

Habitat-specific impacts of climate change in the Mata Atlântica biodiversity hotspot

Luíz Fernando Esser¹  | Danilo M. Neves^{2,3}  | João André Jarenkow¹ 

¹Federal University of Rio Grande do Sul, Porto Alegre, Brazil

²University of Arizona, Tucson, AZ, USA

³Federal University of Minas Gerais, Belo Horizonte, Brazil

Correspondence

Luíz Fernando Esser, Federal University of Rio Grande do Sul, Porto Alegre, Brazil.
Email: luizesser@gmail.com

Editor: Janet Franklin

Abstract

Aim: Elucidate the potential impacts of climate changes on the distribution and conservation of the multiple habitats of the *Mata Atlântica* biodiversity hotspot, which are often treated as a unique entity in ecological studies.

Location: The whole extension of the South American Atlantic Forest Domain plus forest intrusions into the neighbouring Cerrado and Pampa Domains, which comprises rain forest ('core' habitat) and five environmentally marginal habitats, namely high elevation/latitude forest, rock outcrop habitats, riverine forest, semideciduous forest and *restinga* woodlands.

Time period: Current (2000) and future scenarios (2050 and 2070).

Major taxa studied: Tree species.

Methods: We modelled the responses of 282 diagnostic tree species, using multiple algorithms and distinct scenarios of climate change (828,234 projections).

Results: Potential loss of suitable environment summed 50.4% in semideciduous forest, 58.6% in riverine forest and 66% in rock outcrop habitats. Predictions for rain forest (12.2%), *restinga* woodlands (7.6%) and high elevation/latitude forest (5.2%) showed that overall loss of suitable environment will be relatively less severe for these habitats. Habitats that are confined to narrow edaphic conditions, namely rock outcrop habitats and riverine forest, are less studied and will likely suffer the greatest loss of biodiversity because their species are more dispersal limited.

Main conclusions: Because these habitats occupy distinct environmental conditions, lumping them in ecological analyses might lead to erroneous interpretations in studies aiming to evaluate the impacts of global change in the *Mata Atlântica* biodiversity hotspot. This reinforces the importance of our approach and urges for conservation strategies that account for habitat heterogeneity in the *Mata Atlântica* and other species-rich environments.

KEYWORDS

biodiversity conservation, communities' distribution models, habitat conservation, macroecology, tree communities, vegetation

1 | INTRODUCTION

The *Mata Atlântica* of South America is renowned worldwide for being one of the 36 biodiversity hotspots for conservation prioritization (Mittermeier, Turner, Larsen, Brooks, & Gascon, 2011; Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000; Williams et al., 2011). Less known facts, however, are that (a) the hotspot status is specifically referring to its core vegetation type, the rain forest, and that (b) the *Mata Atlântica* also houses a diverse and complex mosaic of vegetation types, with their occurrence and distribution determined by the harshest extremes of five key environmental factors (Figure 1; Neves et al., 2017; Scarano, 2009). Thus, vegetation types are defined here as a plant assemblage and its associated environmental conditions (hereafter 'habitat'). Following Walter (1971), these factors can be classified into azonal (non-climatic) and zonal (climatic). The distribution of azonal habitats in the *Mata Atlântica* is determined by rocky substrates (rock outcrop dwarf-forests and savannas, henceforth rock outcrop habitats), salinity (white-sand woodlands, henceforth *restinga* woodlands) or waterlogged soils (tropical riverine forests, henceforth riverine forest), while the distribution of zonal habitats is determined by frost (montane and subtropical riverine forests, henceforth high elevation/latitude forest), drought stress (semideciduous forests) or high levels of rainfall (cloud and rain forest, henceforth rain forest).

In a seminal article, Scarano (2009) argued that environmentally marginal habitats in the *Mata Atlântica* comprise an impoverished subset of rain forest species that can tolerate the harshest extremes of their environmental conditions. A recent study, however, showed that all *Mata Atlântica* habitats are strikingly distinct both floristically and environmentally (Neves et al., 2017), suggesting that marginal habitats are not simply a nested subset of the more diverse *Mata Atlântica* rain forest. For conservation purposes, a pertinent

takeaway message in Neves et al. (2017) is that a substantial portion of the plant diversity in the *Mata Atlântica* might be neglected if the spatial design for new protected areas is solely based upon studies that places these multiple habitats together (e.g., Zwiener et al., 2017).

Currently, marginal habitats receive much less protection compared with the rain forest (Neves et al., 2017), despite harbouring 3,160 tree species that are not found anywhere else in the world, including in the rain forest of the *Mata Atlântica*. Yet, current levels of fragmentation and the continuous habitat loss are high throughout the *Mata Atlântica*, raising several concerns in the scientific community (Galindo-Leal, Jacobsen, Langhammer, & Olivieri, 2003; Joly, Metzger, & Tabarelli, 2014; Neves et al., 2017; Tabarelli, Cardoso Da Silva, & Gascon, 2004; Tabarelli, Pinto, Silva, Hirota, & Bede, 2005). In addition to these impacts associated with land use change in *Mata Atlântica* habitats, human-induced climate change (IPCC, 2013) will have widespread effects on *Mata Atlântica*'s ecosystems (Ferro, Lemes, Melo, Loyola, & Fenton, 2014; Lemes, Loyola, & Flammini, 2013; Loyola, Lemes, Brum, Provete, & Duarte, 2014). The persistence of biodiversity through such global change will demand biogeographic shifts at all levels of biological organization (e.g. from populations to communities to functional groups, Bhatta, Grytnes, & Vetaas, 2018; Frainer et al., 2017; McLachlan, Hellmann, & Schwartz, 2007, respectively. See also Barnosky et al., 2017, for a recent review).

In the last decades, ecological niche modelling became a major tool to predict the impacts of climate changes on biodiversity, aiding conservation planning in future, dynamic scenarios (Peterson, 2001; Peterson, Egbert, Sánchez-Cordero, & Price, 2000; Peterson et al., 2002). With the development of novel learning machine algorithms (Guisan & Thuiller, 2005) and more accurate climate change predictions (Moss et al., 2010), we are now capable to reduce analytical

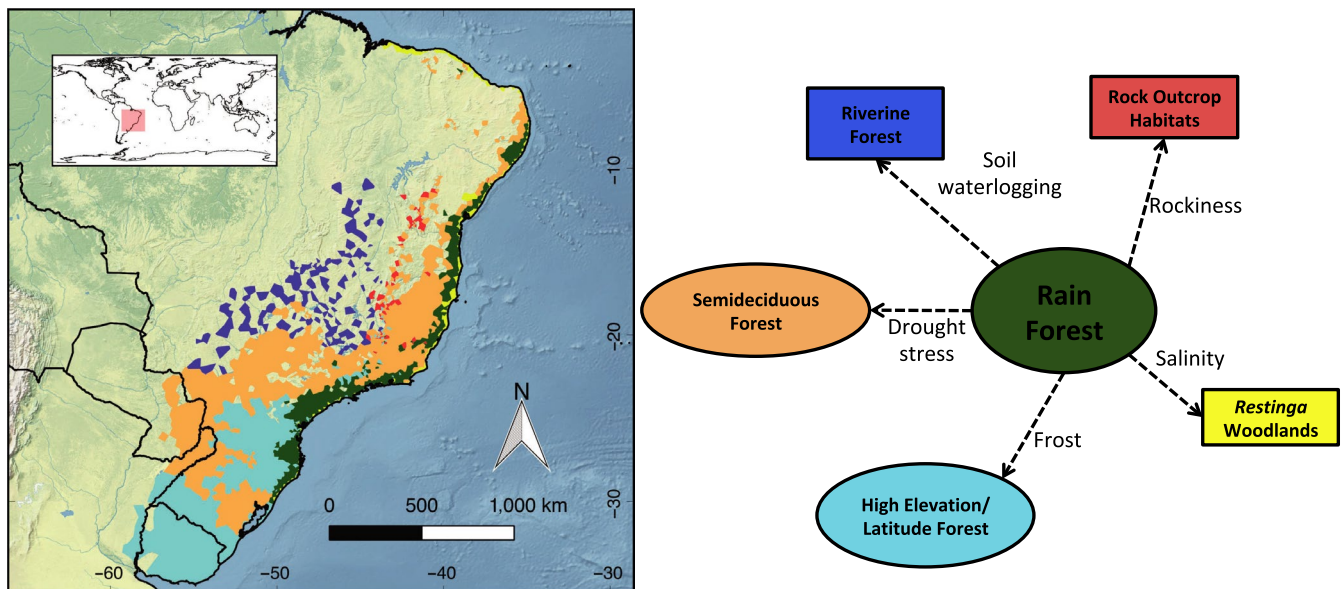


FIGURE 1 Distribution of *Mata Atlântica* habitats in South America (sensu Scarano, 2009) and main environmental factors (arrows) sorting species across these habitats (adapted from Neves et al., 2017). Ellipses indicate zonal habitats, and rectangles indicate azonal habitats

uncertainties and provide the much-needed information to support conservation prioritization while accounting for global change scenarios (Elith et al., 2006). This is of particular relevance for biodiversity hotspots, where species are likely to be more susceptible due to its reduced population sizes caused by habitat fragmentation.

Our goal here is to elucidate the potential impacts of climate changes in *Mata Atlântica* habitats' distribution and conservation. Because *Mata Atlântica* habitats occupy distinct climatic and geographic space, our hypothesis is that climate changes will severely impact all habitats, though to different degrees. In addition, because South America will experience increasing temperatures with reduced water availability (IPCC, 2013), we predict that future climate changes will have less severe impacts in *restinga*, rock outcrop habitats and semideciduous habitats, and more severe impacts in plant communities found at high elevation/latitude and in riverine and rain forests.

2 | METHODS

2.1 | The dataset

We conducted environmental niche modelling for *Mata Atlântica* habitats using diagnostic species obtained from Neves et al. (2017), with their presence points available in NeoTropTree (Oliveira-Filho, 2017). Using diagnostic species to model the climatic distribution of neotropical vegetation has proven a more efficient approach, given its higher TSS and AUC values (Bueno et al., 2017) compared with previous studies (Carnaval & Moritz, 2008; Pena, Kamino, Rodrigues, Mariano-Neto, & de Siqueira, 2014; Werneck, 2011; Werneck, Nogueira, Colli, Sites, & Costa, 2012), and has been effectively used to determine ecological indicators of community types, habitat conditions and environmental changes (Carignan & Villard, 2002; De Cáceres & Legendre, 2009; De Cáceres, Legendre, & Moretti, 2010; De Cáceres, Legendre, Wiser, & Brotons, 2012; Dufrêne & Legendre, 1997; Niemi & McDonald, 2004). To avoid overparameterization (SDMs in this study have three climatic variables as input data; see Section 2.2 below), we first excluded species with <20 records (Thuiller, Guéguen, Renaud, Karger, & Zimmermann, 2019), summing a total of 282 species (see Table S1). These species were classified in Neves et al. (2017) as diagnostic (see Tichy & Chytrý, 2006) of six *Mata Atlântica* habitats, with each habitat being distributed across limited ranges of six environmental gradients: rain forest (warm and wet climates), high elevation/latitude forest (environments associated with seasonal cold), semideciduous forest (seasonal drought), *restinga* (salinity), rock outcrop habitats (seasonal fire and shallow soils) and riverine forests (seasonal soil waterlogging). In order to reflect these limiting environmental conditions in the analyses, we modelled the species of each habitat using distinct geographic delimitations, detailed below (see Figure S2).

Spatial scope for species from high elevation/latitude and rain forests comprised the whole extent of the *Mata Atlântica* and the biogeographical Domains found in the neighbouring South American dry diagonal, namely Caatinga, Cerrado and Chaco. Because species

from semideciduous forests are widely distributed across the dry diagonal, their spatial scope comprised the *Mata Atlântica*, dry diagonal Domains and the neighbouring lowland Amazon (warmer climates). *Restingas*, riverine and rock outcrop habitats are constrained within conditions that are primarily related to soil. Therefore, despite species from *restingas*, riverine and rock outcrop habitats having climatic suitability in other habitats (e.g. rain forests), these species are restricted to specific edaphic conditions (e.g. soil waterlogging in riverine forests). Thus, we modelled the potential distribution of these species within their edaphically suitable areas, which we established as the current distribution of *restingas*, riverine and rock outcrop habitats, respectively. We defined the distribution of the *Mata Atlântica* habitats, dry diagonal Domains and lowland Amazon in geographic space by creating polygons from a set of points. The 6,243 NeoTropTree sites (points) were previously classified into one of the South American biogeographic Domains and into one of the *Mata Atlântica* habitats where applicable. The size of each polygon was then estimated based on the distance between a given site and the other sites around it (wall-to-wall map).

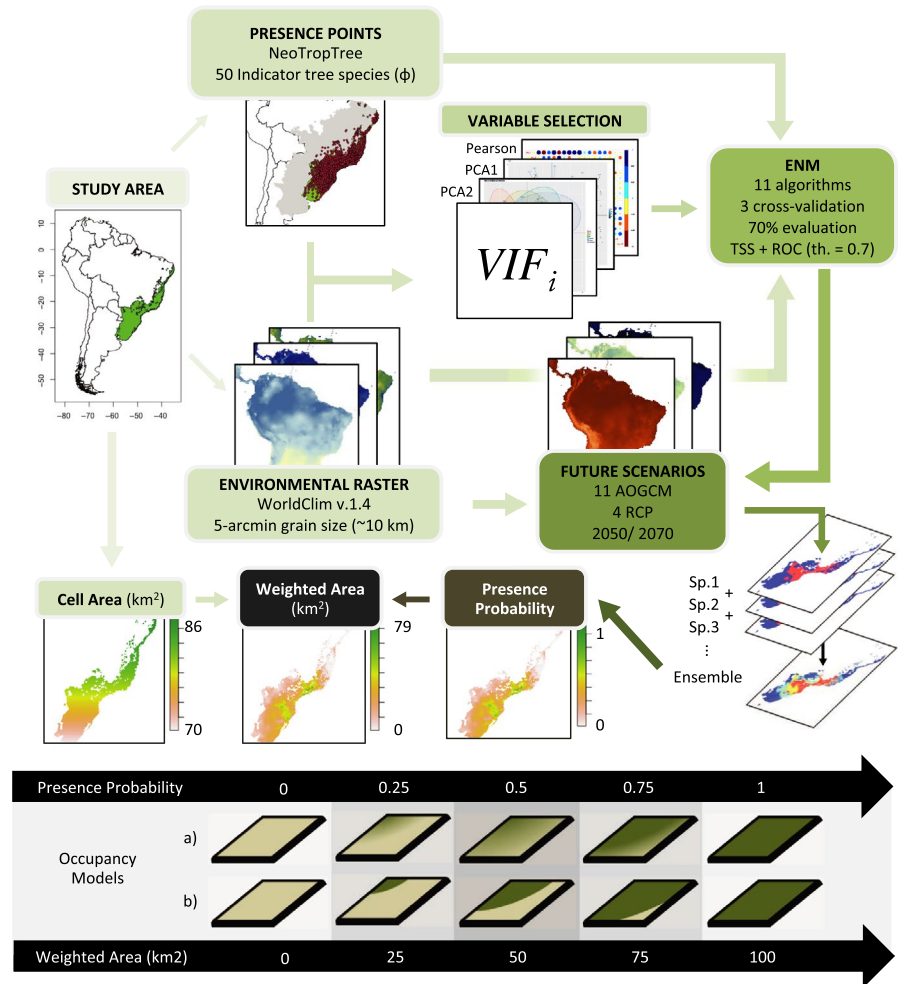
Bioclimatic variables were obtained from WORLDCLIM v.1.4 (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). Climatic layers were obtained at a 5-arcmin grain size (~10 km). This spatial resolution is particularly appropriate for this study because species checklists (sites) in NeoTropTree are defined by a single habitat, following the classification system proposed by Oliveira-Filho (2017), contained in a circular area with a 10 km diameter. NeoTropTree data were originally compiled from an extensive survey of published and unpublished (e.g. PhD theses) literature, particularly those on woody plant community surveys and floristic inventories. New species occurrence records obtained from both major herbaria and taxonomic monographs were then added to the checklists when they were collected within the 10 km diameter of the original NeoTropTree site and within the same habitat. The habitat delimitation was conducted using the package 'DISMO' (Hijmans & Elith, 2015) in R Statistical Environment (R Development Core Team, 2011).

2.2 | Variable selection

Variable selection was very conservative in order to build understandable and ecologically meaningful models (Figure 2). We followed a multiple-step variable selection routine, consisting of the following: (a) using variance inflation factors (VIF) to identify highly collinear variables, which were progressively excluded through a stepwise procedure. VIFs were computed using two methods: VIFcor (threshold = 0.5) and VIFstep (threshold = 10; see Marquardt, 1970, for method details). We then extracted bioclimatic values from presence points and (b) performed a principal components analyses (PCA) to visualize which variables were more effective in segregating the climatic space of each habitat relative to the climatic space of all other habitats. We also (c) performed PCAs for each habitat separately to assess which climatic variables showed higher correlations with the first three principal components (there was a negligible increase in constrained variance by adding a fourth component). Lastly, we (d)

FIGURE 2 Methods summary.

Environmental niche models (ENM) were projected to 11 Atmosphere Ocean General Circulation Models (AOGCM) and four representative concentration pathways (RCP) to 2050 and 2070. To calculate potential occupied area, the presence probability rasters were multiplied by cell area rasters, generating a weighted area raster, following two approaches: (i) considering a presence-absence map with a threshold = 0.5, that is, each cell with presence probability >0.5 sum 100 km² (grid cell size) of the total potential area. (ii) Considering that cells could be partially occupied, that is, occupancy models that are either gradually fading (a) or abruptly changing (b) ecotones



used Pearson's correlation to test whether all variables selected for a given habitat showed low correlation (cut-off = $-0.5 < p < .5$). We also legitimated the variable selection with literature review, which allowed us to select variables that better represented the climatic space occupied by the species of each habitat, while taking into account their ecological relevance (see Table S3).

2.3 | Environmental niche modelling

Models were calculated in three independent cross-validation runs with 30% of data kept to evaluate the model and two evaluation methods (true skill statistic, TSS, and area under the receiver operating characteristic, AUC) for every algorithm available in 'BIOMOD2' R Package (Thuiller, Georges, Engler, Georges, & Thuiller, 2014; generalized linear models, generalized additive models, boosted regression trees, classification tree analysis, artificial neural networks, Bioclim, flexible discriminant analysis, multiple adaptive regression splines, random forest and MaxEnt). We only kept ensemble models with TSS higher than 0.7. We generated 1,000 pseudoabsences through different background areas for each habitat, since they have distinct spatial scopes in our analyses (see section 2.1 and Figure S2 for more details). A caveat to this approach is the recommendations of Barbet-Massin, Jiguet, Albert, and Thuiller (2012) regarding

the use of lower pseudoabsences in some algorithms. Nonetheless, here we followed Thuiller (2014), which points out that the main advantage of BIOMOD2 lies in the capability to compare and combine multiple algorithms using the same set of initial data and parameterization. We controlled for spatial autocorrelation in our models using a generalized least squares framework (Zuur, Ieno, Walker, Saveliev, & Smith, 2009), which consists in modelling alpha diversity as a function of predicting variables using different spatial correlation structures (exponential, gaussian, spherical, linear and rational quadratics) and then selecting the best model (highest delta AIC relative to the null model; i.e. no spatial autocorrelation). We then built a raster with cell sizes as values weighted by presence probabilities to provide a more conservative measure of the potential area occupied by each habitat (Figure 2). Models were projected to CMIP5 data (Coupled Model Intercomparison Project Phase 5; downscaled at 5-arc-minute spatial resolution) using all General Circulation Models available in WORLDCLIM v.1.4 (Hijmans et al., 2005) to the four Representative Concentration Pathways (RCP2.6, 4.5, 6.0 and 8.5) to the years of 2050 and 2070 (BCC-CSM1-1, CCSM4, GISS-E2-R, HadGEM2-AO, HadGEM2-ES, IPSL-CM5A-LR, MIROC-ESM-CHEM, MIROC-ESM, MIROC5, MRI-CGCM3 and NorESM1-M), summing 88 scenarios and a total of 828,234 projections. Species projections were summed into an alpha diversity raster for each habitat and weighted by the

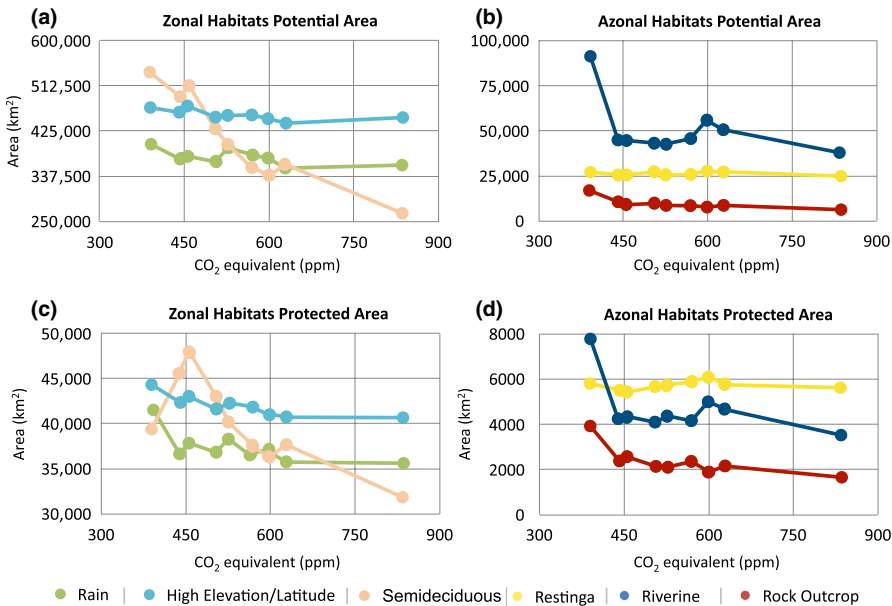


FIGURE 3 Potential area (in km²) of *Mata Atlântica* habitats (total area in a and b; protected area in c and d) through scenarios of increase in CO₂ concentration

maximum number of species before generating habitat suitability maps (Figure 2). Ensemble models were generated for each habitat by first summing their diagnostic species distribution maps and then dividing the resulting map by the number of diagnostic species in a given habitat. This generated a final suitability map (ranging from zero to one) for each habitat.

Finally, to assess the potential conservation status of *Mata Atlântica* habitats, we overlaid the current and future distributions of each habitat on to the coverage of protected areas in the World Database on Protected Areas (IUCN & UNEP-WCMC, 2015).

3 | RESULTS

3.1 | Potential area and conservation status

Our models showed that in current climatic conditions, the existing network of protected areas is more effective in protecting the potential distribution of azonal habitats (17.4% compared to only 9.0% in zonal habitats, Figure 3). Semideciduous forest is the least protected habitat, with only 7.1% of its potential area (537,640.29 km²) occurring within protected areas (39,320.39 km²). Amongst azonal habitats, riverine forest was the least protected, with only 8.5% of its potential area (91,492.64 km²) occurring within protected areas (7,816 km²). On average, 13.8% of the potential distributions of marginal habitats are found within protected areas, which is higher than the potential distribution of rain forest occurring within protected areas (10.2%; 41,203.47 km²).

From current conditions to the worst climate change scenario, the high elevation/latitude forest was the least affected, with 5.2% of potential area shrinkage, followed by *restinga* (7.6%), and rain forest (12.2%). In contrast, future scenarios for semideciduous, riverine and rock outcrop habitats were worrisome. Potential area shrinkage in future climatic scenarios can be as high as 50.4% in semideciduous

forest, 58.6% in riverine forest and 66% in rock outcrop habitats. This loss of climatically suitable areas across all habitats is also reflected in their levels of protection. From current to worst scenario, *restinga* woodlands are predicted to lose climatic suitability in 6.6% of its currently protected area, followed by high elevation/latitude (8.0%), rain (13.6%) and riverine (55.3%) forests. The current network of protected areas in rock outcrop habitats is predicted to undergo the most severe impacts of climate change, with 60.1% of shrinkage in areas of climatic suitability for species of rock outcrop habitats in these protected areas. Conversely, shrinkage in areas of climatic suitability for species of semideciduous forest (50.4%) will mainly occur outside protected areas (19.0% of protected area loss).

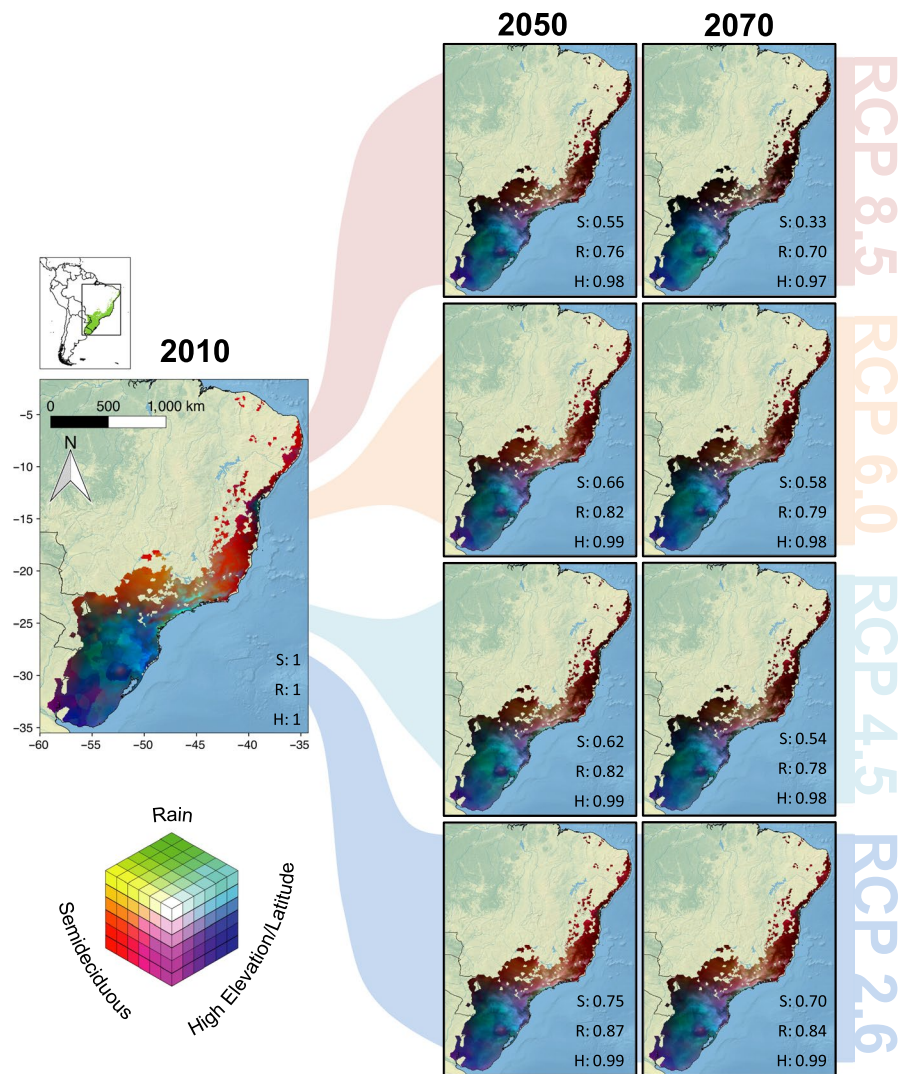
3.2 | Distribution of azonal habitats

Riverine forests, which are mainly found in Central Brazil, and rock outcrop habitats, which are mainly found in the transition between *Mata Atlântica* and Cerrado, are predicted to lose higher levels of climatic suitability in lower latitudes (see Figures S4 and S5). *Restinga* is predicted to lose lower amounts of suitable climatic space relative to the other *Mata Atlântica* habitats, suggesting higher climatic stability across coastal white-sand environments in eastern South America (see Figures S6 and S7).

3.3 | Distribution of zonal habitats

Our results showed a substantial degree of overlap in the climatic spaces occupied by species from high elevation/latitude, semideciduous and rain forests (for decoupled maps check Figures S8, S9 and S10). This suggests that the abrupt contours that are currently used for delimiting the distribution of these three habitats might be too simplistic (Figure 4). Under current climatic conditions, for instance, our models showed that for 3.7% of the geographic space covered

FIGURE 4 Distribution of zonal habitats through climate change scenarios yielded by environmental niche modelling of their diagnostic species (see Table S1 and Section 2). Habitats were plotted using a red-green-blue colour scheme. The brightest shades of red, green and blue represent the highest probability of occurrence of species from semideciduous, rain and high elevation/latitude forests, respectively. If a grid cell is potentially occupied by two habitats, its colour will represent an intermediate palette between the colours for these two habitats. White indicates presence of all habitats, while black indicates full absence. Pearson's correlations between current and each of the future distribution maps are given for semideciduous, rain and high elevation/latitude forests (S, R and H, respectively)



by zonal habitats, there is an equivalent probability that a given area (~100 km²) is suitable for species from high elevation/latitude, semideciduous and rain forests. This intercept increases through scenarios, varying from 6.2% of overlap in RCP2.6/2070 and RCP6.0/2070 to 7.1% in RCP8.5/2070.

Climatic overlap between two habitats is even higher. Species from high elevation/latitude and rain forest showed the highest degree of overlap in climatic suitability, ranging from 14% in current climatic conditions to 24.3% in RCP8.5/2070. In contrast, species from semideciduous and rain forests showed a much lower degree of overlap in climatic suitability (6.7% in current climate), which decreases over time (1.2% in RCP8.5/2070). Unique climatic space (i.e., suitable for species of a single habitat) is highly variable across high elevation/latitude, semideciduous and rain forests, and unstable through time. Potential climatic uniqueness for rain forest species ranges from 1.1% in current climate conditions to 0.5% in RCP8.5/2050, reaching a minimum of 0.2% in RCP6.0/2050. Semideciduous forest showed both the highest degree of climatic uniqueness and future instability, ranging from 25.1% in current climatic conditions to only 8% in RCP8.5/2070. Species from high elevation/latitude forest

showed 18.9% of potential climatic uniqueness, which decreases to 18.1% in RCP8.5/2070 and 13.8% in RCP4.5/2050 (Figure 5).

3.4 | Climatically stable areas

Areas in southeastern Brazil showed a high probability of climatic stability for species of all three zonal habitats (Figure 6). These potential refugia occur mainly in Rio de Janeiro and São Paulo states. Potential refugia for species of high elevation/latitude forest are also found in southern Brazil and Uruguay. Potential refugia for species of semideciduous forests are scattered across central and southeastern Brazil, with larger areas in Minas Gerais state. The distribution of protected areas shows a low level of coincidence with these postulated refugia (Figure 6), ranging from 13.4% in high elevation/latitude and semideciduous forest to 32.8% in rain forests.

Areas in eastern and central-western Brazil showed a high probability of climatic stability for species of azonal habitats. Existing protected areas in the Federal District and across Minas Gerais state (e.g., Canastra National Park) are potential refugia for species of riverine forest. Potential refugia for species of rock outcrop habitats

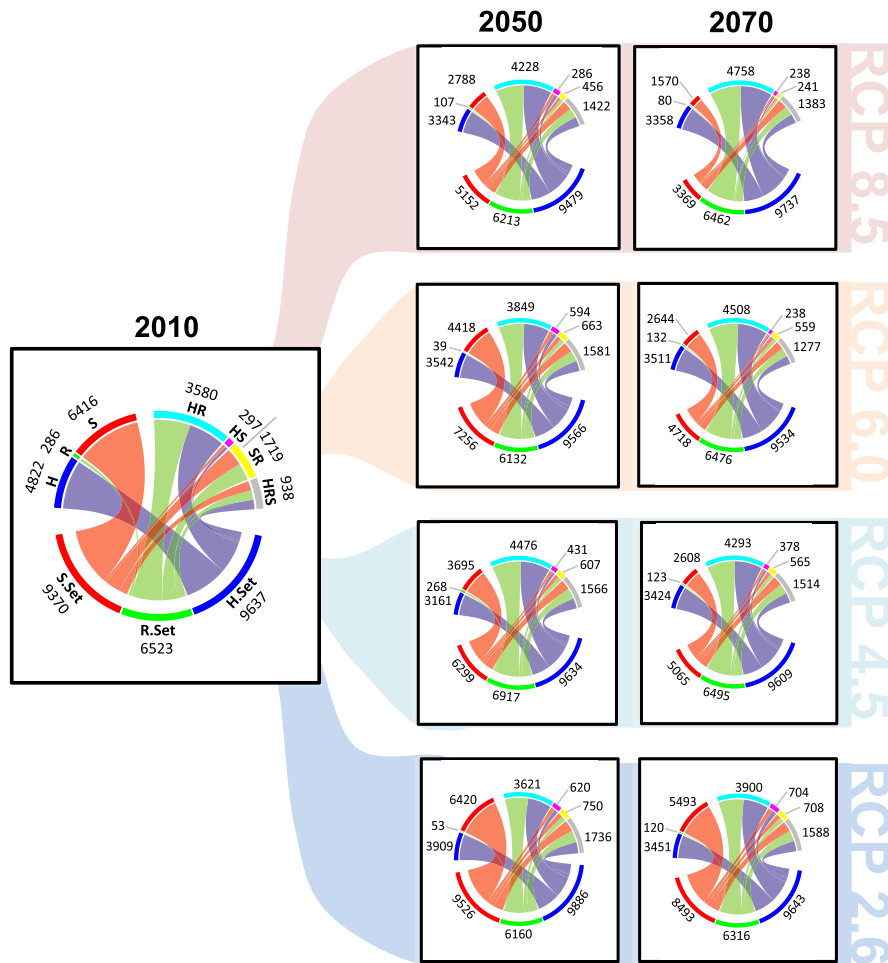


FIGURE 5 Number of grid cells per zonal habitat and their intercepts through climate change scenarios. Bottom groups represent the total number of grid cells of semideciduous (S.Set), rain (R.Set) and high elevation/latitude forests (H.Set). Upper-left groups represent grid cells that in our models are uniquely covered by semideciduous (S), rain (R) and (H) high elevation/latitude forests. Upper-right groups represent grid cells where three (high elevation/latitude-rain-semideciduous, HRS) or two habitats overlap (semideciduous-rain, SR; high elevation/latitude-semideciduous, HS; high elevation/latitude-rain, HR). Habitats with climatic suitability ≥ 0.33 in a grid cell were considered present. Chord diagrams were made using circlize R package (Gu, Gu, Eils, Schlesner, & Brors, 2014)

are scattered in Minas Gerais state (Gandarela and Caparaó National Parks, and Brigadeiro State Park). Large areas of climatic stability areas for species of *restinga* woodlands are found in northeastern Brazil, across the coastline of Bahia, Alagoas and Pernambuco states. However, these climatically stable *restinga* woodlands are mostly found outside existing protected areas (only 19.9% within protected areas; Figure 6).

4 | DISCUSSION

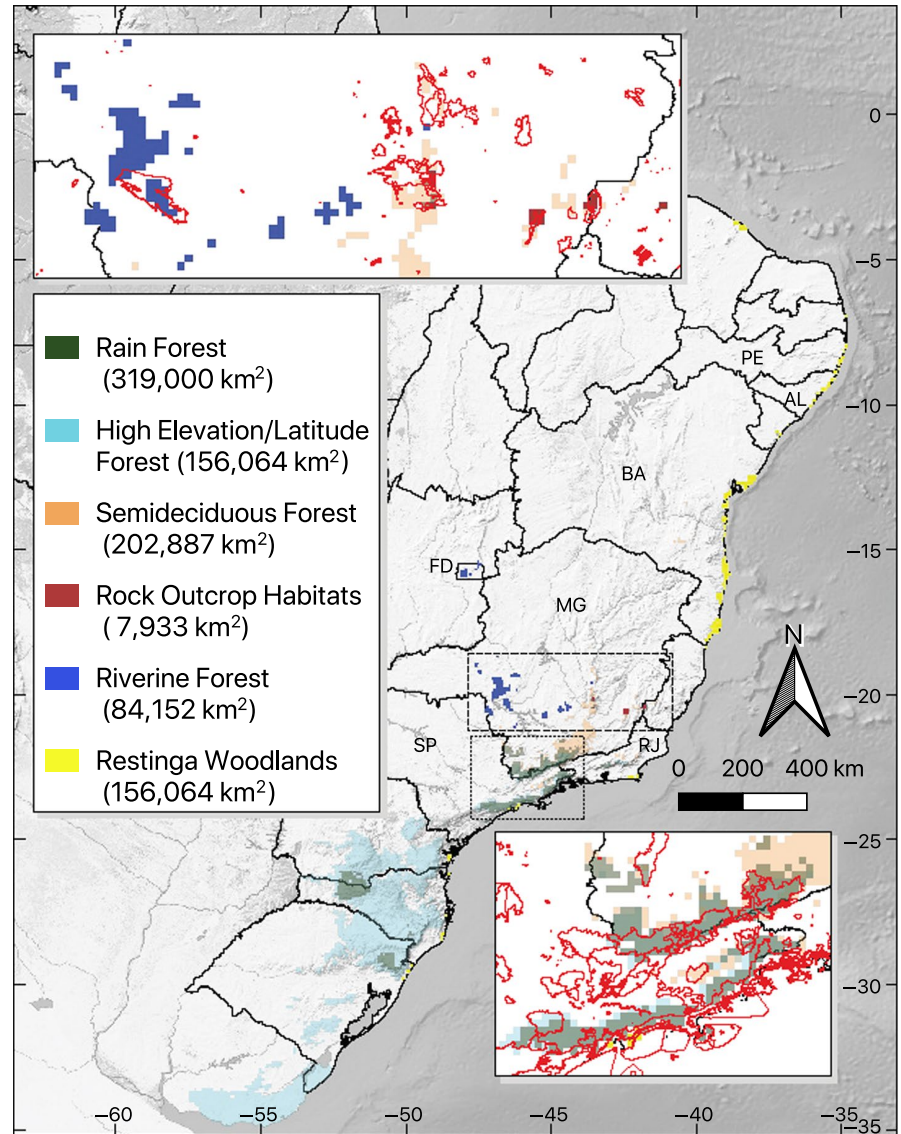
Here, we showed that both core and marginal habitats of the *Mata Atlântica* will be severely impacted by human-induced climate change, though to different, uneven degrees. For instance, considering variation from current conditions to the most pessimistic scenario of climate change in our models (RCP8.5/2070), rain forest is likely to be more climatically stable relative to semideciduous, riverine and rock outcrop habitats, but more impacted than high elevation/latitude forest and *restinga* woodlands. These findings are of relevance for conservation planning predicated on the protection of biodiversity under climate change scenarios. Because there is a considerable level of plant endemism in both core and marginal habitats (Neves et al., 2017), a portion of such species could be neglected if future conservation strategies prioritise regions of highest climatic

stability regardless of habitat heterogeneity (e.g., Lemes et al., 2013; Ferro et al., 2014; Loyola et al., 2014; Zwiener et al., 2017; Sobral-Souza, Vancine, Ribeiro, & Lima-Ribeiro, 2018), but core and marginal habitats are unevenly distributed across these stable regions.

4.1 | Potential area and conservation status

Through the scenarios, protected areas in riverine forest will have more stable climates across the southeastern portion of its current distribution, highlighting the importance of these areas for protecting viable population sizes of riverine species. Congruent with the results for riverine forest, our future scenario models showed that rock outcrop habitats will lose more climatically suitable areas in their lower latitudes, suggesting that southernmost sites may function as climatic refugia for this hyperdiverse habitat (Neves et al., 2018). However, given the scattered spatial configuration of these rock outcrop sites, dispersal is likely to be very limited, which suggests that conservation strategies might need to consider new protected areas that connect these outcrop islands through the lowlands. In fact, previous studies (Mews, Pinto, Eisenlohr, & Lenza, 2014; Neves et al., 2018) provided evidence that rock outcrop habitats and their surrounding lowland savannas are likely to form a continuous meta-community with spatial variation in woody plant population sizes being mainly driven by source-sink dynamics (Pulliam & Danielson,

FIGURE 6 Climatic stability in *Mata Atlântica* habitats yielded by ecological niche models of 269 diagnostic tree species. Coloured grid cells (stable sites) represent areas where all diagnostic species of a given habitat are predicted to occur in all 89 scenarios of current and future climates (four concentrations of atmospheric carbon for the years 2050 and 2070, 11 AOGCMs). Red contours indicate the current network of protected areas in South America. Black contours represent the national borders and state limits in Brazil. Values in parentheses indicate the amount of climatically stable areas in square kilometres for each habitat. Acronyms represent Brazilian states mentioned in the Results: Alagoas (AL), Bahia (BA), Federal District (FD), Minas Gerais (MG), Pernambuco (PE), Rio de Janeiro (RJ) and São Paulo (SP)



1991). Therefore, here we stress that protected areas aiming to secure biodiversity of rock outcrop habitats should not be limited to rock outcrop areas. Rather, effective protected areas should function as ecological corridors connecting multiple rock outcrop sites through lowland environments.

Our models showed that while climate in *restinga* woodlands are expected to be more stable over time when compared to other habitats, this level of stability is highly variable within its distribution, with central and southern *restingas* being relatively more stable. In addition to this uneven impact of climate change across *restinga* woodlands, coastal environments are also expected to be affected by erosion and sea level raise (EUROSION, 2004; IPCC, 2013). This suggests that conservation planning for *restinga* woodlands will require a high degree of complexity, with its effectivity depending on strategies that account for geomorphological variation changes associated with both climate and land use change. *Restinga* has suffered massive fragmentation due to high human occupation in coastal areas and a rapidly developing, unplanned tourism industry.

Amongst zonal habitats, semideciduous forest is predicted to be the most impacted, losing 64% of its current potential distribution under the most pessimistic scenario (RCP8.5/2070). Moreover, while our models predict climatic stability for species of semideciduous forest in southeastern Brazil, there is a high degree of potential area shrinkage for species of semideciduous forests in northeastern Brazil (see Figure S10). These results therefore suggest that conservation strategies aiming to protect suitable climatic space for these northern species would have to consider corridors that could potentially link their current and future suitable climates. Conversely, high elevation/latitude and rain forests are relatively stable over time, indicating the need for tailor-made conservation strategies for each habitat of the *Mata Atlântica*. Nonetheless, biodiversity in these forests is poorly and unequally captured by the current network of protected areas, especially in southern Brazil (Saraiva, dos Santos, Overbeck, Giehl & Jarenkow, 2018). Here, we suggest that accounting for climate change scenarios, in addition to multi-dimensional biodiversity assessments

as in Saraiva et al. (2018), might improve current and future conservation strategies for these neglected high elevation/latitude and rain forests.

4.2 | Climate change and compositional complexity

Previous studies (Neves et al., 2017; Oliveira-Filho, Budke, Jarenkow, Eisenlohr, & Neves, 2015; Oliveira-Filho & Fontes, 2000) that addressed climatic differentiation amongst *Mata Atlântica* habitats showed that while these habitats are floristically distinct, such compositional differentiation is only partially explained by variation in current climatic conditions. Our models not only supported the idea that delimiting the distribution of *Mata Atlântica* habitats is no easy task, but also showed that such complexity will likely increase under climate change, that is, because we currently lack a complete understanding of the factors that control the distribution of species through space and climatic gradients, predicting climate-driven biogeographical shifts is inherently uncertain.

There are many potentially important factors in determining the distribution of species that we have not accounted for adequately and that should be considered/addressed in future studies (see Neves et al., 2018; Titeux, Dufrene, Jacob, Paquay, & Defourny, 2004). Amongst these factors, the importance of biotic processes (e.g. competition, natural enemies) to species distributions and community composition is the most neglected in the literature, especially in studies addressing compositional turnover under climate change scenarios. Here, we highlight that accounting for biotic processes and assessing how they may potentially vary through time is not trivial for studies aiming to accurately predict the impacts of global change on biodiversity.

4.3 | Climatic stability and protected areas

Biodiversity loss from climate change arises because species move to track suitable climate, and agricultural lands, urban development or transportation corridors may stop their movement (Hannah, Midgley, Hughes, & Bomhard, 2005; Heller & Zavaleta, 2009). Protected areas and biodiversity-friendly land uses lessen these barriers to movement (Urban, 2015), but the data needed to inform land use managers require insights from ecologists in which the movements of various species are modelled under multiple climate scenarios. In our models, climatically stable areas are mostly outside the existing protected areas (83.8%). We, therefore, suggest that the areas identified as climatically stable in our analyses should be incorporated into systematic conservation planning and restoration projects to preserve *Mata Atlântica* habitats. Altogether, these areas function as probable refugial areas and climatically stable corridors connecting unstable protected areas to currently protected refugial areas.

5 | CONCLUSIONS

Our study showed that 'lumping' the natural heterogeneity of the *Mata Atlântica* can bring great havoc for future conservation

strategies, and highlighted three additional factors to be considered in conservation planning for this biodiversity hotspot: (a) we still have little understanding of how climate controls species distribution across the *Mata Atlântica*, and therefore, the future distribution of species from zonal habitats, namely high elevation/latitude, semideciduous and rain forests, is highly uncertain. New conservation strategies will need to account for such uncertainty when estimating which areas in geographic space are more likely to protect species from a given habitat and which areas are likely to represent climatic overlaps that are suitable for species from two or more habitats. (b) The maintenance of habitat area through time will likely depend on major biogeographical shifts (see results for semideciduous forests). Thus, new conservation strategies will need to account for the climatic space that will likely facilitate gradual migration under a changing environment. (c) Under climate change scenarios, spatial rearrangements for species of azonal habitats can only occur within the range that comprises their edaphic requirements, namely rock outcrops (rock outcrop habitats), seasonally waterlogged soils (riverine forest) and white-sand saline soils (*restinga* woodlands). This leads to a more limited array of conservation strategies for these habitats. Thus, for azonal habitats, considering conservation strategies that prevent the currently high levels of fragmentation associated with land use change is a must.

Further studies assessing climate changes impacts in habitats may trace how areas might change in (diagnostic) species composition and richness over time, culminating in the emergence of new habitats. In terms of azonal habitats, plant-soil relationship should be addressed carefully, considering influences of climate on substrates, as well as the suitability for plants under new combination of climate and edaphic conditions.

ACKNOWLEDGEMENTS

We thank Marinez Siqueira, Gerhard Overbeck and Demétrio Guadagnin for their insightful considerations on an earlier version of this manuscript. We also thank two anonymous referees for their valuable contributions to this manuscript. D.M.N. was funded by a collaborative research grant from the US National Science Foundation (DEB-1556651) during the time this research was completed.

DATA AVAILABILITY STATEMENT

All environmental layers are available in the WORLDCLIM database (<http://www.worldclim.org>). Species data are available in the NeoTropTree website (<http://www.neotropree.info>).

ORCID

Luiz Fernando Esser  <https://orcid.org/0000-0003-2982-7223>

Danilo M. Neves  <https://orcid.org/0000-0002-0855-4169>

João André Jarenkow  <https://orcid.org/0000-0003-2747-3468>

REFERENCES

- Barbet-Massin, M., Jiguet, F., Albert, C. H., & Thuiller, W. (2012). Selecting pseudo-absences for species distribution models: How, where and how many? *Methods in Ecology and Evolution*, 3(2), 327–338. <https://doi.org/10.1111/j.2041-210X.2011.00172.x>
- Barnosky, A. D., Hadly, E. A., Gonzalez, P., Head, J., Polly, P. D., Lawing, A. M., ... Zhang, Z. (2017). Merging paleobiology with conservation biology to guide the future of terrestrial ecosystems. *Science*, 355, eaah4787. <https://doi.org/10.1126/science.aah4787>
- Bhatta, K. P., Grytnes, J. A., & Vetaas, O. R. (2018). Downhill shift of alpine plant assemblages under contemporary climate and land-use changes. *Ecosphere*, 9(1), e02084. <https://doi.org/10.1002/ecs2.2084>
- Bueno, M. L., Pennington, R. T., Dexter, K. G., Kamino, L. H. Y., Pontara, V., Neves, D. M., ... de Oliveira-Filho, A. T. (2017). Effects of quaternary climatic fluctuations on the distribution of Neotropical savanna tree species. *Ecography*, 40(3), 403–414. <https://doi.org/10.1111/ecog.01860>
- Carignan, V., & Villard, M.-A. (2002). Selecting indicator species to monitor ecological integrity: A review. *Environmental Monitoring and Assessment*, 78, 45–61.
- Carnaval, A. C., & Moritz, C. (2008). Historical climate modelling predicts patterns of current biodiversity in the Brazilian Atlantic forest. *Journal of Biogeography*, 35, 1187–1201. <https://doi.org/10.1111/j.1365-2699.2007.01870.x>
- De Cáceres, M., & Legendre, P. (2009). Associations between species and groups of sites: Indices and statistical inference. *Ecology*, 90, 3566–3574. <https://doi.org/10.1890/08-1823.1>
- De Cáceres, M., Legendre, P., & Moretti, M. (2010). Improving indicator species analysis by combining groups of sites. *Oikos*, 119, 1674–1684. <https://doi.org/10.1111/j.1600-0706.2010.18334.x>
- De Cáceres, M., Legendre, P., Wiser, S. K., & Brotons, L. (2012). Using species combinations in indicator value analyses. *Methods in Ecology and Evolution*, 3, 973–982. <https://doi.org/10.1111/j.2041-210X.2012.00246.x>
- Dufrêne, M., & Legendre, P. (1997). Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecological Monographs*, 67, 345–366. <https://doi.org/10.2307/2963459>
- Elith, J., H. Graham, C., P. Anderson, R., Dudík, M., Ferrier, S., Guisan, A., ... E. Zimmermann, N. (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, 29(2), 129–151. <https://doi.org/10.1111/j.2006.0906-7590.04596.x>
- EUROSION (2004). *Living with coastal erosion in Europe – Sediment and space for sustainability*. 40 p, Luxembourg: European Commission.
- Ferro V. G., Lemes P., Melo A. S., Loyola R., Fenton B. (2014). The Reduced Effectiveness of Protected Areas under Climate Change Threatens Atlantic Forest Tiger Moths. *PLoS ONE*, 9(9), e107792.
- Frainer, A., Primicerio, R., Kortsch, S., Aune, M., Dolgov, A. V., Fossheim, M., & Aschan, M. M. (2017). Climate-driven changes in functional biogeography of Arctic marine fish communities. *Proceedings of the National Academy of Sciences of the United States of America*, 114(46), 12202–12207. <https://doi.org/10.1073/pnas.1706080114>
- Galindo-Leal, C., Jacobsen, T. R., Langhammer, P. F., & Olivieri, S. (2003). State of the hotspots: The dynamics of biodiversity loss. In C. Galindo-Leal, & I. G. de Câmara (Eds.), *The Atlantic Forest of South America: Biodiversity status, threats, and outlook* (pp. 12–23). Washington, DC: Center for Applied Biodiversity Science and Island Press.
- Gu, Z., Gu, L., Eils, R., Schlesner, M., & Brors, B. (2014). circlize implements and enhances circular visualization in R. *Bioinformatics*, 30, 2811–2812.
- Guisan, A., Thuiller, W. (2005). Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, 8(9), 993–1009.
- Hannah, L., Midgley, G., Hughes, G., & Bomhard, B. (2005). The view from the Cape: extinction risk, protected areas and climate change. *BioScience*, 55(3), 231–242.
- Heller, N. E., & Zavaleta, E. S. (2009). Biodiversity management in the face of climate change: a review of 22 years of recommendations. *Biological Conservation*, 142(1), 14–32.
- Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). *Very high resolution interpolated climate surfaces for global land areas*. *International Journal of Climatology*, 25, 1965–1978.
- Hijmans, R. J., & Elith, J. (2015). *Species distribution modeling with R*. R CRAN Project, 79 pp. Retrieved from <http://www.idg.pl/mirrors/CRAN/web/packages/dismo/vignettes/sdm.pdf%5Cnpapers://e21e3140-ccc7-4142-911c-e74fc5ceecf7/Paper/p10162>
- IPCC (2013). *IPCC Fifth Assessment Report (AR5)*. IPCC, s. 10–12. Cambridge: Cambridge University Press.
- IUCN and UNEP-WCMC (2015). *The World Database on Protected Areas (WDPA)*. Retrieved from www.protectedplanet.net
- Joly, C. A., Metzger, J. P., & Tabarelli, M. (2014). Experiences from the Brazilian Atlantic Forest: Ecological findings and conservation initiatives. *New Phytologist*, 204(3), 459–473. <https://doi.org/10.1111/nph.12989>
- Lemes, P., Loyola, R. D., & Flammini, A. (2013). Accommodating Species Climate-Forced Dispersal and Uncertainties in Spatial Conservation Planning. *PLoS ONE*, 8(1), e54323.
- Loyola, R. D., Lemes, P., Brum, F. T., Provete, D. B., & Duarte, L. D. S. (2014). Clade-specific consequences of climate change to amphibians in Atlantic Forest protected areas. *Ecography*, 37(1), 65–72.
- Marquardt, D. W. (1970). Generalized inverses, ridge regression, biased linear estimation, and nonlinear estimation. *Technometrics*, 12(3), 591–612.
- McLachlan, J. S., Hellmann, J. J., & Schwartz, M. W. (2007). A framework for debate of assisted migration in an era of climate change. *Conservation Biology*, 21(2), 297–302. <https://doi.org/10.1111/j.1523-1739.2007.00676.x>
- Mews, H. A., Pinto, J. R. R., Eisenlohr, P. V., & Lenza, E. (2014). Does size matter? Conservation implications of differing woody population sizes with equivalent occurrence and diversity of species for threatened savanna habitats. *Biodiversity and Conservation*, 23(5), 1119–1131. <https://doi.org/10.1007/s10531-014-0651-4>
- Mittermeier, R. A., Turner, W. R., Larsen, F. W., Brooks, T. M., & Gascon, C. (2011). Global biodiversity conservation: The critical role of hotspots. In F. Zachos & J. Habel (Eds), *Biodiversity hotspots* (pp. 3–22). Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-642-20992-5_1
- Moss, R. H., Edmonds, J. A., Hibbard, K. A., Manning, M. R., Rose, S. K., Van Vuuren, D. P., ... & Meehl, G. A. (2010). The next generation of scenarios for climate change research and assessment. *Nature*, 463(7282), 747.
- Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403(6772), 853–858. <https://doi.org/10.1038/35002501>
- Neves, D. M., Dexter, K. G., Pennington, R. T., Bueno, M. L., de Miranda, P. L. S., & Oliveira-Filho, A. T. (2018). Lack of floristic identity in campos rupestres—A hyperdiverse mosaic of rocky montane savannas in South America. *Flora*, 238, 24–31. <https://doi.org/10.1016/j.flora.2017.03.011>
- Neves, D. M., Dexter, K. G., Pennington, R. T., Valente, A. S. M., Bueno, M. L., Eisenlohr, P. V., ... Oliveira-Filho, A. T. (2017). Dissecting a biodiversity hotspot: The importance of environmentally marginal habitats in the Atlantic Forest Domain of South America. *Diversity and Distributions*, 23(8), 1–12. <https://doi.org/10.1111/ddi.12581>
- Niemi, G. J., & McDonald, M. E. (2004). Application of ecological indicators. *Annual Review of Ecology, Evolution, and Systematics*, 35, 89–111. <https://doi.org/10.1146/annurev.ecolsys.35.112202.130132>
- Oliveira-filho, A. T. (2017). *NeoTropTree, Flora arbórea da Região Neotropical: Um banco de dados envolvendo biogeografia, diversidade e conservação*. Retrieved from <http://www.neotropree.info>
- Oliveira-Filho, A. T., Budke, J. C., Jarenkow, J. A., Eisenlohr, P. V., & Neves, D. R. M. (2015). Delving into the variations in tree species composition and richness across South American subtropical Atlantic and Pampean forests. *Journal of Plant Ecology*, 8(3), 242–260. <https://doi.org/10.1093/jpe/rtt058>

- Oliveira-Filho, A. T., & Fontes, M. A. L. (2000). Patterns of floristic differentiation among Atlantic Forests in Southeastern Brazil and the influence of climate. *Biotropica*, 32(4b), 793–810. <https://doi.org/10.1111/j.1744-7429.2000.tb00619.x>
- Pena, J. C. D. C., Kamino, L. H. Y., Rodrigues, M., Mariano-Neto, E., & de Siqueira, M. F. (2014). Assessing the conservation status of species with limited available data and disjunct distribution. *Biological Conservation*, 170, 130–136. <https://doi.org/10.1016/j.biocon.2013.12.015>
- Peterson, A. T. (2001). Predicting species' geographic distributions based on ecological niche modeling. *The Condor*, 103, 599–605. [https://doi.org/10.1650/0010-5422\(2001\)103\[0599:PSGDBO\]2.0.CO;2](https://doi.org/10.1650/0010-5422(2001)103[0599:PSGDBO]2.0.CO;2)
- Peterson, A. T., Egbert, S. L., Sánchez-Cordero, V., & Price, K. P. (2000). Geographic analysis of conservation priority: Endemic birds and mammals in Veracruz, Mexico. *Biological Conservation*, 93(1), 85–94. [https://doi.org/10.1016/S0006-3207\(99\)00074-9](https://doi.org/10.1016/S0006-3207(99)00074-9)
- Peterson, A. T., Ortega-Huerta, M. A., Bartley, J., Sanchez-Cordero, V., Soberon, J., Buddemeier, R. H., & Stockwell, D. R. B. (2002). Future projections for Mexican faunas under global climate change scenarios. *Nature*, 416(6881), 626–629. <https://doi.org/10.1038/416626a>
- Pulliam, H. R., & Danielson, B. J. (1991). Sources, sinks, and habitat selection: A landscape perspective on population dynamics. *The American Naturalist*, 137, S50–S66. <https://doi.org/10.1086/285139>
- R Development Core Team (2011). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.
- Saraiva, D. D., Santos, A. S. D., Overbeck, G. E., Giehl, E. L. H., & Jarenkow, J. A. (2018). How effective are protected areas in conserving tree taxonomic and phylogenetic diversity in subtropical Brazilian Atlantic Forests? *Journal for Nature Conservation*, 42, 28–35.
- Scarano, F. R. (2009). Plant communities at the periphery of the Atlantic rain forest: Rare-species bias and its risks for conservation. *Biological Conservation*, 142(6), 1201–1208. <https://doi.org/10.1016/j.biocon.2009.02.027>
- Sobral-Souza, T., Vancine, M. H., Ribeiro, M. C., & Lima-Ribeiro, M. S. (2018). Efficiency of protected areas in Amazon and Atlantic Forest conservation: A spatio-temporal view. *Acta Oecologica*, 87, 1–7.
- Tabarelli, M., Cardoso Da Silva, J. M., & Gascon, C. (2004). Forest fragmentation, synergisms and the impoverishment of neotropical forests. *Biodiversity and Conservation*, 13(7), 1419–1425. <https://doi.org/10.1023/B:BIOC.0000019398.36045.1b>
- Tabarelli, M., Pinto, L. P., Silva, J. M. C., Hirota, M., & Bede, L. (2005). Challenges and opportunities for biodiversity conservation in the Brazilian Atlantic Forest. *Conservation Biology*, 19(3), 695–700. <https://doi.org/10.1111/j.1523-1739.2005.00694.x>
- Thuiller, A. W., Georges, D., Engler, R., Georges, M. D., & Thuiller, C. W. (2014). Package 'biomod2'. *Species distribution modeling within an ensemble forecasting framework*. <https://CRAN.R-project.org/package=biomod2>.
- Thuiller, W. (2014). Editorial commentary on 'BIOMOD – Optimizing predictions of species distributions and projecting potential future shifts under global change'. *Global Change Biology*, 20, 3591–3592. <https://doi.org/10.1111/gcb.12728>
- Thuiller, W., Guéguen, M., Renaud, J., Karger, D. N., & Zimmermann, N. E. (2019). Uncertainty in ensembles of global biodiversity scenarios. *Nature Communications*, 10(1), 1446. <https://doi.org/10.1038/s41467-019-09519-w>
- Tichy, L., & Chytrý, M. (2006). Statistical determination of diagnostic species for site groups of unequal size. *Journal of Vegetation Science*, 17, 809–818. <https://doi.org/10.1111/j.1654-1103.2006.tb02504.x>
- Titeux, N., Dufrene, M., Jacob, J., Paquay, M., & Defourny, P. (2004). Multivariate analysis of a fine-scale breeding bird atlas using a geographical information system and partial canonical correspondence analysis: environmental and spatial effects. *Journal of Biogeography*, 31(11), 1841–1856.
- Urban, M. C. (2015). Accelerating extinction risk from climate change. *Science*, 348(6234), 571–573.
- Walter, H. (1971). *Ecology of tropical and subtropical vegetation*. Edinburgh, UK: Oliver & Boyd.
- Werneck, F. P. (2011). The diversification of eastern South American open vegetation biomes: Historical biogeography and perspectives. *Quaternary Science Reviews*, 30, 1630–1648. <https://doi.org/10.1016/j.quascirev.2011.03.009>
- Werneck, F. P., Nogueira, C., Colli, G. R., Sites, J. W., & Costa, G. C. (2012). Climatic stability in the Brazilian Cerrado: Implications for biogeographical connections of South American savannas, species richness and conservation in a biodiversity hotspot. *Journal of Biogeography*, 39, 1695–1706. <https://doi.org/10.1111/j.1365-2699.2012.02715.x>
- Williams, K. J., Ford, A., Rosauer, D. F., De Silva, N., Mittermeier, R., Bruce, C., ... Margules, C. (2011). Forests of East Australia: The 35th biodiversity hotspot. In *Biodiversity hotspots* (pp. 295–310). Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-642-20992-5_16
- Zuur, A. F., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. New York: Springer Science & Business Media. <https://doi.org/10.1007/978-0-387-87458-6>
- Zwiener, V. P., Padial, A. A., Marques, M. C. M., Faleiro, F. V., Loyola, R., & Peterson, A. T. (2017). Planning for conservation and restoration under climate and land use change in the Brazilian Atlantic Forest. *Diversity and Distributions*, 23(8), 955–966. <https://doi.org/10.1111/ddi.12588>

BIOSKETCHES

Luíz Fernando Esser is a PhD student in Botany at the Federal University of Rio Grande do Sul, Brazil. He is interested in biodiversity evolution and environmental niche evolution, focusing on what influences the establishment of plant communities in space and time. Danilo M. Neves is a professor of macroecology at the Federal University of Minas Gerais, Brazil. He is interested in the evolutionary dimension of community ecology, with an emphasis on historical biogeography of terrestrial biomes. João André Jarenkow is a research professor at the Federal University of Rio Grande do Sul. His main research interests include phytogeography and plant community ecology of southern Brazilian Atlantic rain forests.

Author contributions: L.F.E. conceived the ideas, applied the methodology and led the writing; D.M.N. contributed for the improvement of writing and the methods; J.A.J. improved the writing and supervised the first author.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Esser LF, Neves D, Jarenkow JA.

Habitat-specific impacts of climate change in the Mata Atlântica biodiversity hotspot. *Divers Distrib*. 2019;25:1846–1856. <https://doi.org/10.1111/ddi.12984>