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

Tarciso C. C. Leão1,2,3 | Jason R. Reinhardt2 | Eimear Nic Lughadha1 | Peter B. Reich2,4

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
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 phytoecographic 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 (Laurnce et al., 2006), and biotic homogenization of plant assemblages (Löbo 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).

## 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
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://floradobra.sil.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 MIROCS; 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 MIROCS (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 emissions 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 x 0.25 degree grid cells occupied by each of the land use states (Hurttt 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 (Hurttt 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:

\[
\text{Land use suitability}_\gamma = \alpha_{\gamma, \text{primary vegetation}} + \alpha_{\gamma, \text{secondary vegetation}} + \alpha_{\gamma, \text{pastures & rangeland}} + \alpha_{\gamma, \text{crops}} + \alpha_{\gamma, \text{urban}}
\]

where $\gamma$ = loss of habitat suitability proportional to the overall loss of species richness relative to the primary vegetation baseline (Newbold et al., 2015); $\beta$ = relative compositional similarity to the primary
vegetation (see fig. 3b in Newbold et al., 2016); $\alpha = \text{relative difference in species richness among range size groups within each land use (Newbold et al., 2018)}$; $r = \text{index for range size groups: first, second and third quantiles of range size}$; and $c = \text{index for spatial grid cell (Table 1)}$.

### 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 $r$):

$$\text{Habitat suitability}_s = \sum_{c=1}^{n} \text{environmental suitability}_c \times \text{land use suitability}_c$$

(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 $m$:

$$\text{Change in habitat suitability} = \frac{1}{n} \sum_{m=1}^{n} \frac{2050 \text{ habitat suitability}_s - 2015 \text{ habitat suitability}_s}{2015 \text{ habitat suitability}_s}$$

(3)

### 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. $\gamma = \text{loss of habitat suitability proportional to the overall loss of species richness relative to the primary vegetation baseline (Newbold et al., 2015)}$; $\beta = \text{relative compositional similarity to the primary vegetation (see fig. 3b in Newbold et al., 2016)}$; $\alpha = \text{relative difference in species richness among range size groups within each land use (Newbold et al., 2018)}$. Range size groups refer to first, second and third quantiles |
|---|---|---|---|---|---|
| **Land use** | **Range size** | $\gamma$ | $\beta$ | $\alpha$ | $\gamma^*\beta^*\alpha$ |
| 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 |
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 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.
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
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 ($\beta = 0.46–0.44$, $R^2 = .21–.20$, $t$-value = 24–23, $p$-value $< .0001$, variation associated with scenarios SSP2-RCP4.5 and SSP5-RCP8.5), and negligibly by climate change ($\beta = 0.028–0.044$, $R^2 < .01$, $t$-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 $\alpha$ coefficient in the land use model), and an independent effect observed on the macroscale (i.e. without the $\alpha$ coefficient: $\beta = 0.04–0.08$, $R^2 = .01–.02$, $t$-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 ($\beta = 0.09–0.10$, $R^2 = .01$, $t$-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 ($\beta = −0.007–0.014$, $R^2 << .01$, $t$-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:
\[ \beta = 0.188 – 0.289, \quad R^2 = .04 – .08, \quad t\text{-value} = 9 – 14, \quad p\text{-value} << .0001, \]
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).

### 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).

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AUTHOR CONTRIBUTIONS
TCCL conceived the initial idea and study design with support from JRR and PBR. TCCL compiled the data, wrote scripts for modelling and analysed modelling outputs. TCCL wrote the manuscript with contributions from ENL, PBR and JRR. All authors contributed with revisions and approved the manuscript.

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.ksn02v74h. 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://lulc.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_brasil&v=393.175); (d) bioclimatic variables (WorldClim, https://www.worldclim.org/); (e) soil attributes (SoilGrids, https://soilgrid.org/).

ORCID
Tarciso C. C. Ledo https://orcid.org/0000-0002-7029-1582

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**BIOSKETCH**

**Tarciso Leão** is a Research Fellow at the Royal Botanic Gardens, Kew. His research focuses on factors affecting species geographic range size and vulnerability to extinction, and understanding the impacts of major threats to tropical plant species. 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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