

UNIVERSIDADE FEDERAL DO PARANÁ

GABRIEL MITSUO INAGUE

DISTRIBUIÇÃO DA DIVERSIDADE E FUNCIONALIDADE DA VEGETAÇÃO  
DAS RESTINGAS EM CENÁRIOS DE MUDANÇAS CLIMÁTICAS



CURITIBA

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Dissertação apresentada ao Programa de Pós-Graduação em Botânica, Setor de Ciências Biológicas, Universidade Federal do Paraná, como parte dos requisitos para a obtenção do título de Mestre em Botânica.

Orientadora: Prof<sup>ª</sup>. Dr<sup>ª</sup>. Márcia C. M. Marques  
Coorientador: Prof. Dr. Victor P. Zwiener

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*"A imaginação às vezes nos leva a mundos  
que nunca existiram, porém, sem ela, nós  
não iríamos a lugar nenhum."*

*— Carl Sagan*

## RESUMO

É esperado que as mudanças climáticas imponham condições ambientais extremas aos ecossistemas, as quais podem potencialmente afetar os padrões de biodiversidade e serviços ecossistêmicos através do tempo e espaço. Projetar a distribuição de espécies em cenários climáticos futuros permite-nos avaliar os impactos das mudanças climáticas em comunidades biológicas. Utilizando modelagem de nicho ecológico, nós comparamos as condições atuais com a de cenários climáticos futuros previstos para 2050 para determinar potenciais mudanças nos padrões espaço-temporais das diversidades taxonômica e funcional da vegetação lenhosa das Restingas do sul e sudeste do Brasil. Especificamente, nossa finalidade foi: i) prever a distribuição das diversidades taxonômica e funcional atual e futura (2050); ii) estimar a partição da diversidade beta nos cenários presente e futuro (2050); e iii) prever a distribuição de atributos funcionais chave para a entrega de múltiplos serviços ecossistêmicos. Nós geramos modelos de nicho ecológico para 796 espécies de plantas lenhosas para as quais estimamos as mudanças espaço-temporais dos componentes da diversidade beta, as médias ponderadas da comunidade (CWM) e os índices de diversidade funcional de atributos selecionados. O cenário de maiores emissões de gases do efeito estufa (pessimista) indicou um aumento geral de uma perda de espécies da Restinga três vezes maior se comparado ao cenário otimista, enquanto que na escala regional (ecorregião), a perda de espécies pode chegar a atingir porcentagens tão altas quanto 19%. Por outro lado, a diversidade beta foi prevista para ser maior no futuro, com o componente de substituição de espécies tendo uma maior contribuição do que o aninhamento. A projeção de CWM mostrou-se contrastante entre atributos funcionais e ecorregiões, sugerindo um futuro aumento em alguns atributos (densidade da madeira, comprimento da semente e do fruto) e uma diminuição em outros (altura máxima da planta). No geral, a divergência e riqueza funcional poderão diminuir no futuro, enquanto que a uniformidade funcional poderá aumentar. Nosso estudo fornece uma comparação dos efeitos dos cenários extremos das mudanças climáticas na biodiversidade da frequentemente marginalizada vegetação das Restingas.

Palavras-chave: Heterogenização da beta diversidade; Homogeneização da diversidade funcional; Mata Atlântica; Partição da diversidade; Modelagem de nicho ecológico; Vegetação costeira.

## ABSTRACT

Climate change is expected to impose extreme environmental conditions which may potentially affect the biodiversity and ecosystem services patterns through time and space. Projecting the species distributions in future climate scenarios allows us to evaluate the climate change impacts over biological communities. Applying ecological niche modeling, we compared current and future climate scenarios predicted for 2050 to determine potential changes in the spatio-temporal patterns of taxonomic and functional diversities of the woody plant species in south and southern Brazilian *Restinga*. Specifically, we aimed to: i) predict the current and future 2050 distribution of woody plant species taxonomic and functional diversities; ii) estimate the partition of beta diversity in the current and future scenarios; and iii) predict the distribution of functional traits key the delivery of multiple ecosystem services. We generated ecological niche models for 796 woody plant species for which we estimated the spatio-temporal changes of beta diversity, and the functional indices and community-weighted means (CWM) of selected traits. The high greenhouse gases emission (pessimist) scenario indicated an overall threefold increase in woody plant species loss if compared to the optimistic scenario, whereas at regional scales, species loss may reach percentages as high as 19%. Conversely, beta diversity may increase in the future, with the turnover component having a greater contribution than nestedness. The CWM projections emphasized contrasts among traits and ecoregions, with an increase in some traits (stem wood density, seed length and fruit length) and a decrease in others (maximum plant height). Functional divergence and richness may decrease in future, while functional evenness, may increase. Our study provides a comparison between climate change extreme scenarios effects on the biodiversity of the frequently marginalized *Restinga* vegetation.

Key words: Atlantic Forest; Beta diversity heterogenization; Coastal vegetation; Diversity partitioning; Functional diversity homogenization; Ecological niche modeling.

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## 1 INTRODUÇÃO GERAL

O crescimento das concentrações atmosféricas de gases do efeito estufa é atribuído à ação antropogênica como a queima de combustíveis fósseis e o desmatamento (BEERLIN; ROYER, 2011). Nos ambientes terrestres e oceânicos superficiais, o aquecimento global, desde 1880, já corresponde a um aumento de 0,85° C de temperatura média (IPCC, 2014) e a estimativa desde o período pré-industrial é de aproximadamente 1° C (BINDOFF *et al.*, 2013; SMITH *et al.*, 2015).

Entre os efeitos das mudanças climáticas de causa antropogênica, a intensificação da perda de biodiversidade é um dos mais preocupantes (PARMESAN; YOHE, 2003; BUTCHART *et al.*, 2010; CBD SECRETARIAT, 2010; WWF, 2012). Existe um grande volume de evidências de que as mudanças climáticas já ocasionaram globalmente diversas respostas biológicas nos organismos vivos. Alterações genéticas, morfológicas, fenológicas e demográficas já foram detectadas em diversas espécies e, como resultado, teias alimentares serão afetadas e novas interações surgirão em detrimento de mudanças na distribuição de muitas espécies (SCHEFFERS *et al.*, 2016). Como resultado da redistribuição de espécies, uma grande parcela da vida na Terra deverá ser afetada (PECL *et al.*, 2017). Associado a isso, mudanças nas interações ecológicas poderão gerar efeitos desconhecidos e alterações em todos os níveis ecológicos. Na iminência destes novos regimes ambientais surge a demanda de se criar outras formas de lidar com as condições emergentes, o que é um cenário desafiador para a humanidade (PECL *et al.* 2017).

A manutenção da vida humana na Terra depende de que os processos e funções ecossistêmicas estejam intactos e em funcionamento para a provisão de inúmeros bens e serviços, incluindo aqueles relacionados à adaptação em novas condições climáticas (MARTIN; WATSON, 2016). As funções ecossistêmicas são provenientes de processos ecossistêmicos desempenhados pelos organismos que compõem o ecossistema como reflexo da expressão somada de seus atributos funcionais que, individualmente ou coletivamente (ao nível da comunidade), afetam os recursos do ambiente e o próprio *fitness* das espécies (LAVOREL; GARNIER, 2002; VIOLLE *et al.*, 2007; LUCK *et al.*, 2009). Como as mudanças climáticas implicam em alterações das condições ambientais, a

degradação dos ecossistemas afeta diretamente a sua resiliência (COLLS *et al.*, 2009), a qual pode chegar a atingir um ponto de virada na qual a recuperação e auto-organização são impossibilitadas de ocorrer (CARPENTER *et al.*, 2001). A resiliência ecossistêmica é a capacidade do ecossistema de sofrer um distúrbio e retornar ao estado de equilíbrio que possuía antes do mesmo e pode ser medida pela diversidade funcional. Como consequência, a ação dos impactos antropogênicos sobre a mesma influencia os serviços ecossistêmicos ao afetar diretamente os processos ecossistêmicos (HOOPER *et al.*, 2005), os quais representam a expressão conjunta dos atributos funcionais.

Atributos funcionais têm sido amplamente utilizados para relacionar diversos níveis ecológicos, desde indivíduos e espécies até os ecossistemas (HOOPER *et al.* 2005). Como o componente vegetal de um ecossistema terrestre é o que representa a maior proporção da biomassa, a vegetação tende a influenciar majoritariamente as estruturas físicas dos mesmos, bem como os ciclos de energia, água e nutrientes (MOOR *et al.* 2015). Uma maneira de analisar a influência desse fenômeno na funcionalidade ecossistêmica é quantificar o efeito da dominância em cada atributo, já que a hipótese de razão da massa estabelece que os atributos das espécies dominantes na comunidade conduzem significativamente as funções ecossistêmicas (GRIME, 1998). Uma das formas de se medir estes efeitos é agregando os atributos das espécies da comunidade e estimando as contribuições relativas de determinados atributos (GARNIER *et al.* 2007). O efeito da dominância de atributos pode ser determinado pelo valor da média dos atributos na comunidade, ponderada pela abundância (“*community-weighted mean*”, ou “CWM”, VIOLLE *et al.*, 2007). Essa medida de diversidade funcional permite o desenvolvimento de modelagens preditivas de distribuição espacial de atributos funcionais, além de mudanças em potencial devido a alterações na composição (como em LAVOREL *et al.*, 2011).

A diversidade funcional não é igualmente afetada por todas as espécies, já que o conjunto de atributos funcionais de cada espécie contribui diferentemente nos processos ecossistêmicos (MOUCHET *et al.*, 2010). Para além do efeito de dominância, os componentes da diversidade funcional têm a propriedade de descrever o espaço funcional e podem ser medidos por três índices multidimensionais: riqueza funcional (FRic), uniformidade funcional (FEve) e

divergência funcional (FDiv; VILLÉGER *et al.*, 2008). A propriedade complementar dessas facetas da dimensão funcional permite-nos preencher o espaço funcional de uma comunidade com as distribuições das abundâncias das espécies (MOUCHET *et al.*, 2010). Enquanto o FRic delimita as dimensões do espaço funcional através de seu volume, o FEve descreve a regularidade das abundâncias das espécies distribuídas nesse espaço funcional e o FDiv, quão longe as abundâncias se encontram do centro do espaço funcional (MOUCHET *et al.*, 2010).

Enquanto a diversidade funcional representa a dimensão dos atributos funcionais que as espécies em geral exibem, a diversidade taxonômica representa como a riqueza de espécies em uma comunidade contribui para sua biodiversidade. Podemos compreender a diversidade taxonômica em escala regional através da exploração da diversidade beta das comunidades em escala local (SOCOLAR *et al.*, 2016). Essa última é medida pela diversidade alfa em um sítio e a diversidade beta, por sua vez, quantifica o número de diferentes unidades composicionais em uma região (TUOMISTO, 2010). Além de permitir a comparação entre comunidades locais e regionais, a diversidade beta também indica o grau de diferenciação entre as comunidades, e pode ser particionada em dois componentes: substituição de espécies e aninhamento (BASELGA, 2010). O aninhamento ocorre quando as biotas de sítios com um número menor de espécies representam sub-conjuntos dos sítios mais ricos em espécies. Já a substituição de espécies indica a troca de uma espécie por outra em um sítio devido à filtragem ambiental e a limitações na dispersão.

Para calcular os componentes da diversidade beta, utilizam-se os dados de ocorrência de cada espécie em cada sítio da comunidade. Em estudos macroecológicos que incluem cenários futuros, uma maneira de obtê-los é através da modelagem de nicho, a qual gera o índice de adequabilidade de habitat para cada espécie da comunidade em cada cenário projetado. Apesar de que prever as exatas ocorrências futuras de espécies para calcular as abundâncias pode representar um grande desafio, o índice de adequabilidade nos viabiliza assumi-lo como *proxy* de abundância em cenários futuros (WEBER *et al.*, 2017).

Abordagens macroecológicas da distribuição da biota permitem

compreender fenômenos ecológicos que ocorrem simultaneamente em extensas áreas. Como a distribuição de espécies ao nível continental é altamente influenciada pelo clima (MCGILL, 2010), a modelagem de nicho é uma abordagem eficiente e amplamente difundida para os estudos macroecológicos, que ao predizer a distribuição das espécies, possibilita prever as respostas espaciais e evolutivas das distribuições das espécies (DINIZ-FILHO *et. al.* 2009).

A modelagem de nicho associa informações sobre as características abióticas que definem o nicho atual de uma espécie com a distribuição espacial de cada característica, projetando, assim, o nicho potencial dessa espécie, de acordo com os requisitos ecológicos necessários (WIENS *et al.*, 2009). Os modelos preditivos de distribuição potencial são capazes de indicar áreas potenciais de ocorrência de determinada espécie em locais de ocorrência desconhecida, de modo que sejam precursores para a projeção de distribuições futuras em diversos cenários de mudanças climáticas (WILLIAMS; BLOIS, 2018).

### 1.1 AS RESTINGAS DO SUL E SUDESTE DO BRASIL

Ao longo de quase todo o litoral brasileiro, na área geológica chamada de planície costeira ou litorânea, a vegetação distribui-se em uma estrutura de mosaico caracterizado por grande heterogeneidade florística e estrutural. Conhecida como Restingas (ou Restinga), essa vegetação apresenta fisionomias predominante herbáceas, arbustivas ou arbóreas, dispostas adjacientemente sobre um solo formado de depósitos costeiros arenosos e rochosos do Quaternário (CONAMA, 1999) os quais, por sua vez, são relacionados aos efeitos geológicos ocorridos entre períodos glaciais e interglaciais (ARAÚJO e LACERDA, 1987). Floristicamente, as Restingas representam as fitofisionomias costeiras associadas à Mata Atlântica, (MORELLATO; HADDAD, 2000; OLIVEIRA-FILHO; FONTES, 2000) a qual, somada com manguezais e campos de altitude, formam um complexo vegetacional (RIZZINI, 1979).

As planícies litorâneas no eixo sudeste-sul do Brasil variam em função de singularidades geológicas, oceanográficas e climáticas, as quais refletem as peculiares paisagens (SILVEIRA, 1964). No Espírito Santo, ocorre a formação Barreiras e o litoral é marcado pela intercalação de afloramentos rochosos e

penhascos com extensas planícies costeiras (SILVEIRA, 1964). Desde o Rio de Janeiro até a metade de Santa Catarina (Cabo de Santa Marta), o litoral prossegue com a proximidade, a oeste, da cadeia de montanhas da Serra do Mar, exibindo extensas planícies, muitas vezes indentadas, ocorrendo a formação de ilhas, baías e lagoas (SILVEIRA, 1964). O clima varia de tropical a subtropical em ambas as regiões, com alta pluviosidade causada pela interceptação do alto relevo da Serra do Mar (MAACK, 1947). A região mais meridional da costa brasileira compreende a faixa territorial do Cabo de Santa Marta (SC) até o Chuí (RS), sendo o clima subtropical (MAACK, 1947), e o relevo, formado por amplas planícies sedimentares arenosas, onde ocorrem lagoas conjugadas e uma elevação basáltica na região de Torres (RS) (SILVEIRA, 1964).

O solo predominantemente quartzoso, a alta intensidade de luz solar, a influência marinha da umidade e maresia, a presença de rios, estuários e lagos (PEREIRA, 1990), fazem das Restingas um ambiente estressante para muitas espécies vegetais, propiciando que apenas uma seleção de espécies da comunidade sejam capazes de sobreviver e perpetuar-se frente a esses fatores abióticos. Essa singularidade faz com que as florestas de Restinga sejam particularmente interessantes do ponto de vista taxonômico e funcional (MARQUES *et al.*, 2015). Estima-se que 40% das espécies lenhosas dessas florestas sejam compartilhadas com fragmentos do interior. No trecho que compreende os litorais sul e sudeste brasileiro a diversidade é alta, com 1.588 espécies vegetais, sendo 4% exclusivas desse tipo vegetacional, o que sugere certo grau de endemismo (MARQUES *et al.*, 2015). Embora seja importante em termos de conservação da biodiversidade e da funcionalidade da Mata Atlântica como um todo (SCARANO, 2009), as Restingas são historicamente negligenciadas. Isso é refletido na ameaça de impactos antrópicos caracterizada pela ampliação de áreas urbanas (GOUDIE, 2013), muito relacionada à intensa atividade turística e grande pressão imobiliária. No entanto, estes ecossistemas apresentam funções importantes, tais como a proteção de corpos d'água, a retenção de sedimentos e dunas, a formação de solos e a ciclagem de nutrientes (MARQUES *et al.*, 2015). Esses e outros aspectos reforçam a necessidade de esforços de conservação e restauração das Restingas (ZAMITH; SCARANO, 2006).

Estimativas globais futuras acerca dos efeitos das mudanças nas condições climáticas sobre as Restingas mostram diversas tendências em relação à precipitação e à temperatura. Até 2100, as previsões para a porção sul e sudeste da Mata Atlântica, por exemplo, indicam aumento de temperatura de 2,5°C e 3°C e aumento de 25% a 30% na precipitação (RAN1, 2013). Ambos os fatores (temperatura e precipitação) estão diretamente envolvidos na regulação dos processos biológicos e químicos, e estão entre os fatores ambientais mais importantes para o desenvolvimento das plantas (BEIER, 2004). Somado a isto, mudanças no uso da terra (HOF *et al.*, 2011), o aumento de caça predatória, invasão de espécies exóticas (BECHARA *et al.*, 2013) representam outros fatores antrópicos diretos que acentuarão a degradação desses ecossistemas.

Neste estudo, foram analisados os aspectos taxonômicos e funcionais da vegetação lenhosa das Restingas no sul e sudeste do Brasil. Comparamos as distribuições das espécies e das funcionalidades ecossistêmicas do presente com as projetadas para o cenário pessimista e otimista de emissões de gases do efeito estufa para o ano de 2050. A partir dessas comparações, buscamos prever os efeitos das mudanças climáticas sobre a vegetação das Restingas, a fim de direcionar medidas de conservação da biodiversidade e mitigação e adaptação desses sistemas ecológicos.

## 2 CAPÍTULO I

### **AS MUDANÇAS CLIMÁTICAS AMEAÇAM AS DIVERSIDADES TAXONÔMICA E FUNCIONAL DA VEGETAÇÃO LENHOSA DAS RESTINGAS NO BRASIL†**

†Artigo preparado de acordo com as normas da revista *Perspectives in Ecology and Conservation*

**Climate change threatens the woody plant taxonomic and functional diversities of the *Restinga* vegetation in Brazil**

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## Abstract

Climate change may impose extreme conditions which potentially affect species' distributions, leading to spatio-temporal variation in biodiversity and ecosystem services patterns. Here we compared current climate conditions to future climate scenarios projected to 2050 to assess potential changes in the spatio-temporal patterns of the taxonomic and functional diversities of the woody species of the *Restinga* vegetation in Brazil. We generated Ecological Niche Models (ENM) for 796 woody plant species from which we estimated the spatio-temporal changes of beta diversity components, the community-weighted means (CWM) of selected traits and functional diversity indices. The pessimistic scenario indicated an overall threefold increase in woody plant species loss compared to the optimistic scenario, whereas at regional scales, species loss may reach percentages as high as 19%. Conversely, beta diversity may increase in the future, in which the turnover component had a greater contribution than nestedness. The CWM projection emphasized contrasts among traits and ecoregions, with an increase in most analysed traits (stem wood density, seed length and fruit length) and a decrease in one of them (maximum plant height). Functional divergence and richness may decrease in future, while functional evenness may increase. Our study highlighted important potential changes in the distribution of biodiversity that could lead to biotic homogenization in the *Restinga* vegetation and calls for the inclusion of this marginalized vegetation in plans for mitigation and adaptation to climate change.

## Introduction

The impacts of climate change on the world's ecosystems have already been documented on every continent, ocean and in most taxonomic groups (Scheffers et al., 2016). Greenhouse gases atmospheric concentrations are reaching levels never seen in recent history nor estimated over the past 20 million years (Beerling and Royer, 2011). Coupled with the intensification of habitat loss and aggressive land-use change, climate change represents one of the main threats to biodiversity and associated ecosystem services, particularly to tropical regions where most of the biodiversity is concentrated (Asner et al., 2010; Zwiener et al., 2017).

One of the most species-rich and yet highly degraded tropical domains is the Atlantic Forest (Mittermeier et al., 2011). This highly diverse South-American ecosystem complex formed by multiple physiognomies has

approximately 28% left of its original vegetation cover (Rezende et al., 2018). Sadly, it is considered one of the 'hottest of the hotspots' (Laurance, 2009) and one of the three most vulnerable to climate change (Béllard et al., 2014). One of its most heterogeneous physiognomies is the *Restinga* vegetation, a mosaic of distinct coastal physiognomies dominated by herbs, shrubs and trees occurring side by side (Marques et al., 2015), and where peripheral plant communities face more extreme environment conditions than the hinterland forests (Scarano, 2002).

Despite exhibiting some floristic, functional and historical connections to other Atlantic Forest ones, at least 4% of Atlantic Forest plant species are endemic to the *Restinga* forest physiognomies (Marques et al., 2015). The biodiversity in these ecosystems is under serious threat as they are considered extremely vulnerable to climate change and highly exposed to deforestation and biological invasion (Zamith and Scarano, 2006). As such, species displacement (Pecl et al., 2017) and extinction (Waller et al., 2017), related to climate change, may entail irreversible consequences to the many aspects of biodiversity and ecosystem services. Indeed, services such as sediment retention, protection from sea-level rise and extreme high tide events are key to human well-being and climate change mitigation (Scarano and Ceotto, 2015).

Taxonomic diversity, i.e., the species composition and abundance at a given location and time, can be measured locally (alpha), among locations (beta) and regionally (gamma; Whittaker, 1972). Beta diversity indicates the degree of differentiation among communities and can be partitioned into two components: turnover and nestedness (Baselga, 2010). Disentangling these components allows beta diversity to be scaled up to regional levels (Socolar et al., 2016). The nestedness phenomenon occurs when the biotas of sites with less species are subsets of the biotas at richer sites, while spatial turnover denotes the replacement of some species by others due to environmental sorting and spatial constraints. Disentangling the beta diversity components represents an important tool for understanding the anthropogenic effects on the distribution of taxonomic diversity (Kraft et al., 2011).

Climate change is predicted to alter the environment and, by extension, the spatial distribution of biodiversity and ecosystem functioning. Species may

locally adapt or track suitable conditions, however, given spatio-temporal restrictions to dispersal many species are expected to go locally extinct or retract their distribution leading to ecosystem degradation (Carpenter et al., 2001; Colls et al., 2009). Evidence shows that species responses to climate change may lead to biotic homogenization or heterogenization of ecological communities with detrimental effects to biodiversity (Hidasi-Neto et al., 2019; Socolar et al., 2016; Zwiener et al., 2018). Such changes directly affect the delivery of ecosystem services crucial to human well-being (Díaz et al., 2007). A way to assess these changes is by measuring functional diversity (Hooper et al., 2005), which represents the combined expression of functional traits. Functional diversity is not equally affected by all species, as the set of functional traits of each species matters differently to ecosystem processes (Mouchet et al., 2010). Combining different facets of diversity (i.e., taxonomic and functional) may represent an effective approach to estimate the effects of climate change on ecosystem structure and processes. In fact, considering the current land use changes and increasing impacts of climate disturbances in tropical ecosystems, measuring the different biodiversity levels adequately could account as an urgent task in Latin America (see Pearson et al., 2019).

Here we assessed the potential effects of climate change on woody plants of the *Restinga* vegetation in Brazil. Based on species checklists from local studies we generated ecological niche models and compiled functional traits for 796 woody plants to: i) predict the current and future distribution of taxonomic and functional diversities; ii) estimate the beta diversity between current and future scenarios and compare the relative contribution of turnover and nestedness; and iii) predict the distribution of functional traits indispensable to the delivery of multiple ecosystem services. Ultimately, our results contribute to the discussion of biotic homogenization and heterogenization that affect ecological communities and may jeopardize the conservation of biodiversity and human well-being.

## **Methods**

### *Study region and occurrence data*

The study encompasses the forest component of the *Restinga* vegetation of South and Southeastern Brazil (States of *Espírito Santo*, *Rio de Janeiro*, *São Paulo*, *Paraná*, *Santa Catarina* and *Rio Grande do Sul*; Fig. 1A), a well-defined floristic zone in historical and ecological terms (Marques et al., 2011). This vegetation is part of the Atlantic Forest complex, and include the Edaphic System of First Occupation and the Lowland Dense Rain forest in the Brazilian vegetation classification (IBGE, 1992). The study region was defined by overlapping the area of Edaphic System and Lowland Forest from the IBGE vegetation map ([www.ibge.gov.br](http://www.ibge.gov.br)) and the area of *Restinga* vegetation from the *SOS Mata Atlântica* map ([www.maps.sosma.org.br](http://www.maps.sosma.org.br)). We divided the study region (5 km<sup>2</sup> grid resolution) into five ecoregions – eco-0, eco-5, eco-12, eco-16 and eco-18 (Fig. 1) – considering the regionalization proposed by Cantídio and Souza (2019), which was based on a spatially contiguous estimation of floristic dissimilarity and ecosystem variation.

In order to create a checklist of woody plant species occurring in the *Restinga* vegetation, we gathered floristic and phytosociological studies from the literature based on a list previously compiled by Marques et al. (2015). The search resulted in 47 published studies, which were developed in 44 sites and comprised 796 native woody plant species (occurrence data ranged from 10 to 2435 records) of 89 families. Henceforth, the occurrence data of each species was compiled from SpeciesLink (<http://splink.cria.org.br/>) and GBIF (<http://gbif.org/>). Synonymies and misspelled names were resolved using the information provided by specialists at *Flora do Brasil 2020* (<http://floradobrasil.jbrj.gov.br/>). See Appendix A for more details about the obtention and preparation of the occurrence data.

### *Climatic data and ecological niche modeling*

A total of 19 climatic variables for future climate projections were compiled from the WorldClim database (Hijmans et al., 2005), which are based on the IPCC Fifth Assessment Report. The first six principal component analysis (PCA) axes from current conditions projected to three global climate models (CCSM4, GISS-E2-R and MIROC5) for 2050 optimistic (RCP 2.6) and

pessimistic (RCP 8.5) scenarios were chosen as proxy for the climatic variation in the region. These variables and the occurrence data of 796 woody species were used to estimate geographic distributions with ecological niche modeling (ENM) for the present time and for both 2050 scenarios (see details in Supplementary Material, Appendix A). Our models were performed in package 'dismo' (Hijmans et al., 2012) in R using the Maxent implementation, and considered all the assumptions stated by Peterson (2001).

### *Species loss assessment*

In order to calculate the number and percentages of projected species loss, we compared the current distribution of the *Restinga* woody plant species to the future RCP 2.6 and 8.5 scenarios' presence-absence matrices obtained from niche modeling. To determine the magnitude of distribution, we separated the species into range categories by calculating the quartiles based on the range of the most ubiquitous species (*Securidaca diversifolia*) and classifying the species in narrow (1st quartile), intermediate (2nd quartile) and wide (3rd and 4th quartiles) distribution. In addition, we determined the pattern of range dynamics (i.e., expansion, retraction and stabilization) every species in each range category presented in both future scenarios. We also calculated the net retraction rate (expansion minus retraction) for each species. We considered a potential local extinction event when the species showed no suitability in the future scenarios (i.e, 100% retraction).

### *Taxonomic beta diversity partitioning*

We partitioned beta diversity into nestedness and turnover components in order to estimate the taxonomic beta diversity – Sørensen total dissimilarity index ( $\beta_{sor}$ ) – of each ecoregion by calculating the sum of its components in the current, RCP 2.6 and RCP 8.5 scenarios. Simpson's dissimilarity index ( $\beta_{sim}$ ) was used to represent turnover and nestedness was represented by Sørensen's beta diversity component of nestedness ( $\beta_{sne}$ ). Further on, we took the present time presence–absence matrices to compute the dissimilarity for

each focal grid cell between present time and future scenarios considering  $\beta_{sim}$  and  $\beta_{sne}$  components of temporal change, and the sum of both values (i.e.,  $\beta_{sor}$ ). Both analyses were calculated with the functions 'beta.multi' and 'beta.temp', respectively, available in the 'betapart' package (Baselga and Orme, 2012; R Core Team, 2017).

### *Plant traits and functional diversity*

Five functional traits for each species were compiled from the 'UFPR Atlantic Forest trait' dataset, complemented with information from the literature and herbaria. The traits used were maximum plant height (Hmax), wood density (WD), leaf area (LA), seed length (SL) and fruit length (FL). These traits were chosen because of their association to key ecological functions and services for these coastal forest ecosystems. The missing trait values were imputed with 'phylopars' function in 'Rphylopars' package (Goolsby et al., 2017) considering the macroevolutionary parameters under the Brownian Motion model. The mean percentage of imputed trait data was 43%, what is considered reliable (Penone et al., 2014). For this procedure, we obtained a phylogenetic tree of all 796 species (Appendix C) from 'V.PhyloMaker' package (Jin and Qian, 2019), which is based on an extended version of the GBOTB megatree (Smith and Brown, 2018). All analyses were performed in R (R Core Team, 2017).

To measure functional diversity, we calculated the community-weighted mean of each trait mentioned above and the three components of functional diversity with the following multidimensional indices: functional richness (FRic), functional evenness (FEve) and functional divergence (FDiv; Villéger et al., 2008). The complementary nature of these facets allows us to fill the functional space of a community with the distributions and abundances of the species (Mouchet et al., 2010). While FRic defines the dimensions of the functional space by its volume, FEve describes how regularly of the species abundances are distributed in the functional space and FDiv, how far high species abundances are from the center of the functional space (Mouchet et al., 2010). All the functional metrics were calculated with the 'dbFD' function implemented in the 'FD' package (Laliberté and Shipley, 2011) and were performed in R (R Core Team, 2017). ENM's environmental suitability index was used as a proxy of species abundance (Weber et al., 2017).

## Analyses

Two-way permutational ANOVA was used to compare the averages of the taxonomic beta diversity components ( $\beta_{sim}$ ,  $\beta_{sne}$  and  $\beta_{sor}$ ),  $\beta_{sim}$  and  $\beta_{sor}$  temporal change and the functional diversity indices (FDiv, FEve, FRic and CWM of all five traits) of the climate scenarios (present, RCP 2.6 and RCP 8.5) for each ecoregion, using the ‘aovp’ function in the ‘lmPerm’ package (Wheeler and Torchiano, 2016). The datasets with significant variations were submitted to the Fisher’s Least Significant Difference test (LSD) employing Bonferroni’s correction with  $p < 0.05$ , using the ‘LSD.test’ function in the ‘agricolae’ package (Mendiburu, 2017; Table S1–5) performed in R (R Core Team, 2017).

## Results

### *Species loss assessment*

Overall, our models suggested expressive losses in woody-plant species of the *Restinga* vegetation for future climatic scenarios (Fig. 1). The RCP 8.5 presented more than three times higher species loss rate than RCP 2.6 (0.75% and 0.25%, respectively). The highest individual ecoregion proportional rate of projected species loss occurred in eco-5, the northernmost ecoregion (14% in RCP 2.6 and 19% in RCP 8.5), whilst the lowest was in eco-16, located in the central region of the study area (1% in RCP 2.6 and 1.6% in RCP 8.5; Fig. 1). Regarding the range dynamics, the species in the optimistic scenario exhibited 10.0%, 80.5% and 9.7% of expansion, retraction and stabilization, respectively (Table S6). The pessimistic scenario showed a more contrasting pattern than the previous scenario as expansion and retraction presented even higher rates, reaching 11.3% and 82.7%, respectively, although stability was lower, representing 6.2 % of species only (Table S6). Furthermore, the optimistic scenario had not only a net retraction rate 1% lower than the pessimistic, but also a 3% higher stability rate. Comparing the patterns of range distribution with

present, 2050's RCP 2.6 and RCP 8.5 showed that narrow distributions decrease (80.65%, 80.60% and 80.50%, respectively) whilst wide (6.03%, 6.04 and 6.07%, respectively) and intermediate distributions (13.31%, 13.35% and 13.41%, respectively) increase.

### *Taxonomic beta diversity partitioning*

All beta diversity components significantly changed from the current scenario to the future scenarios (ANOVA, Table S2). In the whole area (eco-all) and all individual ecoregions,  $\beta_{sim}$  was significantly higher ( $p < 0.05$ ) than  $\beta_{sne}$  within each scenario, except for eco-5, where  $\beta_{sne}$  was higher than  $\beta_{sim}$  (Table S1). Additionally, in all regions,  $\beta_{sor}$  increased in the future scenarios (Fig. 2; Table S2). For all ecoregions,  $\beta_{sor}$  was higher in RCP 8.5 than in RCP 2.6 and present scenarios. All the individual beta diversity measures ( $\beta_{sim}$ ,  $\beta_{sne}$  and  $\beta_{sor}$ ) were higher in RCP 2.6 and RCP 8.5 than in the present scenario, except in eco-0, where the present  $\beta_{sim}$  was indeed higher than in future scenarios (Table S2). Moreover, RCP

8.5 showed even higher indices than RCP 2.6, except for the  $\beta_{sim}$  of eco-5 and eco-12, where no significant difference was found.

In the temporal pairwise comparison among scenarios,  $\beta_{sim}$  and  $\beta_{sne}$  of the present–RCP 2.6 pair were significantly higher than the present–RCP 8.5 pair, except for  $\beta_{sim}$  in eco-18 and  $\beta_{sne}$  in eco-0, where there were no differences detected with ANOVA (Fig. S1; Table S3).

### *Functional traits and diversity distribution*

Comparing the present time to future scenarios (RCP 2.6; RCP 8.5), the CWM for all five traits changed, in most ecoregions and for the whole study area (Fig. 3; Table S4). In addition, all five ecoregions did not show the same tendencies for changes in future scenarios, especially eco-0 (located at the southern limit of the study area), and eco-5 and eco-12 (the northernmost ecoregions; Fig. 3). In general, there was a decrease in maximum height (Hmax), except for the opposite result in eco-0, (Fig. 3A; Table 4), and an

increase in stem wood density (SWD), seed length (SL) and fruit length (FL) (Figs. 3C, 3D and 3E, respectively; Table S4). Leaf area (LA) did not exhibit change for the whole area (eco-all), but eco-5 and eco-12 had increased values, whilst eco-16 and eco-18, decreased.

Seemingly to the CWMs, the values within each functional diversity index showed a congruent pattern of variation in future scenarios (Fig. 4). Functional divergence (FDiv; Fig. 4A) and functional richness (FRic; Fig. 4C) decreased, whilst functional evenness (FEve; Fig. 4B) increased. The only exception was FDiv in eco-0, which increased in the pessimistic future scenario (Fig. 4A; Table S5).

## Discussion

In general, we found that climate change has the potential to critically alter the woody plant biodiversity in the *Restinga* vegetation by 2050. The results point to a potential taxonomic heterogenization and functional homogenization, which indicate the first stages of a sequential process of long-term biodiversity loss and biotic homogenization. The gauged increase of taxonomic beta diversity in pessimistic future scenarios accompanied by the predicted loss of species suggests subtractive taxonomic heterogenization, where the loss of few highly ubiquitous species boosts beta diversity (Socolar et al., 2016). In addition, the higher turnover in relation to nestedness indicates the replacement of some ubiquitous species by non-ubiquitous ones despite the observed overall richness reduction. The combination of higher beta diversity values and species loss supports the heterogenization hypothesis, which states that an increase in beta diversity corresponds to a decrease in the mean of distribution range sizes either through the incursion of micro-endemic species (e.g., non-ubiquitous species) into the study area or through the net contraction of species ranges (Ochoa-Ochoa et al., 2012). Nevertheless, the decrease in the number of narrow-ranged species may be a sign that some non-ubiquitous and/or endemic species are predicted to be lost, what may contribute to a process of taxonomic homogenization in the future. Regarding the functional dimension, however, we observed an ongoing process of functional

homogenization whereby the mean of key traits changes and clings towards one direction. Future environmental filters will potentially constrain species functional diversity to more acclimated trait values, narrowing the functional space. The taxonomic and functional outcomes forecast by our results are alarming, considering that human impacts extend beyond the climatic factors, therefore the estimated detrimental impacts on biodiversity are likely conservative and may act in synergy with other anthropogenic impacts, potentially leading to an even worse scenario of expressive loss of biodiversity and functions (Hidasi-Neto et al., 2019; Prieto-Torres et al., 2020).

Climate change may impose particular ecological filters that constrain the occurrence of trait diversity. At a single trophic level, disturbance, if in low intensity and frequency, may increase species richness (McCabe and Gotelli, 2000), on the other hand, it may lead to species loss, as only species at a certain range of the functional traits are allowed to establish and perpetuate. As our models predicted species loss in local, regional and continental scales, climate change in the *Restinga* vegetation may represent an intense and growing disturbance phenomenon. The regional scale (study area), representing gamma diversity, may witness the loss of two species in the optimistic scenario and six species in the pessimistic, all with narrow distribution. The models indicated that the species *Unonopsis aurantiaca* may disappear in both contrasting future scenarios of the study area where it is endemic, what endorses the concerning result of our models. In the more localized scale (ecoregions), species loss reached striking levels, making up to 134 of projected lost species by eco-5 in the pessimistic scenario, which represents 19% of its current estimated woody plant species number. Moreover, the unsettling levels of species loss and displacement will potentially hinder ecosystem processes in the *Restinga* vegetation and, by extension, the provision of ecosystem services crucial to human well-being.

The general projected increase of wood density and decrease of maximum height (and leaf area in a couple of ecoregions) suggest that these ecosystems might face dryer and warmer environmental conditions in 2050, as woody plant species are driven towards a more conservative ecological strategy, although further studies are necessary to explore this matter. The

above-mentioned homogenization of functional diversity is attributed to the decrease of two out of the three aspects of functional diversity measures, FRic and FDiv. This outcome indicates a narrower functional space with declining species abundances in more extreme trait values. Although FEve showed, instead, an overall increase in future projections, this result is rather expected, considering the significant loss of projected species richness and environmental suitability (proxy of abundance). Moreover, an increase in FEve, coupled with a decrease in FRic, has been observed in the latitudinal gradient of taxonomic diversity (Schumm et al., 2019) and after mass extinction events (Edie et al., 2018). In these cases, despite major loss of species, the majority of, if not all, functional groups will persist, even with very few species and lower abundances, so the distribution of the species' abundances tends to be more uniform.

The *Restinga* is one of the most vulnerable marginal ecosystems of the Atlantic Forest (Scarano, 2009). Our models have indicated drastic effects of climate change on the diversity and functionality of these systems in a near future. Nevertheless, other current menaces such as deforestation, biological invasion and land-use change (Zamith and Scarano, 2006) are not expected to decrease nor cease in the near future, and they can act in synergy with climate change. The future conservation of the *Restinga* can be more uncertain than the outcome pointed out in this work, as we have addressed only one threat. It is important to highlight that this vegetation is typically composed by species with high phenotypic plasticity (Zamith and Scarano, 2006), which could affect species distribution. Another relevant aspect is that part of these *Restinga* plant communities is also structured by the facilitation process, especially in non-forest areas at initial stages of succession (Dalotto et al., 2018). Thus, incorporating the information on the species phenotypic plasticity, biological interactions and even considering sea-level rise in future models could promote higher refinement to predictions of the effects of climate change on the *Restinga* vegetation.

The used method for estimating abundance from environmental suitability is a practical approach to capture changes in species distributions and their functionalities. Despite the evidence of significant correlation

between the suitability index and abundance, several factors may contribute to some degree of uncertainty in the results. For instance, (i) ENMs may inaccurately estimate species-environment correlation due to limited environmental representability within accessible areas; (ii) local factors and biological interactions not anticipated by the models may limit the occurrence of species at a given site; and (iii) correlative models assume niche stability, when in fact it is dynamic. In spite of the methodological limitations and associated uncertainty, ENM endorses conjecturing over large spatial and temporal scales, and allows exploring macroecological community assembly processes (Distler et al., 2015).

Understanding the relationship between the distribution of the taxonomic and functional facets of biodiversity across spatio-temporal scales and different scenarios is crucial to guide conservation strategies that deal with the uncertainty of the future. The predicted higher future turnover associated to decreasing species richness should be considered when planning protected areas in the *Restinga* vegetation, otherwise it would risk losing species and functions (Tuomisto et al., 2003). Moreover, the conservation of the *Restinga* is also vulnerable to law subterfuges (Marques et al., 2015). Tackling this and many other issues to attain healthier ecosystems is paramount not only for the intrinsic value and maintenance of the Atlantic Forest biodiversity, but also to preserve ecosystem services essential to the prevalence of the Brazilian coastal natural wonders as well as the traditional peoples and communities that rely on its integrity.

### **Conflicts of interest**

None declared.

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## Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi: <https://doi.org/10.1016/j.pecon.2020.12.006>.

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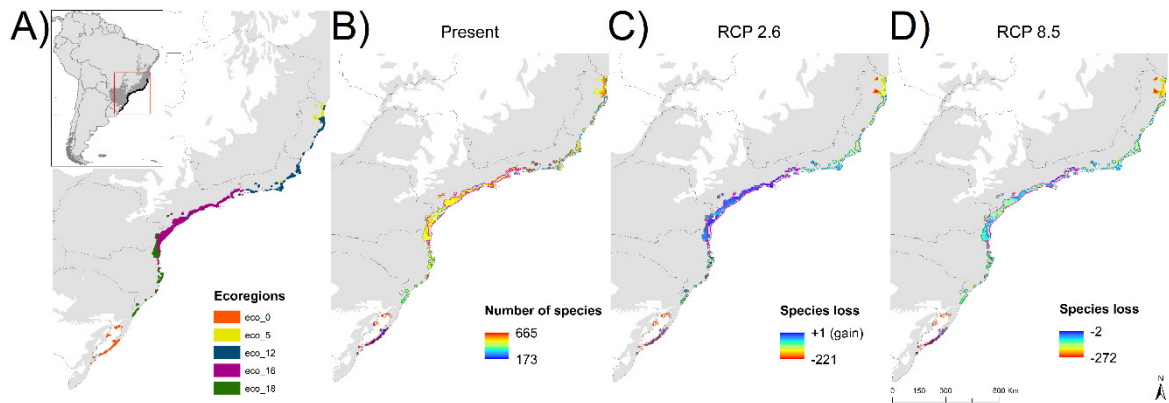
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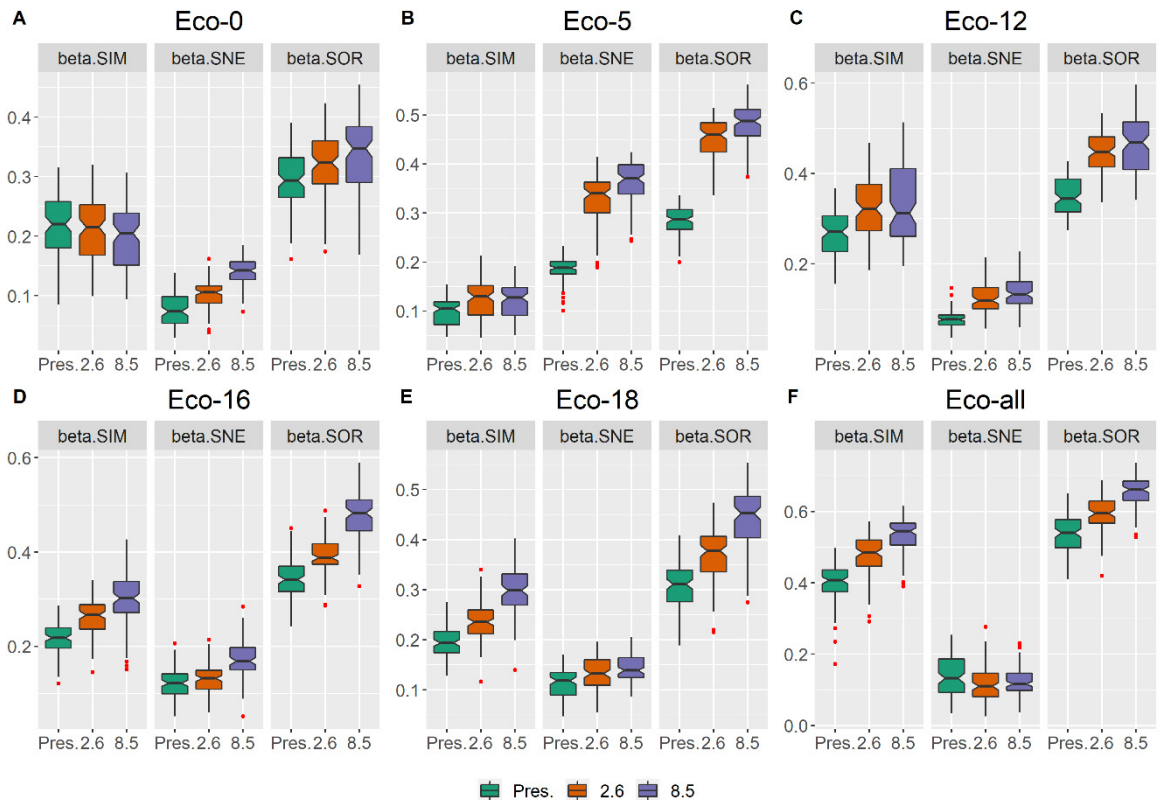
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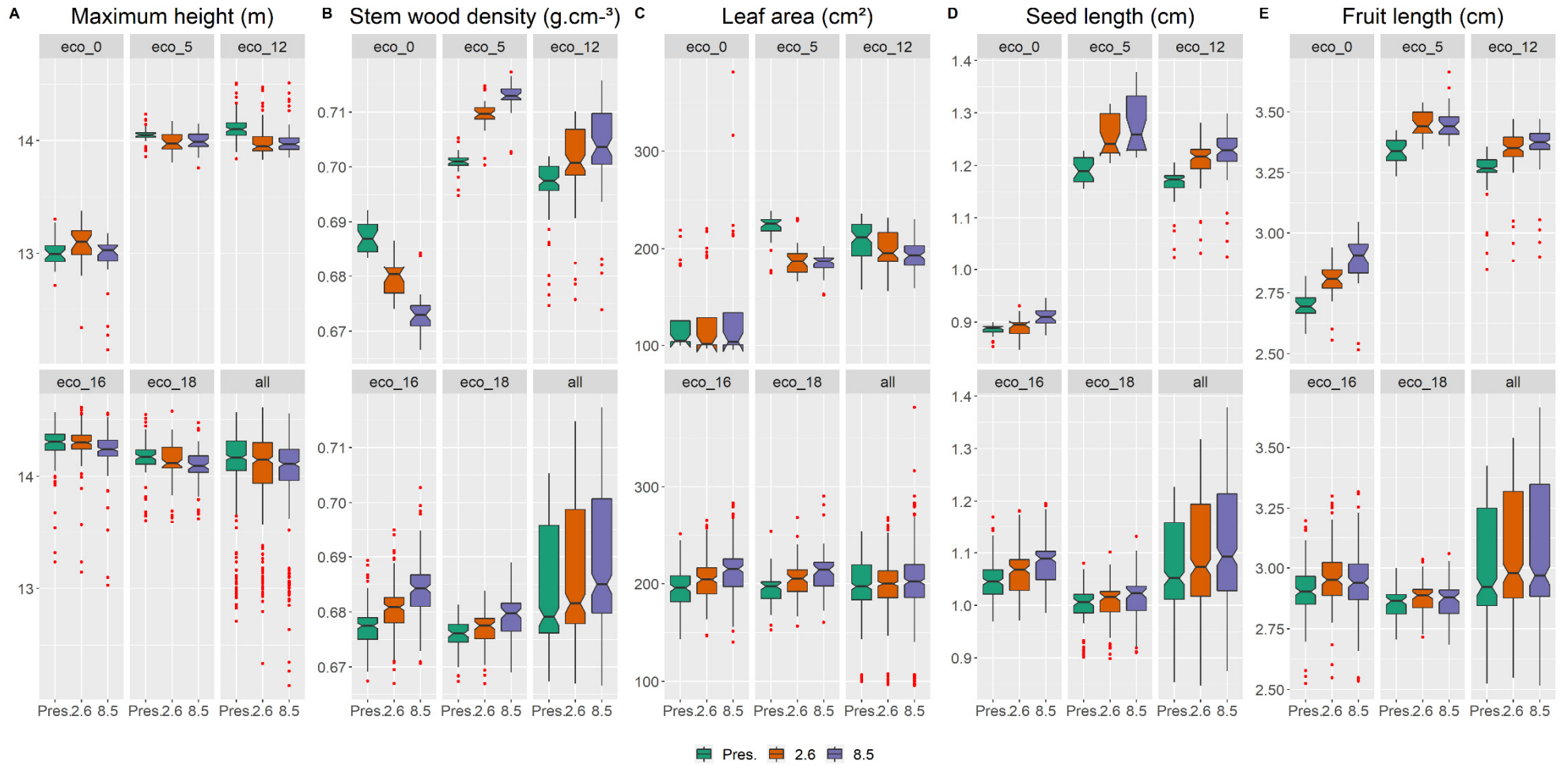
## FIGURES



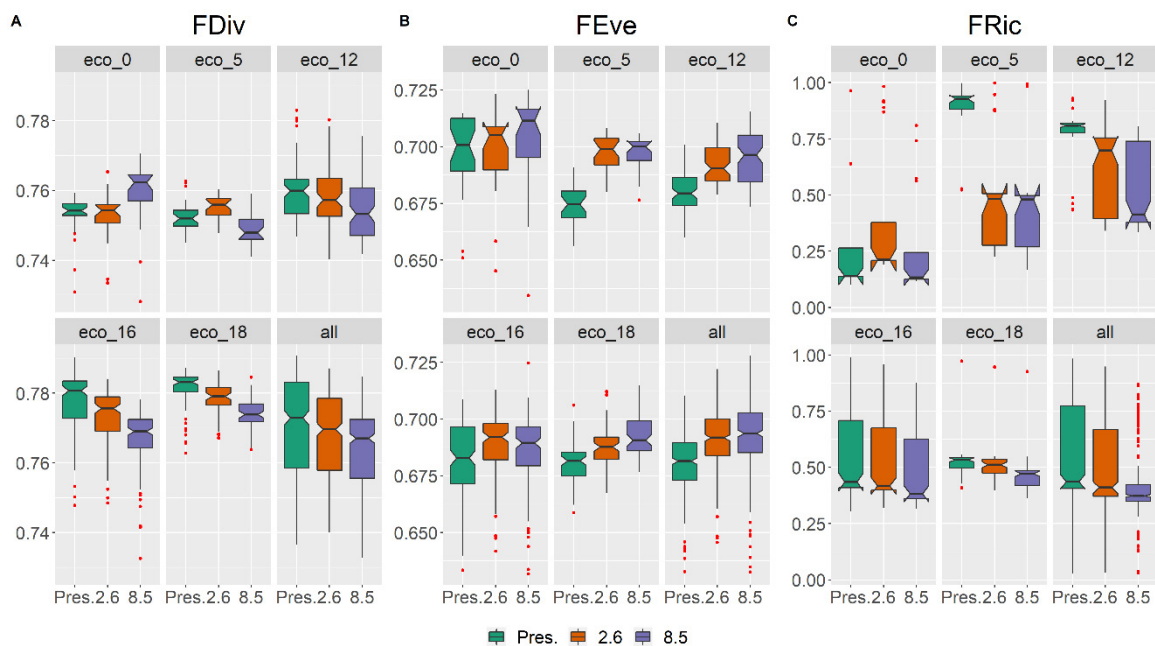
**Fig. 1.** Study ecoregions eco-0, -5, -12, -16 and -18 plus eco-all – assigning to the whole summed up area – (A), current number of species (B), and future projected species loss (C and D). A buffer of 20 km was created around the final ecoregions to fit the shapefiles and the distribution raster resolution and to better integrate the total area, specially the isolated and smaller ones, in more detail.



**Fig. 2.** Boxplots of each taxonomic Sørensen's beta diversity ( $\beta_{sor}$ ) and its components of turnover ( $\beta_{sim}$ ) and nestedness ( $\beta_{sne}$ ) in five ecoregions (A, B, C, D and E) and in the whole area (F) in the present and future scenarios.



**Fig. 3.** Functional traits' community-weighted mean (CWM) boxplots of five functional traits in five ecoregions (eco-0, eco-5, eco-12, eco-16 and eco-18) and in the whole area (eco-all) at the present and in future scenarios.



**Fig. 4.** Functional diversity indices boxplots (FDiv (A), FEve (B) and FRic (C)) in five ecoregions (eco-0, -5, -12, -16 and -18) and in the whole area (eco-all) at the present and in future scenarios.

## Appendix A – Supplementary material

### Methods for climatic data and ecological niche modeling

#### *Species occurrence data*

The 144,375-occurrence data from 796 woody plant species collected from SpeciesLink and GBIF databases were projected in ArcGis and cleaned up. This process consists in excluding problematic and imprecise occurrence data like duplicated and improbable points such as those on the sea and out of the distribution range according to *Flora do Brasil* (<http://floradobrasil.jbrj.gov.br/>) and *Tropicos* (<http://www.tropicos.org/>). After cleaning species occurrence data, we applied a spatial filtering procedure to reduce sampling bias. Occurrences from the same species that were closer than 20 km were excluded and we also only considered species that contained a minimum of 10 occurrences points inside South America, after data cleaning and spatial filtering. We opted for 20 km based on assessment of the number of species having a minimum of 10 occurrences. In fact, increasing such filtering distance (e.g., 25 km) would drastically reduce the number of species with at least 10 occurrences in the study, whereas considering smaller distances and species with less than 10 occurrences could lead to biased models (Zwiener et al., 2020). Increasing such filtering distance would drastically reduce the number of species in the study, whereas considering smaller distances and species with less than 10 occurrences could lead to biased models. We used the Maxent implementation in the ‘dismo’ (Hijmans et al., 2012) R package, all feature classes (as the default), raw output, and no clamping. It is important to highlight that for this study, despite that WorldClim 1.4 uses climatic variables from 1960 to 1990, the species occurrences are not restricted

to that period of time.

### *Climatic data*

Climatic variables were compiled from the WorldClim 1.4 database (Hijmans et al., 2005) at a spatial resolution of 5'. The 19 variables summarize precipitation and temperature tendencies and represent annual seasonal tendencies as well as limiting and extreme environmental drivers (Hijmans et al., 2005). The set of variables for future climate projections was chosen based on the IPCC Fifth Assessment Report. We selected the global climate models (GCM) CCSM4, GISS-E2-R and MIROC5 and two contrasting representative concentration pathways (RCP 2.6 and RCP 8.5) for the year 2050 (the average for 2041-2060). The GCMs were selected based on the variability of climate predictions. We randomly sampled 1,000 pixels of bioclimatic rasters from all GCMs of the CMIP5 (Coupled Model Intercomparison Project Phase 5) RCP 2.6 and RCP 8.5 scenarios, available for 2050 in the WorldClim database, extracted the respective bioclimatic variables and performed a non-metric multidimensional scaling (NMDS) based on Euclidean distances. We selected contrasting GCMs, in terms of predictions, based on the ordination plot of the NMDS. Hereupon, the bioclimatic variables were submitted to principal component analysis (PCA) in order to reduce the dimensionality and collinearity of environmental layers, which was based on a correlation matrix of standardized variables. Finally, we chose the first six principal components axes as a proxy for the climatic variables in the ecological niche modeling, as they account for >95% of the variation. Moreover, despite WorldClim 1.4 uses climatic variables from 1960 to 1990, the species occurrences are not restricted to that period of time.

### *Ecological niche modeling*

Ecological niche modeling approach was used to predict suitable areas where each species could naturally occur in the present and in the future, based on 19 WorldClim (Hijmans et al., 2005) environmental variable models and potential dispersal dynamics. Its core assumptions are that environmental conditions are crucial components of a species' ecological niche and that the equilibrium between them has been reached where they occur (Peterson et al., 2011; Soberón and Nakamura, 2009). Other assumptions are that species interactions play null or little effect on large-scale distributional patterns (Soberón and Nakamura, 2009; but see Anderson, 2017; Inderjit et al., 2017), and that phenotypic plasticity would potentially take place despite the fact it is unlikely to be precisely predicted in order to be incorporated into niche modeling. As dispersal is a pivotal factor in determining species distributions, a calibration area buffer of either 100 or 200 kilometers - for restricted (i.e., regional) and wide (i.e., continental) distributions, respectively - was created around each occurrence point and a convex hull polygon of minimum bounding geometry was drawn in ArcGIS. The resulting polygon represented the M dimension, which depicts the potential areas where the species could physically reach, and was used in the niche modeling.

The maximum entropy (Maxent) method was used to construct niche models (Phillips et al., 2006). It was chosen over other available modeling methods given its high performance and suitability for presence-only data (Elith et al., 2006; Peterson et al., 2011). The settings were: five bootstraps replications, raw output and a threshold of 5% lower values of training presences over the mean estimate to produce binary predictions (Merow et al., 2013; Peterson et al., 2011). Other settings were kept as the default.

The geographical distribution estimates for each species in the future were derived from overlaying the thresholded projections of the three global circulation

models and selecting only the areas where the three models overlapped. The climatic data and ENM processing were performed with the package 'dismo' (Hijmans, et al., 2012) and scripts available at <https://github.com/narayanibarve/ENMGadgets>. All analyses in this work were performed in R (R Core Team, 2017).

To evaluate models, we randomly split the data into training (70%) and testing (30%) datasets. Due to lack of true absence data, we used omission error as a performance metric using the function 'kuenm\_omrat', implemented in the R package 'kuenm' (<https://github.com/marloncobos/kuenm>) with default parameters (threshold = 5). We only considered models that presented error rate  $\leq 5\%$  on testing data. Final models were calibrated with all occurrences and applied in the subsequent biodiversity analyses.

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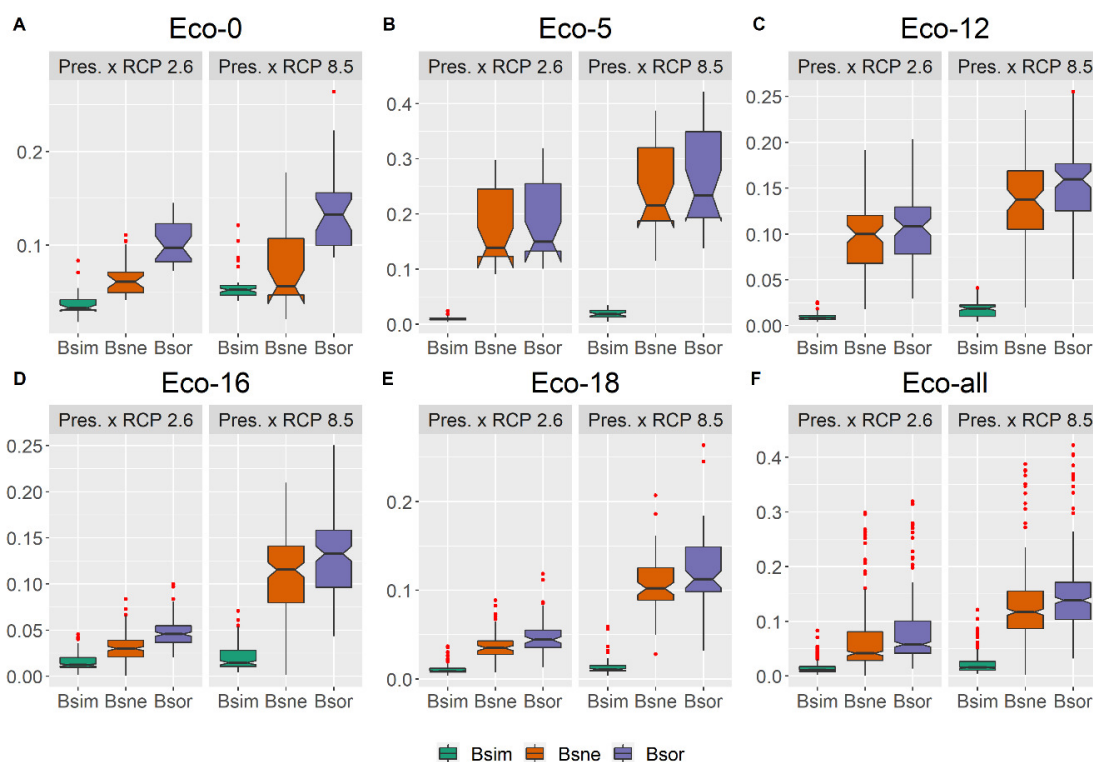
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## Figures and tables



**Fig.**

**S1.** Temporal pairwise comparison boxplots for each ecoregion in each present-future scenario pair.

**Table S1.**  $\beta_{sim}$  and  $\beta_{sne}$  comparison in each scenario ANOVA (DF = 1) and Fisher's LSD (post hoc) results in each ecoregion ('ecoreg') and scenario. Significance codes: 0 (\*\*\*), 0.001 (\*\*), 0.01 (\*) and 0.05 (·).

Ecoreg.	Scenario	ANOVA		Post hoc	
		F-value	p	$\beta_{sim}$	$\beta_{sne}$
				mean ( $\pm$ SD)	mean ( $\pm$ SD)
eco-0	Pres.	554.2	<2e-16***	0.2184 $\pm$ 0.0496 (a)	0.0775 $\pm$ 0.0559 (b)
eco-5	Pres.	543.4	<2e-16***	0.0982 $\pm$ 0.0296 (b)	0.1849 $\pm$ 0.04 (a)
eco-12	Pres.	1332	<2e-16***	0.2697 $\pm$ 0.0418 (a)	0.0784 $\pm$ 0.0453 (b)
eco-16	Pres.	408.5	<2e-16***	0.218 $\pm$ 0.0424 (a)	0.1229 $\pm$ 0.0378 (b)
eco-18	Pres.	358.4	<2e-16***	0.1942 $\pm$ 0.0509 (a)	0.1136 $\pm$ 0.0531 (b)
eco-all	Pres.	1222	<2e-16***	0.4023 $\pm$ 0.0524 (a)	0.1372 $\pm$ 0.0475 (b)
eco-0	2.6	378.3	<2e-16***	0.2143 $\pm$ 0.053 (a)	0.1032 $\pm$ 0.0521 (b)
eco-5	2.6	378.3	<2e-16***	0.1261 $\pm$ 0.0275 (b)	0.326 $\pm$ 0.0412 (a)
eco-12	2.6	378.3	<2e-16***	0.3307 $\pm$ 0.0488 (a)	0.1244 $\pm$ 0.065 (b)
eco-16	2.6	378.3	<2e-16***	0.2611 $\pm$ 0.0342 (a)	0.1306 $\pm$ 0.0408 (b)
eco-18	2.6	378.3	<2e-16***	0.2359 $\pm$ 0.0302 (a)	0.1334 $\pm$ 0.0364 (b)
eco-all	2.6	378.3	<2e-16***	0.4787 $\pm$ 0.0524 (a)	0.1146 $\pm$ 0.054 (b)
eco-0	8.5	96.58	<2e-16***	0.1986 $\pm$ 0.0278 (a)	0.1406 $\pm$ 0.0233 (b)
eco-5	8.5	1776	<2e-16***	0.3622 $\pm$ 0.025 (b)	0.3622 $\pm$ 0.0494 (a)
eco-12	8.5	458.4	<2e-16***	0.3307 $\pm$ 0.0192 (a)	0.135 $\pm$ 0.0337 (b)
eco-16	8.5	382.5	<2e-16***	0.3 $\pm$ 0.0323 (a)	0.1755 $\pm$ 0.0312 (b)
eco-18	8.5	794	<2e-16***	0.3 $\pm$ 0.03 (a)	0.1443 $\pm$ 0.0314 (b)
eco-all	8.5	3867	<2e-16***	0.5317 $\pm$ 0.0549 (a)	0.1233 $\pm$ 0.0453 (b)

**Table S2.** ANOVA (DF = 2) and Fisher's LSD (post hoc) results of  $\beta_{sim}$ ,  $\beta_{sne}$  and  $\beta_{sor}$  comparison among all three scenarios, with each variable ('var.') in each ecoregion ('ecoreg.'). Significance codes: 0 (\*\*\*), 0.001 (\*\*), 0.01 (\*) and 0.05 (·).

Ecoreg.	Var.	ANOVA		Post hoc		
		F-value	p	Pres.	2.6	8.5
				mean ( $\pm$ SD)	mean ( $\pm$ SD)	mean ( $\pm$ SD)
eco-0	$\beta_{sim}$	3.836	0.0227*	0.2184 $\pm$ 0.0496 (a)	0.2143 $\pm$ 0.053 (ab)	0.1986 $\pm$ 0.0278 (b)
eco-5	$\beta_{sim}$	18.21	3.47e-08***	0.0982 $\pm$ 0.0296 (b)	0.1261 $\pm$ 0.0275 (a)	0.1216 $\pm$ 0.025 (a)
eco-12	$\beta_{sim}$	23.96	2.25e-10***	0.2697 $\pm$ 0.0418 (b)	0.3307 $\pm$ 0.0488 (a)	0.3224 $\pm$ 0.0192 (a)
eco-16	$\beta_{sim}$	95.13	<2e-16***	0.218 $\pm$ 0.0424 (c)	0.2611 $\pm$ 0.0342 (b)	0.3 $\pm$ 0.0323 (a)
eco-18	$\beta_{sim}$	185.9	<2e-16***	0.1942 $\pm$ 0.0509 (c)	0.2359 $\pm$ 0.0302 (b)	0.3 $\pm$ 0.03 (a)
eco-all	$\beta_{sim}$	153.6	<2e-16***	0.4023 $\pm$ 0.0524 (c)	0.4787 $\pm$ 0.0524 (b)	0.5317 $\pm$ 0.0549 (a)
eco-0	$\beta_{sne}$	166.6	<2e-16***	0.0775 $\pm$ 0.0559 (c)	0.1032 $\pm$ 0.0521 (b)	0.1406 $\pm$ 0.0233 (a)
eco-5	$\beta_{sne}$	516.6	<2e-16***	0.1849 $\pm$ 0.04 (c)	0.326 $\pm$ 0.0412 (b)	0.3622 $\pm$ 0.0494 (a)
eco-12	$\beta_{sne}$	99.27	<2e-16***	0.0784 $\pm$ 0.0453 (c)	0.1244 $\pm$ 0.065 (b)	0.135 $\pm$ 0.0337 (a)
eco-16	$\beta_{sne}$	67.39	<2e-16***	0.1306 $\pm$ 0.0378 (b)	0.1229 $\pm$ 0.0408 (b)	0.1755 $\pm$ 0.0312 (a)
eco-18	$\beta_{sne}$	28.05	6.92e-12***	0.1136 $\pm$ 0.0531 (c)	0.1334 $\pm$ 0.0364 (b)	0.1443 $\pm$ 0.0314 (a)
eco-all	$\beta_{sne}$	5.733	0.00361**	0.1372 $\pm$ 0.0475 (a)	0.1146 $\pm$ 0.054 (b)	0.1233 $\pm$ 0.0453 (ab)
eco-0	$\beta_{sor}$	14.73	7.94e-07***	0.2959 $\pm$ 0.0633 (c)	0.3175 $\pm$ 0.0546 (b)	0.3392 $\pm$ 0.0223 (a)
eco-5	$\beta_{sor}$	835.5	<2e-16***	0.2831 $\pm$ 0.0413 (c)	0.452 $\pm$ 0.0351 (b)	0.4838 $\pm$ 0.045 (a)
eco-12	$\beta_{sor}$	154.3	<2e-16***	0.3481 $\pm$ 0.063 (c)	0.4469 $\pm$ 0.0844 (b)	0.4657 $\pm$ 0.0351 (a)
eco-16	$\beta_{sor}$	252.7	<2e-16***	0.3409 $\pm$ 0.0475 (c)	0.3917 $\pm$ 0.0498 (b)	0.4755 $\pm$ 0.0397 (a)
eco-18	$\beta_{sor}$	165.1	<2e-16***	0.3078 $\pm$ 0.0555 (c)	0.3694 $\pm$ 0.0484 (b)	0.4443 $\pm$ 0.0267 (a)
eco-all	$\beta_{sor}$	146.6	<2e-16***	0.5395 $\pm$ 0.0428 (c)	0.5933 $\pm$ 0.051 (b)	0.655 $\pm$ 0.0414 (a)

**Table S3.** ANOVA (DF = 1) and Fisher's LSD (post hoc) results of the temporal  $\beta_{sim}$  and  $\beta_{sne}$  comparison among the pairwise scenarios, with each variable ('var.') in each ecoregion ('ecoreg.'). Significance codes: 0 (\*\*\*), 0.001 (\*\*), 0.01 (\*) and 0.05 (·).

Ecoreg.	Var.	ANOVA		Post hoc	
		F-value	p	Pres. vs 2.6	Pres. vs 8.5
				mean ( $\pm$ SD)	mean ( $\pm$ SD)
eco-0	$\beta_{sim}$	19.36	5.14e-5***	0.058 $\pm$ 0.014 (a)	0.0382 $\pm$ 0.02 (b)
eco-5	$\beta_{sim}$	23.63	1.05e-5***	0.0187 $\pm$ 0.0044 (a)	0.0103 $\pm$ 0.0685 (b)
eco-12	$\beta_{sim}$	77.35	2.17e-15***	0.018 $\pm$ 0.0039 (a)	0.0093 $\pm$ 0.0377 (b)
eco-16	$\beta_{sim}$	12.48	4.78e-4***	0.0206 $\pm$ 0.009 (a)	0.0156 $\pm$ 0.0149 (b)
eco-18	$\beta_{sim}$	3.938	0.0493*	0.0113 $\pm$ 0.0074 NA	0.0143 $\pm$ 0.0155 NA
eco-all	$\beta_{sim}$	42.54	1.33e-10***	0.0216 $\pm$ 0.0109 (a)	0.0147 $\pm$ 0.0511 (b)
eco-0	$\beta_{sne}$	2.634	0.11	0.0645 $\pm$ 0.014 NA	0.0799 $\pm$ 0.02 NA
eco-5	$\beta_{sne}$	12.85	7.27e-4***	0.2465 $\pm$ 0.0044 (a)	0.1741 $\pm$ 0.0685 (b)
eco-12	$\beta_{sne}$	41.48	1.33e-9***	0.1377 $\pm$ 0.0039 (a)	0.0947 $\pm$ 0.0377 (b)
eco-16	$\beta_{sne}$	425.4	<2e-16***	0.1102 $\pm$ 0.009 (a)	0.0318 $\pm$ 0.0149 (b)
eco-18	$\beta_{sne}$	266.6	<2e-16***	0.1078 $\pm$ 0.0074 (a)	0.0376 $\pm$ 0.0155 (b)
eco-all	$\beta_{sne}$	220.3	<2e-16***	0.1246 $\pm$ 0.0109 (a)	0.0616 $\pm$ 0.0511 (b)

**Table S4.** ANOVA (DF = 2) and Fisher's LSD (post hoc) results of the community-weighted means comparison among all three scenarios, with each variable ('var.') in each ecoregion ('ecoreg.'). Significance codes: 0 (\*\*\*), 0.001 (\*\*), 0.01 (\*) and 0.05 (·).

Ecoreg.	Var.	ANOVA		Post hoc		
		F-value	p	Pres. mean ( $\pm$ SD)	2.6 mean ( $\pm$ SD)	8.5 mean ( $\pm$ SD)
eco-0	Hmax	3.853	0.0252*	13.002 $\pm$ 0.1295 ab	13.094 $\pm$ 0.2016 a	12.938 $\pm$ 0.1195 b
eco-5	Hmax	4.232	0.0179*	14.053 $\pm$ 0.2159 a	13.99 $\pm$ 0.1909 b	13.994 $\pm$ 0.1448 ab
eco-12	Hmax	22.59	1.02e-09***	14.12 $\pm$ 0.2682 a	13.999 $\pm$ 0.17 b	14.003 $\pm$ 0.1261 b
eco-16	Hmax	3.136	0.0444*	14.273 $\pm$ 0.0814 a	14.281 $\pm$ 0.0659 a	14.229 $\pm$ 0.1875 a
eco-18	Hmax	1.811	0.166	14.147 $\pm$ 0.1014 NA	14.125 $\pm$ 0.2281 NA	14.086 $\pm$ 0.1813 NA
eco-all	Hmax	2.905	0.0552·	14.093 $\pm$ 0.0875 a	14.066 $\pm$ 0.1824 a	14.026 $\pm$ 0.1968 a
eco-0	SWD	121.9	<2e-16***	0.6872 $\pm$ 0.1195 a	0.6796 $\pm$ 0.1295 b	0.6732 $\pm$ 0.2016 c
eco-5	SWD	116.6	<2e-16***	0.7009 $\pm$ 0.1448 c	0.7093 $\pm$ 0.2159 b	0.7126 $\pm$ 0.1909 a
eco-12	SWD	24.57	1.97e-10***	0.6966 $\pm$ 0.1261 c	0.7013 $\pm$ 0.2682 b	0.7039 $\pm$ 0.17 a
eco-16	SWD	73.68	<2e-16***	0.6773 $\pm$ 0.1875 c	0.6805 $\pm$ 0.0814 b	0.6843 $\pm$ 0.0659 a
eco-18	SWD	17.52	9.7e-08***	0.6758 $\pm$ 0.1813 b	0.677 $\pm$ 0.1014 b	0.6793 $\pm$ 0.2281 a
eco-all	SWD	15.35	2.7e-07***	0.6842 $\pm$ 0.1968 c	0.6869 $\pm$ 0.0875 b	0.6892 $\pm$ 0.1824 a
eco-0	LA	0.543	0.583	126.26 $\pm$ 0.2016 NA	126.84 $\pm$ 0.1195 NA	139.83 $\pm$ 0.1295 NA
eco-5	LA	36.4	5.28e-12***	219.16 $\pm$ 0.1909 a	189.1 $\pm$ 0.1448 b	182.99 $\pm$ 0.2159 b
eco-12	LA	15.89	3.3e-07***	209.13 $\pm$ 0.17 a	196.82 $\pm$ 0.1261 b	192.33 $\pm$ 0.2682 b
eco-16	LA	19.99	5.02e-09***	196.76 $\pm$ 0.0659 c	205.98 $\pm$ 0.1875 b	214.59 $\pm$ 0.0814 a
eco-18	LA	12.16	1.04e-05***	194.45 $\pm$ 0.2281 b	203.54 $\pm$ 0.1813 a	211.17 $\pm$ 0.1014 a
eco-all	LA	2.352	0.0957·	195.32 $\pm$ 0.1824 a	195.67 $\pm$ 0.1968 a	200.22 $\pm$ 0.0875 a
eco-0	SL	16.78	7.97e-07***	0.885 $\pm$ 0.1295 b	0.8895 $\pm$ 0.2016 b	0.9103 $\pm$ 0.1195 a
eco-5	SL	33.56	2.42e-11***	1.191 $\pm$ 0.2159 b	1.2581 $\pm$ 0.1909 a	1.2794 $\pm$ 0.1448 a
eco-12	SL	45.4	<2e-16***	1.1665 $\pm$ 0.2682 b	1.21 $\pm$ 0.17 a	1.2251 $\pm$ 0.1261 a
eco-16	SL	25.48	3.51e-11***	1.047 $\pm$ 0.0814 c	1.065 $\pm$ 0.0659 b	1.0815 $\pm$ 0.1875 a
eco-18	SL	2.772	0.0649·	0.9965 $\pm$ 0.1014 NA	1.003 $\pm$ 0.2281 NA	1.0138 $\pm$ 0.1813 NA
eco-all	SL	12.93	2.84e-06***	1.0635 $\pm$ 0.0875 b	1.088 $\pm$ 0.1824 a	1.1038 $\pm$ 0.1968 a
eco-0	FL	29.75	2.05e-10***	2.6982 $\pm$ 0.1195 c	2.7957 $\pm$ 0.1295 b	2.8873 $\pm$ 0.2016 a
eco-5	FL	33.5	2.5e-11***	3.3395 $\pm$ 0.1448 b	3.4508 $\pm$ 0.2159 a	3.4538 $\pm$ 0.1909 a
eco-12	FL	25.34	1.03e-10***	3.2597 $\pm$ 0.1261 b	3.3394 $\pm$ 0.2682 a	3.3591 $\pm$ 0.17 a
eco-16	FL	7.156	8.77e-4***	2.9073 $\pm$ 0.1875 b	2.957 $\pm$ 0.0814 a	2.9446 $\pm$ 0.0659 a
eco-18	FL	1.439	0.24	2.8504 $\pm$ 0.1813 NA	2.8711 $\pm$ 0.1014 NA	2.863 $\pm$ 0.2281 NA
eco-all	FL	8.318	2.61e-4***	2.9959 $\pm$ 0.1968 b	3.0557 $\pm$ 0.0875 a	3.0612 $\pm$ 0.1824 a

**Table S5.** ANOVA (DF = 2) and Fisher's LSD (post hoc) results of the functional diversity indices comparison among all three scenarios, with each variable ('var.') in each ecoregion ('ecoreg.'). Significance codes: 0 (\*\*\*), 0.001 (\*\*), 0.01 (\*) and 0.05 (·).

Ecoreg.	Var.	ANOVA		Post hoc		
		F-value	p	Pres.	2.6	8.5
				mean(±SD)	mean (±SD)	mean (±SD)
eco-0	FDiv	7.513	0.00102**	0.7527 ± 0.0062 (b)	0.7526 ± 0.0062 (b)	0.7594 ± 0.0081 (a)
eco-5	FDiv	15.67	1.76e-06***	0.7527 ± 0.0071 (a)	0.7553 ± 0.0047 (a)	0.7492 ± 0.0086 (b)
eco-12	FDiv	8.708	22.3e-5***	0.7597 ± 0.0091 (a)	0.7577 ± 0.0041 (a)	0.7544 ± 0.0123 (b)
eco-16	FDiv	66.73	<2e-16***	0.7776 ± 0.0044 (a)	0.7738 ± 0.005 (b)	0.7674 ± 0.0168 (c)
eco-18	FDiv	32.83	4.6e-13***	0.7807 ± 0.0033 (a)	0.7781 ± 0.0079 (b)	0.7737 ± 0.0137 (c)
eco-all	FDiv	27.48	2.34e-12***	0.7703 ± 0.0045 (a)	0.7681 ± 0.0074 (b)	0.7638 ± 0.015 (c)
eco-0	FEve	1.327	0.271	0.698 ± 0.0076 NA	0.6987 ± 0.0169 NA	0.705 ± 0.0086 NA
eco-5	FEve	72.28	<2e-16***	0.6741 ± 0.0084 (b)	0.6966 ± 0.0175 (a)	0.6971 ± 0.0092 (a)
eco-12	FEve	53.33	<2e-16***	0.6799 ± 0.0086 (b)	0.6921 ± 0.0188 (a)	0.6949 ± 0.0086 (a)
eco-16	FEve	8.566	22.5e-5***	0.6819 ± 0.0081 (b)	0.6892 ± 0.0084 (a)	0.6866 ± 0.0073 (a)
eco-18	FEve	33.64	2.51e-13***	0.68 ± 0.0069 (c)	0.6879 ± 0.0084 (b)	0.6922 ± 0.0134 (a)
eco-all	FEve	69.37	<2e-16***	0.6815 ± 0.0076 (b)	0.6913 ± 0.0078 (a)	0.6923 ± 0.0189 (a)
eco-0	FRic	1.774	0.176	0.2849 ± 0.2733 NA	0.3846 ± 0.3121 NA	0.2534 ± 0.2238 NA
eco-5	FRic	43.48	<2e-16***	0.8837 ± 0.1322 (a)	0.49 ± 0.2455 (b)	0.4254 ± 0.2028 (b)
eco-12	FRic	59.86	<2e-16***	0.8001 ± 0.0922 (a)	0.5959 ± 0.1777 (b)	0.5471 ± 0.1818 (b)
eco-16	FRic	3.567	<2e-16***	0.5289 ± 0.1781 (a)	0.5113 ± 0.1694 (ab)	0.4756 ± 0.1697 (b)
eco-18	FRic	11.23	<2e-16***	0.5201 ± 0.0707 (a)	0.5063 ± 0.0682 (a)	0.4656 ± 0.0701 (b)
eco-all	FRic	30.7	1.11e-13***	0.546 ± 0.0882 (a)	0.4607 ± 0.1271 (b)	0.4228 ± 0.1369 (b)

**Table S6.** Number of species in each range category for the study area in the climatic scenarios.

Range category	2050 RCP 2.6			2050 RCP 8.5		
	Expansion	Retraction	Stability	Expansion	Retraction	Stability
Intermediate	10	77	19	11	88	7
Narrow	69	537	36	77	537	28
Wide	1	25	22	2	32	14
Total	80 (10.0 %)	639 (80.5 %)	77 (9.7 %)	90 (11.3 %)	657 (82.7 %)	49 (6.2 %)

## Phylogenetic tree

((((((((((((Symphyopappus\_casarettoi:45.259634,Moquiniastrium\_polymorphum:45.259634,(((Austroeupatorium\_inulaefolium:17.695347,Tithonia\_diversifolia:17.695347):5.294113,(Baccharis\_singularis:1.787296,Baccharis\_semiserrata:1.787296,Baccharis\_patens:1.787296,Baccharis\_oblongifolia:1.787296,Baccharis\_longiattenuata:1.787296,Baccharis\_lateralis:1.787296,Baccharis\_crispa:1.787296,Baccharis\_dracunculifolia:1.787297):21.202163):7.684679,((Eremanthus\_erythropappus:9.356008,(Piptocarpha\_axillaris:2.231807,Piptocarpha\_angustifolia:2.231807,Piptocarpha\_rotundifolia:2.231808):7.1242):2.527079,(Vernonanthura\_puberula:1.079406,Vernonanthura\_petiolaris:1.079406,Vernonanthura\_discolor:1.079406,Vernonanthura\_beyrichii:1.079406):10.80368):18.791052):7.620132,(Trixis\_antimenorrhoea:18.180717,Stiffia\_chrysantha:18.180717):20.113554):6.965364,Dasyphyllum\_spinescens:45.259635):47.472002,Escallonia\_bifida:92.731637):0.998575,((((((Schefflera\_calva:0.626424,Schefflera\_angustissima:0.626424):4.240055,((Schefflera\_selloi:0.471605,Schefflera\_macrocarpa:0.471605):1.501848,Schefflera\_morotoni:1.973453):2.893026):7.442248,(Oreopanax\_fulvus:6.730207,Oreopanax\_capitatus:6.730208):5.578519):0.082152,(Dendropanax\_monogynus:10.14907,Dendropanax\_australis:10.14907,Dendropanax\_cuneatus:10.149071):2.241808):6.471233,Schefflera\_vinosa:18.862111):5.692138,Aralia\_warmingiana:24.554249):61.086405,Sambucus\_australis:85.

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### 3 CONSIDERAÇÕES FINAIS

Neste estudo foram apontadas as possíveis consequências das mudanças climáticas para as dimensões taxonômica e funcional da diversidade da vegetação lenhosa na porção meridional da Restinga brasileira. Nossos resultados indicaram a potencial perda de espécies e consequentes processos de heterogenização da diversidade taxonômica beta e homogeneização da diversidade funcional para o ano de 2050. Estes resultados alertam para consequências drásticas na biodiversidade das Restingas em cenários de mudanças climáticas globais, as quais incluem as mudanças climáticas, eventos climáticos extremos, poluição e expansão de novos ecossistemas e impõem uma enorme pressão à entrega diversos desses serviços (CHAPIN *et al.*, 2008). O entendimento a partir da observação dos impactos das mudanças climáticas, associados com processos ecossistêmicos fundamentais para a manutenção da vida, permitiram prever os possíveis cenários futuros.

A abordagem macroecológica da modelagem de nicho permitiu que prevíssemos de que maneira as futuras condições climáticas afetarão a biodiversidade das Restingas, além de gerar modelos da atual e futura distribuição das diversidades dessa frequentemente ignorada fitofisionomia da Mata Atlântica. Apesar de ser ofuscada pelos ecossistemas centrais da Mata Atlântica (Scarano, 2002), as restingas, como um ecossistema marginal, preservam e mantém uma grande parte da diversidade e das funcionalidades do bioma como um todo (MARQUES *et al.*, 2015; MILLENIUM ECOSYSTEM ASSESSMENT, 2005).

A vulnerabilidade desses ecossistemas também é devido à instabilidade costeira provocada pelo aumento do nível do mar (VOUSDOUKAS *et al.*, 2020). Apesar desse possível avanço do mar sobre as áreas costeiras ser um processo relevante para estudo nesse tipo de ambiente (BARNARD *et al.*, 2019), esse fator não

foi considerado neste estudo. Infelizmente, o acesso a esses modelos de elevação do nível do mar é oneroso, o que impossibilitou a inclusão desse fator sobre as modelagens de nicho.

Apesar das limitações, nossos resultados ressaltam a importância dessa vegetação costeira que, similarmente como ocorre em outros lugares do mundo (SPALDING *et al.*, 2014), é consideravelmente povoada, altamente ameaçada por impactos antrópicos e subterfúgios legais, e frequentemente negligenciada em planos de conservação. Por fim, advogamos para que os ecossistemas das Restingas sejam mais efetivamente considerados em estratégias de mitigação e adaptação a mudanças climáticas.

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