
**PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA, EVOLUÇÃO E
BIODIVERSIDADE**

**ECOLOGIA ESPACIAL APLICADA À CONSERVAÇÃO DA BIODIVERSIDADE
EM PAISAGENS FRAGMENTADAS**

VINICIUS RODRIGUES TONETTI

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VINICIUS RODRIGUES TONETTI

Tese apresentada ao Instituto de Biociências do Câmpus de Rio Claro, Universidade Estadual Paulista, como parte dos requisitos para obtenção do título de Doutor em Ecologia, Evolução e Biodiversidade.

Orientador: Dr. Marco Aurélio Pizo

Coorientador: Dr. Milton Cezar Ribeiro

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TÍTULO DA TESE: Ecologia espacial aplicada à conservação da biodiversidade em paisagens fragmentadas

AUTOR: VINICIUS RODRIGUES TONETTI

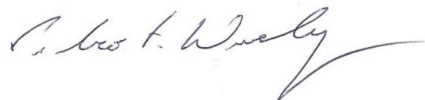
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Rio Claro, 06 de março de 2023

Às milhões de vítimas da pandemia de Covid-19

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“Não encontrei no edifício do pensamento nenhuma categoria sobre a qual descansar a minha cabeça. Em compensação, que belo travesseiro é o caos!”

Emil Cioran

“A natureza como um todo, assim como as araras-azuis, depende daquele que tem sido o seu maior inimigo”

Fernando Fernandez citando o artigo no qual o orientador desta tese relata o intrigante caso das araras que dependem de um dos seus maiores predadores (tucano-toco) para reproduzir no Pantanal – *“Os mastodontes de barriga cheia e outras histórias: Crônicas de biologia e conservação da natureza”*.

Pizo, MA et al. 2008. Conservation puzzle: Endangered hyacinth macaw depends on its nest predator for reproduction. *Biological Conservation* 141(3):792-796.

Resumo

Essa tese está dividida em três capítulos em formato de artigos científicos que encontram-se publicados em revistas internacionais. O primeiro capítulo, corresponde ao primeiro estudo a sintetizar o conhecimento e fornecer o estado da arte sobre heterogeneidade de paisagens com base em uma revisão sistemática abrangente da literatura de 661 artigos publicados entre 1982 e 2019. O segundo capítulo teve como objetivo avaliar como a regeneração florestal em grande escala baseada num método de restauração de baixo custo pode mitigar os efeitos da perda e fragmentação de habitat associados a futuras alterações climáticas na distribuição de aves e mamíferos arbóreos num hotspot de biodiversidade tropical; além de encontrar áreas com diferentes riquezas potenciais atuais e futuras de espécies e avaliar como a restauração passiva pode reduzir o risco de extinção de espécies. No terceiro capítulo nós identificamos os 30% de remanescentes florestais mais importantes para conservação no Domínio da Mata Atlântica na América do Sul com base em três componentes de diversidade de aves: (1) ocorrência geral de espécies, (2) ocorrência de espécies ameaçadas e (3) diversidade de traços funcionais. Avaliamos a extensão da sobreposição entre áreas prioritárias usando o diferentes abordagens e analisamos a eficiência da atual rede de Áreas Protegidas na proteção da biodiversidade no clima atual e futuro potencial (considerando cenários para 2040 e 2080).

Palavras-chave: aves, conservação da biodiversidade, ecologia de paisagens, heterogeneidade de paisagens, mata atlântica, mudanças climáticas

Abstract

This thesis is divided into three chapters in the format of scientific articles that are published in international journals. The first chapter corresponds to the first study to synthesize knowledge and provide the state of the art on landscape heterogeneity based on a comprehensive systematic literature review of 661 articles published between 1982 and 2019. The second chapter aimed to evaluate how regeneration large-scale forestry based on a low-cost restoration method can mitigate the effects of habitat loss and fragmentation associated with future climate change on the distribution of birds and arboreal mammals in a tropical biodiversity hotspot; in addition to finding areas with different potential current and future species richness and evaluating how passive restoration can reduce the risk of species extinction. In the third chapter we identify the 30% of forest remnants most important for conservation in the Atlantic Forest Domain in South America based on three components of bird diversity: (1) general occurrence of species, (2) occurrence of threatened species and (3) diversity of functional traits. We assess the extent of overlap between priority areas using different approaches and analyze the efficiency of the current network of Protected Areas in protecting biodiversity in the current and potential future climate (considering scenarios for 2040 and 2080).

Key-words: Atlantic Forest, biodiversity conservation, birds, climate change, landscape ecology, landscape heterogeneity

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Introdução geral

O Antropoceno e a urgência em mitigar os seus efeitos na biodiversidade

Desde o seu surgimento, há centenas de milhares de anos, os seres humanos desenvolveram surpreendente capacidade de adaptação e ocupação dos mais diversos tipos de ambientes. Mesmo sem os aparatos tecnológicos disponíveis atualmente, a espécie humana habitou alguns dos locais mais extremos do planeta, como cordilheiras com baixa concentração de oxigênio, desertos quentes, e o inóspito ártico (Ilardo and Nielsen 2018). Essas ocupações sempre estiveram acompanhadas de impactos ambientais (Redman 1999). No passado, esses impactos eram causados sobretudo pela caça, modificação das paisagens pelo uso do fogo, desenvolvimento da agricultura e disseminação de espécies exóticas (Redman 1999, Pereira et al. 2012, Ellis et al. 2021). Ainda que impactos na biodiversidade por causas antrópicas, incluindo registros de extinção de espécies, tenham se iniciado há pelo menos 50.000 anos (Barnosky et al. 2004, Ellis et al. 2021), foi em meados do século XVIII, após a segunda fase da revolução industrial, que as consequências das ações humanas se acentuaram (Ellis et al. 2010, Dirzo et al. 2014).

Atualmente, a extinção de espécies por causas antrópicas estão acontecendo em níveis tão elevados que alguns autores sugerem que o planeta está experimentando um novo período de extinção em massa (Barnosky et al. 2011, Ceballos et al. 2015). A lista vermelha publicada em setembro de 2021 pela União Internacional pela Conservação da Natureza (IUCN) indica que cerca de 30% de todas as 138.374 espécies avaliadas estão sob algum grau de ameaça (<https://www.iucnredlist.org/resources/summary-statistics>). Além das extinções, as consequências das atividades humanas na biodiversidade incluem alterações nas abundâncias das populações e composição das comunidades, perda de diversidade genética e mudanças nas distribuições geográficas e interações

bióticas (Dirzo et al. 2014, Ceballos et al. 2017). As alterações no planeta, sobretudo em relação às mudanças na cobertura da terra e modificação da composição da atmosfera, têm acontecido de forma tão acentuada que as suas evidências poderão ser notadas durante milhões de anos (Lewis and Maslin 2015). Esses fatores fazem com que as sociedades humanas tenham se tornado uma força geofísica global, caracterizando uma nova era geológica, o “Antropoceno” (Steffen et al. 2007, Dirzo et al. 2014).

A destruição de habitats, somada aos efeitos das mudanças climáticas, estão entre as principais causas da perda de biodiversidade no Antropoceno (Haddad et al. 2015, Lewis and Maslin 2015, Newbold et al. 2016, Tilman et al. 2017). Ambientes naturais outrora contínuos foram fragmentados e substituídos por pastagens, lavouras, áreas urbanas e outros tipos de cobertura da terra criados pelo homem (Haddad et al. 2015). Com a população humana ainda em crescimento, há um contínuo aumento da demanda por produtos agrícolas, como alimentos e biocombustíveis, de modo que é esperado que a supressão de vegetação nativa para o estabelecimento de novas áreas destinadas para pastagens e cultivos continue em expansão (Foley et al. 2011). Embora a maior parte da perda de vegetação natural em algumas das áreas mais biodiversas do planeta tenha ocorrido durante o último século, sobretudo nos trópicos, essas regiões ainda sofrem com a perda e fragmentação de habitats (Hansen et al. 2013). Para exemplificar, entre os anos de 1992 e 2015 cerca de 148 milhões de hectares de áreas de vegetação nativa foram suprimidas em *hotspots* de biodiversidade em todo o mundo, sendo que destes, 54 milhões de hectares (Mha) correspondem a florestas (Hu et al. 2021). Apenas na América do Sul, 268 Mha de áreas naturais sofreram alterações entre 1985 e 2018 (Zalles et al. 2021).

Somado às alterações nas paisagens, as mudanças climáticas causadas pela emissão de gases causadores do efeito estufa apresentam riscos para a biodiversidade. Após a segunda fase da revolução industrial, o aumento na emissão de gases do efeito

estufa causou mudanças na composição de gases na atmosfera sem precedentes na história recente do planeta (IPCC 2021). O acúmulo desses gases vem causando alterações climáticas com consequentes efeitos na biodiversidade, dentre eles estão alterações nas interações entre as espécies, como dispersão de sementes (Sales et al. 2021), predação (Laws 2017) e polinização (Settele et al. 2016), perda de variabilidade genética (Bálint et al. 2011), mudanças na distribuição (Peterson et al. 2011) e extinção de espécies (Thomas et al. 2004). Os efeitos das mudanças climáticas podem acentuar os impactos negativos da supressão e fragmentação de habitats naturais na biodiversidade (Oliver and Morecroft 2014). Dessa maneira, compreender a interação desses dois fatores é essencial para a conservação da biodiversidade a longo prazo (Sutherland et al. 2013).

Heterogeneidade de paisagens: o estado da arte e perspectivas futuras

Conciliar a expansão agrícola e fragmentação de habitats naturais com a manutenção da biodiversidade é um dos maiores desafios dos conservacionistas. Sob a perspectiva da ecologia de paisagens, uma das alternativas para alcançar esse objetivo e que é frequentemente discutida está relacionada com o papel da heterogeneidade de paisagens em áreas agrícolas (Benton et al. 2003, Fahrig et al. 2011). Desde o surgimento da ecologia de paisagens como disciplina, boa parte dos estudos focou no paradigma habitat-matriz, segundo o qual os remanescentes de vegetação natural são tratados como “ilhas” circundadas por “oceanos” (equivalentes às matrizes) hostis à biodiversidade nativa (Franklin and Lindenmayer 2009). No entanto, matrizes antropogênicas podem não ser totalmente inóspitas à biodiversidade por fornecerem diferentes recursos, como alimento e abrigo, além de promoverem o fluxo dos indivíduos entre os fragmentos de vegetação nativa, apresentando, portanto, extrema relevância para a manutenção da biodiversidade (Prevedello and Vieira 2010, Wright et

al. 2012). Sendo assim, é crucial compreender como a heterogeneidade dos diferentes tipos de cobertura da terra pode afetar a biodiversidade.

Estudos sugerem que paisagens mais heterogêneas podem ser benéficas para a biodiversidade em comparação com regiões nas quais monoculturas são predominantes (Driscoll et al. 2013). Além da heterogeneidade de composição das paisagens, i.e. a variabilidade dos diferentes tipos de cobertura da terra, a heterogeneidade de configuração, ou seja, como os diferentes fragmentos estão espacialmente arranjados em relação a, por exemplo, isolamento, tamanho e formato, podem influenciar na magnitude dos processos ecológicos ocorrendo dentro de cada fragmento (Li and Reynolds 1995). Dentre os poucos estudos que avaliaram os efeitos da heterogeneidade de composição e configuração da paisagem separadamente, Perović et al. (2015) notaram que a diversidade taxonômica de borboletas pode variar com a heterogeneidade de composição da paisagem, ao passo que a heterogeneidade de configuração afeta em maior grau a diversidade funcional do grupo. Assim, é de extrema relevância estabelecer uma agenda de pesquisa que vise compreender melhor os efeitos da heterogeneidade da paisagem e seus diferentes componentes na biodiversidade (Fahrig et al. 2011, Tschardt et al. 2012).

No entanto, apesar da relevância da heterogeneidade da paisagem e do crescente número de publicações sobre o tema ao longo dos anos, o uso adequado de suas definições ainda precisa ser mais bem esclarecido, assim como quais componentes da heterogeneidade estão sendo investigados. As inconsistências existentes na literatura em relação às diferentes definições e como os termos são tratados podem fazer com que a comunicação entre a comunidade científica e os tomadores de decisão seja prejudicada, o que é crucial para a legislação e criação de protocolos e diretrizes de planejamento do uso da terra (Heink and Kowarik 2010). Somado a isso, diferentes métodos de quantificação da heterogeneidade da paisagem podem gerar diferentes resultados, o que

pode prejudicar a construção de um corpo de conhecimento mais robusto sobre o tema. Alguns autores já destacaram a dificuldade em definir e quantificar a heterogeneidade (Li and Reynolds 1995). Dessa maneira, um dos objetivos desta tese é tentar elucidar como os conceitos e quantificações a respeito da heterogeneidade de paisagens têm sido tratados na literatura científica (Figura 1). Além disso, nós fornecemos também o estado-da-arte sobre o assunto, identificando as regiões e biomas onde os estudos precisam ser intensificados, destacamos lacunas de conhecimento e apontamos para as perspectivas futuras, fornecendo diretrizes sobre como os estudos podem abordar o tema.

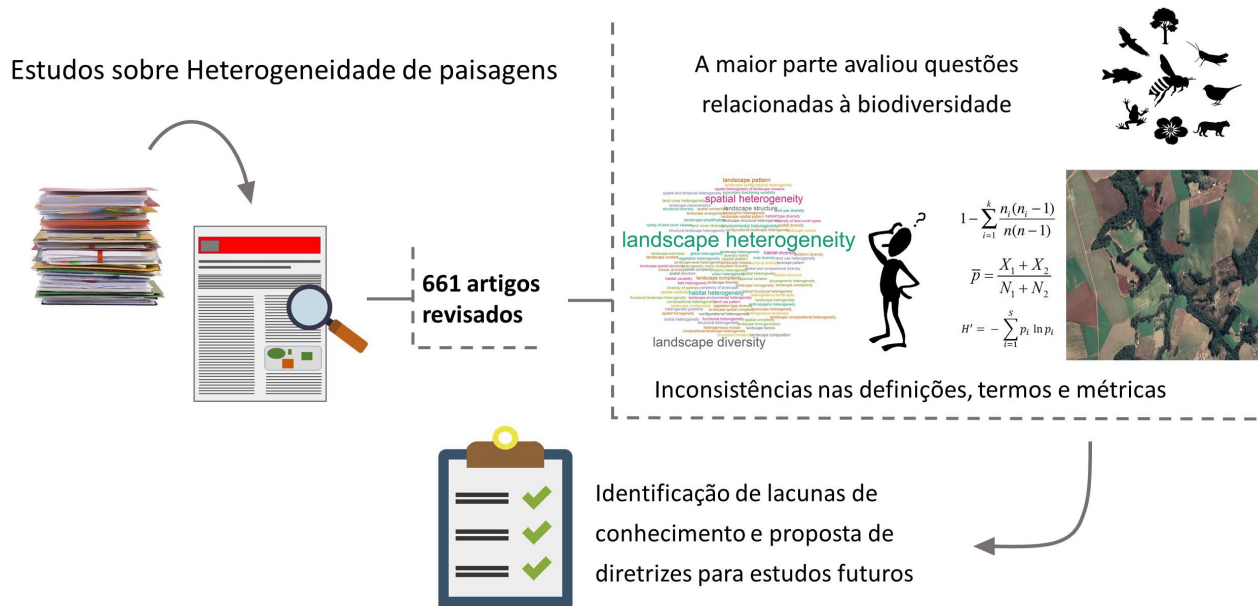


Figura 1. Resumo gráfico da revisão realizada no capítulo 1 desta tese que teve como objetivo avaliar como a heterogeneidade de paisagens é tratada na literatura em relação às definições, métricas e outros aspectos espaço-temporais.

A importância da regeneração florestal na recuperação da biodiversidade em paisagens fragmentadas

Apesar de abrigarem elevada riqueza de espécies e apresentarem altos níveis de endemismo, os ambientes tropicais, sobretudo as florestas, estão entre os ecossistemas que mais sofreram com a perda de habitat nos últimos séculos, (Haddad et al. 2015,

Alroy 2017, Kehoe et al. 2017, Raven et al. 2020). Isso faz com que essas regiões sejam prioritárias para a conservação da biodiversidade (Myers et al. 2000). Para exemplificar a magnitude das perdas de vegetação nativa que essas regiões sofreram, estima-se que atualmente cerca de 70% de toda a vegetação florestal do planeta estão a menos de 1 km da borda dos remanescentes onde se localizam e, dessa maneira, em grande proximidade com ambientes modificados pelo ser humano, como plantações agrícolas, centros urbanos e rodovias (Haddad et al. 2015). Essa proximidade causa impactos para biodiversidade que habita e se desloca entre os fragmentos. Associada à fragmentação, as mudanças climáticas esperadas para as próximas décadas podem ter consequências drásticas para a biodiversidade, de modo que estratégias mitigadoras são necessárias para a conservação das espécies a longo prazo. Uma estratégia que pode ser empregada para esse fim é a restauração de ambientes degradados (Holl 2017a).

A recuperação de florestas tropicais pode acontecer por meio de duas estratégias principais: (1) restauração ativa, que consiste em uma série de intervenções diretas, como o plantio de árvores, que visam favorecer e acelerar o processo de regeneração e (2) a restauração passiva, que consiste em cessar o efeito causador de distúrbio ambiental permitindo que as florestas regenerem de forma natural, com pouca ou sem intervenção humana (Figura 2, Holl 2017b). Apesar da restauração ativa em geral acontecer em menor intervalo de tempo e ser eficiente para conservar a biodiversidade, a sua aplicação em larga escala pode ser limitada devido aos seus custos elevados quando comparado à restauração passiva (Holl and Brancalion 2020). Por outro lado, apesar de fatores que podem limitar a restauração passiva, como a baixa disponibilidade de sementes no solo e baixa oferta de propágulos em paisagens com pouca cobertura vegetal, essa estratégia pode ser mais adequada para a recuperação de áreas extensas devido ao seu relativo baixo custo (Holl 2017a). Apesar dessas limitações e das elevadas taxas de desmatamento, é estimado que cerca de 12% das florestas tropicais do

mundo estão passando por um processo de regeneração natural (Wright 2010), o que sugere que estimular a restauração passiva como estratégia para mitigar a perda de biodiversidade a longo prazo pode ser eficaz.

Ainda que florestas secundárias não apresentem os mesmos níveis de biodiversidade em comparação a florestas primárias (Gibson et al. 2011), ambientes em regeneração podem ser cruciais para a manutenção da biodiversidade, além de promoverem serviços ecossistêmicos importantes, como provisão de água e estoque de carbono (Chazdon et al. 2009, Brancalion et al. 2018). Assim, identificar regiões que apresentem maior potencial de regeneração natural e avaliar o potencial do aumento de áreas florestais causado pela recuperação de ambientes degradados na mitigação dos efeitos das mudanças climáticas, pode auxiliar no planejamento do uso da terra.

Dessa maneira, no segundo capítulo desta tese o nosso objetivo foi projetar a distribuição potencial de espécies de vertebrados (aves e mamíferos arborícolas) em diferentes cenários de paisagem (com regeneração passiva e sem regeneração) e clima (considerando e sem considerar os efeitos das mudanças climáticas) na região da Mata Atlântica brasileira. Para gerar o cenário de regeneração, nós utilizamos modelos espacialmente explícitos que consideram a quantidade de floresta e configuração da paisagem na chuva de sementes promovida pela fauna frugívora (Figura 2). Os modelos assumem que regiões próximas de fragmentos florestais apresentam maior chance de regeneração natural devido à maior quantidade de sementes na matriz. Além de evidenciar o potencial da restauração passiva de áreas degradadas na mitigação dos efeitos da perda de habitat e mudanças climáticas, essas análises podem auxiliar na identificação de áreas prioritárias para a conservação do domínio.

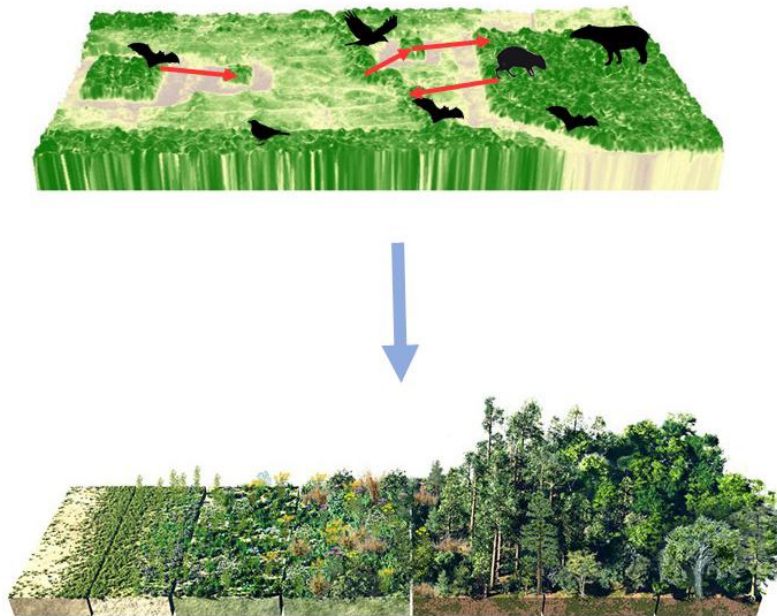


Figura 2. Esquema mostrando que a movimentação da fauna frugívora entre os remanescentes de vegetação nativa (parte superior da figura) pode promover chuva de sementes em matrizes antrópicas, favorecendo a regeneração natural (parte inferior da figura).

Selecionando áreas para a conservação em florestas tropicais fragmentadas

A delimitação e proteção de áreas naturais é uma das principais estratégias utilizadas para a conservação da biodiversidade. Áreas Protegidas são em sua maioria eficazes na manutenção de populações, e podem salvaguardar espécies ameaçadas por serem, em alguns casos, o último reduto de táxons de distribuição restrita, sendo portanto fundamentais para evitar extinções no futuro próximo (Margules and Pressey 2000, Cazalis et al. 2020). Somado a isso, áreas protegidas podem proporcionar importantes serviços ecossistêmicos, como o fornecimento e regulação da qualidade da água e estoque de carbono. Portanto, diversas iniciativas regionais e globais clamam por aumentar a quantidade de áreas protegidas no mundo.

No terceiro capítulo desta tese nós utilizamos uma abordagem baseada em ecologia de paisagens e em diferentes componentes da diversidade das aves para

identificar áreas prioritárias para a conservação da biodiversidade (Figura 3). Além de identificar as áreas mais importantes, nós também avaliamos a sobreposição entre as regiões apontadas pelos diferentes componentes e a eficácia da rede de Áreas Protegidas na conservação da biodiversidade tanto no cenário climático atual quanto em cenários climáticos futuros. Com as mudanças climáticas é esperado que as espécies sofram mudanças nas suas áreas de distribuição (Guisan et al. 2017), o que pode acarretar em mudanças das áreas prioritárias para a conservação no futuro. Portanto, é de extrema importância considerar os efeitos das possíveis mudanças climáticas ao selecionar áreas para a conservação.

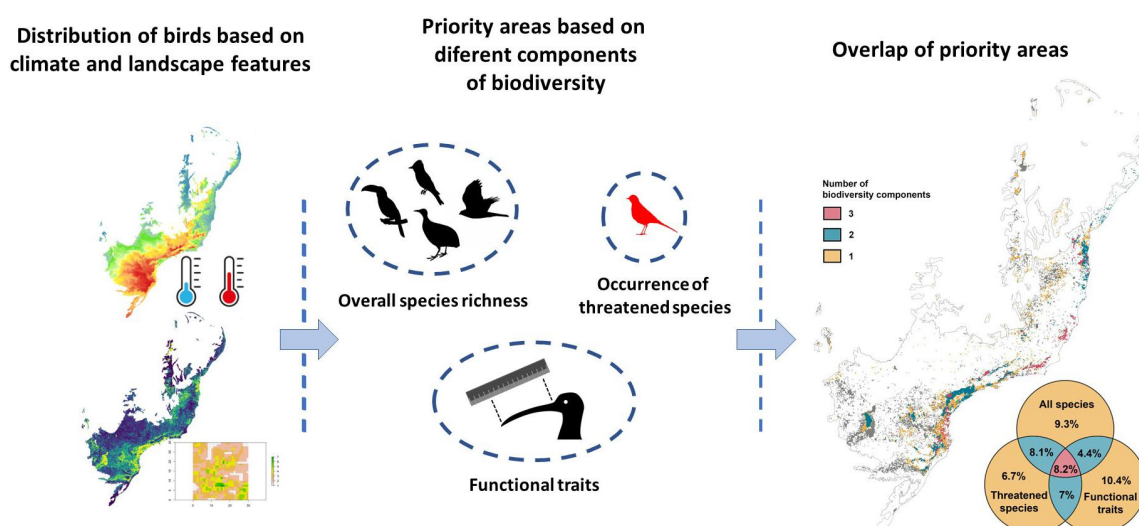


Figura 3. Esquema mostrando o modelo adotado na priorização de áreas importantes para a conservação na Mata Atlântica. Após projetar a distribuição de centenas de aves em diferentes cenários climáticos (parte esquerda da figura), diferentes componentes da diversidade de aves foram utilizados em um algoritmo de priorização de áreas para a conservação (centro), e por fim a sobreposição dessas diferentes áreas e em diferentes cenários foi avaliada (parte direita da figura).

A Mata Atlântica como modelo de estudo

A Mata Atlântica é o segundo maior domínio florestal da América do Sul, menor apenas que a Amazônia. Suas florestas estendem-se do litoral do nordeste ao sul do Brasil, alcançando o interior do continente até a parte leste do Paraguai e Argentina (Muylaert et al. 2018). A sua grande extensão territorial (162 milhões de hectares)

associada ao gradiente latitudinal (variando de -3 à -33°) e altitudinal (0 – 2.900 m) faz com que diferentes regiões climáticas e biogeográficas sejam encontradas no domínio (Muyllaert et al. 2018, Marques et al. 2021). Devido à sua grande área e diferentes regiões biogeográficas (Marques et al. 2021), um elevado número de espécies e endemismo pode ser encontrado no domínio. Atualmente, 2.645 espécies de tetrápodes e cerca de 15.000 de plantas com sementes foram registradas, das quais 36% e 57% são endêmicas da Mata Atlântica (Zappi et al. 2015, Figueiredo et al. 2021).

No entanto, a despeito de sua enorme biodiversidade, a Mata Atlântica é um dos domínios florestais mais devastados em todo o mundo. As estimativas da quantidade de vegetação nativa variam entre 28 e 34 milhões de hectares em sua porção brasileira (Rezende et al. 2018, Rosa et al. 2021, Tonetti et al. 2022), o que corresponde a menos de 30% de sua vegetação original. Além disso, mais de 80% dos remanescentes são considerados pequenos (<50 ha) e isolados, distando em média 1.440 metros uns dos outros (Ribeiro et al. 2009). Áreas antes cobertas por vegetação nativa foram substituídas por matrizes de uso antrópico, sobretudo pastagens, monoculturas, cultivos agrícolas e áreas urbanas. Ainda que a perda de áreas naturais na Mata Atlântica tenha acontecido de forma mais acentuada durante o ciclo do café (~1800 - 1930) e a quantidade de floresta nativa tenha aumentado em diversas regiões devido a regeneração natural nas últimas décadas (Dean 1996), o desmatamento total do domínio voltou a crescer nos últimos anos. Apenas no primeiro semestre de 2022, a área de floresta nativa desmatada na Mata Atlântica foi de ~21.000 hectares (MapBiomass 2022).

Devido à enorme parcela da população que reside dentro de seus limites (cerca de 120 milhões de pessoas), ~70% do PIB do país é gerado no domínio (<https://www.sosma.org.br/conheca/mata-atlantica/>). Dessa maneira, a região pode ser considerada adequada para o desenvolvimento de estudos que visam orientar planos de conservação sem gerar prejuízos ao desenvolvimento de atividades econômicas. Assim,

os capítulos 2 e 3 desta tese utilizaram a Mata Atlântica como modelo de estudo e objetivaram, em essência, propor o manejo de matrizes antrópicas visando otimizar o espaço destinado à biodiversidade e a produção agrícola, além de identificar áreas importantes para a conservação. O fato de a quantidade de pastagens pouco produtivas na Mata Atlântica ser grande (~30 milhões de hectares; Latawiec et al. 2015), sugere que pode não haver conflito entre a expansão da agricultura e aumento da proteção dos remanescentes florestais e estímulo à regeneração de áreas degradadas caso novas áreas agrícolas sejam estabelecidas em regiões já antropizadas.

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Capítulo 1 - Landscape heterogeneity: Concepts, quantification, challenges, and future perspectives

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Landscape heterogeneity: concepts, quantification, challenges and future perspectives

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Conflict of interest

No conflict of interest is declared by the authors.

Abstract

The intrinsic complexity, variety of concepts and numerous ways to quantify landscape heterogeneity (LH) may hamper a better understanding of how its components relate to ecological phenomena. Our study was the first to synthesize the knowledge and provide

the state-of-the-art on the subject based on a comprehensive systematic literature review of 661 articles published between 1982 and 2019. Definitions, terminology, and measurements of LH were diverse and conflicting. Most articles (534 out of 661) did not provide any definition for LH, and we found a great variation among the studies that did. According to our review, only 10 studies measured the effects of different land cover types on biotic or abiotic process (functional LH). The remaining 651 studies measured physical attributes of the landscape without mentioning that different land cover types may impact biotic and abiotic processes differently (structural LH). The metrics most frequently used to represent LH were “Shannon diversity index” and “proportion of land cover type”. Most metrics used as proxies of LH also coincided with those used to represent non-heterogeneity metrics, such as fragmentation and connectivity. We identify knowledge gaps, indicate future perspectives, and propose guidelines that should be addressed when researching LH.

Keywords: functional heterogeneity, habitat heterogeneity, landscape composition, landscape configuration, landscape ecology, spatial heterogeneity, structural heterogeneity

Introduction

Landscape ecology is closely linked to the concept of landscape heterogeneity (LH), which is the qualitative or quantitative variation of landscape elements (Risser 1987, Li and Reynolds 1994, 1995, Pickett and Cadenasso 1995, Turner et al. 2001, Fahrig et al. 2011; Box A). LH has two main components: composition and configuration. The variety of land cover types, known as compositional LH (Li and Reynolds 1995), provides different environmental conditions (e.g., light incidence and temperature) and resource availability (e.g., shelter and food) for organisms, while the

spatial arrangement of land cover types, or configurational LH (Box A), influences the magnitude of processes that occur within and between patches (Li & Reynolds, 1995) and is tightly related with patch size and connectivity. Hence, compositional and configurational LH affect several biotic and abiotic processes, including species diversity (Regolin et al., 2020), movement of individuals (Romero et al., 2009), predation (Kauffman et al., 2007), pest control (Gardiner et al., 2009), pollination (Boscolo et al., 2017), nutrient cycling (LeClare et al., 2020), and fire occurrence (Vega-García & Chuvieco, 2006). Humans may also be influenced by LH, such as in the provision of urban ecosystems services (Hamstead et al., 2016), and human welfare wellbeing (Finder et al., 1999).

LH can be further described under a structural and functional perspective. Structural LH considers the attributes of a landscape, “regardless” of the effects different land cover types have on biotic and abiotic processes. The choice of the structural components is usually based on prior knowledge or assumptions regarding the studied organism. This type of approach usually assumes that metrics such as number of patches and edge amount are sufficient to characterize landscapes (Li & Reynolds, 1995; Fahrig et al., 2011). The lack of clearly stating what are these assumptions and the ecological processes they are representing can induce to the mistaken conclusion that the attributes of the landscape are solely responsible for the patterns found, and not a proxy of an underlying ecological process. Conversely, functional LH considers how different land cover types affect a target species or biological group, or how they influence abiotic processes such as nutrient flow (Li & Reynolds, 1995; Fahrig et al., 2011). In other words, the realization of biological processes will depend on how organisms “perceive” the environment, and consequently will be influenced by the variation of functional LH.

Landscapes may be evaluated by their physical attributes (structural LH) combined with their compositional and/or configurational aspects, such as the proportion of land cover type and edge amount (e.g., Duflot et al. 2014; “Structural [composition and/or configuration]” in Fig. 1). Similarly, landscapes can be described considering the effects of different land cover types on biotic and abiotic process (functional LH) combined with its compositional and/or configurational aspects (e.g., Perović et al. 2015; “Functional [composition and/or configuration]” in Fig. 1). Therefore, LH can be perceived, studied, and represented under several perspectives depending on the subject conveying the research and on the study target (see examples of the different components of LH and a conceptual scheme in Box A).

The complexity of the topic may hamper a clear understanding of which LH components and perspectives have been assessed in empirical research (Tschardt et al. 2012). Moreover, different methods for quantifying LH may yield different results, which may hinder the construction of a more robust body of knowledge in the field and, consequently, environmental decision making. Li and Reynolds (1995) highlighted that the difficulty in defining and quantifying LH originates in the concept itself, which is usually related to specific research questions and data types. Despite the relevance of LH and the increasing number of publications addressing this topic over the last four decades, a synthesis of LH literature is still needed. Therefore, unlike other studies that reviewed the effects of LH on animal diversity (Tews et al. 2004), our study was the first to synthesize the knowledge and provide the state-of-the-art on the subject based on a comprehensive systematic literature review. Specifically, we identified (1) how LH is defined and quantified; (2) the scope of studies and biological response variables investigated in relation to LH; (3) the spatial scales most used; and (4) provide a summary of knowledge gaps, indicating future perspectives and proposing guidelines that should be addressed when researching LH. We hypothesized that the definitions

and metrics used to quantify LH will be varied across studies, making comparisons across studies and general conclusions harder to be made. Regarding the scale and variables used to measure LH, we hypothesize that those are not clearly stated, again making it difficult to compare results across studies besides creating difficulties in reproducing approaches across biomes and geographic areas. Lastly, we hypothesize that the scattered definitions and lack of consistency among studies weakness the real consequences of LH in biodiversity and landscape conservation. To address these issues, we propose guidelines to help with strengthening the outcomes of LH studies.

Review methods

We performed a comprehensive search in the Web of Science database (clarivate.com/webofsciencegroup) using the following keywords and Boolean operator search criteria: “landscape heterogeneity” OR “landscape diversity” OR “landscape homogeneity” OR “landscape simplification” OR “spatial heterogeneity” OR “functional heterogeneity” OR “temporal heterogeneity” OR “structural heterogeneity” AND “landscape”. We restricted the search to the following research areas: “Ecology”, “Environmental Sciences”, “Biodiversity Conservation”, “Geography Physical”, “Forestry”, “Remote Sensing”, “Environmental Studies”, “Plant Sciences”, “Zoology”, “Agriculture Multidisciplinary”, “Marine Freshwater Biology”, and “Biology”. We restricted the search until the end of 2019 (Fig. 1), which resulted in 2,879 articles. As we were interested in heterogeneity measurements, we only considered articles in which authors had claimed to have quantified LH and, after carefully reading all 2,879 articles (mainly the title and abstract, but in some cases, the full text), 661 publications were eligible for our analysis.

To characterize the definitions and measurements, we extracted from each study (1) the LH definitions given, (2) the LH components investigated

(compositional/configurational), (3) the LH perspectives investigated (structural/functional; Box A), and (4) the metrics used as proxies of LH. We also recorded (5) the research topic (including taxonomic groups and level of biological organization), and (6) the spatial scale used. All the components evaluated in this review were only considered when explicitly said by the authors to avoid misinterpretations and subjectivity.

The landscape metrics, scope of studies, and variables related to LH, were, in general, specific to each study. Therefore, to synthesize the information, we grouped similar terms in the same class; for instance, “proportion of pasture” was classified as “proportion of land cover type” (Fig. 2). Definitions of LH were also synthesized (Tables S1 and S2); for example, when configurational LH was defined as “*the degree of spatial complexity of the landscape pattern*” (Fahrig et al., 2015), we classified it as “heterogeneity in spatial arrangement of land cover types” (Table S2). To ensure consistency, only the first author (VT) performed these classifications.

We determined five extent classes based on the smallest analytical unit of landscape scales, i.e. polygons from which LH metrics were extracted: (1) local, when studies sampled local landscape scales (usually small regular polygons, such as squares and circles) – studies were considered local even if different landscape scales (polygons) were spread over larger areas (e.g., crop fields spread over a country); (2) regional, when studies were based on regional maps that were smaller than a country but larger than a local unit (e.g., a watershed or a province); (3) national, (4) continental, and (5) global extents occurred when landscape maps corresponded to the territory of a country, a continent, or the entire world, respectively. The extent classes are different from the scale of the study. For example, if LH metrics were extracted from circles surrounding sampling sites spread across a country, the extent class was defined as “local”, while the study can be considered as in the national scale.

We only assigned articles as having structural/functional or compositional/configurational measures of LH when explicitly stated by the authors. Similarly, we did not assume which metric was used to quantify LH or non-heterogeneity aspects unless explicitly written (even for the most often used metrics, such as the “Shannon diversity index”; McGarigal et al. 2009). Additionally, to provide an overview of other descriptive aspects of LH studies, we also extracted data on the terms most used to refer to LH, geographic coverage (e.g. countries, biomes), spatial and temporal aspects (pixel size, time scale and number of temporal observations), and the landscape models (heterogeneous mosaic, binary, or continuous model). Such descriptive information is found in the Supporting Information file.

Landscape heterogeneity in the literature: definitions and important terms

Our review comprised 37 years (1982 – 2019), with gaps from 1983 to 1988 and from 1990 to 1992. The number of publications on LH has increased over the years since the first publication in 1982 (Fig. 1), but in different rates over the years. Most articles (534 out of 661) did not provide any definition for LH, and we found a great variation among the studies that provided definitions. For instance, the spatial component of the landscape was not considered in some articles, such as “landscape diversity can be considered an attribute of landscape health and landscape stability.” (Yeh and Huang 2009), or LH was defined under specific conditions to comply with the goals, e.g., the “number of vegetation types in 500 m radius of site” (Pereoglou et al., 2016). Among all studies that defined LH ($n = 127$), 24.4% considered both compositional and configurational components by explicitly stating the investigated component in the definitions (the “spatial variation of the composition and configuration of landscapes;” Li et al. 2015) or implicitly (the “land-cover types and

their spatial arrangements” Singh et al. 2017). Lastly, only two articles considered temporal aspects in their definitions (Deutschewitz et al., 2003; Wang et al., 2017).

Among all 127 articles with a LH definition, a total of 51 different references were cited, with 52.7% of the articles citing at least one reference. The most cited references were Fahrig et al. (2011; n=16), followed by Li and Reynolds (1995; n=9) and Li and Reynolds (1994; n=5). These three references consider LH as a compositional and configurational variability of landscapes. However, some studies adapted the original definitions from these references, as for Corro et al. (2019), which defined LH as “the number and amount of land uses” and cited Fahrig et al. (2011). Although this definition is comprised by the reference, it considers only one aspect of LH described by Fahrig et al. (2011).

There are striking differences between studies that measured LH under the structural and functional perspectives. We found only 10 (0.01%) studies that explicitly stated that functional LH was measured, with the definition of functional LH consistently used. For instance, Azevedo et al. (2000) assigned weights to forest patches according to their regeneration time, with higher weights assigned to older patches as they would offer more resources for birds. In contrast, 158 (24%) studies measured structural LH, but only three explicitly provided a definition of the term (Mairota et al., 2013; Ye et al., 2015; Fahrig et al., 2015) that were similar and accounted for physical attributes of the landscape, without considering organisms and ecological processes.

From the seven publications that used biological variables in functional LH articles, only one studied a community (Perović et al., 2015). Contrarily, from the 102 articles that used biological variables in structural LH studies, 80 investigated communities and 22 studied populations (Fig. 3). Concerning LH components, most articles (75%) did not state if they measured compositional or configurational LH (Fig. S1), even though they employed metrics commonly used as proxies for these

components. In 17.4% of the reviewed articles the authors explicitly state that both compositional and configurational LH were analyzed, while in 5.4% and in 1.6% of the articles, only compositional or configurational attributes of landscapes were measured, respectively. Fahrig et al. 2011, the most cited reference, defined compositional LH as “the number and proportions of land cover types” and configurational LH as “the spatial arrangement” of them. However, we found 10 distinct definitions of compositional LH in 46 articles that cited Fahrig et al. (2011) (Tables S1 and S2).

Landscape metrics quantifying and representing landscape heterogeneity

A total of 203 metrics were used to measure LH, while 238 were used to measure other landscape features (e.g., fragmentation and connectivity). The metrics most frequently used to represent LH were “Shannon diversity index” and “proportion of land cover type” (Fig. 2). Most metrics used as proxies of LH also coincided with those used to represent non-heterogeneity metrics (Fig. 2). For instance, although “number of land cover types” and “patch richness” commonly quantify LH (McGarigal and Marks 1994), we found that most studies employed them to measure other landscape features (Fig. 2). Regarding compositional heterogeneity, the metrics most commonly used were those describing the amount of land cover types (e.g., “proportion and number of land cover types”) and the number and proportional abundance of patch types in the landscape. For configurational LH, the metrics most frequently used were “patch size” and “edge density” (Fig. 2). The same metrics were also applied by different authors as proxies for different types of LH. For instance, the “proportion of a land cover type” was considered as structural and compositional LH and as heterogeneity and non-heterogeneity metrics (Fig. 2). This result highlights the difficulty in interpreting the type of LH authors aimed to address when not explicitly stated.

Studies also used remote sensing metrics as proxies of canopy cover quality, including the normalized difference vegetation index (NDVI), the enhanced vegetation index (EVI), and semivariograms (Garrigues et al., 2008; Horning et al., 2010). These parameters can summarize the distribution of biophysical properties of the vegetation and are good indicators of heterogeneity over landscapes, making them suitable proxies for LH as long as pixel values are used instead of categorical maps (Garzia et al., 2018; Sugai et al., 2019). Finally, 27.5% of the articles did not specify the metric used to represent LH.

Scope of landscape heterogeneity studies

Most articles (45%) addressed the effects of LH on biodiversity patterns (Fig. S2), while others addressed biodiversity-related topics, such as agricultural yield (12.7%), human induced changes (4.7%), ecosystem services (3.2%), and conservation (1.5%; Fig. S2). These last research topics addressed LH by evaluating natural landscape patterns and/or by quantifying how these patterns changed in space and time. About 24% of the articles evaluated LH without accounting for any response variable, being treated as “landscape analysis” (Fig. S2). For example, studies aimed at identifying sites with high LH (Perko et al., 2017), analyzing landscape changes over the years (Li et al., 2005), or proposing approaches to quantify LH (Hamstead et al. 2016).

Biological response variables related to landscape heterogeneity

Biological data were used in 55.5% of the articles, with the most frequent response variable being species richness (18.4% of all variables), species abundance (11.3%), and species diversity (7%; Fig. S2). The biological groups most frequently

studied were insects (27.5%), birds (24%), plants (18.7%), and mammals (14%; Fig. 3), reflecting a general taxonomic bias in biodiversity research worldwide (Troudet et al. 2017). Regarding the biological level of organization, our results revealed that communities (rather than populations or individuals), are far more common response variables (72.2% of studies that used biological data; Fig. 3).

Scale and extent

Most studies used local extent analyses (57.5%), followed by regional (33.7%), national (6.2%), continental (2.3%), and only one global mapping analysis. Wider extents would, for example, investigate changes in LH over different time periods in a watershed (classified as regional extent; Wang and Wang 2013). Despite its importance, 3.9% of studies did not inform which spatial scale (mapping polygons size) was employed for mapping. From those that evaluated landscapes delimitations based on circles, squares and rectangles and used a single landscape scale, 70% did not justify the choice of the scale used. For the remaining 30% that did justify the scale employed, more than half (66%) chose the scale based on the biology of the studied organism. For most biological groups, local scale was the most frequently employed scale, except for vertebrates, which had a larger contribution of regional and national extents (Fig. S3). Circular buffers were the most frequent delimitation within all biological groups (Fig. S3). Only 25% of studies used more than one scale such as several circular buffer sizes and most of multiscale studies were conducted at local extents (Fig. S3). Refer to the Supporting Information file for more details on landscape – and temporal – scales and extents used.

Inconsistencies, Knowledge gaps, and future perspectives

The literature related to LH may be inserted in a wider context of ecological research concerned with understanding the role of heterogeneity in determining ecological patterns (Stein et al., 2014). Given the correlated nature between LH and the current scenario of climate change, conversion and destruction of natural areas, and biodiversity loss (Barnosky et al., 2011), research accounting for such challenges are extremely relevant to support the development of conservation strategies and to evaluate existing conservation plans. A conceivable strategy to guarantee the integrity of ecological processes and long-term conservation of species is to preserve patches of natural vegetation embedded in heterogeneous landscapes (Benton et al., 2003; Perfecto & Vandermeer, 2010).

There is an imbalance of the taxonomic groups studied (Fig. 3). Except for most insect species, some of the most-studied groups (birds, plants, and mammals) comprise “charismatic species” which are often used as “umbrella species” in conservation actions (Barua 2011). In most studies insects were used as the focal group, mainly because they are taxonomically diverse, virtually occupy any terrestrial environment, are widely used as bioindicators, have medical or veterinary concerns, and are agricultural and forestry pests (Hill 1997). Focusing on underrepresented groups, such as reptiles, amphibians, invertebrates other than insects, and microorganisms, should be the main concern in future studies. By reducing taxonomic bias, knowledge gaps related to the role LH has on governing ecological processes and biodiversity patterns (species occurrence, richness, and abundance) could be narrowed. Furthermore, at the landscape level, key ecosystem processes can be driven by many understudied taxa, and valuable ecological processes will remain unknown if LH studies remain focusing on the same taxonomic groups. For example, chelonians (turtles) can account for a significant portion of dispersed seeds in terrestrial environments (Falcón et al., 2020). Hence,

understanding how chelonians are distributed and moving in heterogeneous landscapes can be relevant for ecological restoration, as seed dispersal is essential for natural regeneration.

Additionally, the level of organization of these groups and the mechanisms governing them are influenced in distinct ways by LH. Species richness can be modulated by environmental heterogeneity in many aspects, including LH (Tews et al., 2004). Species coexistence, persistence, and diversification should govern the main ecological mechanisms that regulate broad patterns (e.g.: species distribution) across ecological systems. For instance, positive correlations between LH and bird richness may result from a dependence of the taxa on similar environmental variables or on different but spatially covariant variables (Kissling et al., 2007). Therefore, searching for a causal inference in LH studies may assist in understanding the mechanisms that promote biodiversity in heterogeneous landscapes, thus supporting practical conservation measures.

Movement and dispersal ability (Doherty & Driscoll, 2018), habitat preference (Sánchez-Clavijo et al., 2019) and species interactions (Boscolo et al., 2017) are important factors affecting the response of every organism to LH. Given communities are represented by a set of species with unique ecological requirements, response of communities to LH are often the output of countless ecological processes in which determining the underlying ecological mechanisms is quite challenging (Wiens et al., 1993). Therefore, focusing on the functional dimension of landscapes could enable a better understanding of these mechanisms. Estimating the effects of different types of land cover to different species in a community may not be easy or feasible in most cases, and this may explain the fact that only one study used the functional perspective in community studies.

Few articles explored the effects of LH on the spread of diseases (Suwonkerd et al. 2002, Overgaard et al. 2003; Fig. S2). Nonetheless, new diseases, such as the one causing the COVID-19 pandemic, exemplifies the urgency of understanding how landscape features (including LH) may affect the emergence and spread of diseases.

Regarding the way in which the authors refer to LH, the lack of clear definitions in 80.8% of studies, summed with the inconsistencies on the terminology, suggest that a fundamental shortfall of the literature on LH is due to an issue as basic as properly defining LH. As both components of LH (composition and configuration) may have different effects on biodiversity (Fahrig et al. 2011, Tschamntke et al. 2012), it is crucial to adequately classify, define, and specify which component is being addressed. Determining the relative effects of composition and configuration allows a better understanding of the mechanisms driving diversity patterns and further improve strategies for landscape management (Duflot et al. 2017). Although most studies failed in specifying the LH components analyzed (Fig. S1), the proportion of published articles that specify it has increased over the years (Fig. 1).

Most LH metrics were used interchangeably by different authors to represent compositional and/or configurational aspects (Fig. 2) as, theoretically, most metrics are proxies of both composition and configuration. For example, the “Shannon diversity index” considers the number and proportion of patches of different land cover types and is frequently used as a measure of landscape composition (Fig. 2). In turn, the “number of patches” is influenced by the degree of landscape fragmentation, which is related to the spatial arrangement (landscape configuration). Given the complex relationship between landscape composition and configuration, researchers should seek to minimize such interdependence when planning the experimental design of their studies.

Fragmented landscapes are commonly correlated with heterogeneity and consequently the same metrics applied to quantify habitat loss or fragmentation *per se*

were also used to measure LH, and vice versa (e.g., patch and edge density and patch richness; Fig. 2). Because LH increases with more dispersed and intermixed land cover types (Yaacobi et al., 2007), metrics referring to the spatial arrangement of single class patches were also used as proxies of LH, such as “nearest-neighbor distance”, “interspersion-juxtaposition”, and “contagion index” (Šímová & Gdulová, 2012).

Guidelines to address landscape heterogeneity in ecological research

Our literature review provided insights on how to address LH accounting for the distinct components and perspectives. We suggest six steps to be considered when assessing LH (Fig. 4):

(1) Use previous knowledge to test the influence of heterogeneity on the processes of interest under hypothesis-based rather than explorative approaches (Fig. 4). In our review, we identified studies in which the mechanism relating landscape heterogeneity and biodiversity was unclear. Without a clearly stated mechanism prevents us from determining the likelihood of distinct ecological processes occurring (e.g., Marboutin and Aebischer 1996, Jeanneret et al. 2003). The processes of interest may also refer to an abiotic aspect involved in higher-level ecosystem processes. For instance, soil nutrients should vary less in landscapes situated in flat terrains in comparison to mountainous regions, therefore, in this case, landscape variables other than terrain heterogeneity should be considered (Hu et al., 2019).

(2) The definition of LH and its components (composition and configuration) should be explicitly stated. Analyzing LH without asserting and defining the components being addressed may hamper the comprehension of how landscape composition and configuration affects biotic and abiotic factors separately. This could lead to misunderstandings among researchers and the non-scientific community, including stakeholders, and hinder advances in the field (Heink & Kowarik, 2010). Few

studies analyzed the effects of compositional and configurational LH separately. For instance, Perović et al. (2015) found that compositional LH in agricultural landscapes influenced the taxonomic diversity of butterflies while configurational LH was mostly associated with their functional diversity. These are important findings to guide landscape management in conservation plans, and future research should be concerned with the independent role of compositional and configurational LH. To avoid misinterpretations, we suggest using definitions and terms that are a consensus in the landscape ecology literature. Although ecological terms can be understood within the context in which they are used (Hodges, 2008), clearly stating the definition being used may aid to understand the many aspects related to LH.

(3) Choose metrics that measure heterogeneity based on its implications with response variables. There are several methods to quantify LH (Li & Reynolds, 1994) and adequate metrics should represent the effect presumed in the ecological processes. Although heterogeneous landscapes are generally more fragmented in human-dominated regions, the use of metrics that are proxies of landscape fragmentation (e.g., patch and edge density and patch richness; Fig. 2) are discouraged to quantify LH since even with a high number of patches, their proportion in different categories (land cover types) could be uneven. Metrics that consider both the number and the proportion of landscape units, such as Shannon and Simpson diversity indexes, are more suitable (McGarigal, 2014). As discussed, there are several ways to quantify LH components, and selecting metrics that quantify composition or configuration may be difficult. Therefore, researchers should clearly state which component is being addressed and the metrics being used as proxies of LH and the reasons why predictors are expected to affect the response variable(s) chosen. Nonetheless, deciding on the appropriate metrics depends directly on the definition of LH and its components.

(4) To improve communication and provide adequate interpretation of results, authors should clearly state the effect of LH (based on the adopted definition) on the phenomenon of interest (dependent variable). The literature on LH is highly diverse and is already represented by hundreds of articles. However, we believe that a certain level of standardization on terminologies and concepts related to LH may enhance the ability of the scientific community in communicating their findings and transferring the knowledge produced into decision making actions.

(5) Clearly stating the scale and resolution used is fundamental when comparing and interpreting LH. The appropriate scale should be selected to represent the phenomenon of interest (e.g., species richness, fire incidence). For instance, Duflot et al. (2016) investigated the effects of LH on carabid beetles establishing 1 km-edge squares based on the home range of the focal group. In addition, we suggest a multi-scale approach to evaluate the scale of effect of the investigated parameters on dependent variables (Jackson & Fahrig, 2015; Tschardt et al., 2005), as the effect of LH on biodiversity at small scales (e.g., a local field) may be different from the effect of LH at larger scales (Weibull et al. 2000, Chust et al. 2003).

(6) Promote research that focuses on the functional perspective of LH. Because movement abilities and resource exploitation differ between taxonomic groups, functional components of landscapes provide useful approaches to investigate organisms under a functional perspective (Tschardt et al., 2012; Fahrig et al., 2011). However, as functional LH requires information on how different land cover types influence species demographic and behavioral processes, its application is not a trivial task. Moreover, subtle differences in land cover types that are not apparent to humans and/or remote sensors may also affect species preferences and dispersal (Fahrig et al. 2011; Box A). Despite the potential of functional LH in improving our understanding of how species interact with their environments, structural LH is easier to quantify as it

uses a series of metrics that are commonly applied as proxies of biodiversity (Duelli, 1997). The low number of studies that employ a functional approach in LH analysis (Fig. 1) also indicates a research gap that should be addressed by future studies, especially as functional approaches can indicate how different land cover types and their spatial arrangement affect both biotic and abiotic processes, such as species abundance and nutrient cycling.

Moreover, studies that investigate LH over different time periods can benefit from employing the same scale and resolution to support comparisons over different periods. Although arbitrary delimitations may appear to have no scientific basis to assess ecological responses, LH measures in such extents are useful to support public policies related to biodiversity and ecosystem services such as watershed management (Qiu & Turner, 2015).

Some of the mechanisms and hypotheses underlying how LH could affect biodiversity patterns are exemplified below and points out that heterogeneity is not always a determinant factor in the process of interest. Distinct land cover types influence the ability of organisms to exploit different yet essential resources. This process, called “landscape complementation” is affected by the heterogeneity of land cover types and the spatial arrangement of different patches in landscapes, as both can influence the mobility of organisms (Dunning et al. 1992). Thus, LH may have a positive effect on species richness and abundance for several taxonomic groups (Benton et al., 2003). However, as LH increases, patch size (habitats) tends to decrease, eventually becoming so small that they may not provide enough resources to organisms, and thus might no longer sustain viable populations (Duelli, 1997). This suggests that the occurrence of overall taxa is greatest at intermediate levels of LH and, thus, the intermediate disturbance hypothesis would drive the species richness-LH relationship (Redon et al., 2014; Fahrig et al., 2011), specially for taxa with wider niches. Groups

with wide niches may be able to obtain resources in both extremes of the spectrum: from homogeneous to extremely fragmented, heterogeneous landscapes (Tews et al., 2004; Redon et al., 2014). In contrast, sensitive/specialist organisms with narrow niches tend to be negatively affected by LH, since they require larger areas, which is the case of certain forest understory birds (Powell et al., 2015), arboreal mammals (Moraes et al., 2018), and amphibians (Becker et al., 2007).

Following these six suggested steps and considering the knowledge gaps identified, we believe the literature on LH can become more cohesive and indicate more explicitly how patterns and processes are related to the different aspects of LH.

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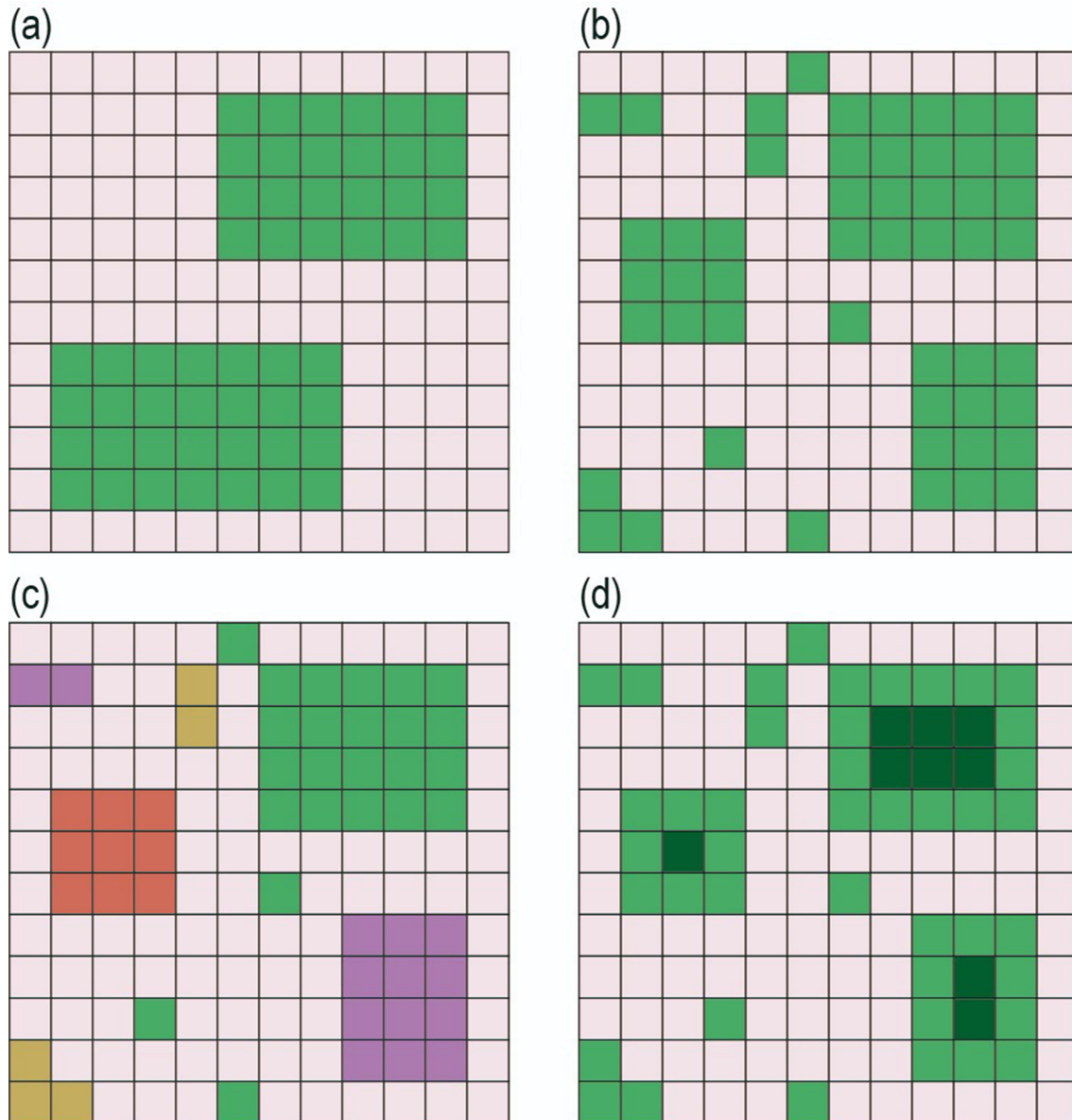
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Box A.

Schematic representation of the different dimensions of landscape heterogeneity (LH).



Each square represents a pixel of a categorical mapping (i.e., the smallest possible mapping unit in which pixels of the same color have the same categorical value). The four landscapes (a - d) represent patches of land cover types (colored pixels) and a matrix (light gray pixels). The area occupied by the matrix and the patches is the same in all four landscapes, however, the components values (composition and configuration) and perspectives (structural and functional) differ. Landscape (a) has the same

compositional LH (diversity of land cover types) of landscape (b), but landscape (b) shows a more complex spatial patterning than (a) and, consequently, higher values of configurational LH. In landscape (c), pixels of different colors represent different land cover types. Therefore, compositional LH in landscape (c) is higher than (b), even though both have the same configurational LH. Landscape (d) has the same land cover types of landscape (b); however, it is represented under the “perception” of a species for which edge-pixels (i.e., pixels that have direct contact with the matrix; light green pixels) have lower habitat suitability than pixels that are not in contact with the matrix (core pixels; dark green). The difference in suitability between edge-core areas may affect the occurrence of a given species and may be described as different land cover classes. Areas located in patch edges may be affected by the surrounding matrix, thus differences in environmental conditions (e.g., light incidence and temperature) between fragments (core and edge) could be expected (Turner et al., 2001). These differences could affect vegetation structure, species occurrence, ecological interactions, and several other biotic and abiotic processes, which in landscape ecology, are widely known as edge-effects (Turner et al., 2001). In summary, in contrast with landscape (b), which only the structural perspective is considered, landscape (d) exemplifies functional LH in which edge effects are considered for a given species. Another way to analyze the landscape from a functional perspective would be to assign different weights in the analyzes that are concerned with the effects of different land cover types (c). These weights can vary according to the biological group or abiotic factor, so that for a given species some type of land cover can provide more (or less) resources and, thus, influence a certain ecological process.

Figure legends

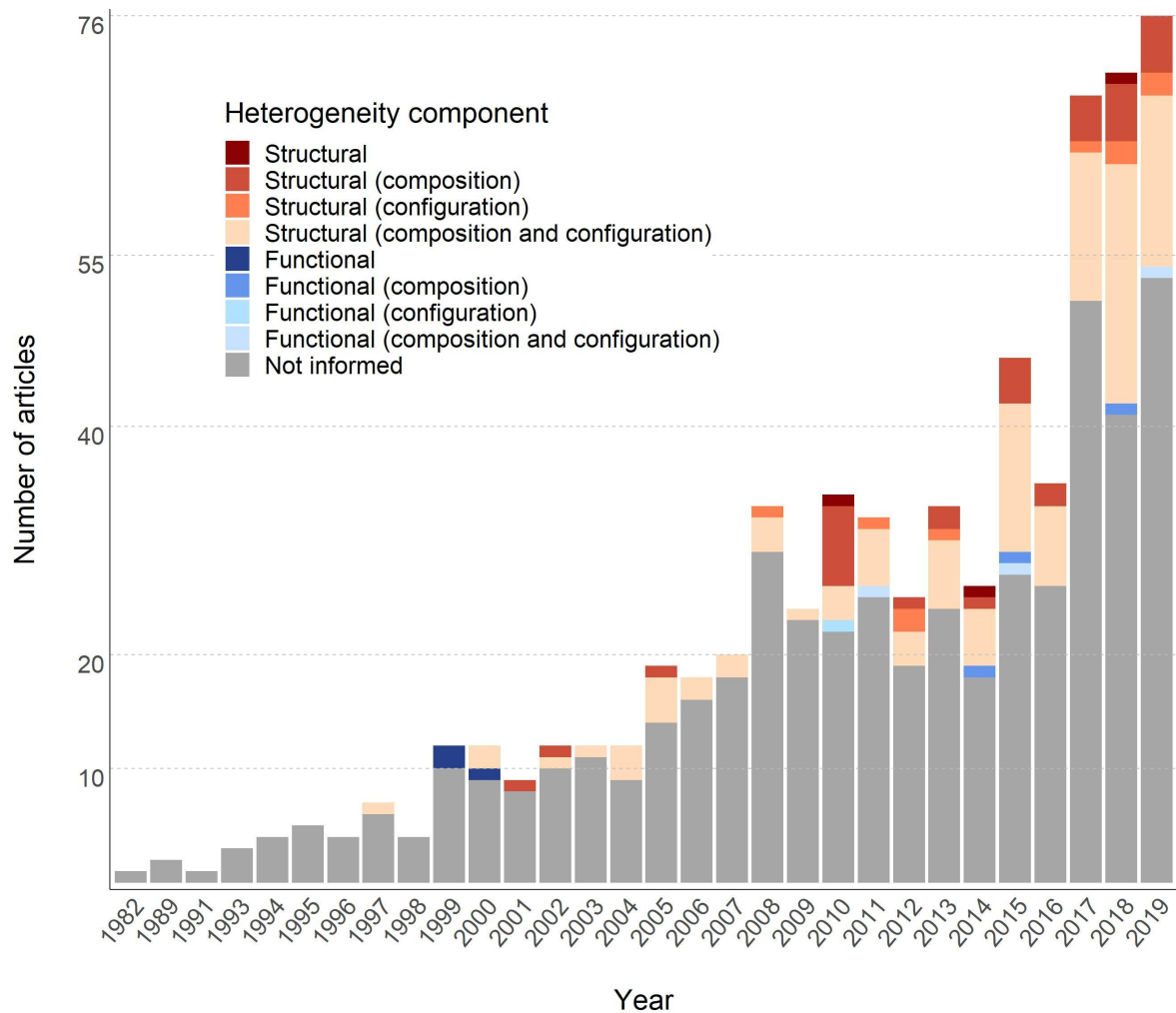


Fig. 1. Number of articles per year that addressed landscape heterogeneity. Colored bars indicate the proportion of articles in which authors stated that distinct types of heterogeneity (compositional/configurational; structural /functional) were measured – see definitions and discussion on these terms in Box A. The type of heterogeneity was attributed only when authors explicitly stated them.

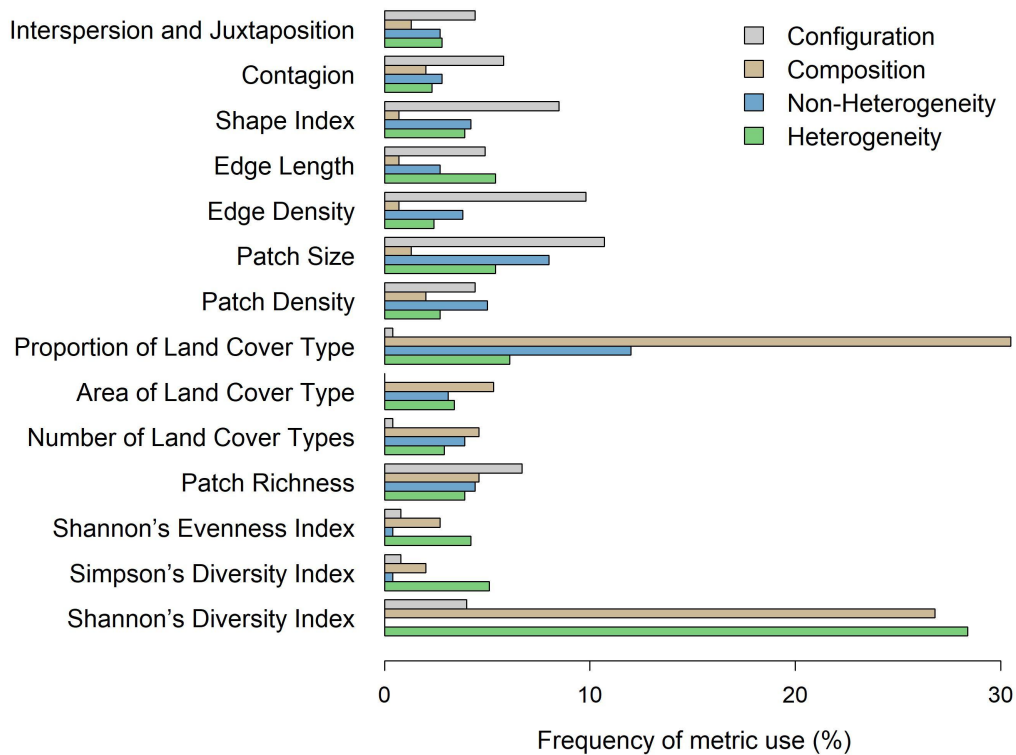


Fig. 2. The ten most frequently used metrics assigned by the authors as proxies of landscape heterogeneity (green bars) and of other landscapes aspects unrelated to landscape heterogeneity (blue bars). The percentage of studies in which each metric was considered as a proxy for configurational LH are indicated by gray bars and for compositional LH by light brown bars. Note that the summed numbers do not correspond to the total amount of articles reviewed (661) as the quantity of metrics employed varied among studies.

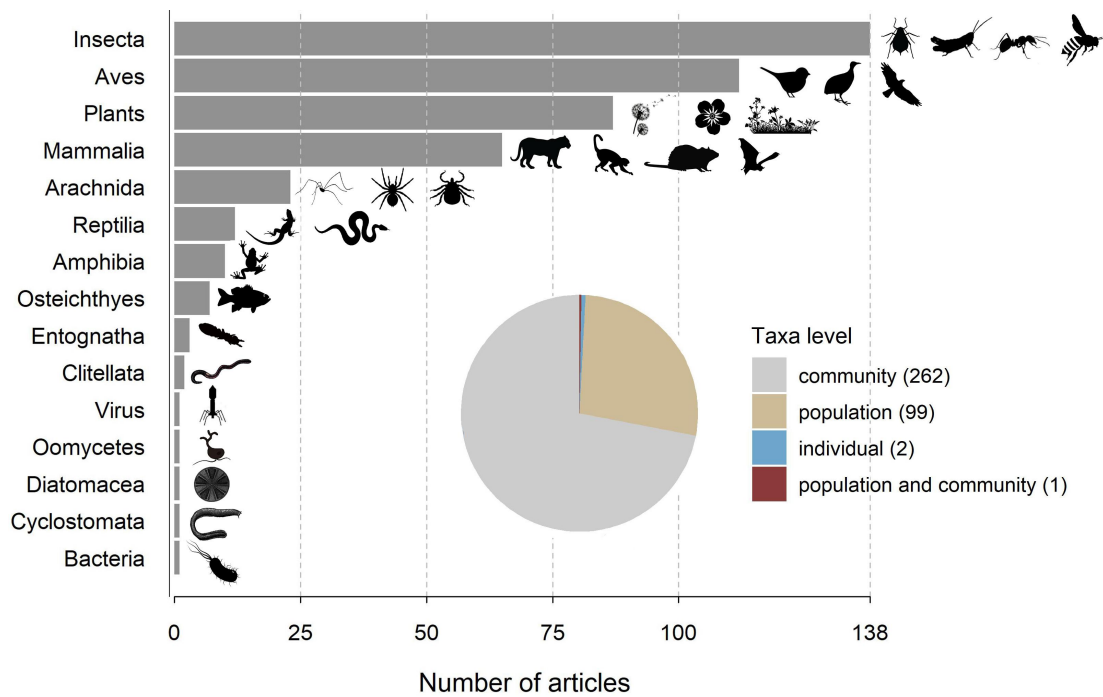


Fig. 3. Frequency with which different taxonomic groups were used as a dependent variable in studies that measured landscape heterogeneity. The pie chart indicates the proportion of the level of organization of the taxa studied. Note that the summed numbers do not correspond to the total amount of articles reviewed (661) as the quantity of metrics employed varied among studies.

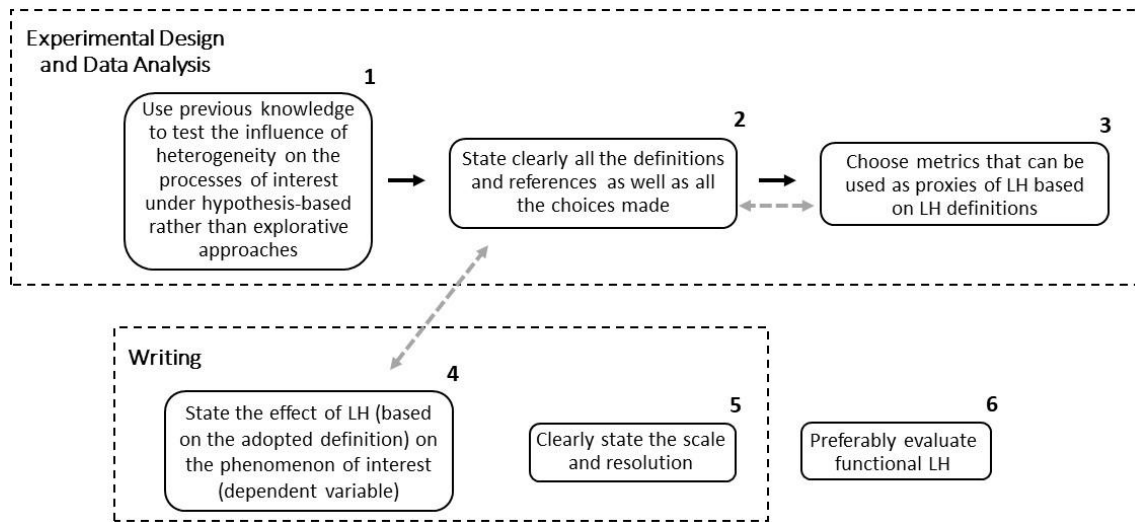


Fig. 4. Steps suggested for each stage in studies that aim to quantify landscape heterogeneity.

Supporting Information

To provide an overview of landscape heterogeneity (LH) studies, we compiled the terms most-used by authors to refer to LH, countries, and biomes where LH was measured, spatial and temporal resolution aspects (pixel size, time scale, and number of temporal observations), and the landscape models.

Terms on Landscape Heterogeneity

In total, 93 different terms are used in the reviewed articles to refer to LH and the discussion of the use of each of them is not the scope of our review. The terms most used by the authors are “landscape heterogeneity”, “landscape diversity” and “spatial heterogeneity” (Figure S4). We employ throughout this review the term “landscape heterogeneity”. Although the term “landscape diversity” is broadly used, there is a non-trivial difference to the term “landscape heterogeneity”. Whereas the word “heterogeneity” implies in integration of interactions among different entities, diversity implies divergence, and refers to the range of different things without integration between them (Kolumbus et al., 2016). In the context of landscape ecology, diversity thus indicates a quantity of different landscape elements without addressing the differences in particular. Heterogeneity, conversely to diversity, refers to the expression of the differences between individual elements.

We also do not encourage the use of the term “spatial heterogeneity”, once the word “spatial” is too broad, and can refer for example to the heterogeneity of any element in space (*e.g.* biological species; Hodapp *et al.*, 2018). Terms that are associated to the word “habitat”, as “habitat heterogeneity”, also do not seem to be accurate, once habitat in ecology takes into account species perception and thus may be more related to functional heterogeneity that represents only one type of LH (see above).

“Landscape pattern” and “landscape structure” seems too vague and can refer to other aspects of landscapes, as vegetation only.

Geographic coverage and biases

Regarding the geographical coverage, non-simulated studies (i.e., studies that did not use simulated landscapes) were mainly concentrated in Europe (50% of sampling locations), North America (19%), and Asia (18.2%), whereas South America, Africa, Oceania, and Central America corresponded together to 13.1% (Figure S5). Most of the Asian landscapes analyzed were concentrated in China (68.4%). US and China, together accounted for 27.7% of the localities studied (Figure S5), being the two countries with the largest number of studies. Almost 70% of the landscapes studied were in North America and Europe (Figure S5), which is also a tendency in other fields of ecology (Martin et al., 2012).

The approximate geographic coordinates and the corresponding biome, according to Olson et al. (2001), of where LH studies were conducted were extracted using Google Earth (google.com/earth). To evaluate if the number of studies were evenly distributed across biomes, we performed a G-test between the number of studies in each biome and the ice-free land area these biomes occupy on Earth.

Landscapes analyzed were mostly from Temperate Broadleaf and Mixed Forests (41.2% of sampling locations), Mediterranean forests - woodlands and scrublands (15.3%), and temperate conifer forests (11.5%); while only 0.1% were mangroves (Figure S6). Conversely, biomes such as deserts and xeric shrublands (20.6% of ice-free land area), tropical and subtropical grasslands, savannas, and shrublands (14.9%), and tropical and subtropical moist broadleaf forests (14.6 %) occupy the largest areas on Earth. The remaining 11 biomes considered by Olson et al. (2001) were represented by 32% of sampled locations. Thus, the number of studies expected considering the area

occupied does not necessarily correspond to the number of observed studies per biome (G-test, $P < 0.05$; Figure S6). For example, the number of studies performed in temperate broadleaf and mixed forests ($N = 318$) is statistically higher than the expected number of studies proportional to its area (73 expected studies; 9.4% of ice-free land area on Earth; Figure S3).

Most of the studied landscapes are located in Europe and North America (Figure S5). This bias of knowledge towards temperate regions has been documented in several ecological research areas, such as ecoacoustics (Scarpelli et al., 2020) and species invasion (Pyšek et al., 2008). Wealthy countries usually invest more in scientific research (Gálvez et al., 2000; Annan, 2003), resulting in greater efforts to investigate their own territories in comparison to countries with less economic resources, which are coincidentally located in tropical regions (Martin et al., 2012). On the other hand, the terrestrial distribution of species has an opposite trend, with increasing biodiversity towards the tropics (Gaston, 2000). In addition to the higher species richness in tropical regions, LH may have greater relevance for maintaining biodiversity and ecosystems functioning in these regions (Arroyo-Rodríguez et al., 2020).

Similarly, most articles focused on temperate biomes (Figure S6), whereas geographical knowledge gaps were evident in tropical and subtropical regions, comprising forests, savannas, grasslands, and shrublands. Despite the high levels of species richness and endemism in tropical biomes, they also suffer from intense deforestation, and are considered priority areas for biodiversity conservation worldwide (Buchanan et al., 2011). Therefore, increasing efforts to improve scientific knowledge in the tropics is of extreme importance given the current scenario of biodiversity loss (Lindenmayer et al., 2018).

Extent, scale, and resolution

Articles that used multiscale approaches corresponded to 23% of the 661 articles analyzed. They employed either regular (61.1%; 404 out 661) or irregular (38.9%; 257 out 661) polygons as landscape analysis units. Among the articles that used irregular polygons, 35.8% (92 out 257) of them used municipalities, watershed, or reserves as boundaries. The mean size of regular polygons used as circular buffers was 1180 m-radii $\pm$ 2069 S.D. (N = 614; Figure S7) and the average edge of square polygons was 6832 m $\pm$ 14,001 S.D. (N = 139; Figure S8). Such wide variation in the scales of regular polygons may reflect the variation in the extent of studies from local to global, as well as the large range of body mass and area of occurrence of the studied organisms. The large range of variation in scale and extent demands different mapping resolution and different levels of detail. Thus, as expected, mapping resolution also varied. The most used value of pixel size was 30 m-edge (28.9%), with the larger pixel size used being 43.709 m-edge (Figure S9). In addition to pixel size, the number of classes employed also varied where the mean number of classes used was 11 $\pm$ 11 S.D. (N = 683 as some studies used more than one map; Figure S10).

Temporal landscape heterogeneity

Landscapes are dynamic, therefore are heterogeneous in a spatio-temporal perspective (Li & Reynolds, 1995). As ecological processes may range from days to centuries (as lifetime spans of organisms vary greatly) the temporal scale of LH may also vary (Risser, 1987). Accordingly, 21% of the articles analyzed considered temporal changes when defining LH, stating that LH includes spatial and temporal variations in landscape properties (Deutschewitz et al., 2003; Wang et al., 2017).

Temporal LH was used to investigate the influence of crop rotation in agricultural regions and the effects of these changes on species assemblages (Bertrand et

al., 2016), the effects of forest regeneration and species richness (Marull et al., 2015), the effects of fires over different periods of time (Viedma et al., 2009), and the effects of different economic cycles (Pereira et al., 2017).

The mean number of temporal observations (i.e., number of different mappings that represent each period) was 9 ± 24.2 ($n = 139$), ranging from 2 to 221, and the temporal breadth spanned from 1750 to 2054 (Figure S11). Maps of a remote past, as those of the 18th century, were generated based on landscape modelling or based on historical maps, while maps for future periods were generated based on landscape modelling. The temporal scale of most studies was two years (27%), followed by four years (16.2%) and three years (14.2%), and only about 13% of studies represented long-term assessments (≥ 10 years). Even though defining a long-term study is debatable since time periods differ according to the study's goal, prolonged investigations are required to determine ecological responses to drivers of ecosystem change and to better understand complex ecosystem processes (Lindenmayer et al., 2012). Finally, 94.3% of studies that investigated temporal LH analyzed the period after the 1990s, coinciding with the emergence of an ecological approach in landscape ecology (Turner et al., 2001).

Landscape models

The landscape models were considered to be either (1) heterogeneous mosaic, in which landscapes are formed by patches of different land cover classes, with no variation within land cover classes; (2) binary, which uses only two land cover classes (patches are generally considered as “habitat” or “non-habitat”); and (3) continuous model, in which landscapes are represented by the pixel value that may assume any continuous value (McGarigal et al. 2009).

Heterogeneous mosaics were the most employed landscape model (85.3%), followed by continuous (12.8%) and binary models (1.9%). Arguably, the application of

remote sensing tools and data on ecological research has contributed to address the effects of environmental changes on biodiversity over large spatio-temporal scales (Pettorelli et al., 2014). Land-cover mapping relying on categorical classes became the reference to describe environmental changes over large scales. As most maps are based on classified satellite imagery, an increase in the availability of remote sensing products likely promoted the use of heterogeneous mosaics in observational studies (Yu et al., 2014). In fact, the use of satellite imagery associated to large-scale biodiversity datasets has been encouraged to improve the understanding of the effects of LH on natural and managed ecosystems (Fahrig et al., 2011).

Regarding continuous models, 38% (32 out of 84) of the articles were also interested in methodological approaches. This may indicate an increasing interest in the development and improvement of continuous models to address biodiversity changes at large scales. Finally, from the articles using binary models, 46.1% (6 out of 13) were interested in simulation approaches, which often simplify landscapes into habitat and non-habitat categories to model biological parameters such as behavioral responses (Nonaka & Holme, 2007; Romero et al., 2009), population models (Stoddard, 2010), and metacommunity models (Ryberg & Fitzgerald, 2016).

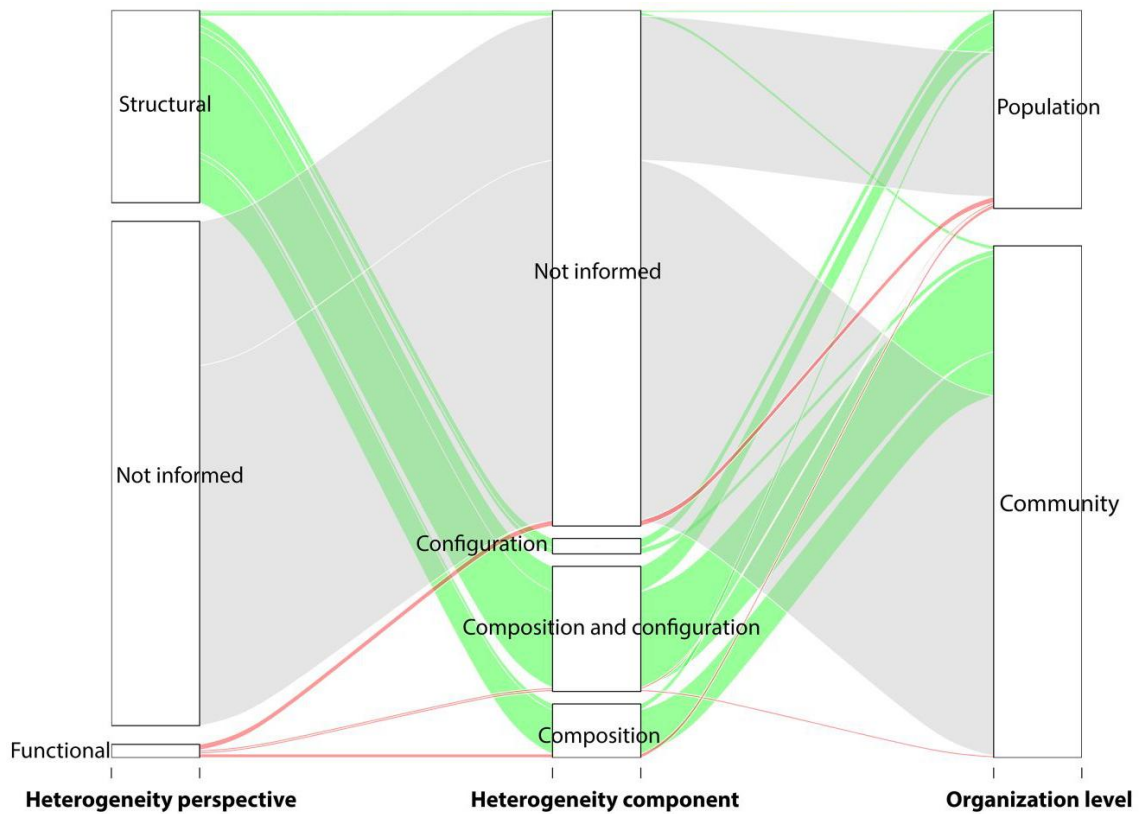


Figure S1. Alluvial diagram showing the relationship among the landscape heterogeneity perspective (structural, functional, or not informed by the authors) and the level of organization of biological variables studied (community or population). In this analysis we removed studies that used non-biological response variables.

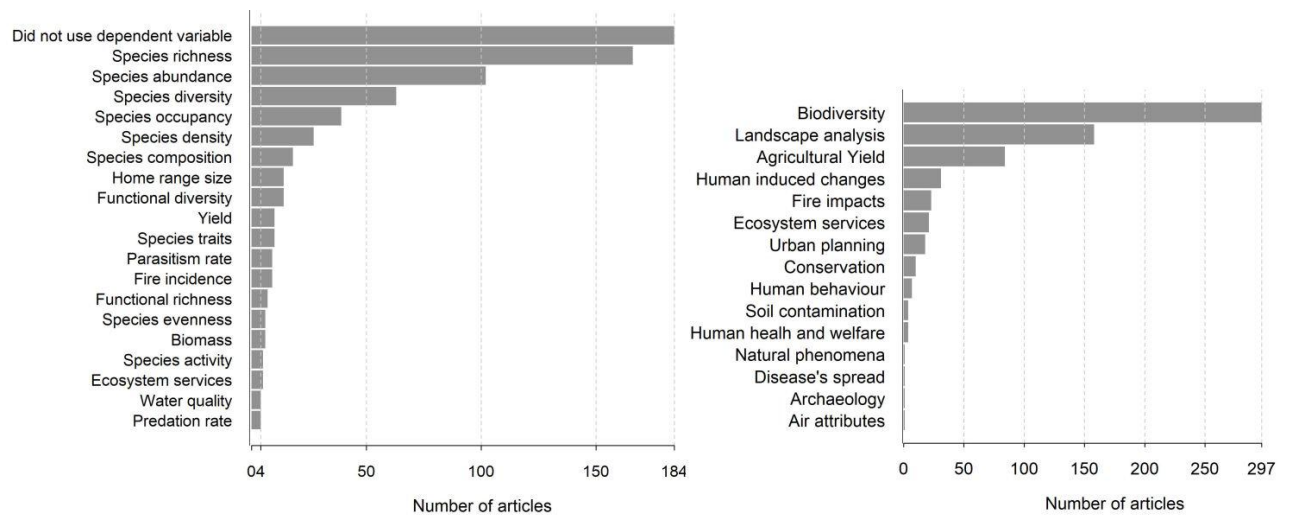


Figure S2. Frequency of scopes present in the articles investigated (right panel) and frequency in which dependent variables were used in studies that measured landscape heterogeneity (left panel).

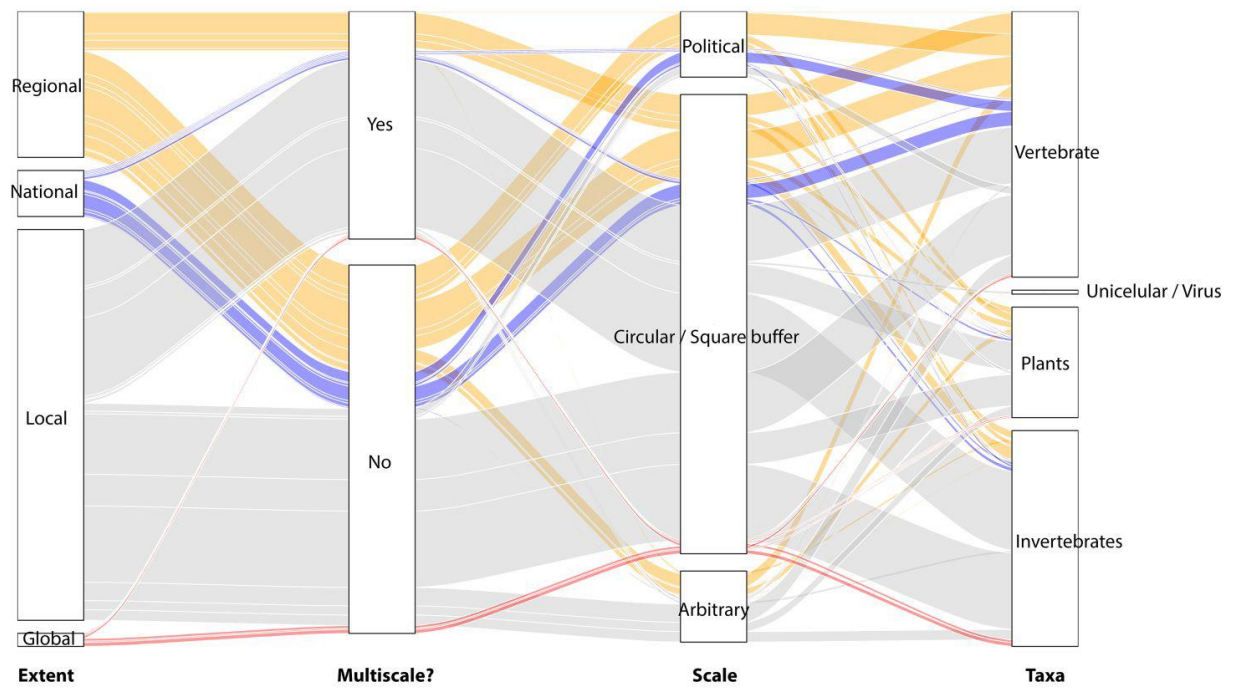


Figure. S3. Alluvial diagram showing the relationships among extent, scale, and taxa in the reviewed articles. In this analysis we removed studies that omitted the scale and that used non-biological response variables. Examples of arbitrary scale are watersheds and ownerships.

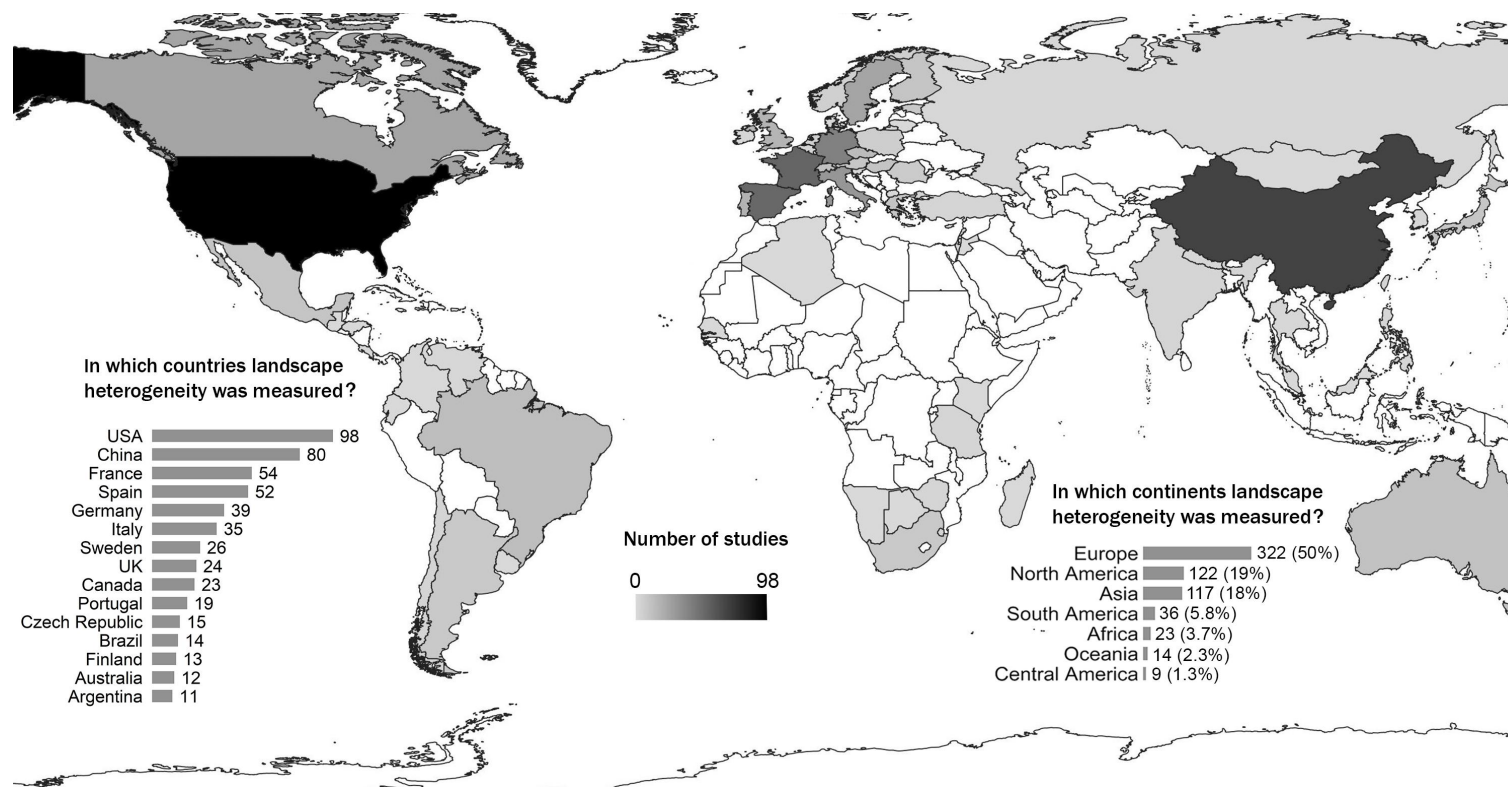


Figure S5. Geographical distribution of the articles addressing landscape heterogeneity. Shades of gray indicate countries where landscape heterogeneity was measured, while white indicates countries where no study was performed and black indicates countries in which the maximum number of studies has been reached (98; US). The 15 countries with the higher number of sampling locations are represented in the bar plot in the lower left corner and the numbers of sampling locations in each continent are in the lower right corner.

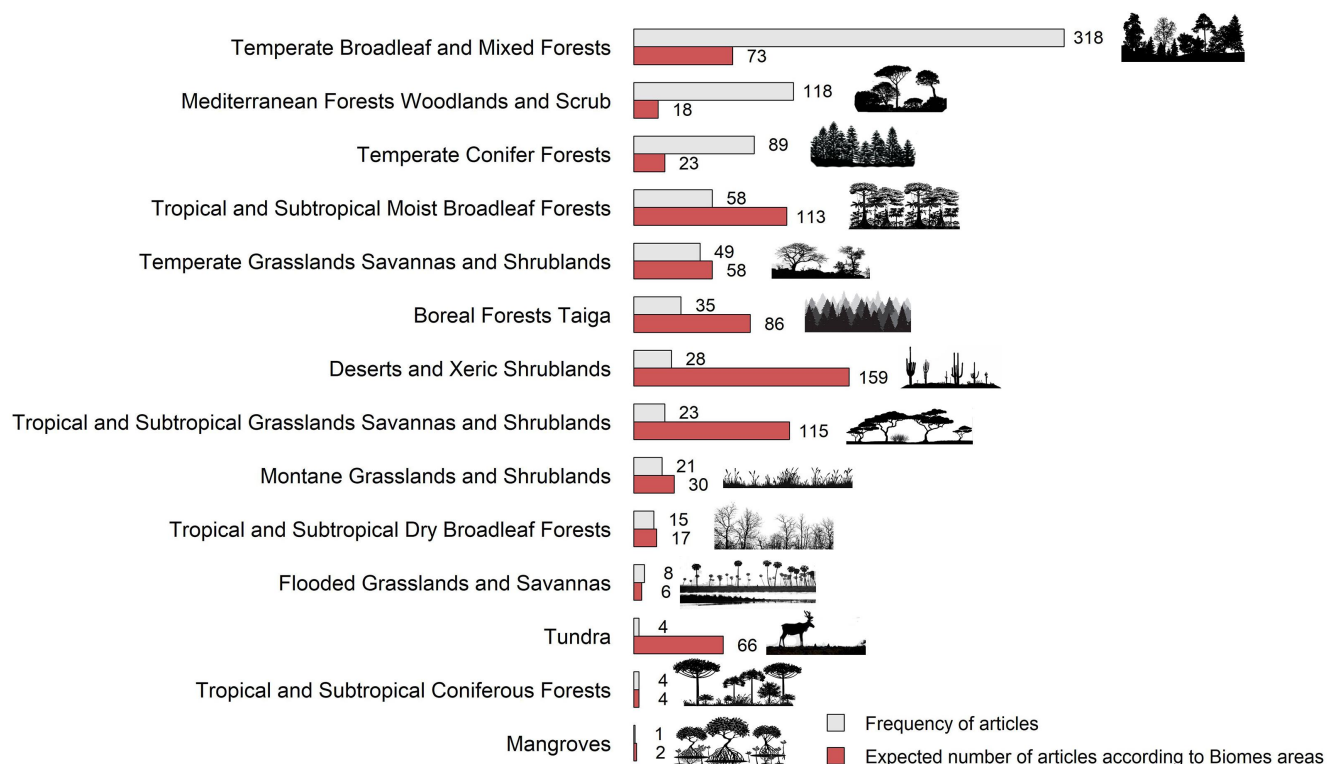


Figure S6. Number of studies performed in each biome (light gray bars) and the expected number of studies in relation to the area of each biome (orange bars; contingency table of G-test).

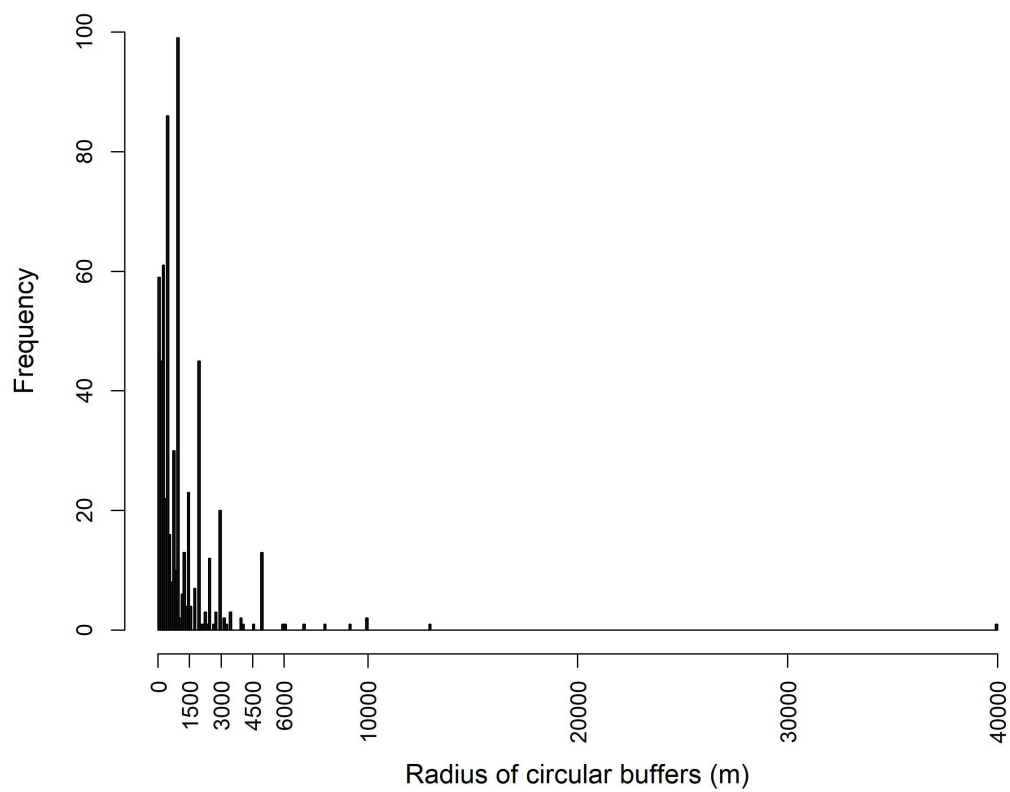


Figure S7. Frequency of the radius of circular buffers used as landscape analysis unities.

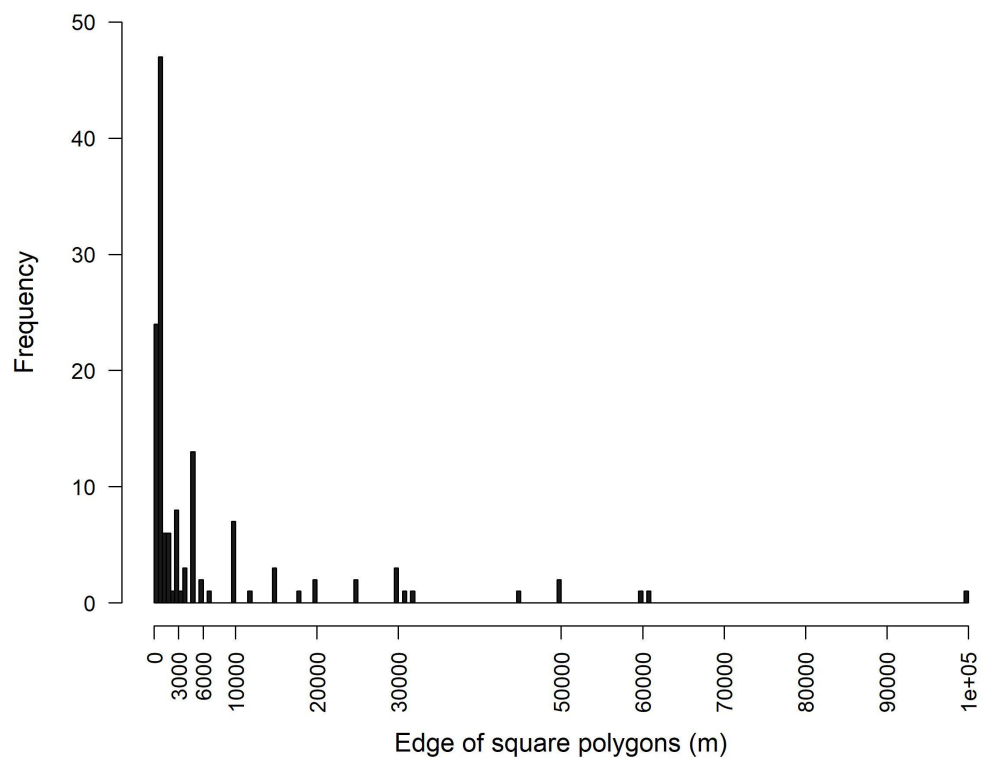


Figure S8. Frequency of the edge of square buffers used as landscape analysis unities.

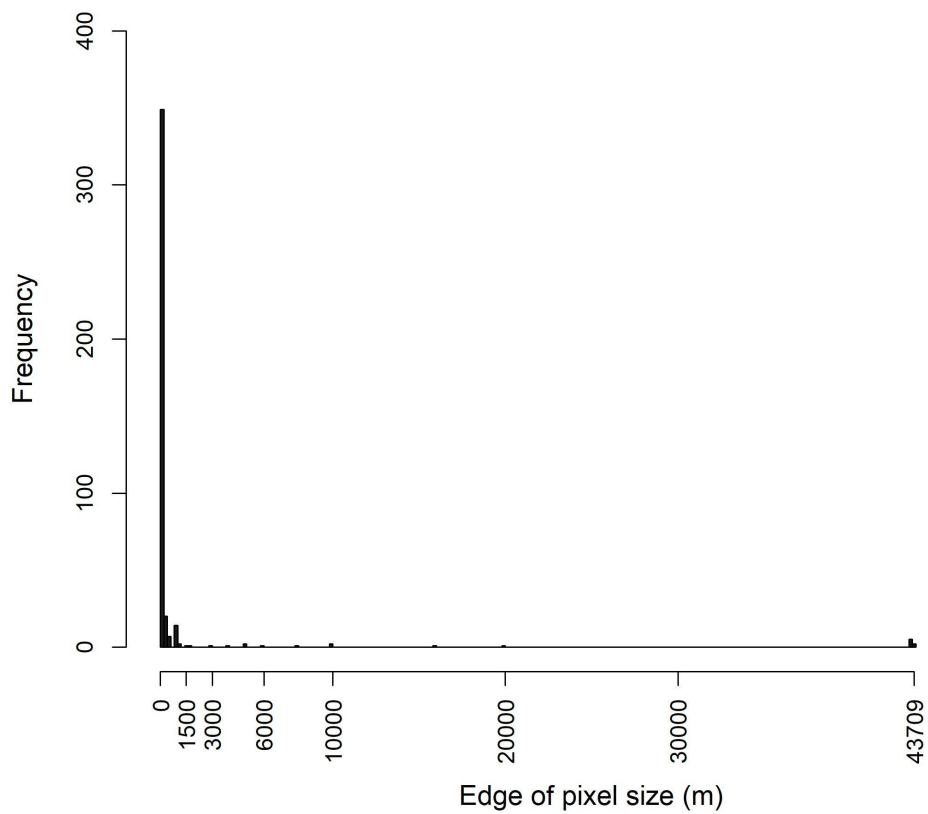


Figure S9. Frequency of the edge of pixels used in mappings

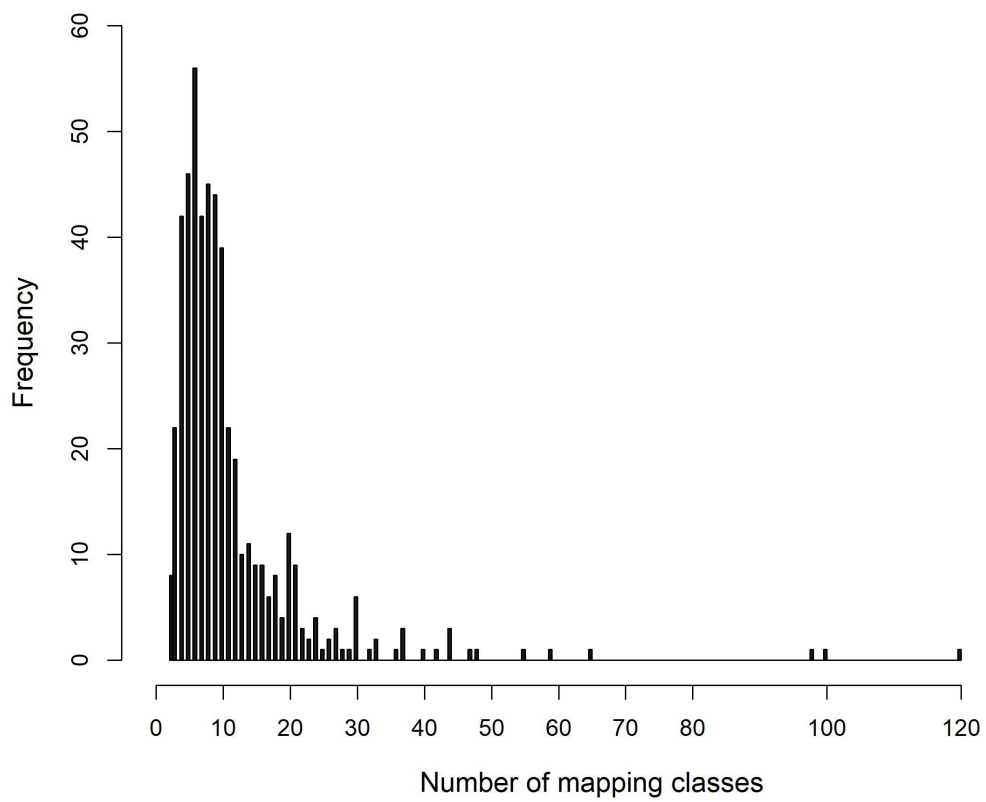


Figure S10. Frequency of the number of mapping classes.

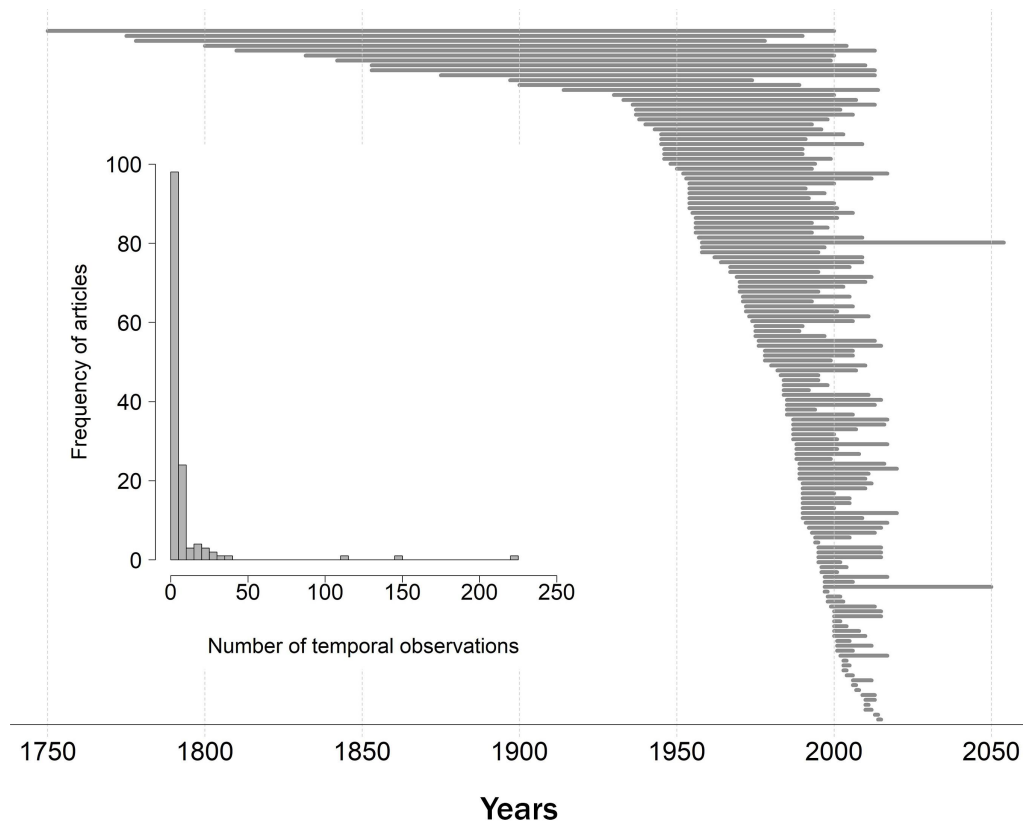


Figure S11. Time scale of studies that measured temporal heterogeneity. Each horizontal bar represents a study with the year it began and ended (x-axis). The histogram shows the number of observations in studies that measured temporal heterogeneity. Mappings for future years and those based on remote past (e.g. XVIII century) were elaborated based on simulations.

Table S1. Definitions of compositional landscape heterogeneity provided by the authors (left column) and the references used to cite these definitions (right column). Numbers in parenthesis indicate the number of articles that used each definition.

Definitions of compositional heterogeneity	References
Proportion of land cover types (14)	Concepción et al. 2008; Fahrig et al. 2011; Li and Reynolds 1994; Miguët et al. 2013
Proportion and number of land cover types (10)	Fahrig et al. 2011; Fahrig and Nuttle 2005; Gustafson 1998; Herzog et al. 2001; Li and Reynolds 1993; Li and Reynolds 1994; Li and Reynolds 1995; Riitters et al. 1995
Heterogeneity of land cover types (10)	Concepción et al. 2008; Duelli 1997; Fahrig and Nuttle 2005; Fahrig et al. 2011; Gustafson 1998; Perović et al. 2015
Number of land cover types (3)	—
Number and area of land cover types (3)	Fahrig et al. 2011; O'Neill et al. 1988; Trani and Giles 1999; Turner 2005
Heterogeneity and proportion of land cover types (2)	Fahrig et al. 2011; Gustafson 1998; Li and Reynolds 1995; Turner 2005
Number and area of land cover types and influence of land cover types on the natural ecosystem (1)	—
Presence of patches of semi-natural and	Fahrig et al. 2011

agricultural habitats (1)	
Non-spatial attributes of a landscape (1)	—
Number of patches (1)	—

Table S2. Definitions of configurational landscape heterogeneity provided by the authors (left column) and the references used to cite these definitions (right column). Numbers in parenthesis indicate the number of articles that used each definition.

Definitions of configurational heterogeneity	References
Heterogeneity in spatial arrangement of land cover types (29)	Concepción et al. 2008; Duelli 1997; Fahrig et al. 2011; Fahrig and Nuttle 2005; Gustafson 1998; Jaeger 2000; Li and Reynolds 1993; Li and Reynolds 1995; Miguët et al. 2013; O’Neill et al. 1988; Trani and Giles 1999; Turner 2005
Heterogeneity in spatial arrangement of land cover types and patch shape (3)	Fahrig et al. 2011; Li and Reynolds 1994
Heterogeneity in spatial arrangement of land cover types and type of edge (2)	Li and Reynolds 1994
Spatial arrangement of land cover types, type of edge, and patch shape (1)	Li and Reynolds 1995
Heterogeneity in spatial arrangement of land cover types, number of land cover types, and size of patches (1)	Fahrig et al. 2011; Perović et al. 2015

Heterogeneity in spatial arrangement of land cover types, number and size of patches (1)	Duelli 1997; Fahrig et al. 2011
Heterogeneity in spatial arrangement of land cover types, number, size and compaction of patches, and occurrence of edges (1)	Herzog et al. 2001; Li and Reynolds 1994; Riitters et al. 1995
Number, size, and complexity of patches and connectivity (1)	—
Size and distribution of patches (1)	—
Number, size, and shape of patches (1)	Concepción et al. 2008; Duelli 1997
Structural connectivity (1)	—
Edge density (1)	—
Edge length (1)	—
Grain size of land cover types (1)	Fahrig et al. 2011

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RESEARCH ARTICLE

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Forest regeneration may reduce the negative impacts of climate change on the biodiversity of a tropical hotspot

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ABSTRACT

Aim: Evaluate how large-scale forest regeneration based on a low-cost restoration method may mitigate the effects of habitat loss and fragmentation associated to future climate changes on the distribution of birds and arboreal mammals in a tropical biodiversity hotspot; find areas with different current and future potential species richness and assess how passive restoration can reduce the risk of species extinction.

Location: Brazilian Atlantic Forest (BAF).

Methods: We built a forest regeneration scenario via a model of seed dispersal based on the potential movement of frugivorous fauna and projected the potential distribution of 356 bird species and 21 arboreal mammals based on Species Distribution Models (SDM) which employed 79,462 occurrence records and four algorithms for different climate and landscape scenarios. SDM were based on climate and landscape predictors separately and the results were combined into maps of species richness. Finally, we assessed the species' risk of extinction based on the species-area relationship.

Results: Without considering the effects of climate change, the potential distribution area for each species increases on average by 72.5% (SD = 8%) in the scenario of potential regeneration. Climate change decreases the area of potential occurrence of 252 species, which may suffer a mean reduction of 74.4% (SD = 9.3%) in their current potential distribution areas. BAF regions with the largest amounts of forest had the greatest potential richness of species. In future climate scenario, 3.4% of species may become extinct, but we show that large-scale regeneration may prevent these extinctions.

Main conclusions: Despite the possible negative impacts of climate change on the distribution of 67% of the studied species, which would increase the risk of species extinction, our analysis indicated that promoting large-scale BAF restoration based on natural regeneration may prevent biodiversity loss.

KEYWORDS: Atlantic Forest, birds, ecological niche models, primates, seed dispersal, species distribution models

1 INTRODUCTION

The modification of natural habitats is one of the main causes of the current biodiversity loss (Newbold, 2018). This can be especially relevant in tropical forests, which combine high species richness and severe fragmentation and area reduction (Alroy, 2017; Haddad et al., 2015). In addition to the ongoing modification of natural habitats, climate changes are imposing a challenge to biodiversity (Scarano & Ceotto, 2015). The changes on Earth's climate induced by human activities may cause further reductions and/or shifts on species distributions (Lyra et al., 2017; Parmesan & Yohe, 2003). Therefore, it is of utmost importance to understand the effects of the interplay between habitat loss, fragmentation and climate change for the conservation of natural habitats (Tilman et al., 2017).

Due to the interlinkages of ecological processes, conservation measures that address different threats to biodiversity in an integrated manner may have a greater chance of being successful (Díaz et al., 2020). In this regard, forest restoration can be employed to mitigate the effects of climate changes by promoting at the same time the carbon sink and biodiversity conservation functions of forests (Matos et al., 2020; Poorter et al., 2021). An analysis involving secondary tropical forests spread across different continents showed that the time for the recovery to 90% of old-forest conditions is less than a decade for soil and less than 25 years for plant functioning (Poorter et al., 2021). Tropical forests growing ~50 years after land abandonment may sustain tree species richness comparable to old-growth forests (Rozendaal et al., 2019), which also results in a substantial carbon stock increment (Martin, Newton, & Bullock, 2013). Richness and density of primates rise significantly in tropical forests regenerating from only five to 19 years (Chapman et al., 2020), and both species richness and phylogenetic diversity of birds may be high in these forests (Hughes, Edwards, Sayer, Martin, & Thomas, 2020).

Unsurprisingly, forest restoration is considered one of the 17 UN Global Goals that addresses the main development challenges on sustainable development (goal 15, "Life on Land"; <https://sdgs.un.org/goals>). Other global initiatives also aim to restore natural environments. The Convention of Biological Diversity suggests the restoration of 15% of all degraded lands in the planet (Latawiec, Strassburg, Brancalion, Rodrigues, & Gardner, 2015), and an association between the IUCN and the Government of Germany have launched a global goal to restore 350 million hectares of forests (the Bonn Challenge; <https://www.bonnchallenge.org/>). Furthermore, in the year of 2021 the UN has launched the decade for restoration, a call for the protection and revitalization of ecosystems around the world (<https://www.decadeonrestoration.org/>).

To minimize the costs of allocating land for forest restoration, areas with greater potential for crop production may be cultivated while areas with low agricultural aptitude should be designed for the conservation of biodiversity (Latawiec et al., 2015). In addition of being restored through "active regeneration" – i.e. when a series of human interventions promote forest growth (e.g. planting trees) – degraded areas can be recovered through passive restoration (or natural regeneration), which occurs when the prior anthropogenic disturbance is ceased and forests can naturally recover (Brancalion et al., 2016; Holl, 2017a). In addition to having lower costs as compared to active restoration, a meta-analysis indicated that natural regeneration was more effective in promoting the diversity of birds, plants, and invertebrates (Crouzeilles et al., 2017).

Although there are many studies about the effects of natural regeneration on biodiversity, most of them are carried out at local scales and relatively few explored the potential of large scale natural regeneration in tropical forests (Crouzeilles et al., 2017). In addition to advancing the understanding of the effects of the interplay between habitat fragmentation and climate change, studies that aim to disentangle how the large scale restoration of forests based on low-cost methods might influence species occurrence and their risk of extinction can be useful for identifying priority areas for conservation and the design of conservation actions and policies. In this context, we present how natural regeneration based on a seed dispersal model may affect the occurrence and the risk of extinction of species in a highly fragmented tropical forest domain, the Brazilian Atlantic Forest (BAF). The seed rain promoted by frugivorous animals on anthropogenic matrixes favors natural regeneration and can be used as a strategy to recover areas in large scales at relatively low costs (Chazdon, 2017; Figure 1). This may be especially relevant in tropical environments, where most trees are dispersed by animals (Corlett, 2017).

Thus, our aims are (1) to evaluate how forest regeneration may affect the amount of area potentially available for species occurrence, estimating its potential in mitigating the effects of climate change; (2) to identify areas with higher species richness that should be prioritized for biodiversity conservation; and (3) to estimate the chance of species extinction due to climate change by considering current landscapes and a potential regeneration scenario. We expected that forest regeneration could reduce the chance of species extinction by increasing the amount of forest within landscapes.

2 METHODS

2.1 Natural forest regeneration models and scenarios of landscape restoration

We first employed a model of potential natural forest regeneration based on the seed dispersal from forest patches into the matrix promoted by the movement of frugivorous animals (Niebuhr, 2018; Figures 1 and 3). After that, we projected the potential distribution of a set of selected species of forest birds and arboreal mammals (primates and sloths) in four different scenarios that considered both current and potential future conditions of climate and landscape. The two climate conditions were (1) the current and (2) a future climate scenario based on the expected climate change, while the two landscapes were (a) the current configuration of the BAF native forest remnants and (b) our scenario of BAF regeneration. We choose the taxonomic groups for which we predicted distributions because they are considered good indicators of habitat quality and are of conservation concern in fragmented environments (Arroyo-Rodríguez & Fahrig, 2014; Pizo & Tonetti, 2020), thus serving as environmental indicators of priority areas for biodiversity conservation.

The theoretical models of potential natural forest regeneration proposed here are based on three main ecologically rooted assumptions extracted from reviews and recent large-scale studies relating landscape ecology, seed dispersal, and natural regeneration. Our

main assumption is that, since most of the seed dispersal is led by animals in the tropics (Corlett, 2017; Howe & Smallwood, 1982), places which receive a larger load of seed rain have the higher probability of natural regeneration, mainly degraded and open areas that are abandoned or subject to less intense human management (Molin, Gergel, Soares-Filho, & Ferraz, 2017; Silva, Batistella, Moran, & Lu, 2017). Second, we assume that the richness and abundance of the main frugivorous animals (e.g. bats, birds, non-flying mammals, reptiles and even invertebrates) increase within larger forest patches (Böhning-Gaese, 1997; Bovo et al., 2018; Kirika, Bleher, Böhning-Gaese, Chira, & Farwig, 2008; Magioli, Ribeiro, Ferraz, & Rodrigues, 2015; Figure 3). Accordingly, the higher the richness and abundance of frugivorous animals, the higher the probability that they spread seeds around forest patches and for long distances (McConkey et al., 2012). Third, we assume that seed dispersal decreases as the distance of forest patches increases (Bullock et al., 2018; Camargo, Pizo, Brancalion, & Carlo, 2020; Nathan & Muller-Landau, 2000; Figures 1 and 3). In combination, these assumptions mean that sites closer to larger forest patches have higher seed deposition, which leads to a higher potential for natural regeneration.

To operationalize these premises, we first classified BAF forest patches into five size classes, corresponding theoretically to different functional assemblages of seed dispersers (Table S1). The size classes were (1) up to 10 ha (< 10), (2) between 11 and 25 ha, (3) between 26 and 50 ha, (4) between 51 and 250 ha, and (5) higher than 250 ha (Figure 3). Species abundance and diversity thresholds in tropical forests are generally assessed in terms of habitat amount in the landscape (e.g. Muylaert, Stevens, & Ribeiro, 2016; Tambosi, Martensen, Ribeiro, & Metzger, 2014), but hardly using patch size and connectivity. In BAF, there is evidence that forest patches separated by size thresholds of 60 and 2050 ha present different functional assemblages of mammals (Magioli et al., 2015).

We selected the above-mentioned patch size classes to allow for variation within the seed dispersal process derived from the smaller patches (< 250 ha), which comprehend 95% of the forest patches in BAF (Ribeiro, Metzger, Martensen, Ponzoni, & Hirota, 2009), and considering that a great part of the seed dispersal that leads to regeneration is driven by small bodied species (Galetti et al., 2013). We then created curves of potential natural forest regeneration around these patches using an exponential function which assigns a decreasing chance of forest regeneration as one walks away from the edges of forest patches. The exponential distribution is defined by the scale parameter (λ), which determines the decreasing rate of the curves in relation to the distance of forest patches, varied among the different size classes of forest patches, according to an expected scale of mobility of the disperser animals (Table S1). Even though the decrease of these curves alone is monotonic, when the curves of potential regeneration around multiple patches in different landscape arrangements are combined, complex spatial patterns of potential natural regeneration are created by our models (Figure 3).

Continuous values for the chance of seed dispersal (and consequently forest regeneration) were estimated for each pixel in the landscape, and they decrease as forest fragment distance increases (Figure 3). Although these values may be estimated for virtually any type of matrix, we established scenarios of forest regeneration only for pastures because BAF regeneration is more likely to occur in these areas (Latawiec et al. 2015). Pastures are more likely to be abandoned than other types of land use, allowing BAF and other tropical forests to regenerate (Rezende, Uezu, Scarano, & Araujo, 2015). Pasture map used in our analysis was developed by the Processing and Geoprocessing Lab (LAPIG; <https://www.lapig.iesa.ufg.br/lapig/>; Table S2; available in <https://pastagem.org>). Since this is an initiative to map Brazilian pastures, we considered only the Brazilian portion of Atlantic Forest. We established a threshold of 0.5 in the continuous values of forest

regeneration to create a scenario of landscape restoration, i.e., we assumed that all pixels with a potential natural regeneration of ≥ 0.5 would be converted to forests (Figures 1 and 3). Although arbitrary, with this threshold value our amount of forest regeneration is similar to the one proposed by the Atlantic Forest Restoration Pact. A chance of natural regeneration below 0.5 was considered too low for the analysis (see below; Crouzeilles et al., 2019; Melo et al., 2013).

2.2 Study area

Extending from the Brazilian coast (from northeastern to southern Brazil) to the inner southern parts of the continent, the Atlantic Forest is the second largest tropical forest domain in South America, and is mostly distributed in Brazil (99% of its area; Muylaert et al. 2018). Despite its high species richness and endemism, the Atlantic Forest was severely devastated in the last centuries, and only 28% of its native vegetation persist (Rezende et al., 2018; Figure 2). Moreover, most (80%) native forest patches are small (< 50 ha) and distant from each other (1,440 m in average; Ribeiro et al. 2009). The high latitudinal and altitudinal gradient of the Atlantic Forest causes great variation in climate and vegetation and its domain can be divided into different biogeographic regions (Figure 2). Due to limited availability of pasture data (see above), only the Brazilian portion of the Atlantic Forest was considered in our analyses (BAF; Figure 2).

High species richness and endemism associated with high devastation rates make the domain a priority region for biodiversity conservation (Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000; Pizo & Tonetti, 2020). Because forest remnants are fragmented and surrounded by different land cover types, BAF is an appropriate region for evaluating how natural forest regeneration may promote biodiversity in human-dominated environments. BAF delimitation and forest remnants considered in this study (Figure 2) were processed by

the Spatial Ecology and Conservation Lab at the São Paulo State University, Brazil (LEEC – UNESP) in an association with Agroicone, a Brazilian non-governmental organization (Ribeiro et al. in prep.; <https://www.agroicone.com.br/>) and are detailed in Table S2.

2.3 Species distribution models

We projected the potential distribution of forest birds, primates, and sloths in BAF via SDM approach. SDM identifies areas with different suitability for the occurrence of species based on predictor variables (Guisan, Thuiller, & Zimmermann, 2017). We employed two categories of predictor variables – (1) climatic and (2) landscape. Species distribution at biogeographic scales (e.g. within a domain) is usually determined by climatic variables, while species occurrence at mesoscales, within a smaller regions, such as watersheds, are influenced by landscape ones (Peterson et al., 2011). We modeled species distribution separately based on climatic and landscape predictors and identified areas in which both predictors indicated suitability to species occurrence (Sobral-Souza, Santos, Maldaner, Lima-Ribeiro, & Ribeiro, 2021; Figure 4).

Several SDM studies that predict species occurrence under future scenarios assume static conditions of landscapes, which may be unrealistic as land cover is usually dynamic (Martin, Van Dyck, Dendoncker, & Titeux, 2013). Some investigations have shown that considering different landscape scenarios in SDM may result in more accurate predictions (Regos et al., 2018; Visconti et al., 2016), probably because the different predictors (climate and landscape) that influence the distribution of species operate at different scales (Sobral-Souza et al., 2021).

To build the climate SDM we used the 19 WorldClim 1.4 variables with 30-arc seconds resolution (~1 km). These variables are also known as “bioclimatic” as they are biologically meaningful and derived from temperature and precipitation data collected in

weather stations around the world (1960 – 1990 temporal range, <https://www.worldclim.org/data/v1.4/worldclim14.html>). We considered bioclimatic variables within BAF delimitation and, to avoid correlation among them, we applied a Variance Inflation Test (VIF) using the USDM package in the R environment (Naimi, Hamm, Groen, Skidmore, & Toxopeus, 2014). From the 19 variables, we eliminated those with VIF values ≥ 5 (Guisan et al., 2017), and used the remaining five, namely: mean diurnal range (bio 2); mean diurnal range / temperature annual range (bio 3); mean temperature of the wettest quarter (bio 8); precipitation of the wettest month (bio 13); and precipitation of the coldest quarter (bio 19).

In addition to the current climate, we projected the potential distribution of species for 2070 using the 6.0 representative concentration pathway (RCP). The emission of greenhouse gases is simulated by RCP scenarios according to different trends of human activity (IPCC, 2014). We opted for using an intermediated RCP scenario over the scenarios of highest (RCP = 8.5) and lowest gas emission (RCP = 2.6), as both are unlikely to occur and should not be used in environmental planning studies (Hausfather & Peters, 2020). To reduce the effect of uncertainty in the different general circulation models of the RCP scenario, we projected species distributions for three different models – MIROC ESM, HadGEM2-AO, and GFDL-ESM2G and averaged environmental suitability of these three models. We selected these models following Sanderson, Knutti, & Caldwell (2015), that suggest choosing the models least related to each other.

To build the landscape SDM, we calculated the following landscape variables based on the BAF remnant map (30-m resolution): habitat amount, edge amount (edge depth = 30 m), functionally connected area, and patch size. The functionally connected area is the sum of the area of all patches closer than a gap-crossing distance – here we considered the value of 60 m. We used these variables because they are widely known to influence the occurrence

of vertebrates (Baguette & Van Dyck, 2007; Fahrig, 2013; Pfeifer et al., 2017), and the value of edge depth and gap crossing were chosen based on the literature (Graham & Socha, 2019; Uezu, Metzger, & Vielliard, 2005). With the increase of forest amount in the regeneration scenario, it is expected that the values of the four landscape variables will also increase. Despite the relative value of edge amount in relation to habitat amount may diminish, its absolute value is also expected to increase (Figure S1). These variables were calculated for each landscape scenario (current and potential regeneration) with the aid of LSMetrics (Niebuhr et al., 2020; Niebuhr, 2018; https://github.com/LEEClab/LS_METRICS), a package designed to calculate landscape metrics in the GRASS GIS environment (Neteler, Bowman, Landa, & Metz, 2012).

For both habitat and edge amount, we considered a moving window of 2 km (i.e., for each central pixel we considered an average value of all pixels within a 2 km-distance). This distance was based on the scale at which the landscape may affect the occurrence of the studied species (Barros, Peres, Pizo, & Ribeiro, 2019; Gestich, Arroyo-Rodríguez, Ribeiro, da Cunha, & Setz, 2019). As elevation has proven to be an important variable in predicting species distribution (Guisan et al., 2017), we added this layer to the landscape variables and, after applying a VIF test (threshold value = 5), we removed edge amount to avoid high correlation among variables. After calculating landscape variables using 30-m pixel size, we resampled the data to the same resolution of bioclimatic variables (~1 km), a suitable resolution for SDM. We calibrated the SDM for the current landscape layers, in which species are currently distributed, and projected for both the current landscape and the potential regeneration scenario.

We downloaded species occurrence data with the aid of the spocc package in the R environment (Chamberlain, 2020) from the following databases: Global Biodiversity Information Facility (GBIF; <https://www.gbif.org>); iNaturalist (<https://www.inaturalist.org>);

VertNet (<http://vertnet.org>); eBird (<https://ebird.org>); and Integrated Digitized Biocollections (iDigBio; <https://www.idigbio.org>). We also considered primates and sloths occurrences in datasets of the Atlantic Forest region (Culot et al., 2019; Santos et al., 2019). We only considered primate and sloth data locations assigned as “precise” or with a geographic accuracy of 1 km according to the authors (Culot et al., 2019; Santos, et al., 2019). We excluded occurrence data recorded prior to 1980 to avoid mismatching between species presence and landscape features. The literature suggests that BAF forest remnants suffered no substantial changes in most of the domain from the 1980s onward (Ribeiro et al. 2009). Endemic birds considered in this study are listed in Vale et al. (2018), non-endemic ones in Hasui et al. (2018), primates (endemic and non-endemic) in Reis et al. (2015), and sloths in Santos et al. (2019). We only considered species that have forest as main habitat type according to IUCN (<https://www.iucnredlist.org>) and included taxonomical synonyms in our searches.

To avoid spatial correlation and model overfitting, we spatially rarefied points keeping a distance of at least 10 km between them with the aid of the spThin package in R (Aiello-Lammens, Boria, Radosavljevic, Vilela, & Anderson, 2015; Guisan et al., 2017; Peterson et al., 2011). To avoid potential location errors, we discarded species occurrence near biodiversity institutions, urban areas, state capitals and with zero decimal values for latitude and longitude with the aid of the package CoordinateCleaner in R (Zizka et al., 2019). Moreover, we plotted species occurrence and searched for potential outliers and records that failed to correspond to the expected distribution of the species based on our knowledge and on databases such as IUCN and Wiki Aves (<https://www.wikiaves.com/>). After these filtering procedures, we only modeled species with at least 10 occurrence points. We assumed this to be the minimum number of occurrences to sample a gradient of

environmental variability adequate to estimate areas environmentally suitable for the species studied (Peterson et al. 2011).

As the study area in SDM should ideally consider the area accessible for the organisms (Barve et al., 2011), for each species we used a background region based on a minimum convex polygon of the occurrence points (comprising geographical extreme occurrences) and summed by a buffer of two coordinate degrees (~ 220 km). We then cropped variables for each species using the convex hull and sampled 5,000 background points. We considered these types of backgrounds more adequate than using the entire BAF for all species, which could result in model overfitting and the overestimation of model evaluation (Barve et al., 2011; Guisan et al., 2017; Peterson et al., 2011). This approach is similar to other analyses employing SDM in BAF (Sales, Kissling, Galetti, Naimi, & Pires, 2021).

As there is no single best algorithm for use in SDM (Qiao, Soberón, & Peterson, 2015), we combined the prediction of four different algorithms of presence-only data: bioclim, domain, random forest and maxent via the sdm package in R (Naimi & Araújo, 2016). For each species we ran 10 replicates of each algorithm assigning 70% of the occurrence points to training the models, and 30% to evaluate each run via bootstrapping (Peterson et al., 2011), resulting in 40 models per species for climate variables (four algorithms, 10 replicates) plus 40 models for landscape variables. Ensemble projections for the 10 replicates were performed via a weighted mean for the individual models based on a threshold that maximizes specificity + sensitivity considering the True Skill Statistic test (Allouche et al. 2006). We used the lowest presence-threshold in the raster of continuous values from the ensemble of the 40 individual models to create binary maps for each species (presence / absence; Liu et al. 2016). Then, we combined maps of climatic and landscape

suitability and analyzed regions where both landscape and climate were suitable for species occurrence (Figure 4).

After training the models for the current scenarios of climate and landscape, we projected the SDM for both current and future climate, current landscape configuration and future potential landscape regeneration. We added the binary maps of the potential distribution of species and identified areas with different potential species richness and suitable areas for the occurrence of species in the following scenarios: (1) current climate and current landscape, (2) current climate and future regenerated landscape, (3) future climate and current landscape, and (4) future climate and future regenerated landscape. To calculate the area of occurrence of species in each scenario, we considered suitable areas only within forest patches (upper line in Figure 5). As forest patches may be small, to facilitate the visualisation of species richness in different regions, we calculate the mean values of potential species richness considering only forest patches in hexagonal grids ($\sim 1,000 \text{ km}^2$ hexagons, bottom line in Figure 5; see the potential species richness in forest fragments in Figure S2).

2.4 Assessment of extinction risk

Based on the relation between geographical range and probability of extinction, we evaluated the percentage of species that would become extinct in the future in the two different BAF landscape scenarios (current and with regeneration). We evaluated extinction risk assessment based on an equation developed by Thomas et al., (2004), which takes into account the average proportional loss of distribution area for each species: $E = 1 - \{(1/n) [\sum (A_{\text{fut}} / A_{\text{original}})]\}^z$ in which E is the proportion of extinct species, n the number of species, A_{fut} the future occupied area, A_{original} the original occupied area and z a constant that reflects

the proportion of species overlap between areas (Tjørve & Tjørve, 2008). Based on the literature, we set $z = 0.25$ (Brooks & Balmford, 1996; Thomas, Cameron, et al., 2004).

3 RESULTS

We identified ~ 34 million hectares (Mha) of native forest remnants in the BAF, while in our scenario of forest regeneration, the amount of regenerated forest sum 13 Mha (Figure 3). We predicted the potential distribution of 377 species in the four different scenarios (Figure 5): 356 of which are forest-dwelling birds and 21, arboreal mammals (19 primates and 2 sloths; Tables S3 and S4). We obtained 79,462 occurrence points (211 points per species on average; SD = 219; Figure S3) and 30,160 individual models were employed to predict distributions; half of them were based on climate and half on landscape predictors.

Without considering the effects of climate change, each species would have its potential distribution area increased by 72.5% on average (SD = 8%) in our scenario of forest regeneration (Figure 6, “Current climate / regenerated landscape” bar; Table S5). Climate change alone may decrease the potential distribution of 67% of species, which represents a mean reduction of 74.4% (SD = 28.7%) in their potential distribution areas compared to the current landscape and climate scenario. For those species that may have their distribution areas reduced because of climate change, our regeneration scenario points to a mean increase of 75.3% (SD = 9.3%) in their future potential distribution areas (“future climate / regenerated landscape” scenario). In contrast, climate change may increase the potential distribution areas of 33% of species to an average increment of 10.5% (SD = 14.5%) of their current potential distribution (“future climate / current landscape” scenario). For these species, if our regeneration scenario also occurred, they would experience a mean increase of 54.6% (SD = 29.5%) of areas suitable to their occurrence.

Forest remnants that showed higher potential species richness concentrate mainly near the coast, in the Serra do Mar biogeographical region, the Araucaria region, in the central part of the state of Bahia and in the northern portion of Bahia interior forests (Figures 3 and 5). Brejos Nordestinos, Diamantina, São Francisco and Pernambuco regions presented lowest potential species richness. This pattern of species richness was consistent for all scenarios (Figure 5). In the future climate scenario, 3.4% of species may become extinct. When only species that may suffer reductions in their areas due to climate change effects are considered, 7.1% of them may disappear, a figure even higher if we consider endemic species (Table 1). Our regeneration scenario may zero the extinction probability of species, except for the endemic species that may suffer reductions in their distribution areas because of climate change, even with forest regeneration (Table 1).

4 DISCUSSION

4.1 Natural forest regeneration and biodiversity

Despite the possible negative impacts of climate change on the distribution of 67% of the studied species, our analysis indicated that, as expected, promoting natural forest regeneration at large scales may not only prevent biodiversity loss but also increase the potential distribution area of species that may be impacted by climate change in future scenarios. The 252 species that might be negatively impacted by climate change may suffer a reduction of 74.4% (SD = 28.7%) of their potential distribution area when considering future climate and current landscape scenarios. However, if our natural regeneration scenario is considered, these same species might increase their potential distribution area by 75.3% (SD = 9.3%) in the future climate scenario (Figure 6). From these 252 species, except for six species that may zero their potential distribution areas with climate change regardless of the landscape scenario, the remaining species might increase their area of occurrence with

forest regeneration. Several tropical forest species of birds and arboreal mammals, including endemic species, tolerate fragmented and secondary forests (Develey & Phalan, 2021; Pizo & Tonetti, 2020), which suggests that the regenerated environments could be used for many of the studied taxa (but see Santos, Bailey, Ribeiro, Chiarello, & Paglia 2019).

Thus, as expected, with the increase of forest amount in the regeneration scenario as modeled here, it may be possible to reduce the proportion of species that would become extinct because of future climate change. In an assessment of the risk of extinction of Atlantic Forest birds due to deforestation, endemic species were the most vulnerable (Brooks & Balmford, 1996). Indeed, the potential loss of area of distribution due to climate change may also increase the extinction risk in different environments around the world, including other tropical forests (Thomas, Cameron, et al., 2004). Loss of species may have deleterious cascading effects on biodiversity. Some studies have identified that endemic large-bodied birds (Vidal et al., 2014) and primates (Bufalo, Galetti, & Culot, 2016) are key elements involved in seed dispersal in tropical forests. Therefore, the loss of such large-bodied frugivores in BAF because of climate change may pledge seed dispersal systems with consequences for the dynamics of forest ecosystems (Sales et al., 2021).

Our models indicated that regions with higher forest amounts (such as Serra do Mar, Araucaria, and northern Bahia; Figures 2 and 5) have higher chances of natural regeneration and, thus, sustain a higher number of species, both in the present and future scenarios. Other studies found similar results (de Souza et al., 2011; Santos et al., 2020; Vale et al., 2018; Zwiener et al., 2017). When considering models based on landscape predictors only, species richness was higher in regions where landscapes have higher amounts of forest (Figure 4; Figure S4). These results were expected as the studied taxa are forest-dwelling species (Pizo & Tonetti, 2020; Reis et al., 2015; Santos et al., 2019).

Contrary to areas with high forest amount, regions where forest patches are small and distant to each other may show lower chance of forest regeneration and sustain lower potential species richness according to our models. Although some may presume that the higher the species richness the higher is the importance of an area for conservation, this must be interpreted with caution. In our study, some severely devastated regions that presented comparatively fewer potential species richness in all scenarios are relevant for the conservation of tropical biodiversity, as the Pernambuco Endemism Center in BAF (PEC; Figure 2). PEC is remarkable for its endemism of birds, mammals, and other groups, harboring several species on the brink of extinction (Develey & Phalan, 2021; Garbino, Rezende, Fernandes-Ferreira, & Feijó, 2018; Pizo & Tonetti, 2020). Therefore, when planning natural forest regeneration in large scales based on seed dispersal, it might be important to use restoration techniques beyond passive restoration to increase the amount of forest in landscapes with low amount of remaining forest (such as the PEC). These techniques may comprise the mixed restoration approach – i.e., when less human input than used in active regeneration is employed. This has lower costs when compared to active regeneration and may increase the chances of regeneration and decrease the time needed for new forest formations to be established (Brancalion et al., 2016).

4.2 Forest restoration as an auxiliary measure of biodiversity conservation

Although secondary forests are relevant for the maintenance of species and ecological processes in human-dominated landscapes, older forests are crucial to preserve most of the original biodiversity and as sources of individuals that can establish populations in regenerated areas, especially in fragmented landscapes (Gibson et al., 2011). As in other tropical environments (e.g. Meyfroidt & Lambin, 2008; Smith et al., 2021), evidence shows a process of “rejuvenation” of forests in BAF. Young forests increased at a rate of ~150.000

ha annually since 2000, however the loss of older forests occurred at rate of ~100.000 to 200.000 ha annually in the same period (Rosa et al., 2021). It is thus important that forest monitoring is carried out properly so that the allocation of areas for natural regeneration does not cause forest loss in other regions.

Regarding climate change, some of the imposed challenges to biodiversity may not be properly mitigated by increasing forest amount only. Population and community responses to altered climate may also drive complex changes on species interactions with consequences difficult to predict (Oliver & Morecroft, 2014), as for example, changes in phenology that can alter frugivory, seed dispersal, and pollination (Scranton & Amarasekare, 2017). With a more direct impact on forest regeneration, global warming is also expected to increase the frequency and intensity of fires in tropical forests, resulting in negative consequences to species persistence and to the growth of early forests (Herawati & Santoso, 2011). Added to the effects of fire, prolonged droughts caused by climate change may hinder seedling recruitment and survival, which may further compromise natural regeneration (Anderson-Teixeira et al., 2013). In sum, despite having several benefits, forest restoration should be seen as an auxiliary measure in the mitigation of the effects of climate change and landscape conversion and should be associated with policies that aim to drastically reduce carbon emissions and deforestation (Holl & Brancalion, 2020). Restoration policies that promote actions to enrich and accelerate the succession rate of secondary and regenerating forests might also be important, to account for the already increased loss of mature forests.

4.3 Tropical forest regeneration and model limitations

The summed area of native forest remnants in our BAF map (~ 34 Mha; Figure 3) is similar to previous spatial analysis, which identified ~ 28 – 32 Mha of native forests in the

domain (Rezende et al., 2018; Rosa et al., 2021). Our regeneration scenario indicated an addition of 13 Mha of forests in BAF (Figure 2), an area close to the 15 Mha of native forests that the Atlantic Forest Restoration Pact aims to restore (Crouzeilles et al., 2019; Melo et al., 2013). The total area of pastures in BAF sum ~ 38 Mha. Therefore, for the amount of regenerated forests indicated in our study to be recovered (~ 13 Mha), 34% of current pastures need to be set aside for this purpose. Despite the area of regenerated forests in pastures indicated in our models seem excessive, studies suggest that the area of unproductive or underused pastures in BAF is also high – with the consequence that degraded pastures are often the land use class more prone to regenerate into forest (Silva et al., 2017). The cattle stocking rates in BAF are on average 1.17 animals per hectare, considered an extremely low production efficiency (Latawiec et al., 2015). It is estimated that 47% of pastures in Brazil could increase production by twice or even more (Santos et al., 2020). Thus, areas that could be allocated for conservation indicated in our regeneration model can be viable if productivity is increased in pastures that have low potential for forest regeneration.

Not all pastures that we identified as suitable to be converted into forests are unproductive and, thus, will not be destined for this purpose. Furthermore, although seed dispersal is one of the most important factors to promote forest regeneration, some other aspects may limit natural regeneration such as topography (Rezende et al., 2015; Silva et al., 2017), the past intensity of land use, and the amount of soil nutrient available (Crouzeilles et al., 2016; Mendes et al., 2019; but see Rozendaal et al., [2019]). Socioeconomic factors such as the size of rural villages and the possibilities of farm credit might also influence how prone are landowners to convert their lands into crops, what might affect forest regeneration (Silva et al., 2017). Our model of forest regeneration is based on theoretical seed dispersal curves and their response to forest patch size and proximity and, although rooted in the

literature, has limitations on its prediction of areas with higher potential of seed deposition and natural regeneration. Data-driven models that use seed dispersal data sampled at landscape-scale or natural regeneration data and take these aspects into account can generate more accurate results. For instance, Crouzeilles et al., (2020) developed a modeling approach based on machine learning algorithms to fit natural regeneration data from remote sensing to environmental and socioeconomic variables. Even though they used more complex models, they concluded that the most important variable to predict natural regeneration at large scales was the proximity to forest (Crouzeilles et al., 2020), which is the main assumption of our models. Therefore, we believe that data-driven approaches might have more reliable predictions locally and may be useful for driving location restoration planning, but do not change from our approach on a biogeographical scale.

Overall, most tropical forests have high potential for natural regeneration (Wright, 2010), which is also the case for the Atlantic Forest (Crouzeilles et al., 2019). There are evidences showing that even tropical regions where past land use intensity were high and forest cover low (~10 %), the area of naturally regenerated forests was substantial (Baptista & Rudel, 2006; Brancalion et al., 2016; Crouzeilles et al., 2019; Lira, Tambosi, Ewers, & Metzger, 2012; Mendes et al., 2019; Rezende et al., 2015). Moreover, the amount of degraded area is also large in other tropical regions (Lamb, Erskine, & Parrotta, 2005). This suggests that our natural regeneration model may be a viable strategy to passively restore degraded areas in several tropical forest regions and pinpoint regions where natural regeneration may be more successful.

Regarding species distribution, although SDM is an adequate approach to predict species occurrence at large scales, some limitations should be considered. In addition to the intrinsic errors of models to detect all areas potentially suitable for a species indicating otherwise unsuitable areas (Guisan et al., 2017; Peterson et al., 2011), these models may not

be adequate in predicting population parameters (Lee-Yaw, McCune, Pironon, & Sheth, 2021). The risk of species extinction could be better estimated if variations of population size were assessed (<https://www.iucnredlist.org/assessment/process>). Moreover, despite considering the effects of landscape and climate on SDM may potentially improve predictions, some limitations need to be recognized, as the fact that climate and landscape might affect species disproportionately depending on the taxonomic group and the studied region (Betts, Illán, Yang, Shirley, & Thomas, 2019; Newbold, 2018; Vermaat et al., 2017).

Finally, to be successful a landscape regeneration program must include multiple stakeholders, involve local communities, use democratic and inclusive approaches, and consider political issues, so that restoration is economically and socially viable (Díaz-García, López-Barrera, Pineda, Toledo-Aceves, & Andresen, 2020; Holl, 2017b). Summed to all factors expressed favoring tropical forest regeneration in our study area, the Atlantic Forest Law establishes that rural landowners are not allowed to suppress forest patches at intermediate and advanced stages of regeneration (http://www.planalto.gov.br/ccivil_03/_ato2004-2006/2006/lei/111428.htm). This provides some protection to the recovering areas, increasing the chances of success of a large-scale regeneration program in the domain. Therefore, in sum, our study reinforces that the regeneration of a tropical forest domain can have high benefits for biodiversity, is feasible in economical and legislation terms, pending, however, the political will to effectively occur.

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BIOSKETCH

All authors are broadly interested on spatial ecology and biodiversity conservation, specially in tropical environments. They conduct research that aim to guide the selection of priority areas for the conservation of biodiversity based on spatial modelling, on aspects of animal-plant interaction involving frugivory and seed dispersal, and on landscape and movement ecology.

TABLE 1 Percentage of species that may become extinct under future climate conditions (RCP 6.0). *n* is the number of species in each group. *Future no-regeneration* corresponds to the scenario of future climate and current forest configuration in the Brazilian Atlantic Forest, and *Future regeneration* corresponds to the scenario of future climate associated with our regeneration scenario. *All spp* consider all species studied, *Endemic spp* refers to endemic species, *All spp area reduced* corresponds to the species that may suffer reductions in their distribution areas, and *Endemic area reduced* to the endemic species that may suffer reductions in their distribution areas.

Species group	Future no-regeneration	Future regeneration
All spp	3.4	0
Endemics spp	4.9	0
All spp area reduced	7.1	0
Endemic area reduced	8.8	1.9

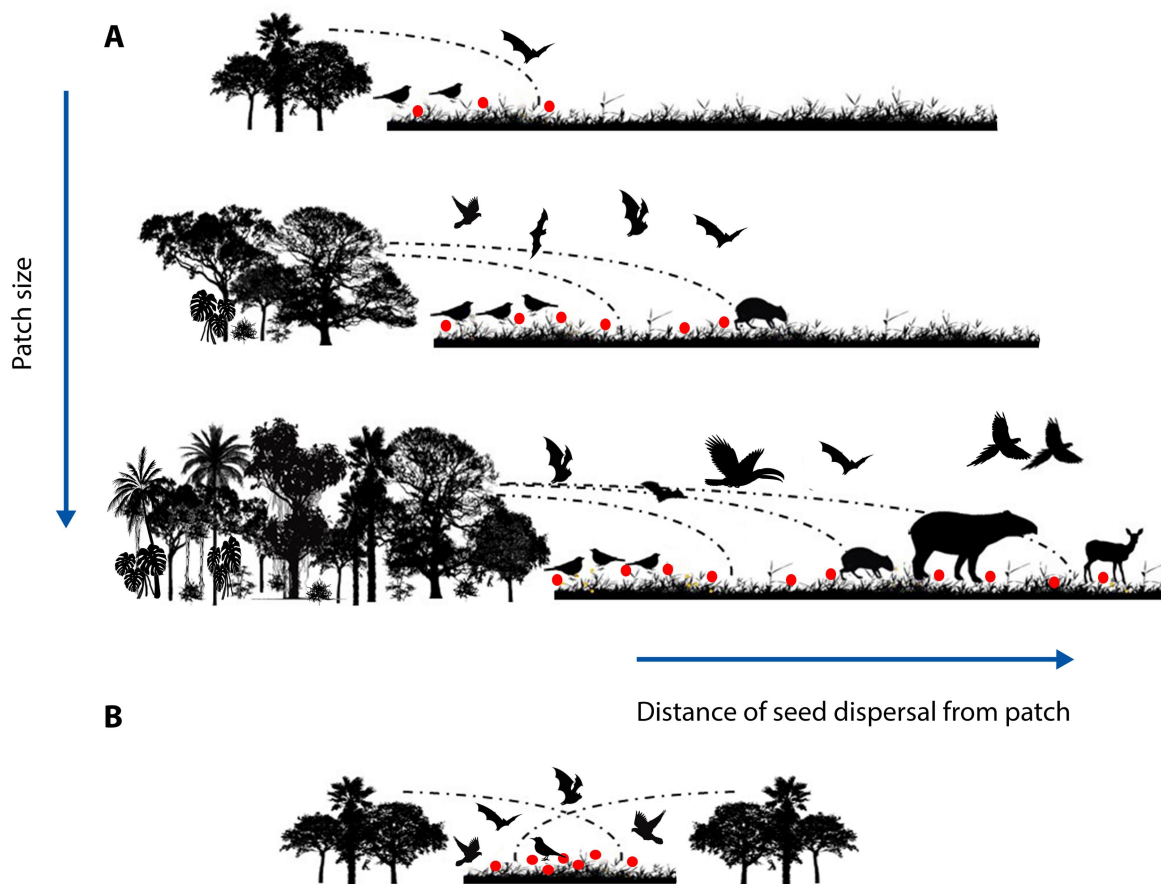


FIGURE 1 Scheme of the assumptions of our forest regeneration models. (A) Larger forest patches may sustain assemblages of frugivorous animals with greater species richness and abundances, increasing the rate of seed dispersal to the surrounding matrix and, consequently, the chance of natural forest regeneration. (B) As a consequence, the matrix in landscapes containing large amounts of forest fragments close to each other have greater natural regeneration. Seed dispersal (red dots) decreases as the distance from forest patches increases.

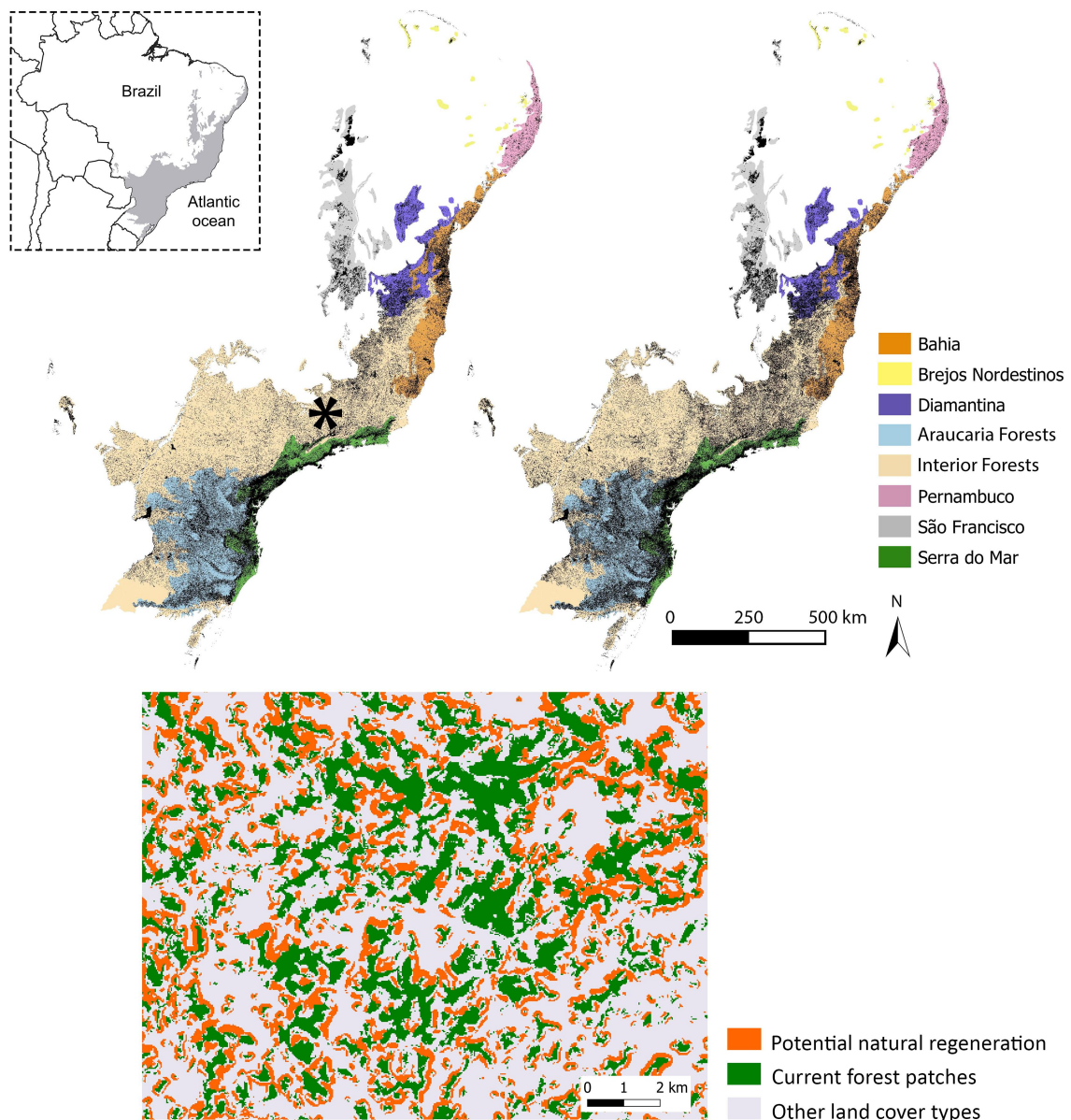


FIGURE 2 Biogeographical regions of the Brazilian Atlantic Forest (BAF) based on Silva & Casteleti (2003) and landscape scenarios used in our analysis. BAF forest remnants are in black. At the top left we show the current scenario of BAF landscape and, on the right, the scenario based on our potential forest regeneration model, with an increment of ~13 Mha of forests. At the bottom, a landscape is represented showing the current forest remnants in green and areas with natural regeneration potential on pastures in orange. Areas in orange are considered forest in our scenario of landscape restoration. The asterisk on the map at the top left indicates the location of the landscape.

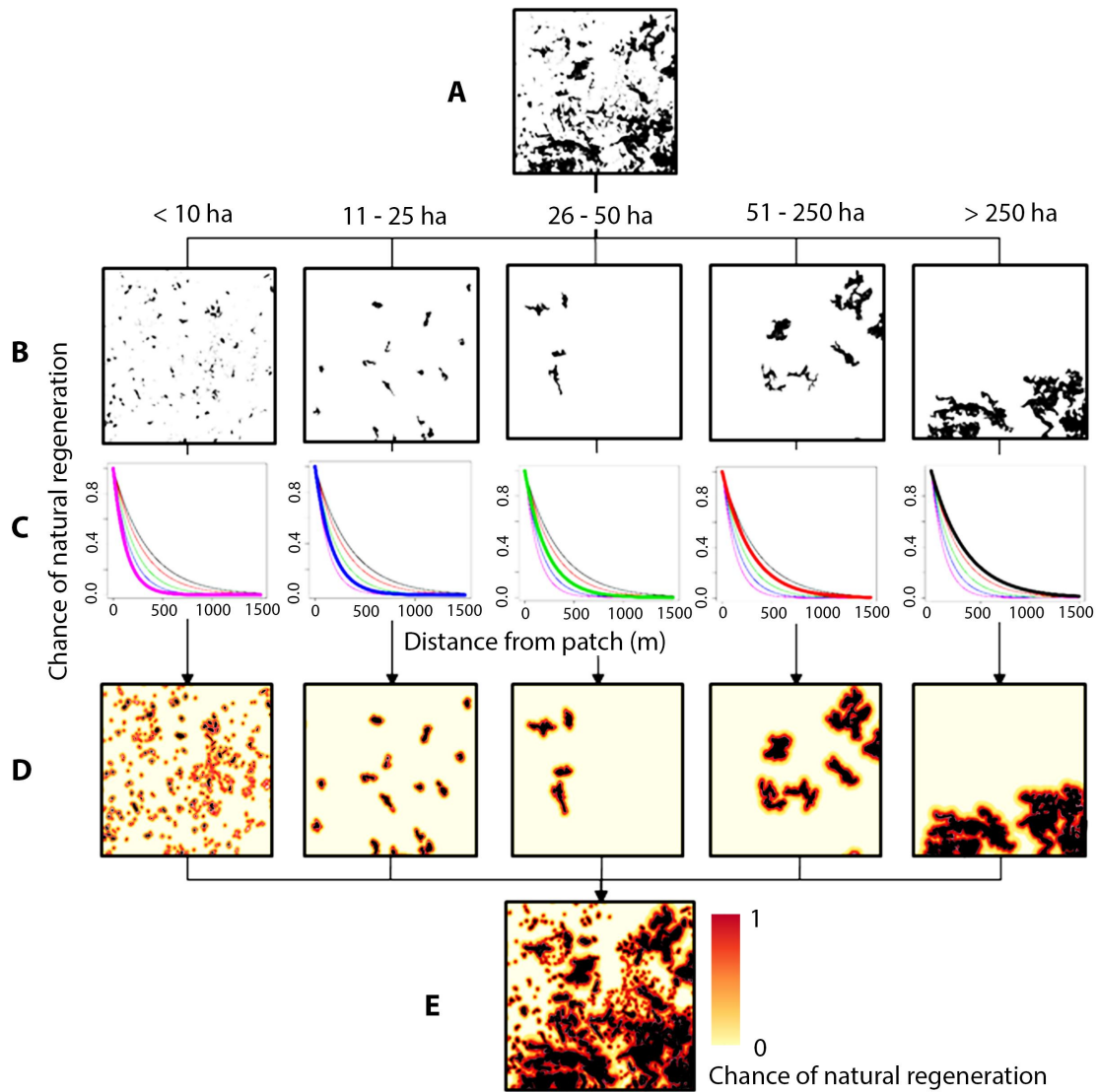


FIGURE 3 Flowchart for the elaboration of maps of potential of natural regeneration in the matrix. The forest remnants (in black) of a binary forest map (forest / non-forest; A) are classified into five patch size classes (B), and curves of forest regeneration potential are simulated for the fragments of each size class (C), so that individual maps (D) of forest regeneration potential of each fragment size class are created and summed into a final map of natural regeneration potential (E). The color gradients in frames D and E indicate areas with different chances of regeneration, with red for higher chances and light yellow for lower.

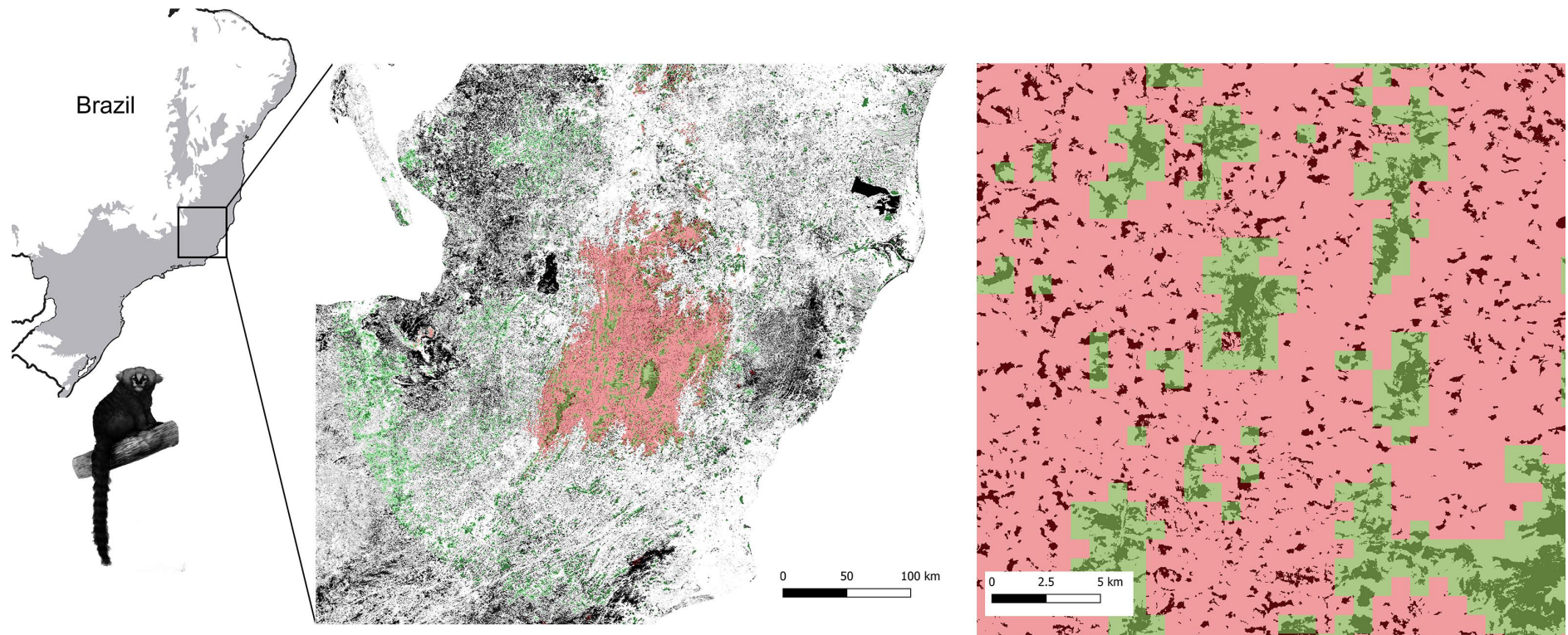


FIGURE 4 Results of species distribution models based on climate (in red) and on landscape predictors (in green) for one of the modeled species, the Buffy-headed Marmoset *Callithrix flaviceps*, in the scenario of current climate and current landscape. Note that there are areas where only either the climate or the landscape is suitable for the species occurrence. Only forest patches (in black) that presented both climatic and landscape suitability were considered to calculate the potential distribution area in the different scenarios.

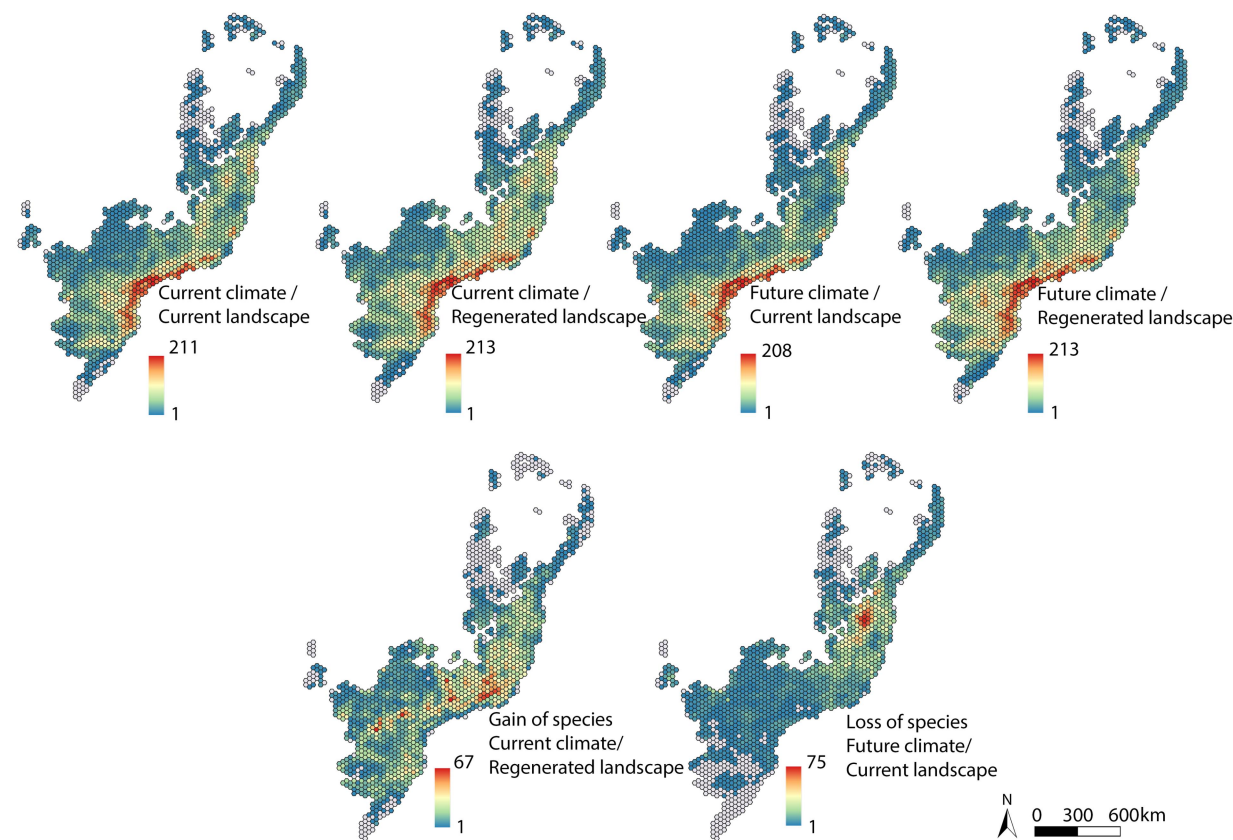


FIGURE 5 Potential species richness (maps at the top of the figure) of forest birds, primates, and sloths in the four different scenarios considering current/future climate (RCP 6.0) and current/regenerated landscapes. Maps at the bottom represent regions with different potential gains of species due to forest regeneration in the current climate and potential loss of species due to the effects of climate change in the current landscape. Species richness follows a color gradient that varies from blue for lower values to red for higher. Areas in gray are those where the potential species richness is zero. To facilitate the visualization of potential species richness in different regions of the study area, maps represent the mean values of potential species richness considering only forest patches in a hexagonal grid (~1,000-km²-area).

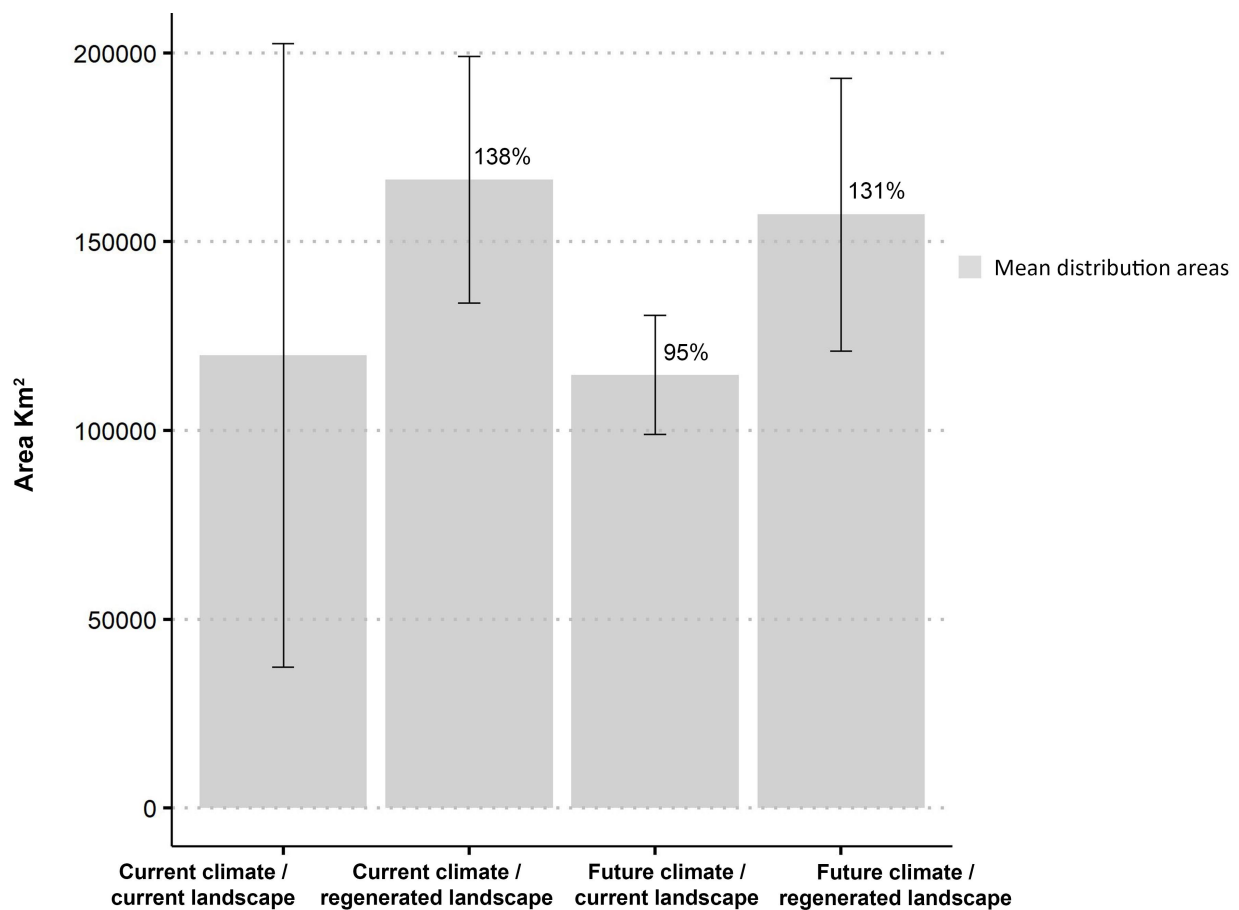


FIGURE 6. Mean distribution area (in square kilometers) of the 377 species in each of the scenarios listed on the X axis. Lines represent the Standard Deviation, and numbers above the bars the percentage of area in relation to the current scenario.

Supplementary Material

Forest regeneration may reduce the negative impacts of climate change on the biodiversity of a tropical hotspot

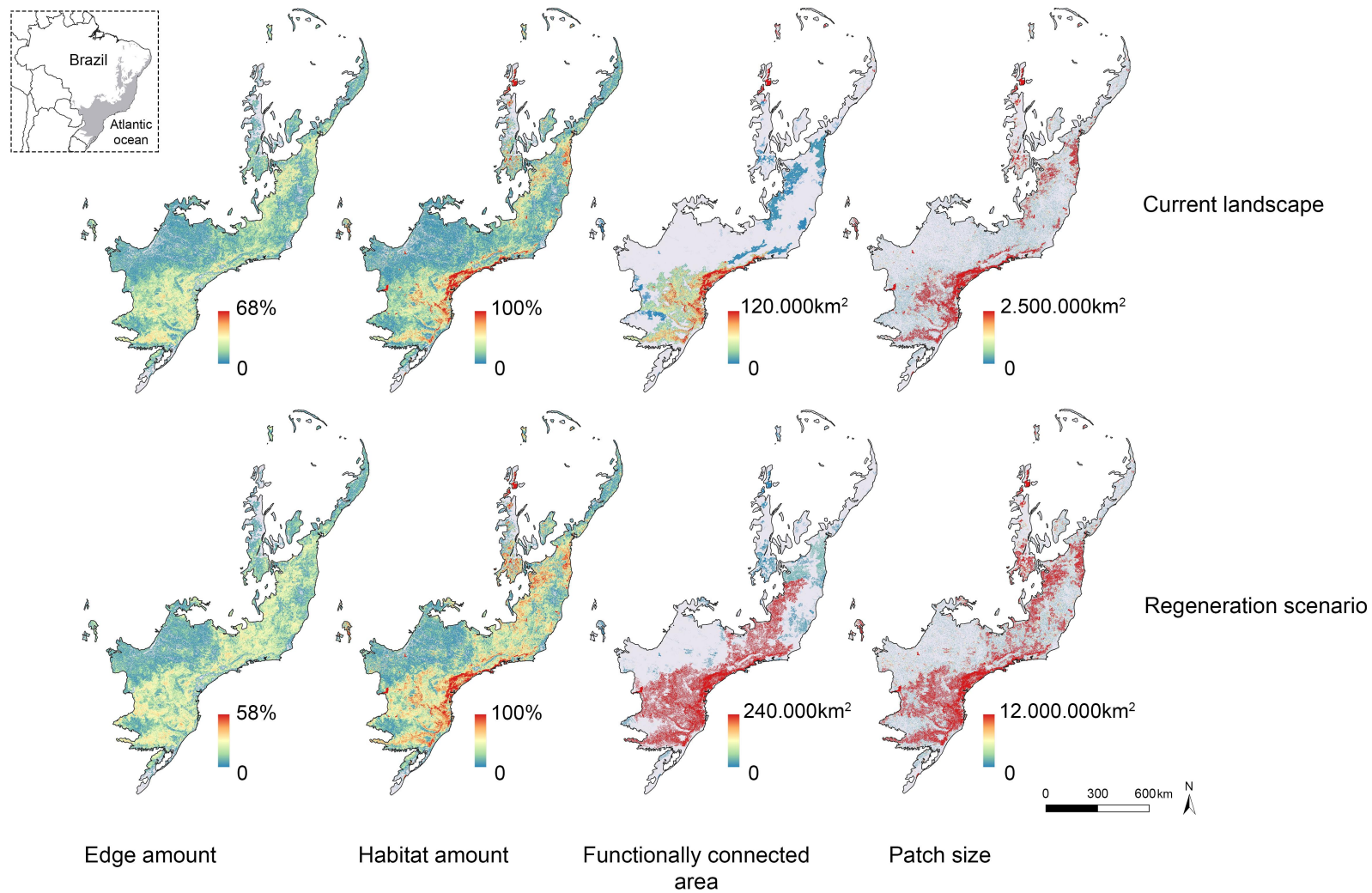


FIGURE S1. Landscape variables in the current landscape scenario (maps at the upper part of the figure) and in the regeneration scenario (in the bottom). The values of all landscape variables increased with the increase of habitat amount in the regeneration scenario.

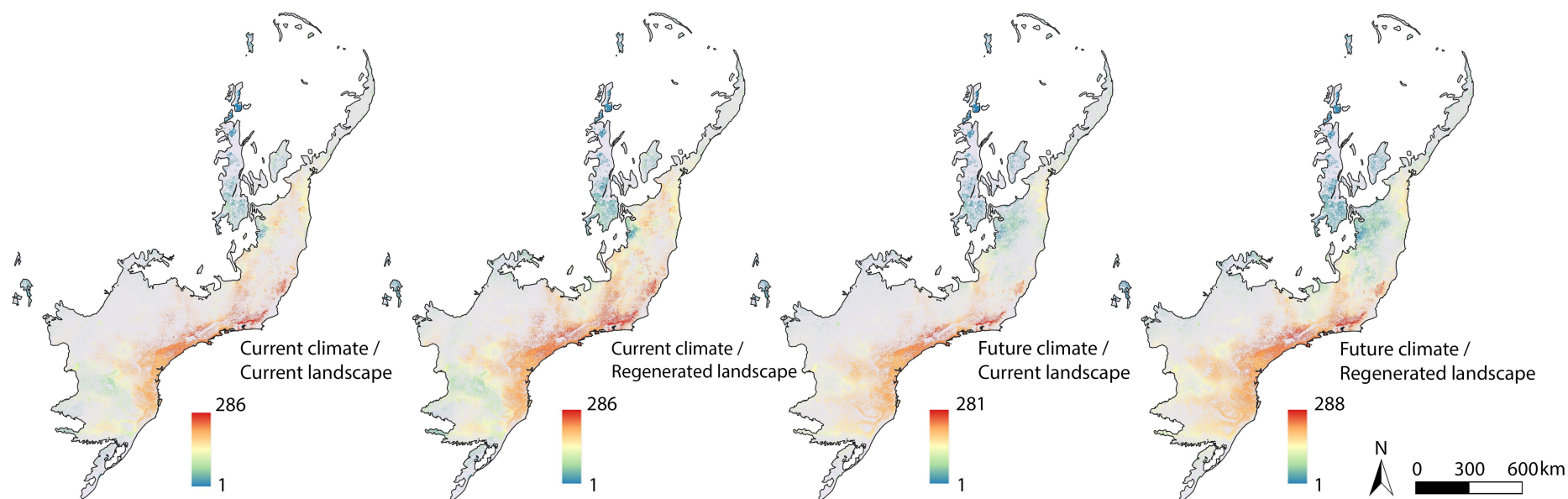


FIGURE S2. Potential species richness of forest birds, primates, and sloths in the Brazilian Atlantic Forest patches under the four different scenarios considering current/future climate (RCP 6.0) and current/regenerated landscapes. Species richness follows a color gradient that varies from blue for lower values to red for higher. Areas in gray are those where the potential species richness is zero – mostly deforested areas.

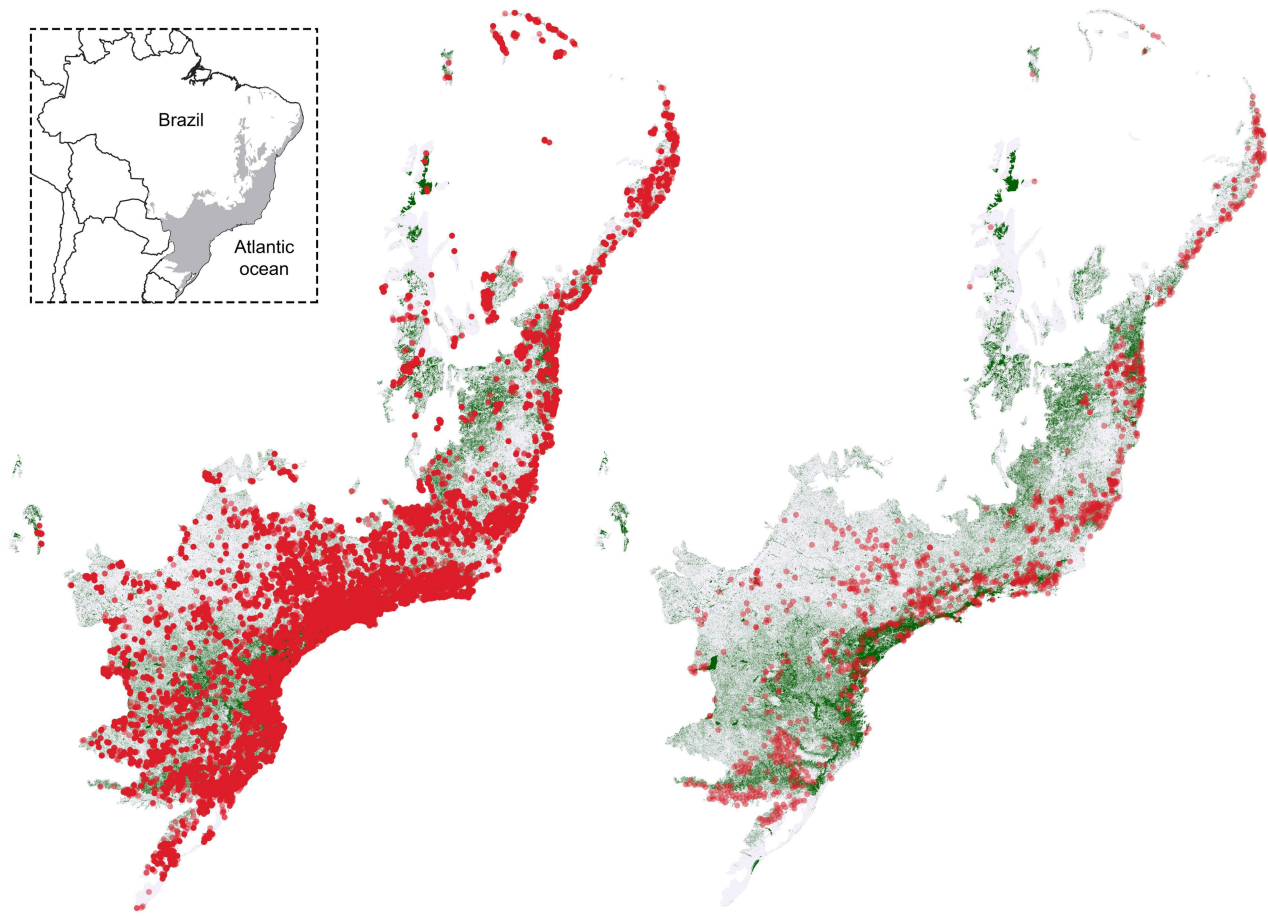


FIGURE S3. Occurrence records (red dots) employed in Species Distribution Models. In total, 79,777 occurrence points of birds (left panel; $n = 78,312$) and primates (right panel; $n = 1,150$) were used.

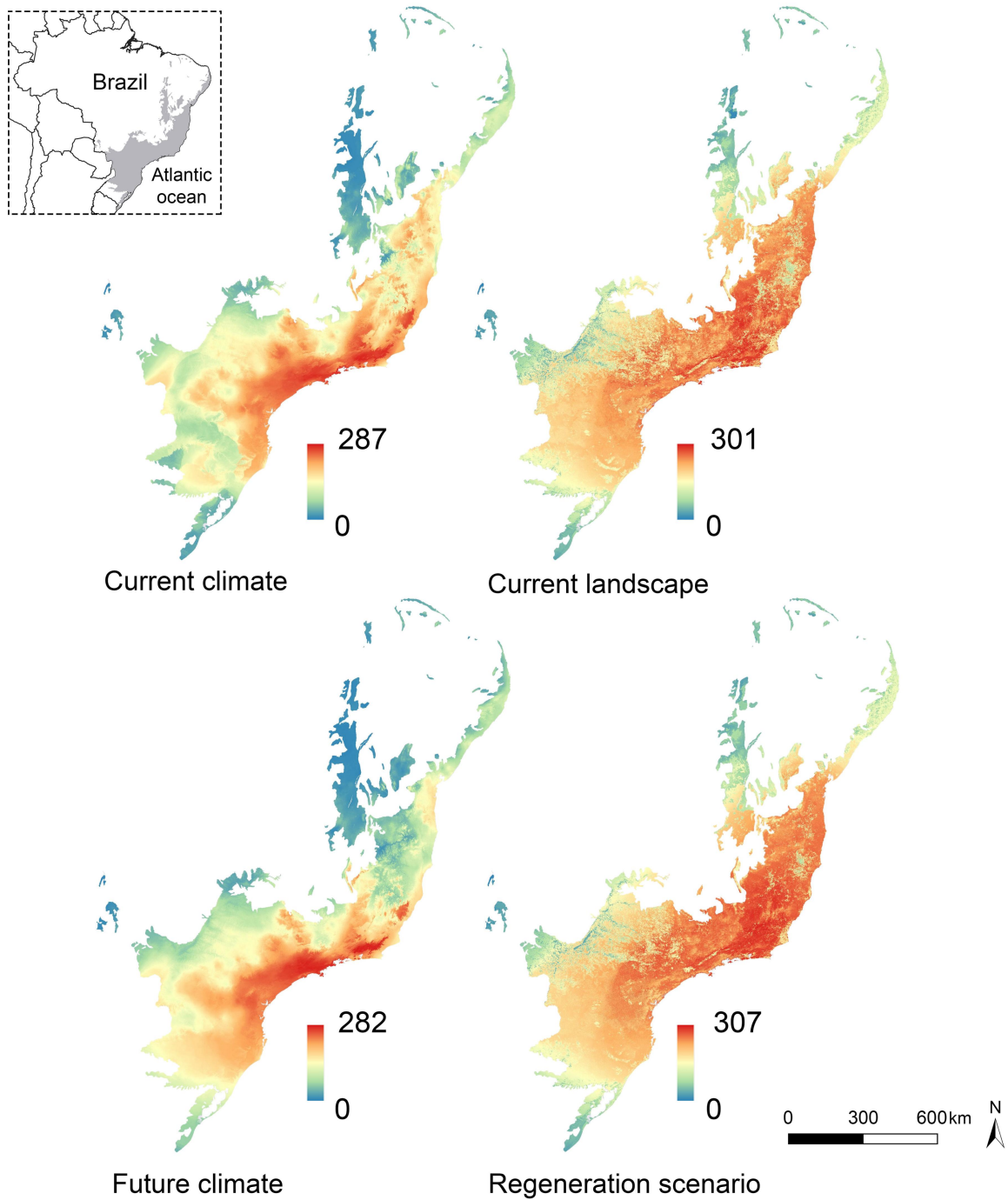


FIGURE S4. Maps of species richness resulting from climate and landscape-only predictors considering both current and future scenarios.

Table S1. Forest patch size classes, animal mobility scales, and function parameters used to model the natural forest regeneration. The natural regeneration potential (NRP) was defined as $NRP(d, S) = \exp(-d/\lambda_s)$, where d is the distance from the forest patch into the matrix, S is the size of the patch, and λ_s is scale the parameter defined below, adjusted so that the natural regeneration potential would decrease to approximately 0.05 when the distance to the forest patch reaches the scale of animal mobility.

Patch Size (ha)	Animal mobility scale (m)	λ_s
< 10	350	130
11 to 25	500	170
26 to 50	650	220
51 to 250	850	290
> 250	1000	350

TABLE S2. Description of the layers used for modeling the natural regeneration potential for the Atlantic Forest (AF). The forest map was a mosaic between two different maps, used to define forests in different parts of the AF limit.

Input variable	Map	Institution	Source	Comment
Atlantic Forest limit	Integrative AF limit	Laboratório de Ecologia Especial e Conservação (LEEC), Universidade Estadual Paulista (UNESP)	1	We used the part of the integrative limit of the AF within Brazil to conduct our study
Forest map	Land use	Fundação Brasileira para o Desenvolvimento Sustentável (FBDS)	2	Map resampled from the 5 m (original resolution) to 30 m and used to define forests (class “forest”) within the AF limit from the Ministério do Meio Ambiente (MMA/IBGE – see ref. 1 below)
	AF remnants	Fundação SOS Mata Atlântica/ Instituto Nacional de Pesquisas Espaciais (INPE)	3	Map used to define forests within the regions included in the Atlantic Forest limit of the AF law (law n. 11.428/2006) but not in the AF limit from MMA/IBGE (see ref. 1 below) – mostly areas in Northeastern Brazil. We consider the classes forest (“mata”), restinga, and mangrove (“mangue”).

Pasture map	Map of Brazilian pastures	Laboratório de Processamento e Geoprocessamento (LAPIG), Universidade Federal de Goiás (UFG)	4	We considered only natural regeneration within mapped pastures that did not overlap with urban areas, roads, or water bodies.
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¹ Muylaert, R. L., Vancine, M. H., Bernardo, R., Oshima, J. E. F., Sobral-Souza, T., Tonetti, V. R., Niebuhr, B. B., & Ribeiro, M. C. (2018). UMA NOTA SOBRE OS LIMITES TERRITORIAIS DA MATA ATLÂNTICA. *Oecologia Australis*, 22(03), 302–311.

<https://doi.org/10.4257/oeco.2018.2203.09>

Access: <https://github.com/LEEClab/ATLANTIC-limits>

² FBDS, 2017. Mapeamento do Uso do Solo dos biomas Cerrado e Mata Atlântica na escala 1:20.000, Projeto de Apoio à Implantação do CAR. Fundação Brasileira para o Desenvolvimento Sustentável, Rio de Janeiro.

Access: geo.fbds.org.br

³ Atlas dos remanescentes florestais da Mata Atlântica: período 2014/2015, relatório técnico. Fundação SOS Mata Atlântica / Instituto Nacional de Pesquisas Espaciais – INPE. São Paulo: Fundação SOS Mata Atlântica, 2021.

Access: <https://www.sosma.org.br/iniciativas/atlas-da-mata-atlantica/>

⁴ Parente, L., Ferreira, L., Faria, A., Nogueira, S., Araújo, F., Teixeira, L., & Hagen, S. (2017). Monitoring the brazilian pasturelands: A new mapping approach based on the landsat 8 spectral and temporal domains. *International Journal of Applied Earth Observation and Geoinformation*, 62, 135–143. <https://doi.org/10.1016/j.jag.2017.06.003>

Access: <https://pastagem.org/>

TABLE S3 Species of birds studied, the number of occurrence points used to build the SDM, and the areas of their potential distribution in hectares in the different BAF scenarios; *Number of points* corresponds to the number of occurrences used in the models for each species; *Current climate / current landscape* corresponds to the current climate and landscape scenario; *Current climate / regenerated landscape* is the scenario with current climate and regenerated landscape; *Future climate / current landscape* is the scenario with future climate and regenerated landscapes; and *Future climate / regenerated landscape* the scenario with future climate models associated to the regeneration scenario. ^{end} are Atlantic Forest endemic species according to Vale, Tourinho, Lorini, Rajão, & Figueiredo (2018).

Species	Number of points	Current climate / current landscape	Current climate / regenerated landscape	Future climate / current landscape	Future climate / regenerated landscape
<i>Aburria jacutinga</i> ^{end}	50	8,764,234	11,347,028	11,590,791	14,987,933
<i>Accipiter bicolor</i>	134	20,814,658	29,192,882	22,453,624	31,379,742
<i>Accipiter poliogaster</i>	43	10,021,145	12,467,381	10,136,331	12,417,976
<i>Acrobatornis fonsecai</i> ^{end}	18	1,187,452	1,484,298	183,256	216,285
<i>Amadonastur lacernulatus</i> ^{end}	189	8,923,551	11,223,793	9,442,719	11,800,485
<i>Amazona brasiliensis</i> ^{end}	22	494,535	517,849	69,666	70,915
<i>Amazona farinosa</i>	53	11,207,695	17,306,979	12,636,621	19,688,615
<i>Amazona pretrei</i> ^{end}	48	1,535,576	2,497,515	1,580,124	2,525,201

<i>Amazona rhodocorytha</i> ^{end}	97	5,944,339	9,095,011	6,570,019	10,098,167
<i>Amazona vinacea</i> ^{end}	181	18,090,380	24,515,653	16,895,573	22,735,689
<i>Anabacerthia amaurotis</i> ^{end}	115	11,039,427	13,719,504	11,540,831	14,273,019
<i>Anabacerthia lichtensteini</i> ^{end}	163	12,862,829	17,045,938	14,378,074	18,541,963
<i>Anabazenops fuscus</i> ^{end}	197	14,029,742	19,188,876	15,690,912	21,603,471
<i>Antilophia galeata</i>	186	7,352,517	12,335,404	5,438,008	9,254,467
<i>Antrostomus rufus</i>	115	16,051,665	24,282,507	14,265,525	21,530,890
<i>Antrostomus sericocaudatus</i>	26	6,527,344	7,833,868	6,879,979	8,299,953
<i>Arremon semitorquatus</i> ^{end}	166	9,309,076	13,316,632	10,525,394	14,732,721
<i>Asio stygius</i>	77	11,920,319	16,254,350	12,303,693	15,846,759
<i>Attila rufus</i> ^{end}	412	20,572,490	28,478,176	20,668,178	28,104,031
<i>Automolus lammi</i> ^{end}	14	244,665	326,891	68,556	75,703
<i>Automolus leucophthalmus</i> ^{end}	497	22,746,792	31,792,398	25,046,548	34,915,731
<i>Baryphthengus ruficapillus</i> ^{end}	316	19,639,834	27,456,910	20,157,198	27,617,962
<i>Batara cinerea</i>	249	15,729,076	20,746,587	14,336,649	18,035,216
<i>Biatas nigropectus</i> ^{end}	72	9,731,446	12,271,219	10,828,624	13,350,841

<i>Campephilus robustus</i> ^{end}	336	20,203,064	27,860,060	19,575,788	26,626,672
<i>Campylorhamphus falcularius</i> ^{end}	218	20,084,270	28,126,721	17,116,784	23,036,698
<i>Campylorhamphus trochilirostris</i>	61	10,658,898	15,918,785	13,233,088	20,251,012
<i>Capsiempis flaveola</i>	323	17,294,906	25,221,200	15,711,520	22,476,730
<i>Carpornis cucullata</i> ^{end}	219	10,739,945	13,293,942	10,922,715	13,427,932
<i>Carpornis melanocephala</i> ^{end}	84	7,009,181	8,391,963	7,500,454	8,864,501
<i>Caryothraustes canadensis</i>	96	8,336,174	12,046,607	8,668,755	12,363,298
<i>Castanozoster thoracicus</i> ^{end}	54	9,270,773	12,268,998	6,521,793	8,358,934
<i>Celeus flavescens</i>	492	26,187,163	36,473,304	26,961,890	37,312,979
<i>Celeus galeatus</i> ^{end}	25	9,151,078	11,844,685	10,357,334	13,627,841
<i>Ceratopipra rubrocapilla</i>	111	4,730,172	6,564,884	4,611,378	6,415,906
<i>Cercomacra brasiliana</i> ^{end}	46	5,900,485	10,000,051	4,983,164	8,113,089
<i>Cercomacra laeta</i>	26	168,754	178,399	3,886	3,886
<i>Chamaeza campanisona</i>	311	16,042,714	20,701,484	15,164,042	19,372,548
<i>Chamaeza meruloides</i> ^{end}	129	11,027,284	14,861,923	9,788,762	12,573,754
<i>Chamaeza ruficauda</i> ^{end}	96	9,323,093	11,706,185	6,249,234	7,683,780

<i>Chiroxiphia caudata</i> ^{end}	876	22,622,932	31,418,947	20,742,424	28,549,300
<i>Chiroxiphia pareola</i>	121	3,703,286	5,065,251	3,087,459	3,972,584
<i>Chlorophanes spiza</i>	145	13,105,482	17,118,311	14,373,078	1,877,0183
<i>Chlorophonia cyanea</i>	234	19,671,059	26,830,953	17,378,936	23,018,033
<i>Chlorostilbon notatus</i>	97	3,912,354	4,990,311	3,275,295	3,937,543
<i>Cichlocolaptes leucophrus</i> ^{end}	162	10,731,340	13,388,866	9,806,109	12,083,105
<i>Claravis pretiosa</i>	157	17,429,243	26,077,598	17,603,339	26,179,044
<i>Clibanornis dendrocolaptoides</i> ^{end}	67	9,663,306	12,424,083	8,042,520	10,208,564
<i>Clytolaema rubricauda</i> ^{end}	227	15,233,500	20,758,175	15,061,208	19,773,408
<i>Coccyzus euleri</i>	49	5,911,518	7,485,952	5,187,653	6,387,526
<i>Conopias trivirgatus</i>	114	17,382,197	24,054,703	18,974,325	25,549,062
<i>Conopophaga cearae</i> ^{end}	23	512,021	565,520	178,329	186,587
<i>Conopophaga lineata</i>	672	23,734,404	32,780,774	21,099,083	29,015,871
<i>Conopophaga melanops</i> ^{end}	280	13,613,963	17,838,429	13,455,132	17,620,756
<i>Contopus cinereus</i>	277	25,026,495	34,754,610	24,301,311	33,588,946
<i>Corythopsis delalandi</i>	261	18,681,435	28,242,254	18,950,178	28,609,876

<i>Cotinga maculata</i> ^{end}	10	284,980	380,806	141,345	172,987
<i>Cranioleuca obsoleta</i> ^{end}	252	12,184,691	16,560,424	11,081,962	14,975,096
<i>Cranioleuca pallida</i> ^{end}	332	12,701,361	17,804,567	12,178,238	16,254,558
<i>Crax blumenbachii</i> ^{end}	15	800,887	1,297,225	542,344	803,940
<i>Crypturellus noctivagus</i>	108	12,846,800	18,570,759	13,581,420	19,398,014
<i>Crypturellus obsoletus</i>	630	26,052,340	36,329,738	24,015,429	33,137,779
<i>Crypturellus soui</i>	101	7,490,601	10,927,780	8,427,004	12,496,733
<i>Crypturellus undulatus</i>	88	10,853,257	17,463,521	11,824,285	19,040,661
<i>Crypturellus variegatus</i>	39	1,613,639	2,262,217	1,626,753	2,249,102
<i>Cyanerpes cyaneus</i>	144	6,893,024	9,389,914	9,248,291	14,227,569
<i>Cyanocorax caeruleus</i> ^{end}	297	9,430,368	11,626,735	9,192,225	11,363,265
<i>Dacnis nigripes</i> ^{end}	85	9,409,690	13,206,789	8,577,093	11,515,296
<i>Dendrocincla taunayi</i> ^{end}	11	96,173	99,642	0	0
<i>Dendrocincla turdina</i> ^{end}	321	21,158,618	29,064,165	23,457,820	31,999,385
<i>Dendrocolaptes platyrostris</i>	492	28,086,892	39,032,436	24,768,715	34,044,276
<i>Dendroplex picus</i>	114	4,033,993	5,183,004	3,726,253	4,668,346

<i>Dixiphia pipra</i>	48	3,716,123	5,430,792	3,535,989	5,007,658
<i>Dromococcyx pavoninus</i>	124	16,476,533	23,102,965	18,685,459	25,571,891
<i>Drymophila ferruginea</i> ^{end}	291	20,405,194	28,626,044	22,483,946	31,286,553
<i>Drymophila genei</i> ^{end}	52	3,556,528	6,139,322	3,148,799	5,313,871
<i>Drymophila malura</i> ^{end}	285	17,494,607	23,803,238	15,092,294	19,634,075
<i>Drymophila ochropyga</i> ^{end}	192	16,962,047	24,099,251	18,267,669	25,764,237
<i>Drymophila rubricollis</i> ^{end}	131	12,869,490	16,795,791	12,398,409	15,509,738
<i>Drymophila squamata</i> ^{end}	179	10,412,984	13,703,267	10,437,340	13,369,021
<i>Dysithamnus mentalis</i>	723	24,648,741	33,885,375	21,855,699	29,907,032
<i>Dysithamnus plumbeus</i> ^{end}	20	1,296,601	2,259,303	307,879	554,209
<i>Dysithamnus stictothorax</i> ^{end}	220	13,713,953	18,545,779	12,296,268	16,038,550
<i>Dysithamnus xanthopterus</i> ^{end}	76	5,379,166	6,728,156	3,348,014	3,985,698
<i>Elaenia chilensis</i>	12	1,523,364	2,031,221	886,929	1,135,688
<i>Eleoscytalopus indigoticus</i> ^{end}	241	14,274,407	18,842,209	14,682,275	18,744,440
<i>Eucometis penicillata</i>	87	13,369,229	20,890,569	13,136,707	20,519,686
<i>Euphonia chalybea</i> ^{end}	218	14,663,193	18,691,566	14,833,404	18,961,003

<i>Euphonia pectoralis</i> ^{end}	431	19,282,343	25,858,190	17,061,690	22,338,230
<i>Formicivora iheringi</i>	23	1,535,854	2,920,093	980,118	1,581,304
<i>Formicivora serrana</i> ^{end}	85	5,940,037	9,350,640	3,845,672	6,120,101
<i>Galbula ruficauda</i>	504	15,381,715	23,140,921	15,816,853	24,036,107
<i>Geotrygon montana</i>	281	21,221,346	29,179,490	18,408,320	24,860,447
<i>Glaucidium brasilianum</i>	24	4,147,513	9,335,097	4,649,334	10,460,724
<i>Glaucidium minutissimum</i> ^{end}	114	10,387,102	12,953,659	11,144,066	14,412,630
<i>Glaucis dohrnii</i> ^{end}	18	1,311,173	2,185,612	1,337,263	1,990,698
<i>Glaucis hirsutus</i>	162	13,038,452	18,677,688	12,873,792	18,584,290
<i>Grallaria varia</i>	193	13,548,322	17,411,410	12,987,659	16,374,670
<i>Habia rubica</i>	440	23,185,399	31,922,710	21,638,026	2,931,5561
<i>Haplospiza unicolor</i> ^{end}	295	19,743,362	27,091,023	17,422,581	23,006,098
<i>Harpagus bidentatus</i>	20	5,704,461	8,454,552	5,809,933	8,381,624
<i>Harpagus diodon</i>	235	22,307,629	31,461,482	20,222,840	27,905,648
<i>Heliobletus contaminatus</i> ^{end}	213	13,571,983	17,017,073	13,050,317	16,131,670
<i>Heliothryx auritus</i>	118	7,578,239	9,934,131	6,127,179	7,449,176

<i>Hemithraupis flavicollis</i>	112	7,802,712	11,302,064	7,724,234	10,958,867
<i>Hemithraupis guira</i>	302	21,078,474	27,790,879	15,944,737	20,504,767
<i>Hemithraupis ruficapilla</i> ^{end}	671	18,435,729	25,517,143	20,122,712	27,551,002
<i>Hemitriccus diops</i> ^{end}	207	16,582,837	22,937,264	14,513,521	19,142,593
<i>Hemitriccus furcatus</i> ^{end}	39	2,464,902	3,536,822	1,975,571	2,703,600
<i>Hemitriccus griseipectus</i>	43	419,664	441,660	157,652	160,219
<i>Hemitriccus kaempferi</i> ^{end}	18	201,089	247,649	0	0
<i>Hemitriccus margaritaceiventer</i>	189	11,653,519	18,944,488	10,989,328	17,816,641
<i>Hemitriccus mirandae</i> ^{end}	11	40,593	41,009	8,882	9,021
<i>Hemitriccus nidipendulus</i> ^{end}	305	17,585,992	24,884,594	18,633,348	26,263,490
<i>Hemitriccus obsoletus</i> ^{end}	112	15,059,681	19,737,395	13,546,587	17,010,758
<i>Hemitriccus orbitatus</i> ^{end}	209	13,510,019	18,525,795	14,650,564	19,659,055
<i>Hemitriccus striaticollis</i>	46	3,908,330	5,720,976	2,832,941	3,602,186
<i>Herpsilochmus atricapillus</i>	221	9,588,852	14,814,044	5,125,550	8,067,847
<i>Herpsilochmus pileatus</i> ^{end}	47	904,692	1,011,204	25,605	34,070
<i>Herpsilochmus rufimarginatus</i>	353	17,753,775	24,091,757	19,072,441	25,439,844

<i>Hylocharis sapphirina</i>	60	5,895,489	8,656,404	5,755,740	8,473,356
<i>Hylopezus nattereri</i> ^{end}	136	14,079,355	18,217,986	12,425,540	15,377,829
<i>Hylopezus ochroleucus</i>	35	4,116,496	6,463,437	3,663,040	5,513,434
<i>Hylophilus amaurocephalus</i>	276	15,316,906	23,054,115	10,862,485	15,953,063
<i>Hylophilus poicilotis</i> ^{end}	398	18,499,844	25,256,033	17,311,490	22,989,375
<i>Hylophilus thoracicus</i>	108	3,786,344	5,929,490	3,422,261	5,023,409
<i>Hypoedaleus guttatus</i> ^{end}	301	23,206,562	32,397,955	20,311,172	27,807,116
<i>Ilicura militaris</i> ^{end}	310	15,158,283	20,781,004	14,457,247	19,503,277
<i>Iodopleura pipra</i> ^{end}	59	10,902,384	14,148,813	9,675,380	12,222,508
<i>Jacamaralcyon tridactyla</i> ^{end}	45	4,737,250	7,848,301	4,375,733	7,121,730
<i>Laniisoma elegans</i> ^{end}	24	1,817,850	2,088,606	1,458,693	1,592,128
<i>Lanio cristatus</i>	26	2,851,259	4,115,733	3,692,669	5,200,351
<i>Laniocera hypopyrra</i>	10	954,028	1,292,854	924,191	1,382,643
<i>Lathrotriccus euleri</i>	789	26,339,055	36,261,945	20,598,650	28,127,901
<i>Legatus leucophaius</i>	507	23,333,405	31,879,967	23,870,475	33,097,603
<i>Lepidocolaptes falcinellus</i> ^{end}	342	14,783,721	18,798,494	14,211,471	17,876,385

<i>Lepidocolaptes squamatus</i> ^{end}	219	8,589,929	13,096,392	7,621,052	11,490,455
<i>Leptasthenura setaria</i> ^{end}	279	13,921,148	18,234,709	12,674,715	16,109,882
<i>Leptasthenura striolata</i> ^{end}	63	4,096,512	5,541,536	2,956,314	3,988,127
<i>Leptodon cayanensis</i>	309	22,695,305	31,707,050	22,108,344	30,308,655
<i>Leptodon forbesi</i> ^{end}	29	324,879	373,798	38,164	39,760
<i>Leptopogon amaurocephalus</i>	835	26,979,029	37,333,032	24,343,361	33,272,255
<i>Leptotila rufaxilla</i>	658	26,278,062	36,226,488	23,683,195	32,361,179
<i>Leptotila verreauxi</i>	38	5,516,001	9,191,809	5,319,145	8,584,101
<i>Lipaugus lanioides</i> ^{end}	81	14,433,099	20,527,041	12,500,619	16,948,586
<i>Lipaugus vociferans</i>	40	3,001,625	4,074,239	2,977,408	3,980,009
<i>Lochmias nematura</i>	574	21,420,770	29,655,706	18,949,623	25,730,723
<i>Lophornis chalybeus</i> ^{end}	85	8,772,492	11,065,240	8,233,201	10,247,283
<i>Machaeropterus regulus</i> ^{end}	52	3,534,185	4,731,143	3,401,860	4,526,169
<i>Mackenziaena leachii</i> ^{end}	305	15,003,407	19,127,814	12,375,094	15,442,847
<i>Mackenziaena severa</i> ^{end}	318	20,610,169	28,544,373	20,047,425	27,462,600
<i>Macropsalis forcipata</i> ^{end}	73	13,564,489	17,670,438	11,445,491	14,493,537

<i>Malacoptila striata</i> ^{end}	355	16,075,743	22,641,598	18,759,705	26,701,126
<i>Manacus manacus</i>	519	19,368,246	27,119,333	22,914,852	31,743,132
<i>Megascops atricapilla</i> ^{end}	124	15,320,583	20,651,316	14,669,924	19,381,916
<i>Megascops sanctaecatarinae</i> ^{end}	110	9,558,807	11,788,411	9,236,703	11,530,770
<i>Melanerpes flavifrons</i> ^{end}	309	19,357,283	26,387,905	18,686,431	24,965,294
<i>Merulaxis ater</i> ^{end}	82	4,498,552	5,156,497	5,330,941	6,177,694
<i>Micrastur ruficollis</i>	272	26,116,525	35,994,659	22,978,898	31,359,897
<i>Micrastur semitorquatus</i>	315	26,858,708	37,312,840	24,402,133	33,573,750
<i>Mionectes oleagineus</i>	69	8,435,609	12,254,982	7,524,463	10,576,326
<i>Mionectes rufiventris</i> ^{end}	421	21,376,569	29,648,350	20,045,967	27,514,781
<i>Momotus momota</i>	78	10,726,344	16,437,953	11,047,060	17,106,307
<i>Monasa morphoeus</i>	19	1,405,333	2,385,452	974,567	1,349,406
<i>Monasa nigrifrons</i>	35	808,242	1,356,692	1,920,824	3,097,312
<i>Myiarchus swainsoni</i>	718	27,129,533	37,903,687	26,550,899	37,112,306
<i>Myiobius atricaudus</i>	112	15,837,045	22,487,208	14,133,062	19,759,253
<i>Myiobius barbatus</i>	156	18,206,121	25,288,785	16,781,844	22,516,837

<i>Myiornis auricularis</i> ^{end}	487	25,443,106	35,461,406	27,116,627	37,592,755
<i>Myiothlypis flaveola</i>	426	14,725,227	22,194,317	10,816,272	16,688,863
<i>Myiothlypis leucoblephara</i>	724	18,214,656	24,564,434	15,377,413	19,621,099
<i>Myiothlypis rivularis</i>	159	15,941,683	21,002,077	18,519,481	24,540,980
<i>Myrmoderus loricatus</i> ^{end}	87	7,281,879	10,993,630	4,015,119	5,976,327
<i>Myrmoderus ruficauda</i> ^{end}	26	2,234,045	4,119,619	1,493,110	2,633,933
<i>Myrmoderus squamosus</i> ^{end}	216	12,420,613	16,223,402	12,744,590	16,438,439
<i>Myrmotherula axillaris</i> ^{end}	178	8,286,769	11,709,585	9,740,259	1,397,5271
<i>Myrmotherula minor</i> ^{end}	46	2,785,895	3,274,254	2,366,231	2,722,335
<i>Myrmotherula unicolor</i> ^{end}	155	7,311,161	9,566,162	7,520,022	9,797,227
<i>Myrmotherula urosticta</i> ^{end}	39	1,377,647	1,670,468	715,955	787,842
<i>Nemosia pileata</i>	503	18,428,096	27,060,908	21,306,833	30,803,467
<i>Neopelma aurifrons</i> ^{end}	19	3,508,372	5,481,029	2,896,917	4,406,958
<i>Neopelma chrysolophum</i> ^{end}	104	6,168,812	9,353,485	5,353,145	7,804,308
<i>Nonnula rubecula</i>	73	18,187,455	25,436,791	20,590,670	28,579,137
<i>Notharchus swainsoni</i> ^{end}	81	10,075,338	13,746,704	13,474,214	18,046,526

<i>Nyctibius aethereus</i>	19	8,223,903	13,996,088	8,217,589	13,961,324
<i>Nyctibius grandis</i>	22	5,577,896	8,943,882	9,135,951	14,707,255
<i>Nyctiphrynus ocellatus</i>	89	15,535,758	23,260,478	17,838,498	26,477,278
<i>Odontophorus capueira</i> ^{end}	235	21,429,513	29,582,084	19,051,694	25,925,636
<i>Onychorhynchus swainsonii</i> ^{end}	37	4,778,050	5,640,416	5,472,703	6,392,591
<i>Orchesticus abeillei</i> ^{end}	99	8,636,698	10,805,725	8,360,946	10,073,048
<i>Ortalis araucuan</i> ^{end}	115	6,843,827	9,450,213	6,684,510	9,365,836
<i>Ortalis guttata</i>	265	22,463,546	30,532,712	23,951,175	32,564,974
<i>Ortalis squamata</i> ^{end}	140	3,905,693	4,646,003	3,774,201	4,551,912
<i>Orthogonys chloricterus</i> ^{end}	146	7,425,445	8,969,279	8,057,023	9,802,986
<i>Oxyruncus cristatus</i>	151	14,055,971	19,200,464	11,768,149	15,445,692
<i>Pachyramphus castaneus</i>	464	24,430,791	33,831,321	22,941,566	31,351,779
<i>Pachyramphus marginatus</i>	117	13,253,974	17,791,522	15,110,682	20,212,640
<i>Pachyramphus polychopterus</i>	714	27,430,195	38,020,538	28,009,454	39,019,876
<i>Pachyramphus validus</i>	564	27,037,593	37,627,727	23,224,257	32,019,369
<i>Pachyramphus viridis</i>	325	21,464,762	28,837,402	18,740,624	25,202,326

<i>Panyptila cayennensis</i>	54	9,296,170	12,710,104	10,533,790	14,761,378
<i>Patagioenas cayennensis</i>	16	1,051,797	1,532,523	1,331,989	2,106,716
<i>Patagioenas plumbea</i>	399	22,722,783	31,691,923	21,272,278	29,052,924
<i>Penelope obscura</i>	733	19,615,340	27,069,443	19,818,025	27,200,796
<i>Penelope supercilialis</i>	292	16,410,683	23,834,532	18,654,234	27,794,001
<i>Phaethornis eurynome</i> ^{end}	407	23,804,417	33,272,116	22,662,831	31,198,707
<i>Phaethornis idaliae</i> ^{end}	49	4,292,744	6,926,469	4,376,427	6,964,356
<i>Phaethornis pretrei</i>	727	15,313,089	22,721,048	14,021,831	20,674,215
<i>Phaethornis ruber</i>	268	10,545,309	14,145,205	10,655,429	14,217,786
<i>Phaethornis squalidus</i> ^{end}	146	8,422,425	10,939,646	8,432,694	10,740,430
<i>Pheugopedius genibarbis</i>	276	12,233,610	17,621,797	12,256,023	17,809,078
<i>Phibalura flavirostris</i> ^{end}	96	13,324,195	18,578,184	12,816,893	17,011,522
<i>Philydor atricapillus</i> ^{end}	257	16,474,243	21,865,830	16,828,682	21,906,284
<i>Philydor rufum</i>	454	22,524,261	30,969,862	18,789,057	25,373,717
<i>Phyllomyias fasciatus</i>	535	24,746,719	33,684,356	21,710,121	29,673,400
<i>Phyllomyias griseocapilla</i> ^{end}	207	15,184,928	20,817,850	14,792,326	19,459,354

<i>Phyllomyias virescens</i> ^{end}	229	18,913,818	25,853,541	16,611,425	21,807,335
<i>Phylloscartes beckeri</i> ^{end}	13	271,102	481,212	10,061	11,310
<i>Phylloscartes ceciliae</i> ^{end}	12	118,169	126,218	25,813	26,229
<i>Phylloscartes difficilis</i> ^{end}	74	6,611,513	8,341,170	5,938,094	7,232,683
<i>Phylloscartes eximius</i> ^{end}	66	16,608,788	24,418,578	16,633,005	24,322,752
<i>Phylloscartes kronei</i> ^{end}	87	1,625,713	1,877,039	938,069	1,064,773
<i>Phylloscartes oustaleti</i> ^{end}	95	12,750,904	17,261,946	10,691,303	13,920,524
<i>Phylloscartes paulista</i> ^{end}	48	3,607,529	4,015,050	4,248,544	4,721,360
<i>Phylloscartes sylviolus</i> ^{end}	50	5,393,877	6,107,889	5,994,507	6,878,730
<i>Phylloscartes ventralis</i>	453	20,525,722	28,260,989	17,885,267	23,790,331
<i>Piculus aurulentus</i> ^{end}	339	17,624,850	23,420,280	15,624,576	19,959,786
<i>Piculus flavigula</i>	166	19,774,657	27,432,416	21,712,273	30,113,881
<i>Picumnus exilis</i> ^{end}	51	2,396,346	2,951,804	1,769,001	2,040,728
<i>Picumnus fulvescens</i>	23	171,807	205,530	47,670	53,013
<i>Picumnus limae</i>	18	52,389	53,568	34,694	35,319
<i>Picumnus nebulosus</i>	111	8,661,122	10,856,865	5,872,868	7,506,491

<i>Picumnus pernambucensis</i> ^{end}	37	294,556	307,393	27,409	27,617
<i>Picumnus temminckii</i> ^{end}	426	13,611,812	17,735,456	14,632,454	18,716,754
<i>Pionopsitta pileata</i> ^{end}	310	15,083,828	19,393,851	14,275,101	18,074,143
<i>Pionus maximiliani</i>	848	23,942,293	33,289,186	23,181,097	32,006,602
<i>Pipra fasciicauda</i>	46	3,116,117	5,028,405	3,400,403	5,705,780
<i>Pipraeidea bonariensis</i>	254	11,643,804	16,101,486	11,175,707	15,151,344
<i>Pipraeidea melanonota</i>	508	21,972,897	30,300,259	19,382,957	26,139,215
<i>Piprites chloris</i>	66	26,592,671	37,351,906	26,549,095	37,264,823
<i>Piprites pileata</i> ^{end}	59	17,627,487	24,446,126	19,359,156	26,735,960
<i>Platyrrinchus leucoryphus</i> ^{end}	47	6,035,447	7,555,896	8,425,131	10,705,250
<i>Platyrrinchus mystaceus</i>	615	23,308,148	31,973,226	18,931,096	25,511,315
<i>Poecilotriccus fumifrons</i>	42	1,390,692	1,579,014	194,358	216,632
<i>Poecilotriccus plumbeiceps</i>	21	3,478,743	5,234,490	1,986,951	2,585,153
<i>Polioptila lactea</i> ^{end}	28	3,928,938	5,361,542	378,447	461,297
<i>Primolius maracana</i>	317	17,764,946	27,112,117	19,307,600	29,181,571
<i>Procnias nudicollis</i> ^{end}	372	20,901,880	28,310,394	19,574,262	25,929,522

<i>Pseudastur polionotus</i> ^{end}	167	26,082,385	36,329,391	27,339,018	38,117,682
<i>Psilorhamphus guttatus</i> ^{end}	127	11,670,588	15,083,551	13,484,761	17,068,420
<i>Pteroglossus aracari</i>	190	12,772,623	19,680,080	14,371,829	22,132,769
<i>Pteroglossus bailloni</i> ^{end}	143	13,959,104	19,408,839	15,833,506	21,629,977
<i>Pteroglossus inscriptus</i>	13	207,195	232,245	4,510	4,580
<i>Pulsatrix koeniswaldiana</i> ^{end}	254	20,340,940	29,491,393	21,508,339	30,283,745
<i>Pulsatrix perspicillata</i>	48	17,992,958	27,491,952	19,650,728	29,648,836
<i>Pyriglena atra</i> ^{end}	14	154,113	209,138	0	0
<i>Pyriglena leucoptera</i> ^{end}	609	22,472,914	31,198,151	23,175,268	31,884,200
<i>Pyroderus scutatus</i>	221	22,438,844	31,785,806	23,605,896	33,429,352
<i>Pyrrhura cruentata</i> ^{end}	45	2,819,132	4,528,875	2,713,661	4,216,417
<i>Pyrrhura frontalis</i> ^{end}	750	24,784,119	34,319,958	22,799,805	31,150,689
<i>Pyrrhura leucotis</i> ^{end}	51	9,622,575	14,408,397	10,413,609	15,527,224
<i>Ramphastos dicolorus</i> ^{end}	634	21,872,908	30,294,569	19,829,127	27,067,361
<i>Ramphastos vitellinus</i>	303	16,451,276	22,300,205	17,390,940	23,090,614
<i>Ramphocaenus melanurus</i>	190	15,774,456	21,019,633	17,691,394	23,872,696

<i>Ramphocelus bresilius</i> ^{end}	439	17,664,610	24,542,507	18,534,747	25,807,744
<i>Ramphodon naevius</i> ^{end}	192	7,036,451	8,555,235	7,245,866	8,869,150
<i>Ramphotrigon megacephalum</i>	73	11,227,679	14,913,826	13,637,833	18,121,536
<i>Rhopias gularis</i> ^{end}	224	11,519,182	14,937,834	1,1050,252	14,167,617
<i>Rhopornis ardesiacus</i> ^{end}	10	618,880	963,257	340,214	546,923
<i>Rhynchocyclus olivaceus</i>	39	2,357,349	2,978,449	674,946	797,972
<i>Saltator fuliginosus</i> ^{end}	218	21,504,245	30,161,065	20,016,685	27,490,425
<i>Saltator maximus</i>	12	375,949	754,535	118,933	159,872
<i>Saltator similis</i>	1041	26,896,109	37,523,089	25,609,431	35,481,390
<i>Saltatricula atricollis</i>	113	11,007,231	17,636,022	6,891,220	10,972,606
<i>Schiffornis turdina</i>	64	4,087,561	5,398,248	2,583,834	3,273,421
<i>Schiffornis virescens</i> ^{end}	561	22,384,582	30,750,385	20,001,281	26,885,840
<i>Schistochlamys melanopis</i>	81	9,758,647	15,836,282	922,3034	15,164,944
<i>Sclerurus scansor</i> ^{end}	348	19,129,063	26,022,572	16,742,848	21,965,681
<i>Scytalopus iraiensis</i> ^{end}	28	5,230,466	7,054,700	2,757,862	3,679,138
<i>Scytalopus pachecoi</i> ^{end}	35	2,527,976	3,709,600	568,156	899,905

<i>Scytalopus petrophilus</i> ^{end}	43	1,834,296	3,093,635	848,487	1,287,997
<i>Scytalopus speluncae</i> ^{end}	188	14,056,595	17,961,386	13,125,257	16,322,975
<i>Selenidera maculirostris</i> ^{end}	185	23,144,182	32,300,602	24,277,580	33,503,459
<i>Sittasomus griseicapillus</i>	876	28,105,905	38,758,835	24,699,187	33,966,213
<i>Spizaetus melanoleucus</i>	142	19,932,378	28,051,781	21,315,299	29,511,654
<i>Spizaetus ornatus</i>	64	21,265,755	29,190,731	23,806,776	32,799,300
<i>Spizaetus tyrannus</i>	320	25,324,450	35,393,474	22,561,385	31,033,630
<i>Sporophila falcirostris</i> ^{end}	122	16,517,126	22,863,018	15,102,147	20,422,402
<i>Sporophila frontalis</i> ^{end}	152	11,579,203	15,225,451	10,441,850	13,061,975
<i>Stephanophorus diadematus</i>	344	14,745,349	19,035,526	13,874,241	17,653,091
<i>Strix huhula</i>	41	10,491,602	16,157,344	10,874,767	16,740,627
<i>Strix hylophila</i> ^{end}	149	15,105,547	21,168,957	11,760,447	15,359,025
<i>Strix virgata</i>	156	19,940,843	27,643,913	22,870,998	31,803,570
<i>Synallaxis cinerascens</i>	349	17,685,565	23,626,018	14,905,360	19,015,612
<i>Synallaxis cinerea</i> ^{end}	21	1,383,615	1,987,090	147,590	191,028
<i>Synallaxis hypospodia</i>	28	4,064,247	6,751,054	4,914,677	8,347,970

<i>Synallaxis infuscata</i> ^{end}	23	183,881	193,942	13,808	14,017
<i>Synallaxis ruficapilla</i>	745	22,735,065	31,396,326	20,077,123	27,555,859
<i>Synallaxis scutata</i>	51	5,535,985	8,090,468	2,389,684	3,429,061
<i>Syndactyla rufosuperciliata</i>	389	17,657,879	23,368,724	15,055,865	19,121,985
<i>Tachyphonus coronatus</i> ^{end}	1044	20,904,378	29,064,651	19,581,686	26,714,102
<i>Tangara brasiliensis</i> ^{end}	78	4,862,288	6,890,873	4,581,957	6,354,705
<i>Tangara cyanocephala</i> ^{end}	301	16,983,558	22,182,452	16,687,892	21,729,203
<i>Tangara cyanoventris</i> ^{end}	297	13,805,546	20,356,969	10,915,915	15,931,900
<i>Tangara desmaresti</i> ^{end}	262	9,142,196	12,496,316	8,873,661	11,316,913
<i>Tangara fastuosa</i> ^{end}	28	223,640	231,134	4,857	4,857
<i>Tangara preciosa</i>	267	14,574,861	18,454,464	13,563,518	16,981,615
<i>Tangara seledon</i> ^{end}	441	24,460,628	34,025,472	26,091,198	36,277,835
<i>Taraba major</i>	419	15,534,232	24,249,825	15,919,063	25,017,613
<i>Terenura maculata</i> ^{end}	200	17,094,372	23,416,672	17,352,915	23,385,447
<i>Terenura sicki</i> ^{end}	13	172,293	197,064	57,593	65,156
<i>Tersina viridis</i>	823	26,861,415	37,240,121	25,934,032	35,957,259

<i>Thalurania glaucopis</i> ^{end}	828	23,553,715	32,487,536	21,889,839	29,696,021
<i>Thalurania watertonii</i> ^{end}	12	54,609	57,385	6,523	6,523
<i>Thamnomanes caesius</i>	34	3,000,376	3,910,481	2,036,703	2,415,289
<i>Thamnophilus aethiops</i>	14	465,183	822,258	155,847	174,791
<i>Thamnophilus ambiguus</i> ^{end}	219	8,161,453	12,150,829	8,958,176	13,736,504
<i>Thamnophilus caerulescens</i>	1136	25,060,356	34,532,982	20,717,305	28,402,265
<i>Thamnophilus doliatus</i>	31	2,326,610	4,840,639	1,628,904	3,353,982
<i>Thamnophilus palliatus</i>	206	7,061,917	10,300,990	6,496,536	9,567,133
<i>Thamnophilus pelzelni</i>	220	13,922,258	21,852,577	13,898,666	21,889,006
<i>Thamnophilus ruficapillus</i>	478	18,959,615	26,230,670	16,384,732	21,844,181
<i>Thamnophilus torquatus</i>	81	13,449,095	20,623,769	8,841,672	12,508,737
<i>Thraupis cyanoptera</i> ^{end}	353	18,417,410	24,756,780	16,955,872	22,208,542
<i>Thraupis ornata</i> ^{end}	373	19,874,577	28,027,842	21,451,440	29,522,965
<i>Thripophaga macroura</i> ^{end}	25	2,515,209	3,678,791	1,516,703	2,063,765
<i>Tijuca atra</i> ^{end}	49	2,380,386	3,426,008	1,925,264	2,599,447
<i>Tinamus solitarius</i> ^{end}	182	15,733,586	20,861,010	16,973,219	22,548,617

<i>Tityra cayana</i>	301	27,021,356	37,294,660	23,667,721	32,406,004
<i>Tityra inquisitor</i>	164	18,663,671	26,584,275	19,209,831	26,667,195
<i>Todirostrum poliocephalum</i> ^{end}	689	16,678,732	23,406,264	19,522,775	27,138,346
<i>Tolmomyias poliocephalus</i>	55	3,501,780	4,759,454	2,820,242	3,733,470
<i>Tolmomyias sulphureus</i>	38	9,430,298	13,121,719	8,225,707	10,974,201
<i>Touit melanonotus</i> ^{end}	69	10,514,361	13,824,697	11,213,107	14,554,877
<i>Touit surdus</i> ^{end}	67	3,290,491	4,252,846	1,527,735	1,808,622
<i>Trichothraupis melanops</i>	643	20,785,723	28,670,036	19,611,038	26,438,628
<i>Triclaria malachitacea</i> ^{end}	127	12,947,830	16,540,093	12,508,737	15,795,481
<i>Trogon curucui</i>	79	9,770,373	15,478,027	11,278,680	18,936,647
<i>Trogon rufus</i>	249	20,737,150	28,418,502	17,946,468	24,098,557
<i>Trogon surrucura</i>	797	25,347,835	35,495,337	22,924,219	31,869,905
<i>Trogon viridis</i>	282	23,422,501	32,192,703	25,895,313	35,707,250
<i>Turdus albicollis</i>	706	26,374,027	36,411,964	22,996,245	31,583,191
<i>Turdus flavipes</i>	439	23,807,887	32,874,102	21,733,783	29,482,997
<i>Turdus fumigatus</i>	23	3,169,477	4,552,883	3,259,335	4,679,032

<i>Veniliornis affinis</i>	15	342,781	527,147	1,1449	17,486
<i>Veniliornis maculifrons</i> ^{end}	25	1,270,511	2,083,541	1,131,039	1,574,712
<i>Veniliornis spilogaster</i>	64	14,997,856	19,963,464	13,865,290	17,729,974
<i>Vireo chivi</i>	1015	27,791,503	38,527,077	25,692,906	35,574,579
<i>Xenops minutus</i>	266	18,452,590	24,428,293	19,290,114	25,659,113
<i>Xenops rutilans</i>	623	27,106,288	37,499,843	23,601,594	32,124,008
<i>Xiphocolaptes albicollis</i>	320	22,809,380	31,351,709	18,949,345	25,500,560
<i>Xiphocolaptes falcistrostris</i>	13	1,000,380	2,470,939	756,478	1,638,480
<i>Xipholena atropurpurea</i> ^{end}	37	2,185,195	2,738,572	1,693,852	1,981,053
<i>Xiphorhynchus atlanticus</i> ^{end}	11	220,379	261,666	50,723	54,054
<i>Xiphorhynchus fuscus</i> ^{end}	643	25,291,907	35,145,964	23,528,874	32,396,220
<i>Xiphorhynchus guttatus</i>	55	3,232,066	4,232,376	3,076,357	3,897,366

TABLE S4 Species of primates and sloths studied, the number of occurrence points used to build the SDM, and the areas of their potential distribution in hectares in the different BAF scenarios; *Number of points* corresponds to the number of occurrences used in the models for each species; *Current climate / current landscape* corresponds to the current climate and landscape scenario; *Current climate / regenerated landscape* is the scenario with current climate and regenerated landscape; *Future climate / current landscape* is the scenario with future climate and regenerated landscapes; and *Future climate / regenerated landscape* the scenario with future climate models associated to the regeneration scenario. ^{end} are Atlantic Forest endemic species according to Reis, Peracchi, Batista, & Rosa, (2015).

Species	Number of points	Current climate / current landscape	Current climate / regenerated landscape	Future climate / current landscape	Future climate / regenerated landscape
<i>Alouatta belzebul</i>	14	109,634	131,353	12,559	16,098
<i>Alouatta caraya</i>	23	3,298,401	5,473,813	2,354,574	3,775,034
<i>Alouatta guariba</i> ^{end}	325	16,737,782	22,148,174	15,429,177	20,087,740
<i>Brachyteles arachnoides</i> ^{end}	29	3,627,027	4,338,333	2,647,880	3,065,255
<i>Brachyteles hypoxanthus</i> ^{end}	18	766,053	1,340,594	324,809	483,571
<i>Bradypus torquatus</i> ^{end}	39	1,251,082	1,587,271	1,375,427	1,626,545
<i>Bradypus variegatus</i>	122	8,989,263	15,045,595	8,517,418	14,370,164
<i>Callicebus coimbrai</i> ^{end}	12	43,507	70,707	36,013	83,752

<i>Callicebus nigrifrons</i>	50	3,370,080	5,375,489	1,328,034	1,944,693
<i>Callicebus personatus</i> ^{end}	21	742,184	1,078,234	722,477	995,661
<i>Callithrix aurita</i> ^{end}	56	2,324,320	3,679,208	1,203,689	1,683,097
<i>Callithrix flaviceps</i> ^{end}	10	202,546	316,275	44,131	47,323
<i>Callithrix geoffroyi</i> ^{end}	40	2,801,299	4,899,758	2,889,493	5,115,003
<i>Callithrix jacchus</i>	51	979,286	1,104,741	994,690	1,137,909
<i>Callithrix kuhlii</i> ^{end}	40	1,147,901	1,605,590	4,163	5,135
<i>Leontopithecus chrysomelas</i> ^{end}	21	694,444	1,183,150	26,854	58,703
<i>Leontopithecus chrysopygus</i> ^{end}	14	429,170	691,530	31,572	37,539
<i>Leontopithecus rosalia</i> ^{end}	17	113,937	216,146	2,776	4,372
<i>Sapajus flavius</i> ^{end}	14	138,223	195,885	26,784	38,997
<i>Sapajus nigritus</i> ^{end}	224	19,156,124	27,780,956	19,572,735	27,968,376
<i>Sapajus xanthosternos</i> ^{end}	10	524,303	879,504	2,706	4,302

TABLE S5 Mean area and the standard deviation in parenthesis (in square kilometers) of potential distribution area of species in the current landscape and current climate scenario in the Brazilian Atlantic Forest (BAF; *Current area*), increase of species potential distribution area in the scenario of regeneration with current climate (*Gain of area with BAF regeneration*), loss of species potential distribution area with climate change in the current landscape scenario (*Loss of area with climate change*), and increase of species potential distribution area with the regeneration of BAF with climate change (*Gain of area in climate change scenario*). n = the number of species for each group.

Species group	Current area	Gain of area with BAF regeneration	Loss of area with climate change	Gain of area in climate change scenario
All species (n = 377)	119,934 (82,535)	46,540 (32,652)	5,170 (15,770)	42,455 (31,603)
All birds (n = 356)	125,057 (81,089)	48,374 (32,200)	5,196 (16,162)	44,237 (31,149)
Endemic birds (n = 182)	109,082 (73,862)	39,450 (28,927)	3,776 (13,251)	35,551 (28,046)
Non-endemic birds (n = 175)	141,391 (85,012)	57,498 (32,890)	6,649 (18,603)	53,117 (31,728)
All mammals (n = 21)	32,117 (53,195)	15,093 (23,371)	4,713 (5,991)	11,905 (22,871)
Endemic mammals (n = 16)	31,687 (58,759)	13,319 (23,557)	3,974 (5,180)	10,602 (23,054)
Non-endemic mammals (n = 5)	33,493 (34,613)	20,768 (24,434)	7,078 (8,348)	16,073 (24,369)

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Capítulo 3 - The Protected Areas network may be insufficient to protect bird diversity in a fragmented tropical hotspot under different climate scenarios

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Research Letters

The Protected Areas network may be insufficient to protect bird diversity in a fragmented tropical hotspot under different climate scenarios



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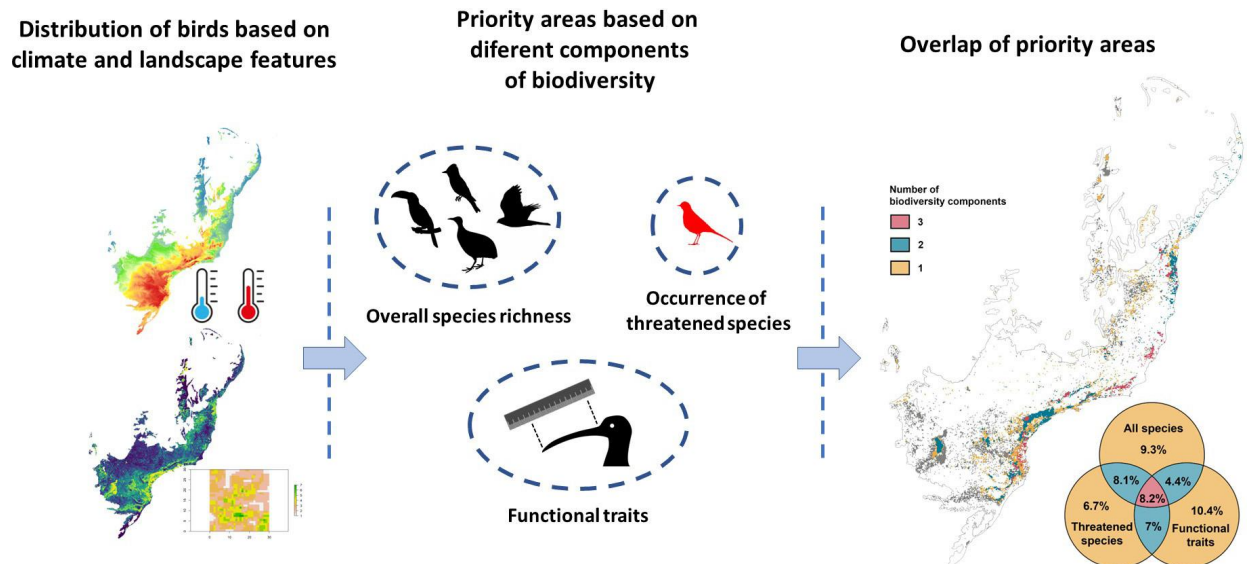
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HIGHLIGHTS

- Overlap of priority areas for bird conservation based on three diversity components is low

- The current Protected Areas network does not cover the most important areas
- Climate change can has a low impact on priority areas for conservation
- We show priority areas where the current Protected Areas network could be expanded

GRAPHICAL ABSTRACT



ABSTRACT

We identified the 30% most-important forest remnants for conservation in the Atlantic Forest domain in South America based on three bird diversity components: (1) overall species occurrence, (2) occurrence of threatened species, and (3) diversity of functional traits. We evaluated the extent of overlap among priority areas using the different approaches and analysed the efficiency of the current Protected Areas network at protecting biodiversity in current and potential future (2040 and 2080) climate scenarios. The overlap among the most important areas is low among the different bird diversity components in all climate scenarios, and few changes were found in priority areas between the current and future scenario. The proportion of species that reached the minimum amount of their distribution areas protected varied from zero to 4% depending on the climate scenario and the species conservation status (threatened or not). Priority

areas based on the occurrence of threatened species were less correlated to areas based on the overall species occurrence than to functional traits in all climate scenarios, suggesting that there might be considerable differences between species composition and their functionalities. Our analyses point out the main regions where resources should be allocated to conservation of birds in a mega-biodiversity region.

Keywords: Atlantic Forest, birds, climate change, functional traits, landscape ecology, species distribution models, Zonation

Introduction

The establishment of Protected Areas (hereafter PA) has long been used as a cornerstone strategy for conserving biodiversity worldwide (Cazalis et al., 2020; Margules and Pressey, 2000; Wauchope et al., 2022). Although the amount of terrestrial PA has increased in recent years, it is well below the minimum requirements for long-term maintenance of biodiversity (~16% of the terrestrial surface are currently protected; UNEP-WCMC and IUCN, 2020). Evidence suggests that the land area that should be preserved to maintain biodiversity and provide important ecosystem services such as water quality regulation and carbon storage may vary from 44 to 70% (Allan et al., 2022; Jung et al., 2021). In view of the need to expand the PA network, one of the targets of the first draft of the post-2020 Global Biodiversity Framework proposes protecting 30% of land surface area by 2030, the “30 by 30 target” (CBD, 2021; Jung et al., 2021). This means there is a need to identify important areas for conservation, especially in tropical environments with high biodiversity and high levels of habitat loss (Barlow et al., 2018; Haddad et al., 2015; Myers et al., 2000).

While prioritizing areas based on overall species occurrence may effectively capture a large portion of biodiversity, focusing on threatened taxa can be relevant in avoiding imminent extinctions (Ricketts et al., 2005). A rather different approach – adopting strategies that consider functional diversity - may benefit ecosystem processes and resilience to environmental changes (Carlucci et al., 2020; Martello et al., 2018; Violle et al., 2007). Although it is possible to use different approaches for prioritizing areas for conservation, some striking incongruences can be found when using different aspects of biodiversity (Belote et al., 2021; Brum et al., 2017; Sibarani et al., 2019; Sobral et al., 2014). In addition, climate change can cause shifts in species distributions and mean that critical areas for conservation may be different in the future (Avalos and Hernández, 2015). These factors make the process of selecting priority areas for conservation challenging.

In this article we used a landscape-based approach to identify important areas for bird conservation in a fragmented tropical biodiversity hotspot, the Atlantic Forest in South America. We focused on forest birds because they are a diverse group that can be used as indicators of habitat quality (Alexandrino et al., 2016). Our aims were to (1) identify, in line with the “30 by 30” target, the 30% most important regions for different components of bird diversity: overall species occurrence, the occurrence of threatened species, and functional traits; (2) evaluate congruences and divergences among the most important areas based on these three components; (3) evaluate how priority regions for conservation may be different under future climate scenarios; and (4) assess the efficiency of the current PA network at preserving bird diversity and identify regions where it could be expanded.

Material and Methods

The Atlantic Forest (AF) is a highly fragmented tropical forest domain in South America (Fig. 1). Distributions of forest birds in the domain were predicted using the Species Distribution Models approach. Characterization of the study area and models used to predict species distribution can be read in the Supplementary Material.

Functional traits

We considered two classes of functional traits of the 368 bird species studied (Table S1): (1) morphological and (2) foraging attributes of species. Five morphological measurements were used: (1) the hand-wing index; (2) tail/wing, and (3) tarsus/wing relationships, which may indicate locomotory characteristics of species (Bregman et al., 2016); (4) bill shape (bill length/width ratio), which can be used as a proxy of dietary traits (Bovo et al., 2018), and (5) body mass (values were log-transformed to reduce the influence of extreme values) which is related to physiology and ecology of birds and the amount of food consumed (Bovo et al., 2018). The hand-wing index was collected from Tobias et al. (2022). The other morphological measurements were extracted from the literature (Rodrigues et al., 2019), specimens deposited in the Museum of Zoology of the University of São Paulo, and individuals measured in the field by the authors. When possible, we measured two males and two females and extracted a mean value to account for species variability. Ecological data were obtained from the literature (Wilman et al., 2014) and represent continuous values of the proportional composition of the food birds consume (invertebrates, vertebrates, fruits, nectar, seed, and other plant material) as well as the foraging strata species occupy (ground, understory, mid to high, canopy or aerial). In line with other authors (Bregman et al., 2016), we then used the mean values of traits for each species to conduct a Principal Component Analysis of

morphological traits and of foraging attributes. This allowed us to characterize the large variation in functional traits in a smaller number of dimensions.

Identification of priority areas in different scenarios

To identify priority areas we used the Zonation algorithm (Moilanen et al., 2014). Based on the distribution of individual features, Zonation produces a hierarchical prioritization rank in which pixel values vary from 0 to 1. We choose the Core Area Zonation (CAZ) as a removal rule. CAZ gives more weight to features with smaller distribution (Moilanen et al., 2014). Only forest patches were considered in the analysis (see a description of the study area and database used in the Supplementary Material).

We used layers of the following three classes of features: (1) overall species occurrence, (2) globally threatened species occurrence (BirdLife International, 2022), and (3) distribution of functional traits of birds. We mapped the functional traits of birds following a similar approach used by Brum et al. (2017) and Sibarani et al. (2019). We first split the first axis of the PCA of morphological data (which accounted for 98% of the variance in morphological data) and the first four axes of foraging data (which explained 81% of variation) into 10% quantiles and then converted into categorical variables (each of the percentile is a category). We then built a matrix of binary variables each species has and multiplied this matrix by the occurrence of species in the study area. The result was distribution maps of each trait so that the same trait can represent a pixel by more than one species (Box S1).

Using the continuous raster ranked by Zonation we identified the 30% most-important pixels as priority areas for conservation according to each biodiversity component. We considered the distribution of species separately for the different climate scenario (current, 2040 and 2080). To evaluate the congruence among priority

areas, we superimposed the 30% most important areas for each feature class in each climate scenario to identify the amount of area that overlap. We also performed a Kendall rank correlation test among the continuous ranks in different periods and for different bird diversity components.

We accounted for the amount of area of each 30% binary priority map with the current PA network considering the IUCN classes I-IV. PA data were downloaded from the protected planet database (<https://www.protectedplanet.net/>). The current PA network covers 12.2% of AF forest patches, and to expand it to 30% we identified the 17.8% top priority forest remnants beyond the already protected ones using the current PA network as an input in the Hierarchical Removal mask in the Zonation software (Moilanen et al., 2014).

To evaluate the current PA's coverage, we accounted for the proportion of species that achieved minimum targets of their distributional ranges covered by reserves. One of the targets, first proposed by Rodrigues et al. (2004), set the minimum amount of the distributional range of a species varying from 10% for species with more than 250.000 km² of distributional range increasing to 100% for species with small geographical ranges (<1.000 km²). A log-linear interpolation is applied to values between these two thresholds (Butchart et al., 2015; Rodrigues et al., 2004). Like other studies (Belote et al., 2021), we also set a target to protect at least 30% of the species distributional range. The efficiency of the priority landscapes was evaluated based on the current and 2080 potential distribution of species, and the best landscapes considered were those based only on the current distribution of species – i.e. to set the targets we did not consider the potential future distribution of species.

Results

The amount of overlap among the 30% most important areas for biodiversity conservation is low in both current and 2080 climate scenarios (Fig. 1 and S1). Most areas where the 30% top priority regions for conserving the three different bird diversity components overlap are represented by large forest patches near the coast (Figs 1 and 4). Bird diversity components with higher overlap are overall species occurrence and occurrence of threatened species (Figs 1 and 2). The Kendall rank correlation test among the continuous raster showing the rank of priority areas according to Zonation was also low among the different bird diversity components in all climate scenarios, and as for the overlap of the 30% most important areas of binary maps, overall species occurrence and occurrence of threatened species are more correlated among each other when compared to areas important according to functional traits (Fig. S1 and S2; Tables S2 to S4).

Although we have identified potential important areas for conservation in 2040, we are only showing figures for the current and the 2080 climate scenarios for practical reasons. In 2040, we estimate around 52% of species will have a reduced distribution, with the mean loss running at 11.5% (S.D. = 18.4%) of current distribution; and 48% of species can increase a mean of 5.6% (S.D. = 5%) in their distributional areas. In the 2080 scenario, 52.4% of species can suffer a mean contraction of 9.7% (S.D. = 19.2%), 47.5% of species can increase their areas in 3.9% (S.D. = 6.5%) and eight species can have no potential distributional areas available, suggesting that they can be extinct (Table S1).

Only 2.9% of the species reached the target of the amount of areas protected proposed by Rodrigues et al. (2004) in the current climate scenario, and 4% in the 2080 climate scenario. Only 0.5% of the species reached at least 30% of their distributional

ranges covered by PA in the current climate scenario and 1.1% for the 2080 climate. For threatened species only, none has reached the minimum distributional range covered by PA in the current nor in the 2080 climate scenario for both targets.

Whereas the current PA network leads to a low percentage of species reaching their distributional ranges, the top 12.2% of the ranked landscape could adequately safeguard from 5.5 to 61% of species depending on the threatened status and climate scenario (Fig. 2). The amount of the top 30% of most important areas covered by reserves is low for all bird diversity components investigated with slight variations in the different climate scenarios (Table 1). Despite that, pixel values of the continuous raster of the Zonation priority rank are higher when comparing regions within and outside PA in the current and 2080 climate scenarios (Figs. S3 and S4). All the differences were significant under the Wilcoxon rank sum test ($p < 0.05$). Fig 3 shows areas in the AF where the current PA network can be expanded.

Discussion

To our knowledge our study is the only one which included landscape metrics when projecting the potential distribution of species to find priority areas for conservation. Similar to others (Kremen et al., 2008; Sibarani et al., 2019), our analysis considered only forest patches. As landscape features influence the persistence of populations of forest birds, considering their effects may provide a more accurate representation of species distribution (Guisan et al., 2017; Pizo and Tonetti, 2020). Large forest patches where bird species richness and endemism are higher presented greater overlap among the three different approaches used (Fig. 1; Pizo and Tonetti, 2020; Ribeiro et al., 2009; Silva and Casteleti, 2003). Other studies that aimed at identifying important areas for the occurrence of plants (Murray-smith et al., 2009;

Zwiener et al., 2017) and amphibians (Trindade-Filho et al., 2012) in the AF region have reported similar results. In spite of that, some small fragments also showed high overlap among the three different prioritization approaches, which reinforces the point that some areas which are not large blocks of native vegetation should be prioritized (Fig. 1; Kremen et al., 2008; Riva and Fahrig, 2022).

A substantial mismatch when comparing priority areas using different approaches was observed in other regions of the globe (Brum et al., 2017; Mazel et al., 2014; Sibarani et al., 2019; Sobral et al., 2014). Interestingly, the occurrence of threatened species was less correlated to the overall species occurrence than to functional traits in all climate scenarios, and when the three approaches were compared, overall species occurrence and functional traits were the less correlated (Fig. S2; Tables S2 to S4). This suggests that there might be considerable differences between species composition and their functionalities (Bełcik et al., 2020). It is expected that areas where functional richness is higher are more resilient to environmental disturbances and can be more relevant in promoting ecosystem processes in fragmented landscapes (e.g. seed dispersal, and pollination; Barros et al., 2019; Bregman et al., 2016).

Prioritization of important areas for conservation under different climate scenarios

Other study also found high overlap when comparing priority areas in current and potential future scenarios based on the distribution of plants, invertebrates and birds in a temperate region (Critchlow et al., 2022). Under the effects of global warming, species are expected to shift their distributions to track changing climatic conditions, which means that they commonly move towards the poles and top of mountains (Guisan et al., 2017). The AF comprises high latitudinal and altitudinal ranges (Muylaert et al., 2018) and species richness is expected to increase in the south of the study area and in

areas where elevation is higher (Figs S5 and S6). Because these shifts on species distributions can be complex (Vanderwal et al., 2013), species are likely to shift their distributions in a non-unidirectional, with some birds can potentially moving to the southern parts of the study region while others to higher altitude regions, which may partially explain the high overlap among priority areas in the current and both future climate scenarios.

Regions pointed to expand the current PA network are also similar in different climate scenarios (Fig. 3). Despite the expansion of PA can be effective to mitigate the negative effects of climate change by, for example, providing habitat for species that may perform movements to other regions (Lehikoinen et al., 2021) and sequester carbon (Melillo et al., 2016), it should be seen as an auxiliary measure to conserve biodiversity in the future. Expanding the extent of the protected area network will clearly be an important adaptation strategy to support the region's biodiversity as the climate changes. Nevertheless, reducing emissions globally must remain the key focus of climate change efforts (Holl and Brancalion, 2020; Tonetti et al., 2022).

Efficiency of the current PA network

Like other studies, our analysis corroborates the assertion that the effectiveness of PA could be enhanced with conservation planning (Brum et al., 2017; Critchlow et al., 2022; Jenkins et al., 2015; Margules and Pressey, 2000; Venter et al., 2018). The percentage of overall or threatened species which reached the minimum amount of their distributional areas covered by the current PA under the two different targets evaluated is lower when compared to the proportion of species that can achieve the thresholds of distributional areas protected by the best 12.2% of landscapes pointed by the Zonation analysis (Fig. 3). The effectiveness of the PA network in covering the distribution of

species has also proven to be limited in other parts of the world (Belote et al., 2021; Rodrigues et al., 2004). Obviously, the importance of the current PA network should not be overshadowed because it does not properly cover the areas pointed as important by our analysis (Cazalis et al., 2020; Develey and Phalan, 2021; Magioli et al., 2021; Tonetti et al., 2017).

Limitations, opportunities, and future perspectives

Because of the notorious limited amount of resources countries expend on biodiversity conservation (specially in developing tropical regions, where biodiversity is high; McClanahan and Rankin, 2016), studies that aim to use holistic approaches to prioritize areas for the creation of new reserves are essential to maximize biodiversity benefits outcomes PA can provide. Even if it can not be possible to protect 30% of the forest remnants in tropical fragmented forests, those regions where there are overlap among all components of biodiversity should be prioritized to expand the current PA network, as those forest patches in the eastern portion of AF (Fig. 3). It is indispensable that not only the expansion of the new PA network be promoted but also the proper management of the reserves be guaranteed. In addition to the investment of resources, creating new effective reserves requires good management and the integration of political, institutional, and governance aspects (Geldmann et al., 2019; Schleicher et al., 2019; Wauchope et al., 2022).

Although forest birds are good environmental quality indicators (Alexandrino et al., 2016), including other taxonomic groups can provide a more comprehensive perspective of biodiversity (Critchlow et al., 2022). In addition, taking social aspects into account are of utmost relevance when expanding PA networks. The displacement of people from their original areas for the establishment of reserves involves ethical and

social justice issues which by themselves should justify that actions like these are not promoted. In addition, the exclusion of local communities and Indigenous peoples from the natural areas they occupy can negatively impact biodiversity by creating conflicts between communities and natural areas (Dawson et al., 2021; Rechciński et al., 2019). Lastly, because there are large areas of unproductive pastures in the AF as in other tropical areas worldwide (Latawiec et al., 2015), there might be few trade-offs between increasing sustainable agricultural production and promoting biodiversity conservation in these regions. Actually, as other tropical forests, the AF shows several restoration opportunities to increase its amount of natural areas (Banks-Leite et al., 2014; Tonetti et al., 2022). Thus, our analyses can contribute to conservation in a mega-biodiversity region by pointing out areas where resources could be better allocated.

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Tables

Table 1 Percentage of the 30% most important areas for the different components of bird diversity covered by protected areas.

Climate scenario	Overall species occurrence	Threatened species occurrence	Functional traits
Current climate	15	13.1	21.1
2040 climate	15.5	14.5	20.7
2080 climate	17	14.3	19.8

Figures

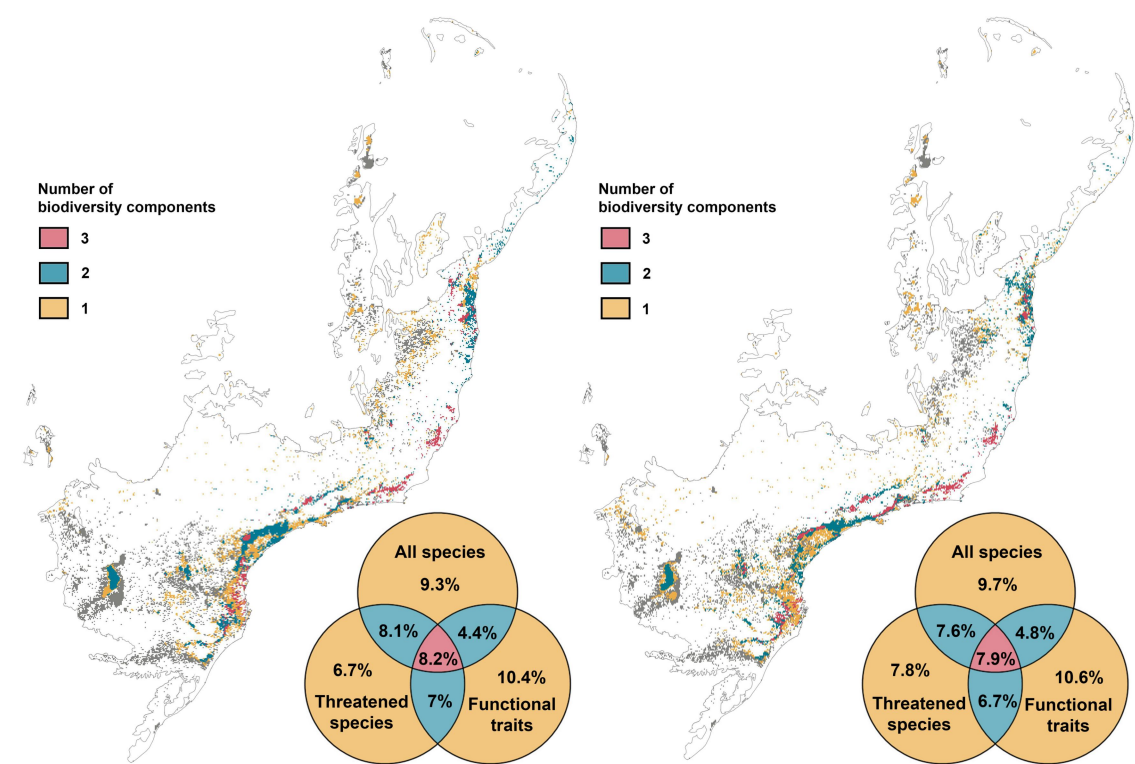


Fig. 1. Overlap among priority areas based on the different bird diversity components analysed (overall species occurrence, occurrence of threatened species and functional traits) in different climate scenarios (current climate scenario in the left panel and 2080 climate scenario in the right panel). The Venn diagrams show the percentage of overlap of the Atlantic Forest patches representing the 30% top priority areas for the different bird diversity components analysed. Colors in the maps show forest patches with different amounts of overlap. Forest patches in which none of the biodiversity components showed importance are in light gray.

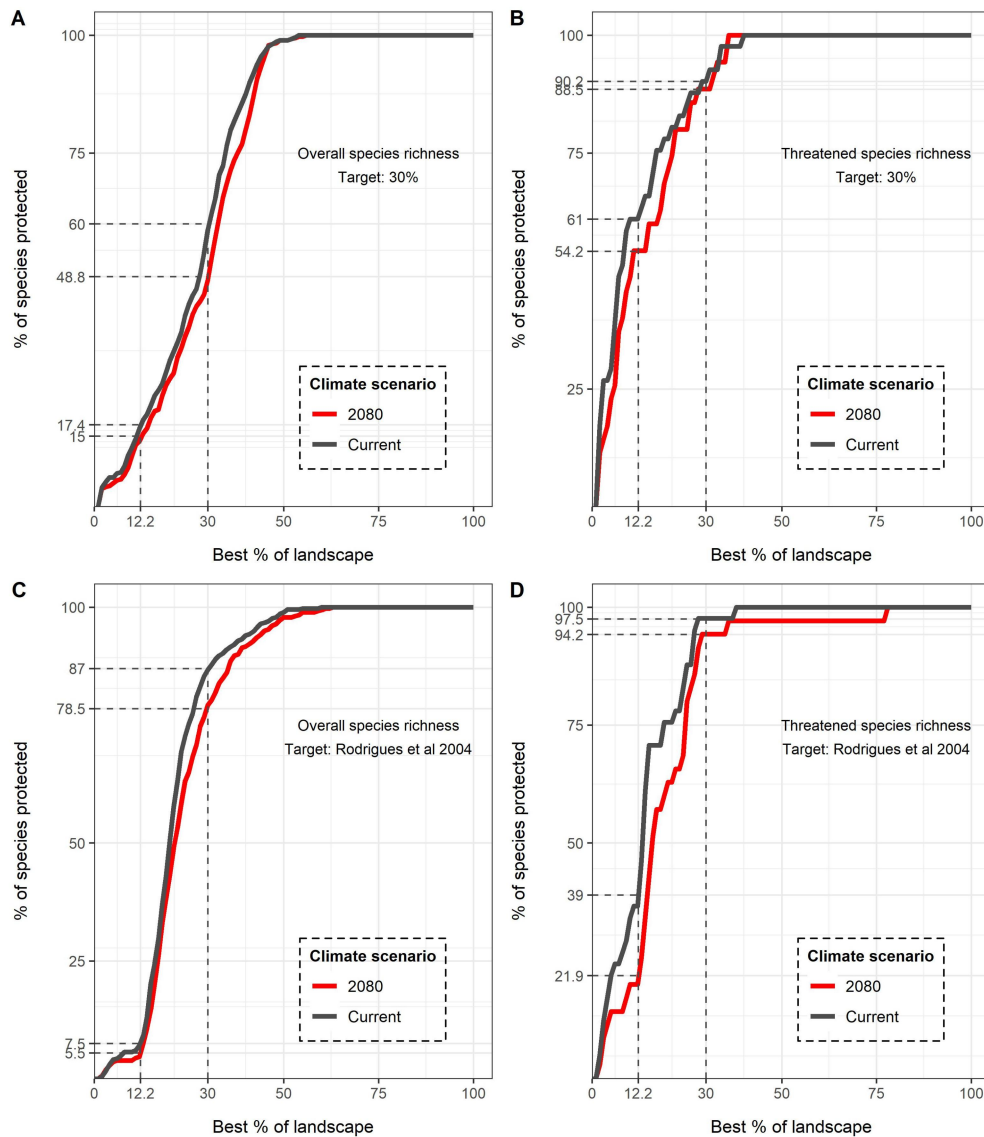


Fig. 2. Percentage of total (left panels) and threatened species (right panels) that might achieve thresholds of their occurrence areas protected according to two targets: (1) at least 30% of distributional areas protected (panels A and B), and (2) the target proposed by Rodrigues et al. (2004; panels C and D) – and considering different thresholds for the continuous Zonation priority rank maps (x-axis). Black lines represent the distribution of species under the current climate scenario and red lines under the 2080 climate scenario. Zonation priority rank landscapes considered are those indicated by the current distribution of species only.

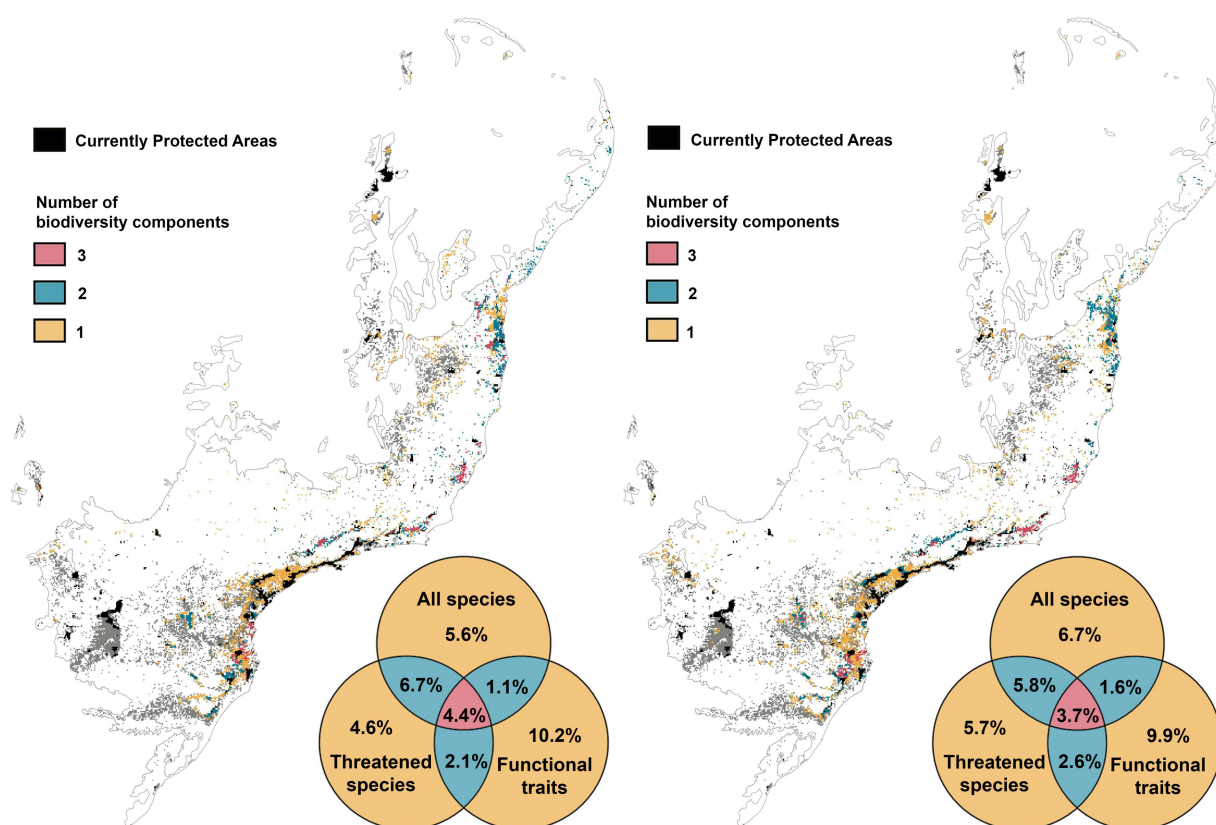


Fig. 3. Overlap among the priority areas that could be protected to increase the current protected areas network to 30% of the AF remnants. Priority areas were identified based on the different bird diversity components analysed (overall species occurrence, occurrence of threatened species and functional traits) in different climate scenarios (current climate scenario in the left panel and 2080 climate scenario in the right panel). The Venn diagrams show the percentage of overlap of the Atlantic Forest patches representing the 17.8% top priority areas for the different components analysed when considering the 12.2% of forest patches already protected (represented in black). Colors in the maps show forest patches with different amounts of overlap. Forest patches in which none of the biodiversity components showed importance are in light gray.

Supplementary Material

Study area

About 2,645 species of Tetrapoda can be found in the Atlantic Forest in South America (AF; Figueiredo et al., 2021). Regarding birds, 1025 species have been registered in the region (Figueiredo et al., 2021; Pizo and Tonetti, 2020; Vale et al., 2018). Despite the high number of species and endemism, after centuries of devastation, only 28% of its native vegetation currently persists (Rezende et al., 2018), and most of the forest remnants are small and isolated from each other (Ribeiro et al., 2009). As many other tropical forest domains, AF is a priority region for biodiversity conservation worldwide (Mittermeier and da Fonseca, 2021; Myers et al., 2000). Due to its fragmentation, it may be considered an appropriate region to be used as a model to identify important areas for conservation in anthropic landscapes. We opted to use a comprehensive delimitation among the different boundaries of AF (Muylaert et al., 2018). Forest remnants were represented by a 30-m pixel raster processed by the Spatial Ecology and Conservation Lab at the São Paulo State University, Brazil (LEEC – UNESP; Ribeiro et al. in prep.) in an association with Agroicone (<https://www.agroicone.com.br/>).

Species occurrences

Species occurrence layers were generated based on the Species Distribution Models (SDM) approach. SDM comprises correlative methods that predict suitable areas for the occurrence of species based on environmental layers and geographic locations (Guisan et al., 2017; Peterson et al., 2011). For each species, our models were based on two classes of predictor variables – (1) climate and (2) landscape. To better

represent species distributions, we only considered areas of potential distribution those that were suitable under both classes. Climatic variables usually defines species occurrence at large biogeographic scales, while the landscape influences the distribution regionally (Peterson et al., 2011; Sobral-Souza et al., 2021).

For the climatic models we considered the 19 bioclimatic variables from the WordClim 2.1 database (<https://www.worldclim.org/data/worldclim21.html>). These variables are derived from temperature and precipitation data collected during the years of 1970 and 2000 in weather stations distributed around the world and were used to represent the current climate scenario (Fick and Hijmans, 2017). To avoid correlation among the 19 variables, we performed a VIF (threshold = 5), and a Pearson correlation test (threshold = 0.7) considering the region of study and eliminated those with values higher than thresholds. After removing correlated variables, we used the following: BIO 02, BIO 03, BIO 08, BIO 09, BIO 13, BIO 18 and BIO 19.

To predict suitable areas for species occurrence according to landscape, we calculated the following variables based on our 30-m resolution raster with the aid of the LSMetrics package in the GRASS GIS environment (https://github.com/LEEClab/LS_METRICS/wiki; Niebuhr, 2018): (1) edge amount considering pixels less than 60 m from edge and for each pixel a mean value around a 1.000 m moving window was calculated (Hagen-Zanker, 2016), (2) area of patches functionally connected considering that species may cross a 60 m-distance in matrix, (3) forest percentage (moving window = 1.000 m), and (4) patch area. These distances for edge depth, moving window, and gap crossing were chosen based on the literature (Graham and Socha, 2019; Uezu et al., 2005). We also considered elevation in association to the landscape variables as it proved to be important to predict species distributions (Guisan et al., 2017; Peterson et al., 2011). We applied the same

correlation tests used on climatic layers (VIF [threshold = 5] and Pearson correlation [threshold = 0.7]) and the five variables were retained. After calculating landscapes variables, to use it in SDM models cell size was resampled to the same resolution (2.5 minutes) of climatic variables using the nearest-neighbor method.

Spatial occurrence of species were obtained from the following databases: Global Biodiversity Information Facility (GBIF; <https://www.gbif.org>); iNaturalist (<https://www.inaturalist.org>); VertNet (<http://vertnet.org>); eBird (<https://ebird.org>); and Integrated Digitized Biocollections (iDigBio; <https://www.idigbio.org>) considering taxonomical synonyms with the aid of the spocc R package (Chamberlain, 2020). We excluded occurrence data recorded before 1980 to avoid mismatch between species presence and landscape features (Ribeiro et al., 2009). We only considered species that have forest as major habitat type according to IUCN (<https://www.iucnredlist.org>).

We avoided spatial correlation of species occurrences by rarifying points keeping the distance of at least 10 km among each other with the aid of the package spThin in R (Aiello-Lammens et al., 2015; Guisan et al., 2017; Peterson et al., 2011). Species occurrences that are less than 100 m from biodiversity institutions, urban areas, state capitals and with zero values in latitude and longitude decimals were removed to avoid potential location errors with the aid of the package CoordinateCleaner in R (Zizka et al., 2019). We also plotted species occurrence and searched for potential outliers and records that did not correspond to the expected distribution of the species based on our knowledge and on the WikiaAves (<https://www.wikiaves.com/>) database. After these filtering procedures, we only predicted the distribution of species with at least 10 occurrence points (Guisan et al., 2017; Peterson et al., 2011).

For each species we used a background region based on a minimum convex polygon of the occurrence's points (comprising the geographical extremes occurrences)

summed by a buffer of two coordinates degrees (~ 220 km). We then cropped variables for each species using the convex hull and sampled 5,000 background points. We considered these restricted backgrounds for each species more adequate than using the entire BAF for all species, what could result in model overfitting and overestimate model evaluation (Barve et al., 2011; Guisan et al., 2017; Peterson et al., 2011).

We employed the stack distribution models approach combining the prediction of the following algorithms of presence-only data: bioclim, domain, random forest, and maxent. For each species we ran 10 replicates of each algorithm splitting 70% of occurrence points to training the models and 30% for evaluation in each run using the bootstrap approach. This resulted in 40 models per species for climate variables (four algorithms, 10 replicates) and 40 models per species for landscape variables. The ensembles projections of the 10 replicates were performed using a weighted mean of the different individual models based in a threshold that maximizes specificity + sensitivity considering the True Skill Statistic test (Allouche et al., 2006). We used the lowest presence-threshold in the raster of continuous values that resulted from the ensemble of the 40 individuals models to create binary maps for each species (presence / absence; Liu et al., 2016). Then, we combined maps of climatic and landscape suitability and only considered pixels where both landscape and climate were suitable for species occurrence. Models were run in the sdm package in the R environment (Naimi and Araújo, 2016).

After training models for the current scenarios of climate and landscape, we projected the SDM in both current and future climate scenarios assuming the current AF forest patches configuration. We projected the potential distribution of species for the year of 2040 and 2080 using intermediate scenarios of climate change (SSP 370). As scenarios that predict low effects of climate change and those that predict very intense

effects are unlikely to occur (Hausfather and Peters, 2020), we project the distribution of species in an intermediate climate change scenarios (the SSP 370; IPCC, 2022). We also did not project the distribution of species in the temporally more distant scenario (2100), as it can be less accurate (Hausfather and Peters, 2020). We averaged the predicted future distribution of species using three different general circulation models (MIROC-ES2L, GFDL-ESM4, and MRI-ESM2). These models were selected because are less related to each other (Sanderson et al., 2015).

Tables

Table S1. Number of occurrence points and threaten category of the studied bird species. ^{end} = species endemic to the Atlantic Forest, PE = species that might be possibly extinct in the 2080 climate scenario for having no potential distribution areas available in the future.

Species	Number of occurrence points	Globally threatened (BirdLife 2020)
<i>Aburria jacutinga</i> ^{end}	94	EN
<i>Accipiter bicolor</i>	182	
<i>Accipiter poliogaster</i>	54	
<i>Accipiter striatus</i>	24	
<i>Accipiter superciliosus</i>	53	
<i>Acrobatornis fonsecai</i> ^{end}	18	VU
<i>Amadonastur lacernulatus</i> ^{end}	188	VU
<i>Amazona brasiliensis</i> ^{end}	22	
<i>Amazona farinosa</i>	50	
<i>Amazona pretrei</i> ^{end}	52	VU
<i>Amazona rhodocorytha</i> ^{end}	97	VU
<i>Amazona vinacea</i> ^{end}	210	EN
<i>Anabacerthia amaurotis</i> ^{end}	135	
<i>Anabacerthia lichtensteini</i> ^{end}	277	
<i>Anabazenops fuscus</i> ^{end}	197	
<i>Antilophia galeata</i>	243	

<i>Antrostomus rufus</i>	186	
<i>Antrostomus sericocaudatus</i>	75	
<i>Arremon semitorquatus</i> ^{end}	166	
<i>Asio stygius</i>	109	
<i>Attila rufus</i> ^{end}	412	
<i>Automolus lammi</i> ^{end}	14	EN
<i>Automolus leucophthalmus</i> ^{end}	635	
<i>Baryphthengus ruficapillus</i> ^{end}	468	
<i>Batara cinerea</i>	310	
<i>Biatas nigropectus</i> ^{end}	85	VU
<i>Brotogeris chiriri</i>	719	
<i>Brotogeris tirica</i> ^{end}	549	
<i>Cacicus cela</i>	78	
<i>Campephilus robustus</i> ^{end}	470	
<i>Campylorhamphus falcularius</i> ^{end}	260	
<i>Campylorhamphus trochilirostris</i>	75	
<i>Capsiempis flaveola</i>	483	
<i>Carpornis cucullata</i> ^{end}	219	
<i>Carpornis melanocephala</i> ^{end}	84	VU
<i>Caryothraustes canadensis</i>	96	
<i>Castanozoster thoracicus</i> ^{end}	53	
<i>Celeus flavescens</i>	610	
<i>Celeus galeatus</i> ^{end}	79	VU
<i>Ceratopipra rubrocapilla</i>	110	
<i>Cercomacra brasiliana</i> ^{end}	46	

<i>Cercomacra laeta</i>	26	
<i>Chamaeza campanisona</i>	451	
<i>Chamaeza meruloides</i> ^{end}	129	
<i>Chamaeza ruficauda</i> ^{end}	122	
<i>Chiroxiphia caudata</i> ^{end}	1067	
<i>Chiroxiphia pareola</i>	121	
<i>Chlorophanes spiza</i>	144	
<i>Chlorophonia cyanea</i>	379	
<i>Chlorostilbon notatus</i>	97	
<i>Cichlocolaptes leucophrus</i> ^{end}	162	
<i>Claravis pretiosa</i>	239	
<i>Clibanornis dendrocolaptoides</i> ^{end}	104	
<i>Clytolaema rubricauda</i> ^{end}	237	
<i>Coccyzus euleri</i>	83	
<i>Colibri serrirostris</i>	372	
<i>Conopias trivirgatus</i>	192	
<i>Conopophaga cearae</i> ^{end}	23	
<i>Conopophaga lineata</i>	867	
<i>Conopophaga melanops</i> ^{end}	280	
<i>Contopus cinereus</i>	378	
<i>Corythopsis delalandi</i>	404	
<i>Cotinga maculata</i> ^{end}	10	CR
<i>Cranioleuca obsoleta</i> ^{end}	340	
<i>Cranioleuca pallida</i> ^{end}	332	
<i>Crax blumenbachii</i> ^{end}	15	EN

<i>Crypturellus noctivagus</i>	108	
<i>Crypturellus obsoletus</i>	817	
<i>Crypturellus soui</i>	100	
<i>Crypturellus undulatus</i>	132	
<i>Crypturellus variegatus</i>	39	
<i>Cyanerpes cyaneus</i>	144	
<i>Cyanocorax caeruleus</i> ^{end}	344	
<i>Dacnis nigripes</i> ^{end}	85	
<i>Dendrocincla taunayi</i> ^{end, PE}	11	
<i>Dendrocincla turdina</i> ^{end}	397	
<i>Dendrocolaptes platyrostris</i>	682	
<i>Dendroplex picus</i>	114	
<i>Dixiphia pipra</i>	48	
<i>Dromococcyx pavoninus</i>	233	
<i>Drymophila ferruginea</i> ^{end}	291	
<i>Drymophila genei</i> ^{end}	51	
<i>Drymophila malura</i> ^{end}	373	
<i>Drymophila ochropyga</i> ^{end}	192	
<i>Drymophila rubricollis</i> ^{end}	174	
<i>Drymophila squamata</i> ^{end}	179	
<i>Dysithamnus mentalis</i>	940	
<i>Dysithamnus plumbeus</i> ^{end}	20	VU
<i>Dysithamnus stictothorax</i> ^{end}	229	
<i>Dysithamnus xanthopterus</i> ^{end}	76	
<i>Elaenia chilensis</i>	14	

<i>Eleoscytalopus indigoticus</i> ^{end}	241	
<i>Eucometis penicillata</i>	115	
<i>Euphonia chalybea</i> ^{end}	269	
<i>Euphonia pectoralis</i> ^{end}	540	
<i>Florisuga fusca</i>	734	
<i>Formicarius colma</i>	205	
<i>Formicivora iheringi</i>	23	
<i>Formicivora serrana</i> ^{end}	85	
<i>Forpus xanthopterygius</i>	1250	
<i>Galbula ruficauda</i>	504	
<i>Geotrygon montana</i>	384	
<i>Glaucidium brasilianum</i>	33	
<i>Glaucidium minutissimum</i> ^{end}	122	
<i>Glaucis dohrnii</i> ^{end}	18	EN
<i>Glaucis hirsutus</i>	162	
<i>Grallaria varia</i>	280	
<i>Habia rubica</i>	600	
<i>Haplospiza unicolor</i> ^{end}	336	
<i>Harpagus bidentatus</i>	20	
<i>Harpagus diodon</i>	341	
<i>Heliobletus contaminatus</i> ^{end}	269	
<i>Heliomaster furcifer</i>	59	
<i>Heliothryx auritus</i>	117	
<i>Hemithraupis flavicollis</i>	112	
<i>Hemithraupis guira</i>	518	

<i>Hemithraupis ruficapilla</i> ^{end}	670	
<i>Hemitriccus diops</i> ^{end}	286	
<i>Hemitriccus furcatus</i> ^{end}	39	VU
<i>Hemitriccus griseipectus</i>	43	
<i>Hemitriccus kaempferi</i> ^{end}	18	VU
<i>Hemitriccus margaritaceiventer</i>	333	
<i>Hemitriccus mirandae</i> ^{end, PE}	11	VU
<i>Hemitriccus nidipendulus</i> ^{end}	305	
<i>Hemitriccus obsoletus</i> ^{end}	121	
<i>Hemitriccus orbitatus</i> ^{end}	209	
<i>Hemitriccus striaticollis</i>	46	
<i>Herpsilochmus atricapillus</i>	300	
<i>Herpsilochmus pileatus</i> ^{end}	39	VU
<i>Herpsilochmus rufimarginatus</i>	502	
<i>Hylocharis sapphirina</i>	59	
<i>Hylopezus nattereri</i> ^{end}	169	
<i>Hylopezus ochroleucus</i>	35	
<i>Hylophilus amaurocephalus</i>	276	
<i>Hylophilus poicilotis</i> ^{end}	504	
<i>Hylophilus thoracicus</i>	108	
<i>Hypoedaleus guttatus</i> ^{end}	449	
<i>Ilicura militaris</i> ^{end}	310	
<i>Iodopleura pipra</i> ^{end}	59	EN
<i>Jacamaralcyon tridactyla</i> ^{end}	45	
<i>Laniisoma elegans</i> ^{end}	24	

<i>Laniocera hypopyrra</i>	10	
<i>Lathrotriccus euleri</i>	1014	
<i>Legatus leucophaeus</i>	655	
<i>Lepidocolaptes falcinellus</i> ^{end}	418	
<i>Lepidocolaptes squamatus</i> ^{end}	219	
<i>Leptasthenura setaria</i> ^{end}	328	
<i>Leptasthenura striolata</i> ^{end}	63	
<i>Leptodon cayanensis</i>	444	
<i>Leptodon forbesi</i> ^{end}	29	EN
<i>Leptopogon amaurocephalus</i>	1086	
<i>Leptotila rufaxilla</i>	843	
<i>Leptotila verreauxi</i>	53	
<i>Lipaugus lanioides</i> ^{end}	81	
<i>Lipaugus vociferans</i>	40	
<i>Lochmias nematura</i>	766	
<i>Lophornis chalybeus</i> ^{end}	85	
<i>Machaeropterus regulus</i> ^{end}	52	
<i>Mackenziaena leachii</i> ^{end}	427	
<i>Mackenziaena severa</i> ^{end}	430	
<i>Macropsalis forcipata</i> ^{end}	98	
<i>Malacoptila striata</i> ^{end}	373	
<i>Manacus manacus</i>	617	
<i>Megascops atricapilla</i> ^{end}	185	
<i>Megascops sanctaecatarinae</i> ^{end}	127	
<i>Melanerpes flavifrons</i> ^{end}	453	

<i>Merulaxis ater</i> ^{end}	82	
<i>Micrastur ruficollis</i>	382	
<i>Micrastur semitorquatus</i>	467	
<i>Mionectes oleagineus</i>	69	
<i>Mionectes rufiventris</i> ^{end}	515	
<i>Momotus momota</i>	78	
<i>Monasa morphoeus</i>	19	
<i>Monasa nigrifrons</i>	35	
<i>Myiarchus swainsoni</i>	942	
<i>Myiobius atricaudus</i>	112	
<i>Myiobius barbatus</i>	156	
<i>Myiopagis caniceps</i>	569	
<i>Myiopagis gaimardii</i>	31	
<i>Myiopagis viridicata</i>	401	
<i>Myiornis auricularis</i> ^{end}	42	
<i>Myiothlypis flaveola</i>	426	
<i>Myiothlypis leucoblephara</i>	936	
<i>Myiothlypis rivularis</i>	217	
<i>Myrmoderus loricatus</i> ^{end}	87	
<i>Myrmoderus ruficauda</i> ^{end}	26	EN
<i>Myrmoderus squamosus</i> ^{end}	216	
<i>Myrmotherula axillaris</i> ^{end}	178	
<i>Myrmotherula minor</i> ^{end}	46	VU
<i>Myrmotherula unicolor</i> ^{end}	155	
<i>Myrmotherula urosticta</i> ^{end}	39	VU

<i>Nemosia pileata</i>	719	
<i>Neopelma aurifrons</i> ^{end}	19	VU
<i>Neopelma chrysolophum</i> ^{end}	104	
<i>Nonnula rubecula</i>	141	
<i>Notharchus swainsoni</i> ^{end}	139	
<i>Nyctibius aethereus</i>	32	
<i>Nyctibius grandis</i>	22	
<i>Nyctiphrynus ocellatus</i>	152	
<i>Odontophorus capueira</i> ^{end}	358	
<i>Onychorhynchus swainsonii</i>	37	
<i>Orchesticus abeillei</i> ^{end}	99	
<i>Ortalis araucuan</i> ^{end}	115	
<i>Ortalis guttata</i>	265	
<i>Ortalis squamata</i> ^{end}	140	
<i>Orthogonys chloricterus</i> ^{end}	146	
<i>Oxyruncus cristatus</i>	209	
<i>Pachyramphus castaneus</i>	609	
<i>Pachyramphus marginatus</i>	117	
<i>Pachyramphus polychopterus</i>	911	
<i>Pachyramphus validus</i>	741	
<i>Pachyramphus viridis</i>	460	
<i>Panyptila cayennensis</i>	54	
<i>Patagioenas cayennensis</i>	27	
<i>Patagioenas plumbea</i>	399	
<i>Penelope obscura</i>	870	

<i>Penelope superciliaris</i>	446	
<i>Phaethornis eurynome</i> ^{end}	535	
<i>Phaethornis idaliae</i> ^{end}	49	
<i>Phaethornis pretrei</i>	955	
<i>Phaethornis ruber</i>	268	
<i>Phaethornis squalidus</i> ^{end}	146	
<i>Pheugopedius genibarbis</i>	276	
<i>Phibalura flavirostris</i> ^{end}	112	
<i>Philydor atricapillus</i> ^{end}	298	
<i>Philydor rufum</i>	605	
<i>Phyllomyias fasciatus</i>	655	
<i>Phyllomyias griseocapilla</i> ^{end}	207	
<i>Phyllomyias virescens</i> ^{end}	300	
<i>Phylloscartes beckeri</i> ^{end}	13	EN
<i>Phylloscartes ceciliae</i> ^{end, PE}	12	CR
<i>Phylloscartes difficilis</i> ^{end}	74	
<i>Phylloscartes eximius</i> ^{end}	134	
<i>Phylloscartes kronei</i> ^{end}	87	
<i>Phylloscartes oustaleti</i> ^{end}	95	
<i>Phylloscartes paulista</i> ^{end}	64	
<i>Phylloscartes sylviolus</i> ^{end}	83	
<i>Phylloscartes ventralis</i>	591	
<i>Piculus aurulentus</i> ^{end}	417	
<i>Piculus flavigula</i>	166	
<i>Picumnus exilis</i> ^{end}	51	

<i>Picumnus fulvescens</i>	23	
<i>Picumnus limae</i>	18	
<i>Picumnus nebulosus</i>	130	
<i>Picumnus pernambucensis</i> ^{end}	37	
<i>Picumnus temminckii</i> ^{end}	551	
<i>Pionopsitta pileata</i> ^{end}	414	
<i>Pionus maximiliani</i>	1146	
<i>Pipra fasciicauda</i>	126	
<i>Pipraeidea bonariensis</i>	335	
<i>Pipraeidea melanonota</i>	681	
<i>Piprites chloris</i>	144	
<i>Piprites pileata</i> ^{end}	59	
<i>Platyrinchus leucoryphus</i> ^{end}	57	VU
<i>Platyrinchus mystaceus</i>	804	
<i>Poecilotriccus fumifrons</i>	42	
<i>Poecilotriccus plumbeiceps</i>	852	
<i>Polioptila lactea</i> ^{end}	94	
<i>Primolius maracana</i>	395	
<i>Procnias nudicollis</i> ^{end}	459	
<i>Pseudastur polionotus</i> ^{end}	176	
<i>Psilorhamphus guttatus</i> ^{end}	167	
<i>Pteroglossus aracari</i>	190	
<i>Pteroglossus bailloni</i> ^{end}	225	
<i>Pteroglossus inscriptus</i>	13	
<i>Pulsatrix koeniswaldiana</i> ^{end}	320	

<i>Pulsatrix perspicillata</i>	59	
<i>Pyriglena atra</i> ^{end, PE}	14	EN
<i>Pyriglena leucoptera</i> ^{end}	765	
<i>Pyroderus scutatus</i>	332	
<i>Pyrrhura cruentata</i> ^{end}	45	VU
<i>Pyrrhura frontalis</i> ^{end}	959	
<i>Pyrrhura leucotis</i> ^{end}	51	VU
<i>Ramphastos dicolorus</i> ^{end}	798	
<i>Ramphastos vitellinus</i>	303	
<i>Ramphocaenus melanurus</i>	190	
<i>Ramphocelus bresilius</i> ^{end}	439	
<i>Ramphodon naevius</i> ^{end}	192	
<i>Ramphotrigon megacephalum</i>	109	
<i>Rhopias gularis</i> ^{end}	224	
<i>Rhynchocyclus olivaceus</i>	39	
<i>Saltator fuliginosus</i> ^{end}	270	
<i>Saltator maximus</i>	12	
<i>Saltator similis</i>	1365	
<i>Saltatricula atricollis</i>	113	
<i>Schiffornis turdina</i>	64	
<i>Schiffornis virescens</i> ^{end}	690	
<i>Schistochlamys melanopis</i>	106	
<i>Sclerurus scansor</i> ^{end}	391	
<i>Scytalopus iraiensis</i> ^{end}	28	EN
<i>Scytalopus pachecoi</i> ^{end}	64	

<i>Scytalopus petrophilus</i> ^{end}	43	
<i>Scytalopus speluncae</i> ^{end}	188	
<i>Selenidera maculirostris</i> ^{end}	266	
<i>Sittasomus griseicapillus</i>	1112	
<i>Spizaetus melanoleucus</i>	204	
<i>Spizaetus ornatus</i>	95	
<i>Spizaetus tyrannus</i>	389	
<i>Sporophila falcirostris</i> ^{end}	122	VU
<i>Sporophila frontalis</i> ^{end}	152	VU
<i>Stephanophorus diadematus</i>	416	
<i>Strix huhula</i>	67	
<i>Strix hylophila</i> ^{end}	211	
<i>Strix virgata</i>	223	
<i>Synallaxis cinerascens</i>	492	
<i>Synallaxis cinerea</i> ^{end}	21	
<i>Synallaxis hypospodia</i>	28	
<i>Synallaxis infuscata</i> ^{end}	23	EN
<i>Synallaxis ruficapilla</i>	960	
<i>Synallaxis scutata</i>	51	
<i>Syndactyla rufosuperciliata</i>	525	
<i>Tachyphonus coronatus</i> ^{end}	1305	
<i>Tachyphonus cristatus</i>	279	
<i>Tangara brasiliensis</i> ^{end}	77	
<i>Tangara cyanocephala</i> ^{end}	325	
<i>Tangara cyanoventris</i> ^{end}	297	

<i>Tangara desmaresti</i> ^{end}	262	
<i>Tangara fastuosa</i> ^{end, PE}	28	VU
<i>Tangara preciosa</i>	347	
<i>Tangara seledon</i> ^{end}	495	
<i>Taraba major</i>	419	
<i>Terenura maculata</i> ^{end}	247	
<i>Terenura sicki</i> ^{end, PE}	13	CR
<i>Tersina viridis</i>	110	
<i>Thalurania glaucopis</i> ^{end}	966	
<i>Thalurania watertonii</i> ^{end, PE}	12	EN
<i>Thamnomanes caesius</i>	34	
<i>Thamnophilus aethiops</i>	14	
<i>Thamnophilus ambiguus</i> ^{end}	219	
<i>Thamnophilus caerulescens</i>	1462	
<i>Thamnophilus doliatus</i>	37	
<i>Thamnophilus palliatus</i>	206	
<i>Thamnophilus pelzelni</i>	220	
<i>Thamnophilus ruficapillus</i>	594	
<i>Thamnophilus torquatus</i>	81	
<i>Thraupis cyanoptera</i> ^{end}	353	
<i>Thraupis ornata</i> ^{end}	373	
<i>Thripophaga macroura</i> ^{end}	25	VU
<i>Tijuca atra</i> ^{end}	49	
<i>Tinamus solitarius</i> ^{end}	256	
<i>Tityra cayana</i>	469	

<i>Tityra inquisitor</i>	321	
<i>Todirostrum poliocephalum</i> ^{end}	689	
<i>Tolmomyias poliocephalus</i>	55	
<i>Tolmomyias sulphurescens</i>	61	
<i>Touit melanonotus</i> ^{end}	69	VU
<i>Touit surdus</i> ^{end}	67	VU
<i>Trichothraupis melanops</i>	861	
<i>Triclaria malachitacea</i> ^{end}	127	
<i>Trogon curucui</i>	79	
<i>Trogon rufus</i>	384	
<i>Trogon surrucura</i>	1111	
<i>Trogon viridis</i>	282	
<i>Turdus albicollis</i>	914	
<i>Turdus flavipes</i>	503	
<i>Turdus fumigatus</i>	23	
<i>Veniliornis affinis</i>	15	
<i>Veniliornis maculifrons</i> ^{end}	25	
<i>Veniliornis spilogaster</i>	84	
<i>Vireo chivi</i>	1297	
<i>Xenops minutus</i>	331	
<i>Xenops rutilans</i>	797	
<i>Xiphocolaptes albicollis</i>	429	
<i>Xiphocolaptes falcistrostris</i>	13	
<i>Xipholena atropurpurea</i> ^{end}	37	VU
<i>Xiphorhynchus atlanticus</i> ^{end, PE}	11	VU

<i>Xiphorhynchus fuscus</i> ^{end}	754
<i>Xiphorhynchus guttatus</i>	55

Table S2. Kendall rank correlation tests for the different bird diversity components in the current climate scenario.

Climate scenario	Overall spp curr	Threatened spp curr	Func traits curr
Overall spp curr	1		
Threatened spp curr	0.35	1	
Functional traits curr	0.16	0.41	1

Table S3. Kendall rank correlation tests for the different bird diversity components in the 2040 climate scenario.

Climate scenario	Overall spp 2040	Threatened spp 2040	Func traits 2040
Overall spp 2040	1		
Threatened spp 2040	0.37	1	
Func traits 2040	0.15	0.41	1

Table S4. Kendall rank correlation tests for the different bird diversity components in the 2080 climate scenario.

Climate scenario	Overall spp 2080	Threatened spp 2080	Func traits 2080
Overall spp 2080	1		
Threatened spp 2080	0.36	1	
Func traits 2040	0.17	0.38	1

Figures

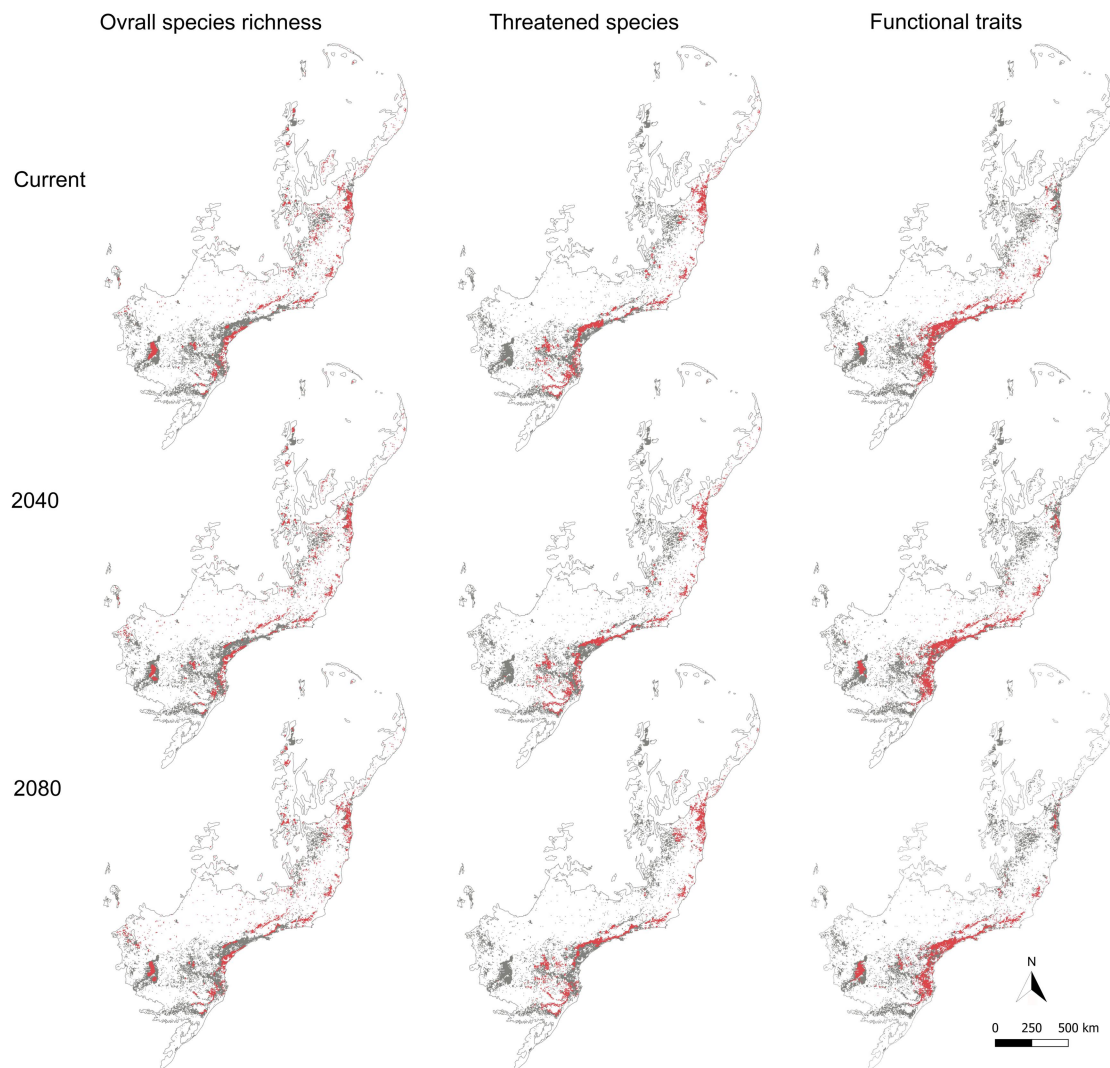


Figure S1. Red regions indicate the 30% most important forest areas under the different bird diversity component (columns) and in different climate scenarios (rows) according to the Zonation prioritization analysis. The remaining 70% of forest patches are in gray.

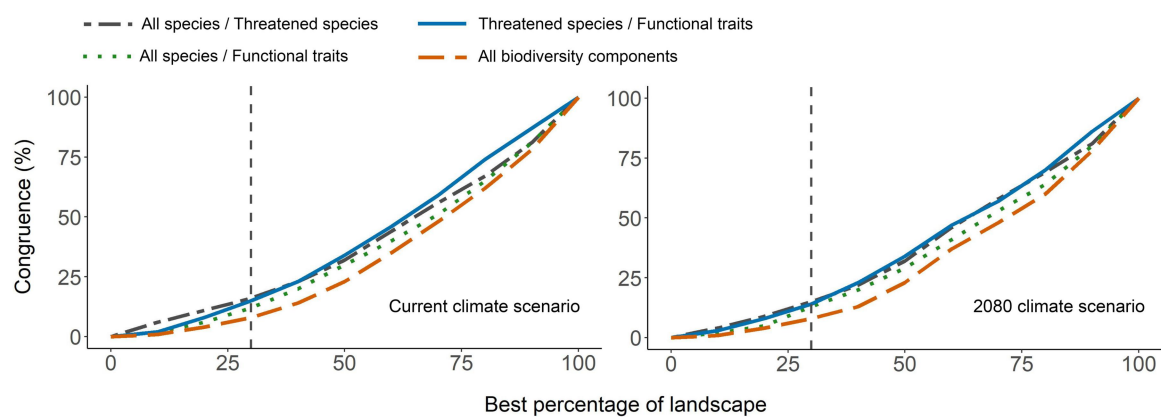


Figure S2. Pairwise and overall congruence of the different bird diversity components analysed in a continuous rank of landscape importance according to zonation. The top 30% most important landscapes for each bird diversity component are indicated by the dashed line in the x-axis.

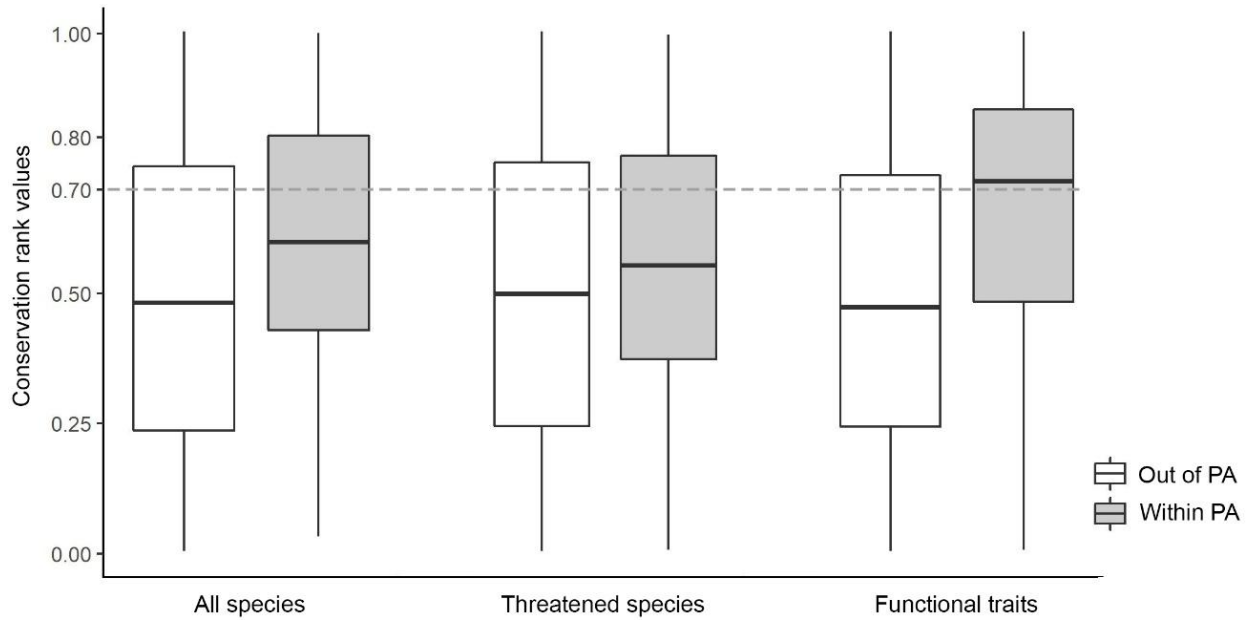


Figure S3. Pairwise differences in current climate scenario of the values of priority rank values between regions within (gray plots) and out (white plots) of protected areas for the current climate scenario. Values above the gray dashed line are from pixels within the top 30% most important areas, showing that for most bird diversity components analysed the median values are below this threshold.

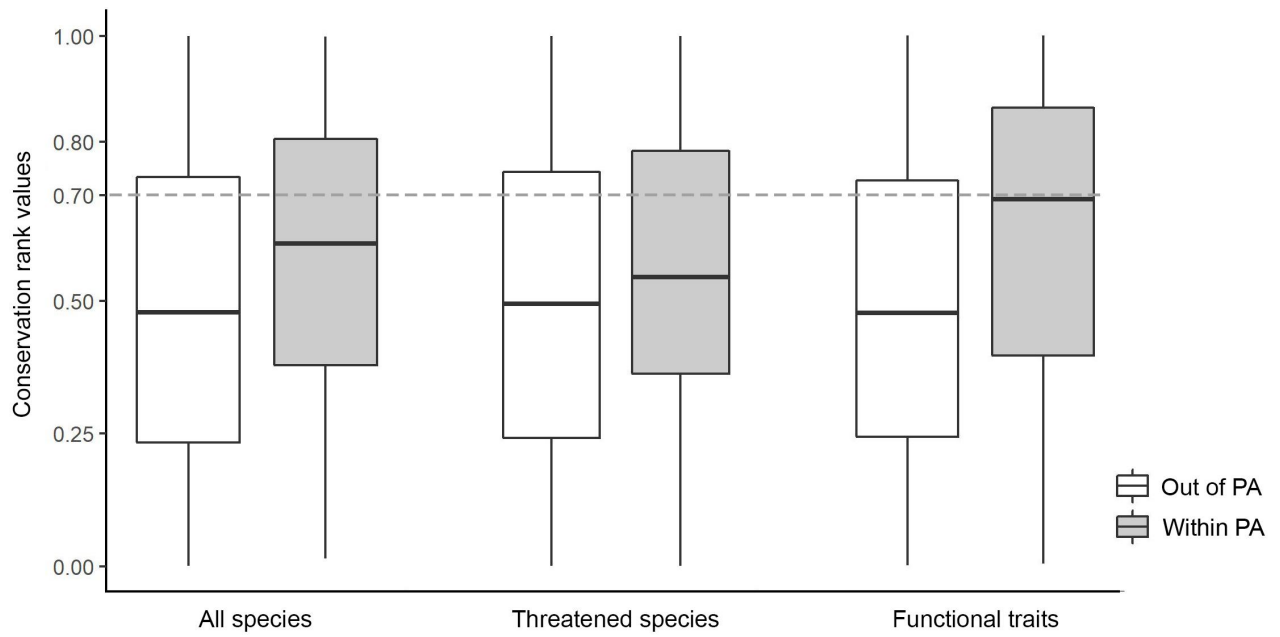


Figure S4. Pairwise differences in 2080 climate scenario of the values of priority rank values between regions within (gray plots) and out (white plots) of protected areas for the current climate scenario. Values above the gray dashed line are from pixels within the top 30% most important areas, showing that for all bird diversity components analysed the median values are below this threshold.

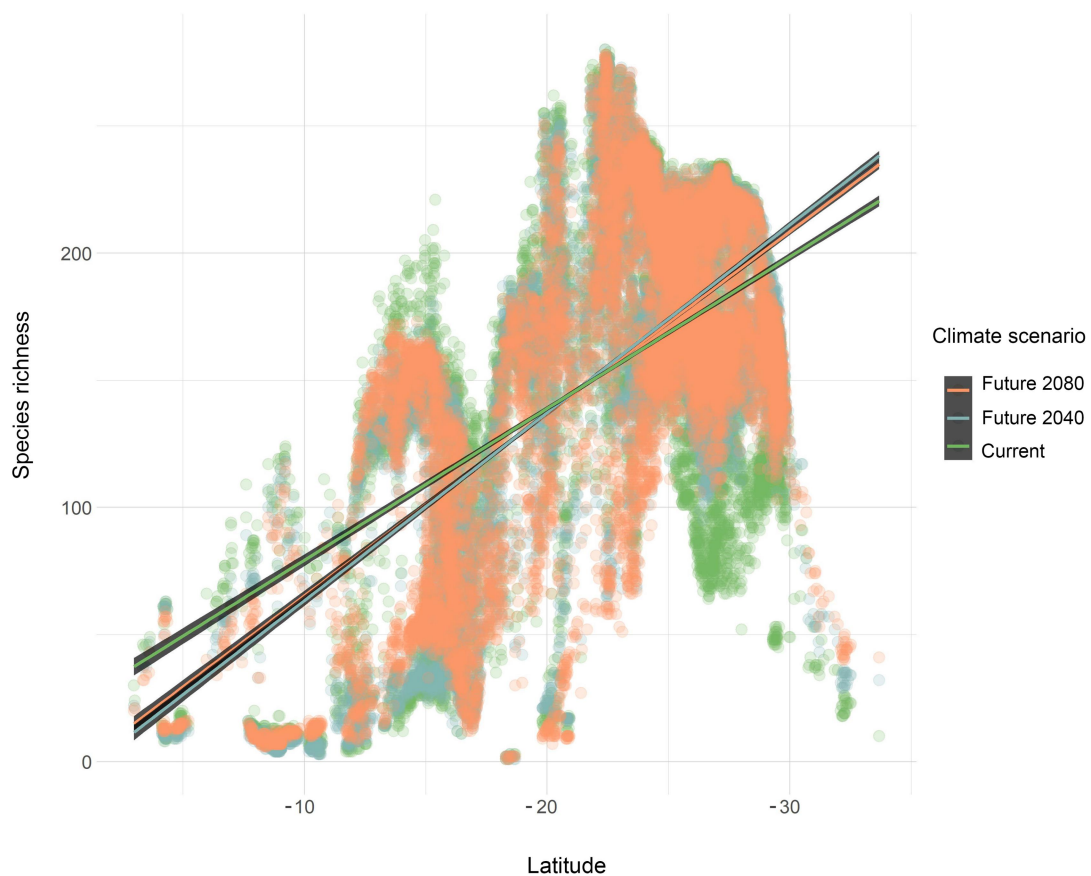


Figure S5. Circles representing bird species richness values in each pixel in a latitudinal range in the different climate scenarios. Linear models with confidence intervals were fitted to data.

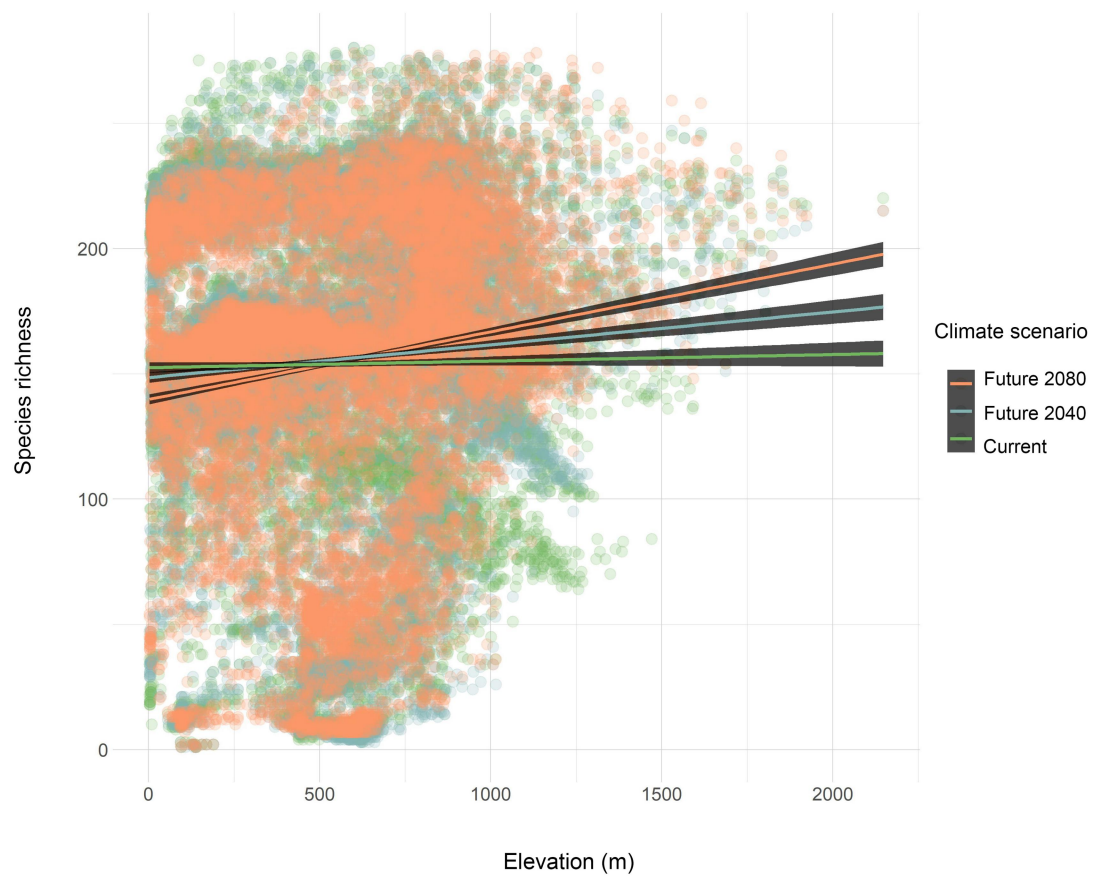
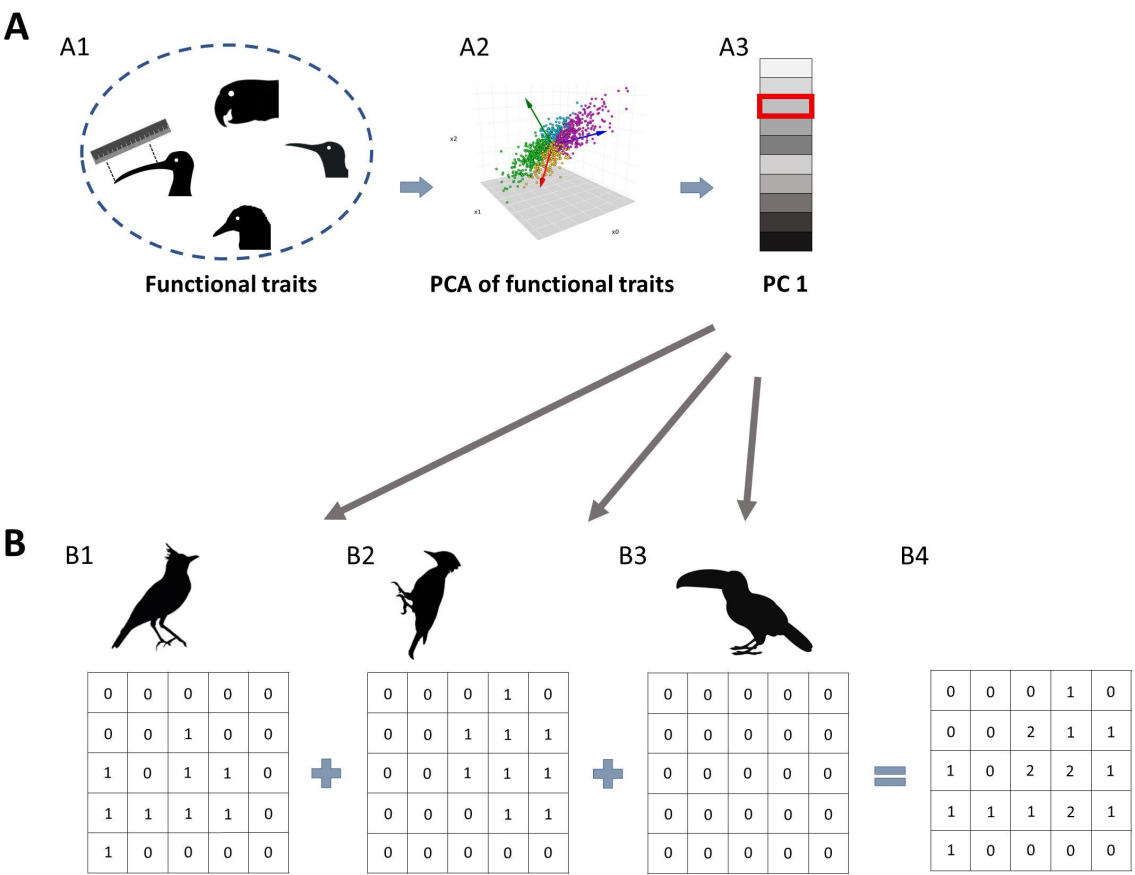


Figure S6. Circles representing bird species richness values in each pixel in a latitudinal range in the different climate scenarios. Linear models with confidence intervals were fitted to data.

Box S1. Workflow of the use of functional and foraging traits of birds for selecting priority areas for conservation.



In the first step (A), we obtained measures of functional and foraging traits for the 368 studied species (A1). With these traits, we performed a Principal Component Analysis (PCA; A2) and selected the first four axes of morphological (which correspond to 98% of the variation in data) and the first four axes of foraging data (81% of variation). We then split each axis into the 10% quantiles (A3).

In the second step (B), to build richness maps of each 10% quantile of each eight PCA components (four components based on morphological data and four for foraging data), we considered the presence (1) or absence (0) of each species in each pixel of the study area (B1 to B3) and if the species represented that value of the quantile considered.

Therefore, if a given species represented the quantile considered, we assigned the value 1 for the pixels our distribution models predicted the species occurrence and 0 for pixels that the species is not supposed to occur (B1 and B2). If a given species does not represent the quantile considered, we assign 0 for all pixels in the distribution area regardless of the species occurrence (B3). In the end, we summed all individual rasters to obtain a layer of the richness of each 10% quantile in the study area (B4). We used the 80 layers of the richness of all quantiles (10 quantiles for each of the eight PCA components) as input in the Zonation software. A similar approach was employed by other authors (Brum et al., 2017; Sibarani et al., 2019).

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Considerações finais

Áreas agrícolas dominam as paisagens em praticamente todos os tipos de ecossistemas terrestres e a extensão dessas áreas apresenta-se em expansão, sobretudo em regiões tropicais, onde encontra-se a maior parte da biodiversidade mundial (Figura 1). Sendo assim, o manejo adequado de paisagens antropizadas é essencial para promover processos ecológicos fundamentais para a manutenção de populações de espécies que sofrem com os efeitos da perda e modificação de habitats naturais. Com esta perspectiva, esta tese tratou de diferentes abordagens baseadas em ecologia espacial, sobretudo ecologia de paisagens, voltadas para a biologia da conservação. Cada um dos capítulos visou, de maneira direta ou indireta, aplicar conhecimentos em ecologia de paisagens para promover a biodiversidade em regiões agrícolas. Ainda que o primeiro capítulo apresente uma abordagem menos aplicada, ao fornecer o estado da arte de um dos assuntos que é um dos pilares da ecologia de paisagens (heterogeneidade espacial), nós propomos algumas medidas práticas que podem ser aplicadas no manejo de paisagens. Por exemplo, ao indicar a escassez de estudos que visam elucidar os diferentes efeitos que a configuração e composição das paisagens têm sobre populações, nós sugerimos que mais investigações como essa sejam realizadas, o que pode orientar estudos que sejam aplicados em medidas de conservação.

O segundo e o terceiro capítulos apresentaram um viés mais aplicado, utilizando como modelo de estudos a Mata Atlântica. No Capítulo 2 ficou demonstrado que a recuperação de áreas degradadas por meio da regeneração florestal natural apresenta potencial de aumentar a área de habitat para espécies florestais sem que áreas destinadas à produção agrícola sejam comprometidas. Os resultados obtidos nesse capítulo vão de encontro com o que já foi encontrado por outros autores – a recuperação do bioma em larga escala é viável do ponto de vista econômico devido sobretudo à elevada

quantidade de áreas degradadas. Sendo assim, como ocorre outros domínios florestais tropicais, a regeneração natural pode ser uma estratégia viável para a recuperação da Mata Atlântica (Latawiec et al., 2015; Díaz-García et al., 2020; Banks-Leite et al., 2014).

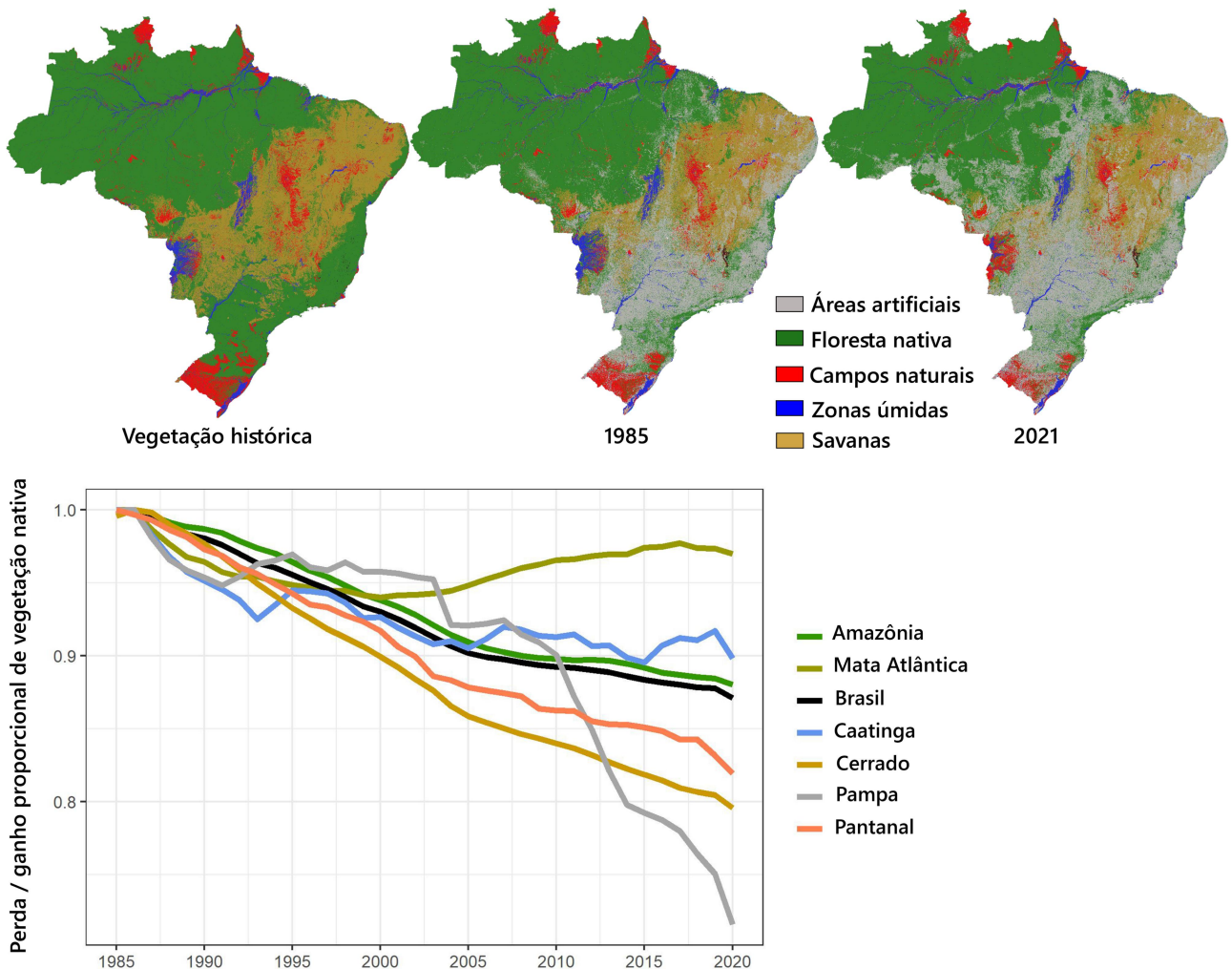


Figura 1 – Conversão de áreas naturais em áreas antrópicas ao longo dos anos no Brasil, exemplificando a magnitude da conversão de vegetação natural em paisagens antrópicas em regiões tropicais. Na parte superior, pode-se observar mapas da cobertura da terra no Brasil em diferentes períodos. O mapa da vegetação histórica foi baseado em dados do Instituto Brasileiro de Geografia e Estatística (IBGE) e a cobertura da terra entre os anos 1985 e 2021 são provenientes da iniciativa MapBiomas (<https://mapbiomas.org/>). Na parte inferior da figura está a perda de vegetação nativa de cada um dos domínios brasileiros e de todo o país (linha preta). A perda de vegetação foi ajustada à proporção da área que cada uma das regiões ocupa para que a mesma escala fosse aplicada. Todas as regiões apresentam tendência de declínio da quantidade de vegetação nativa.

No terceiro capítulo, ao utilizarmos diferentes abordagens para identificar áreas importantes para a conservação utilizando medidas de diversidade taxonômica e funcional de aves, pudemos observar que a sobreposição das áreas importantes para a conservação utilizando diferentes abordagens é baixa. Isso sugere que estudos holísticos que visam o uso de diferentes estratégias sejam necessários para a seleção de áreas importantes para a conservação da biodiversidade (Brum et al., 2017; Sibarani et al., 2019). Nesses capítulos, nós também elaboramos mapas indicando as áreas importantes para a conservação da biodiversidade na região da Mata Atlântica. Esse estudo pode ser considerado inovador por utilizar abordagem baseada em ecologia de paisagens para identificar regiões importantes para a conservação em larga escala. Assim como em estudos prévios que também visaram identificar regiões importantes para a conservação (Kremen et al., 2008), os nossos resultados demonstram a importância de fragmentos florestais pequenos para a conservação.

Síntese dos resultados obtidos em cada capítulo

Capítulo 1

- A maioria dos estudos de ecologia de paisagens que abordam a heterogeneidade espacial não define os conceitos utilizados.
- A sobreposição de métricas utilizadas para fornecer *proxies* de composição e a configuração da paisagem é alta.
- Abordagens que estudam as paisagens baseadas em aspectos estruturais são mais prevalentes do que abordagens que levam em consideração a funcionalidade das paisagens.

- Além de uma síntese de conhecimento do assunto, nós identificamos lacunas de conhecimentos e apontamos para perspectivas futuras em estudos que tratam a heterogeneidade espacial em ecologia de paisagens.

Capítulo 2

- Dentre as ameaças que os efeitos das mudanças climáticas apresentam para a biodiversidade de ambientes tropicais, destaca-se a redução da área de distribuição potencial das espécies.
- A restauração florestal em áreas degradadas por meio da regeneração natural pode aumentar a área de distribuição potencial de espécies florestais.
- A chance de extinção das espécies devido aos efeitos das mudanças climáticas pode ser reduzida com a restauração de áreas degradadas.
- Mapas indicando áreas onde a restauração natural pode ser promovida são fornecidos

Capítulo 3

- A sobreposição das áreas importantes para a conservação identificadas por meio de abordagem taxonômica e funcional das aves é baixa em um domínio florestal fragmentado.
- Ainda que as mudanças climáticas causem mudanças nas áreas de distribuição das espécies, áreas prioritárias para a conservação em cenário climático atual apresentam elevada sobreposição com áreas prioritárias para a conservação em cenários futuros.
- A quantidade de áreas protegidas atuais não é suficiente para proteger as aves da região da Mata Atlântica utilizando diferentes limiares que identificam a quantidade mínima de áreas de distribuição tanto em cenário climático atual quanto futuro.

- Mapas que indicam áreas importantes para a conservação das aves na região da Mata Atlântica são apresentados

Contribuição desta tese para o cumprimento dos Objetivos de Desenvolvimento Sustentável

A Agenda 2030 para o Desenvolvimento Sustentável, adotada por todos os Estados Membros das Nações Unidas (ONU) em 2015, reconhece 17 metas ambiciosas e interconectadas que abordam os principais desafios de desenvolvimento enfrentados em todo o mundo (Figura 2; <https://sdgs.un.org/goals>). Nós especificamos abaixo as metas para as quais nós acreditamos que esta tese pode contribuir.



Figura 2 – Objetivos do Desenvolvimento Sustentável adotados pelos membros das Nações Unidas, com destaque para aqueles em que a presente tese pode contribuir de maneira direta ou indireta.

1 – Erradicar a pobreza: O Capítulo 2 da presente tese indica áreas que podem ser regeneradas na Mata Atlântica. Programas de recuperação da vegetação podem gerar renda e empregos. Estima-se que no início de 2020 mais de 8.000 empregos foram

gerados em programas de restauração ecológica no Brasil (Brancaion et al., 2022). Além disso, o Capítulo 3 apresenta áreas onde a rede de áreas protegidas poderia ser ampliada na região da Mata Atlântica. O estabelecimento de novas Unidades de Conservação pode gerar emprego e renda ao, por exemplo, incentivar o turismo de base comunitária (Souza et al., 2019).

6 – Água e saneamento: O aumento da área de floresta, assim como a expansão das áreas protegidas, podem propiciar diversos tipos de serviços ecossistêmicos, dentre eles a provisão de água (Holl, 2017; Allan et al., 2022).

8 – Trabalho digno e crescimento econômico; 10 – Reduzir desigualdades: As fontes com projetos de restauração e expansão da rede de áreas protegidas, ambos citados no Objetivo 1 acima, podem auxiliar também na redução da desigualdade social e na geração de trabalho e crescimento econômico.

13 – Combater as alterações climáticas: O aumento de áreas florestais (sugerido no Capítulo 2), assim como a expansão das áreas protegidas (Capítulo 3), geram absorção de carbono da atmosfera, auxiliando no combate às alterações climáticas (Holl & Brancaion, 2020; Dobrowski et al., 2021).

15 – Ecossistemas terrestres e biodiversidade: Conforme amplamente discutido ao longo dos capítulos e desta seção, as diversas medidas propostas nessa tese podem contribuir com a conservação de ecossistemas terrestres e conservação da biodiversidade.

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Lista de produções acadêmicas

Além dos capítulos acima, estágio no exterior, créditos obtidos em disciplinas e monitoria em duas disciplinas de graduação, algumas das produções acadêmicas alcançadas durante a elaboração desta tese estão listadas abaixo. Não estão sendo consideradas as produções acadêmicas obtidas antes do início do curso de doutorado.

Artigos científicos publicados

1. Tonetti, V; Niebuhr, BB; Ribeiro, M; Pizo, MA. 2022. Forest regeneration may reduce the negative impacts of climate change on the biodiversity of a tropical hotspot.

Diversity and Distributions

2. Danilo, B; Nobrega, NB; Ferreira, PA; Lopes, L; **Tonetti, V;** et al. ATLANTIC FLOWER-INVERTEBRATE INTERACTIONS: a dataset of occurrence and frequency of floral visits. *Ecology*

3. Silva, R; et al; **Tonetti, V;** et al. 2021. ATLANTIC ANTS: a data set of ants in Atlantic Forests of South America. *Ecology* 103(2):e03580

4. Pizo, MA; **Tonetti, VR.** 2020. Living in a fragmented world: Birds in the Atlantic Forest. *The Condor* 122:1–14.

5. Nagy'Reis, M; et al; **Tonetti, V;** et al. 2020. NEOTROPICAL CARNIVORES: a data set on carnivore distribution in the Neotropics. *Ecology* 101(11):e03128.

6. Ramos, FN; et al; **Tonetti, V**; et al. 2019. ATLANTIC EPIPHYTES: a data set of vascular and non-vascular epiphyte plants and lichens from the Atlantic Forest. *Ecology* 100(2):e02541.
7. Cavarzere, V; Albano, C; **Tonetti, VR**; Pacheco, JF; Whitney, BM; Silveira, LF. 2019. An overlooked hotspot for birds in the Atlantic Forest. *Papéis Avulsos de Zoologia* 59: 20195905.
8. Rodrigues, RC; Hasui, E; Assis, JC; Pena, JCC; Muylaert, R; **Tonetti, VR**; et al. 2019. ATLANTIC BIRD TRAITS: a dataset of bird morphological traits from the Atlantic forests of South America. *Ecology* 100(6), 2019, e02647.
9. Santos, P; et al; **Tonetti, VR**; et al. 2019. NEOTROPICAL XENARTHTRANS: a data set of occurrence of xenarthran species in the Neotropics. *Ecology* 100(7):e02663.
10. Hasui, E; et al; **Tonetti, VR**; et al. 2018. ATLANTIC BIRDS: a data set of bird species from the Brazilian Atlantic Forest. *Ecology* 99(2):497.
11. Muylaert, RL; Vancine, MH; Bernardo, R; Oshima, J; Sobral-Souza, T; **Tonetti, VR**; Niebuhr, BB; Ribeiro, MC. 2018. A note on the territorial limits of the Atlantic forest. *Oecologia Australis* 22: 302 – 311.

- 12. Tonetti, VR;** Rego, MA; Luca, AC; Develey, PF; Schunck, F; Silveira, LF. 2017. Historical knowledge, richness and relative representativeness of the avifauna of the largest native urban rainforest in the world. *Zoologia: An International Journal for Zoology* 34:3 – 18.
- 13. Tonetti, VR;** Gussoni, COA; Pizo, MA. 2017. First egg and standardized nest description of the Southern Bristle-tyrant. *The Wilson Journal of Ornithology* 129(2):372 – 376.
- 14. Cavarzere, VA;** Silveira, LF; **Tonetti, VR;** Develey, P; Ubaid, FK; Regalado, LB; Figueiredo, LFA. 2017. Museum collections indicate bird defaunation in a biodiversity hotspot. *Biota Neotropica* e20170404.
- 15. Tonetti, VR;** Cavarzere, V. 2017. Beta diversity analysis of bird assemblage of a biodiversity hotspot within the Atlantic Forest. *Ornitologia Neotropical* 28:281 – 290.
- 16. Tonetti, VR;** Bocalini, F; Silveira, LF; Del-Rio, G. 2017. Taxonomy and molecular systematics of the Yellow-green Grosbeak. *Revista Brasileira de Ornitologia* 25:176 – 189.

Manuscritos aceitos para a publicação em periódicos científicos

- 1. Tonetti, V;** et al. Landscape heterogeneity: Concepts, quantification, challenges, and future perspectives. Aceito para a publicação no periódico *Environmental Conservation*.

Manuscritos em revisão em periódicos científicos

1. **Tonetti, V**; Bocalini, F; Schunck, F.; Vancine, MH; Butti, M; Ribeiro, M; Pizo, M.
The Protected Areas network may be insufficient to protect bird diversity in a fragmented tropical hotspot under different climate scenarios. Em revisão no periódico *Perspectives in Ecology and Conservation*.
2. Januário, NLE; **Tonetti, V**; Schunck, F; Cavarzere, V. Studies of forest birds over two hundred years in a tropical biodiverse region. Em revisão no periódico *Studies on Neotropical Fauna and Environment*.

Capítulos de livros publicados

1. **Tonetti, VR**; Muylaert, R; Ribeiro, MC. 2019. Fragmentação de habitat. In: Lais Santos de Assis; Marina Campos; Vanessa Jó Girão. (Org.). Manejo de fragmentos florestais degradados. 1ed.Campinas, São Paulo: *The Nature Conservancy*, v., p. 28-47.

Outros tipos de produções bibliográficas

1. **Tonetti, VR**. 2017. Pesquisa realizada com ave rara da Mata Atlântica. Unesp
Ciência, São Paulo – SP

2. Tonetti, VR. 2017. Floresta urbana revela riqueza de aves: Pesquisa da Unesp é publicada em revista internacional. UNESP notícias.

3. Tonetti, VR. 2017. Aves da Cantareira: estudo revela que área abriga ao menos 326 espécies de aves, ou seja, 17% do total registrado no Brasil. Jornal da UNESP.

Palestras e apresentações de trabalhos científicos

1. Tonetti, VR; Niebuhr, BBS; Ribeiro, MC. 2021. The potential of Atlantic Forest in reducing the negative effects of climate change on biodiversity. Apresentado no IV Simpósio de Modelagem de Sistemas Ambientais e Gestão da Paisagem, Universidade Federal de Minas Gerais.

2. Tonetti, VR. 2021. The potential of natural regeneration in mitigating biodiversity loss in a fragmented forest domain. Apresentado nas reuniões do Laboratório de Ecologia de Aves da UNESP Rio Claro.

3. Tonetti, VR. 2021. Landscape heterogeneity. Apresentado no curso de Ecologia de Paisagens ministrado na UNESP Rio Claro.

4. Tonetti, VR. 2020. Landscape heterogeneity: concepts, quantification, challenges and future perspectives. Apresentado no curso de Ecologia de Paisagens ministrado na UNESP Rio Claro.

5. **Tonetti, VR.** 2018. Optimizing space for agriculture and biodiversity based on a landscape ecology-approach. Apresentado nas reuniões do Laboratório de Ecologia de Aves da UNESP Rio Claro.
6. **Tonetti, VR.** 2017. Ecological niche modeling: theoretical bases, purposes and tools. Apresentado na Universidade de Campinas (UNICAMP).
7. **Tonetti, VR.** 2017. Close and little known: the Cantareira birds. Apresentado no evento de divulgação científica “*Vem passarinhar*”, São Paulo.
8. **Tonetti, VR.** 2017. The birds in the largest urban forest in the world. Apresentado no AVISTAR.
9. Cavarzeri, VA; Marchi, VAA; **Tonetti, VR.** 2017. Bird species richness in western Paraná state and citizen science: first approach. Apresentado no Ornithological Congress of the Americas, Argentina.
10. **Tonetti, VR.** 2017. The birds of the largest urban rainforest in the world. Apresentado no II Seminário sobre pesquisas científicas desenvolvidas no Parque Estadual do Jaraguá.
11. Assis, LS. et al. **Tonetti, VR.** 2017. Restoration of disturbed forests in human-modified landscapes: developing a reference document to guide practice. Apresentado no VII World Conference on Ecological Restoration.

Orientações

Coorientação de trabalho de Conclusão de Curso **Ano:** 2017

Curso / Instituição: Graduação em Ciências Biológicas / UNESP Rio Claro

Aluno: Bruno Machado de Freitas.

Título: Comparação entre dois métodos de amostragem de aves: gravadores autônomos e ponto fixo.

Premiações

2021

Melhor trabalho apresentado no IV Simpósio de Modelagem de Sistemas Ambientais e Gestão da Paisagem, Universidade Federal de Minas Gerais.

2019

Top downloaded paper in Ecology, The Ecological Society of America.

2017

Aprovado em primeiro lugar no exame de seleção do PPG em Ecologia & Biodiversidade. Nível doutorado, UNESP Rio Claro.

Revisões de manuscritos em periódicos científicos

Periódico	Quantidade de manuscritos revisados
<i>Ecology and Evolution</i>	1
<i>Mammalian Biology</i>	1
<i>Wilson Journal of Ornithology</i>	1
<i>Ornitología Neotropical</i>	4
<i>Iheringia, Série Zoologia</i>	1
<i>Revista Ciência, Tecnologia & Ambiente</i>	1