RESEARCH ARTICLE

Projected impacts of climate and land use changes on the habitat of Atlantic Forest plants in Brazil

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Abstract

Aim: To provide novel evidence on the average impact of climate and land use changes on habitat suitability for tropical plants and to test previous conclusions on the relative importance of these two drivers in shaping future availability of habitat for tropical plant species.

Location: Brazil's Atlantic Forest domain.

Time period: Plant occurrences recorded between 1960 and 2014. Baseline climate from 1960 to 2000 and land use from 2015. Projected scenarios of climate for 2041–2060 and land use for 2050.

Major taxa studied: Angiosperms.

Methods: We modelled the habitat suitability of 2,232 species of angiosperms from the Atlantic Forest domain, endemic to Brazil, and estimated how future climate and land use may affect species-level habitat suitability under a moderate and a business-as-usual scenario for the year 2050.

Results: Our results suggest that climate change alone will, surprisingly, have only a modest negative impact on the mean habitat suitability, decreasing it by 2% (median = −5 to −7%, variation associated with scenarios). Land use change alone had a more consistent negative impact on habitat suitability, causing mean and median reductions of 4 to 6%. When the effects of climate and land use are combined, the mean habitat suitability was reduced by 4% (median = −9 to −11%).

Main conclusions: The combined impacts of climate and land use changes were substantial, although smaller than expected. Habitat suitability decreased for most species, but it increased substantially for some species, suggesting that the distribution of impacts across species is markedly right skewed. The impacts were typically detrimental to small-ranged species and neutral or beneficial to widespread species. Land use change rather than climate change will likely cause more losses to the habitat of Atlantic Forest plant species within the next several decades.

KEYWORDS
climate change, geographic range size, land use change, plant conservation, species distribution modelling, tropical forest

1 | INTRODUCTION

Projected impacts of climate change on plant species vary across studies, regions and scenarios (Bellard et al., 2012). Projections often point to substantial reductions in habitat suitability and species' range size (Bellard et al., 2012; Gomes et al., 2019; Thomas et al., 2004; Velazco et al., 2019; Warren et al., 2018). The few projections focusing on tropical plants suggest they are highly vulnerable to climate change (Colombo & Joly, 2010; Colwell et al., 2008; Gomes et al., 2019; Miles et al., 2004; Siqueira & Peterson, 2003; Velazco et al., 2019). For instance, studies focusing on tropical plants in South America predicted that potential range size would decline on average 50% for Cerrado trees (based on 162 species, Siqueira & Peterson, 2003), 20%–50% for Atlantic Forest trees (based on 38 species, Colombo & Joly, 2010), 35%–45% for Cerrado plant species (based on 1,553 species, Velazco et al., 2019) and 47%–53% for Amazonian trees (based on 4,935 species, Gomes et al., 2019) by the year 2050. These and other studies support the expectation that tropical species are highly sensitive to climate change, as much as temperate and boreal species (Wright et al., 2009).

However, responses of tropical plant species to climate change are complex and hard to predict (Corlett, 2016). On one hand, tropical plants already live under warm temperatures and are often adapted to narrow ranges of environmental conditions, suggesting they have limited ability to withstand additional warming and adapt to changes (Sheldon, 2019; Wright et al., 2009). On the other hand, a simple (and uncertain) model of biome shifts suggested that tropical regions may be less vulnerable to vegetation change in response to climate change than temperate and boreal ecosystems (Gonzalez et al., 2010), and many tropical lineages may have evolved under global climatic conditions that were warmer than today (McElwain, 2018).

It will be important for conservation planning to know how climate change will affect species and how it compares with other major threats. Some studies suggest that climate change has been, and will continue to be for decades, a less important driver of biodiversity loss in tropical forests than land use change (de Chazal & Rounsevell, 2009; IPBES, 2019; Sala et al., 2005; Schipper et al., 2020; WWF, 2018), though the relative importance of each driver may differ across phytogeographic domains (Silva et al., 2019). If climate change alone is predicted to cause very large losses of suitable habitat and yet be less important than land use change, then the loss of suitable habitat due to their combination may be profound. Deforestation in the Amazon between 1900 and 2013 may have brought a quarter of Amazonian trees to extinction risk (ter Steege et al., 2015). Thus, realistic predictions of the impact of these drivers on habitat suitability and potential range size should include both climate and land use changes.

Predicting how tropical plant species will respond to future climate remains a challenge for myriad reasons. Projected changes in climate differ among regions and across emissions scenarios, including changes in levels, timing and variation in temperature and rainfall, potentially leading to distinct ecological responses across the world (Walther et al., 2002). Projections of finer-scaled and variable aspects of climate change are much more uncertain than coarser-scale

projections of changes in mean temperature. Responses to changes in temperature and precipitation also vary considerably among species. Niche breadth and geographic range size seem partly responsible for differences in species' responses to climate change (Slatyer et al., 2013). Species adapted to narrow niches are likely to lose habitat and unlikely to gain habitat as climate changes (Thuiller et al., 2005). The environmental conditions required by specialist plant species are less likely to be available within dispersal range among the future combinations of temperature, precipitation, soil and other environmental attributes (Sheldon, 2019; Slatyer et al., 2013; Thuiller et al., 2005). In addition, species with smaller geographic range sizes are likely more vulnerable to extinction from climate change (Schwartz et al., 2006; Silva et al., 2019) because they are susceptible to losing larger portions of their occupied habitat due to changes in habitat suitability.

Responses to land use change may also vary among species. As land use intensifies, species with more acquisitive traits (i.e. fast-growing, short-lived) often prevail over species with conservative traits (i.e. slow-growing, long-lived; Carreno-Rocabado et al., 2016). Specifically, habitat fragmentation, a common and well-studied outcome of land use change in tropical forest regions, selects species that are tolerant of edge effects and other fragmentation-induced disturbances, leading to the proliferation of fast-growing and short-lived species (Laurance et al., 2006), and biotic homogenization of plant assemblages (Lôbo et al., 2011; Newbold et al., 2018; Staude et al., 2020; Tabarelli et al., 2012).

Herein, we aim to provide more comprehensive evidence than published heretofore concerning projected changes in habitat suitability of tropical plants due to climate and land use changes, and to test previous conclusions on the scale of these changes and the relative importance of these two drivers to the future availability of tropical plant habitat. Specifically, we investigate how projected changes in climate and land use affect the habitat suitability of 2,232 plant species of Brazil's Atlantic Forest—a relatively well-known and highly threatened tropical region (Joly et al., 2014; Ribeiro et al., 2009). We hypothesize that: (a) projected climate change is highly detrimental to species habitat suitability as concluded by previous investigation (e.g. Colombo & Joly, 2010; Colwell et al., 2008; Gomes et al., 2019; Miles et al., 2004; Siqueira & Peterson, 2003; Velazco et al., 2019); (b) projected land use change will cause substantially larger losses of habitat suitability than projected climate change, as suggested by previous studies (de Chazal & Rounsevell, 2009; IPBES, 2019; Jetz et al., 2007; Sala et al., 2005; Schipper et al., 2020; Silva et al., 2019; WWF, 2018); and (c) species with smaller range sizes are more negatively affected by climate and land use changes (Newbold et al., 2018; Schwartz et al., 2006; Silva et al., 2019; Staude et al., 2020; Thuiller et al., 2005).

2 | METHODS

2.1 | Atlantic Forest species

This study focuses on plant species of Brazil's Atlantic Forest phytogeographic domain, a highly diverse tropical forest region

(Joly et al., 2014). Atlantic Forest originally covered 17% of Brazil (> 1,450,000 km²), extending along the coast from the state of Ceará (3° S) to Rio Grande do Sul (34° S), and beyond Brazil (Galindo-Leal & Câmara, 2003). Proximity to the Atlantic Ocean moderates climatic conditions, and the region includes equatorial and warm temperate climates (Kottek et al., 2006), with annual mean temperature ranging from 13 to 27 °C, and annual precipitation ranging roughly from 1,000 to 2,500 mm. It encompasses mostly forests, but also non-forest vegetation types (IBGE, 2008). The 500-year history of forest clearing and expansion of agriculture and built infrastructure has left the natural vegetation severely fragmented in the region (Galindo-Leal & Câmara, 2003; Ribeiro et al., 2009). The high levels of plant diversity (> 15,000 angiosperm species; Brazil Flora Group, 2019), endemism (50% of angiosperms are endemic to Atlantic Forest; Zappi et al., 2015), habitat loss (84%–89% of original vegetation cover is lost; Ribeiro et al., 2009) and extinction risk (40% of evaluated species are threatened; Martinelli & Moraes, 2013) make the Atlantic Forest a biodiversity hotspot with global priority for conservation (Mittermeier et al., 2004).

2.2 | Occurrences and species sample

We downloaded 3,786,000 raw occurrences of plants from the Species Link Network (http://www.splink.org.br, see the list of herbaria providing records in Supporting Information Appendix S1). We cleaned the species names by removing unusual characters, removing uncertain identifications, and retaining only the binomials (i.e. species level). We checked synonyms and used accepted names according to Brazilian Flora 2020 (Brazil Flora Group, 2019). We matched synonyms and corrected minor spelling errors in the specific epithets using the function *get.taxa()* from the R package 'flora' v.0.2.7 (Carvalho, 2016). We discarded records without an accepted name in Brazilian Flora 2020, which mainly involved illegitimate, invalid or rejected names.

We kept only species occurring in the Atlantic Forest and endemic to Brazil, according to Brazilian Flora 2020 (http://floradobrasil.jbrj.gov.br, Brazil Flora Group, 2019). Occurrences dated before 1960 or lacking collection date were removed to avoid temporal mismatch with climate data. The centroid of the most local administrative unit (i.e. municipality or district) was used as the location for each occurrence. This choice allowed us to include more occurrences and avoid errors in geographic location because specific geographic coordinates were typically not available or unreliable. Administrative units are typically small in the Atlantic Forest region, with a median distance between closest administrative units of 10 km (see more details in Leão et al., 2020). We used the Global Administrative Areas version 2.5 (http://www.gadm.org) as reference for limits of municipalities and districts.

Only species occurring in 15 or more unique locations had their habitat suitability modelled. This procedure ensured that each species had robust range size estimates (Rivers et al., 2011) and a minimum variation in the environmental predictors, which is important to

fit reliable habitat suitability models (Thibaud et al., 2014). Although 15 records is not as restrictive as the minimum of 20–30 often suggested (Guisan et al., 2017), use of this threshold improved substantially the variation of range sizes in our sample (Supporting Information Figure S1). The resulting sample includes 104,000 unique species-year-coordinate records of 2,232 plant species of the Atlantic Forest and endemic to Brazil.

2.3 | Species' observed area of occupancy

Observed area of occupancy was estimated according to the sliding scale method described in Leão et al. (2020). In this method, the area of occupancy is the sum of the grid cell area occupied by the species, where the grid cell size varies in proportion to the scale of the species' geographic range extent. The cell width is set as 1/10th of the maximum distance between occurrences with a minimum cell size of 5 km × 5 km and maximum of 50 km × 50 km. This method is a hybrid between traditional area of occupancy (with fixed cell size) and extent of occurrence, helping to find appropriate cell sizes for the estimation of area of occupancy according to the species' range extent. Use of limits for minimum and maximum cell size avoids underestimation of the area for species with few occurrences and overestimation for species with very sparse distribution.

2.4 | Environmental data

The environmental data initially included the following predictors: (a) 19 bioclimatic variables derived from 'current' climate at 5-min spatial resolution (approximately 9 km at the equator; Fick & Hijmans, 2017; Hijmans et al., 2005); (b) 21 predicted soil attributes from SoilGrids with 1-km spatial resolution (Hengl et al., 2014); and (c) an elevation mosaic of NASA Shuttle Radar Topography Mission (SRTM) images with 90-m spatial resolution (Jarvis et al., 2008). We applied several steps of variable selection to remove correlated predictors and focus on the most important predictors. First, we calculated the correlation among all variables within South American boundaries. When predictors had Pearson correlation above .8, we selected the most directly relevant to plant growth. This procedure selected 22 predictors that are likely important to describe the habitat suitability for plants, which were used in a preliminary modelling stage to evaluate their importance for prediction of habitat suitability using random forests (Supporting Information Table S1). For the final modelling stage, we chose six predictors from the nine having importance values above the mean, according to the mean increase in node purity in the random forest models. Predictors with largest mean increase in node purity are the ones contributing most to improving predictions of species distribution in the models, and are likely among the best available predictors to describe the habitat of those species. These predictors represented important aspects of temperature (temperature seasonality and annual mean temperature), precipitation (precipitation of warmest quarter and annual precipitation) and soil

(clay fraction and available water capacity) (Supporting Information Table S1), and their interaction should provide good discrimination of the plant habitat suitability at the geographic scale of this study.

2.5 | Future climate data

Future climate conditions were obtained from the projections of three Coupled Model Intercomparison Project phase 6 [CMIP6: BCC-CSM2-MR, CNRM-ESM2-1 and MIROC6; WorldClim v.2.1 (Fick & Hijmans, 2017)] and two CMIP5 models [HadGEM2-ES and MIROC5; WorldClim v.1.4, (Hijmans et al., 2005)]. The new CMIP6 models have higher equilibrium climate sensitivity (ECS), which means they generate global scenarios with typically more warming for a given concentration of atmospheric CO_2 than corresponding CMIP5 models (Hausfather, 2019). The three CMIP6 models we chose have ECS values that are relatively low (2.6C, MIROC6), medium (3C, BCC-CSM2-MR) and high (4.8C, CNRM-ESM2-1) among the choices available on WorldClim v.2.1 on August 2020 (ECS values from Hausfather, 2019). We included HadGEM2-ES and MIROC5 (CMIP5 models) because they have been commonly used and extensively tested in South America and Brazil (Chou et al., 2014; Follador et al., 2018; Yin et al., 2013), thus facilitating integration of our results with previous knowledge. The derived bioclimatic variables were used to assess the effects of climate change in the year 2050 (average for 2041–2060, Supporting Information Figures S2 and S3) on two representative concentration pathways (RCP4.5 and RCP8.5; Fick & Hijmans, 2017; Hijmans et al., 2005). RCP4.5 is a moderate scenario in which radiative forcing stabilizes around 2100; it assumes that human societies will make an active effort to reduce greenhouse gas emission by increasing the contribution of non-fossil energy sources and mitigating emissions from land use (Thomson et al., 2011). RCP8.5 is a high emission scenario ('business as usual'), in which human population and demand for energy grow fast, while economic development and improvement in energy technology move slowly, leading to the highest radiative forcing among the RCP scenarios (Riahi et al., 2011).

2.6 | Land use data

Current (2015) and projected future (2050) land use were obtained from the land use harmonization data set (LUH2 v2f), which describes the fraction of 0.25×0.25 degree grid cells occupied by each of the land use states (Hurtt et al., 2020; http://luh.umd.edu). The possible land use states, grouped for analysis purposes, were primary vegetation (forested primary land, non-forested primary land), secondary vegetation (potentially forested secondary land, potentially non-forested secondary land), pastures and rangeland, crops, and urban. We used the projections SSP2-RCP4.5 from MESSAGE-GLOBIOM and SSP5-RCP8.5 from REMIND-MAGPIE (Hurtt et al., 2020; http://luh.umd.edu), which are land use scenarios based on narratives for potential future development pathways known as shared socioeconomic pathways (or SSPs, Popp et al., 2017; Riahi

et al., 2017), and representatives of a 'moderate' scenario and a 'business as usual' scenario, respectively.

2.7 | Environmental suitability model

As this research focused on prediction, we relied on two environmental modelling techniques suited for this purpose (Elith et al., 2008; Prasad et al., 2006): random forests and boosted regression trees. These two approaches are machine learning tree-based methods that typically show superior performance on prediction, selection of relevant variables and fitting of complex models without overfitting the data compared to more traditional regression methods based on stepwise selection (Elith et al., 2008; Hastie et al., 2013). We used the recommended default parameters for the two modelling techniques as performed in R v.3.6.3 (R Core Team, 2020) packages 'biomod2' v.3.4.6 (Thuiller et al., 2020), 'randomForest' v. 4.6–14 (Liaw & Wiener, 2002) and 'gbm' v. 2.1.5 (Greenwell et al., 2019).

In addition to the internal cross-validation performed by each machine learning technique, we performed an external fivefold cross-validation (Guisan et al., 2017; James et al., 2013). Five models were generated for each species and modelling technique based on different training data sets (80% of the data) and evaluated on a test data set (20% of the data). We randomly selected the same number of pseudo-absences as the number of occurrences for a given species, with a minimum of 100 pseudo-absences (Barbet-Massin et al., 2012).

We generated ensemble predictions based on the weighted sum of probabilities from each model as evaluated by the true skill statistic (TSS; Guisan et al., 2017; Thuiller et al., 2020). Our inferences focus on these ensemble predictions. In an effort to exclude potentially unreliable predictions, models with TSS below .8 were not used to build the ensemble predictions.

2.8 | Land use model

We used evidence from site-level surveys to build a model that accounts for the effects of each land use state on habitat suitability based on the reported impacts of each land use on species richness (Newbold et al., 2015) and beta diversity (Newbold et al., 2016), and how these impacts differ among range size groups (Newbold et al., 2018). These three components are included in our model as coefficients weighting the effects of each land use by range size group. For each spatial unit the land use suitability is a function of the sum of the proportion of each land use weighted by their coefficient:

$$\text{Land use suitability}_{rc} = \alpha_{1r}\beta_1\gamma_1 \text{primary vegetation}_c + \alpha_{2r}\beta_2\gamma_2 \text{secondary vegetation}_c +$$
$$\alpha_{3r}\beta_3\gamma_3 \text{ pastures \& rangeland}_c \qquad (1)$$
$$+ \alpha_{4r}\beta_4\gamma_4 \text{crops}_c + \alpha_{5r}\beta_5\gamma_5 \text{urban}_c$$

where γ = loss of habitat suitability proportional to the overall loss of species richness relative to the primary vegetation baseline (Newbold et al., 2015); β = relative compositional similarity to the primary

vegetation (see fig. 3b in Newbold et al., 2016); α = relative difference in species richness among range size groups within each land use (Newbold et al., 2018); r = index for range size group: first, second and third quantiles of range size; and c = index for spatial grid cell (Table 1).

2.9 | Projections into future

We predicted future habitat suitability using the projections for future climate in the models trained on current climate and the projections for future land use accordingly. We followed steps that allowed us to estimate the independent and combined effects of climate and land use changes on habitat suitability (Figure 1).

We further estimated the habitat suitability within proximity of known occurrences. This is a more realistic metric and useful for conservation purposes because it avoids the oversimplistic assumptions that species can occur anywhere with suitable environment or do not occur elsewhere than suggested by observed occurrences. The buffer radius equals the maximum distance between occurrences, which makes it proportional to the species' range extent.

Given the seven steps to verify the independent effects of climate and land use (Figure 1), two modelling techniques and the ensemble, five samples associated with the fivefold cross-validation, five climate models, and two future scenarios, we generated 605 projections for each species, summing to more than 1,300,000 projections.

2.10 | Full habitat suitability model and changes in suitability

The full habitat suitability model is a function of both the environmental suitability (i.e. the suitability given climate and soil) and the

land use suitability (described above). The habitat suitability for the species s was calculated as the sum across grid cells of the product between the environmental suitability and the land use suitability (given the range size group r):

$$\text{Habitat suitability}_s = \sum_{c=1}^{n} \text{enviromental suitability}_{sc} * \text{land use suitability}_{rc} \tag{2}$$

The change in habitat suitability was calculated as the difference between the habitat suitability under climate and land use for the years 2050 and 2015 proportional to the suitability in the year 2015, and averaged across climate models m:

$$\begin{aligned} &\text{Change in habitat suitability} \\ &= \frac{1}{n} \sum_{m=1}^{n} \frac{2050 \text{ habitat suitability}_s - 2015 \text{ habitat suitability}_s}{2015 \text{ habitat suitability}_s} \tag{3} \end{aligned}$$
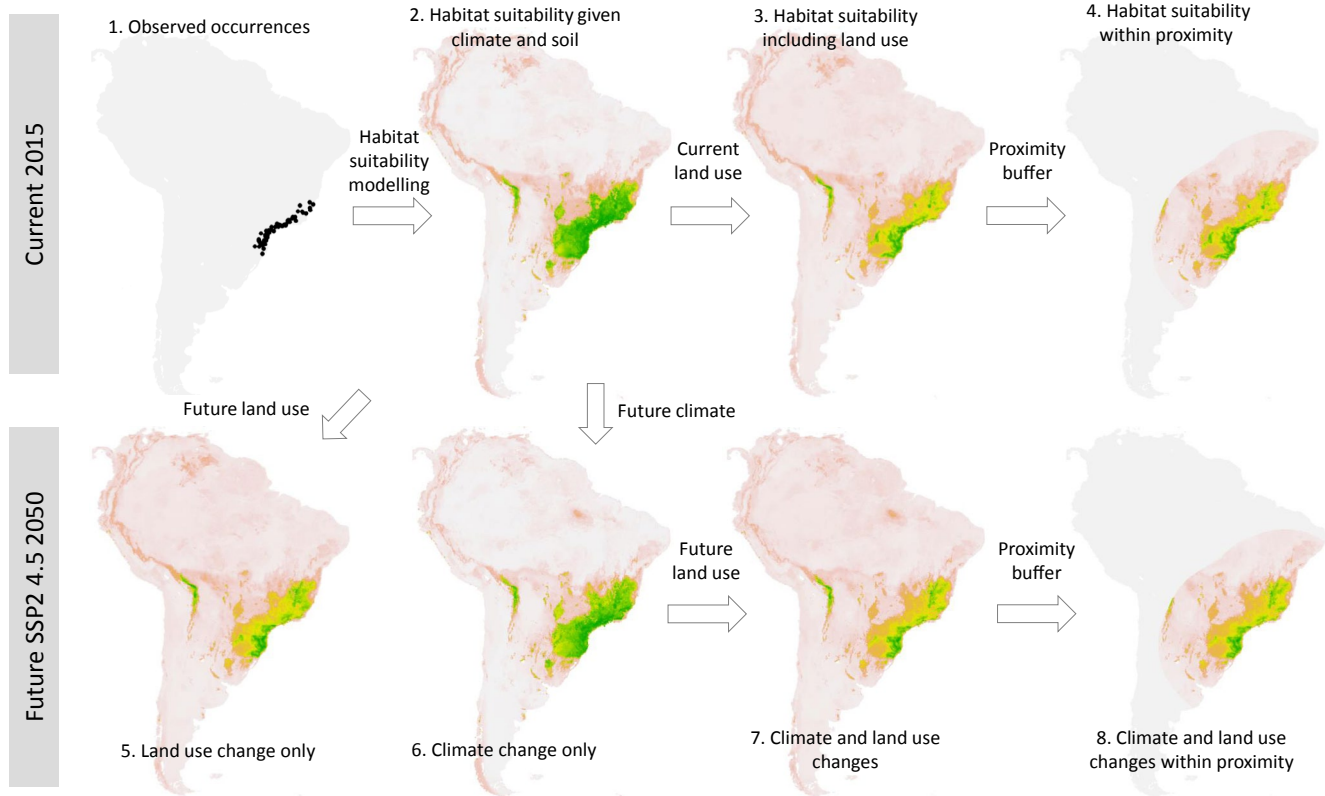
2.11 | Statistical analyses

We summarized the distribution of changes in habitat suitability per species using the mean and median, as both convey information informative to the distribution of values (and enabling direct comparison with prior studies that largely provided mean projections). Differences between the mean and median highlight the skewness in predicted changes in habitat suitability, which is an important aspect of the impacts of climate and land use change, as can be visualized in the frequency distribution plot (Figure 3).

We fitted simple ordinary least-squares regression models to understand how changes in habitat suitability relate to species' area of occupancy and to test the hypothesis that species with smaller range sizes are more negatively affected by changes in climate and land use. For each model, we checked for the relationship between

TABLE 1 Values of the coefficients weighting the impacts of each land use on the habitat suitability. γ = loss of habitat suitability proportional to the overall loss of species richness relative to the primary vegetation baseline (Newbold et al., 2015); β = relative compositional similarity to the primary vegetation (see fig. 3b in Newbold et al., 2016); α = relative difference in species richness among range size groups within each land use (Newbold et al., 2018). Range size groups refer to first, second and third quantiles

Land use	Range size	γ	β	α	γ*β*α
Primary vegetation	Q1	1	1	1.03	1.03
Primary vegetation	Q2	1	1	1.05	1.05
Primary vegetation	Q3	1	1	0.92	0.92
Secondary vegetation	Q1	.92	.94	0.87	0.76
Secondary vegetation	Q2	.92	.94	1.02	0.88
Secondary vegetation	Q3	.92	.94	1.10	0.96
Pastures and rangeland	Q1	.7	.75	0.79	0.42
Pastures and rangeland	Q2	.7	.75	1.02	0.54
Pastures and rangeland	Q3	.7	.75	1.19	0.62
Urban	Q1	.69	.87	0.77	0.46
Urban	Q2	.69	.87	0.90	0.54
Urban	Q3	.69	.87	1.32	0.80
Cropland	Q1	.65	.79	0.68	0.35
Cropland	Q2	.65	.79	0.98	0.50
Cropland	Q3	.65	.79	1.34	0.69

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FIGURE 1 Steps followed to project the effects of predicted future climate and land use changes on species' habitat suitability. The future scenario is based on the shared socioeconomic pathway SSP2 and representative concentration pathway RCP4.5.
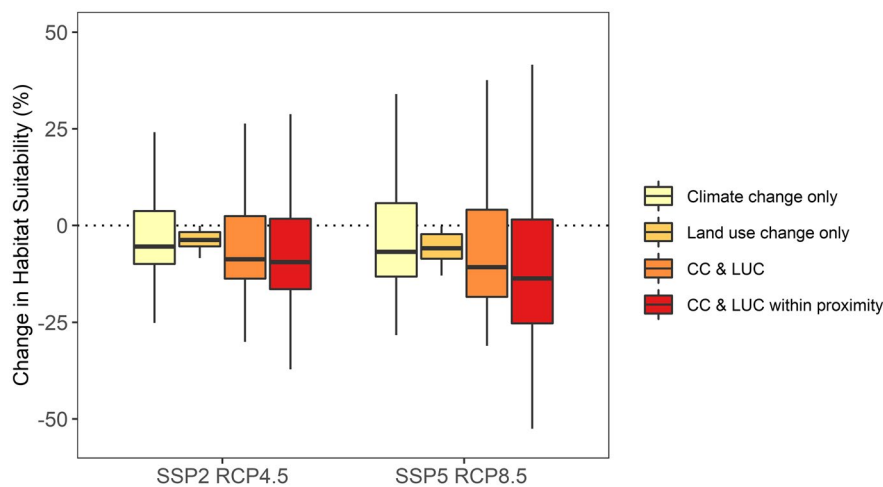
FIGURE 2 Box plot of the predicted effects of climate and land use on the species' habitat suitability given the two scenarios for climate and land use change in the year 2050. The scenario based on the shared socioeconomic pathway SSP2 and the representative concentration pathway RCP4.5 represents moderate levels of change, while the SSP5 RCP8.5 represents extreme levels of change. Effects are mean values from five climate models. Lines inside the boxes show median effects, the lower and upper limits of the boxes show first and third quantiles, respectively, and whiskers show range from minimum to maximum values excluding outliers (not shown). CC = climate change; LUC = land use change

studentized residuals and fitted values and the predictor and transformed area of occupancy either to the logarithmic scale (base 2) or square root, choosing the transformation that performed best in minimizing undesirable trends in residuals and spreading the data more symmetrically. Predictor and response variables were standardized to have means of zero and standard deviations of one, so regression coefficients are comparable between models. Summary statistics, figures and regression models were generated in R v.3.6.3
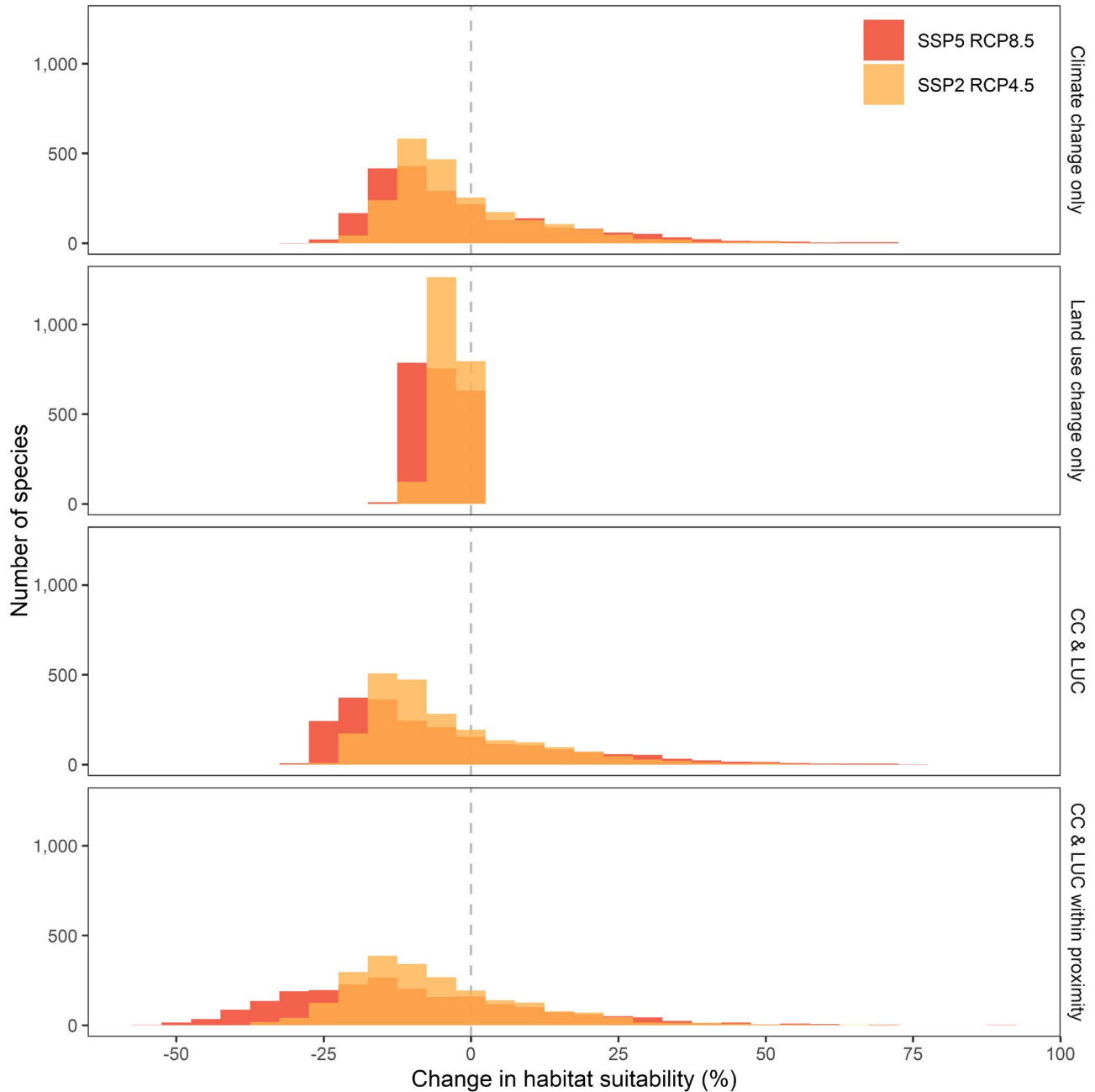
FIGURE 3 Frequency distribution of predicted percent change in habitat suitability (year 2015 to 2050) under SSP2-RCP4.5 and SSP5-RCP8.5 scenarios, and by effects of climate change, land use change, combined climate and land use change, and climate and land use changes within proximity of observed occurrences. The scenario based on the shared socioeconomic pathway SSP2 and the representative concentration pathway RCP4.5 represents moderate levels of change, while the SSP5 RCP8.5 represents extreme levels of change. CC = climate change; LUC = land use change

(R Core Team, 2020) with support of the packages 'ggplot2' v.3.3.0 (Wickham, 2016), 'car' v.3.0–7 (Fox & Weisberg, 2019) and 'doBy' v. 4.6.5 (Højsgaard & Halekoh, 2020).

3 | RESULTS

Projected climate and land use changes showed distinct impacts on future habitat suitability of Atlantic Forest species. When simulating the effects of climate change alone, keeping land use constant, the mean species' habitat suitability decreased by 2% under SSP2-RCP4.5 (median = −5%, min. = −31%, max. = 114%) and by 2% under SSP5-RCP8.5 (median = −7%, min. = −33%, max. = 129%) (Figure 2). Land use change had a more negative mean impact. Simulating the effects of land use change alone, keeping climate constant, reduced the mean species' habitat suitability by 4% under SSP2 (median = −4%, min. = −9%, max. = 0%) and by 6% under SSP5 (median = −6%, min. = −14%, max. = 0%). The combined effects of climate and

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land use change reduced the mean species' habitat suitability by 4% under SSP2-RCP4.5 (median = −9%, min. = −34%, max. = 129%) and 5% under SSP5-RCP8.5 (median = −11%, min. = −36%, max. = 145%). When considering changes in habitat suitability within the proximity of observed occurrences, the combined effects of climate and land use reduced the estimated species' habitat suitability by 6% under SSP2-RCP4.5 (median = −10%) and 10% under SSP5-RCP8.5 (median = −14%) (Figure 2).

A striking aspect of the predicted impacts is the right-skewed distribution of changes in habitat suitability. Few species gained large amounts of habitat suitability—due to projected increases in climate suitability—while the majority of the species lost substantial amounts of habitat suitability (Figure 3). Future habitat suitability was at least 10% smaller for 48% of the species under SSP2-RCP4.5 and for 58% of the species under SSP5-RCP8.5. In contrast, future habitat suitability was at least 10% larger for only 14% of the species under SSP2-RCP4.5 and 16% of the species under SSP5-RCP8.5.

Changes in habitat suitability were strongly associated with observed area of occupancy. Species with smaller area of occupancy lost larger percentages and larger absolute amounts of suitable habitat (Figure 4, Supporting Information Figure S4). Among the species with the 25% smallest observed area of occupancy, 59%–72% were predicted to lose at least 10% of habitat suitability, while only 11%–12% were predicted to gain 10% or more of habitat suitability (variation associated with scenarios SSP2-4.5 and SSP5-8.5; Figure 5). In contrast, among the species with the 25% largest area of occupancy,

31%–38% were predicted to lose at least 10% of habitat suitability, while 17%–23% were predicted to gain 10% or more of habitat suitability (Figure 5).

The strong relationship between species' area of occupancy and percent change in habitat suitability was driven mainly by land use change (β = 0.46–0.44, R^2 = .21–.20, t-value = 24–23, p-value << .0001, variation associated with scenarios SSP2-RCP4.5 and SSP5-RCP8.5), and negligibly by climate change (β = 0.028–0.044, R^2 < .01, t-value = 1–2, p-value = n.s.–.04; Figure 4). The selective impact of land use change reflects both a site-level effect (vide the α coefficient in the land use model), and an independent effect observed on the macroscale (i.e. without the α coefficient: β = 0.04–0.08, R^2 = .01–.02, t-value = 1.9–3.8, p-value = .05–.0001). Random forests models suggested a positive relationship between species' area of occupancy and percent change in habitat suitability (β = 0.09–0.10, R^2 = .01, t-value = 4–5, p-value < .0001), though with effect size much smaller, more variable and less predictable than the effect of land use change (see above). In contrast, the boosted regression trees suggested there is no relationship between area of occupancy and percent change in habitat suitability (β = −0.007–0.014, R^2 << .01, t-value = 0–1, p-value = n.s.), causing the ensemble models to show only a marginally significant weak range-size sensitivity in the independent effects of climate change. However, the combined impacts of climate and land use changes when excluding areas distant from observed occurrences were always strongly and positively dependent on species' area of occupancy (ensemble:
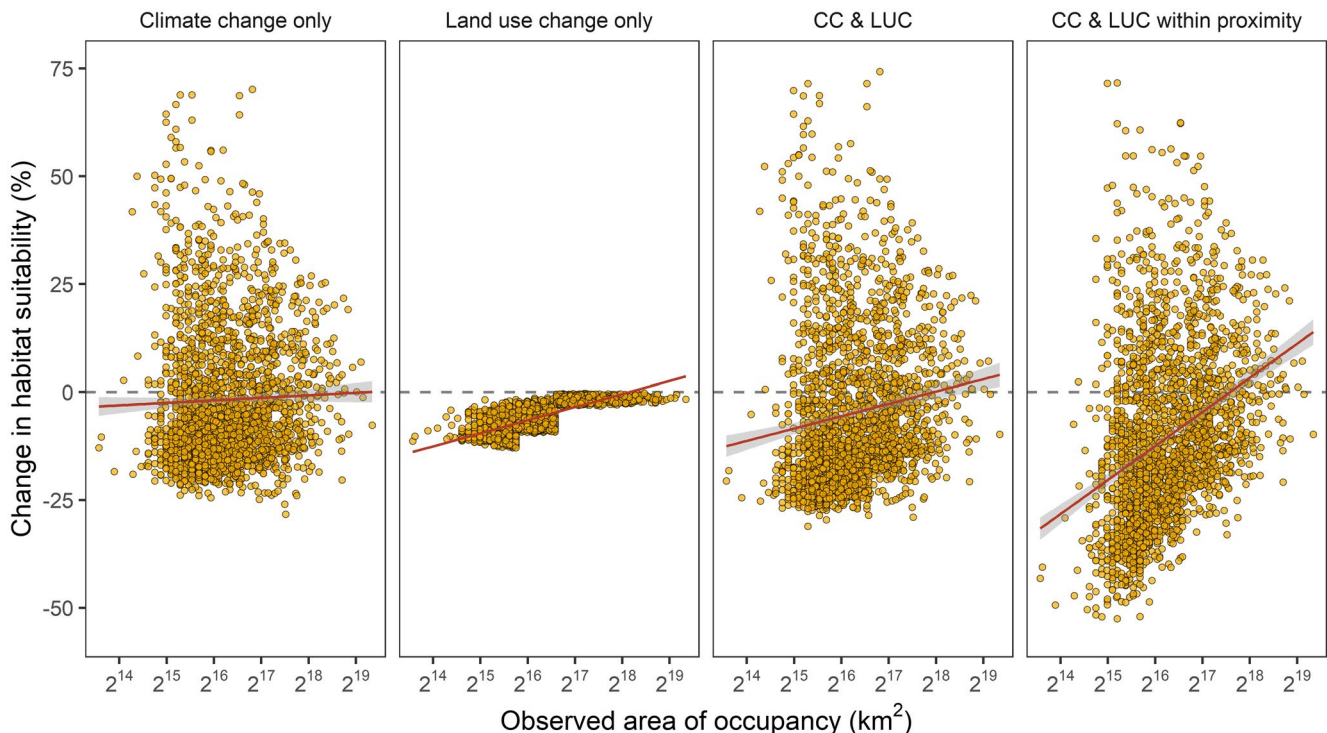
FIGURE 4 Relationship between observed area of occupancy and percent change in species' habitat suitability discriminated by the effects of climate change, land use change, combined climate and land use change, and climate and land use changes within proximity of observed occurrences under scenario SSP5-RCP8.5. CC = climate change; LUC = land use change; RCP representative concentration pathway; SSP = shared socioeconomic pathway
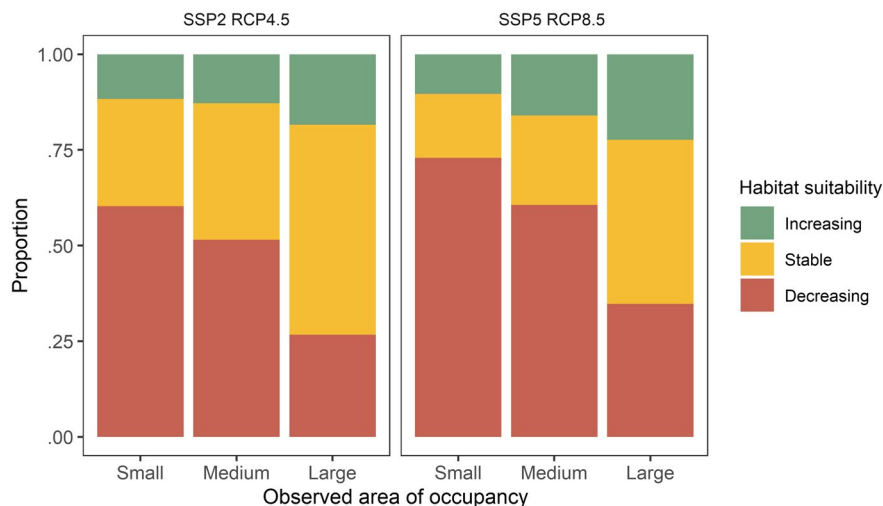
FIGURE 5   Proportion of species with habitat suitability predicted to increase at least 10%, remain similar (between 10% decrease and 10% increase) or decrease at least 10% under two scenarios of climate and land use changes. Species were grouped by observed area of occupancy into small (smallest 25%), medium (intermediate 50%) and large (largest 25%). The scenario based on the shared socioeconomic pathway SSP2 and the representative concentration pathway RCP4.5 represents moderate levels of change, while the SSP5 RCP8.5 represents extreme levels of change. This figure is based on the ensemble of modelling techniques and averaged across climate models. For variation across climate models and modelling techniques, see Supporting Information Figure S5

β = 0.188–0.289, R^2 = .04–.08, t-value = 9–14, p-value << .0001), supporting our expectation that the impacts of climate and land use changes are more detrimental to small-ranged species and more beneficial to widespread species (Figure 4, Supporting Information Figure S4).

4 | DISCUSSION

4.1 | Impacts of land use change versus climate change

Our results show that land use change will likely be responsible for larger total losses of the habitat of Atlantic Forest plants than climate change over the next few decades. This finding agrees with previous studies suggesting that land use change is more important than climate change as a driver of biodiversity loss in tropical forest regions (de Chazal & Rounsevell, 2009; IPBES, 2019; Jetz et al., 2007; Sala et al., 2005; Schipper et al., 2020; WWF, 2018), and in the Atlantic Forest region (Silva et al., 2019).

Climate change (i.e. assuming all other drivers of change are held constant) posed, on average, a lower threat than expected to the habitat suitability for Atlantic Forest plants. For instance, our predicted impacts of climate change were not as negative as those for Cerrado trees (species were predicted to lose 35%–60% of their area of distribution; Siqueira & Peterson, 2003; Velazco et al., 2019), Amazon trees (50% average loss in species area of occupancy; Gomes et al., 2019; Miles et al., 2004), European plants (average of 30% loss in suitable habitat; Thuiller et al., 2005), or plants across the globe (8%–67% of the species predicted to lose > 50% of their

'climatic range'; Warren et al., 2018). Much of the variation among these estimates is likely explained by differences in methods, including modelling assumptions, techniques and predictors, global climate models and future scenarios used. However, the marked contrasts with our results might indicate that Atlantic Forest plants may be under relatively lower threat from climate change compared to species in other habitats (Silva et al., 2019). The proximity of the Atlantic Forest to the Atlantic Ocean buffers the effects of climate change, making temperature and humidity relatively stable (Torres & Marengo, 2014).

4.2 | Effect of species' geographic range size

Our results support the hypothesis that range-restricted species are more negatively affected by the combined effects of climate and land use change, and by the independent effects of land use change (Newbold et al., 2018; Silva et al., 2019; Staude et al., 2020). However, the evidence for the existence of a range size pattern in the independent effects of climate change was inconsistent, failing to support our expectation (Schwartz et al., 2006; Thuiller et al., 2005). Species with the smallest range sizes were most sensitive to the combined changes in climate and land use, particularly when disregarding changes in habitat suitability deemed too far away from observed occurrences. This pattern may be related to two key factors. First, small areas are more vulnerable than large areas to being affected in their entirety by changes in the environment (Gaston & Fuller, 2009; Staude et al., 2020). Second, species confined to a small area are less able to take advantage of increases in habitat suitability that are sparsely spread over a large area. In

contrast, widespread species were most resistant and often benefited from projected changes in climate. Given the relatively large niche breadth of widespread species (Slatyer et al., 2013), it is likely that future combinations of environmental conditions will be more inclusive of their environmental tolerances, as compared to narrowly distributed species.

4.3 | Other considerations

Our results do not indicate gains or losses in geographic range size. They attempt to show changes in habitat suitability, which are quite different. We expect that changes in habitat suitability indicate some of the pressures (positive or negative) that climate and land use may exert on species. Whether species' range will change in response to these pressures is beyond the scope of this study (but critical to conservation). Species may withstand environmental changes and persist in their current area of occupancy despite apparent decreasing suitability (Spicer & Gaston, 1999), and species may not expand their range into areas with increasing suitability due to dispersal limitation (Corlett & Westcott, 2013).

The time-lag between reduction in habitat suitability and loss of area of occupancy may be large enough to hinder our perception of impacts, particularly for long-lived trees. This time-lag is somewhat analogous to the relaxation time associated with extinction debt (Figueiredo et al., 2019; Halley et al., 2016). Given the longevity and generation length of the species, the time-lag may range from a few to hundreds of years. The time-lag should be shorter in cases where the species' range is clearly limited by climate, as observed in some montane species (Morueta-Holme et al., 2015).

Though our results suggest that Atlantic Forest plants may lose lower proportions of their habitat from climate change compared to estimates from elsewhere, this should not be taken as evidence that climate change is not a major threat in the region. On the contrary, centuries of exploitation have already caused the loss of the overwhelming majority of the original habitat (Galindo-Leal & Câmara, 2003; Ribeiro et al., 2009), endangered a large fraction of the plant species (Martinelli & Moraes, 2013), and likely built up a large extinction debt (Joly et al., 2014; Nic Lughadha et al., 2020). Additional losses of habitat suitability for species that are already vulnerable may substantially increase their extinction risk (Moat et al., 2019), and climate change will affect even the species that have been protected from land use changes, such as those in montane regions, rocky outcrops, hilltops and steep slopes, and legally protected areas.

In addition, the large variation in the projected impacts of climate change has an important implication for those species with the largest deviations from predicted averages. In particular, the species losing the largest proportions of their habitat suitability may become subject to threat of extinction. It is also important to highlight that our sample does not include species with fewer than 15 unique records, thus it excludes the majority of the Atlantic Forest species and the species with smallest range sizes, which are the ones most likely be at risk of extinction (Supporting Information Figure S1).

Losses of habitat suitability will be much larger in the high emissions and most intensive land use scenario (SSP5-RCP8.5) than the SSP2-RCP4.5 scenario, particularly due to the impacts of land use change. The new CMIP6 models forecast more extreme changes in climate, and therefore greater losses in habitat suitability (see Supporting Information Figures S4b and S5), which is particularly concerning because previous estimates were based on climate models that typically project smaller changes in climate (Hausfather, 2019). Avoiding the SSP5-RCP8.5 scenario should thus be largely beneficial to the conservation of plant species in the region. For a more thorough explanation of caveats, including those inherent to modelling habitat suitability, please refer to Supporting Information Appendix S2.

4.4 | Conclusion

Land use change rather than climate change will likely cause more losses to the habitat of Atlantic Forest plants during the next several decades. Although the importance of climate change as a driver of biodiversity loss is increasing through time (IPBES, 2019; Schipper et al., 2020), decisions and actions affecting land use change in the coming decades rather than climate change (e.g. protected areas, forest management, land use planning, and forest restoration) will likely continue to be more critical to the short-term conservation of Atlantic Forest species. Whether a species loses or gains suitable habitat depends substantially on current range size and scenarios for climate and land use changes. The evidence indicates that small-ranged species are particularly vulnerable to loss of habitat, while widespread species are more resistant and may often benefit from climate change. Overall, we can expect that the combined effects of climate and land use change will impoverish the Atlantic Forest region. As habitat suitability decreases for most but increases for a few species, the similarity among plant assemblages is bound to increase through time, accelerating the ongoing homogenization of plant communities in Brazil's Atlantic Forest region (Lôbo et al., 2011; Tabarelli et al., 2012; Zwiener et al., 2018) and globally (Newbold et al., 2018; Staude et al., 2020).

AUTHOR CONTRIBUTIONS

DATA AVAILABILITY STATEMENT

The R codes and data supporting this study's findings are available in a Dryad repository at https://doi.org/10.5061/dryad.ksn02 v74h. The raw data that are not shared directly in the repository can be downloaded from their online sources: (a) occurrence records (Species Link Network, http://www.splink.org.br); (b) land use data (harmonized global land use for years 1500–2100, http://luh.umd. edu/data.shtml); (c) list of species endemic to Brazil (Flora do Brasil, http://ipt.jbrj.gov.br/jbrj/resource?r=lista_especies_flora_brasi l&v=393.175); (d) bioclimatic variables (WorldClim, https://www. worldclim.org/); (e) soil attributes (SoilGrids, https://soilgrids.org/).

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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*, 327–338. https://doi. org/10.1111/j.2041-210X.2011.00172.x

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., & Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. *Ecology Letters*, *15*, 365–377. https://doi. org/10.1111/j.1461-0248.2011.01736.x

Brazil Flora Group. (2019). *Brazilian Flora 2020 project - Projeto Flora do Brasil 2020*. v393.179. Instituto de Pesquisas Jardim Botanico do Rio de Janeiro.

Carreno-Rocabado, G., Pena-Claros, M., Bongers, F., Diaz, S., Quetier, F., Chuvina, J., & Poorter, L. (2016). Land-use intensification effects on functional properties in tropical plant communities. *Ecological Applications*, *26*, 174–189. https://doi.org/10.1890/14-0340

Carvalho, G. (2016). flora: Tools for interacting with the Brazilian Flora 2020. R package version 0.2.7. https://CRAN.R-project.org/package=flora

Chou, S. C., Lyra, A., Mourão, C., Dereczynski, C., Pilotto, I., Gomes, J., Bustamante, J., Tavares, P., Silva, A., Rodrigues, D., & Campos, D. (2014). Assessment of climate change over South America under RCP 4.5 and 8.5 downscaling scenarios. *American Journal of Climate Change*, *3*, 512–527.

Colombo, A., & Joly, C. (2010). Brazilian Atlantic Forest lato sensu: The most ancient Brazilian forest, and a biodiversity hotspot, is highly threatened by climate change. *Brazilian Journal of Biology*, *70*, 697–708. https://doi.org/10.1590/S1519-69842010000400002

Colwell, R. K., Brehm, G., Cardelus, C. L., Gilman, A. C., & Longino, J. T. (2008). Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science*, *322*, 258–261. https://doi. org/10.1126/science.1162547

Corlett, R. T. (2016). Plant diversity in a changing world: Status, trends, and conservation needs. *Plant Diversity*, *38*, 10–16. https://doi. org/10.1016/j.pld.2016.01.001

Corlett, R. T., & Westcott, D. A. (2013). Will plant movements keep up with climate change? *Trends in Ecology and Evolution*, *28*, 482–488. https://doi.org/10.1016/j.tree.2013.04.003

de Chazal, J., & Rounsevell, M. D. A. (2009). Land-use and climate change within assessments of biodiversity change: A review. *Global Environmental Change*, *19*, 306–315. https://doi.org/10.1016/j.gloen vcha.2008.09.007

Elith, J., Leathwick, J. R., & Hastie, T. (2008). A working guide to boosted regression trees. *Journal of Animal Ecology*, *77*, 802–813. https://doi. org/10.1111/j.1365-2656.2008.01390.x

Fick, S. E., & Hijmans, R. J. (2017). Worldclim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, *37*(12), 4302–4315. https://doi.org/10.1002/joc.5086

Figueiredo, L., Krauss, J., Steffan-Dewenter, I., & Sarmento Cabral, J. (2019). Understanding extinction debts: Spatio–temporal scales, mechanisms and a roadmap for future research. *Ecography*, *42*, 1973–1990. https://doi.org/10.1111/ecog.04740

Follador, M., Viezzer, J., Egler, M., Becher, M., Hach, L., Pereira, V., & Hartzell, S. (2018). Modelling potential biophysical impacts of climate change in the Atlantic Forest: Closing the gap to identify vulnerabilities in Brazil. In W. Leal Filho & L. Esteves De Freitas (Eds.), *Climate change adaptation in Latin America: Managing vulnerability, fostering resilience* (pp. 33–64). Springer International.

Fox, J., & Weisberg, S. (2019). *An R companion to applied regression* (3rd ed.). Sage. https://socialsciences.mcmaster.ca/jfox/Books/Companion/

Galindo-Leal, C., Câmara, I. D. G. (2003). Atlantic Forest Hotspot status: An overview. In C. Galindo-Leal, & I. D. G. Câmara (Eds.), *The Atlantic Forest of South America: biodiversity status, threats, and outlook* (pp. 3–11). Conservation International.

Gaston, K. J., & Fuller, R. A. (2009). The sizes of species' geographic ranges. *Journal of Applied Ecology*, *46*, 1–9. https://doi. org/10.1111/j.1365-2664.2008.01596.x

Gomes, V. H. F., Vieira, I. C. G., Salomão, R. P., & ter Steege, H. (2019). Amazonian tree species threatened by deforestation and climate change. *Nature Climate Change*, *9*, 547–553. https://doi.org/10.1038/ s41558-019-0500-2

Gonzalez, P., Neilson, R. P., Lenihan, J. M., & Drapek, R. J. (2010). Global patterns in the vulnerability of ecosystems to vegetation shifts due to climate change. *Global Ecology and Biogeography*, *19*, 755–768. https://doi.org/10.1111/j.1466-8238.2010.00558.x

Greenwell, B., Boehmke, B., Cunningham, J. & GBM Developers (2019). gbm: Generalized boosted regression models. R package version 2.1.5. https://CRAN.R-project.org/package=gbm

Guisan, A., Thuiller, W., & Zimmermann, N. E. (2017). *Habitat suitability and distribution models: With applications in R*. Cambridge University Press.

Halley, J. M., Monokrousos, N., Mazaris, A. D., Newmark, W. D., & Vokou, D. (2016). Dynamics of extinction debt across five taxonomic groups. *Nature Communications*, *7*, 12283. https://doi.org/10.1038/ncomm s12283

Hastie, T., Tibshirani, R., & Friedman, J. (2013). *The elements of statistical learning: Data mining, inference, and prediction* (2nd ed, pp. 1–745). Springer.

Hausfather, Z. (2019). CMIP6: The next generation of climate models explained. Carbon brief. https://www.carbonbrief.org/cmip6-the-next-generation-of-climate-models-explained

Hengl, T., de Jesus, J. M., MacMillan, R. A., Batjes, N. H., Heuvelink, G. B. M., Ribeiro, E., Samuel-Rosa, A., Kempen, B., Leenaars, J. G. B., Walsh, M. G., & Gonzalez, M. R. (2014). SoilGrids1km–global soil information based on automated mapping. *PLoS ONE*, *9*, e105992. https://doi.org/10.1371/journal.pone.0105992

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. https:// doi.org/10.1002/joc.1276

Højsgaard, S. & Halekoh, U. (2020). doBy: Groupwise statistics, LSmeans, linear contrasts, utilities. R package version 4.6.5. https://CRAN.R-project.org/package=doBy

Hurtt G. C., Chini L., Sahajpal R., Frolking S., Bodirsky B. L., Calvin K., Doelman J. C., Fisk J., Fujimori S., Klein Goldewijk K., Hasegawa T., Havlik P., Heinimann A., Humpenöder F., Jungclaus J., Kaplan J. O., Kennedy J., Krisztin T., Lawrence D., ... Zhang X. (2020). Harmonization of global land use change and management for the period 850–2100 (LUH2) for CMIP6. *Geoscientific Model Development*, *13*, 5425–5464. https://doi.org/10.5194/gmd-13-5425-2020

IBGE. (2008). *Mapa da área de aplicação da Lei nº 11.428 de 2006*. Instituto Brasileiro de Geografia e Estatística.

IPBES. (2019). Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (S. Díaz, J. Settele, E. S. Brondízio, H. T. Ngo, M. Guèze, J. Agard, A. Arneth, P. Balvanera, K. A. Brauman, S. H. M. Butchart, K. M. A. Chan, L. A. Garibaldi, K. Ichii, J. Liu, S. M. Subramanian, G. F. Midgley, P. Miloslavich, Z. Molnár, D. Obura, A. Pfaff, ... C. N. Zayas, Eds.) (56p). Bonn, Germany: IPBES secretariat.

James, G., Witten, D., Hastie, T., & Tibshirani, R. (2013). *An introduction to statistical learning: With applications in R* (745p). Springer.

Jarvis, A., Reuter, H. I., Nelson, A., & Guevara, E. (2008). Hole-filled SRTM for the globe version 4. Available from the CGIAR-CSI SRTM 90m database (http://srtm.csi.cgiar.org).

Jetz, W., Wilcove, D. S., & Dobson, A. P. (2007). Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biology*, *5*, e157. https://doi.org/10.1371/journal.pbio.0050157

Joly, C. A., Metzger, J. P., & Tabarelli, M. (2014). Experiences from the Brazilian Atlantic Forest: Ecological findings and conservation initiatives. *New Phytologist*, *204*, 459–473.

Kottek, M., Grieser, J., Beck, C., Rudolf, B., & Rubel, F. (2006). World map of the Köppen-Geiger climate classification updated. *Meteorologische Zeitschrift*, *15*, 259–263. https://doi.org/10.1127/0941-2948/2006/0130

Laurance, W. F., Nascimento, H. E., Laurance, S. G., Andrade, A. C., Fearnside, P. M., Ribeiro, J. E., & Capretz, R. L. (2006). Rain forest fragmentation and the proliferation of successional trees. *Ecology*, *87*, 469–482. https://doi.org/10.1890/05-0064

Leão, T. C. C., Nic Lughadha, E., & Reich, P. B. (2020). Evolutionary patterns in the geographic range size of Atlantic Forest plants. *Ecography*, *43*, 1510–1520. https://doi.org/10.1111/ecog.05160

Liaw, A., & Wiener, M. (2002). Classification and regression by randomForest. *R News*, *2*, 18–22.

Lôbo, D., Leão, T., Melo, F. P. L., Santos, A. M. M., & Tabarelli, M. (2011). Forest fragmentation drives Atlantic forest of northeastern Brazil to biotic homogenization. *Diversity and Distributions*, *17*, 287–296. https://doi.org/10.1111/j.1472-4642.2010.00739.x

Martinelli, G., & Moraes, M. A. (2013). *Livro vermelho da flora do Brasil*. Instituto de Pesquisas Jardim Botânico do Rio de Janeiro.

McElwain, J. C. (2018). Paleobotany and global change: Important lessons for species to biomes from vegetation responses to past global change. *Annual Review of Plant Biology*, *69*, 761–787. https://doi.org/10.1146/annurev-arplant-042817-040405

Miles, L., Grainger, A., & Phillips, O. (2004). The impact of global climate change on tropical forest biodiversity in Amazonia. *Global Ecology and Biogeography*, *13*, 553–565. https://doi.org/10.1111/j.1466-822X.2004.00105.x

Mittermeier, R. A., Gil, P. R., Hoffmann, M., Pilgrim, J., Brooks, T., Mittermeier, C. G., & Fonseca, G. A. B. (2004). *Hotspots revisited: Earth's biologically richest and most endangered terrestrial ecoregions*. Cemex and University of Chicago Press.

Moat, J., Gole, T. W., & Davis, A. P. (2019). Least concern to endangered: Applying climate change projections profoundly influences the extinction risk assessment for wild Arabica coffee. *Global Change Biology*, *25*, 390–403. https://doi.org/10.1111/gcb.14341

Morueta-Holme, N., Engemann, K., Sandoval-Acuña, P., Jonas, J. D., Segnitz, R. M., & Svenning, J.-C. (2015). Strong upslope shifts in Chimborazo's vegetation over two centuries since Humboldt. *Proceedings of the National Academy of Sciences USA*, *112*, 12741–12745. https://doi.org/10.1073/pnas.1509938112

Newbold, T., Hudson, L. N., Contu, S., Hill, S. L. L., Beck, J., Liu, Y., Meyer, C., Phillips, H. R. P., Scharlemann, J. P. W., & Purvis, A. (2018). Widespread winners and narrow-ranged losers: Land use homogenizes biodiversity in local assemblages worldwide. *PLoS Biology*, *16*, e2006841. https://doi.org/10.1371/journal.pbio.2006841

Newbold, T., Hudson, L. N., Hill, S. L. L., Contu, S., Gray, C. L., Scharlemann, J. P. W., Börger, L., Phillips, H. R. P., Sheil, D., Lysenko, I., & Purvis, A. (2016). Global patterns of terrestrial assemblage turnover within and among land uses. *Ecography*, *39*, 1151–1163. https://doi.org/10.1111/ecog.01932

Newbold, T., Hudson, L. N., Hill, S. L. L., Contu, S., Lysenko, I., Senior, R. A., Börger, L., Bennett, D. J., Choimes, A., Collen, B., Day, J., De Palma, A., Díaz, S., Echeverria-Londoño, S., Edgar, M. J., Feldman, A., Garon, M., Harrison, M. L. K., Alhusseini, T., ... Purvis, A. (2015). Global effects of land use on local terrestrial biodiversity. *Nature*, *520*, 45–50. https://doi.org/10.1038/nature14324

Nic Lughadha, E., Bachman, S. P., Leão, T. C. C., Forest, F., Halley, J. M., Moat, J., Acedo, C., Bacon, K. L., Brewer, R. F. A., Gâteblé, G., Gonçalves, S. C., Govaerts, R., Hollingsworth, P. M., Krisai-Greilhuber, I., Lirio, E. J., Moore, P. G. P., Negrão, R., Onana, J. M., Rajaovelona, L. R., ... Walker, B. E. (2020). Extinction risk and threats to plants and fungi. *Plants, People, Planet*, *2*, 389–408. https://doi.org/10.1002/ppp3.10146

Popp, A., Calvin, K., Fujimori, S., Havlik, P., Humpenöder, F., Stehfest, E., Bodirsky, B. L., Dietrich, J. P., Doelmann, J. C., Gusti, M., Hasegawa, T., Kyle, P., Obersteiner, M., Tabeau, A., Takahashi, K., Valin, H., Waldhoff, S., Weindl, I., Wise, M., ... van Vuuren, D. P. (2017). Land-use futures in the shared socio-economic pathways. *Global Environmental Change*, *42*, 331–345. https://doi.org/10.1016/j.gloenvcha.2016.10.002

Prasad, A. M., Iverson, L. R., & Liaw, A. (2006). Newer classification and regression tree techniques: Bagging and random forests for ecological prediction. *Ecosystems*, *9*, 181–199. https://doi.org/10.1007/s10021-005-0054-1

R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Riahi, K., Rao, S., Krey, V., Cho, C., Chirkov, V., Fischer, G., Kindermann, G., Nakicenovic, N., & Rafaj, P. (2011). RCP 8.5—A scenario of comparatively high greenhouse gas emissions. *Climatic Change*, *109*, 33–57. https://doi.org/10.1007/s10584-011-0149-y

Riahi, K., van Vuuren, D. P., Kriegler, E., Edmonds, J., O'Neill, B. C., Fujimori, S., Bauer, N., Calvin, K., Dellink, R., Fricko, O., Lutz, W., Popp, A., Cuaresma, J. C., Kc, S., Leimbach, M., Jiang, L., Kram, T., Rao, S., Emmerling, J., ... Tavoni, M. (2017). The Shared Socioeconomic Pathways and their energy, land use, and greenhouse gas emissions implications: An overview. *Global Environmental Change*, *42*, 153–168. https://doi.org/10.1016/j.gloenvcha.2016.05.009

Ribeiro, M. C., Metzger, J. P., Martensen, A. C., Ponzoni, F. J., & Hirota, M. M. (2009). The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. *Biological Conservation*, *142*, 1141–1153. https://doi.org/10.1016/j.biocon.2009.02.021

Rivers, M. C., Taylor, L., Brummitt, N. A., Meagher, T. R., Roberts, D. L., & Lughadha, E. N. (2011). How many herbarium specimens are needed to detect threatened species? *Biological Conservation*, *144*, 2541–2547. https://doi.org/10.1016/j.biocon.2011.07.014

Sala, O., van Vuuren, D., Pereira, H., Lodge, D., Alder, J., Cumming, G., Dobson, A., & Xenopoulos, M. (2005). Chapter 10: Biodiversity across scenarios. In Millennium Ecosystem Assessment, *Volume 2: Scenarios* (pp. 375–408). Island Press. https://www.millenniumassessment.org/documents/document.334.aspx.pdf

Schipper, A. M., Hilbers, J. P., Meijer, J. R., Antão, L. H., Benítez-López, A., Jonge, M. M. J., Leemans, L. H., Scheper, E., Alkemade, R., Doelman, J. C., Mylius, S., Stehfest, E., Vuuren, D. P., Zeist, W.-J., & Huijbregts, M. A. J. (2020). Projecting terrestrial biodiversity intactness with GLOBIO 4. *Global Change Biology*, 26, 760–771. https://doi.org/10.1111/gcb.14848

Schwartz, M. W., Iverson, L. R., Prasad, A. M., Matthews, S. N., & O'Connor, R. J. (2006). Predicting extinctions as a result of climate change. *Ecology*, 87, 1611–1615.

Sheldon, K. S. (2019). Climate change in the tropics: Ecological and evolutionary responses at low latitudes. *Annual Review of Ecology, Evolution, and Systematics*, 50, 303–333. https://doi.org/10.1146/annurev-ecolsys-110218-025005

Silva, J. M. C. d., Rapini, A., Barbosa, L. C. F., & Torres, R. R. (2019). Extinction risk of narrowly distributed species of seed plants in Brazil due to habitat loss and climate change. *PeerJ*, 7, e7333. https://doi.org/10.7717/peerj.7333

Siqueira, M. F. d., & Peterson, A. T. (2003). Consequences of global climate change for geographic distributions of cerrado tree species. *Biota Neotropica*, 3, 1–14. https://doi.org/10.1590/S1676-06032003000200005

Slatyer, R. A., Hirst, M., & Sexton, J. P. (2013). Niche breadth predicts geographical range size: A general ecological pattern. *Ecology Letters*, 16, 1104–1114. https://doi.org/10.1111/ele.12140

Spicer, J. I., & Gaston, K. J. (1999). *Physiological diversity and its ecological implications*. Blackwell Science.

Staude, I. R., Navarro, L. M., & Pereira, H. M. (2020). Range size predicts the risk of local extinction from habitat loss. *Global Ecology and Biogeography*, 29, 16–25. https://doi.org/10.1111/geb.13003

Tabarelli, M., Peres, C. A., & Melo, F. P. L. (2012). The 'few winners and many losers' paradigm revisited: Emerging prospects for tropical forest biodiversity. *Biological Conservation*, 155, 136–140. https://doi.org/10.1016/j.biocon.2012.06.020

ter Steege, H., Pitman, N. C., Killeen, T. J., Laurance, W. F., Peres, C. A., Guevara, J. E., Salomão, R. P., Castilho, C. V., Amaral, I. L., de Almeida Matos, F. D., & de Souza Coelho, L. (2015). Estimating the global conservation status of more than 15,000 Amazonian tree species. *Science Advances*, 1(10), e1500936. https://doi.org/10.1126/sciadv.1500936

Thibaud, E., Petitpierre, B., Broennimann, O., Davison, A. C., & Guisan, A. (2014). Measuring the relative effect of factors affecting species distribution model predictions. *Methods in Ecology and Evolution*, 5, 947–955. https://doi.org/10.1111/2041-210X.12203

Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., Erasmus, B. F. N., de Siqueira, M. F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A. S., Midgley, G. F., Miles, L., Ortega-Huerta, M. A., Townsend Peterson, A., Phillips, O. L., & Williams, S. E. (2004). Extinction risk from climate change. *Nature*, 427, 145–148. https://doi.org/10.1038/nature02121

Thomson, A. M., Calvin, K. V., Smith, S. J., Kyle, G. P., Volke, A., Patel, P., Delgado-Arias, S., Bond-Lamberty, B., Wise, M. A., Clarke, L. E., & Edmonds, J. A. (2011). RCP4.5: A pathway for stabilization of radiative forcing by 2100. *Climatic Change*, 109, 77–94. https://doi.org/10.1007/s10584-011-0151-4

Thuiller, W., Georges, D., Engler, R. & Breiner, F. (2020). biomod2: Ensemble platform for species distribution modeling. R package version 3.4.6. https://CRAN.R-project.org/package=biomod2

Thuiller, W., Lavorel, S., & Araujo, M. B. (2005). Niche properties and geographical extent as predictors of species sensitivity to climate change. *Global Ecology and Biogeography*, 14, 347–357. https://doi.org/10.1111/j.1466-822X.2005.00162.x

Torres, R. R., & Marengo, J. A. (2014). Climate change hotspots over South America: From CMIP3 to CMIP5 multi-model datasets. *Theoretical and Applied Climatology*, 117, 579–587. https://doi.org/10.1007/s00704-013-1030-x

Velazco, S. J. E., Villalobos, F., Galvão, F., & De Marco Júnior, P. (2019). A dark scenario for Cerrado plant species: Effects of future climate, land use and protected areas ineffectiveness. *Diversity and Distributions*, 25(4), 660–673. https://doi.org/10.1111/ddi.12886

Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J.-M., Hoegh-Guldberg, O., & Bairlein, F. (2002). Ecological responses to recent climate change. *Nature*, 416, 389–395. https://doi.org/10.1038/416389a

Warren, R., Price, J., Graham, E., Forstenhaeusler, N., & VanDerWal, J. (2018). The projected effect on insects, vertebrates, and plants of limiting global warming to 1.5°C rather than 2°C. *Science*, 360, 791–795. https://doi.org/10.1126/science.aar3646

Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. Springer.

Wright, S. J., Muller-Landau, H. C., & Schipper, J. (2009). The future of tropical species on a warmer planet. *Conservation Biology*, 23, 1418–1426. https://doi.org/10.1111/j.1523-1739.2009.01337.x

WWF. (2018). Aiming higher. In M. Grooten, & R. E. A. Almond (Eds.), *Living planet report - 2018*. WWF.

Yin, L., Fu, R., Shevliakova, E., & Dickinson, R. E. (2013). How well can CMIP5 simulate precipitation and its controlling processes over tropical South America? *Climate Dynamics*, 41, 3127–3143. https://doi.org/10.1007/s00382-012-1582-y

Zappi, D. C., Filardi, F. L. R., Leitman, P., Souza, V. C., Walter, B. M. T., Pirani, J. R., Morim, M. P., Queiroz, L. P., Cavalcanti, T. B., Mansano, V. F., Forzza, R. C., Abreu, M. C., Acevedo-Rodríguez, P., Agra, M. F., Almeida, E. B. Jr., Almeida, G. S. S., Almeida, R. F., Alves, F. M., Alves, M., … Zickel, C. S. (2015). Growing knowledge: An overview of seed plant diversity in Brazil. *Rodriguésia*, 66, 1085–1113. https://doi.org/10.1590/2175-7860201566411

Zwiener, V. P., Lira-Noriega, A., Grady, C. J., Padial, A. A., & Vitule, J. R. S. (2018). Climate change as a driver of biotic homogenization of woody plants in the Atlantic Forest. *Global Ecology and Biogeography*, 27, 298–309. https://doi.org/10.1111/geb.12695

BIOSKETCH

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All authors are interested in understanding the impacts of global environmental change on plant species.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

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