likely to track
10 their climate niche, even when their range is expected to expand. In addition to
11 deforestation, hunting, and disease spread, climate change may have unprecedented
12 impacts, thus adding up to conservation-defying feedbacks on primate populations'
13 fitness and resilience dynamics. We suggest that climate change should be explicitly
14 considered in global conservation assessments to better support mitigation and adaptation
15 plans for biodiversity in face of climate change. Meanwhile, conservation units may act
16 as "stepping stones" and provide temporary habitat conditions, enough to allow
17 successful climate-driven migrations.

18

19 **Keywords:** range shift; biotic velocity; exposure to novel climates

1 **Introduction**

2 Species' vulnerability to global climate change is usually assessed at broad geographical
3 spatial scales (Thomas, 2010). The relationship between current environmental
4 conditions and species' occurrence is projected into different scenarios of human
5 economic development (Pearson & Dawson, 2003; Pereira *et al.*, 2010). Then, based on
6 the assumptions that climate drives species' distribution at geographical scales (Soberón,
7 2007) and that species' occurrence is in equilibrium with current climate (Early & Sax,
8 2014), researchers attempt to predict the likely effect of climate change on species'
9 distribution.

10 Climate change effects on species' distribution include change in the area
11 predicted as suitable for a given species, displacement of optimal environments from
12 current to future locations and exposure to non-analog climates. The losses in the total
13 area that holds suitable climatic conditions may lead to species' range contractions, due
14 to local extinction in unsuitable sites (Bellard *et al.*, 2012; Cahill *et al.*, 2012). Range
15 contractions have already been observed for some highly-mobile species (Forero-Medina
16 *et al.*, 2011) and after extreme climatic events (Smale & Wernberg, 2013).

17 As climate changes, the optimal environmental conditions for survival of a given
18 species may move from one place to another, and some populations may be able to track
19 such environment or climatic niche. Climate-driven faunal migration of tropical species
20 towards the poles or uphill is expected, as temperature increases (Parmesan & Yohe,
21 2003; Forero-Medina *et al.*, 2011; Gavin *et al.*, 2014). Such movements may, however,
22 force species out of protected areas (Ferro *et al.*, 2014; Lemes, Melo, & Loyola, 2014;
23 Loyola *et al.*, 2014) and affect species' interaction by introducing new predators,
24 pathogens and competitors (Tylianakis *et al.*, 2008). Beyond that, migrations will only

1 allow a species to keep pace with climate change if species move at a minimum velocity
2 that is the same speed of climate change (Carroll *et al.*, 2015). Therefore, the velocity of
3 change in the climate niche must fit the species' dispersal ability (Carroll *et al.*, 2015).

4 Successful migrations are therefore dependent on the species' ability to keep pace
5 with climate change and the existence of permeable routes to allow such migrations.
6 However, habitat loss and fragmentation create landscape mosaics that affect species'
7 movements and may ultimately prevent climate-driven dispersal, thus confining species
8 to unsuitable climates (Gouveia *et al.*, 2016). Therefore, migration towards suitable
9 climates in the future will probably not be possible for several species (Schloss, Nuñez,
10 & Lawler, 2012). As consequence, those species might have to cope with non-analog
11 climate conditions, likely to exceed the amplitude, extremes and seasonality values to
12 which species are adapted (Ribeiro *et al.*, 2016). Novel climate conditions are expected
13 in one-third of the Earth, followed by disappearing of current conditions in many
14 locations (J. W. Williams, Jackson, & Kutzbach, 2007). Thus, some regions may be
15 exposed to harsher novel environmental conditions (J. W. Williams, Jackson, & Kutzbach,
16 2007), whilst some biological taxa may be more vulnerable to such changes (Foden *et al.*,
17 2013; Ribeiro *et al.*, 2016).

18 Amazonian primates are particularly vulnerable to climate change because they
19 inhabit climate conditions close to their upper thermal physiological thresholds (Colwell
20 *et al.*, 2008; Dillon, Wang, & Huey, 2010), which are highly preserved among lineages
21 (Araújo *et al.*, 2013). Even small increases in temperature may lead to deleterious effects
22 on primate populations' fitness (e.g. Sesink Clee *et al.*, 2015). Neotropical primates, in
23 particular, are canopy-dependent and poor dispersers, not likely to be able to track their
24 climatic niches, as climate changes (Schloss, Nuñez, & Lawler, 2012). Due to dispersal
25 limitation, climate-driven movements of tropical species are further limited to the upslope

1 direction (Lawler *et al.*, 2013). Amazonian primate species will also be exposed to non-
2 analog climate conditions at a rate greater than the global average (Ribeiro *et al.*, 2016;
3 T. L. Graham, Matthews, & Turner, 2016).

4 Although lack of empirical evidence is a major problem in climate change
5 literature, effects on primate population structure (Sesink Clee *et al.*, 2015), range size
6 (Meyer, Pie, & Passos, 2014), species' interactions (Wiederholt & Post, 2010), exposition
7 to novel parasites (Barrett *et al.*, 2013), and climate-deforestation feedbacks (Struebig *et*
8 *al.*, 2015) have already been found. Here, we assessed the projected effects of multiple
9 dimensions of climate change on primates that are endemic to the Amazon basin. To allow
10 a comprehensive assessment of such dimensions, we analyzed species' range shift, biotic
11 velocity and exposure to non-analog climates, searching for metric biases and
12 inconsistencies among them.

13

14 **Methods**

15 **Distribution data**

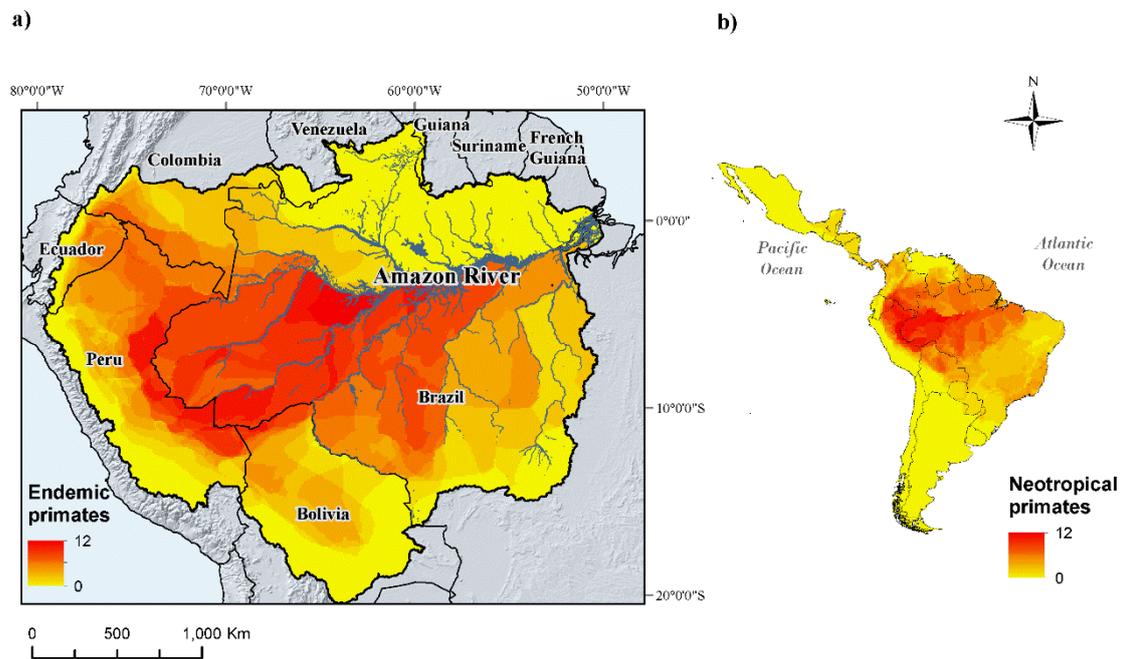
16 The Amazon basin concentrates a high number of species that are vulnerable to climate
17 change (Pacifici *et al.*, 2015). From a conservation perspective, addressing river basins
18 as conservation planning units can potentially benefit biodiversity by not being limited to
19 political units (Eros & Grant, 2015). We defined the species endemic to the Amazon basin
20 as those whose known distribution fall completely within the basin territory, plus a 200km
21 buffer to account for border uncertainty. Range maps were downloaded from the
22 International Union for Conservation of Nature and Natural Resources (IUCN) database
23 (www.iucnredlist.org, date of access: November 15th 2017). Identifying endemics based

1 on range maps is useful for macroecological purposes as it overcomes some species-
2 specific data deficiencies (Young *et al.*, 2009; Swenson *et al.*, 2012; Sales *et al.*, 2017),
3 especially because some of the areas that concentrate the highest number of species
4 vulnerable to climate change are also data-deficient regions, such as the Amazon basin
5 (Pacifci *et al.*, 2015).

6 Point-locality records were collected after defining the primate species that are
7 endemic to the Amazon basin using three free-access databases: the Global Biodiversity
8 Information Facility (GBIF; www.gbif.org); the SpeciesLink project
9 (www.splink.cria.org.br); and the VertNet database (www.vertnet.org). Whenever
10 allowed by the website search, only records previously checked by experts were
11 maintained. We cross-checked all species' records and its known extent of occurrence -
12 IUCN range maps. Occurrences further than 200km from the border of species' IUCN
13 range maps were removed from the dataset. In such a conservative data-cleaning
14 approach, only reliable records were kept. However, some very recent information may
15 not have been considered, but this seems appropriate as it probably has not had sufficient
16 time to be verified. To minimize spatial autocorrelation, we also disaggregated
17 occurrences less than 0.5km from each other.

18 A total of 132 Neotropical primate species had IUCN georeferenced range maps
19 at the search occasion. Of those, 75 primate species were considered endemic to the
20 Amazon basin. Endemic species richness was concentrated south of the Amazon river
21 and follows a west-east gradient, from the Andes mountains downstream (Fig. 1). After
22 cleaning for duplicate occurrence records, pseudo-replicates, and misplacements, we
23 ended up with a total of 12 primate species, whose occurrence is restricted to the Amazon
24 Basin, for which we had more than 15 valid records. The potential distribution of those

1 12 species was then modeled using 869 valid and cross-checked occurrences, with an
2 average of 72 ± 40 records per species.



3
4 **Fig. 1** Primate species richness and the Amazon basin. **a)** Species richness of primate whose occurrence is restricted
5 to the Amazon basin, where reddish color indicates higher species richness. **b)** Primate species richness for the
6 Neotropics.

7

8 **Climate data**

9 We obtained climate information as raster layers, available at the WorldClim database,
10 version 1.4, at 30 seconds resolution. Such files contain information regarding the present
11 climate and were produced by interpolation of data from ground weather stations, as
12 averaged weather values for years 1960-1990 (www.worldclim.org/version1, date of
13 access: November 21th 2017). In this work, we upscaled the downloaded climate
14 information to 0.1° of latitude/longitude, because interpolated data for this region is based
15 on small satellite information (Hijmans et al., 2005), for which uncertainty should prevent

1 finer-scale assessments. WorldClim data are composed of raw or derived data on
2 temperature and precipitation. We modeled the distribution of Amazonian primates as a
3 function of climate predictors thought to be drivers of their distribution - WorldClim
4 bioclimate predictors. Bioclimatic variables are composed of 19 predictors, derived from
5 the raw data, representing annual trends, seasonality, and extreme environmental factors.
6 Therefore, bioclimatic predictors are considered more biologically meaningful and thus
7 often used in species' distribution modeling (Hijmans *et al.*, 2005).

8 To assess the impact of climate change on primate distribution, we projected the
9 relationship between current climate and species' occurrence into future scenarios of
10 climate change. To do so, we downloaded the future expectations of the variables outlined
11 above, projected to the year 2070. Such expectations represent climate scenarios
12 developed by the Fifth Assessment Report (AR5) of The Intergovernmental Panel on
13 Climate Change (IPCC - CMIP5), available at WorldClim
14 (www.worldclim.org/cmip5_30s, date of access: October 21th 2016).

15 Climate scenarios rely on prospects of anthropogenic emission rates of
16 greenhouse gases, especially CO₂ (IPCC, 2014a). Temperature and precipitation values
17 are then predicted according to different emission scenarios. Here, we considered two
18 scenarios (representative concentration pathways *rcp26* and *rcp85*), which are the most
19 extreme expectations of greenhouse gases emission rates considered in AR5. The *rcp2.6*
20 is a stringent mitigation scenario, and *rcp8.5* is baseline "business as usual" scenario
21 without additional efforts to restrain emissions (IPCC, 2014b). There are several climate
22 forecasts with global information. However, each of this model is known to produce
23 different biases, according to the spatial region (Knutti *et al.*, 2008). Here, we considered
24 the HadGEM2-ES (HE) model, the CMIP5 climate forecast with least biased estimates

1 of current temperature and precipitation for the Northern South America (Sierra, Arias,
2 & Vieira, 2015).

3 We reduced the dimensionality of bioclimate predictors to avoid overfitting of
4 species' distribution models, due to the excessive number of variables, with a Principal
5 Component Analysis - PCA. The PCA extracts dominant patterns in a group of predictor
6 variables to later calibrate the model (Reimann *et al.*, 2011). Designed to summarize
7 predictors information into eigenvectors, the PCA removes issues of multicollinearity
8 among model predictors, because PC eigenvectors are orthogonal. We used the
9 eigenvector scores that captured 95% of bioclimate information, thus not the original
10 variables, used to calibrate the species' distribution models in this work. Then, we
11 projected the climate information referred to the future onto the basis coordinates (linear
12 combination) of the PCA, to respect the original eigenvectors rotation.

13

14 **Species' Distribution Modeling**

15 Potential species' distributions were modeled according to the relationship between point-
16 localities and current climate variables. Such models were then projected into future
17 climate change scenarios to predict climate-driven shifts in species' distribution. Despite
18 our thorough data cleaning process, positional errors might still exist in our occurrence
19 dataset, which might ultimately affect the predictive performance of species' distribution
20 models (Graham *et al.*, 2008). However, machine learning techniques, such as maximum
21 entropy and boosted regression trees, are robust to the presence of a moderate level of
22 locational error and still provide useful predictions of species' distributions (Graham *et*
23 *al.*, 2008). Maximum entropy (MaxEnt) also provides the additional advantage of
24 balancing goodness-of-fit with model complexity, by "tuning" model settings in a

1 relatively user-friendly way (Muscarella *et al.*, 2014). Model specification and the choice
2 of modeling parameters affect the performance of species' distribution models (Araújo &
3 Guisan, 2006; Merow, Smith, & Silander, 2013). Model overfitting, for example, is
4 alleviated by species-specific smoothing of settings and also by calibrating and evaluating
5 models with independent datasets (Muscarella *et al.*, 2014).

6 We used MaxEnt, which is a presence-background method in which the species'
7 distribution is an unknown probability along the full background points (non-negative
8 values that add up to one) (Elith *et al.*, 2011). The values of predictor variables at localities
9 with presences restrict the unknown distributions so that the average and variance values
10 of environmental predictor should be therefore close to empirical values (Graham *et al.*,
11 2008; Merow, Smith, & Silander, 2013). The maximum likelihood approach
12 approximates the unknown distribution using the background point distribution that
13 maximizes the entropy subjected to such constraints (Phillips & Dudík, 2008). Therefore,
14 MaxEnt compares the relationship between environmental conditions from species'
15 presences to the conditions along the full background. However, the complexity of the fit
16 to the observed values can be adjusted by transformations on the original predictor values
17 ("feature classes" or FCs) (Peterson, 2011; Muscarella *et al.*, 2014)

18 In this work, we built species' distribution models that potentially maximized
19 model performance. First, we used a species-specific background. Limiting the study area
20 to the regions that are accessible for a species is crucial for the outcome of species'
21 distribution models (Barve *et al.*, 2011). Therefore, the study area should only include the
22 climate conditions the species probably experience and/or are restricted to, due to
23 biogeographical limitations. To do so, our background was defined as the bounding box
24 of each species' occurrence points, plus additional 5 degrees to each bound, a value close
25 to the average dispersal capacity for Amazonian primates (Table 1). Environmental layers

1 were then cropped to match the study extent and 10,000 background points were sampled
2 from background extent rasters (only one per cell, without replacement) (Barbet-Massin
3 *et al.*, 2012).

4 Once we were interested not only in the species' potential distribution but also on
5 the likely effects of climate change, we used the "block" method to partition the
6 environmental dataset. We did so because the block method is ideal for studies that
7 require transferability across space or time and also to account for spatial autocorrelation
8 in species' occurrence dataset (Muscarella *et al.*, 2014). In this method, data is partitioned
9 by the latitude and longitude lines that divide occurrence localities as equally as possible.
10 Occurrences and background are attributed to a bin depending on their location. Then, we
11 iteratively ran k models, with $k-1$ bins for training and the rest for testing. Metrics of
12 model evaluation are summarized across the k iterations (Muscarella *et al.*, 2014).

13 To enhance model performance, we "tuned" MaxEnt models, by selecting among
14 models with different combinations of feature classes - L, LQ, H, LHQ, LQHP, LQHPT
15 (L = linear, Q = quadratic, H = hinge, P = product, T = threshold) (Muscarella *et al.*,
16 2014). The model most supported by each species' occurrence dataset was chosen by the
17 Akaike Information Criteria (Akaike, 1974), corrected for small sample sizes (AICc), a
18 presence-dependent continuous metric recommended to assess the performance of our
19 models (Lawson *et al.*, 2014). "Tuned" models selected by AICc are less overfitted and
20 exhibit lower omission rates than MaxEnt default models (Muscarella *et al.*, 2014).

21 To calculate potential range shifts, we converted continuous predictions of climate
22 suitability into binary maps of "presence" and "absence". We used the minimum
23 predicted value of climate suitability across presence points - the lower presence threshold
24 (Pearson *et al.*, 2007) - as the threshold for converting continuous into binary predictions.

1 Although this is a simple and relatively less used threshold in species' distribution
2 modeling literature, it can potentially uncover informative distributional areas for species
3 with small numbers of occurrence records (Pearson *et al.*, 2007). Much of Amazonian
4 biodiversity presents extensive distributional knowledge gaps (Bush & Lovejoy, 2007)
5 due to access constraint, which in turn creates strong sampling biases towards the
6 neighborhood of cities and the main rivers (Schulman, Toivonen, & Ruokolainen, 2007).
7 Other traditionally used thresholds, such as maximizing the sum of sensitivity and
8 specificity (Peterson *et al.*, 2011), in addition to the small number of occurrence records
9 for some of the species analyzed here, could generate overly stringent predictions, which
10 lead out a much of species' potential distribution. Furthermore, the lower presence
11 threshold has a high success rate in jackknife tests (Pearson *et al.*, 2007), such as the ones
12 used here.

13

14 **Biotic velocity**

15 Climate-driven distributional shifts abound in paleontological records, suggesting that
16 species might move in response to climate change (Schloss, Nuñez, & Lawler, 2012)
17 towards regions with optimal climate conditions (Keppel *et al.*, 2012). Such
18 environments, called "climate refugia", probably provide the best survival opportunities
19 for species in face of climate change (Keppel *et al.*, 2012; Gavin *et al.*, 2014; Ribeiro,
20 Sales, & Loyola, 2018). Besides moving directionally, species must keep pace with
21 climate change velocity to track optimal environmental conditions, which can only if they
22 move above a minimum velocity (Carroll *et al.*, 2015). Therefore, to assess species-
23 specific responses to climate change in terms of range movements, we calculated the
24 "biotic velocity".

1 The biotic velocity corresponds to the time-calibrated distance from a suitable site
2 in the present and the nearest site projected to be climatically similar to the species'
3 optimal conditions in future projected climates (Carroll *et al.*, 2015). Biotic velocity is
4 therefore the minimum speed at which species have to migrate to keep track of its optimal
5 climate conditions (Carroll *et al.*, 2015). Comparison between species' maximum
6 dispersal capacity and the biotic velocity required to maintain its climatic fitness can thus
7 indicate a species' ability to track their climatic niches (Schloss, Nuñez, & Lawler, 2012).
8 Although there are several methods to evaluate the velocity of climate change versus
9 species' dispersal limits (Hamann *et al.*, 2015), the biotic velocity is probably one of the
10 most straightforward of them. A range prediction for the current time is compared to its
11 future counterpart and the geographical distance between both environments is then
12 measured (Ordonez & Williams, 2013). Therefore, we calculated the biotic velocity as
13 the minimum speed at which a species might move from the centroid of its current range
14 towards the centroid of its projected future range. Despite its usefulness, the biotic
15 velocity is however based on a binary classification of the landscape (suitable *vs* non-
16 suitable) and thus penalizes information on local habitat gradients, to incorporate only
17 large-scale range shift patterns (Carroll *et al.*, 2015).

18 To evaluate whether species could track their optimal climatic conditions, biotic
19 velocity was then compared to a measure of species' maximum dispersal velocity,
20 obtained from Schloss *et al.* (2012). For each species, dispersal velocity was modeled as
21 a function of body mass, diet type, and the successive time between generations. When
22 the species-specific value of dispersal velocity was not available, we used the data from
23 its sister taxa, following Perelman *et al.* (2011). Each climate scenario produced a map of
24 potential distribution *per* species. A species was considered able to track its climatic niche
25 when dispersal velocity was larger than biotic velocity, taken for each climate scenario.

1 **Climate change exposure**

2 As climate changes, species may be exposed to novel climatic conditions (John W.
3 Williams & Jackson, 2007), exceeding the values to which they are already adapted
4 (Ameca y Juárez et al., 2013). Across species' ranges, populations may be exposed to
5 different non-analog climatic conditions, in a geographically structured pattern of
6 exposure to climate change (Ribeiro *et al.*, 2016). Here, we quantified the local exposure
7 of primates to climate change across species' ranges within the Amazon basin. We did so
8 by identifying the amplitude (maximum and minimum limits) of climate predictors within
9 the entire range of each species. Such amplitude values characterize the climate
10 conditions of where the species is known to occur. Then, we identified cells within the
11 species' range that are likely to exceed the current climate conditions in future scenarios
12 of climate change (Ribeiro et al., 2016). Areas within species' ranges where future climate
13 conditions are likely to exceed such current climatic variability will, therefore, expose
14 species to non-analog climates, i.e. conditions to which species are supposedly not
15 accustomed.

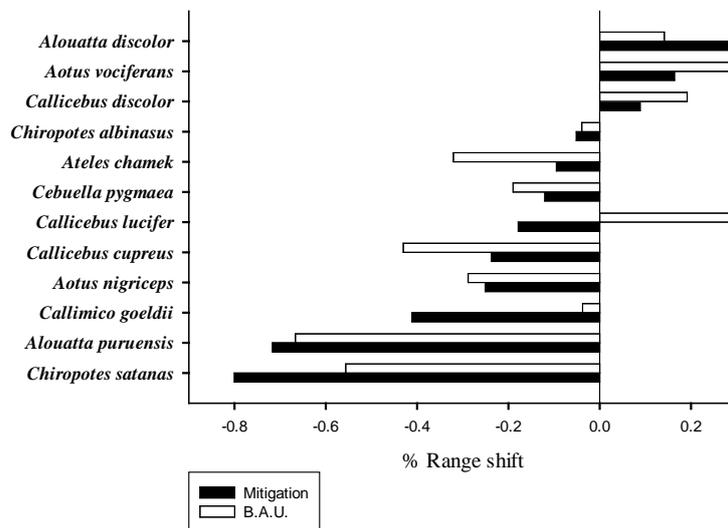
16 We calculated the percent of each species' range that will be exposed to non-
17 analog climate conditions, as described above. In addition, species that were exposed to
18 extreme climatic conditions in more than 80% of their current ranges were classified as
19 "critically exposed" (Ribeiro *et al.*, 2016). Finally, we mapped the magnitude of exposure
20 to climate change according to species richness, to highlight areas likely to exceed the
21 thermal amplitude, i.e. variation in climatic conditions across a species' range of many
22 species. Such regions will impose a greater number of species to harsher climate
23 conditions and may flag "climate change hotspots". Climate metrics were the ones
24 captured in the PCA axes explaining 95% of the variance, described in the "Species'

1 Distribution Modeling” Methods section, which were: mean diurnal range (Bio 2);
 2 temperature seasonality (Bio 4), mean temperature of warmest quarter (Bio 10),
 3 precipitation of driest month (Bio 14), and precipitation of warmest quarter (Bio18).

4

5 Results

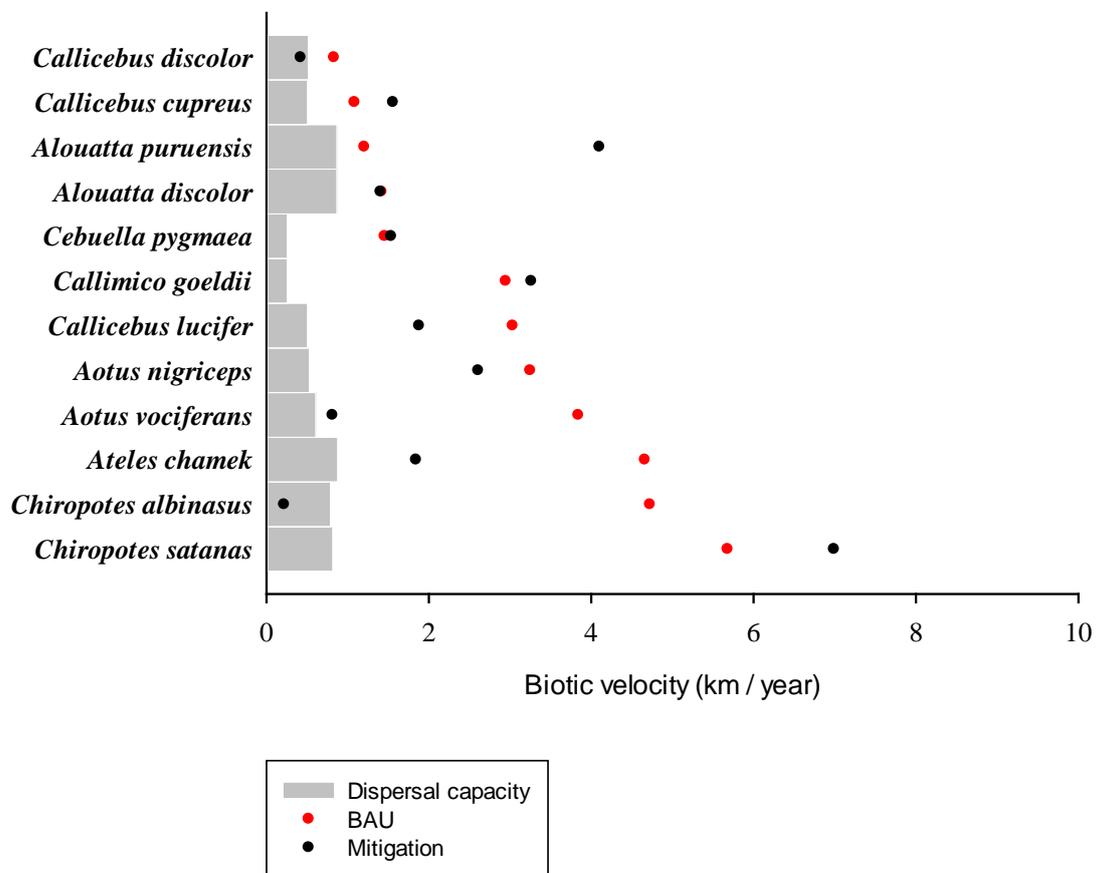
6 Predicted response to climate change greatly varied among the studied species. Most
 7 species were likely to lose suitable climate area on at least one greenhouse gas emission
 8 scenario (Fig. 2, Table 1). Four species were, however, predicted to benefit from climate
 9 change. Interestingly, one species seemed to expand their suitable climate areas only in
 10 the B.A.U. scenario (e.g. *Callicebus lucifer*). On the other hand, some species seemed to
 11 take advantage of some climate change on both greenhouse gas emission scenarios (e.g.
 12 *Alouatta discolor*, *Aotus vociferans*, *Callicebus discolor*). There was no pattern on
 13 expected range shift as for greenhouse gas emission scenarios.



14

15 **Fig. 2** Expected range shift on primate distribution in face of climate change. Percent range shift expected for
 16 Mitigation greenhouse gas emission scenario (*rcp 2.6*) and for Business as usual scenario (*rcp 85*). Bars indicate the
 17 predicted % variation in range size.

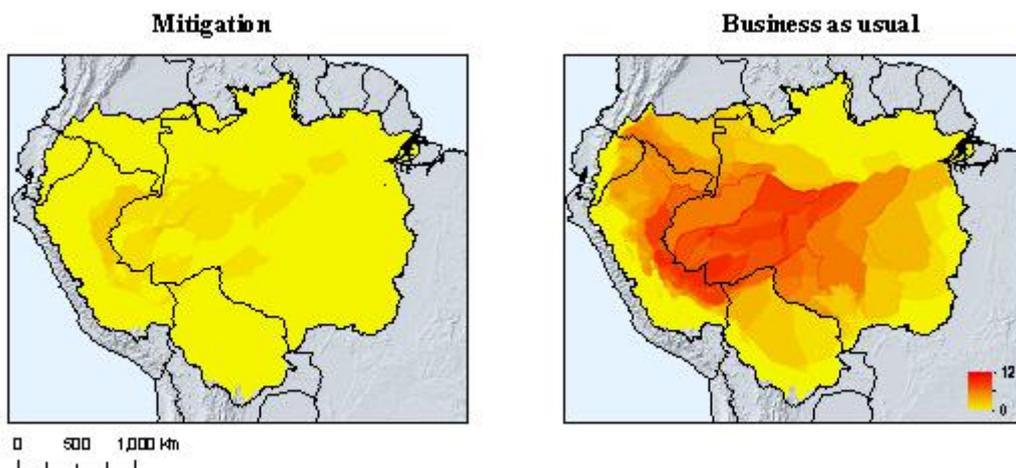
1 Many of the species studied here were not be able to keep pace with projected
 2 climate change, to track their suitable climates (Fig. 3). The difference between species'
 3 dispersal capacity and climate change dispersal requirements was usually greater on the
 4 B.A.U. scenario, i.e. species' climate niche will move in a faster pace. However, some
 5 were able to keep pace with climate change in the Mitigation scenario (e.g. *Callicebus*
 6 *discolor* and *Chiropotes albinasus*). Overall, dispersal capacity of most species was
 7 smaller than dispersal requirements in face of climate change.



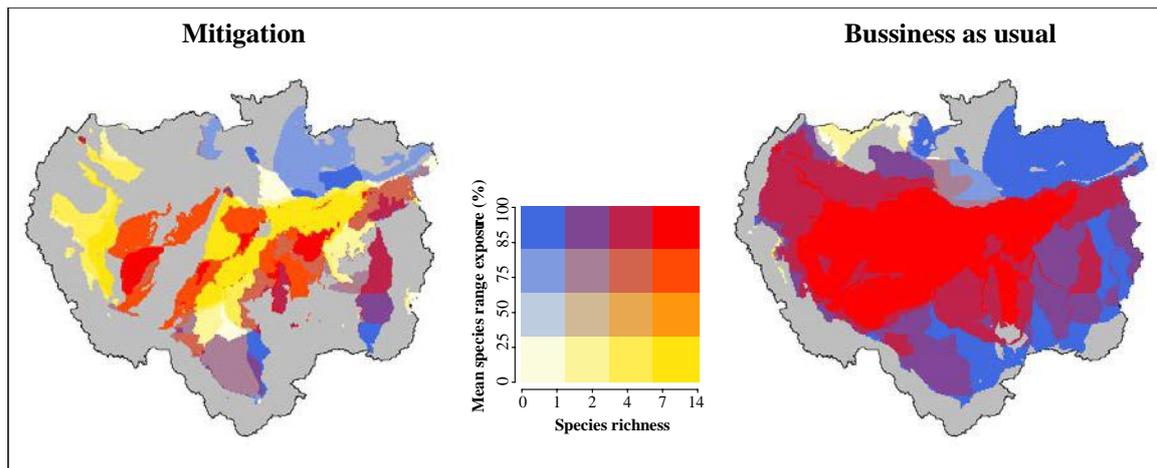
8

9 **Fig. 3** Biotic velocity in relation to primate species' maximum dispersal capacity. Grey horizontal bars indicate the
 10 maximum dispersal capacity a primate species can move, modeled as a function of body size, diet and generation length
 11 (Schloss, Nuñez, & Lawler, 2012). Circles indicate the average speed that the centroid of species' distribution (here
 12 considered to contain the optimal environmental conditions) will move from current time to the year 2070. Black circles
 13 refer to a Mitigation scenario (*rcp 2.6*) of greenhouse gas emission. Red circles refer to a Business as usual (*rcp 8.5*)
 14 greenhouse gas emission scenario.

1 Projections of future climate exposed Amazonian primates to environmental
2 conditions that exceed their current variation in climatic conditions across their ranges
3 (Table S1). Most critically exposed primate species occurred in the central and western
4 portions of the Amazon basin, especially southwards the Amazon river (Fig. 4). Patterns
5 of exposure to climate change across species' ranges were quite similar among climatic
6 variables. In the Mitigation scenario of greenhouse gas emission, 39% of all species (29
7 out of 75) were likely be exposed to non-analog climate conditions in the year 2070, for
8 at least one climatic variable. In the B.A.U. scenario, the number of critically-exposed
9 species raises to 92% of the analyzed species (69 out of 75). The magnitude of exposure
10 to climate change was also affected by the greenhouse gas scenarios (Fig. 5). In the
11 B.A.U., several species were be highly exposed to non-analog conditions across the entire
12 Amazon territory.



13
14 **Fig. 4** Species richness of primates that are critically-exposed to climate change. In the Mitigation scenario, the
15 highest richness of critically-exposed species ($n = 3$) is much smaller than that of the Business as usual ($n = 12$).
16 Critically-exposed species are those exposed to non-analog climates in more than 80% of their geographical ranges, for
17 at least one climate variable.
18



1

2 **Fig. 5** Magnitude of exposure to climate change of Amazon primate species. Exposure to climate change is the
 3 average of the percent of each species' range that is exposed in a given cell. In the Business as usual scenario, most
 4 species will be exposed to non-analog climates in a large portion of their territories.

5

6 **Discussion**

7 Incorporating the multiple dimensions of climate change can be a step forward in debates
 8 regarding future threats to biodiversity conservation. Lack of consensus on accurate
 9 methods and the many sources of uncertainty (Diniz-Filho *et al.*, 2009) hamper
 10 comprehensive assessments about the impacts of climate change on species' distribution
 11 (Rocchini *et al.*, 2011). Here, we used three distinct lines of evidence (range shifts, biotic
 12 velocity, and exposure to non-analog climates) to predict how climate change will affect
 13 the potentially threatened group of the Amazonian primates. Range shift did not exhibit
 14 a consistent pattern among the studied species, with some of them increasing the area
 15 predicted as climatically suitable in different scenarios of climate change. Other metrics,
 16 however, indicate that Amazonian primates face a potentially great threat from climate
 17 change.

18 Predicted range contraction in response to climate change is a pattern found in
 19 primates around the world. Here, most species were indeed likely to exhibit some

1 reduction in suitable climate area. Such range contractions can ultimately lead to local
2 extinction (Urban, 2015), by causing physiological stress on populations inhabiting non-
3 optimal climates (Dillon, Wang, & Huey, 2010). Some species, however, seem to benefit
4 from climate change, with predicted range expansion in one or both greenhouse gas
5 emission scenarios. Range expansion could, in such cases, promote colonization of
6 unoccupied territories and increase population viability in face of climate change. Climate
7 change may, therefore, modify the balance between species that are considered “native”
8 and “non-native” (Mainali *et al.*, 2015), by allowing primate range expansion in this case.
9 Species’ interactions and the existence of permeable migratory routes, in addition to
10 climate suitability, will determine whether such range expansion will be successful.

11 The expected expansion of some species’ ranges is yet not good news because the
12 primates expected to gain climate areas do not seem capable to track their suitable areas.
13 Although the total area that potentially enables positive population growth may expand,
14 species might not be able to get there. Range shift *per se* considers only the total area that
15 is climatically suitable for a species, not its spatial configuration. The optimal
16 environment for Amazonian primates will be displaced and the velocity of this change
17 will exceed the maximum dispersal capacity of most species analyzed here. This pattern
18 is also found for most primates worldwide (Schloss, Nuñez, & Lawler, 2012). In addition
19 to that limited tracking ability, the existence of climate-induced feedbacks on
20 deforestation and fire dynamics in the Amazon (Malhi *et al.*, 2008; Coe *et al.*, 2013),
21 coupled with increased deforestation rates in recent years (Fearnside, 2015), may disrupt
22 landscape dispersal routes for primates.

23 Adding the evidence of exposure to non-analog climates does not bring good news
24 to Amazonian primates. Exposure to climate conditions to which a primate species is not
25 adapted causes physiological stress, fitness reduction and behavioral change (Gould,

1 Sussman, & Sauther, 1999; Milton & Giacalone, 2014). We found that Amazonian
2 primates might not be able to track their optimal environment when exposed to novel
3 climate conditions. In a recent meta-analysis about the effects of climate change on the
4 distribution of threatened species, all primate studies demonstrated negative responses
5 (Pacifci *et al.*, 2017). Contrary to other studies (e.g. Pearson *et al.*, 2014), exposure to
6 climate change within species' ranges was significantly larger in the Business as usual
7 scenario. However, range shift and biotic velocity did not differ substantially between
8 greenhouse gas scenarios. This suggests that actions aimed at mitigation of climate
9 change effects via reductions in greenhouse gas emission will have a positive effect on
10 biodiversity conservation but may not be sufficient to prevent climate-driven extinctions.

11 Although the likely effects of climate change on Amazonian primates creates a
12 dismal scenario, not everything is lost. Conservation units might act as “stepping stones”
13 and facilitate climate-driven migrations. As temperatures increase, conservation units
14 might, therefore, provide habitat conditions that permit species' temporary persistence,
15 enough to allow effective movements towards more suitable climates. In Brazil, where
16 most of Amazon deforestation occurs (Soares-Filho *et al.*, 2006), the network of protected
17 areas covers more than 23% of its territory (Veríssimo *et al.*, 2011). Protected areas,
18 besides buffering against the local effects of climate change (Thomas & Gillingham,
19 2015), might also enhance species' long-term survival by giving them a chance to reach
20 their newly suitable habitats. Therefore, species may persist in fragmented landscapes
21 exposed to climate change, by tracking their suitable environment via migration through
22 protected areas.

23 To sum up, we analyzed the three most widely used approaches to understand how
24 climate change may affect the distribution of the potentially threatened group of
25 Amazonian primates. The overall picture for the studied taxa is not good in terms of

1 vulnerability to climate change. Primates endemic to the Amazon basin are expected to
2 experience climate-driven range shifts and are not likely to track their suitable climates.
3 Confined to unsuitable sites, those primates will be exposed to novel climate conditions
4 in most of their ranges. The combination of such climate change effects will probably
5 cause physiological stress and deleterious effects on population dynamics and fitness
6 (Cahill *et al.*, 2012). Usually neglected in conservation risk assessments, climate change
7 is therefore an imminent threat to Amazon primates, which might face a future harsher
8 than expected so far.

9

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18

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22

Table 1 Summary results of three climate change metrics, calculated for 12 primate species that are endemic to the Amazon Basin. Range shift indicates the percent variation in the area predicted as suitable for species. Biotic velocity is the minimum speed at which species might migrate to track their suitable climate conditions. All metrics were modeled as a function of climate predictors from two greenhouse gas emission expectations for the year 2070: Mitigation (*rcp 26*) and Business as usual (*rcp 85*). Dispersal velocity was taken from Schloss (2012) and is expressed in kilometers per year .

Species binomial	Number of records	Range shift		Biotic velocity		Dispersal Velocity (km/yr)
		Mitigation	B.A.U.	Mitigation	B.A.U.	
<i>Alouatta discolor</i>	68	0.04	0.13	1.21	2.42	0.87
<i>Alouatta puruensis</i>	16	-0.29	-0.25	0.44	1.93	0.87
<i>Aotus nigriceps</i>	60	-0.16	-0.07	0.89	2.13	0.53
<i>Aotus vociferans</i>	27	0.25	0.20	1.45	4.02	0.61
<i>Ateles chamek</i>	229	-0.09	-0.06	0.90	0.17	0.88
<i>Callicebus cupreus</i>	63	-0.28	-0.11	1.29	2.08	0.51
<i>Callicebus discolor</i>	15	0.16	-0.17	1.32	2.09	0.52
<i>Callicebus lucifer</i>	102	0.05	-0.11	0.64	1.43	0.51
<i>Callimico goeldii</i>	86	0.07	-0.13	1.43	1.34	0.26
<i>Cebuella pygmaea</i>	125	-0.05	-0.01	0.23	0.60	0.26
<i>Chiropotes albinasus</i>	50	-0.07	-0.02	0.66	1.35	0.79
Total						

Capítulo 4

Sales LP, Ribeiro BR, Hayward MW, Paglia A, Passamani M & Loyola RD (2017). **Niche conservatism and the invasive potential of the wild boar.**
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Niche conservatism and the invasive potential of the wild boar

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Abstract

1. Niche conservatism, i.e. the retention of a species' fundamental niche through evolutionary time, is cornerstone for biological invasion assessments. The fact that species tend to maintain their original climate niche allows predictive maps of invasion risk to anticipate potential invadable areas. Unravelling the mechanisms driving niche shifts can shed light on the management of invasive species.
2. Here, we assessed niche shifts in one of the world's worst invasive species: the wild boar *Sus scrofa*. We also predicted potential invadable areas based on an ensemble of three ecological niche modelling methods, and evaluated the performance of models calibrated with native vs. pooled (native plus invaded) species records. By disentangling the drivers of change on the exotic wild boar population's niches, we found strong evidence for niche conservatism during biological invasion.
3. Ecological niche models calibrated with both native and pooled range records predicted convergent areas. Also, observed niche shifts are mostly explained by niche unfilling, i.e. there are unoccupied areas in the exotic range where climate is analogous to the native range.
4. Niche unfilling is expected as result of recent colonization and ongoing dispersal, and was potentially stronger for the Neotropics, where a recent wave of introductions for pig-farming and game-hunting has led to high wild boar population growth rates. The invasive potential of wild boar in the Neotropics is probably higher than in other regions, which has profound management implications if we are to prevent their invasion into species-rich areas, such as Amazonia, coupled with expansion of African swine fever and possibly great economic losses.
5. Although the originally Eurasian-wide distribution suggests a pre-adaptation to a wide array of climates, the wild boar world-wide invasion does not exhibit evidence of niche evolution. The invasive potential of the wild boar therefore probably lies on the reproductive, dietary and morphological characteristics of this species, coupled with behavioural thermoregulation.

KEYWORDS

biological invasion, conservation biogeography, ecological niche models, feral pig, invasive alien species

1 | INTRODUCTION

Assessing invasion risk and managing invasive species is a world-wide conservation, economic and social issue (Strubbe, Beauchard, & Matthysen, 2015) and niche shifts during biological invasions are one of the hot topics of current scientific debate (Guisan, Petitpierre, Broennimann, Daehler, & Kueffer, 2014). In fact, understanding processes that drive changes in species' fundamental niches is important for ecology and evolution (Pyrone, Costa, Patten, & Burbrink, 2015; Wiens & Graham, 2005), but is pivotal for understanding biological invasions (Broennimann et al., 2007; Guisan et al., 2014). A species' "fundamental niche" can be defined as the set of environmental conditions where a species can persist indefinitely (Hutchinson, 1957). Competition and other negative interactions lead to reductions in the fundamental niche to create the "realized niche" (Hutchinson, 1957), or the "biotically reduced niche" (Peterson et al., 2011). In this sense, the "invadable niche" would be the portions of the fundamental niche, non-restricted by biotic interactions, but unreachable due to geographic dispersal limitations (Peterson et al., 2011).

Potential invadable areas have historically been assessed through the study or models of ecological niche, which are based on the assumption that climatic similarity between native and exotic ranges is an a priori condition for the establishment of an alien species (Jiménez-Valverde et al., 2011; Peterson, 2003; Thuiller et al., 2005). This assumption is possible because species' fundamental niches are not likely to change over short-to-moderate time spans (Peterson, 2011). Given that these climatic niches exhibit little or no differentiation, the process of niche conservatism is expected during biological invasion (Peterson, 2003, 2011). Therefore, by determining climate tolerances from species' native geographic range, climatically matching regions in non-native ranges can be assessed and mapped (Jiménez-Valverde et al., 2011; Thuiller et al., 2005). If climatic conditions therefore pose long-term and stable constraints on species geographic distribution, potential invadable areas can be anticipated with relative confidence (Peterson, 2003).

Although exciting in their potential for guiding management decisions, ecological niche models can only accurately predict potential invadable areas when niche conservatism is supported. However, initial studies on niche conservatism revealed contrasting patterns of niche shift due to tests of different null hypotheses (Graham, Ron, Santos, Schneider, & Moritz, 2004; Peterson, 1999). After Warren, Glor, and Turelli (2008), niche conservatism was thought to be best measured in terms of statistical difference, i.e. "niche similarity" and "niche equivalence." Despite their transparency, the similarity and equivalence tests only reveal statistically significant differences on species' climate niches, but not the causes underlying such niche shifts (Guisan et al., 2014; Petitpierre et al., 2012; Strubbe, Broennimann, Chiron, & Matthysen, 2013). Hence, absolute values of "equivalence" and "similarity" have little biological meaning unless niche shifts are disentangled into their main drivers of change, namely "niche unfilling" and "niche expansion" (Broennimann et al., 2012; Guisan et al., 2014). In addition to detecting niche shifts, decomposing the changes in terms of niche expansion and unfilling can shed substantial light on the

ecological processes driving biological invasions (Broennimann et al., 2012; Guisan et al., 2014).

Currently present in all continents, except in Antarctica, the wild boar is a member of the family Suidae from Eurasia and North Africa. The wild boar is the oldest intentionally introduced mammal species (for bush meat) and is now one of the most widely distributed species in the world (Long, 2003). Biological traits of the species partially explain its invasive success. Wild boars have fast population growth rates (Taylor, Hellgren, Gabor, & Ilse, 1998) and feed opportunistically on many plants and animals (Ballari & Barrios-García, 2014). Population top-down control by predators is limited throughout its native and exotic ranges due to world-wide small density of large carnivores (Barrios-García & Ballari, 2012; Estes et al., 2011) and widespread defaunation of natural areas (Dirzo et al., 2014). Wild boars also possess weaponry and a low centre of gravity that prevents their preferential capture by all but the largest felids (Hayward, Jędrzejewski, & Jędrzejewska, 2012). Further, their extensive native distribution across Eurasia and North Africa suggests a pre-adaptation to a wide array of climatic conditions (Barrios-García & Ballari, 2012; Long, 2003). In this paper, we assessed the invasive potential of the wild boar *Sus scrofa* globally. Our aim was to test whether wild boars and their hybrids have substantially changed their climatic niches during their global invasion. In addition, we mapped potential invadable areas, where allowed by niche conservatism assumptions.

2 | MATERIALS AND METHODS

2.1 | The wild boar

Wild boars (*S. scrofa*) are ecosystem engineers that turn extensive areas of leaf litter, soil and vegetation, which may ultimately affect fire regimes (Hayward et al., 2016). While the impact of that rooting behaviour on biodiversity is controversial (Siemann, Carrillo, Gabler, Zipp, & Rogers, 2009), the same is not true for economic losses. Wild boar rooting damages crops and husbandry, causing economic losses up to 800 million dollars a year in the USA alone (Pimentel, Zuniga, & Morrison, 2005). Wild boars damage various vegetable crops (Ballari & Barrios-García, 2014; Herrero, García-Serrano, Couto, Ortuño, & García-González, 2006; Pimentel et al., 2005) and also transmit and are reservoirs for several diseases to humans and livestock (Barasona et al., 2014). Impacts of wild boars on wildlife span predation (Ballari & Barrios-García, 2014) to habitat and nest destruction (Barrios-García & Ballari, 2012). Competitive interaction with wild boar leads to native species exclusion, especially peccaries (Gabor & Hellgren, 2000) and other species of the genus *Sus* (Frantz et al., 2016). Despite those negative effects, in some particular areas—such as the Brazilian Pantanal—wild boars are supposed to be a preferential target for bush meat hunters and may thus release native peccaries from over-harvesting (Desbiez, Keuroghlian, Piovezan, & Bodmer, 2011), although this lacks empirical validation.

As they are primarily raised for meat, domesticated pig breeds were selected to increase traits, such as fecundity and population growth rate. Escaped domestic pigs hybridize with wild populations and transmit to them those artificially selected traits, which enhances

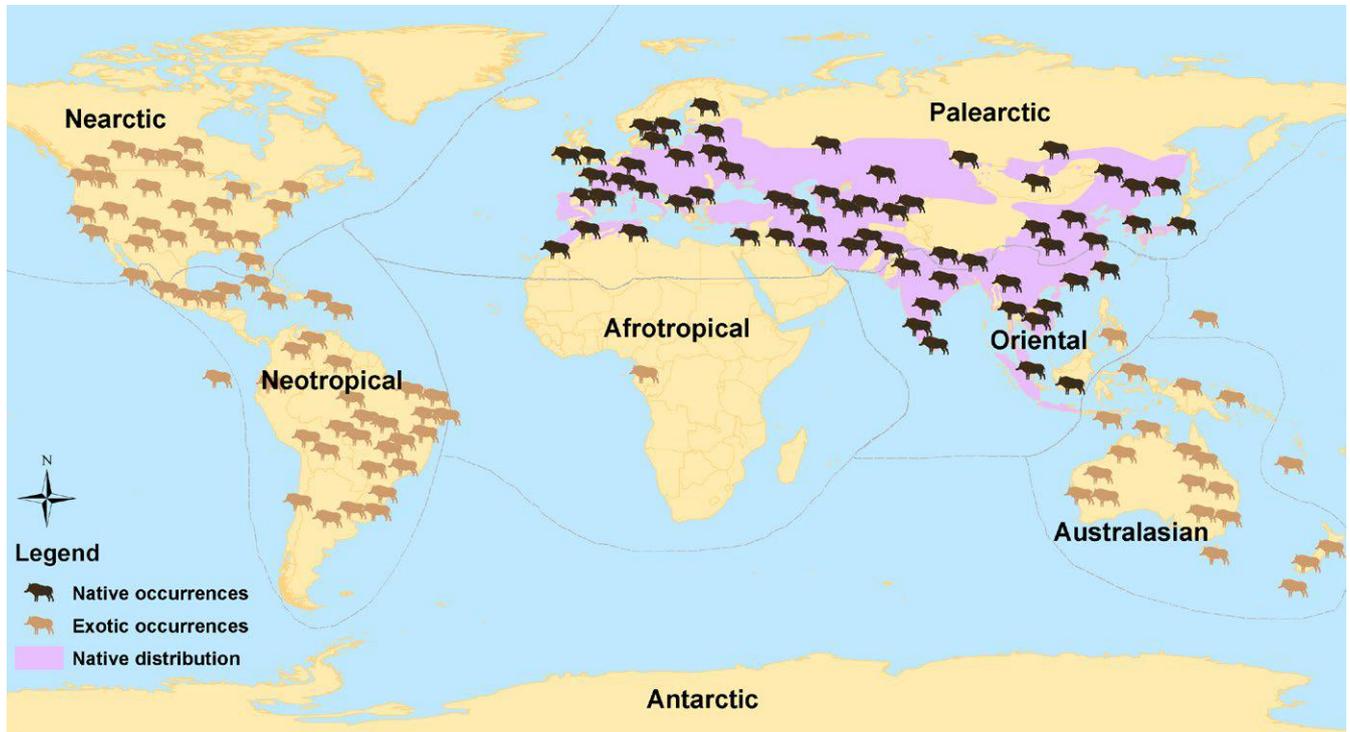


FIGURE 1 Distribution of wild boar *Sus scrofa* around the world. Violet polygon indicates the species' native distribution, according to the IUCN. Dark pigs indicate wild boar occurrences considered native in this study, and pale pigs represent occurrences considered exotic. Only some occurrences used in this work are shown [Colour figure can be viewed at wileyonlinelibrary.com]

hybrid fitness (Fulgione et al., 2016). Hybrid pigs have therefore inherited higher fertility rates and larger litter size from their domestic relatives (Fulgione et al., 2016), while retaining sociability, coupled with associated large group herds, and flexible climatic tolerance from their wild ancestors (Marshall, Dobney, Denham, & Capriles, 2014). The impact of hybrid pigs on both biodiversity and the economy can therefore be even higher than that of wild populations, although those effects are still to be addressed in scientific literature (Barrios-Garcia & Ballari, 2012).

2.2 | Data collection

We collected occurrence data for the wild boar and its hybrids (henceforth jointly named “wild boars”) from different virtual databases, namely the Global Biodiversity Information Facility (GBIF; www.gbif.org), the VertNet (www.vertnet.org), the Biodiversity Information Serving Our Nation (BISON; bison.usgs.gov), the Berkeley Ecoinformatics Engine (Ecoengine; ecoengine.berkeley.edu), the iNaturalist (www.inaturalist.org) and the Invasive Species Compendium (ICS; www.cabi.org/isc). In addition, we exhaustively searched non-formal sources of wild boar occurrence information, primarily game hunting or wildlife sightseeing websites, such as the “Rede Aqui Tem Javali” in Brazil (aquitemjavali.blogspot.com.br), the “Wild Boars in Canada” (wildboarcanada.ca), and “Feral Scan” in Australia (www.feralscan.org.au). A strong geographical bias towards European countries was found in the distribution of wild boar occurrence records within native distribution. Thus, to improve characterization of the

niche space, we did a literature survey on wild boar occurrences from less sampled regions within the native distribution (see Table S1). All occurrences from virtual databases were downloaded with the function `occ` from R package (R Core Team, 2016) `spocc` (Scott, Ram, Hart, & Chamberlain, 2016), and occurrences from other sources were downloaded manually.

Native distribution was defined based on the IUCN range map for *Sus scrofa* (Oliver & Leus, 2008), obtained at www.iucnredlist.org. The use of IUCN range maps to identify species native distribution is considered useful for large-scale modelling studies, as well as to conservation planning, management and wildlife monitoring (Rodrigues, Pilgrim, Lamoreux, Hoffmann, & Brooks, 2006). We also included occurrences up to 200 km from the existing border of the species native range map. Occurrences farther than that to the native polygon were removed from the “native dataset”. By doing so, we accounted for possible uncertainties on the borders of IUCN range maps, to consider highly updated—though perhaps imprecise—species records. A total of 2283 occurrence records was then collected, from which 688 belonged to native distribution, 168 of them to the Australian region, 609 to the Nearctic region, and 736 to the Neotropical region (Figure 1 and Figure S1), covering years from 1970 to 2016. Remaining occurrences were scattered around the globe and not used in this study. Spatial autocorrelation was minimized by randomly removing occurrences less than 0.5 degree of latitude/longitude from each other, from the whole dataset (both native and exotic ranges). This procedure has minimized problems related to spatial autocorrelation in other niche shift studies at geographic scale (Broennimann et al., 2012; Strubbe et al., 2015).

Climate data were produced from interpolation of ground weather stations, from year 1950 to 2000, downloaded from the WorldClim website (www.worldclim.org/version1) and downscaled to 0.5 degrees of latitude/longitude. All WorldClim bioclimatic predictors were used for tests of niche equivalence/similarity between native and exotic ranges, but only five were used to predict potential invadable areas for the wild boar. A factor analysis with Varimax rotation was used to select uncorrelated variables and to avoid collinearity issues (Table S2). Five non-correlated variables were used to fit ecological niche models: BIO2: Mean Diurnal Range (Mean of monthly [max temp–min temp]); BIO5: Max Temperature of Warmest Month; BIO14: Precipitation of Driest Month; BIO15: Precipitation Seasonality (Coefficient of Variation); BIO16: Precipitation of Wettest Quarter.

2.3 | Niche equivalence/similarity tests

We used all predictors at first because tests of niche equivalence/similarity are best performed with the PCA-env method (Broennimann et al., 2012). The PCA-env is calibrated with the full background, i.e. environmental conditions of both native and exotic range, and reduces environmental data dimensionality to the first two main axes in a principal component analysis (PCA). That full background is then compared to the areas effectively occupied by species on each of its ranges. Niche overlap between native and exotic range is then measured in terms of Schoener's *D*, which ranges from no overlap, 0, to complete overlap, 1 (Schoener, 1974; Warren et al., 2008).

The observed niche overlap is then compared to random measures of niche overlap. Niche equivalence and similarity tests are based on comparisons of observed measures of niche overlap to random overlap values, although different null hypotheses are thereby tested. Niche equivalence tests, as initially proposed by Graham et al. (2004), ask whether the compared niches are indistinguishable from each other. Rejection of the null hypothesis on niche equivalence tests indicates that native and exotic niches are not identical (Broennimann et al., 2012; Strubbe et al., 2015). Niche similarity tests, on other hand, were first used in Peterson (1999) work, and test whether niche models calibrated for one species (or population, in our case) predict other species' occurrences better than expected by chance. The niche similarity null hypothesis is that of retained niche resemblance and its rejection indicates that niches are more different than expected by chance. Null hypotheses tests were repeated 1,000 times for each biogeographical region and *p*-values were computed at a 5% level of confidence.

Following Broennimann et al. (2012), niche changes between native and exotic populations were directly measured in a gridded environmental space, not in the geographic space. Kernel density functions were used to produce smoothed densities of both occurrences and environmental availability. Explicitly incorporating environmental availability into niche shift measures reduces erroneous detections of niche changes due to uneven distribution of climate conditions on native and exotic ranges (Guisan et al., 2014). Niche shift analyses were performed using the *ecospat* R package (Di Cola et al., 2017).

Niche equivalence and similarity tests only verify whether niche shifts have occurred, but do not address their causal mechanisms.

To understand the wild boar invasion process, we disentangled niche changes into the processes of unfilling and expansion. Niche unfilling is observed when some environmental conditions within the native niche are available, but unoccupied in the exotic climate (Guisan et al., 2014). Those unoccupied areas probably result from recent colonization and ongoing dispersal. In niche unfilling, the exotic niche is a subset of the native niche, and the species will eventually occupy all available niche space within the exotic range, unless biological interactions restrict range expansion (Guisan et al., 2014). Niche expansion, on other hand, is the result of occupancy of non-analogous climatic conditions to the native range. In other words, niche expansion is observed when the species occupies climate conditions to which it is not supposedly adapted, based on its native distribution climatic limits. Such occupancy in non-analogous climates is probably due to ecological or evolutionary changes on its fundamental niche (Guisan et al., 2014).

Observed niche expansion can also be the outcome of the constrained nature of a species' realized niche. Across an accessible geographic distribution, a species may not occupy its full fundamental niche due to extant or past biotic interactions (Peterson et al., 2011; Soberón, 2007; Soberón & Peterson, 2005). Also, there may be environmental conditions that are favourable to persistence, but non-existent throughout the species' geographic range (Barve et al., 2011). All those conditions may limit the observed occupancy of certain environmental conditions that do belong to the fundamental niche (Hutchinson, 1957). Therefore, observed niche expansion can also result from occupancy of regions within a species' fundamental niche, but outside its geographically accessible area and/or restricted by negative biotic interactions. Also, the correlative nature of the techniques used to disentangle niche shifts into unfilling and expansion implies that a species niche will be always calibrated using observed occurrences from the realized niche (Guisan et al., 2014). Assessing the whole fundamental niche and knowing for sure all the exact conditions favourable for a species is nearly impossible. Therefore, asserting niche expansions may be a doubtful task.

Predicting potential invadable areas for invasive species is only possible when: (1) changes in a species' climatic niche are not observed or (2) observed niche differences are not caused by evolutionary changes in the species fundamental niche (Jiménez-Valverde et al., 2011; Strubbe et al., 2013, 2015). If the exotic niche is a subset of the native one, and niche shifts are therefore caused by niche unfilling rather than expansion, then an ecological niche model calibrated with climatic conditions where the species is known to occur may accurately predict invasion potential (Jiménez-Valverde et al., 2011; Peterson, 2011; Strubbe et al., 2015). Otherwise, the essential assumption of equilibrium between the species' distribution and climate tolerances is violated (Early & Sax, 2014). In cases where climatic equilibrium is not supported, forecasts of invasion risk based on correlative models may not be reliable (Early & Sax, 2014).

2.4 | Ecological niche models

For cases exhibiting evidence for niche conservatism or niche unfilling as the main driver of niche changes, we predicted potential invadable

areas for the wild boar using ecological niche models. Ecological niche models are correlation procedures that capture environmental conditions within which the species is known to be present, based on occurrence and environmental data from geographic information systems (Broennimann & Guisan, 2008; Jiménez-Valverde et al., 2011). Original invasion risk assessments attempted to predict potential invadable areas from climatic conditions present in the species native range (Peterson, 2003; Thuiller et al., 2005). The idea behind this approach is that evolutionary changes on species fundamental niches are not likely to occur within the time-scale of anthropogenic species invasions (Peterson, 1999, 2011). Therefore, if climatic constraints create evolutionary markers carried away during species transportations, then species are supposed to preferentially occupy areas climatically similar to those where they evolved (Peterson, 2011).

Although the predictive accuracy of ecological niche models can often be high, the native-based approach does not incorporate possible niche shifts that may occur during biological invasions (Tingley, Vallinoto, Sequeira, & Kearney, 2014). To allow for less restrictive models in terms of niche conservatism, the use of all occurrences from locations where a species is known to occur has been suggested as a step forward on invasion risk assessments (Jiménez-Valverde et al., 2011; Peterson, 2011). Using distributional data from both native and invaded ranges, possibly small niche shifts could be incorporated into ecological niche models.

To compare the invasion risk maps produced with both calibration scenarios, we fitted ecological niche models using data from the native and the pooled range for the wild boar. Our niche models were therefore calibrated with: (1) occurrences from the wild boar's native distribution (native-based models); or (2) occurrences from all distribution information available (pooled-range-based models) (see Figure S1). All models were projected world-wide. We randomly partitioned wild boar occurrence data into two subsets of calibration (75% of data), and validation (remaining 25%). That data-splitting process was repeated 100 times, in a cross-validation procedure, maintaining the species' observed prevalence unchanged. Those occurrences, coupled with the five previously chosen environmental predictors, were used to model the wild boar potential distribution.

Diverse techniques have been proposed for estimating species climate niches and potential distributions (Franklin, 2009). These methods usually aim to provide a mathematical link between occurrence information for the species and the environmental predictors associated to the location of those occurrences. In this work, ecological niche models are solely meant to provide estimates of the wild boar distributional potential. Niche comparisons were performed using the methods described in the previous section, following Broennimann et al. (2012). We therefore chose methods best suited to estimate the potential distribution of a species, or invasion risk maps (Jiménez-Valverde et al., 2011). In this work, chosen methods do not strongly rely on true absence information and usually lead to overprediction, an intrinsic artefact to the very nature of invasive species (Jiménez-Valverde et al., 2011).

Three different presence-only and presence-pseudoabsence modeling techniques were used: Bioclim, Mahalanobis distance and

Support Vector Machine. In Bioclim, environmental predictors of species' occurrences are treated as multiple distributions of uni-tailed percentiles. The values of each cell grid are evaluated to determine their position in the distribution percentiles. Bioclim then compares the predictor values in a grid cell to the distribution percentiles of the known occurrences of the species to calculate the relative suitability of a given grid cell (Graham & Hijmans, 2006; Hijmans, Phillips, Leathwick, & Elith, 2011). Therefore, values of predictor variables closer to the 50th percentile (the median) are considered the most suitable for species. Distribution tails are not distinguished, i.e. the 10th percentile is equivalent to the 90th percentile.

Species distribution models based on Mahalanobis distance consider the correlations of environmental variables, are scale-independent and useful to determine the similarity between a known sample and an unknown sample (Hijmans et al., 2011). Calculations in the mahal algorithm are based on the Mahalanobis distance (Mahalanobis, 1936). The highest possible value is a function of the correlation between variables in the dataset. Consequently, similarity values are not dependent on the scale of measurements. Bioclim and Mahalanobis distance are presence-only methods (Franklin, 2009). Bioclim models were fitted with the *bioclim* function, and Mahalanobis distance models with the *mahal* function, from the R package *dismo* (Hijmans et al., 2011).

Support Vector Machine models are a machine-learning technique to analyse data and recognize patterns (e.g. species' presences) (Karatzoglou, Smola, & Hornik, 2016). Support Vector Machine models are useful for classification and regression analysis, and usually exhibits good performance under several conditions (Karatzoglou et al., 2016). Support Vector Machine is a presence-background method (Franklin, 2009), for which models were fitted using the function *ksvm* from R package *kernelab* (Karatzoglou et al., 2016). We used an epsilon regression (*eps-svr*) with binary numeric response. All non-binary variables were scaled to mean zero plus variance. The argument *kpar* contains the parameters to be passed on to the kernel function and calculates the appropriate sigma value for the regression. The *ksvm* function, i.e. the kernel function, was used in both training and prediction. Model fitting is performed on output data, via a threefold cross-validation on the training dataset, which is the suggested procedure (Karatzoglou et al., 2016).

Continuous predictions of habitat suitability derived from the three previously described ecological niche models were converted to binary projections. For that, we found the threshold with maximum sensitivity and specificity values in the relative operating characteristic (ROC curve). Then, we calculated the True Skills Statistics (TSS), a measure of model performance that corrects for the dependence on the prevalence of the modelled. The TSS is the measure of choice for presence-absence predictions and ranges from -1 to +1 (Allouche, Tsoar, & Kadmon, 2006). Values close to +1 indicate good prediction and values equal or smaller than zero are not better than random predictions (Allouche et al., 2006).

Ensembles of forecasts tend to produce more robust predictions and reduce variability related to modelling methods used (Diniz-Filho et al., 2009). We therefore created an ensemble of gridded potential

TABLE 1 Summary of statistics describing niche shifts, and their main drivers, during wild boar invasion in the Neotropical, Australian and Nearctic biogeographical regions. Equivalence and Similarity (E→N: from exotic to native; N→E: from native to exotic) are measured in terms of observed niche overlap (Schoener's *D*). Asterisks indicate rejection of null hypothesis (*p*-value < .05), from comparisons of observed vs. random measures of niche overlap. Expansion and Stability are proportions of the exotic niche non-overlapping and overlapping, respectively, with the native niche. Unfilling is the proportion of the native niche, present but non-occupied in the exotic niche (details in text)

	Equivalence	Similarity		Expansion	Stability	Unfilling
		E→N	N→E			
Neotropical	0.36*	0.3*	0.3*	0.02	0.98	0.28
Australian	0.43*	0.4*	0.4*	0.01	0.99	0.08
Nearctic	0.22*	0.2	0.2	0.01	0.99	0.01

distribution maps, originated from the three methods we used here. Ensembles were then created by weighting each model projection (habitat suitability map) according to model performance to discriminate them in terms of accuracy, and only models with TSS > 0.5 were used in final models of potential distribution.

3 | RESULTS

Patterns of niche shift during wild boar invasion were not similar across all studied regions (Table 1). Niche overlap (in terms of Schoener's *D*) between native and invaded niches was overall low (Table 1). The wild boar populations from Australasian region presented the highest values of niche overlap with the native populations of the species (Schoener's $D = 0.4 \pm 0.03$), compared to the Neotropical (Schoener's $D = 0.3 \pm 0.06$) and the Nearctic (Schoener's $D = 0.2 \pm 0.02$). However, we found no evidence that the invaded populations' niches from any of the analysed regions are identical to their native counterparts, although in the Nearctic they were more similar than expected by chance (Figures S2, S3 and S4).

The hypothesis that native and exotic niches are indistinguishable (i.e. niche equivalence) was rejected for all biogeographical regions. However, the hypothesis that niche overlap falls within the 95% confidence limits of the null distributions (i.e. niche similarity) was rejected only for the Neotropical and Australasian region. In these regions, the wild boar's realized niche was apparently different from the one belonging to native populations (Figure S5).

Although some apparent niche shifts were observed, niche stability was high overall ($\text{Stability}_{\text{mean}} = 0.99 \pm 0.006$) and niche expansion was low ($\text{Expansion}_{\text{mean}} = 0.01 \pm 0.006$) in all regions. Niche shifts indicated by rejection of null hypotheses of niche similarity were mostly explained by the process of niche unfilling ($\text{Unfilling}_{\text{mean}} = 0.12 \pm 0.14$). The proportion of climate conditions present in the native range, but unoccupied by exotic populations ranged from 1% in the Nearctic, to 8% in Australasia and up to 28% in the Neotropics.

Because we found evidence for niche conservatism, we created invasion risk maps based on climate suitability, using ecological niche models. Native-based models had a slightly poorer accuracy than pooled-range-based models ($\text{TSS}_{\text{mean}} = 0.62 \pm 0.1$ and $\text{TSS}_{\text{mean}} = 0.68 \pm 0.06$ respectively). Native-based models also accurately predicted most areas where wild boar is known to have invaded

in all but the Australasian region (Figure 2). The Afrotropical biogeographical region was not used for niche comparison in this work due to the small number of valid occurrences ($n = 2$). Although we did not calibrate models with occurrences for that region, both ecological niche model calibration scenarios used here (native vs. pooled range) indicated high climatic suitability for the wild boar on central and south-eastern Africa (Figure 2).

4 | DISCUSSION

We found that during the wild boar invasion into the Neotropical, Nearctic and Australian regions, niche stability was high and niche expansion was low. Although native and exotic populations' niches were not equivalent (sensu Peterson, 1999), climatic matches among occupied ranges were greater than expected by chance (sensu Graham et al., 2004) in only one out of three regions analysed. Niche stability was however corroborated by niche overlap measures (sensu Broennimann et al., 2012) and also by congruent broad-scale predictions of ecological niche models calibrated with native and pooled range data (sensu Peterson, 2003). Niche conservatism is arguably one of the main processes that allows for a species to invade different areas across the globe (Peterson, 2011; Pyron et al., 2015; Strubbe et al., 2015). Although phylogenetic changes in species fundamental niches are expected during the speciation processes (Pyron et al., 2015), such changes are rarely observed at the time-scale of man-made introductions (Peterson, 2011).

Even though niche conservatism seems to be an a priori assumption for predicting potential invadable areas (Jiménez-Valverde et al., 2011), observation of niche changes are increasingly reported (Broennimann et al., 2007; Early & Sax, 2014; Tingley et al., 2014). The validity of those changes is however questioned due to recent unravelling of processes driving niche shifts (Guisan et al., 2014). If species, in their invaded range, only occupy a subset of the environmental conditions that they are usually found in their native range, classic statistical tests may indeed find differences among realized climatic niches. Those differences nevertheless do not arise from expansion into non-analogous climate, as expected from evolutionary adaptation. Niche unfilling might indeed be the pure result of ongoing colonization and slow dispersal (Guisan et al., 2014; Petitpierre et al., 2012; Strubbe et al., 2015). A single snapshot in time may therefore not be sufficient

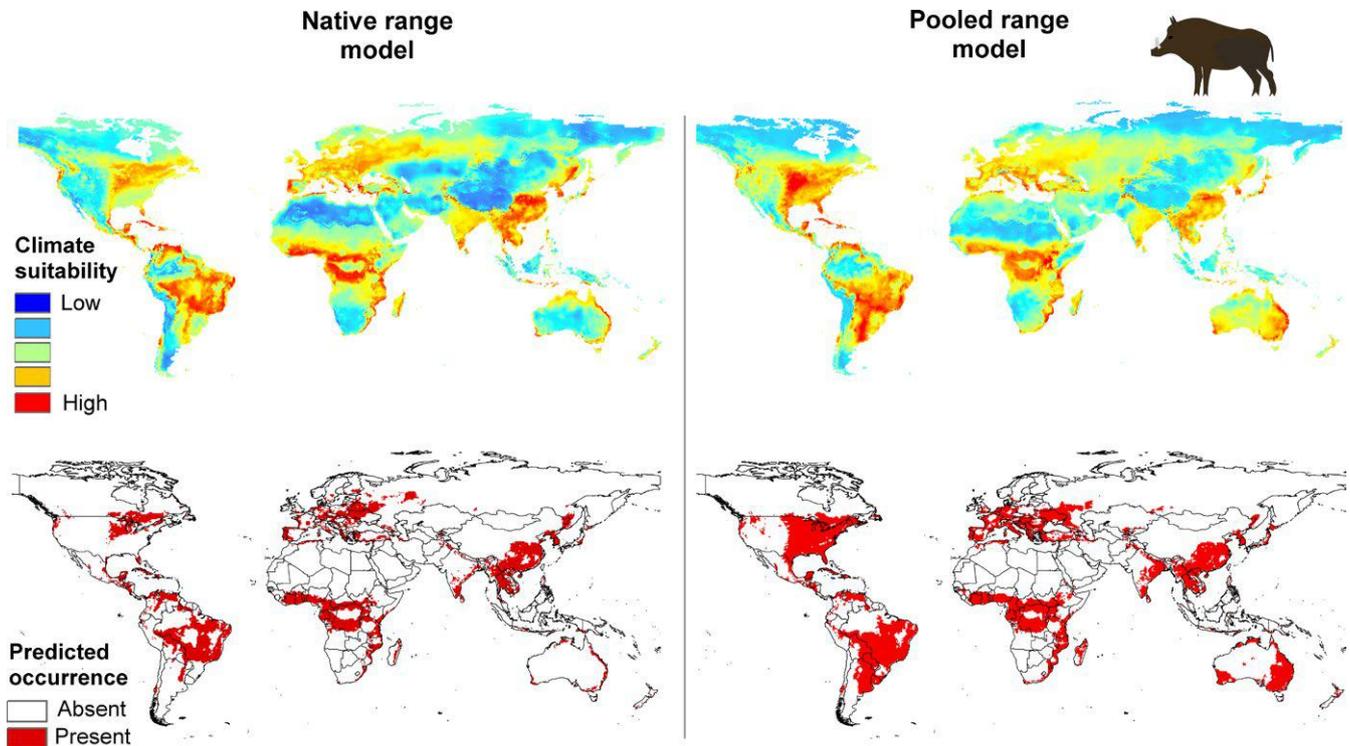


FIGURE 2 Climate suitability and potential invadable areas for the wild boar *Sus scrofa*. On the left, predictions are based on models calibrated solely with occurrences within the species native range (native-based models). On the right, models were calibrated with all locations where the wild boar is known to occur (pooled-range-based models). Continuous predictions are shown on top, where reddish colors indicate high suitability and bluish colors, low suitability. Binary predictions are presented on the downside of the picture, where red color indicates predicted presence and white color, absence [Colour figure can be viewed at wileyonlinelibrary.com]

to capture nuances of these processes. Observed changes on realized niches may in fact mislead understanding of niche shifts during biological invasions. Here, comparisons of native vs. exotic populations revealed that niches were more similar than expected by chance in the Nearctic, although not equivalent in any analysed region, and that differences may be explained by niche unfilling, rather than niche expansion (Guisan et al., 2014). Observed niche shifts due to unfilling of environmental space have already been reported for several non-native vertebrate species, including the wild boar (Strubbe et al., 2013, 2015).

Colonization history and propagule pressure also affect observed niche changes during biological invasions. Niche unfilling seems to be larger for species introduced recently and into a small number of locations, compared to those with ancient colonization history and introduced in several points in space (Strubbe et al., 2015). In this work, niche unfilling was substantially higher for the Neotropics, compared to other locations. Wild boar importation into the Neotropics has a 200-year long history (Skewes & Jaksic, 2015). However, recent waves of introduction on the 1990s for pig-farming and game hunting, followed by escape and inter-country dispersal (Pedrosa, Salerno, Padilha, & Galetti, 2015; Skewes & Jaksic, 2015) have led to explosive population growth in the Neotropics (Pedrosa et al., 2015). Because we found 28% of niche unfilling for the Neotropical region, our results indicate that the invasive potential of wild boar in this region might therefore be extremely high. Preventing expansion of wild boar

distribution into Neotropical species-rich areas such as the Amazon, coupled with potential economic losses and the spread of swine fever, thus requires specific management towards population control in areas already invaded.

Because the niche of non-native populations of wild boars is a subset of its native counterparts' niche, ecological niche models should lead to accurate predictions of potential invadable areas (Strubbe et al., 2015). We found that models calibrated with occurrences within the native distribution indeed predicted areas reportedly struggling with wild boar population expansion, such as the south and southeastern Brazil (Pedrosa et al., 2015), eastern USA (Pimentel et al., 2005) and eastern Australia (Spencer & Hampton, 2005). Such correspondence probably implies that newly occupied areas are climatically similar to the ones the wild boar is already adapted to. Therefore, evolutionary markers from climatic constraints across the native range may still be evident on populations inhabiting exotic ranges (Pyron et al., 2015).

We also found a remarkable convergence on potential invadable areas for the Afrotropical region. Although no data from that region were used to calibrate ecological niche models, both calibration scenarios predicted high climatic suitability for the wild boar in central and southeastern Africa. The Suidae family is a monophyletic group of Cetartiodactyla, composed of 17 species and originated in Africa (Frantz et al., 2016). That origin of extant species is relatively recent—less than 5.3 Ma—and many lineages have and continue to hybridize (Frantz et al., 2016). Climatic constraints on species realized niche may

be the result of adaptation to climates in which species have evolved (Pyron et al., 2015). If fundamental niches are phylogenetically conserved and climate-related evolutionary markers are indeed preserved on related lineages (Pyron et al., 2015), then the high climatic suitability exhibited for the wild boar may in fact be shared with other Afrotropical Suidae species. Furthermore, the diversity of Suidae species in Africa probably prevented wild boar invasion, because humans bred other suids (such as the bush pig *Potamochoerus larvatus*) and transported them through the mainland and towards Mayotte, Comoros, Madagascar and other islands (Frantz et al., 2016). Testing whether phylogenetic niches are preserved among members of the Suidae family is yet to be attempted, but could shed substantial light to the processes driving speciation in that taxa.

One exception to the ecological niche models' predictive ability was nevertheless found. Models calibrated with native occurrences were less able to predict wild boar's exotic occurrences in Australasia, compared to the other regions. Domestic pigs were first established in Australia in 1788 and recreational hunting has been common practice among Caucasian and Aboriginal groups since then (Bengsen, Gentle, Mitchell, Pearson, & Saunders, 2014; Meurk, 2015). Pig hunting is therefore part of subsistence and social practices and contributes substantially to regional economies (Meurk, 2015), despite long-lasting attempts to eradicate feral pig populations in Australian territory (Bengsen et al., 2014). Illegal transportation for game hunt and escapes from pig farms probably increased propagule pressure all over Australia, thus leading to species temporary occupancy of sub-optimal climates. Those populations occupying marginal climates are characterized by sink dynamics and are not expected to persist in time (Colwell & Rangel, 2009; Soberón & Nakamura, 2009).

Also, some of the records from central Australia are from pigs following flooding rivers downstream into Lake Eyre. This is not driven by local climatic events, but rainfall far away in the upstream reaches of the catchments, and so correlations between climate and occurrence is less likely here. Because native-based models were less able to predict wild boar occurrence in the Australasian region, we suggest that predictive maps of invasion risk for that region should be calibrated with pooled range calibration scenarios. Although overall broad-scale differences were small, including all known occurrences of an invasive species allows incorporation of possible non-equilibrium source-sink dynamics and their outcomes, which improves invasion risk assessments at regional scale (Jiménez-Valverde et al., 2011; Peterson, 2011).

Wild boars, like other Suidae members, have a limited ability to eliminate heat. They lack functional sweat glands, have a thick hairy skin and tend to accumulate subcutaneous fat (Bracke, 2011; Fernández-Llario, 2005; Manner & McCrea, 1963). We expected that wild boars would thus preferentially occupy low temperature sites, such as high altitudes and high latitudes, to prevent hyperthermia. However, all models predicted high climatic suitability in warm areas, such as tropical America and Africa. Also, the wild boars' native distribution includes the low-latitude Indian horn, southern China and The Philippines. The occupancy of warm climates suggests that mechanisms other than physiology have evolved in wild boars to prevent

overheating. In response to increased temperature, pigs usually exhibit a series of behavioural patterns, of which the most obvious is wallowing (Olczak, Nowicki, & Klocek, 2015). Wallowing helps wild boars eliminate heat and may have a sexual function in males (Fernández-Llario, 2005). We believe that behavioural flexibility may further allow the wild boars to occupy a wide range of climate conditions and thus overcome many physiological limitations, while also enhancing its invasive potential.

The wild boar is considered one of the worst invasive alien species in the world (Lowe, Browne, Boudjelas, & De Poorter, 2000). Its rapid and large-scale spread into many places world-wide is an issue of great concern for areas as diverse as agriculture, economy and biodiversity conservation. We found that, while niche conservatism explains invasion patterns, the broad native distribution of wild boar is suggestive of a pre-adaptation to a wide array of climate conditions. That large climatic tolerance is probably related to the species' successful invasive potential, which can have unprecedented proportions on newly colonized regions, such as the Neotropics. Our results explain the observed invasive success of the species on several parts of the world, and highlight potential invadable areas to the wild boar.

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AUTHORS' CONTRIBUTIONS

L.P.S., B.R.R., M.W.H., A.P., M.P. and R.L. conceived the ideas and designed the methods; L.P.S. and M.W.H. collected the data; L.P.S. and B.R.R. analysed the data; L.P.S. led the writing; B.R.R., M.W.H., A.P., M.P. and R.L. assisted writing and reviewed the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Climate data used in this work can be downloaded at www.worldclim.org/version1. Wild boar occurrences were collected on freely available web sources, listed in the Materials and methods section. Additional data were obtained from a literature survey, which is provided as Supporting Information. The final spreadsheet containing all occurrences used in this work is archived in the Dryad Digital Repository <https://doi.org/10.5061/dryad.1v3c2> (Sales et al., 2017). All R codes used in this paper are based open-source packages, available at The Comprehensive R Archive Network (cran.r-project.org). All R scripts used in niche overlap and ENM assessments can be downloaded at <http://www.unil.ch/ecospat/home/menuguid/ecospat-resources/tools.html>.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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Considerações finais

Sales LP & Loyola RD (2018). **Modelos de nicho ecológico e o efeito do clima na distribuição das espécies**

Considerações finais

A presente tese buscou prever o efeito do clima e das mudanças climáticas na distribuição de diferentes espécies de vertebrados. Encontramos que, no futuro, novas comunidades serão formadas, devido a perdas por extinção local de espécies que não resistirão às alterações ambientais, e ganhos por colonização de novos habitats previamente desocupados e por espécies ali introduzidas, de forma intencional ou não, pelo homem. Migrações de fauna em resposta às mudanças climáticas, em escala global, interagem com a resistência da matriz, geralmente fragmentada e composta por mosaicos de tipos de uso de solo ao longo da paisagem, permitindo ou impossibilitando que as populações busquem as condições ambientais que definem e pertencem ao seu “nicho climático”. Enquanto isso, as populações que permanecem após alterações ambientais podem não persistir no longo prazo, ainda que o ambiente não se altere mais.

Às populações que não conseguirão migrar, caberá ainda criar mecanismos de conviver com as novas condições climáticas, que invariavelmente virão, apesar de muitas fontes de incerteza tornarem as projeções futura ainda mais imprecisas. Novas espécies continuamente cruzarão barreiras geográficas, intransponíveis sem a presença humana. Essas espécies recém-chegadas, “exóticas”, “invasoras” ou simplesmente “não-nativas”, vão interagir com as comunidades locais e podem ou não se estabelecer localmente, muitas vezes expandindo seu território de forma exponencial, outras vezes sendo eliminadas pela ação do clima ou de interações bióticas. Assim, perda de habitat e fragmentação, mudanças climáticas, efeitos temporais em escala local, regional e global, e a chegada de novos integrantes redefinem continuamente a estrutura e composição das comunidades.

As distribuições das espécies são, dessa forma, dinâmicas, variando no tempo e espaço. Preservar a biodiversidade, nesse contexto, torna-se mais que um desafio logístico, econômico e sociocultural, mas um desafio intelectual: o que preservar? Devemos, sim, buscar soluções aos conflitos entre o homem e a natureza, mas até que ponto as listas de espécies de uma dada região fornecem informação útil à conservação da biodiversidade, dado que a biodiversidade é dinâmica? A perda de habitat por desmatamento é, sem dúvida, uma catástrofe, em termos de redução do número de espécies. Isso é indiscutível e os efeitos da remoção de cobertura vegetal nativa são óbvios e evidentes - ainda que dinâmicas de não-equilíbrio se escondam por trás de paisagens aparentemente ricas em espécies. Mas se sempre houve mudanças na distribuição das espécies, porque as espécies estão continuamente “correndo para permanecer no mesmo lugar” - ou se esforçando para manter suas taxas de crescimento e reprodução em níveis ótimos - deveríamos nos ater aos conceitos de “nativo” e “não-nativo” ao avaliarmos a biota de uma região?

Alfred Russel Wallace, em seu livro *Viagens nos Rios Negro e Amazonas* (1853), afirmou que não há elemento mais interessante ou instrutivo na história natural, senão o estudo da distribuição geográfica dos animais. Se as mudanças climáticas trazem a possibilidade de redefinição das comunidades, pela movimentação das espécies em busca de seus climas ideais, projetar e antecipar o futuro da biodiversidade é, além de poderosa ferramenta de conservação, um belo exercício narrativo. Termina esta tese com mais perguntas do que comecei, o que pode ser bom.