

The geographic range size and extinction risk of plants in the  
Brazilian Atlantic Forest

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## Abstract

The understanding the process of plant species extinction in tropical species-rich regions is substantially incomplete. What makes a species vulnerable to extinction? Are there recognizable species attributes that can help us to predict vulnerability? What are the underlying reasons for high vulnerability? What are the relative contributions of the main drivers of extinction such as land use change and climate change? This doctorate research addresses these questions focusing on the Atlantic Forest region of Brazil. The Atlantic Forest combines an extraordinarily high plant diversity, high human presence, and a relatively well-known flora, making it a region where species extinction is likely to occur and possible to monitor.

Chapter 1 seeks for correlates of extinction risk and insights on potential mechanisms underlying vulnerability to extinction. The chapter provides a first look on the broad ecological patterns in the extinction risk of plants in the Atlantic Forest. It helps to identify which plant groups are more threatened. It uses decision tree, standard regression, and phylogenetic regression to explore the relationships between species attributes and extinction risk. As expected, geographic range size was the main correlate of species extinction risk. Epiphytes (plants growing on other plants, commonly observed in the Atlantic Forest) and species restricted to rocky outcrops and sandy coastal plains ('restinga') were associated with highest extinction risk, and related to extinction risk even after controlling for the effects of geographic range size. Those findings support the notion that slow growth and adaptation to resource-limited environments is a reason for high vulnerability to extinction.

Chapter 1 also shows that extinction risk depends on phylogenetic relationships (i.e. closely related species tend to have similar extinction risk). Therefore, phylogenetically related factors not included in the analysis were likely important to explaining further differences in extinction risk, raising interest to test emerging hypotheses that diversification rate and lineage age explains variation in species' geographic range sizes and extinction risks.

Chapter 2 focused on understanding the variation in species geographic range sizes, which is the single most important predictor of extinction risk. This chapter includes a larger and improved dataset relative to Chapter 1, including evolutionary attributes, a higher resolution phylogeny, double the number of herbarium records, double the number of species (13,785 species, i.e. 90% of angiosperms of the Atlantic Forest), and more complete information on ecological attributes. This dataset allowed to investigate the existence of evolutionary and ecological patterns in the variation of species' geographic range sizes. The chapter shows that lineages with more species tend to have species with smaller range sizes. This trend was particularly strong when focusing on the proportion of species with vulnerably small range size. A two-fold increase in the number of species at the genus level was associated with an average increase of 40% in the number of species with vulnerably small range sizes. The evolutionary histories of the lineages, in particular the rates of speciation and extinction, seem to underlie these observed patterns.

Chapter 2 also addresses associated issues that have been inconclusive in the scientific literature. It shows how the relationship between life form and range size

depends on the vegetation type, which seems to clarify a long-held inconsistency in the literature. It challenges the notion that epiphytes tend to have larger range sizes than terrestrial plants, and suggests that the attributes and mechanisms leading to the rarity of epiphytes may apply to the lineages in which epiphytism evolved as a whole rather than to epiphytic species alone.

Chapter 3 investigates the projected effects of two of the main drivers of plant habitat loss: land use change and climate change. Using habitat suitability modelling, the chapter shows that land use change is likely to have a larger and consistently negative impact on species area of suitable habitat, while climate change will tend to have a more variable and selective impact – varying from largely negative to largely positive depending on the species. Chapter 3 also led to the conclusion that small-ranged and epiphytic species are at particularly high risk of losing area of suitable habitat in the near future.

Finally, this dissertation in its totality provides evidence and inference for recognizing patterns and understanding mechanisms behind the variation in plant species geographic range sizes and extinction risks. I hope the knowledge provided here contributes to improve our understanding of the problem of plant extinction in species-rich tropical forest regions.

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## Preface

Concerns with elevated rates of species extinction and overall biodiversity loss motivated scientists to create the field of conservation biology (Soulé 1985), and motivated governments to create policies to prevent extinctions (e.g., the Endangered Species Act in the United States). In Brazil, the country with the largest known number of vascular plant species (Forzza et al. 2012), such concerns led the federal government to prohibit (or limit) the exploitation of plant species threatened with extinction through federal law in 1965 ('Forest Code,' *Lei n° 4.771, de 15 de Setembro de 1965*'). In 1968, the first government official list of plants threatened with extinction was published in Brazil, with only 13 species – seven of which were orchids (*Portaria IBDF n° 303 de 29 de Maio de 1968*'). That list was updated in 1992 to include 107 plant species<sup>1</sup>, updated again in 2008, and lastly updated in 2014 to include 2,113 plant species officially threatened and protected by federal regulation (*Portaria n° 443 de 17 de dezembro de 2014*').

Despite the relatively large number of species in the most recent list of threatened species, the list likely underestimates the number of threatened species by a large margin. Brazil is home to 36,000 known plant species ([reflora.jbrj.gov.br](http://reflora.jbrj.gov.br)). The number of officially threatened species is thus 6% of the total. However, only 4,600 species had their extinction risk evaluated, and 46% of those were classified as threatened (Martinelli & Moraes 2013). This percentage may overestimate the extinction risk though, particularly if species likely to be threatened had a higher chance to be evaluated. An

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<sup>1</sup> *Portaria IBAMA N° 06-N, de 15 de janeiro de 1992.*

unbiased sample at the world scale suggest that 20% of the world's plant species are threatened with extinction (Brummitt et al. 2015). If 20% of the Brazilian flora might be threatened, then 7,200 species might eventually become protected according to regulations in Brazil. To give an idea, this number of species is more than 7 times the number of plant species currently listed as threatened or endangered in the United States (945 species, according to the U.S. Fish and Wildlife Service<sup>2</sup>), and about half of the total number of vascular plants in the United States and Canada combined (15,447 species, Ulloa Ulloa et al. 2017).

The number of threatened plant species in Brazil is thus potentially very large, which poses an equally large challenge to the management and conservation of all threatened species. The amount of restrictions to the use of natural resources that may be potentially required to protect all threatened species could be prohibitive when taking into account the needs and desires for social and economic development, aside from the challenge of enforcing such restrictions.

Other tropical countries with high species richness may face similar situations as the one described for Brazil. These countries are often at the middle-income level, and still face big challenges in areas such as overcoming poverty, and improving public safety, education and health. The challenges to promoting development in such parts of the world and avoiding species extinctions are by no means easy.

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<sup>2</sup> <https://ecos.fws.gov/ecp0/reports/box-score-report>

In the midst of this big challenge, the understanding of the ongoing process of plant species extinction in tropical species-rich regions is still substantially incomplete. This dissertation aims to improve the understanding of extinction in such regions by focusing on the Atlantic Forest of Brazil.

## Chapter 1

### Predicting extinction risk of Brazilian Atlantic Forest angiosperms<sup>3</sup>

#### Summary

Understanding how plant life history affects species vulnerability to anthropogenic disturbances and environmental change is a major ecological challenge. We examined how vegetation type, growth form, and geographic range size relate to extinction risk throughout the Brazilian Atlantic Forest domain. We used a database containing species-level information of 6,929 angiosperms within 112 families and a molecular-based working phylogeny. We used decision trees, standard regression, and phylogenetic regression to explore the relationships between species attributes and extinction risk. We found a significant phylogenetic signal in extinction risk. Habitat, growth form, and geographic range size were related to species extinction risk, but the effect of growth form was not evident after phylogeny was controlled for. Species restricted to either rocky outcrops or scrub vegetation on sandy coastal plains exhibited the highest extinction risk among habitats, a finding that supports the hypothesis that species adapted to resource-limited environments are more vulnerable to extinction. Among growth forms, epiphytes were associated with the highest extinction risk in non-phylogenetic regression models, followed by trees, whereas shrubs and climbers were associated with

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<sup>3</sup> This research was previously published in the journal *Conservation Biology* (Leão et al. 2014) in collaboration with Carlos R. Fonseca, Carlos A. Peres, and Marcelo Tabarelli. Reproduced with permission from Wiley and Sons.

lower extinction risk. However, the higher extinction risk of epiphytes was not significant after correcting for phylogenetic relatedness. Our findings provide new indicators of extinction risk and insights into the mechanisms governing plant vulnerability to extinction in a highly diverse flora where human disturbances are both frequent and widespread.

## **Introduction**

Terrestrial ecosystems worldwide are experiencing high species extinction rates caused by the growing extent and intensity of anthropogenic activities (Pereira et al. 2010). Habitat conversion and overexploitation are the leading drivers of species extinctions in tropical forests (Brook et al. 2008). Although human disturbances often indistinctly push species toward population decline, vulnerability to extinction often associates with species attributes and evolutionary history (McKinney 1997). While some species are undergoing rapid decline, others are expanding their populations and distribution (McKinney & Lockwood 1999). A key question arising from these opposite species responses is how life history of different species can predict their vulnerability to current disturbances and environmental change (Brook et al. 2008; Henle et al. 2004).

Geographic range size is the most evident predictor of global-scale species extinction risk. The smaller the species range size, the higher the probability that disturbances and environmental changes will affect the entire species range (Gaston & Blackburn 2000). Extent of occurrence and area of occupancy are among the most useful and widely adopted measures of geographic range size and the most common criteria

used by the International Union for Conservation of Nature (IUCN) to assign threat status (Gaston & Fuller 2009). Understanding differences in extinction risk among species therefore critically depends on a robust measure of geographic range size, particularly the extent of occurrence and area of occupancy.

Although several studies have identified some species attributes as strong predictors of extinction risk, most of them have focused on animals (Henle et al. 2004), and little is known about how plant attributes are associated with extinction risk (Stork et al. 2009). For example, large vertebrates are widely considered to be most vulnerable in faunal assemblages because they tend to have low population densities and large spatial requirements, exhibit low fecundity, and be more prone to overexploitation, characteristics that predispose them to high extinction risk (Stork et al. 2009; Turner 1996). Although finding consistent relationships between plant attributes and extinction risk has been difficult (Murray et al. 2002), evidence from both plant and animal studies suggests that attributes related to population size and rates of growth and mortality should be correlated with species vulnerabilities (Henle et al. 2004; Pimm 1991). For tropical forest trees, which comprise the best-known group of tropical plants, shade tolerance, per capita mortality rate, population growth rate, and dispersal capacity are consistently among the most important determinants of population persistence in disturbed environments (Henle et al. 2004). In general, species characterized by small population sizes, high demographic fluctuations, low competitive ability, low dispersal ability, and specialization to restricted habitats are expected to be more vulnerable to extinction in fragmented and disturbed habitats (Henle et al. 2004).

Differences in habitat type and growth form can be associated with differences in relative growth rate (Galmes et al. 2005; Grime & Hunt 1975), another key predictor of extinction risk. Habitats associated with elevated environmental stress, such as excessive droughts or nutrient scarcity, tend to host species with inherently limited growth rates imposed by evolutionary adaptations to stress tolerance (Arendt 1997; Fonseca et al. 2000; Grime 1977). Thus, growth forms adapted to stressful microhabitats, such as some epiphytes and herbs restricted to rocky outcrops, exhibit inherently low growth rates (Benzing 1990; Grime & Hunt 1975). For instance, growth rates of some epiphytes can be lower than those of forest trees that are renowned for their slow growth (Laube & Zotz 2003). Because slow-growing stress-tolerant plants often recover slowly from disturbance events (Grime 1977), slow growth rates are expected to render species more vulnerable to extinction in frequently disturbed habitats (Pimm 1991).

The Atlantic Forest of Brazil is one of the world's biodiversity hotspots. In this area many global extinctions are imminent (Mittermeier et al. 2004). Within the boundaries of the Brazilian Atlantic Forest, there are at least five major vegetation types (Fig. 1), including several forest and non-forest natural habitats that cover a wide range of elevation, precipitation, and temperature gradients and soil types (IBGE 2008; see Methods for details). The Atlantic Forest formerly occupied ~1,500,000 km<sup>2</sup>, 12% of which remains as secondary and old-growth forest distributed across more than 245,000 forest fragments. These forest remnants are typically small (80% are <50 ha), are influenced by edge effects, and consist of secondary forests at intermediate stages of regeneration (Ribeiro et al. 2009). However, the Atlantic Forest still hosts over 15,000

plant species, 45% of which are endemic (Stehmann et al. 2009) and 10% of which are threatened with extinction (Fundação Biodiversitas 2005), although the Brazilian government officially recognizes fewer threatened species.

We examined how habitat type and growth form relate to expert-defined species extinction risk throughout the Brazilian Atlantic Forest domain. We also investigated the additional relevance of these attributes in explaining extinction risk after controlling for geographic range size and explicitly considering the phylogenetic non-independence among species. Finally, we sought to provide evidence to support an appropriate use of life-history attributes as indicators of species extinction risk and evidence-based insights into the mechanisms behind plant vulnerability to extinction.

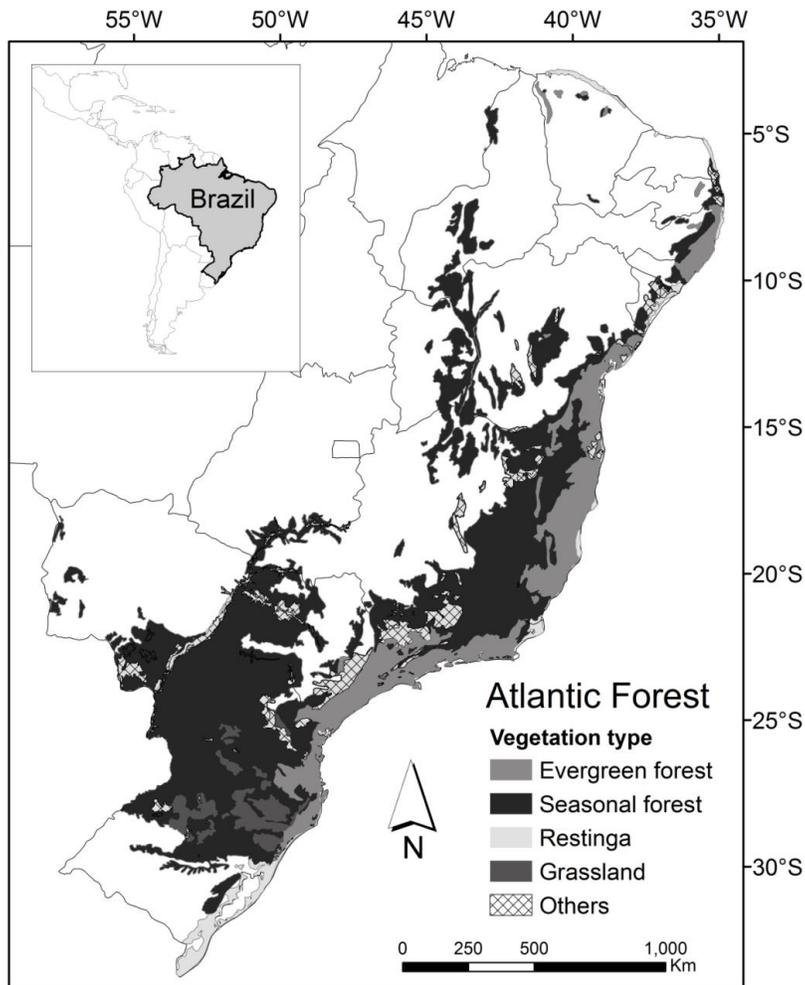


Figure 1. Phytogeographic boundaries and main vegetation types of the Brazilian Atlantic Forest domain (IBGE 2008).

## Methods

### *Database and extinction risk*

The database we used included 6,929 species within 112 angiosperm families of the Brazilian Atlantic Forest flora. This represents roughly 50% of the total number of species and more than 50% of the families of native angiosperms known to the Brazilian

Atlantic Forest domain (Stehmann et al. 2009). We classified extinction risk following the Brazilian Checklist of Threatened and Endangered Flora, which was reviewed by 180 expert botanists and published by Fundação Biodiversitas (2005). We determined that the number of consulted specialists per family was significantly related to the number of threatened species within each family, even after controlling for family size as a covariate ( $t = 2.38$ ,  $df = 193$ ,  $p = 0.02$ ). Therefore, we excluded from the database 92 families because either their level of extinction risk failed to be evaluated by any specialist or the number of consulted specialists was significantly different from the overall mean (chi-square,  $p < 0.10$ ).

We treated the threat status as a continuous response: 0, non-threatened species; 1, vulnerable; 2, endangered; 3, critically endangered; 4, extinct in the wild or globally extinct. Species classified as data deficient in the risk assessment were not included. We estimated the species extent of occurrence and area of occupancy to examine possible effects of geographic range size on the relationships between plant attributes and conservation status. To calculate species-specific extent of occurrences and area of occupancy, we used herbarium data collected from over 60 herbaria through the SpeciesLink network (Supporting Information), which contains 260,690 occurrences of 6,270 species that have been geo-referenced at the municipal county scale across all 26 Brazilian states ( $\sim 8.5$  million  $\text{km}^2$ ). The extent of occurrence for each species was calculated according to the minimum convex polygon (or convex hull) method. Area of occupancy was calculated according to a sliding scale grid cell width with the CAT (Conservation Assessment Tools) extension within ArcView 3.1 (Moat 2007).

### *Species attributes*

We placed each species into categories of growth form, habitat specificity, and level of geographic endemism (Table 1). We distinguished five growth form categories: climber (including scandents), epiphyte, herb, shrub, and tree. Aquatic and parasitic growth forms were excluded from the analyses because of large errors in effect estimates due to small numbers of species in these categories. Growth form is one of the most easily distinguishable plant traits and is related to several functional responses in plants (Diaz & Cabido 1997). We distinguished six categories of vegetation type according to Stehmann et al. (2009): ombrophilous (evergreen) forest, semideciduous (seasonally dry) forest, rocky outcrop, restinga (i.e. scrub vegetation on sandy coastal plains), grassland, and habitat generalist (i.e. species occurring in more than one vegetation type). This classification covers all major plant habitat types across the Brazilian Atlantic Forest (Veloso et al. 1991), and each vegetation type is associated with a distinct set of environmental conditions (Arendt 1997; Grime 1977). The main aggregate sources of information were the Atlantic Forest Vascular Plant Endemism Project (<http://sagui.icb.ufmg.br/bot/mataatlantica/>), SpeciesLink (<http://www.splink.org.br/>), the World Checklist of Selected Plant Families (<http://apps.kew.org/wcsp/home.do>), the Brazilian List of Rare Plants (Giulietti et al. 2009), and the List of the Brazilian Flora (Forzza et al. 2012).

Table 1. Breakdown of angiosperm species into categories of plant traits, extinction risk, and extent of occurrence.

Plant traits	IUCN Red List Category		Extent of occurrence	
	threatened (%)	not threatened (%)	rare <sup>a</sup>	not rare
<i>Growth form</i>				
Climber	46 (4.3)	1026 (95.7)	234 (24.6)	716 (75.4)
Epiphyte	85 (15.3)	471 (84.7)	301 (58.7)	212 (41.3)
Herb	144 (6.3)	2126 (93.7)	730 (38.8)	1153 (61.2)
Shrub	66 (4.9)	1288 (95.1)	396 (33.3)	792 (66.7)
Tree	97 (6)	1520 (94)	354 (23.5)	1150 (76.5)
Aquatic	1 (1.9)	53 (98.1)	6 (12.2)	43 (87.8)
Parasite	0 (0)	103 (100)	30 (34.9)	56 (65.1)
<i>Vegetation type</i>				
Rocky outcrops	43 (19.1)	182 (80.9)	125 (69.4)	55 (30.6)
Grasslands	46 (5.1)	862 (94.9)	291 (40.6)	426 (59.4)
Semideciduous forests	30 (6.2)	456 (93.8)	121 (29.1)	295 (70.9)
Ombrophilous forests	191 (7.1)	2517 (92.9)	1040 (45.3)	1256 (54.7)
Coastal restingas	33 (12.9)	222 (87.1)	73 (32.4)	152 (67.6)
Habitat generalist	101 (4)	2424 (96)	451 (18.9)	1940 (81.1)
<i>Endemism</i>				
Endemic <sup>b</sup>	383 (10.7)	3211 (89.3)	1556 (51.3)	1475 (48.7)
Non-endemic	61 (1.7)	3509 (98.3)	550 (17)	2689 (83)
<b>Total</b>	<b>444 (6.2)</b>	<b>6720 (93.8)</b>	<b>2106 (33.6)</b>	<b>4164 (66.4)</b>

<sup>a</sup>Species with extent of occurrence smaller than 20,000 km<sup>2</sup> were defined as rare, according to the criteria for species categorization adopted by the ICUN. <sup>b</sup>Species were classified as endemic if they were restricted to the Atlantic Forest domain (Stehmann et al. 2009).

### *Phylogenetic tree*

We constructed a dated phylogenetic tree with all species, whereby the branch length was equivalent to the estimated age of each lineage according to Wikström et al. (2001). The topology of the tree containing all species was pruned from the megatree R20100701.new (available at <http://svn.phylodiversity.net/tot/megatrees/>) with the phylomatic tool (Webb & Donoghue 2005) as implemented in Phylocom version 4.2 (Webb et al. 2008). Clades with unresolved nodes were treated as polytomies, which reduced the power of the phylogenetic statistics tests and possibly overestimated phylogenetic conservatism (Davies et al. 2011a). The species and family trees (available in Supporting Information and Fig. 2) showing the phylogenetic distribution of plant attributes and extinction risk were constructed with iTOL (Letunic & Bork 2007).

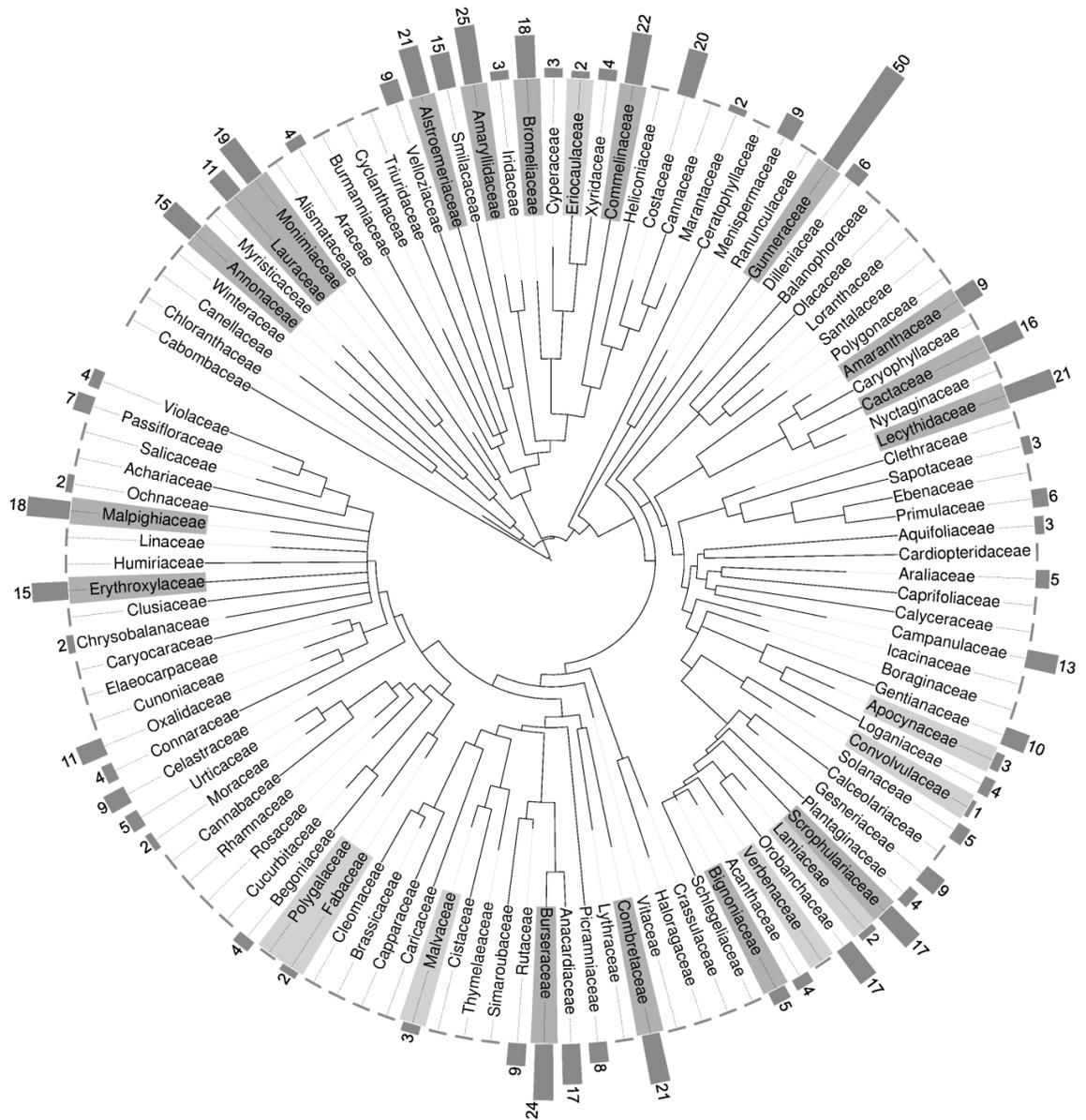


Figure 2. Phylogeny and family level extinction risk of 112 plant families from the Brazilian Atlantic Forest (N = 6,929 study species). Family level extinction risk is represented by percentages of threatened species. Shaded families showed significantly higher (dark grey) and significantly lower (light grey) percentages of threatened species compared to the overall mean.

### *Data analyses*

We measured the strength of the phylogenetic signal in extinction risk, area of occupancy, and extent of occurrence according to the Pagel's  $\lambda$  method and tested for significance with the *phylosig* function in *phytools* package (Pagel 1999; Revell 2012). This method estimates the phylogenetic signal and the likelihood value for each trait in both the original tree and the transformed tree with no phylogenetic signal (i.e.  $\lambda = 0$ ). The likelihood ratio test was then used to compare these trees and test the null hypothesis that there is no phylogenetic signal.

We first explored the relationships between plant attributes and extinction risk with decision-tree analysis, as recommended by Sullivan et al. (2006). We used the QUEST method implemented in SPSS AnswerTree 3.0. The cross-validation procedure was applied 10 times, and the cost of misclassification in decision trees was the same for all trait groups. Further discussions on the use of decision trees to predict extinction risk from species traits can be found in Bielby et al. (2009). We also performed standard and phylogenetic regressions to test the relationship between traits and risk because both of these approaches can be usefully interpreted (Westoby et al. 1995). The use of phylogenetic regression allowed us to test how the independent evolution of certain life history and ecological traits affects present-day variation among species in levels of extinction risk. Phylogenetic regressions were performed using the *compar.gee* function available in the package *ape* version 3.0-8 for R (Paradis et al. 2011). This function uses the generalized estimating equation to apply a phylogenetic correction according to a variance-covariance matrix, which specifies the non-independence among pairs of

species based on their phylogenetic distance (Paradis & Claude 2002). The variance-covariance matrix was constructed using the *corPagel* function, and the lambda value was set equal to the phylogenetic signal in extinction risk ( $\lambda = 0.14$ ; see Freckleton et al. 2002).

## **Results**

### *Phylogenetic signal of extinction risk*

Of 6,929 species of Atlantic Forest plants in our data set, 6.4% were deemed threatened. The estimated extinction risk was higher among close relatives than expected by chance, as evidenced by the phylogenetic signal test ( $\lambda = 0.14$ ,  $p < 0.001$ , see phylogenetic tree in Supporting Information). Significant phylogenetic signal was also detected in the extent of occurrence ( $\lambda = 0.54$ ,  $p < 0.001$ ) and area of occupancy ( $\lambda = 0.47$ ,  $p < 0.001$ ), meaning that closely related species tended to share similar range sizes. The family phylogenetic tree illustrates how extinction risk was skewed toward some lineages (Fig. 2). From all 112 plant families examined, 17 were associated with a higher species extinction risk than the overall mean (Pearson's chi-square tests,  $p < 0.05$ ), while eight families were associated with a significantly lower extinction risk. For example, Bromeliaceae, Cactaceae, Malpighiaceae, Amaryllidaceae, Annonaceae, and Lauraceae had more extinction-prone species than other clades selected by chance. In contrast, Fabaceae, Lamiaceae, Malvaceae, and Verbenaceae had fewer high-risk species than other clades.

### Decision tree analysis

The decision tree analysis indicated that area of occupancy was the most powerful overall predictor of extinction risk, although a significant portion of the variation in extinction risk was additionally explained by other plant attributes. Vegetation type and growth form improved the predictive power of models and explained extinction risk under different classes of area of occupancy (Fig. 3). Species occurring in rocky outcrops were always more extinction prone than those in other vegetation types. Epiphytes also had higher extinction risk than other growth forms. Differences among other vegetation types and extent of occurrence also explained some variation of extinction risk among species.

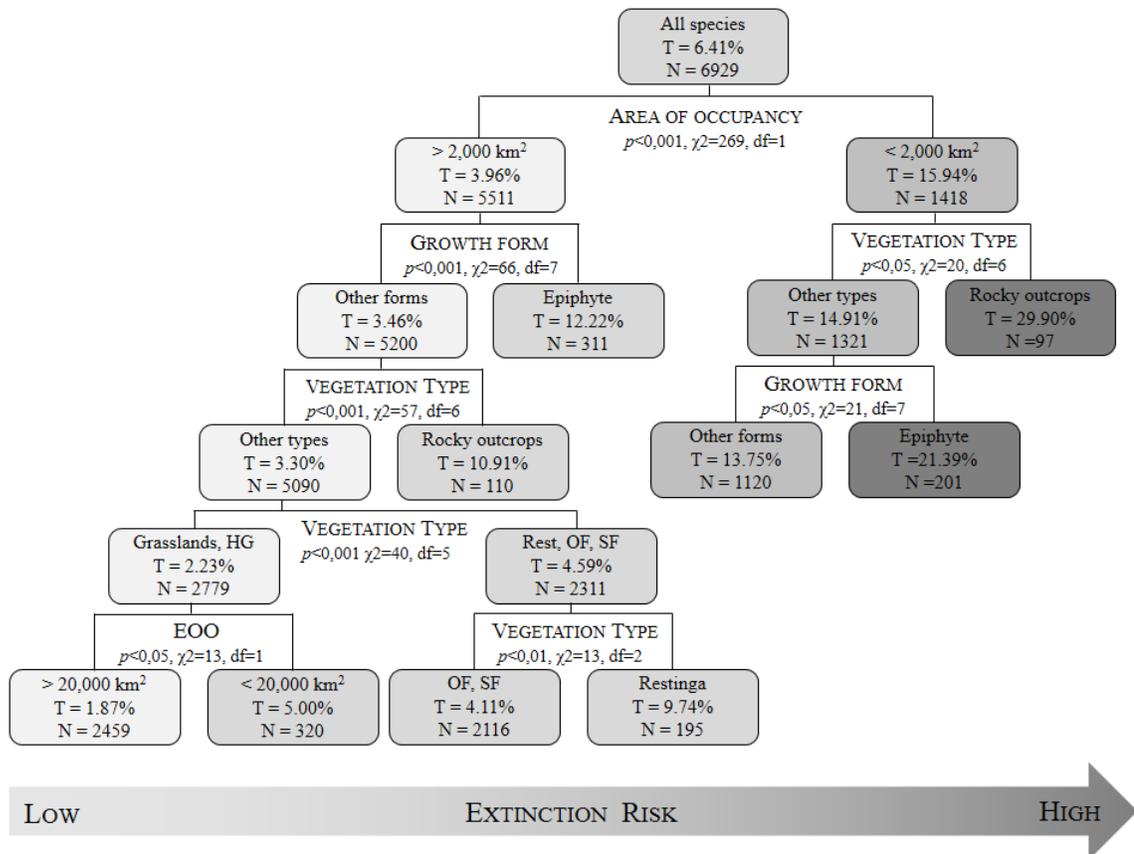


Figure 3. Hierarchical tree resulting from a decision-tree analysis. The tree shows how extent of occurrence and life history enhance partitioning of the species pools into groups with different levels of extinction risk. The tree clearly shows how life history can improve the prediction of extinction risk over and above the area of occupancy and extent of occurrence (EOO). Each tree node contains the predictor variable category, percentage of threatened species (T), and total number of species (N). Abbreviations: Rest, coastal resting; OF, ombrophilous (evergreen) forest; SF, semideciduous forest; HG, habitat generalist.

Overall, 16% of the epiphytes, and 20% and 13% of the species restricted to rocky outcrops and coastal restingas, respectively, were threatened with extinction. These fractions were two to three fold higher than the overall average for all threatened species. Some species groups were under relatively little threat, including climbers (4%) and habitat generalists (4%). This pattern of risk can be partially explained by the geographic distributions of these plant groups because 56% of the rocky outcrop endemics, 44% of all epiphytes, and 24% of the coastal restinga endemics were restricted to an area of occupancy smaller than the critical IUCN value (<2,000 km<sup>2</sup>). Conversely, habitat-generalists and trees were associated with relatively few narrowly distributed species (12% and 17%, respectively).

#### *Standard regression models*

As expected, extent of occurrence and area of occupancy were important predictors of extinction risk (Table 2). Habitat type and growth form were also related to extinction risk in simple uncontrolled models, where plants restricted to either rocky outcrops or

restingas and epiphytes were associated with significantly higher extinction risk than other plants.

According to the non-phylogenetic multiple regression model that included the four predictors, area of occupancy remained an important predictor of risk, while extent of occurrence explained no additional variation in extinction risk. Vegetation type and growth form also significantly explained extinction risk even after controlling for both estimates of geographic range size. In particular, species restricted to rocky outcrops and coastal restingas were still associated with the highest extinction risk, whereas other habitat categories showed no differences among each other. Moreover, in the non-phylogenetic full model, epiphytes were still the single most extinction-prone growth form. Conversely, climbers and shrubs showed significantly lower extinction risk than both trees and epiphytes. Specifically, vegetation type and growth form accounted for 22% of the total variation explained by the full model after the effects of area of occupancy and extent of occurrence had been removed. When area of occupancy and extent of occurrence were removed from the full model, most predictors became more positively related to extinction risk, which clearly showed that part of the variation explained by plant attributes in uncontrolled models reflected differences in range size.

Table 2. Summary of standard and phylogenetic regression models predicting the threat status of plant species in the Brazilian Atlantic Forest.

Model	Standard regression						Phylogenetic regression					
	SLR models		Full model		No-GRS model		SLR models		Full model		No-GRS <sup>a</sup> model	
Predictor	B	SE	B	SE	B	SE	B	SE	B	SE	B	SE
Extent of occurrence <sup>b</sup>	-0.013***	0.001	-0.001	0.002	-	-	-0.011***	0.001	-0.001	0.002	-	-
Area of occupancy <sup>b</sup>	-0.016***	0.001	-0.015***	0.002	-	-	-0.014***	0.001	-0.013***	0.002	-	-
Vegetation type												
Coastal restingas <sup>c</sup>	0.168***	0.030	0.124***	0.030	0.178***	0.030	0.168***	0.029	0.118***	0.029	0.157***	0.030
Grasslands	0.021	0.018	-0.023	0.020	0.019	0.018	0.061*	0.021	0.014	0.022	0.062	0.023
Habitat generalist <sup>d</sup>	-	-	-	-	-	-	-	-	-	-	-	-
Ombrophilous forests	0.053***	0.013	-0.019	0.013	0.050***	0.013	0.044**	0.013	-0.021	0.013	0.041*	0.013
Rocky outcrops	0.342***	0.032	0.212***	0.035	0.312***	0.033	0.254***	0.033	0.165***	0.036	0.258***	0.036
Semideciduous forests	0.064*	0.023	0.039	0.023	0.070**	0.023	0.071*	0.022	0.044	0.023	0.078**	0.023
Growth form												
Climber	-0.035	0.018	-0.051*	0.018	-0.035	0.018	-0.033	0.024	-0.051	0.024	-0.047	0.024
Epiphyte	0.200***	0.023	0.083**	0.023	0.189***	0.023	0.008	0.034	-0.079	0.035	-0.072	0.036
Herb	0.028	0.015	-0.018	0.016	0.013	0.016	-0.011	0.022	-0.039	0.023	-0.030	0.023
Shrub	-0.009	0.017	-0.050*	0.017	-0.016	0.017	0.013	0.020	-0.033	0.020	-0.017	0.020
Tree <sup>d</sup>	-	-	-	-	-	-	-	-	-	-	-	-
Intercept	-	-	0.335***	0.021	0.055***	0.013	-	-	0.355	0.054	0.101	0.053
Observations <sup>e</sup>	-	-	5943		6742		-		5943		5943	
R <sup>2</sup>	-	-	0.079		0.035		-		-		-	

Note: Only species with complete attribute data were considered in each model. The table includes simple linear regressions (SLR models), multiple regressions including all variables (full models) and multiple regressions including only vegetation type and growth form, which did not include geographic range size (no-GRS models). Significance: \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$  (p values adjusted for multiple comparisons with Benjamini-Hochberg method). <sup>a</sup>GRS is the acronym of Geographic Range Size. <sup>b</sup> $\log_2$  extent of occurrence,  $\log_2$  area of occupancy. <sup>c</sup>Restingas' refers to the scrub vegetation on sandy coastal plains. <sup>d</sup>Reference category. <sup>e</sup>Missing cases omitted.

### *Phylogenetic regression models*

Phylogenetic regression analyses reinforced the results that geographic range size and vegetation type were important predictors of extinction risk. Similarly to the non-phylogenetic full model, area of occupancy was negatively related to extinction risk, while extent of occurrence was not significant. Furthermore, species from coastal *restingas* and rocky outcrops still remained highly threatened after taking into account the phylogenetic non-independence of the species. In contrast, the phylogenetic regression analyses produced very different results for growth form. In fact, none of the phylogenetic models detected differences in extinction risk among growth forms. In particular, the higher extinction risk of epiphytes detected in non-phylogenetic models was not significant when the non-independence of the species was taken into account. Again, by removing extent of occurrence and area of occupancy from the full model, it was possible to confirm that part of the predictive power attributed to plant traits was due to their correlation with geographic range size.

### **Discussion**

Vegetation type and growth form were related to extinction risk in angiosperms across the Brazilian Atlantic Forest, even after controlling for variation in geographic range size; thus, these attributes could be used as indicators of extinction risk. For a given range size, plants endemic to either rocky outcrops or *restingas* were more likely to be at risk of extinction than plants in any other vegetation type. Likewise, epiphytes comprised the most extinction-prone growth form. However, threat status had a significant phylogenetic signal, indicating that some families and lineages concentrated a disproportionately high

fraction of the threatened species. Taking into account this phylogenetic structure did not affect the relationship between habitat type and risk of extinction; rather, it rendered differences among growth forms non-significant. This stresses the consistency of rocky outcrops and *restingas* as areas associated with high vulnerability to extinction but indicates that the observed trend for higher extinction risks in epiphytes might not be causal.

#### *Habitat specificity and extinction risk*

Species extinction proneness varied substantially across vegetation types, even when area of occupancy and extent of occurrence were held constant and the phylogenetic structure of all species was considered. Specifically, species restricted to rocky outcrops were most threatened, which is only partially explained by the higher proportion of range-restricted species in this habitat type. This suggests that intrinsic properties of rocky outcrops may be important to understand the mechanisms underlying plant vulnerability to extinction. Rocky outcrops are montane islands facing extremely xeric conditions within a surrounding matrix of humid vegetation and safeguard some of the highest levels of plant endemism anywhere in the tropics (Burke 2003). High levels of beta diversity and endemism in rocky outcrops, along with an increasing frequency of disturbances such as fire, grazing, biological invasions, mining, and overexploitation of plants for trade, are the main determinants of high extinction risk in this habitat type (Jacobi et al. 2007; Meirelles et al. 1999). Like other montane vegetation types, rocky outcrops may also be more vulnerable to species loss due to climate change compared with low-elevation areas (Thuiller et al. 2005b).

In coastal *restinga* plant communities, rarity was relatively unimportant in explaining extinction risk compared with other vegetation types because the risk associated with plants endemic to *restinga* was still significant after area of occupancy and extent of occurrence were controlled for. Land use change is one of the main drivers of extinction risk across *restinga* plant communities because *restinga* is the most densely settled vegetation type and is likely experiencing the highest level of anthropogenic pressure in eastern Brazil (Rocha et al. 2007). The risk associated with species endemic to coastal *restingas* was also largely independent of phylogeny, emphasizing the role of habitat characteristics in explaining extinction risk. In contrast, extinction risk associated with species endemic to seasonally dry or evergreen forests were closely related to geographic range size, emphasizing the importance of range size as a predictor of vulnerability to extinction in these two forest types.

Species extinction risk varies greatly across habitat types worldwide, particularly due to differences in habitat size and rates of habitat loss (Duncan & Young 2000; Sodhi et al. 2008). Although habitat loss is a key determinant of extinction, observed differences in extinction risk can be partially explained by habitat-specific environmental conditions. Habitats exposed to marked environmental stress — such as severe droughts in rocky outcrops (Porembski & Barthlott 2000), *restingas* (Zamith & Scarano 2006) and forest canopy microhabitats associated with epiphytes (Benzing 1990; Zotz & Ziegler 1997) — tend to be primarily occupied by slow-growing species (Arendt 1997; Grime & Hunt 1975), which likely exhibit low rates of population recovery following pulses of disturbance. Because repeated disturbance events are often relentless in areas facing high

anthropogenic pressure, such as the Brazilian Atlantic Forest, more species will likely be extirpated in less resilient communities (Pimm 1991).

*Growth form and extinction risk*

Extinction risk varied among growth forms only when phylogenetic relationships were unaccounted for. We believe, however, that the results from both non-phylogenetic and phylogenetic models are useful if properly interpreted. For conservation purposes, in particular, non-phylogenetic models can be used to produce surrogates of extinction risk. For example, the non-phylogenetic regression models indicated that, in general, epiphytes are likely at higher risk of extinction than other growth forms even after controlling for geographic range size. This corroborates results of previous studies in Southeast Asia that show epiphytes concentrate most extinction-prone species (Sodhi et al. 2008; Turner et al. 1994).

From an evolutionary perspective, however, our phylogenetic models showed there was no evidence of functional relationships between growth forms and extinction risk. The apparently high extinction risk of epiphytes was due to the fact that a few speciose phylogenetic lineages of epiphytes concentrated more high-risk species. Our findings therefore failed to support the notion that epiphytism per se results in higher vulnerability to extinction. For example, among the epiphyte families, Bromeliaceae and Cactaceae concentrated high levels of extinction risk (18% and 16% of all species were threatened, respectively), whereas Gesneriaceae and Araceae were far less extinction prone (9% and 4%, respectively). Moreover, phylogenetically related traits not

considered here may be important in explaining differences in extinction risk among epiphytes. For example, Bromeliaceae and Cactaceae include a large number of species with crassulacean acid metabolism (CAM), whereas this photosynthetic pathway is less prevalent in Araceae and Gesneriaceae species (Zotz & Ziegler 1997). Species with crassulacean acid metabolism typically grow slower than those with other photosynthetic pathways (i.e. C3 and C4; Lüttge 2004), and CAM epiphytes are also expected to have smaller population sizes relative to other epiphytes (Zotz 2004). In addition, we did not consider patterns of speciation that could be related to extinction risk, such as the age and rate of evolution of different phylogenetic lineages (Davies et al. 2011b).

Trees were the second most threatened growth form across the Brazilian Atlantic Forest according to non-phylogenetic models. Although not significant, trees appeared as the most threatened growth form in the full phylogenetic model. This contrasts with findings from elsewhere that herbs other than grasses (Wiegmann & Waller 2006) and shrubs (Duncan & Young 2000; Kolb & Diekmann 2005) are often more extinction prone. Key mechanisms driving trees toward extinction are forest loss and fragmentation, decline of pollinators and seed dispersers, and timber extraction (Tabarelli et al. 2004).

The amount of variation explained by our models was limited, but this could be improved by incorporating other life history traits such as dispersal ability (Duncan & Young 2000) and dependence on specific modes of animal seed dispersal and pollination vectors (Bond 1994; Sodhi et al. 2008). However, we expect that a large amount of variation in extinction risk cannot be explained by any combination of biological traits because of the complex and idiosyncratic nature of human-imposed threats and

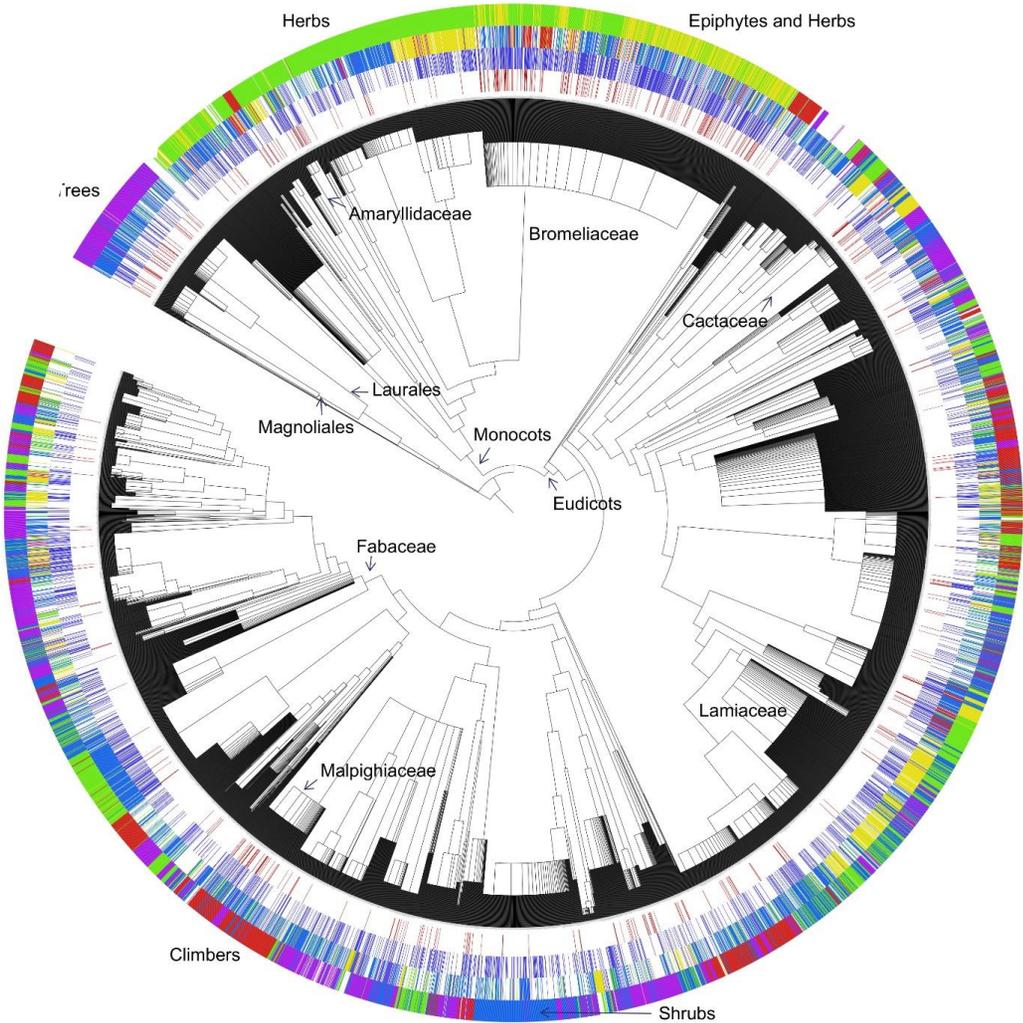
uncertainties associated with estimates of species extinction risk. Despite such limitations, we found evidence for a unifying mechanism explaining plant extinction risk across the Atlantic Forest domain. High extinction risk and slow growth life histories appear to be disproportionately concentrated in plants restricted to rocky outcrops and *restingas* and in the most drought-adapted epiphyte lineages (e.g. Bromeliaceae and Cactaceae). In ecosystems where disturbances are both frequent and diffuse, such as the Atlantic Forest, low-resilience species associated with low rates of net population recovery are likely to be most vulnerable to extinction. An increasingly severe regime of human-induced disturbances and community hyper-dynamism across the Atlantic Forest may therefore disproportionately aggravate threats to species expressing an intrinsically low capacity for population recovery. We hope our findings can aid future attempts to identify extinction-prone species in highly diverse tropical floras, thereby refining regional-scale conservation planning across one of the world's most important biodiversity hotspots.

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**Supplementary Material**



- Color strip 1(internal) - Risk-list
  - Red: Threatened
- Color strip 2 - Extent of Occurrence
  - Blue: Small range size (<20.000 km<sup>2</sup>)
- Color strip 3 - Habitat
  - Red: Rocky outcrop
  - Yellow: Grassland
  - Green: Seasonal forest
  - Blue: Ombrophilous forest
  - Purple: Restinga
  - White: Habitat generalist
- Color strip 4 (external) - Growth Form
  - Red: Climber
  - Yellow: Epiphyte
  - Green: Herb
  - Blue: Shrub
  - Purple: Tree
  - White: Unknown

Figure S1. Phylogenetic tree containing all species and plant attributes. A vectorized version (pdf) allowing to zooming in and seeing details is available at

<https://doi.org/10.1111/cobi.12286>

## Chapter 2

# Evolutionary and ecological patterns in the geographic range size of Atlantic Forest plants<sup>4</sup>

### Summary

Species' geographic range size is arguably the single most important predictor of vulnerability to extinction and a key metric in ecology. Despite this, patterns of specific variation in range size and their underlying reasons are still poorly understood. For example, emerging hypotheses on how evolutionary history affects range size were scarcely tested, and the relationships found between range size and plant life forms are inconsistent. We focused in the Atlantic Forest angiosperm flora, which has the highest (and best-known) plant diversity in Brazil and a high risk of species extinction. We investigated whether and how the genus species richness, net diversification rate and age of the most recent common ancestor, and species' life forms and habitats are associated with geographic range size. We estimated the species' area of occupancy (and extent of occurrence) of 13,785 plant species native to the Atlantic Forest based on over 500,000 unique occurrences. We used ordinary and weighted least squares regression, and phylogenetic generalized least squares to analyze how the predictors affect the geographic range size. The set of predictors was able to explain up to a quarter of the variation in

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<sup>4</sup> This research was conducted in collaboration with Peter B. Reich.

median species' area of occupancy and up to 40% of the variation in the proportion of species with vulnerably small area of occupancy. The larger the genus and net diversification rate, the smaller the average species range size. Genus age had a very weak positive association with range size. Herbs had area of occupancy 60% smaller than trees. Epiphytic and rupicolous habitats had clearly the smallest species' range sizes and the highest proportions of species with vulnerably small ranges. The results suggest that dynamics of diversification considerably affect the species range size. It also clarifies how range size associates with life forms, and suggests that the vegetation type mediates this relationship. Finally, this work reveals poorly known patterns of range size variation and some of the mechanisms driving variation in range size and vulnerability to extinction.

## **Introduction**

The species' geographic range size is a summary of the area over which a species is distributed and is a powerful indicator of the species' vulnerability to extinction (Gaston 2003; Leão et al. 2014). Because of this, it is a key metric in the fields of ecology and conservation biology. The distribution of geographic range sizes varies many orders of magnitude across regions of the world, taxonomic groups and life forms (Brown et al. 1996; Gaston 2003). Although there is consistent evidence supporting some patterns of range size variation among groups of animals (e.g. body size patterns), the patterns of range size variation among plants is much less known and consistent (Murray et al. 2002), especially among tropical plants. Perhaps the major known pattern in plant range size is associated with the available area of habitat; the larger the area of habitat the larger the range size (Gallagher 2016; Morueta-Holme et al. 2013). Other emerging, but poorly

tested, patterns of range size are associated with characteristics of the species, in particular their evolutionary history and life forms.

The evolutionary history of plant lineages seems to explain a considerable amount of variation in species' geographic range size (Lozano & Schwartz 2005; Paul et al. 2009; Schwartz & Simberloff 2001) and extinction risk (Davies et al. 2011b). Plant taxa with larger number of species have higher proportion of rare species, which suggests that rates of net diversification and/or patterns of taxonomic delimitation affect species' range sizes (Lozano & Schwartz 2005; Schwartz & Simberloff 2001). Old species tend to occupy a larger proportion of their extent of occurrence than young species among neotropic *Psychotria* (~20% of the variance explained, Paul et al. 2009). Young and fast-evolving plant lineages have higher extinction risk in the Cape region of South Africa, probably due to a naturally small species' geographic range size (Davies et al. 2011b). These findings support the existence of a biologically relevant effect of the evolutionary history on current plant species' geographic range sizes.

Patterns of range size associated to plant life forms and ecological attributes are elusive. The ways life forms relate to range size varies across continents and vegetation types, with unclear reasons for observed differences (Murray et al. 2002). For example, life forms associated with the largest range size may be trees (such as in Great Britain, Kelly & Woodward 1996) or herbs (such as in Australia, Gallagher 2016; Oakwood et al. 1993). Dispersal mode and seed size also show a context-dependent relationship with range size (Murray et al. 2002). These studies, however, come from mostly temperate and other non-tropical regions of the world. In the tropics, studies focusing on species'

extinction risk revealed that epiphytes (Leão et al. 2014; Sodhi et al. 2008; Turner et al. 1994) and plants adapted to rocky outcrops (Leão et al. 2014) are especially rare and vulnerable to extinction. Because available evidence is quite limited, patterns of range size variation associated with life forms and ecological attributes of tropical plant species are still to be characterized.

Geographic range size is probably the single most relevant factor affecting species' extinction risk. A species that occurs in a small area or extent is vulnerable to disappear completely due to habitat loss and environmental change (Gaston 2003; Gaston & Fuller 2009). In fact, critically small range size as defined under the criterion B1 (extent of occurrence) or criterion B2 (area of occupancy) is the main reason to include a species in the IUCN Red List (Brummitt et al. 2015; Gaston & Fuller 2009). It is true that a full account of extinction risk also depends on factors such as population size and trend, and presence of disturbances causing declines in population size or range size (IUCN 2012). However, the relevance of range size to predict extinction risk stands out given that most species, if not all, with declining populations will ultimately show small range size before extinction; and even species with stable populations but small range size are vulnerable to disappear due to significant habitat loss. Thus, understanding the patterns and mechanisms of range size variation is key to understand species' vulnerability to extinction.

With more than 36,000 known plant species, Brazil is the country with the largest plant diversity in the world, and the Atlantic Forest has the largest known plant diversity in Brazil, making it one of the richest known floras in world (Fontoura et al. 2012). The

largely fragmented and disturbed Atlantic Forest (Ribeiro et al. 2009) has more than 15,000 known flowering plant species, which represents more than 30% of Brazil's known flora (Forzza et al. 2010) and 60% of Brazil's known threatened plant species (Martinelli & Moraes 2013). It is also a region home to most of Brazil's population and economic activity (Scarano & Ceotto 2015). The combination of an extraordinarily high plant diversity with high human pressure makes the Atlantic Forest an ecoregion where a considerable number of plant species is likely to go extinct in this century. Beyond its high conservation appeal, the Atlantic Forest currently provides a unique opportunity to investigate the existence of patterns in the range size of tropical plants. It has one of the best collected tropical flora on a large geographical scale, with millions of herbarium records digitally available (Species Link Network, [inct.splink.org.br](http://inct.splink.org.br)), allowing for the estimation of species' range size on an unprecedented scale.

Previous research investigating predictors of extinction risk in the Atlantic Forest found that closely related species tend to have similar geographic range size, although the causal factors remain unclear (Leão et al. 2014). In this study, we build a new dataset including evolutionary attributes, more plant occurrences and species, and an improved phylogeny to investigate evolutionary and ecological patterns in the variation of species' geographic range size. Focusing on the Atlantic Forest's flowering plants, we tested the hypotheses that lineages' species richness (Lozano & Schwartz 2005; Schwartz & Simberloff 2001), and net diversification rate and age (Davies et al. 2011b; Paul et al. 2009) affect the species' geographic range size. Moreover, we investigated how life forms and habitats relate to species' range size, filling a gap in the basic knowledge about

the distribution of plant species in the Atlantic Forest, and complementing previous analysis on how these relate to the extinction risk (Leão et al. 2014).

## **Methods**

### *Species occurrences*

We downloaded 3,785,741 raw occurrences of plants from more than 100 herbaria and digital collections through the Species Link Network ([www.splink.org.br](http://www.splink.org.br), see the list of herbaria in the supplementary material). After applying several data cleaning procedures (e.g. synonyms matching and coordinates checking), filtering only native species occurring in the Atlantic Forest (according to Flora do Brasil, [reflora.jbrj.gov.br](http://reflora.jbrj.gov.br)) and keeping only one species occurrence per administrative unit regardless of the collection date, 501,689 occurrences from 13,785 species remained and were analyzed in this study (i.e. 90% of all native angiosperms recognized for the Atlantic Forest). A single occurrence may encompass multiple herbarium records collected at the same administrative unit on different dates or different locations within the administrative unit. We used the centroid of the most local administrative unit (i.e. district or municipality) as the reference coordinate for each occurrence. The limits of municipalities and districts were obtained from the database of Global Administrative Areas version 2.5 ([www.gadm.org](http://www.gadm.org), accessed July 2015).

### *Cleaning steps*

We conducted several cleaning and standardizing procedures on the occurrence data before using it for analysis. All unusual characters in the species binomials were removed

(e.g. "?", "\_", ".", "#", "\*", etc). All binomials with uncertain classification were removed (i.e. "cf.", "aff.", or at genus level "sp.", "spp."). Only the species level was kept, which means that subspecies and variations were not considered.

Synonyms were checked and accepted names were adopted according to The Plant List ([www.theplantlist.org](http://www.theplantlist.org)), or Flora do Brasil ([reflora.jbrj.gov.br](http://reflora.jbrj.gov.br)) when there was no accepted name at The Plant List database. Algorithms for matching synonyms and adjusting minor spelling errors in the raw binomials were applied during the synonym checking process through the function `TPL()` in the R package "Taxonstand" (Cayuela & Oksanen 2016) and the function `get.taxa()` from the package "flora" (Carvalho 2016). No spelling corrections were allowed on genus name, and only minor corrections were allowed on specific epithet to assure that only correct species would be matched to misspelled binomials. All records that could not be matched with an accepted name at The Plant List or Flora do Brasil were discarded. Discarded names were mainly illegitimate, invalid or rejected names.

Records with no administrative unity, with coordinates that were likely wrong or with no coordinates (e.g., positioned in the ocean, coordinates not matching reported administrative unit, and coordinates equal zero) were removed. We kept only occurrences within South America boundaries.

#### *Estimation of geographic range size*

The species area of occupancy (AOO) was generated applying the "sliding scale" method proposed by Willis et al. (2003). In the sliding scale, the width of the grid cell varies

among species, and it was defined as one tenth of the maximum distance between occurrences. A minimum (5 x 5 km) and maximum (50 x 50 km) cell size was set to avoid undesired distortions, such as the area of occupancy being too small when there are too few occurrences available, or the area being too large when there are few occurrences with very sparse distribution. Species area of occupancies were estimated in R with the support of the packages “raster” (Hijmans 2016), “sp” (Bivand et al. 2013) and “rgdal” (Bivand et al. 2016).

A species area of occupancy smaller than 2,000 km<sup>2</sup> was considered “vulnerably small” in accordance with the criterion B2 of the IUCN Red List (IUCN 2012). Although a full account of the vulnerability to extinction should consider other factors beyond range size, very small range size is a good indicator of vulnerability to extinction (Gaston 2003; Gaston & Fuller 2009).

The extent of occurrence was defined as the area in squared kilometers of the smallest convex hull that enclosed all occurrences of the species, as computed by the quickhull algorithm (Barber et al. 1996) through function *convhulln()* of the package “geometry” (Habel et al. 2015). The extent of occurrence was calculated only for species with three or more occurrences in distinct locations. For a matter of simplicity, we focused the analyses on the area of occupancy, and showed the results associated with extent of occurrence only at the supplementary material.

### *Phylogeny*

We built a dated phylogeny with all Atlantic Forest's species present in the reference mega-phylogeny (Qian & Jin 2015; Zanne et al. 2014). We used the method described in Qian and Jin (2015) under 'Scenario 3', which is a similar approach used by 'PhyloMatic' to add new taxa to the topology and 'BLADJ' to assign branch lengths (Webb et al. 2008). The reference mega-phylogeny includes 14% of the species (1,950 species), 73% of the genera (1,481 genera) and 100% of the families in our list of species. We decided to focus the analyses at the genus level, where there is good compromise between coverage of the Atlantic Forest plants and precision of the phylogenetic information. We pruned the species phylogeny to the genus level (i.e. genus at the tip) and removed all genera not present in the reference mega-phylogeny, resulting in a phylogenetic tree with 1,481 genera placed at the tip (henceforth referred to as 'genus tree', Figure S1). We processed and edited the phylogenetic tree with support of the R packages 'ape' (Paradis et al. 2004) and 'phytools' (Revell 2012). Final figures of circular phylogenetic trees were designed with iTOL (Letunic & Bork 2016).

### *Predictor variables*

We calculated the number of species per genus according to the number of accepted names of native species in the Atlantic Forest as recognized by Flora do Brasil 2020 and after correcting synonyms according to The Plant List. Names were standardized according to The Plant List in order to match names in the reference mega-phylogeny. We calculated genus age as the time distance (in millions of years, My) from the present to the node of the most recent common ancestor that includes all extant species of the

genus. Age estimates are the same as in the mega-phylogeny (Qian & Jin 2015; Zanne et al. 2014). We calculated the net diversification rate through dividing the number of species in the genus by the square root of the genus age. Because genus age varied five orders of magnitude while number of species varied only two, we transformed genus age to the square root so both had similar magnitude of variation and impact on the estimation of net diversification rate.

The species life forms and habitats were classified according to the Flora do Brasil 2020 ([reflora.jbrj.gov.br](http://reflora.jbrj.gov.br)) as accessed through the R package ‘flora’ version 0.2.7 (Carvalho 2016). In the cases where multiple life forms or habitats were associated to a single species, we applied a decision criterion to choose only one per species, according to the following weight order: climber > tree > shrub > herbs. The life form with higher weight was selected. For example, a species classified as tree and shrub at Flora do Brasil 2020, was classified here as tree. Similarly, in the cases where a species was associated with multiple habitats, we chose the habitat with higher weight in the order: aquatic > parasitic > rupicolous > epiphytic > terricolous.

### *Statistical analyses*

We used ordinary least squares and phylogenetic generalized least squares to analyze the effects of the predictors on geographic range size. The former assumes independence of the model residuals, while the latter allows model errors to be correlated and to have unequal variance (Pinheiro & Bates 2000). Specifically, in the phylogenetic generalized least squares, the phylogenetic distances between pairs of species (or genera) were used

to set the covariance among observations (Orme et al. 2013; Revell 2010). The phylogenetic signal ( $\lambda$ ) was estimated simultaneously with regression parameters, and the values in the variance-covariance matrix were adjusted according to the  $\lambda$  transformation (Orme et al. 2013; Revell 2010). We used the ‘ppls’ function in the R package ‘caper’ to perform phylogenetic regressions (Orme et al. 2013). We conducted all analyses in R version 3.3.0 (R Core Team 2016).

Except for the correlation between the number of species and net diversification rate ( $r = .56$ ), there were no significant correlations among predictors. This allowed fitting multiple regression models and estimating regression coefficients without significant collinearity effects and variance inflation (Fox & Weisberg 2011).

We analyzed the response variable using three distinct levels: (1) species area of occupancy, (2) species median area of occupancy per genus, and (3) genus total area of occupancy (i.e. area occupied by all species of the genus). The first level (species as unit) was used when investigating the effects of life form and habitat on individual species area of occupancy. The second level (median per genus as unit) was used when investigating the effects of number of species, net diversification rate, genus age and all predictors combined. We focused the analyses on the second level, given it allowed us to investigate all predictors, in addition to being the best compromise between coverage of the Atlantic Forest plants and precision of the phylogenetic-derived information. We adopted the median area of occupancy as opposed to the mean because of the highly skewed distribution of area of occupancy, making the median a more representative value of the population. Finally, we analyzed the data at the third level (sum of all species in the

genus) to verify how genus attributes affect the area of occupied by the whole genus, providing further information to understand the relationship between attributes and geographic range size.

We did not analyze the effects of age at first level due to the limited number of species with molecular data and lack of important ancestors in the phylogeny, making species age estimates (i.e. divergence time) overestimated and highly uncertain (Hodge & Bellwood 2015). This limitation reduces considerably our ability to test the age-range relationship at species level.

We further analyzed the effects of the same set of predictors on the proportion of species with area of occupancy smaller than the vulnerability threshold (i.e.  $<2,000 \text{ km}^2$ ). This threshold is the same used in the criteria B2 of the IUCN Red List to categorize a species as ‘vulnerable’ to extinction (IUCN 2012). This binary analysis shows more clearly how the predictors affect rarity and provides a more valuable reference to understand the vulnerability to extinction.

We applied transformations that helped spread the data more symmetrically and make it more appropriate to use in the regression modeling. We found the best transformations with the assistance of the ‘symbox’ function in the R package ‘car’ (Fox & Weisberg 2011). We transformed area of occupancy, species richness and net diversification rate to the logarithmic scale (base 2), and genus age to the square root scale.

We applied a systematic approach to fitting appropriate models. We checked for non-constant variance and deviations from normality in the model residuals. Both response and predictor variables were transformed when it helped to achieve linearity and better residual properties. Given that the models predicting the proportion of small-ranged species had variance of the error term correlated with the number of species in the genus, we used weighted least squares regression (weights = square root of the number of species) instead of ordinary least squares in those occasions to improve the efficiency of model estimation (Fox 2016; Fox & Weisberg 2011).

In order to ease the interpretation of the results, we mentioned the acronym of the regression method when presenting summary statistics, as follow: OLS, ordinary least squares; PGLS, phylogenetic generalized least squares; WLS, weighted least squares.

## **Results**

Species' area of occupancy ranged from 25 km<sup>2</sup> to 1,500,000 km<sup>2</sup>, with median of 30,000 km<sup>2</sup> and mean of 78,300 km<sup>2</sup>. This represents a right skewed distribution where most species have small range sizes (Figure 1). To give an idea of the spatial variation in range size, we mapped the mean area of occupancy and the standard deviation on 0.5° x 0.5° grid cells across the Atlantic Forest (Figure 2).

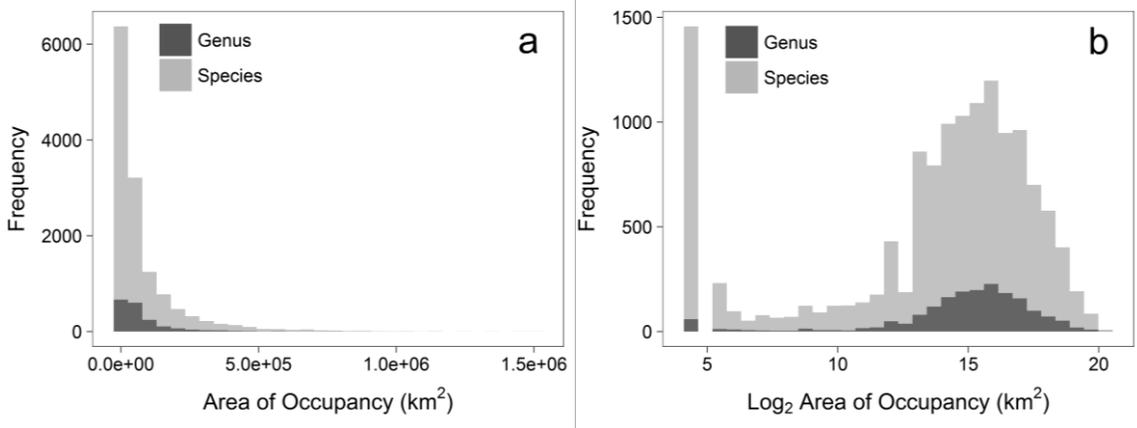


Figure 1. Frequency distribution of the (a) untransformed and (b)  $\log_2$  transformed species area of occupancy and genus median area of occupancy of Atlantic Forest angiosperms.

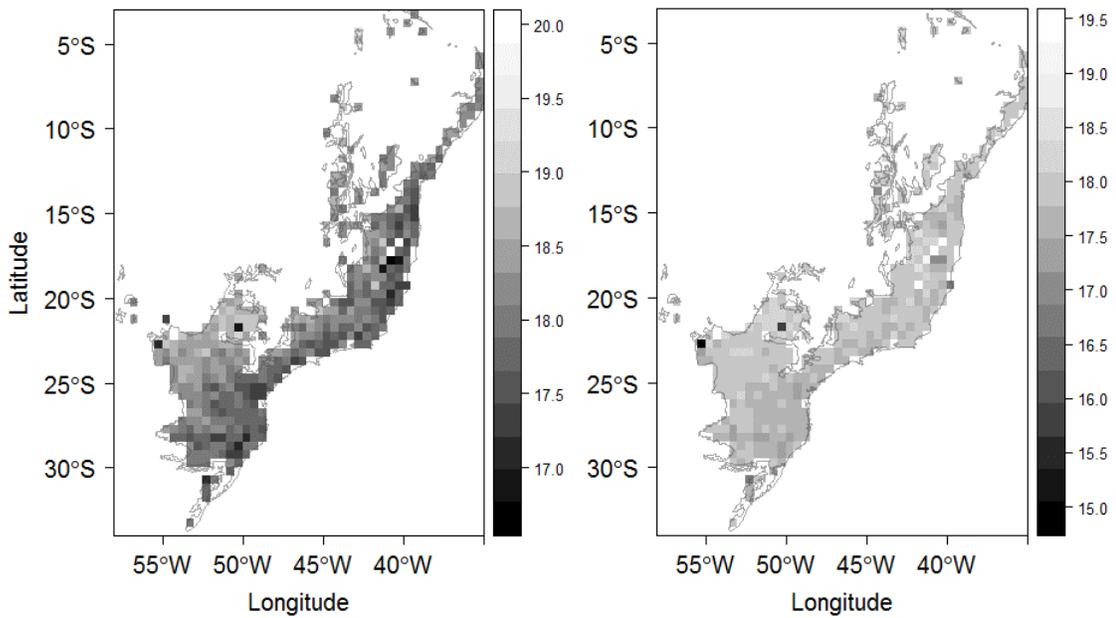


Figure 2. Spatial distribution of  $\log_2$  transformed species area of occupancy (mean, on the left; standard deviation, on the right) across the Atlantic Forest region summarized at 2852  $0.5^\circ \times 0.5^\circ$  grid cells.

*Evolutionary history and median species' area of occupancy at genus level*

The number of species in the genus explained 12% of the variance in median area of occupancy when controlled for phylogenetic relatedness (Table 1). The larger the number of species, the smaller the average species' area of occupancy. A two-fold increase in the number of species was associated with 25% reduction in median area of occupancy (Figure 3a).

Net diversification rate in the genus explained around 11% of the variation in median area of occupancy when controlled for phylogenetic relatedness (Table 1). The higher the diversification rate, the smaller the average species' area of occupancy. A two-fold increase in diversification rate was associated with 20% reduction in median area of occupancy (Figure 3b).

Genus age showed weak but statistically significant effect on median area of occupancy, explaining only 1% of the variation in the response (Table 1). The effect of age was positive and significant even when controlled for the number of species in the genus, showing that age has independent effects. The older the genus, the larger the average area of occupancy (Figure 3c).

The effect of net diversification is slightly weaker than the observed for number of species. Given that net diversification is a ratio between number of species and age, it is clear that most of the effect associated with net diversification rate is due to the number of species rather than the genus age. This highlights the importance of the number of species as a simple and good predictor of range size. The effect of age was positive and

significant even when controlled for the number of species in the genus, showing that age has independent effects. The older the genus, the larger the average area of occupancy (Figure 3c). Age is partially responsible for the effects of net diversification rate, although its partial contribution is much weaker than the number of species. For example, genera with same number of species and two and ten million years old had expected difference in median area of occupancy of only 5,000 km<sup>2</sup>. The weak effect and low explanatory power of age raise concerns whether a similar result would be observed on a different dataset. It is worth noting that current estimates of age include considerable uncertainty, which makes its statistical effects and explanatory power smaller than it truly is.

Table 1. Performance of the predictors in simple regression models explaining median area of occupancy per genus. Data included 1,225 genera. Area of occupancy, net diversification rate and number of species per genus were log<sub>2</sub> transformed, and genus age was square-root transformed. OLS - ordinary least squares; PGLS - phylogenetic generalized least squares.

Models	OLS model					PGLS model				
	Coef.	SE	p-value	R <sup>2</sup>	AIC	Coef.	SE	p-value	R <sup>2</sup>	AIC
Diversification rate	-.331	.025	<2E-16	.129	5036	-.314	.025	<2E-16	.115	4920
Number of species	-.428	.030	<2E-16	.144	5015	-.378	.029	<2E-16	.122	4911
Genus age	.092	.025	3.3E-04	.011	5192	.090	.029	.002	.008	5060
Life form	-	-	3.2E-14	.053	5143	-	-	4.8E-05	.018	5051
Habitat	-	-	< 2E-16	.103	5086	-	-	6.1E-08	.039	5038

The multiple regression model including number of species and genus age as predictors explained 13% of the variance in median area of occupancy, which is the maximum that evolutionary attributes could explained when controlled for phylogenetic relatedness (Table S1). We avoided making inference from models that include both number of species and net diversification rate due to the collinearity among these predictors and consequent inflated variance of coefficients (Table S2). For the same age, the higher the number of species, the lower the median area of occupancy. Because an increasing number of species on constant age means increasing net diversification rate, this results also means there is a negative relationship between net diversification and area of occupancy.

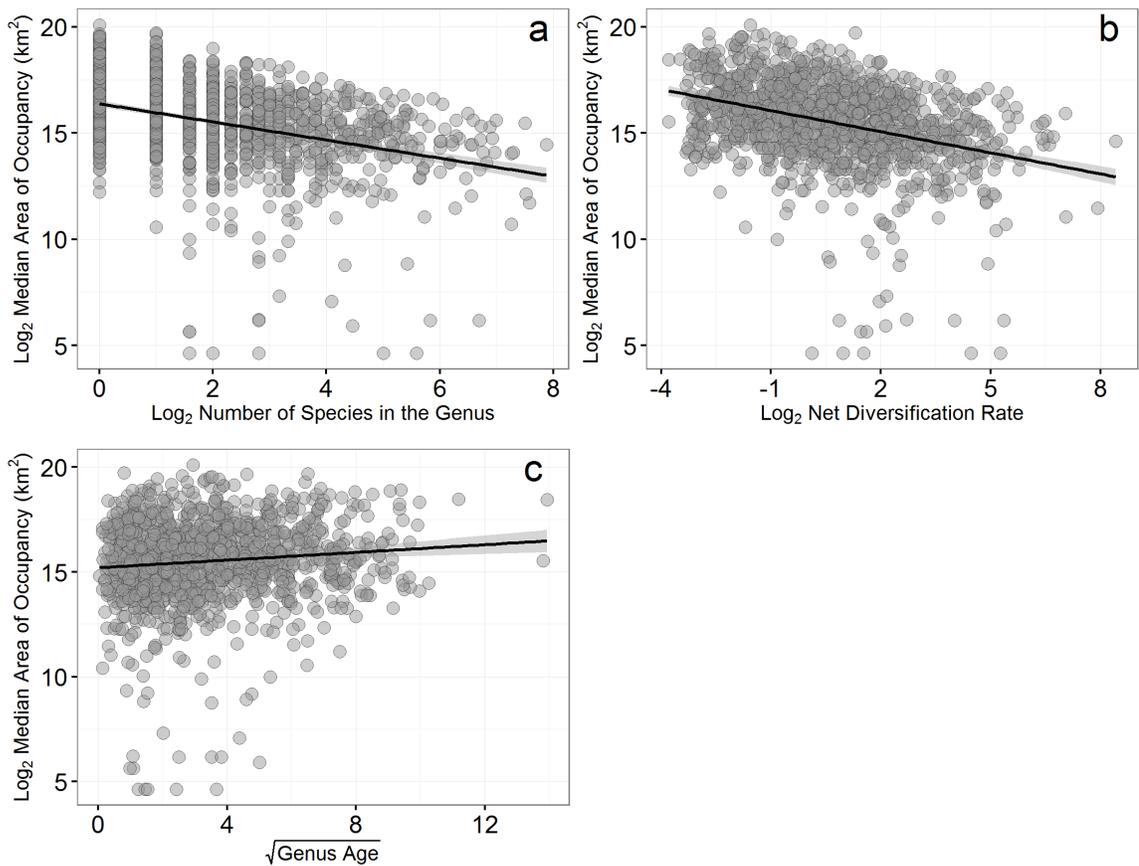


Figure 3. Bivariate relationships between median area of occupancy at genus level ( $\log_2$  transformed) and: (a) number of species in the genus ( $\log_2$  transformed), (b) net diversification rate ( $\log_2$  transformed), and (c) age of the genus most recent common ancestor (square-root transformed). Shaded area shows the 95% confidence interval.

*Evolutionary history and total genus' area of occupancy*

The number of species in the genus was a very strong predictor of the total area of occupancy of the genus (i.e. the area occupied by all species combined), explaining 45% of its variation (PGLS,  $t = 32$ ,  $p\text{-value} = <2E-16$ , Figure 4a). A two-fold increase in the number of species was associated with 56% increase in the genus' total area of occupancy. Net diversification rate explained a slightly smaller amount of variation in genus' total area of occupancy (PGLS:  $R^2 = 33\%$ ) and had a smaller effect size (PGLS: 39% increase in genus' area of occupancy for every two-fold increase in net diversification, Figure 4b). Genus age showed no bivariate relationship with genus' area of occupancy, although it showed significant effects after controlling for the number of species ( $t = 4.65$ ,  $p\text{-value} = 3.6E-06$ ). For the same number of species, the older the genus the larger the genus' total range size.

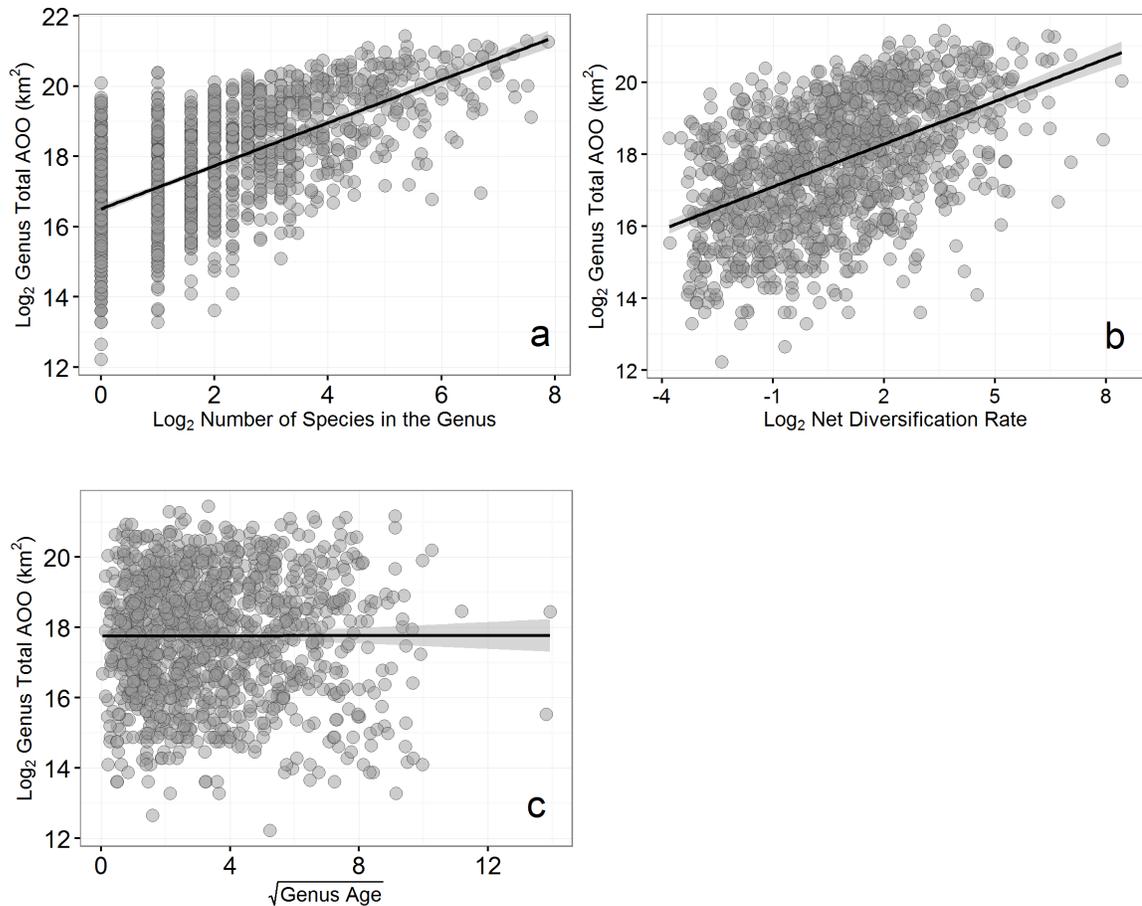


Figure 4. Bivariate relationships with the genus' total area of occupancy and: (a) number of species ( $\log_2$  transformed), (b) net diversification rate ( $\log_2$  transformed), and (c) age of the genus most recent common ancestor (square-root transformed). Shaded area shows the 95% confidence interval.

*Life forms, habitats and species' area of occupancy*

Herbs were consistently associated with the smallest area of occupancy among life forms, while trees and climbers were associated with the largest area of occupancy (Figure 5a). Herbaceous species had mean area of occupancy 60% smaller than tree species ( $t = -13.2$ ,  $df = 13,279$ ,  $p < 2E-16$ ). Shrubs had intermediate area of occupancy, which was 45%

larger than herbaceous species ( $t = 5.9$ ,  $df = 13,279$ ,  $p = 3E-9$ ), and 40% smaller than tree species ( $t = -6.8$ ,  $df = 13,279$ ,  $p = 1E-11$ ). At the genus level, results were similar. Genera with mostly herbaceous species had between 40 and 50% smaller (variation due to whether it was controlled or not for phylogenetic relatedness) median area of occupancy than genera with mostly trees.

Differences in area of occupancy among life forms depended on the vegetation type (Figure S2). Differences were larger and more significant on forests than open fields. Herbaceous species had significantly smaller area of occupancy than tree species on forests ( $\beta_{\text{herbs}} = -1.85$ ,  $t\text{-value} = -15.7$ ,  $p < 2E-16$ ), but not as smaller on open fields ( $\beta_{\text{herbs}} = -0.81$ ,  $t\text{-value} = -1.4$ ,  $p = 0.16$ ).

Habitat discriminated area of occupancy slightly better than life form (Figure 5b). At the species level, habitat explained only 4% of the variation in area of occupancy. Most habitat types showed only small deviation from the average area of occupancy. However, epiphytic and rupicolous habitats were associated with outstanding smaller mean area of occupancy, while aquatic was associated with larger area of occupancy. Epiphytic species had the lowest area of occupancy among habitat types (four times smaller than terricolous; OLS:  $t = -17$ ,  $df = 13,274$ ,  $p < 2E-16$ ), followed by rupicolous species (three times smaller than terricolous; OLS:  $t = -11.7$ ,  $df = 13,274$ ,  $p < 2E-16$ ). Aquatic species had area of occupancy twice as large as terricolous species ( $t = 5.3$ ,  $df = 13,274$ ,  $p = 1E-7$ ). At the genus level, habitat type explained 10% of the variation in median area of occupancy according to the ordinary least squares model, but only 4% in

the phylogenetic least squares model (Table 1). This shows that habitat is a powerful predictor of area of occupancy and is largely confounded with phylogeny.

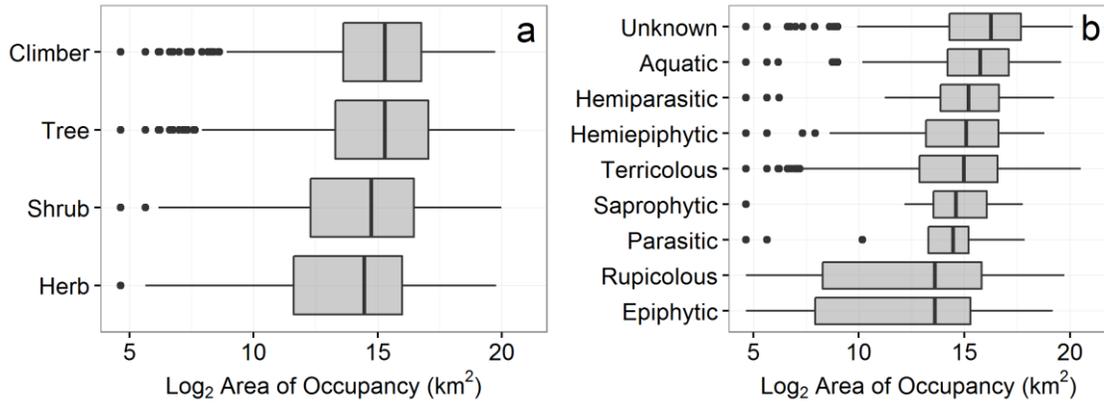


Figure 5. Box-plot of species' area of occupancy (log<sub>2</sub> transformed) across life forms (a) and habitats (b).

*Full model predicting median area of occupancy*

Our full multiple regression model predicting median species' area of occupancy at the genus level included number of species, age, life form and habitat. Net diversification rate was not included due to the collinearity with number of species. The full model explained 24% of the variation in the median species' area of occupancy under the ordinary least squares model, and 17% under the phylogenetic generalized least squares model (Table 2). Evolutionary attributes and life forms each represented approximately half of the contribution to explained variation in median area of occupancy. The marginal effects in the full model were consistent with the effects observed in the simple regression models, except for genus age – which had smaller effect size and was statistically non-significant in the full model. Although effects were smaller in the full

model, which shows some dependent effects, most effects were largely independent on other predictors. Specifically, effect sizes in the full model in comparison to simple models were 3% smaller for number of species ( $\beta = -0.36$  on multiple PGLS vs.  $\beta = -0.38$  on simple PGLS), 56% smaller for genus age (0.04 vs. 0.09), 25% smaller for epiphytic habitat (0.97 vs. 1.30), 5% smaller for rupicolous habitat (0.97 vs. 1.30), and 24% smaller for herbaceous life form (-0.61 vs. -0.80). Number of species in the genus stood out as having the strongest and most precise marginal effect on area of occupancy. All else being equal, a two-fold increase in the number of species was associated with a 24% decrease in the median area of occupancy (Figure 6). Results were similar when adopting extent of occurrence instead of area of occupancy as a measure of range size (Table S3).

Table 2. Summary of the multiple regression models including all predictors (full models). Response variable: median species' area of occupancy per genus ( $\log_2$  transformed). Predictors: number of species in the genus ( $\log_2$  transformed), genus age (square-root transformed), most frequent life form in the genus and most frequent habitat in the genus. Data includes 1,225 genera, summarized based on data for 11,370 species. Tree and terricolous were reference categories for testing differences among growths and habitats. OLS: ordinary least squares; PGLS: phylogenetic generalized least squares.

Predictors	OLS				PGLS			
	Coef.	SE	t-value	p-value	Coef.	SE	t-value	p-value
(Intercept)	16.721	0.145	115.013	<2E-16	16.379	0.463	35.359	<2E-16
Number of species	-0.390	0.029	-13.405	<2E-16	-0.365	0.029	-12.517	< 2E-16
Genus age	0.009	0.024	0.383	0.702	0.041	0.026	1.574	0.116
Life form								
Climber	-0.101	0.167	-0.607	0.544	-0.103	0.184	-0.560	0.576
Herb	-0.648	0.142	-4.574	5.3E-06	-0.609	0.181	-3.371	0.001
Shrub	-0.191	0.159	-1.203	0.229	-0.308	0.168	-1.832	0.067
Tree	-	-	-	-	-	-	-	-
Habitat								
Aquatic	0.268	0.232	1.155	0.248	0.245	0.242	1.011	0.312
Epiphytic	-1.290	0.201	-6.427	1.9E-10	-0.970	0.288	-3.372	0.001
Hemiepiphytic	-0.485	0.468	-1.037	0.300	-0.468	0.479	-0.979	0.328
Hemiparasitic	-0.745	0.463	-1.607	0.108	-0.474	0.516	-0.918	0.359
Parasitic	-1.442	1.261	-1.144	0.253	-1.436	1.252	-1.147	0.252
Rupicolous	-1.382	0.277	-4.984	7.1E-07	-1.379	0.281	-4.907	1E-6
Saprophytic	-0.488	0.804	-0.607	0.544	-0.358	0.816	-0.439	0.661
Terricolous	-	-	-	-	-	-	-	-
Unknown	1.217	0.449	2.712	0.007	0.980	0.447	2.193	0.028
R <sup>2</sup>	0.238				0.169			
AIC	4896				4875			

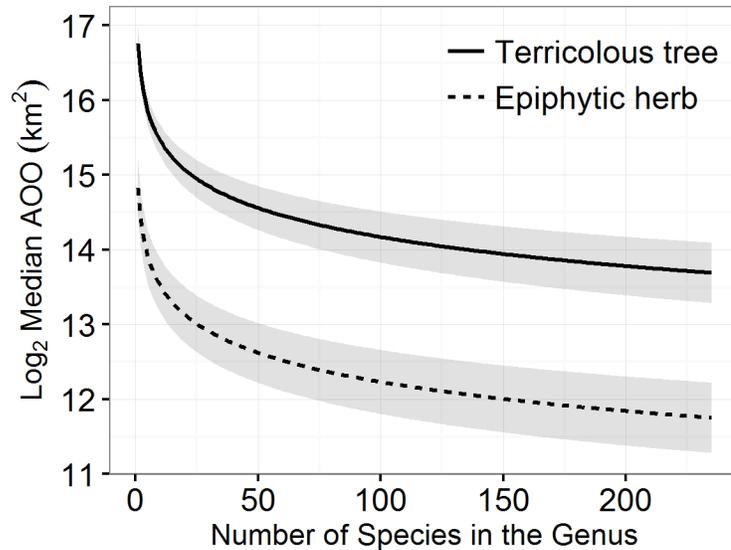


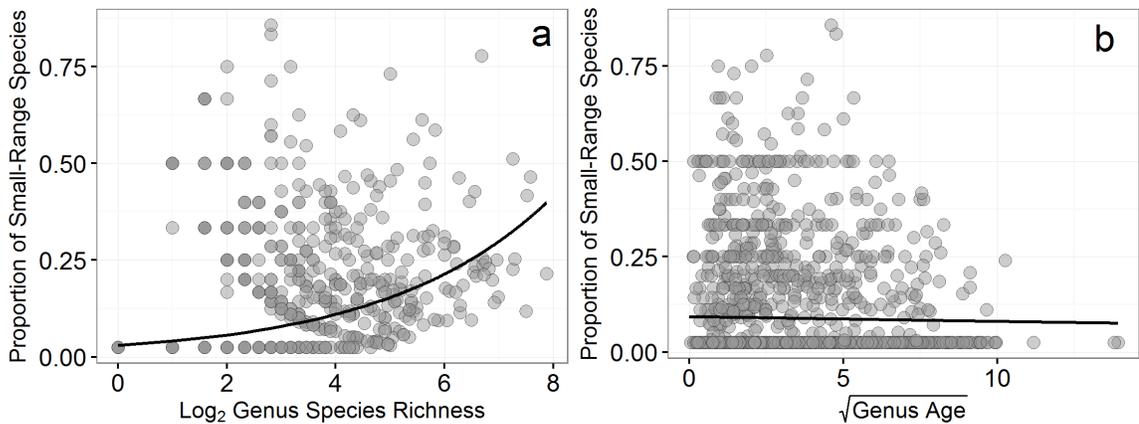
Figure 6. Predicted median area of occupancy as a function of the number of species in the genus on two contrasting ecological groups (terricolous tree and epiphytic herbs). Shaded area shows the 95% confidence interval. Mean functions were obtained from the full ordinary least squares model (Table 2).

*Proportion of species with vulnerably small area of occupancy*

The number of species in the genus explained 35% of the variation in the proportion of species with area of occupancy smaller than the vulnerability threshold (i.e. <2,000 km<sup>2</sup>). The larger the number of species, the larger the proportion of species with vulnerably small area of occupancy. A two-fold increase in the number of species in the genus was associated with 40% increase in the proportion of small-range species in the genus (WLS:  $\beta = 0.48$ ,  $t = 25$ ,  $p < 2e-16$ ,  $df = 1,223$ ,  $R^2 = 0.35$ ; Figure 7a). This relationship is much stronger and more precise than the ones observed with median area of occupancy, showing that the number of species in the genus is a particularly good predictor of the

vulnerability to extinction. A similar result holds when controlling for phylogenetic dependence (PGLS:  $\beta = 0.51$ ,  $t = 24$ ,  $p < 2e-16$ ,  $df = 1,223$ ,  $R^2 = 0.32$ ). Genus age showed no significant effects on the proportion of species with area of occupancy smaller than the vulnerability threshold (Figure 7b).

The proportion of species with area of occupancy smaller than the vulnerability threshold varied among life forms (Figure 7c) and decreased in the following order: herbs (23%, 95% CI: 22-24%), shrubs (20%, 95% CI: 19-21%), trees (16%, 95% CI: 15-17%) and climbers (12%, 95% CI: 11-14%). Among habitats, rupicolous and epiphytic stood out with the highest proportion of small-range species (Figure 7d): 32% of rupicolous (95% CI: 29-36%), 32% of epiphytic (95% CI: 30-34%), 17% of terricolous (95% CI: 16-18%) and only 9% of aquatic had small-range (95% CI: 6-12%). Estimates for other habitats were not as precise, in particular for parasitic (95% CI: 3-44%) and saprophytic (95% CI: 0-15%).



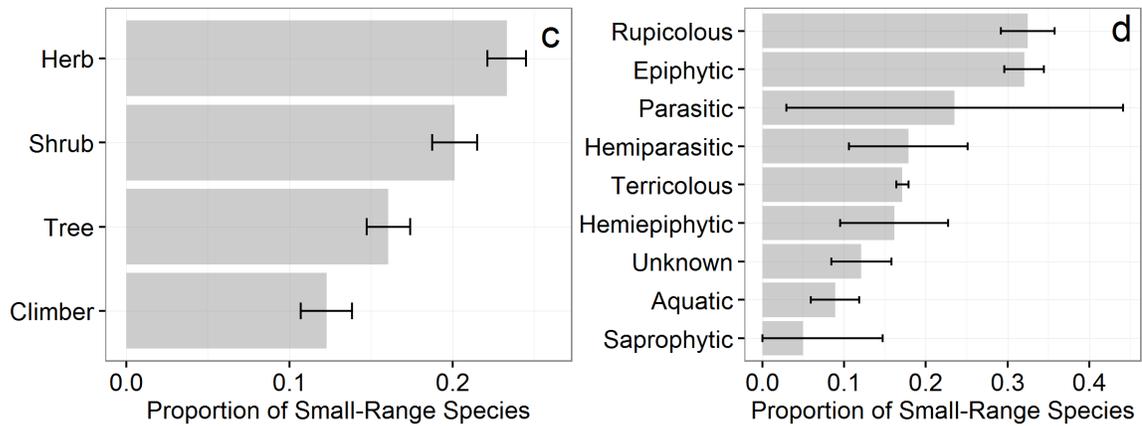


Figure 7. Proportion of species with area of occupancy smaller than the threshold of vulnerability (i.e. <math> < 2,000 \text{ km}^2 </math>) as a function of the number of species in the genus (a), square-root of the genus age (b), life form (c), and habitat (d). Error bars show the 95% confidence interval. Mean functions and errors obtained from weighted least squares regression (a, b) and logistic regression (c, d).

*Full model predicting the proportion of species with vulnerably small area of occupancy*

The full model explained 40% of the variation in the proportion of species with vulnerably small area of occupancy under the weighted least squares regression, and 38% under the phylogenetic generalized least squares (Table 3). These predictors were clearly more powerful to predict the proportion of species with small area of occupancy than the average species' area of occupancy. In particular, the number of species in the genus had marked influence on the expected proportion of small-range species. All else being equal, a two-fold increase in the number of species was associated with 36 to 42% increase (WLS-PGLS) in the proportion of species with vulnerably small area of occupancy. For example, genera with 10 species, consisting mostly of terrestrial trees and with mean age of 17 My had expected percentage of species with vulnerably small area of occupancy of

9% (1 vulnerable species). If the number of species in the genus increased to 50 (e.g. *Calyptranthes*) or 100 (e.g. *Ocotea*, *Miconia*), that percentage increased to 20% (10 species) and 28% (28 species) respectively (Figure 8). In particular, species-rich genera of epiphytic herbs were the most likely to have species with vulnerably small area of occupancy. Genera of epiphytic herbs with 10 species were expected to have 25% of its species (i.e. 2-3 species) with area of occupancy below the threshold of vulnerability. If the number of species in the genus increased to 50 (e.g. *Cattleya*, *Nidularium*), 100 (e.g. *Neoregelia*, *Acianthera*) or 150 (e.g. *Aechmea*), the expected percentage increased to 32%, 46% and 57%, respectively.

Table 3. Full multiple regression models predicting the proportion of species with area of occupancy smaller than the vulnerable threshold (< 2,000 km<sup>2</sup>). Predictors: number of species in the genus (log<sub>2</sub>), genus age (square-root), life form (most frequent in the genus) and habitat (most frequent in the genus). Data includes 1,225 genera, summarized based on data for 11,370 species. Tree and terricolous were reference categories for testing differences among growths and habitats. WLS – weighted least squares regression, PGLS – phylogenetic generalized least squares regression.

Predictors	WLS				PGLS			
	Coef.	SE	t-value	p-value	Coef.	SE	t-value	p-value
(Intercept)	-5.049	0.111	-45.410	< 2E-16	-5.201	0.105	-49.310	< 2E-16
Number of species	0.448	0.019	23.558	< 2E-16	0.513	0.021	24.350	< 2E-16
Genus age	-0.004	0.017	-0.231	0.817	-0.006	0.017	-0.346	0.730
Life form								
Climber	-0.463	0.122	-3.808	1.5E-04	-0.403	0.121	-3.321	0.001
Herb	0.167	0.107	1.568	0.117	0.130	0.103	1.266	0.206
Shrub	-0.043	0.113	-0.378	0.705	-0.079	0.115	-0.686	0.493
Tree	-	-	-	-	-	-	-	-
Habitat								
Aquatic	-0.568	0.198	-2.866	0.004	-0.428	0.168	-2.547	0.011
Epiphytic	0.705	0.133	5.300	1.4E-07	0.577	0.146	3.962	7.8E-05
Hemiepiphytic	-0.117	0.350	-0.335	0.738	-0.045	0.339	-0.133	0.894
Hemiparasitic	0.066	0.362	0.182	0.855	0.115	0.336	0.341	0.733
Parasitic	1.011	1.023	0.988	0.323	0.634	0.915	0.694	0.488
Rupicolous	0.760	0.201	3.782	1.6E-04	0.642	0.201	3.193	0.001
Saprophytic	-0.927	0.773	-1.200	0.231	-0.659	0.583	-1.131	0.258
Terricolous	-	-	-	-	-	-	-	-
Unknown	-0.594	0.394	-1.508	0.132	-0.339	0.326	-1.041	0.298
R <sup>2</sup>	0.403				0.377			
AIC	4370				4107			

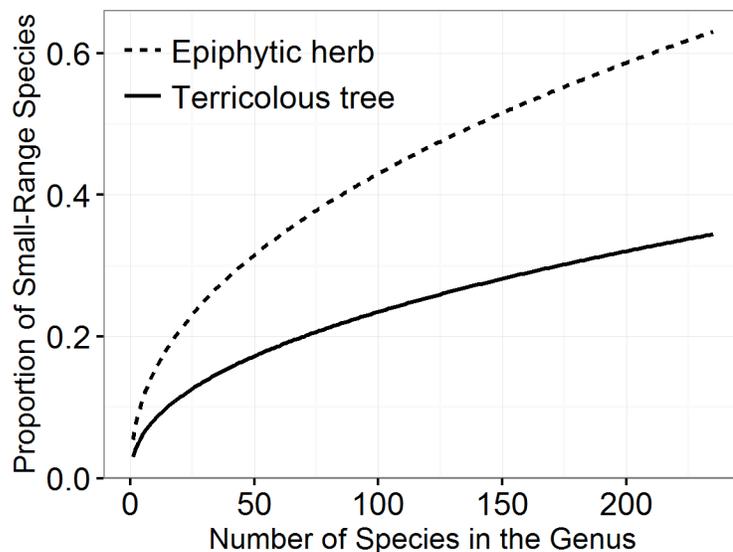


Figure 8. Proportion of species with area of occupancy smaller than the vulnerable threshold ( $<2,000\text{km}^2$ ) as a function of the number of species in the genus for two contrasting ecological groups (terricolous trees and epiphytic herbs). Genus age kept at 17 My (mean value). Mean function obtained from the full weighted least squares model (Table 3).

## Discussion

Our results support the hypothesis that the geographic range sizes of Atlantic Forest's flowering plants are related to their evolutionary history, life form and habitat. Lineages with larger number of species and higher net diversification rates have species with smaller range size. Genus age has a weak positive effect on range size, which is not clearly significant. The observed evolutionary patterns suggest that current ranges depend on historical dynamics of speciation and extinction. Life forms and habitats clearly relate with species range size. Herbaceous species have the smallest ranges among life forms, while tree species have the largest. Epiphytic and rupicolous habitats associate with the

smallest species range sizes and largest proportions of species with critically small range. Assuming that range size is a main component of the vulnerability to extinction, these findings significantly improve our understanding of the current risk of extinction of plant species.

#### *Species richness and net diversification rate*

Genera with more species show larger genus range size (i.e. the aggregate range of all species in the genus). A large number of species likely enables the genus to colonize a broader diversity of habitats, which in turn leads to a larger area occupied by the genus (Gaston & Blackburn 1997). Likewise, a large genus range size entails more opportunities for differentiation, fostering high diversification rates and large number of species (Jansson & Davies 2008). Thus, there is likely a positive feedback between genus' total range size and genus' number of species, where a large range size foster diversification and vice versa.

Genera with more species have smaller average species range size. We believe that the key to understanding the relationship between the number of species and the average species range size rests on the dynamics of diversification and, in particular, on the rates of speciation and extinction. First, the high importance of species richness in the phylogenetic analyses suggests that net diversification is an important mechanism explaining range size. This is true because differences in the number of species among closely related taxa most likely mean differences in net diversification rates (Jansson & Davies 2008). Second, the positive effect of genus age on average species range size

when controlling for species richness reinforces the importance of net diversification as a mechanism influencing the sizes of the ranges. Assuming that most new species start with a small range, the higher the speciation rate, the higher tend to be the number of small-range species at any given time. Assuming that species with smaller range sizes are more vulnerable to extinction (Gaston 2003; Gaston & Fuller 2009), as the proportion of small-range species in a lineage increases, the higher tend to be the extinction rate in that lineage. If the extinction rate is low, then there is an accumulation of small-range species. Thus, a high ratio between speciation and extinction leads both to an elevated number of species and an increased proportion of small-range species (Lozano & Schwartz 2005; Schwartz & Simberloff 2001). This rationale helps understanding how a lineage's dynamics of diversification affects current species range size and vulnerability to extinction.

#### *Lineage's age*

Our results suggest that the effect of age on range size is weak, which is consistent with previous investigation among neotropical shrubs of the genus *Psychotria* (Paul et al. 2009), although the effect of age in our dataset was much weaker (1% vs. 7%). It is worth noting that Paul et al. (2009) tested the effects of age on the species level, which is more precise than our test of genus age vs. average range size. Perhaps, with more accurate age estimates we would have found a stronger effect of age. The fact that both studies found similar effects supports the notion that there is a positive relationship between age and area, though not as strong as some have initially suggested (Willis 1922).

### *Life form*

The pattern of herbs and trees having respectively the smallest and the largest range size among life forms agrees with findings in Great Britain where trees had the largest range (Kelly 1996), and contrasts with studies in Australia where shrubs had the smallest range and herbs the largest (Gallagher 2016; Hunter 2003; Oakwood et al. 1993). Interestingly, the relationship between life form and range size is apparently context-dependent, making it hard to find a single pattern that fits all (Kelly 1996; Murray et al. 2002). The similarities and differences in range size patterns between the Atlantic Forest, Great Britain and Australia may be explained by similarities and differences in vegetation types. The dominance of grasslands, savannas and shrublands in Australia's drier landscape contrasts with the natural dominance of forests in Great Britain and Atlantic Forest's moister landscapes (Olson et al. 2001), which may be an underlying reason for why herbs have larger range sizes in Australia. Perhaps, herbs are favored to have larger range sizes in open fields and are disfavored in forests. Supporting this hypothesis, herbs had a relatively smaller range size than trees in forests as compared to open fields in the Atlantic Forest region (see Table S4, Figure S2). It is true that the forest structure imposes more barriers for long-distance dispersal than open fields for both herbs and trees (e.g. Nathan et al. 2002). However, forests may impose additional barriers to the dispersal of herbaceous species as compared to trees. First, herbs are less competitive in reaching light than trees due to smaller stature, which may drive them to occur in lower densities and smaller range sizes (assuming a positive correlation between abundance and range size, Gaston 2003). Second, herbs might disperse especially poorly on forests

because many of them are restricted to the forest understory, where wind dispersal is deeply inefficient (Howe & Smallwood 1982; Nathan et al. 2002), and dispersal of many relies on ants or specialized birds with restricted home ranges (Wunderle 1997). In contrast, herbs are the dominant life form in open fields, and can take full advantage of the stronger winds for dispersal, as is consistent with the higher proportion of wind-dispersed species in open fields as compared to forests (e.g. Jacobi & Carmo 2011). Finally, because area of habitat is positively associated with species range size (Gallagher 2016; Morueta-Holme et al. 2013), dominant life forms in dominant vegetation types tend to be associated with larger range sizes. If this rationale is true, then we should expect herbs to have larger range sizes in regions dominated by open fields, and trees to have larger ranges in regions dominated by forests.

### *Habitat*

Epiphytes and rupicolous species are at the lower end of the range size distribution among flowering plants in the Atlantic Forest. This contrasts with previous conclusions that epiphytes have larger range than terrestrial species (Hunter 2003; Ibisch et al. 1996; Kessler 2002). It was already noticed that epiphytes have small range sizes in the Atlantic Forest (Fontoura & Santos 2010; Fontoura et al. 2012), which is inconsistent with the generalizations from studies in the Andean region (Ibisch et al. 1996; Kessler 2002). Yet, epiphytes are still considered to have larger range sizes than terrestrial species (Zotz 2016). The contrasting findings between the literature and our study may be explained by (1) differences in taxonomic scale of the analysis (epiphytic families vs. entire angiosperms), (2) difference in range size patterns between Andean and Atlantic Forest,

and (3) differences in data quality and analytical methods among studies. Because the aforementioned studies in the Andean region focused on epiphytic families, they could not compare the range size of epiphytes versus other ecological groups on a broad taxonomic scale. Even in the Atlantic Forest, differences in average range size between epiphytic, terrestrial and rupicolous species are smaller if restricting the analysis to the families containing epiphytic species, although epiphytic species still have smaller range than terrestrial (Figure S3a). In addition, our phylogenetic analysis support the notion that epiphytes have smaller range size than terrestrial even when comparing close relatives.

The finding that epiphytes have smaller average range size does not mean that epiphytism is associated with smaller range size at all scales. Analyses within individual families may yield distinct results. For example, epiphytic species had smaller range than terrestrial within Orchidaceae, but larger range within Bromeliaceae and Araceae, and not significantly different for other families of epiphytes (Figure S4) which is reasonably consistent with the evidence from the Andes (Ibisch et al. 1996; Kessler 2002). It is true that the general trend is disproportionately affected by Orchidaceae – because it is the largest family –, but even within Bromeliaceae, epiphytic species indeed have small range sizes. Epiphytic bromeliad have about the same mean area of occupancy (30,700 km<sup>2</sup>) and a little more than a third of the median area of occupancy (4,750 km<sup>2</sup>) of epiphytic orchids (mean AOO = 29,500 km<sup>2</sup>, median AOO = 12,500 km<sup>2</sup>), which is similar to the area of occupancy estimated for all epiphytic species combined (mean AOO = 34,000 km<sup>2</sup>, median AOO = 12,500 km<sup>2</sup>). Truly exceptional are the range sizes of rupicolous bromeliads (mean AOO = 9,000 km<sup>2</sup>, median AOO = 150 km<sup>2</sup>, 145 species)

and terrestrial bromeliads (mean AOO = 28,500 km<sup>2</sup>, median AOO = 1,500 km<sup>2</sup>), which are much smaller than the average for all rupicolous and terrestrial (rupicolous: mean AOO = 54,500 km<sup>2</sup>, median AOO = 12,500 km<sup>2</sup>; terricolous: mean AOO = 83,500 km<sup>2</sup>, median AOO = 32,500 km<sup>2</sup>). Thus, although epiphytism can be associated with larger range in restrict taxonomic scales, this does not change the fact that they tend to have absolute small range sizes. In particular, the observed larger range of epiphytic species within Bromeliaceae has more to do with the unusually small range of terrestrial and rupicolous bromeliads than with a supposedly large range of epiphytes.

Perhaps more insightful to understanding the rarity of epiphytes is to focus on lineages where epiphytism evolved. Families and genera rich in epiphytic species had much smaller range size than lineages without epiphytes (Figure S5), and this pattern cannot be solely explained by epiphytism. Mechanisms of diversification and particular adaptations on these lineages may hold some of the reasons for small range size.

Epiphytic lineages, particularly within Orchidaceae and Bromeliaceae, are associated with high net diversification rates, especially in the Atlantic Forest where bromeliad epiphytes show unusually high diversification rate (highest known among Bromeliaceae; Givnish et al. 2014). For example, the ability to rapidly speciate through hybrid and polyploid speciation (as fast as within few generations) can both boost the species richness and accumulate species with small range sizes (Pinheiro et al. 2010; Rieseberg & Willis 2007). Key innovations, such as CAM photosynthesis, leaf trichomes for water and nutrient absorption, tanks for water storage, pollinia and new pollination strategies enabled the colonization of new adaptive zones such as the epiphytic and rupicolous

habitats and probably accelerated diversification rates (Givnish et al. 2014; Givnish et al. 2015). The two most important epiphytic families (Orchidaceae and Bromeliaceae) are among the top three families in number of species (Forzza et al. 2010), and they have much lower average range sizes than the other richest families in the Atlantic Forest (i.e. Fabaceae, Asteraceae and Poaceae; Figure S6, Table S6). Epiphytic lineages are key responsible for both the extraordinarily high plant diversity and vulnerability to extinction in the Atlantic Forest.

## **Conservation implications**

### *Species richness, diversification rates and extinction risk*

Lineages with large number of species and high net diversification rates include more species with critically small range size, which is consistent with the finding that those lineages have high species extinction risk (Davies et al. 2011b). In fact, species richness and net diversification rates were even more important to predict the proportion of species with vulnerably small range sizes than to predict average species range size. Because species with very small ranges are vulnerable to extinction, species-rich lineages tend to lose more species through time. This supports the notion, found on another hotspot of plant diversity, that the lineages more likely to lose species are those producing new species more quickly (Davies et al. 2011b). In fact, high evolutionary turnover rate, a situation combining both high speciation and extinction rates, seems a noteworthy characteristic of the flowering plants evolution in the neotropics (Antonelli et al. 2015; Jansson & Davies 2008). Bromeliaceae and Orchidaceae may be good examples of families with high evolutionary turnover, given that they each comprise an

extraordinarily high number of species (probably due to high speciation rates; Givnish et al. 2015) with extraordinarily small species range size (probably leading to high extinction rates; Gaston 2003; Gaston & Fuller 2009). In contrast, some lineages have low species richness, low net diversification and species with large range sizes (thus, probably small extinction risks), being on the opposite extreme of the evolutionary turnover dynamic (e.g. Anacardiaceae, Meliaceae and Combretaceae). Thus, recognizing differences in lineages' evolutionary dynamics seems key to understand current extinction risk of plants in the Atlantic Forest.

The fact that species-rich lineages concentrate the species naturally vulnerable to extinction is a sign of strength of biodiversity to persist under extinction pressures, because a high species' vulnerability to extinction tend to be balanced at the genus level by a large number of species in that genus. Species-rich lineages have more closely related species, meaning that the loss of a single species tend to be less damaging to the evolutionary diversity than if it occurs in a species-poor lineage (Lozano & Schwartz 2005).

*Reasons for vulnerability: natural vs. anthropogenic*

Although many species have small range size due to habitat loss and other human-driven impacts, it is clear that many others have small range size due to evolutionary and ecological reasons. Regardless of the reason, all species with extremely small range size are vulnerable to disappear due to further habitat loss and associated environmental changes, as well as broader environmental changes (e.g., climate change). The reasons

for vulnerability are relevant to understanding the actual contribution of human impacts vs. natural evolutionary and ecological dynamics to explain current extinction risk. A species from a plant lineage with extremely high species richness and diversification rate, with many closely related species and naturally occupying a very restrict range has a vulnerability to extinction better explained by the evolutionary process, in particular the dynamics of speciation and extinction, than by human impacts. On the other hand, a species that was originally abundant and widespread, and driven to rarity due to overexploitation and habitat loss (e.g. Brazilwood, *Paubrasilia echinata*) has a vulnerability status caused by human impacts. Because humans are directly responsible for the decline and vulnerability of these latter species, appealing to a sense of responsibility may help to engage people and attract funds towards their recovery and conservation. Distinguishing whether the vulnerability to extinction is natural or anthropic is thus useful not only to acknowledge clearly distinct conservation stories, but also to assist conservation efforts.

#### *Synergy of vulnerability to extinction*

It is concerning that species with the smallest range sizes also have life histories conferring them additional vulnerability to human disturbances. Plants adapted to epiphytic and rupicolous habitats tend to grow at slower rates than plants adapted to terrestrial habitats due to the marked environmental stress imposed by the first two habitats (Arendt 1997; Benzing 1990; Grime & Hunt 1975; Porembski & Barthlott 2000; Schmidt & Zotz 2002) and their adaptive slow-growth ecological strategy. All else being equal, slow growing plants are at higher vulnerability to local extinction because they

require a longer time to recover the original population size after disturbances – such as forest degradation, overharvesting, increased frequency of fire, livestock grazing and invasive species – causing population decline. In frequently disturbed and hyperdynamic forest habitats (Laurance et al. 2002), such as the small fragments of secondary forest in the Atlantic Forest (Tabarelli et al. 2004), slow growing species are likely to decline and eventually disappear, as already have been observed among trees (Laurance et al. 2006). In fact, many epiphytes are likely disappearing on small fragments of disturbed secondary forests (Koester et al. 2013).

## **Caveats and limitations**

### *Species delimitation problem*

The number of species in a genus can reflect aspects of the evolutionary history of the genus, such as net diversification rate, but can also reflect bias in species delimitation (Agapow et al. 2004; Schwartz & Simberloff 2001). The criteria for classifying distinct plants – i.e. those with differences in morphology, genetic composition, evolutionary history and/or with isolated reproduction – into multiple or single species may vary across plant families and taxonomists (Knapp et al. 2005; McDade 1995), and this may have an effect on the species range sizes (Brown et al. 1996; Schwartz & Simberloff 2001). In some cases, geographic distribution can be used as a criteria for taxonomic delimitation (McDade 1995), which makes a species' range clearly dependent on the taxonomic delimitation. Whether distinct plant populations are classified into multiple or single species affects species' range size because each of the multiple species occupies

only a fraction of the range size occupied by a single species that aggregates all distinct populations (Brown et al. 1996).

In particular, some plant lineages impose more difficulties to set a clear taxonomic delimitation due to factors such as rates of hybridization, intra-specific variation, convergent evolution and cryptic speciation (Agapow et al. 2004; McDade 1995; Rieseberg & Willis 2007). For example, cryptic speciation, a process forming distinct species with subtle differences, may lead to the underestimation of the number of species and the overestimation of the species' range size, because taxonomists would likely group multiple cryptic species under a single species name (Rieseberg & Willis 2007; Soltis & Soltis 2009). Some lineages may show high levels of hybridization, blurring species boundaries and making differences among species to vary in a continuous rather than discrete fashion (Agapow et al. 2004; Rieseberg & Willis 2007), as it appears to be the case among orchids of the genus *Epidendrum* in the Atlantic Forest (Pinheiro et al. 2010). Even though it is important to be aware of the potential confounding effect of the species delimitation, the most complicated cases where the delimitation is unclear seems to be uncommon (McDade 1995). Thus, it seems reasonable to assume that species delimitation is mostly consistent across lineages and that variation in species richness among lineages is mostly due to evolutionary processes.

#### *Quality of age estimates*

Age estimates of most recent common ancestors are still imprecise, as is evident through the large variations in age estimates across studies on the same taxa (see Stevens 2017).

For example, the estimated crown age for many genera of Bromeliaceae was much older in Zanne et al. (2014) than in Givnish et al. (2011). While the former predicted crown age for the genera *Tillandsia* and *Vriesea* as 32 and 42 Mya respectively, the latter predicted crown age of 12-14 My for the whole Tillandsioideae clade (which include *Tillandsia*, *Vriesea* and others). These uncertainties likely diminish the ability to find any age-related pattern and certainly increase skepticism about any pattern that is observed. On the other hand, estimates of species richness are much more accurate, which perhaps can partially explain the stronger and more precise effect of species richness as compared to net diversification – variable dependent on both species richness and age.

## **Conclusion**

Through testing the existence of specific patterns in the variation of range size among Atlantic Forest flowering plants, we showed that species richness, net diversification, life forms and habitats considerably affect the species' range size. We suggested that the dynamic of speciation and extinction is a mechanism underlying the variation in range size, and pointed out the strength of the plant diversity to persist – given high vulnerability to species extinction tend to be balanced by a high number of species at the genus level. We suggested that vegetation type, particularly the contrast between open fields and forests, mediates the relationship between life form and range size, which clarifies a long-held inconsistency in the literature. We challenged the notion that epiphytes have larger range size than terrestrial plants, and recommended a focus on lineages where epiphytism evolved (e.g. Bromeliaceae, Orchidaceae) to understand important reasons for the high levels of plant diversity, rarity and vulnerability to

extinction in the Atlantic Forest and similar floras. Finally, given (1) the gap in knowledge about patterns of variation in plant range size, (2) that range size is critical to the vulnerability to extinction, and (3) the Atlantic Forest has an extraordinarily high plant diversity and species' extinction risk, we believe this work significantly improve the knowledge about ecology and conservation of plants.

### **Acknowledgments**

We are particularly grateful to all herbaria that provided plant occurrences through the Species Link network (see list of herbaria in the supplementary material), without which this work would impossible. We are grateful to members of the Forest Ecology Lab and Jeannine Cavender-Bares Lab, and other colleagues at University of Minnesota for providing insightful comments and criticism, in particular Jose Eduardo Meireles, Jason Reinhardt, Daniel Stanton and Arindam Banerjee. Tarciso Leão received Doctoral Fellowship from CAPES n. 1145/12-6, Interdisciplinary Doctoral Fellowship from University of Minnesota and support from the Institute on the Environment.

## Supplementary Material

Table S1. Explained variance and fit of multiple regression models predicting the median species' area of occupancy per genus ( $\log_2$  transformed).

Model	OLS models			PGLS models		
	R <sup>2</sup>	AIC	BIC	R <sup>2</sup>	AIC	BIC
Age + Species Richness + Habit + Habitat	0.238	4896	4973	0.169	4875	4946
Species Richness + Net Diversification	0.149	5010	5031	0.127	4907	4923
Age + Species Richness	0.148	5010	5031	0.126	4908	4923
Age + Species Richness + Net Diversification	0.149	5012	5038	0.127	4909	4930
Age + Net Diversification	0.142	5020	5040	0.128	4914	4929
Habit + Habitat	0.105	15764	15831	0.054	15739	15800

Table S2. Variance inflation factor (VIF) for each predictor in multiple regression models (OLS). SR: species richness. Div: diversification rate. For more details, see the summary of each regression model below.

Model	SR	Div	Age
SR + Div	3.6	3.6	
SR + Age	1.0		1.0
Div + Age		1.4	1.4
SR + Div + Age	13.7	19.2	5.4

Table S3. Summary of the multiple regression models including all predictors (full models). Response variable: median species' extent of occurrence per genus ( $\log_2$  transformed). Predictors: number of species in the genus ( $\log_2$  transformed), genus age (square-root transformed), most frequent life form in the genus and most frequent habitat in the genus. Data includes 1,225 genera. Tree and terricolous were reference categories for testing differences among growths and habitats. OLS: ordinary least squares; PGLS: phylogenetic generalized least squares.

Predictors	OLS				PGLS			
	Coef	SE	t value	Pr(> t )	Coef	SE	t value	Pr(> t )
(Intercept)	21.171	0.165	128.553	0	21.204	0.856	24.761	0
Number of species	-0.371	0.033	-11.278	4.00E-28	-0.350	0.032	10.772	0
Genus age	-0.014	0.027	-0.528	0.598	0.036	0.032	1.126	0.261
Life form								
Climber	0.162	0.189	0.855	0.393	0.116	0.224	0.517	0.605
Herb	-0.608	0.160	-3.792	1.57E-04	-0.800	0.215	-3.720	2.09E-04
Shrub	-0.424	0.180	-2.360	0.018	-0.432	0.196	-2.201	0.028
Tree	-	-	-	-	-	-	-	-
Habitat								
Aquatic	0.967	0.263	3.681	2.43E-04	0.710	0.281	2.531	0.011
Epiphytic	-0.762	0.227	-3.353	8.24E-04	-1.005	0.361	-2.783	0.005
Hemiepiphytic	0.433	0.530	0.816	0.415	-0.028	0.553	-0.050	0.960
Hemiparasitic	-0.596	0.525	-1.135	0.256	-0.359	0.653	-0.550	0.583
Parasitic	-0.410	1.429	-0.287	0.774	-0.211	1.421	-0.149	0.882
Rupicolous	-1.575	0.314	-5.014	6.13E-07	-1.631	0.320	-5.104	3.86E-07
Saprophytic	1.172	0.911	1.288	0.198	1.039	0.961	1.082	0.280
Terricolous	-	-	-	-	-	-	-	-

Unknown	1.049	0.508	2.063	0.039	0.933	0.500	1.866	0.062
R <sup>2</sup>			0.180				0.145	
AIC			5201				5159	

Table S4. Area of occupancy (mean and standard deviation) for all species, species occurring in open fields and not in forests (“Open Field”), and species occurring in forests and not in open fields (“Forest”).

Life Form	All		Open Field		Forest	
	Mean	SD	Mean	SD	Mean	SD
Climber	84981	118369	72745	92139	75049	105632
Herb	57704	96278	61873	94001	41704	74100
Shrub	77610	128914	59647	95641	59738	106814
Tree	109623	171046	152524	192379	98604	155210

Table S5. Mean and standard deviation of the species’ area of occupancy per family. Only families with 50 or more species are included in this table. Species = number of species of the family included in the estimates of area of occupancy and included in our dataset.

Family	AOO mean	AOO SD	Species
Bromeliaceae	25,447	63,276	620
Amaryllidaceae	27,742	42,078	50
Begoniaceae	28,062	71,947	168
Gesneriaceae	29,118	48,663	123
Eriocaulaceae	31,158	64,487	147
Marantaceae	31,505	42,150	93

Orchidaceae	31,839	46,670	1257
Araceae	40,623	57,802	194
Acanthaceae	41,133	76,431	183
Oxalidaceae	49,660	66,890	62
Dioscoreaceae	57,783	79,436	54
Cucurbitaceae	58,864	73,695	77
Iridaceae	59,992	114,352	85
Melastomataceae	60,453	100,068	523
Loganiaceae	63,134	100,148	54
Cactaceae	63,857	84,463	76
Piperaceae	65,448	119,454	252
Lamiaceae	67,894	114,423	193
Rutaceae	72,292	138,360	86
Chrysobalanaceae	73,163	115,338	61
Myrtaceae	74,120	145,138	607
Asteraceae	74,573	114,576	828
Poaceae	75,824	101,184	681
Apocynaceae	76,510	112,384	336
Plantaginaceae	77,426	130,902	55
Annonaceae	78,811	121,270	93
Arecaceae	78,913	98,125	57
Solanaceae	81,721	117,032	299
Malpighiaceae	85,596	123,717	189
Lauraceae	88,659	125,981	196
Verbenaceae	91,025	175,909	119
Primulaceae	92,928	138,144	63
Malvaceae	93,002	143,844	275
Celastraceae	94,968	133,897	67
Polygalaceae	95,567	108,102	80
Erythroxylaceae	96,023	135,449	65
Rubiaceae	96,746	159,723	469

Phyllanthaceae	97,047	146,945	52
Sapindaceae	97,575	149,320	181
Passifloraceae	98,156	139,691	76
Sapotaceae	99,902	129,036	72
Lythraceae	102,480	116,134	53
Euphorbiaceae	105,262	163,304	294
Convolvulaceae	114,569	114,337	128
Cyperaceae	122,114	148,561	328
Amaranthaceae	131,023	177,676	51
Moraceae	132,225	147,431	92
Bignoniaceae	133,151	162,591	181
Fabaceae	134,085	188,829	921
Boraginaceae	160,299	189,128	64

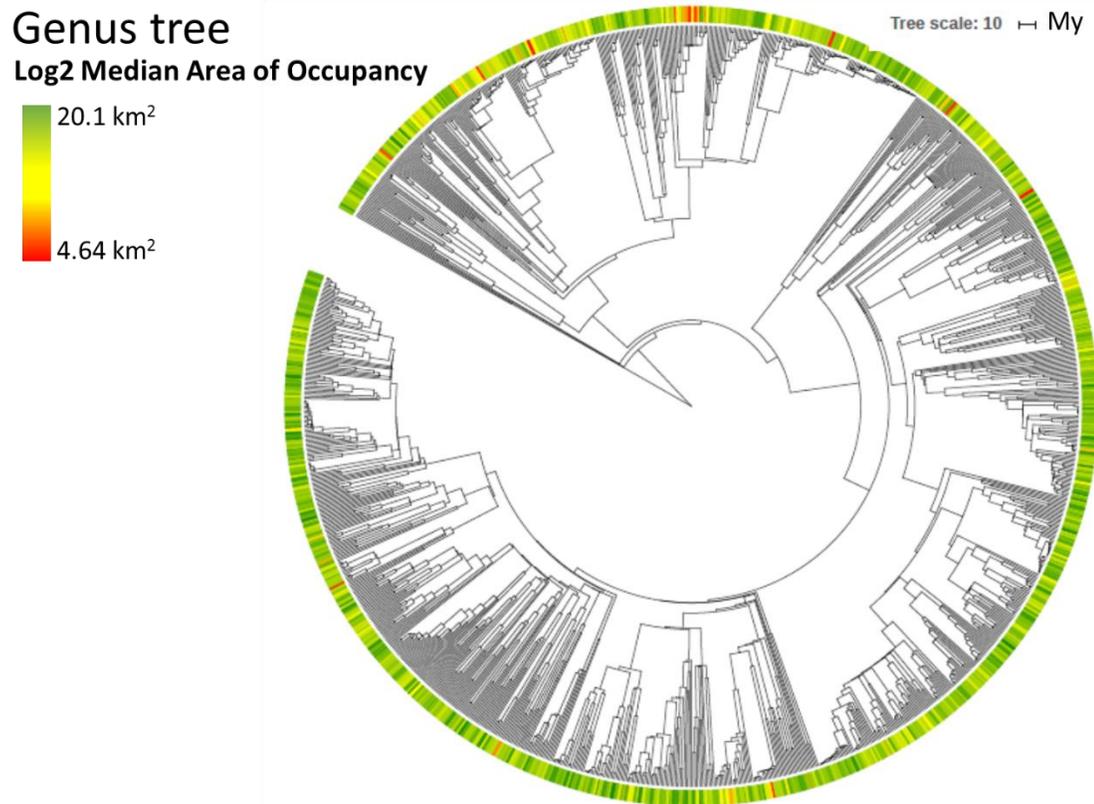


Figure S1. Phylogenetic tree containing 1,481 genera (placed at the tip) used in our phylogenetic analyses. See the attached pdf file with a full resolution version of this tree, which allows for zooming.

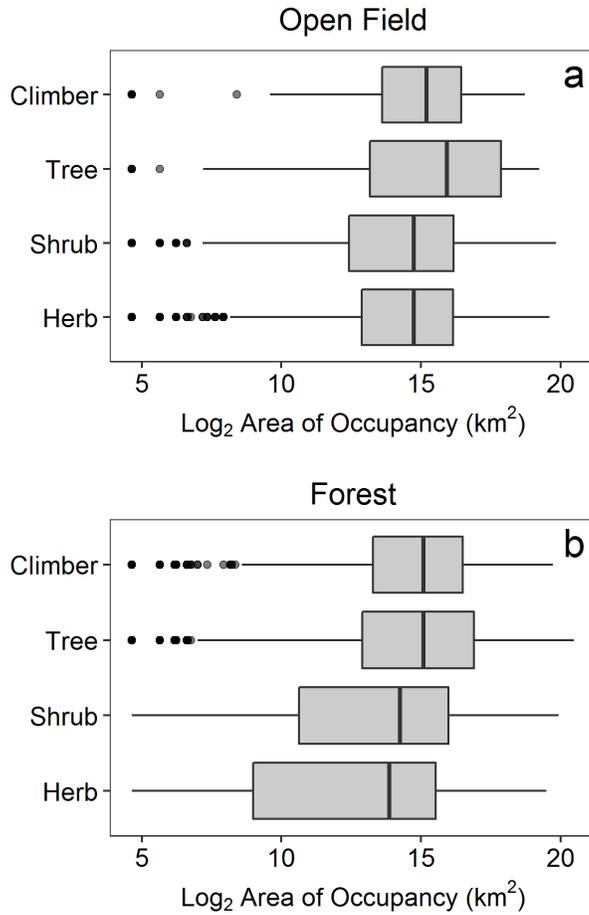


Figure S2. Area of occupancy among life forms in two contrasting vegetation types: open fields (a) and forests (b). The contrast allows visualizing the smaller area of occupancy of herbs in forest as compared to open fields.

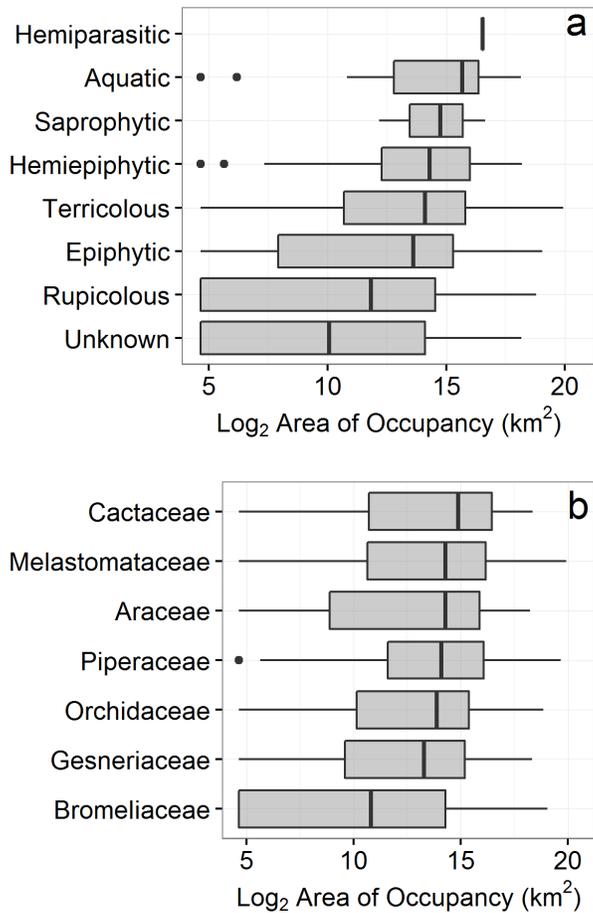


Figure S3. Distribution of species' area of occupancy across habitats when including only major epiphytic families (a), and distribution of species' area of occupancy across these families (b).

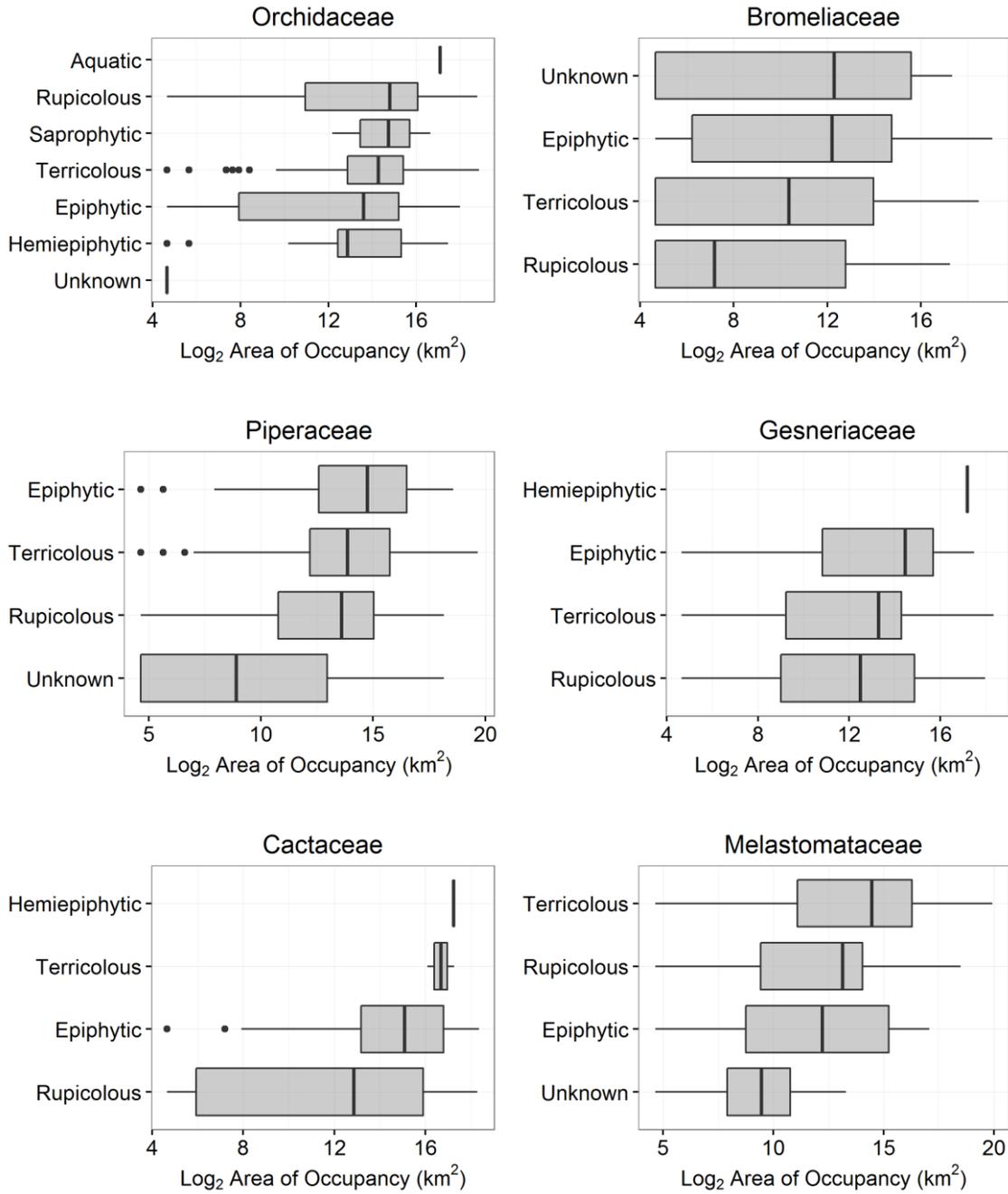


Figure S4. Distribution of species' area of occupancy across habitats among the six families with most number of epiphytic species.

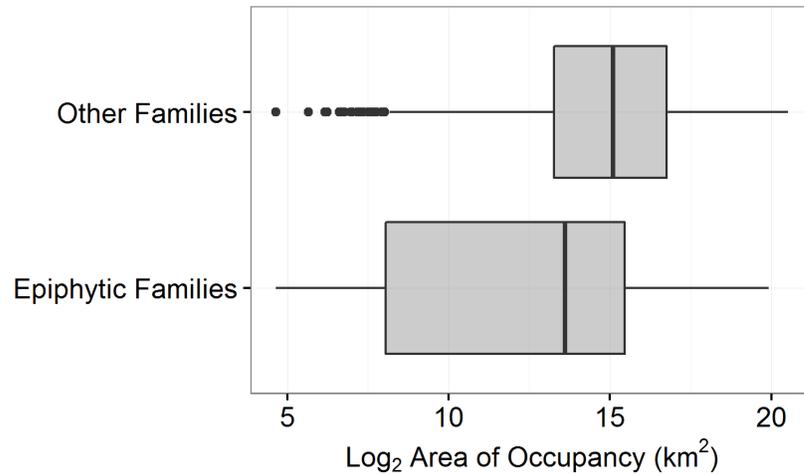


Figure S5. Distribution of species' area of occupancy on families with epiphytic species and on all other families. This contrast shows how families of epiphytes have much smaller species' area of occupancy than other families.

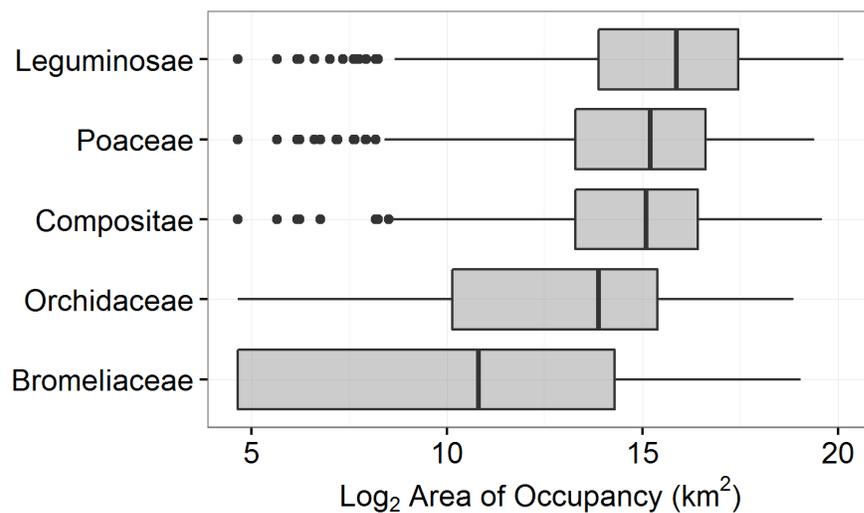


Figure S6. Distribution of species' area of occupancy among the five most species-rich families in the Atlantic Forest. Notice that the epiphytic families (Orchidaceae and Bromeliaceae) have much smaller areas of occupancy.

## Chapter 3

### **Projected impacts of climate and land use on the area of suitable habitat and potential range size of Atlantic Forest plant species<sup>5</sup>**

#### **Summary**

Responses to climate and land use changes vary across regions and species. Previous research suggest that both climate and land use changes may cause substantial reductions in species' geographic range sizes, including for tropical plants, although supporting evidence is limited. We gathered occurrences and estimated the geographic range size of thousands of plant species from the Atlantic Forest in Brazil to investigate how projected future climate and land use may affect species' area of suitable habitat and potential area of occupancy (i.e. a portion of the suitable habitat likely to be occupied) using predictions from habitat suitability modelling under a mitigation (RCP4.5 SSP2) and a business-as-usual (RCP8.5 SSP5) scenario for the year 2050. Our results suggest that climate change alone had modest impact on the mean species' area of suitable habitat, increasing it by 4% under the mitigation scenario (median = -2%) and by 9% under BAU (median = -0.1%). Land use alone had a more consistent and much stronger negative impact to the average species' area of suitable habitat, causing mean reductions of 10% under mitigation (median = -10%) and 33% under BAU (median = -33%). When combining the

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<sup>5</sup> This research was conducted in collaboration with Jason Reinhardt and Peter B. Reich.

effects of climate and land use, and constraining the suitable habitat to areas more likely to be colonized (i.e. a more realistic outcome), the mean species' potential area of occupancy was reduced by 7% under the mitigation scenario (median = -14%) and by 30% under BAU (median = -39%). Climate change was mainly responsible for the selective nature of the impacts, which were typically detrimental to rare and beneficial to widespread species. Epiphytes stood out as the ecological group with largest predicted losses in suitable habitat, while aquatic species were associated with largest gains from climate change and smallest losses from land use change. Overall, these results should be interpreted with caution, as our models have important limitations, including those inherent to many habitat suitability modelling techniques. This study suggests that future climate and land use may reduce the area of suitable habitat for many species ('losers') and increase for few species ('winners'), likely aggravating the undergoing homogenization of plant communities.

## **Introduction**

Projected impacts of climate change on plant species vary across studies, regions and scenarios (Bellard et al. 2012). Often, projections are grim, pointing to substantial reductions in habitat suitability and species' range size (Bellard et al. 2012; Thomas et al. 2004; Thuiller et al. 2005b; Warren et al. 2018). Such conclusions build a general expectation that climate change will be highly detrimental to biodiversity. For instance, predictions for European plants suggested that species could lose on average 30% of their area of suitable habitat (Thuiller et al. 2005a) and more than 50% could become vulnerable to extinction under the assumption of no dispersal (Thuiller et al. 2005b). In a

global study, the proportion of plants predicted to lose at least 50% of their area of suitable habitat varied from eight to 67%, depending on the scenario for climate change (Warren et al. 2018).

There are few predictions focusing on tropical plants (Hannah et al. 2011), and they suggest such species are highly vulnerable to climate change (Colombo & Joly 2010; Colwell et al. 2008; Miles et al. 2004; Siqueira & Peterson 2003). For instance, studies focusing in Brazil predicted the potential range size would decline on average 50% on Cerrado trees (based on 162 species, Siqueira & Peterson, 2003) and 20-50% on Atlantic Forest trees (based on 38 species, Colombo & Joly, 2010). Such studies join others to support expectations that tropical species are as sensitive as temperate and boreal species to the effects of climate change (Wright et al. 2009). On the one hand, such high sensitivity of tropical species could be possible because they are already living near the upper limit of temperature in the planet (potentially reducing the amount of additional warming they can withstand), and they tend to be adapted to narrow ranges of environmental conditions (Wright et al. 2009). On the other hand, many tropical lineages evolved under global climatic conditions that were warmer than today and/or during ice-free periods of Earth history. Some projections, suggest that climate change has been and is going to continue to be substantially less important as a driver of biodiversity loss in tropical forests (more so than in any other ecosystem), particularly when compared to the impacts of land use change (see Fig. 1 in de Chazal & Rounsevell, 2009; Fig. 10.17 in O. Sala et al., 2005; O. E. Sala et al., 2000). If climate change can cause large losses of suitable habitat and yet be relatively less important than land use change, then the amount

of suitable habitat to be lost to the combination of climate and land use changes would potentially be extremely large.

Realistic predictions of future changes in species' area of suitable habitat and potential range size should include land use, in addition to climate change (de Chazal & Rounsevell 2009). Land use change alone was predicted to account for over 90% of the biodiversity loss in tropical forests between 1970 and 2050 (de Chazal & Rounsevell 2009; Sala et al. 2005). Land use is also a more immediate and hypothetically manageable threat than climate change. For example, establishing and enforcing a system of protected areas, and making urban and agricultural landscapes more "biodiversity friendly" are potential pathways to reduce the negative impacts of land use. In contrast, solutions to mitigate climate change encompass a reduction in the global emission of greenhouse gases, which is an action out of reach for local and regional decision makers.

There are many reasons why it is challenging to predict how tropical plant species will respond to future climate and land use. Changes in climate differ among regions, including changes in levels, timing and variation in temperature and rainfall, potentially leading to distinct ecological responses across the world (Walther et al. 2002). And responses to changes in temperature and precipitation vary considerably among species. Niche breadth and geographic range size seem partly responsible for differences in species' responses to climate change (Thuiller et al. 2005a). Species adapted to narrow niche spaces are particularly likely to lose habitat and unlikely to gain habitat as climate changes. The sets of environmental conditions required by environmental specialists are less likely to be available in the future sets of conditions. Species with small geographic

range also tend to be more vulnerable to extinction from climate change (Schwartz et al. 2006), because they are susceptible to lose larger portions of their occupied habitat due to changes in habitat suitability. Geographic range size is an indicator of the overall species' vulnerability to extinction, among other ecological and evolutionary processes, making it useful for applications in conservation and beyond (Gaston 2003; Gaston & Fuller 2009).

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, and with high specific leaf area) often seem to prevail over species with conservative traits (i.e. slow-growing, long-lived species; Carreno-Rocabado et al. 2016). Specifically, habitat fragmentation, a common and well-studied outcome of land use intensification in tropical forest regions, selects species that are tolerant to edge effects, changes in microclimate and other disturbances associated with fragmentation, leading to the proliferation of fast-growing and short-lived species (Laurance et al. 2006; Tabarelli et al. 2008), and the biotic homogenization of plant communities (Lôbo et al. 2011; Tabarelli et al. 2012).

Herein, we aim to provide novel evidence on the species-level responses of tropical plants to climate and land use changes, and test previous findings on the relative importance of climate and land use to the loss of plant habitat in the tropics. Specifically, we investigate how projected changes in climate and land use affect the area of suitable habitat and potential area of occupancy of 4,500 plant species from the Atlantic Forest in Brazil – a relatively well-known tropical flora. We include a larger number of species and/or larger variety of ecological groups (i.e. growth forms and habitat types) than previous studies focusing on tropical regions. We hypothesize that (1) projected climate

change is highly detrimental to species potential area of occupancy, as suggested by previous investigation (e.g. Colombo & Joly 2010; Colwell et al. 2008; Miles et al. 2004; Siqueira & Peterson 2003); and (2) projected land use change will cause substantially larger losses of suitable habitat than projected climate change (de Chazal & Rounsevell 2009; Jetz et al. 2007; Sala et al. 2005; Sala et al. 2000). In addition, we investigate potential underlying reasons for differences in species response to climate and land use changes. Specifically, we tested expectations that species with smaller range sizes are more negatively affected by climate change (Schwartz et al. 2006; Thuiller et al. 2005a), and that there are differences in responses among growth forms and habitat types, which are relevant to understand geographic range size and extinction risk in the region (Leão et al. 2014; Leão & Reich 2018).

## **Methods**

### *Plant occurrences*

We compiled occurrences of Atlantic Forest angiosperms within South America boundaries (excluding islands) through the Species Link Network ([www.splink.org.br](http://www.splink.org.br), see the list of herbaria providing records in the supplementary material). The dataset includes only species occurring in the Atlantic Forest of Brazil, according to Brazilian Flora 2020 ([floradobrasil.jbrj.gov.br](http://floradobrasil.jbrj.gov.br)). Occurrences dated before 1960 or without date of collection were removed to avoid temporal mismatch with climate data. The resulting occurrence dataset includes 754,000 unique species-year-coordinate records of 12,800 species.

### *Environmental data*

The environmental data initially included the following predictors: (1) 19 bioclimatic variables derived from ‘current’ climate (representative of 1960-1990) at 5 minutes spatial resolution (approximately 9 km at the equator, WorldClim v.1.4, Hijmans et al. 2005); (2) 119 predicted soil attributes from SoilGrids with 1 km spatial resolution (Hengl et al. 2014); and (3) an elevation mosaic of SRTM images with 90 meters spatial resolution (Jarvis et al. 2008). We then verified the correlation among all these variables within South America boundaries, and selected the predictors deemed most directly relevant to plant occurrence and with Pearson correlation below 0.8. There were particularly high correlations among soil attributes at varying depths; when those were correlated above our 0.8 threshold, we kept the ones closer to the surface. Given this variable selection process, 22 predictors were retained and used in the modelling stage (Table S1).

Table S1. Environmental predictors included in the modelling. Sources: elevation (Jarvis et al. 2008), bioclimatic (Hijmans et al. 2005), and soil predictors (Hengl et al. 2014).

Code name	Description
Elevation	Elevation SRTM 90m
Bio1	Annual Mean Temperature
Bio2	Mean Diurnal Range (Mean of monthly (max temp - min temp))
Bio4	Temperature Seasonality (standard deviation *100)
Bio12	Annual Precipitation
Bio15	Precipitation Seasonality (Coefficient of Variation)

Bio17	Precipitation of Driest Quarter
Bio18	Precipitation of Warmest Quarter
Bio19	Precipitation of Coldest Quarter
OCSTHA_M_30cm_1km_ll	Soil organic carbon stock in tons per ha for depth interval 0.00 m - 0.30 m
SNDPPT_M_sl1_1km_ll	Sand content (50-2000 micro meter) mass fraction in % at depth 0.00 m
SLTPPT_M_sl1_1km_ll	Silt content (2-50 micro meter) mass fraction in % at depth 0.00 m
CLYPPT_M_sl1_1km_ll	Clay content (0-2 micro meter) mass fraction in % at depth 0.00 m
BLDFIE_M_sl1_1km_ll	Bulk density (fine earth) in kg / cubic-meter at depth 0.00 m
CECSOL_M_sl1_1km_ll	Cation exchange capacity of soil in cmolc/kg at depth 0.00 m
CRFVOL_M_sl1_1km_ll	Coarse fragments volumetric in % at depth 0.00 m
BDTICM_M_1km_ll	Absolute depth to bedrock (in cm)
BDRLOG_M_1km_ll	Probability of occurrence (0-100%) of R horizon
AWCh1_M_sl1_1km_ll	Available soil water capacity (volumetric fraction) for h1
WWP_M_sl1_1km_ll	Available soil water capacity (volumetric fraction) until wilting point
HISTPR_1km_ll	Cummulative probability of organic soil
SLGWRB_1km_ll	Sodic soil grade based on WRB soil types and soil pH

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### *Future climate*

Future climate conditions were derived from the projections of the earth system model HadGEM2-ES, and the derived bioclimatic variables were used to assess the effects of climate change in year 2050 (average for 2041-2060, Figure S1) on two representative

concentration pathways (RCP4.5 and RCP8.5; WorldClim v.1.4, Hijmans et al. 2005). The scenarios represents two possible futures for greenhouse gas emissions and land use (Moss et al. 2008). RCP4.5 is a mitigation scenario where the radiative forcing stabilizes around 2100; it assumes human societies will make an active effort to reducing greenhouse gas emission through increasing the contribution of non-fossil energy sources and mitigating emission from land use (Thomson et al. 2011). RCP8.5 is a high emission scenario ('business as usual'), where 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).

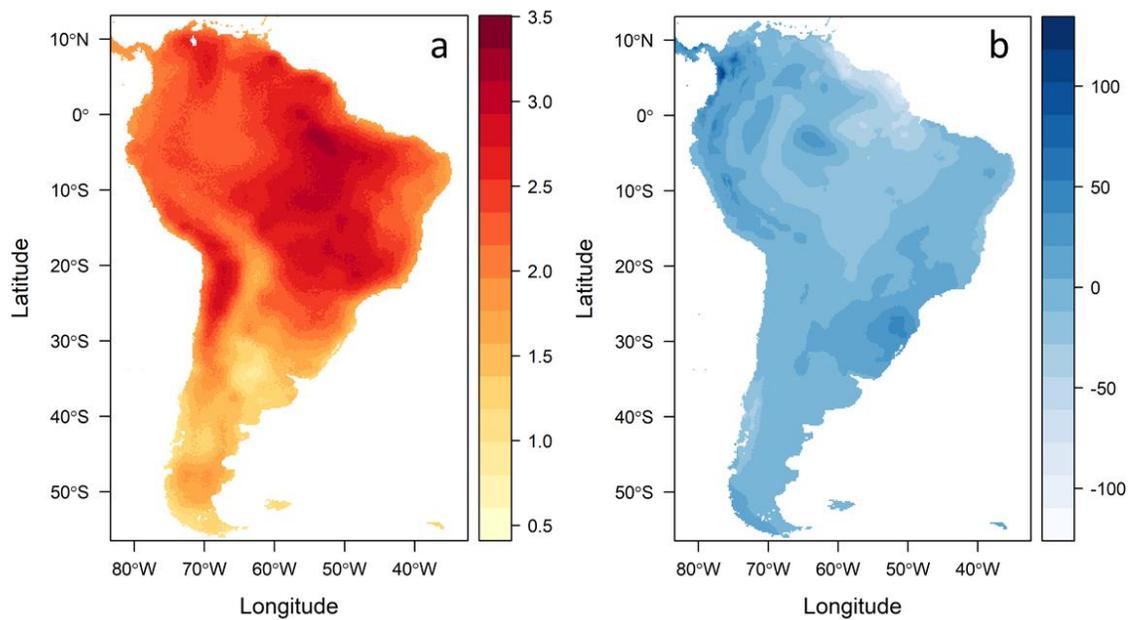


Figure S1. Predicted change in annual mean temperature (°C, a) and annual precipitation (mm, b), calculated as the difference between year 2050 under the mitigation scenario (RCP4.5) and the observed average from 1960-1990.

## *Land use*

Land use for current (2015) and future (2050) were obtained from the land use harmonization LUH2 v2f, which describes the fraction of 0.25 x 0.25 degree grid cells occupied by each of the 12 land use states (Hurtt et al. in prep, luh.umd.edu). We used the projections RCP4.5 SSP2 from MESSAGE-GLOBIOM and RCP8.5 SSP5 from REMIND-MAGPIE (Hurtt, Chini, Sahajpal, Frohking, & others, *in prep*, luh.umd.edu), as representatives of a ‘mitigation’ scenario and a ‘business-as-usual’ scenario (or BAU), respectively. These land use scenarios were built based on narratives for potential future development pathways, which are known as Shared Socioeconomic Pathways (or SSP, Popp et al. 2017; Riahi et al. 2017). The proportion of land use states on each grid cell were then used to estimate the percentage of habitat for native plant species (Figure S2). Cells with less than 10% of habitat were considered unsuitable and applied as a mask over the raster output from the habitat suitability modelling. The calculation of the percentage of plant habitat was based on the equation:

$$habitat\% = primf + primn + .5 * secdf + .5 * secdn + .25 * rangeland$$

where primf: forested primary land, primn: non-forested primary land, secdf: potentially forested secondary land, and secdn: potentially non-forested secondary land. For example, if only one of these five habitat types occurred in the grid cell, it would be necessary to cover at least 10% of primary land, 20% of secondary land or 40% of rangeland to not be classified as unsuitable habitat. The threshold of 10% for the amount

of habitat in the landscape is a conservative estimate, given the 20-30% threshold necessary to the persistence of some species (Fahrig 2003; Joly et al. 2014).

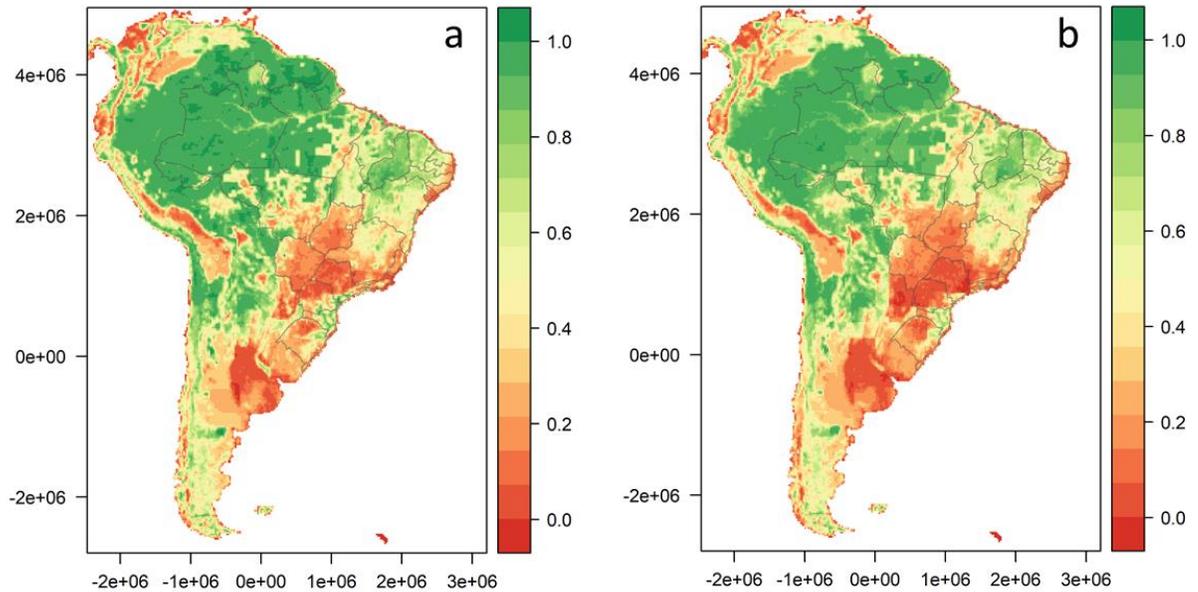


Figure S2. Proportion of plant habitat suitability according to the land use scenarios under the mitigation scenario (i.e. RCP4.5 SSP2) in 2015 (a) and 2050 (b). Refer to the methods for details on how the proportion of plant habitat was calculated (section *Land use*).

### *Geographic range size*

Estimates of observed area of occupancy were obtained from Leão and Reich (2018), according to the 5-to-50 km sliding scale (adapted from Willis et al. 2003).

### *Habitat suitability modelling*

Only species with 15 or more unique locations had their habitat suitability modeled. For each species, we generated background points (“pseudo-absences”) randomly distributed over South America at a number 10 times larger than then number of observed unique

locations (Hijmans & Elith 2017). Each species had their occurrences and background points distinguished into five randomly assigned folds, thus we could run a 5-fold cross validation (James et al. 2013). Five models were generated for each species based on a training data set (80% of the data) and evaluated using a test data set (20% of the data). We extracted values for each of the 22 environmental predictors at each location of observed occurrence and background points, and used those as predictors in random forests regression (James et al. 2013; Liaw & Wiener 2015). The models generated (1) continuous predictions of habitat suitability for each species on grid cells with 5' resolution and extending to entire South America, which were then (2) projected into a raster using the South America Albers Equal Area Conic projection and 10 km spatial resolution; and (3) converted into binary suitability by applying a threshold based on the maximum sum of specificity and sensitivity, as recommended by Liu et al. (2005) and Jiménez-Valverde and Lobo (2007). Our modelling approach used tools available in available in R (version 3.4.3, R Core Team 2017) through the packages “raster” (Hijmans 2017), “dismo” (Hijmans et al. 2017), “sp” (Bivand et al. 2013), “rgdal” (Bivand et al. 2017), “randomForest” (Liaw & Wiener 2015), “foreach” (Revolution Analytics & Weston 2015), and “doParallel” (Microsoft Corporation & Weston 2017).

### *Species' potential area of occupancy*

The species' potential area of occupancy is the area of suitable habitat located in the proximity of the observed occurrences. Each species had its proximity buffer with a radius of 1/5 of the maximum distance among observed occurrences (Figure S3). With this metric we expect to get more realistic predictions (though certainly not accurate for

all) of areas that the species can potentially occupy, given that the species might already occur in the surroundings of known occurrences. It seems reasonable that the size of this proximity buffer depends on the species range extent, a metric inspired in the sliding scale applied for estimating area of occupancy (Moat 2007; Willis et al. 2003). For the sake of simplicity, we estimated the potential area of occupancy only for the combined effects of climate and land use change, which shows the most realistic outcome.

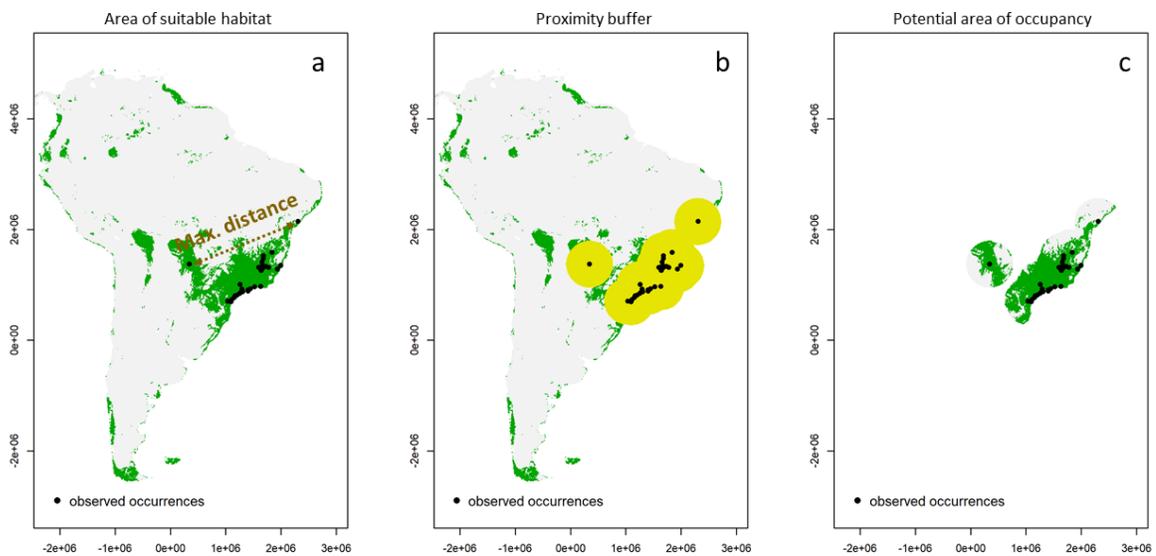


Figure S3. To estimate the species' potential area of occupancy we (a) calculated the maximum distance between observed occurrences, (b) created buffers around each occurrence with radius of 1/5 of the maximum distance, and (c) removed areas of suitable habitat that were outside the buffer. The buffer radius in this figure has 420 km.

### *Projections into future*

We used the bioclimatic variables derived from future scenarios (year 2050, either RCP4.5 or RCP8.5) as predictors of the same random forest model developed for

estimating current area of suitable habitat. The binary suitability maps were generated based on a threshold based on the maximum sum of specificity and sensitivity (Jiménez-Valverde & Lobo 2007; Liu et al. 2005). We then applied the land use masks and proximity buffers to estimate the independent effects of climate and land use changes on the species' area of suitable habitat and species' potential area of occupancy (see details on Figure S4).

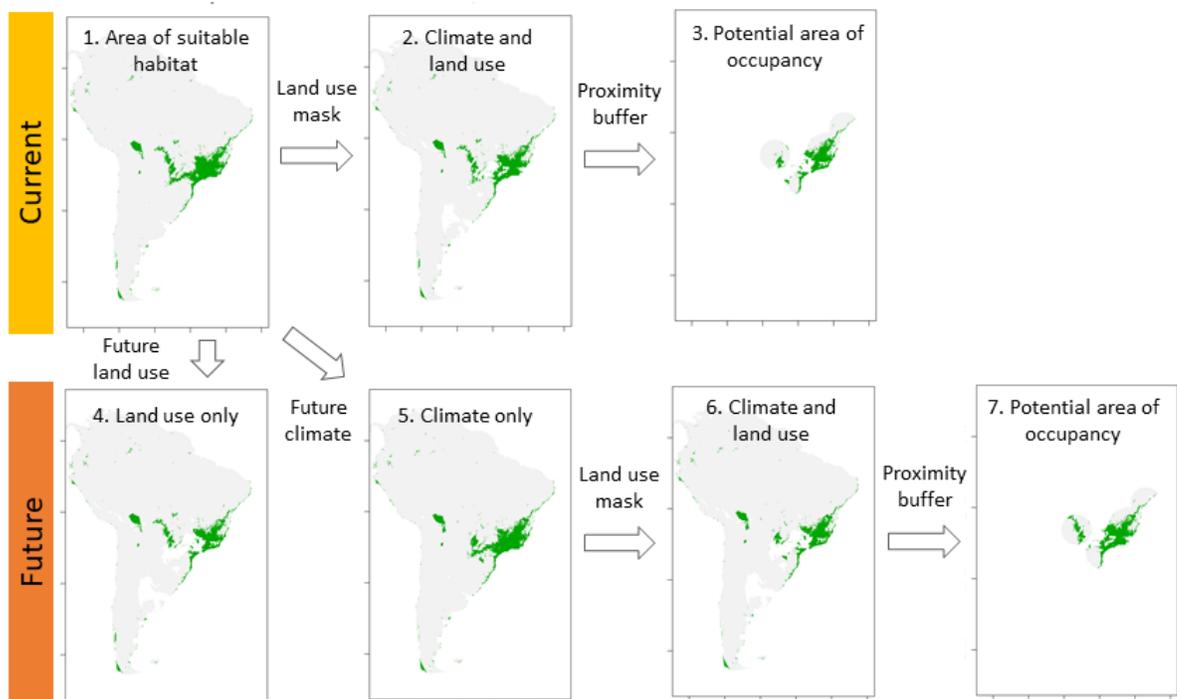


Figure S4. Steps followed to observe the effects of climate and land use change on area of suitable habitat, and to estimate the species' potential area of occupancy.

#### *Area estimates*

The resulting raster map had equal area projection with square grid cells of 10 km width (100 km<sup>2</sup> per cell). Thus, the area estimates were obtained by summing the area of the

cells predicted to be suitable habitat in each of the seven situations described in Figure S4. The area used in the analysis were the mean of the three intermediate cross-validated estimates (i.e. excluding the lowest and highest area estimates generated in the 5-fold cross validation).

### *Model evaluation and selection*

We applied strict criteria to selecting models for inference. We made inference only for species in which (1) the potential area of occupancy varied no more than 70% on average (among the three intermediate cross-validated models) both on current and future projections, (2) the models had average AUC equal or larger than 0.8 (considered good or excellent, Araujo et al. 2005), and (3) average pseudo R-squared of at least 25%. With such criteria, we hope to have excluded unreliable predictions due to high variance in area estimates, poor model fit and low explained variance. Inferences were made on mean area estimates for 4,571 species, which were averaged from the three intermediate cross-validated estimates on each species, and analyzed with ordinary least square regressions. Figures were built with R package “ggplot2” (Wickham 2016).

## **Results**

Projected climate and land use changes showed distinct impacts on future species’ area of suitable habitat. Climate change had a more variable impact on species’ area of suitable habitat (Figure 1). When projecting climate change alone, and keeping land use constant, the mean species’ area of suitable habitat increased by 4% under the mitigation scenario (RCP4.5, median = -2%, min. = -64%, max. = 137%) and increased by 9% under BAU

scenario (RCP8.5, median = -0.1%, min. = -67%, max. = 164%). Even though the mean effect was positive, most species were negatively affected by climate change, as shown by the negative median. Land use had a more negative and consistent impact on species' area of suitable habitat. When projecting land use change alone, and keeping climate constant, the mean species' area of suitable habitat was reduced by 10% under the mitigation scenario (SSP2, Figure S4-4, median = -10%, min. = -36%, max. = 4%) and reduced by 33% under the business-as-usual scenario (henceforth BAU, SSP5, median = -33%, min. = -94%, max. = 0.5%). The combined effects of climate and land use change caused a mean reduction in the species the species' area of suitable habitat of 4% under mitigation (RCP4.5 SSP2) and 21% under BAU (RCP8.5 SSP5).

Of course, projected increases in the species' area of suitable habitat do not mean the species are going to occupy it, particularly because the suitable habitat might be too far away from species' occurrences. To get a better sense of the species' 'potential' area of occupancy, we created an additional metric excluding the areas of suitable habitat that were deemed too far away (i.e. more than 1/5 of the maximum distance among occurrences) from observed occurrences and unlikely to be occupied (Figure S3). This metric suggests the combined effects of climate and land use change would reduce the species' potential area of occupancy by 7% under mitigation (median = -14%) and 30% under BAU (median = -39%). The species' potential area of occupancy, as opposed to the species' area of suitable habitat, allows a more realistic visualization of the resulting effects of climate and land use and enables a more practical applicability for conservation, thus it is often our focus of inference.

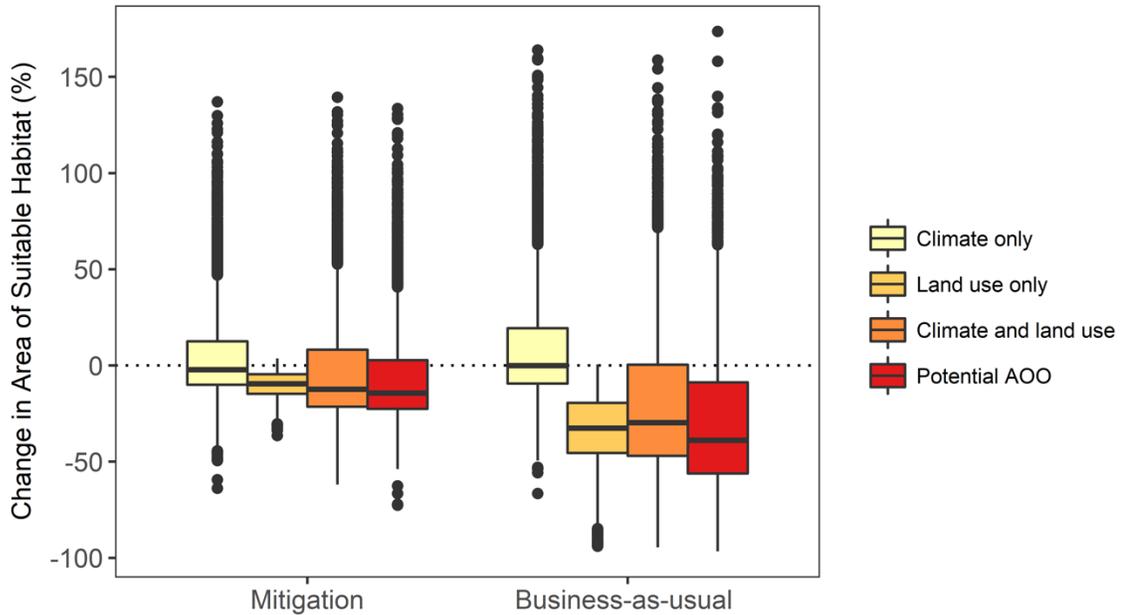


Figure 1. Box plot of the effects of climate and land use on the species’ area of suitable habitat in the two scenarios for climate and land use change at year 2050. Potential area of occupancy (AOO) takes into account the effects of climate and land use, and exclude areas considered too far away from observed occurrences. Lines inside the boxes show median effects.

Projected climate and land use changes generated more losers than winners. Future potential area of occupancy was at least 10% smaller for 59% of the species under mitigation and for 74% of the species under BAU. In contrast, future potential area of occupancy was at least 10% larger for only 19% of the species under mitigation and 15% of the species under BAU. Specifically, few species gained very large areas of suitable habitat – mostly due to projected increases in climate suitability –, while the majority of the species lost substantial amounts of suitable habitat (Figure 2).

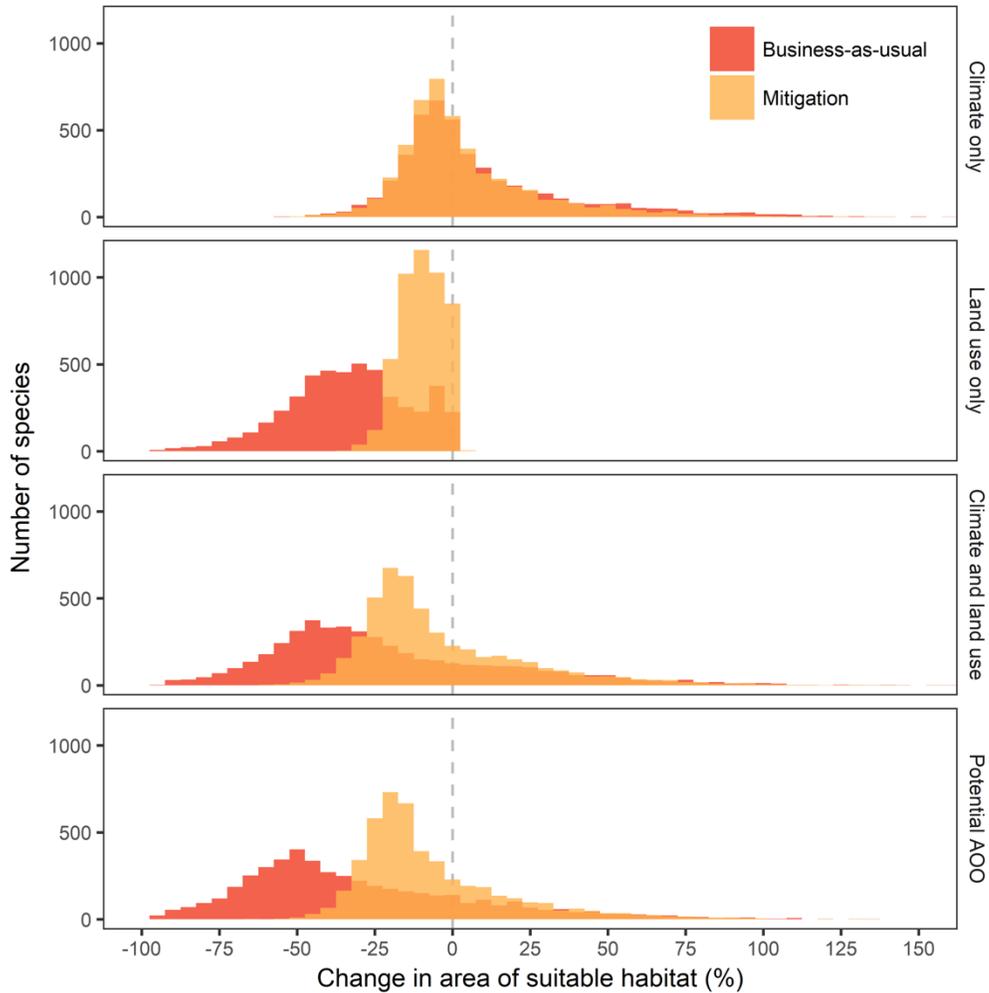


Figure 2. Frequency distribution of percent change (year 2050 - current) in the area of suitable habitat under mitigation (RCP4.5 SSP2) and business-as-usual (RCP8.5 SSP5), and by effects.

Changes in potential area of occupancy were directly dependent on the observed area of occupancy. Species with smaller area of occupancy lost larger percentages and larger absolute areas of suitable habitat (Figure 3). An increase in 100,000 km<sup>2</sup> was associated with an average 8.5 percent point larger potential area of occupancy. Species with area of occupancy below 200,000 km<sup>2</sup> (i.e. 76% of the species) were predicted on

average to lose some potential area of occupancy under the mitigation scenario. Species with the 10% smallest area of occupancy (i.e.  $< 42,500 \text{ km}^2$ ) were predicted on average to lose 17% of their potential area of occupancy under mitigation, and lose 44% under BAU. On the other end of the spectrum, species with the 10% largest areas of occupancy (i.e.  $> 350,000 \text{ km}^2$ ) were predicted on average to expand by 10% their potential area of occupancy under mitigation and contract by 6% under BAU. This shift among the species with largest range sizes from an average expansion under the mitigation scenario to an average contraction under BAU highlights the extreme negative impact of the BAU scenario – mainly due to negative effects of projected land use.

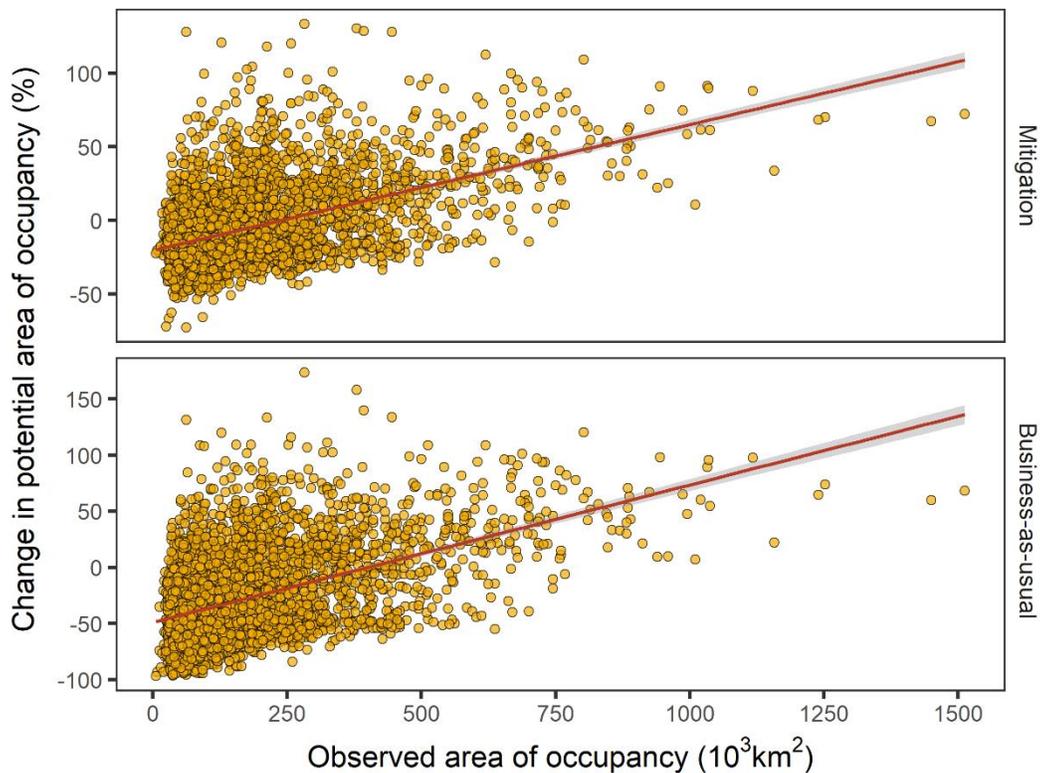


Figure 3. Relationship between observed area of occupancy and projected percent change in species' potential area of occupancy under two scenarios for climate and land use change.

The strong relationship between species' area of occupancy and percent change in area of suitable habitat was driven mainly by climate change ( $R^2 = .28$ ,  $t$ -value = 43,  $p$ -value =  $<2e-16$ , mitigation scenario), and just a little by land use change ( $R^2 = .01$ ,  $t$ -value = 6.5,  $p$ -value =  $1e-10$ , mitigation scenario; Figure 4). The impact of climate change was positively and strongly related to species' area of occupancy. This was true whether the impact was measured as percent change (Figure 4) or absolute change (Figure S5) in species' area of suitable habitat. Thus, the effects of climate change were contrasting between rare and widespread species, being mostly detrimental for the former and mostly beneficial for the latter. The impact of land use change on species' area of suitable habitat was positively and weakly related to species' area of occupancy when measured as percent change in area (Figure 4). However, it was negatively and strongly related to area of occupancy when measured as absolute change (Figure S5). Species with larger area of occupancy lost larger amounts of suitable habitat due to land use change. The impact of land use change was thus less selective, reducing the area of suitable habitat more or less proportionally to species' range size.

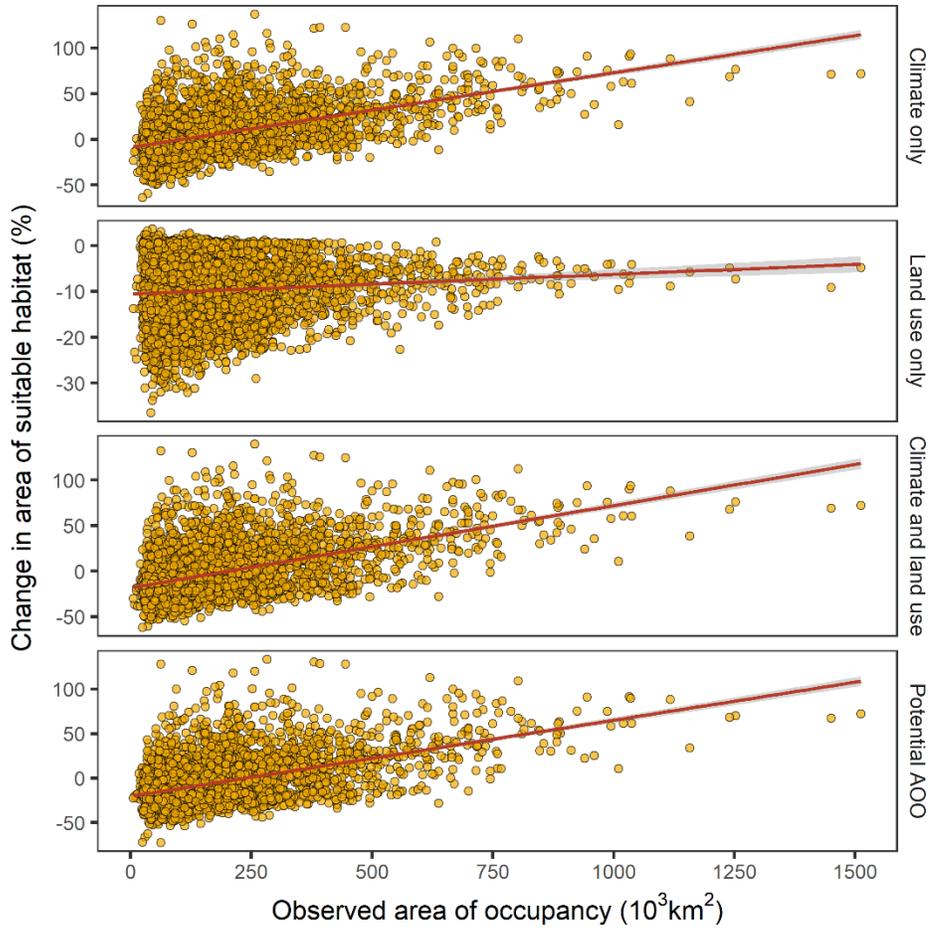


Figure 4. Relationship between observed area of occupancy and percent change in species' area of suitable habitat discriminated by the effects of climate change, land use change, combined climate and land use change, and restricting area of suitable habitat to potential area occupancy under the mitigation scenario.

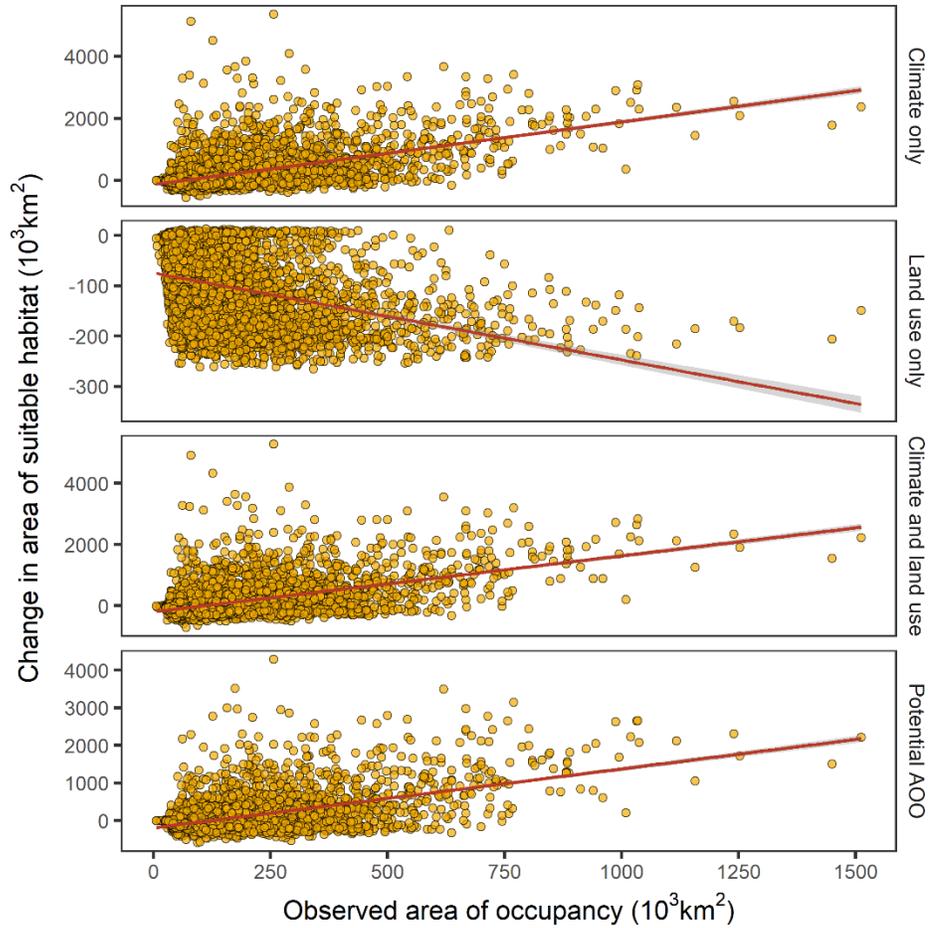


Figure S5. Relationship between observed area of occupancy and change in species' area of suitable habitat as projected if there was only change in climate, only change in land use, combined climate and land use change, and restricting area of suitable habitat to potential area of occupancy under the mitigation scenario. Notice that the y-axes show changes in absolute values, which is different from the proportional values in Figure 4.

Overall, rare species were predicted to lose larger proportions of their potential area of occupancy. Among the species with the 25% smallest observed area of occupancy, 71% were predicted to lose at least 10% their potential area of occupancy in the mitigation scenario. In the same group, only 4% were predicted to gain 10% or more

of potential habitat (Figure 5). In contrast, among the species with the 25% largest area of occupancy, 30% were predicted to lose at least 10% their potential habitat, while 50% were predicted to gain 10% or more of potential habitat under mitigation (Figure 5).

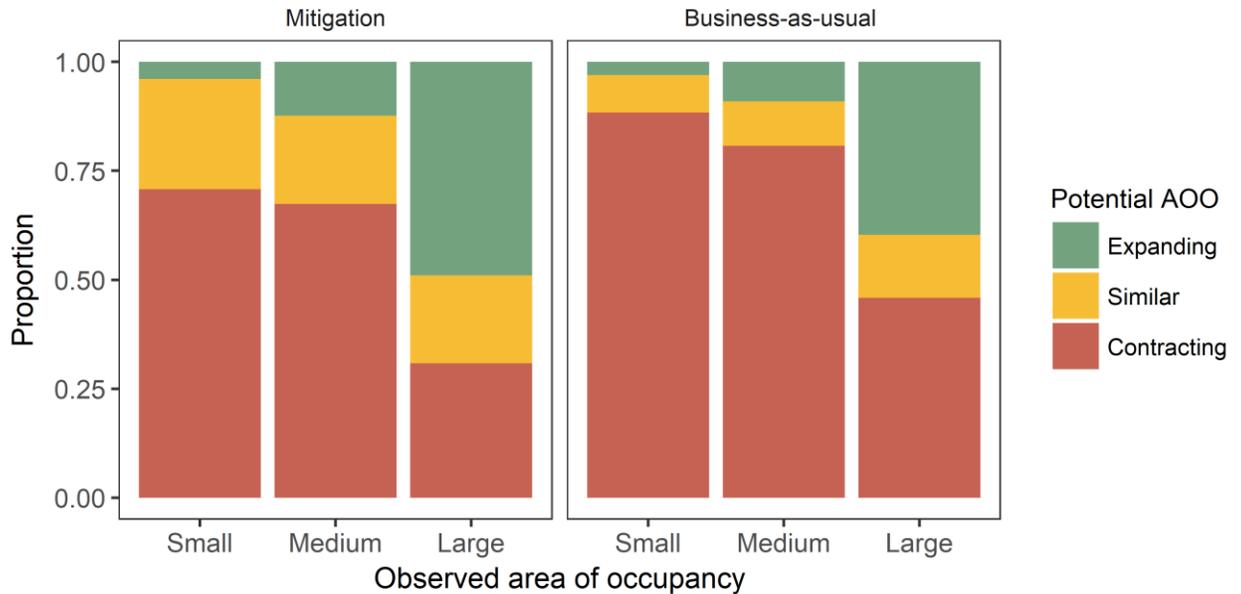


Figure 5. Proportion of species with potential area of occupancy expected to expand (at least 10% larger), remain similar (between 10% decrease and 10% increase) or contract (at least 10% smaller) under two scenarios of climate and land use changes. Species were grouped by observed area of occupancy into small (smaller 25%), medium (intermediate 50%) and large (largest 25%).

The large variation in the impacts of climate and land use has important implications for those species with largest deviations from predicted averages. In particular, the species losing largest proportions of their suitable habitat may become under extinction threat. In this sense, there was a striking difference between the mitigation and the BAU scenario (Figure 6). In the mitigation scenario, less than 1% of

the species lost 50% or more of their potential area of occupancy, while in the BAU scenario that increased to 35%. This effect was driven mainly by land use change, thereby emphasizing the importance of land use choices to the species' extinction risk.

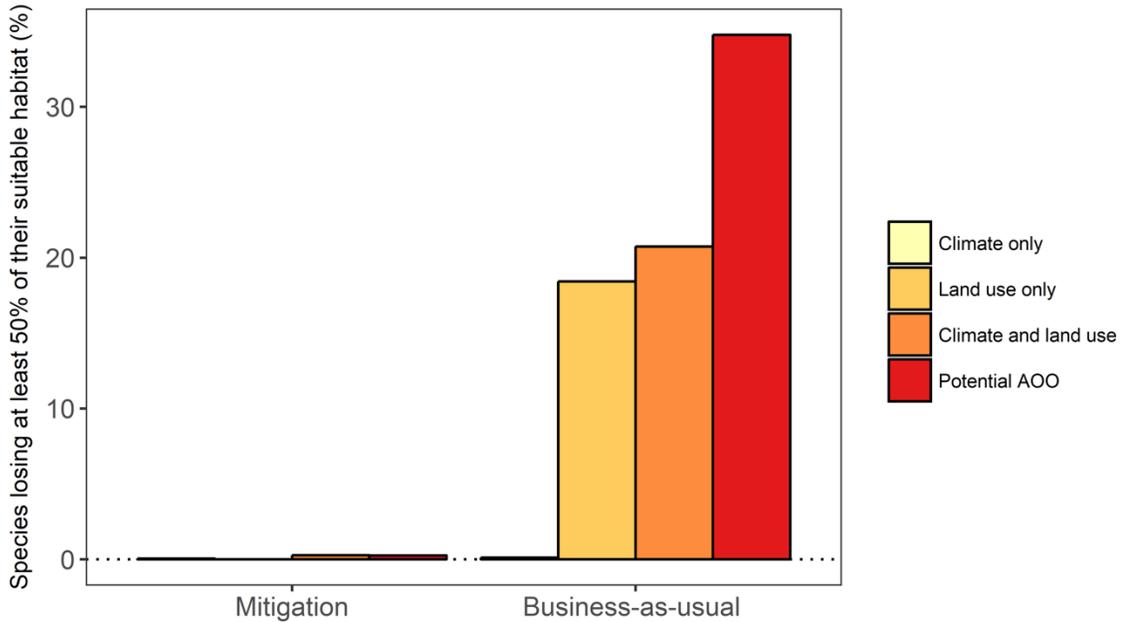


Figure 6. Percentage of species losing more than 50% of their area of suitable habitat in two scenarios. Effects were discriminated as if there was only climate change, only land use change, combined climate and land use changes, and removing areas unlikely to be occupied (i.e. potential area of occupancy).

### *Ecological groups*

Predicted changes in potential area of occupancy differed among ecological groups (Table 1). Epiphytes showed largest losses in potential area of occupancy, while aquatic species showed largest gains. That epiphytes have the smallest average potential area of occupancy (current and future, Figure 7) and the largest absolute and proportional losses in potential area of occupancy (Figure 8 and Figure 9), make them particularly sensitive

and vulnerable to future changes in climate and land use. Epiphytic species were predicted on average to lose 17% of their current potential area of occupancy under mitigation and lose 47% under BAU. In contrast, aquatic species were predicted on average to gain 8% of their potential area of occupancy under mitigation and lose 3% under BAU (Table 1). With the exception of aquatic species, most species in other habitat categories were predicted to lose potential area of occupancy. Because of the species gaining large areas of potential area of occupancy, most habitats showed average absolute gains under mitigation (Figure 9). However, this changed drastically under BAU, when all habitat groups (except aquatic) showed average loss in absolute areas (Figure 9). These illustrate the severe negative impacts of the BAU scenario, offsetting most gains projected under the mitigation scenario.

Table 1. Percentage change in species' potential area of occupancy by habitat and scenario.

Habitat	N	Mitigation					Business-as-usual				
		Mean	Median	SD	Min.	Max.	Mean	Median	SD	Min.	Max.
Epiphyte	337	-16.8	-18.5	14.0	-52.5	70.7	-46.5	-50.6	23.1	-92.1	77.9
Rupicolous	250	-8.6	-16.5	24.5	-53.9	128.0	-34.1	-44.4	38.7	-95.6	133.9
Hemiepiphyte	48	-9.8	-12.7	17.8	-36.0	46.2	-35.0	-43.6	30.0	-96.4	50.0
Terricolous	3754	-6.7	-14.3	24.8	-72.6	133.6	-29.5	-38.7	37.9	-96.7	173.6
Hemiparasite	41	0.8	-2.6	25.8	-38.5	64.0	-18.3	-23.9	36.7	-92.7	63.7
Aquatic	141	7.7	1.5	32.3	-46.2	128.2	-3.1	-9.6	44.4	-89.9	133.6

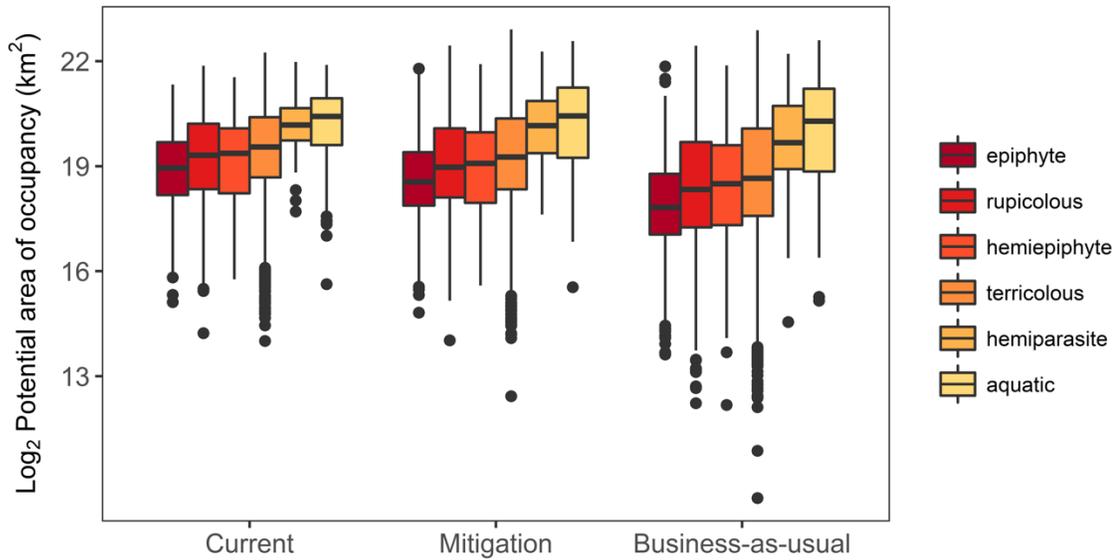


Figure 7. Box plot of the species' potential area of occupancy (log-2 transformed) across habitat categories under current conditions and projected climate and land use in 2050 under mitigation and business-as-usual.

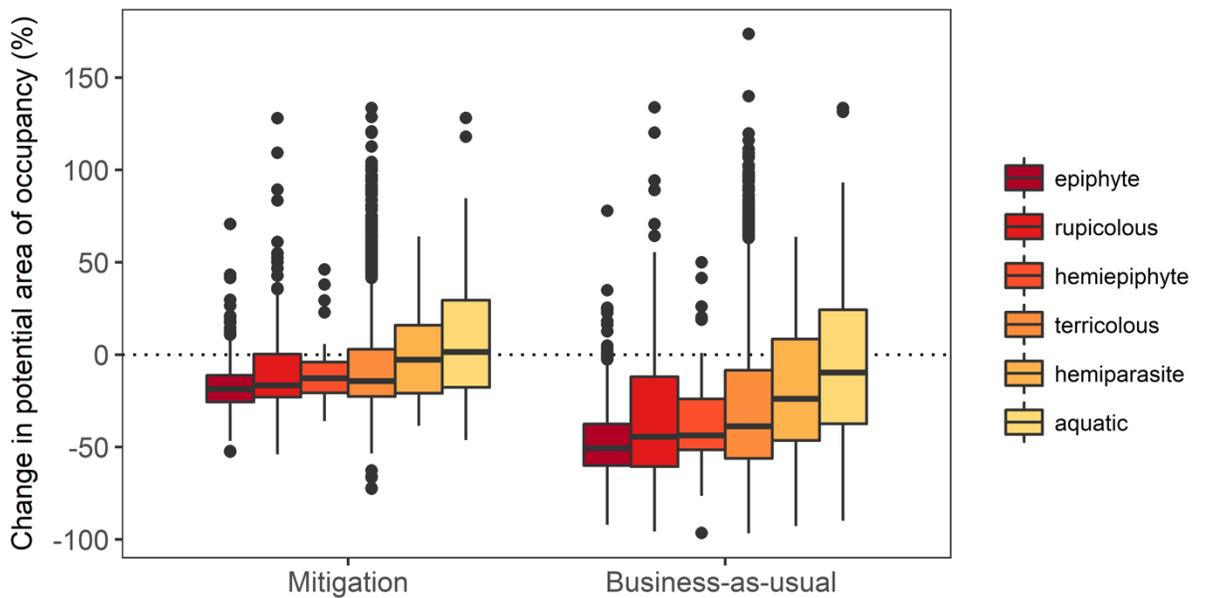


Figure 8. Percent change in species' potential area of occupancy across habitat groups in two scenarios for future climate and land use.

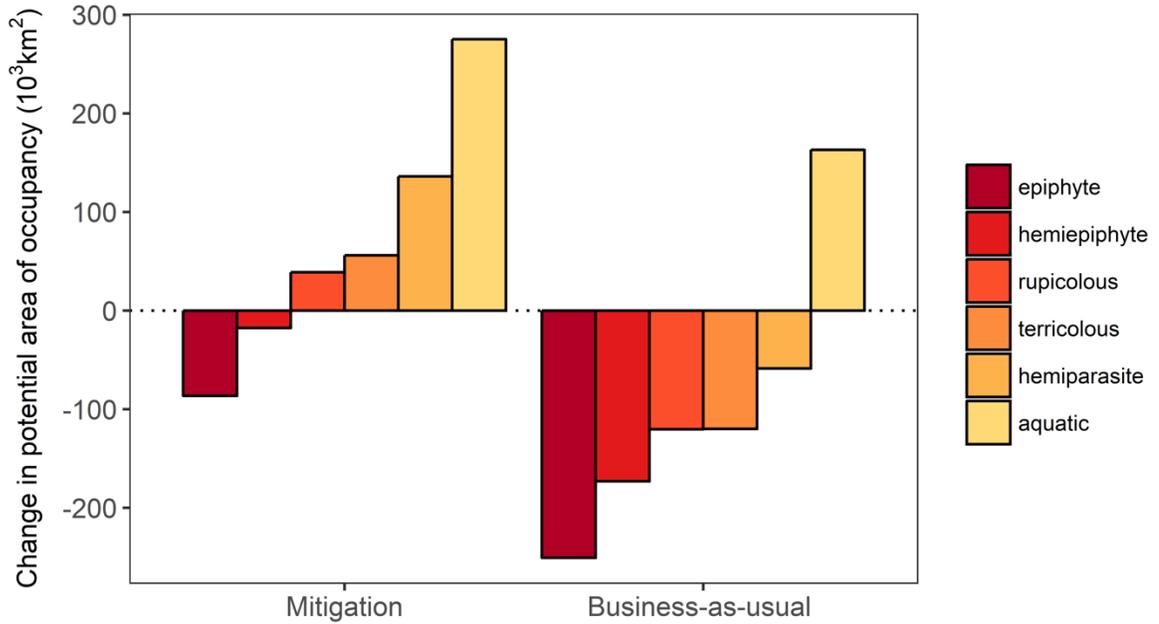


Figure 9. Mean change in species' potential area of occupancy across habitats and scenarios for climate and land use change in year 2050.

The main responsible for the sensitivity among habitat groups was climate change. Accordingly, epiphytes were the most negatively affected by climate change, while aquatic species were the most benefited (Figure S6, Figure S7). The effects of land use change were less distinct among habitat groups, although epiphytes still were associated with most negative impacts.

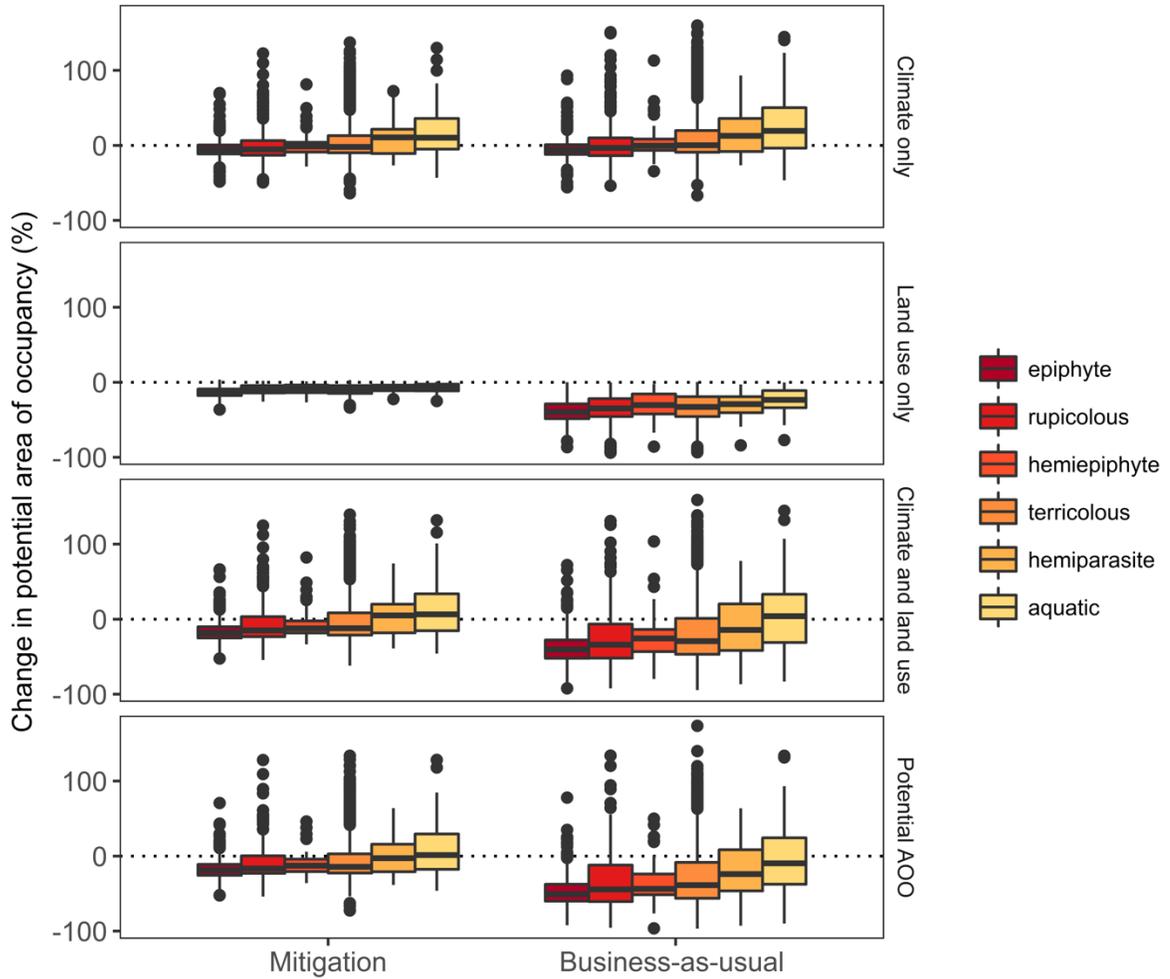


Figure S6. Percent change in species' potential area of occupancy across habitat groups in two scenarios for future climate and land use, discriminated by the effects of climate change, land use change, combined climate and land use change, and taking into account occupancy.

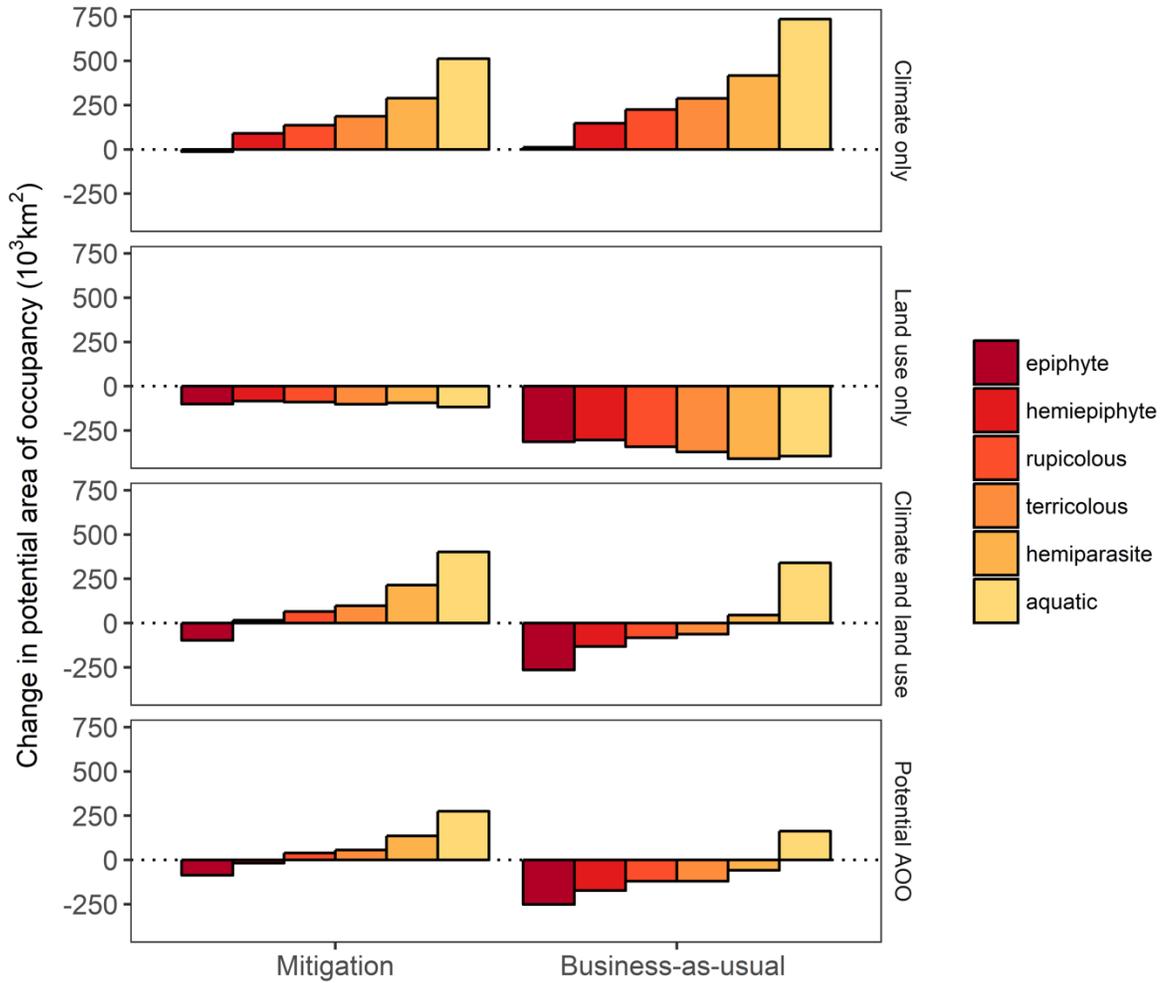


Figure S7. Mean change in species' potential area of occupancy across habitats and scenarios, discriminated by the effects of climate change, land use change, combined climate and land use change, and taking into account occupancy.

There were no differences in average sensitivity to climate and land use change among growth forms (Figure 10). However, growth form became substantially more important after controlling for confounding factors, suggesting it has a relevance to understand to understand species sensitivity (see details below and Table 2).

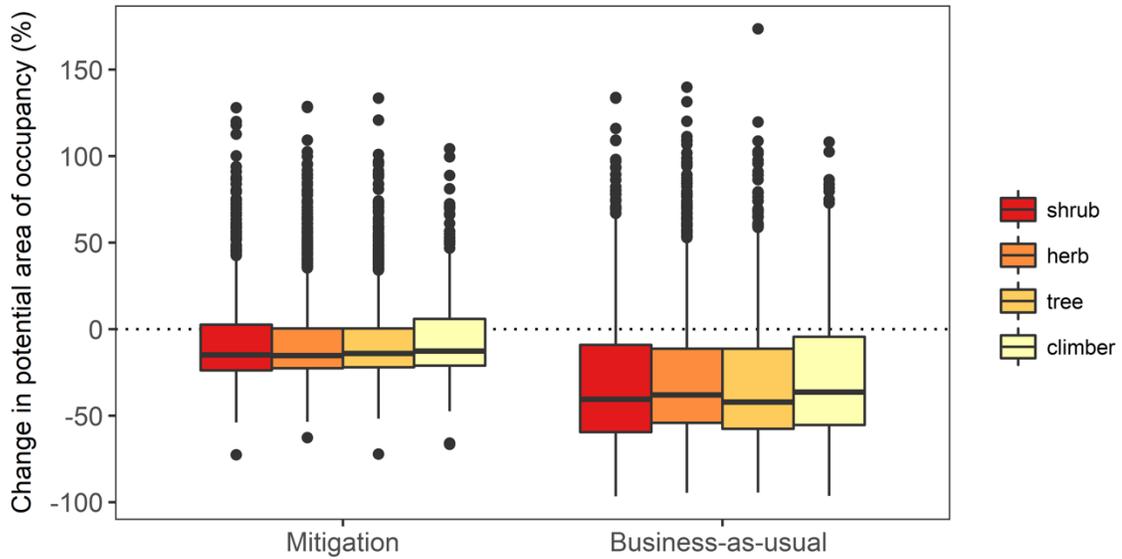


Figure 10. Percent change in species' potential area of occupancy across growth forms in two scenarios for future climate and land use.

#### *Modelling species' sensitivity*

To investigate whether the effects of the predictors of sensitivity are consistent after controlling for each other (in addition to northing and easting position), we fit a multiple regression model including all predictors and the percent change in potential area of occupancy as response variable (Table 2). As expected, observed area of occupancy, area of suitable habitat, being epiphyte or aquatic remained important predictors, reinforcing their relevance to understanding the mechanisms of sensitivity to climate and land use changes. Growth form gained importance after controlling for confounding effects.

Holding all other predictors equal, trees were associated on average with largest losses in potential area of occupancy among growth forms (on average lost 3 percent points more than shrubs) while herbs were associated with smallest losses (on average lost 2.6 percent points less than shrubs).

Given the effects of climate and land use vary across space (Figure S1 and Figure S2), we added as predictors the position of the centroid (northing and easting) of the species' area of suitable habitat. Position had a strong effect in the area of habitat predicted to be lost. Suitable habitat located towards south and east lost on average much larger areas. This effect was likely driven by the intensification of land use projected on southern and eastern portions of Brazil (particularly southeastern region, see Figure S2), which highlights the importance of development to the fate of species in the region.

Table 2. Summary table of the multiple regression model predicting the percent change in species' potential area of occupancy under 2050 mitigation. Model includes 4,571 species, and  $R^2 = 0.59$ . Terricolous and shrub were reference categories for the categorical predictors habitat and growth form. Area of occupancy and area of suitable habitat units are  $10^3 \text{ km}^2$ , and northing and easting are in km.

Predictor	Estimate	SE	t-value	p-value
(Intercept)	-50.507	0.907	-55.7	0
Area of occupancy	0.064	0.002	31.744	5.7E-200
Area of suitable habitat	0.005	0.0004	12.529	1.99E-35
Easting	-0.005	0.001	-6.049	1.58E-09
Northing	0.022	0.001	37.623	5.2E-270
<i>Habitat</i>				
Epiphyte	-2.961	0.993	-2.982	2.88E-03
Hemiepiphyte	-3.197	2.314	-1.382	0.17

Hemiparasite	-0.525	2.513	-0.209	0.83
Terricolous	-	-	-	-
Rupicolous	0.390	1.058	0.3688	0.71
Aquatic	4.807	1.424	3.3765	7.40E-04
<i>Growth form</i>				
Tree	-3.026	0.653	-4.631	3.73E-06
Climber	-0.620	0.776	-0.799	0.42
Shrub	-	-	-	-
Herb	2.557	0.671	3.8	1.42E-04

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## Discussion

Our results suggest that changes in potential area of occupancy will depend on species' range size, particularly with reference to the effects of climate change. Species with the smallest range sizes were most sensitive, while most widespread species were most resistant and often benefited from projected changes in climate. This pattern concurs with previous analyses, where plant species with the smallest range sizes were the most vulnerable to climate change (Broennimann et al. 2006; Thuiller et al. 2005a). Range-restricted species may be the most negatively affected by climate change for few reasons. Small range size associates with narrow niche breadth (Slatyer et al. 2013), which means that a more specific set of environmental conditions is required for the species to thrive and survive (Brown et al. 1996). As the climate changes, these narrow sets of environmental conditions are less likely to be available, particularly within a reasonable

distance from current occurrences. In addition, the area of suitable habitat may be particularly fragmented for species with narrow niches, where patches of suitable habitat may be immersed on a matrix of unsuitable habitat. If the species has low dispersal ability and/or low colonization ability (potentially many of them, though not necessarily: Gaston 2003; Lester et al. 2007), then it is unlikely to migrate and follow the movement of its suitable habitat. Finally, small areas are more likely than large areas to be affected on its entirety (or on larger proportions) by land use change (Gaston & Fuller 2009). Even though our results suggest the effect of land use is not as dependent on range size (compared to the effects of climate change), species with smaller range size were indeed more negatively affected by land use. These support the notion that range-restricted species are particularly vulnerable to projected climate and land use changes.

In contrast, widespread species have attributes that minimize losses and maximize gains in suitable habitat under a changing climate. First, widespread species tend to have a large niche breadth (Slatyer et al. 2013). As showed by Thuiller et al. (2005a), there seems to be a positive linear relationship between niche breadth and percentage of remaining suitable habitat under projected climate change. Chances are that future combinations of environmental conditions will be more inclusive of environmental tolerances of widespread species, as opposed to the environmental tolerances of narrowly distributed species. Second, plant species with large geographic range are expected to have large genetic variation (Frankham 1996), creating better opportunities for rapid evolutionary adaptation to changes in the environment (Hoffmann & Sgro 2011; Jump et al. 2008), which goes beyond than what our models can typically capture, but reinforce

the notion that widespread species can succeed under projected climate change. Third, the large spatial spread means that a larger extent of apparently unoccupied suitable habitat are within reach through dispersal (or may already be occupied at low density).

Our results suggest that the isolated effects of climate change (i.e. assuming all other drivers of change are hold constant) pose on average a lower than expected threat to the area of suitable habitat for plants of the Atlantic Forest of Brazil. For instance, our predicted impacts of climate change were not as grim as those for Cerrado trees (Siqueira & Peterson 2003; nearly all 162 species were predicted to reduce by >50% the potential distributional area), Amazon trees (Miles et al. 2004, 43% of the species were predicted to be non-viable), European plants (Thuiller et al. 2005a, average of 30% loss in suitable habitat), and the plants across the globe (Warren et al. 2018, 8-67% of the species predicted to lose >50% of their 'climatic range'). Much of the variation among these estimates might be explained by differences in methods, including timeframe considered, global climate models, future scenarios, technique for modelling habitat suitability, definition of 'potential range size,' subset of species evaluated, whether dispersal was taken into account, among others. However, the large contrast with our results may be an indication that Atlantic Forest plants may be under relatively lower threat by climate change, as compared to species on those other habitats.

The Atlantic Forest occur along the east coast of South America, and the proximity with the Atlantic Ocean may buffer the effects of climate change, making temperature and humidity more stable. It is expected that vegetation types in the Atlantic Forest region be rearranged across space, and the climatic suitability for specific

vegetation may decrease or increase. For example, while the dense ombrophilous forest is expected to have net loss in suitability, the open ombrophilous forest (a forest type adapted to periods of drought) was projected to gain 167% in habitat suitability (Follador et al. 2018). This may correlate with gains in suitability for some species.

In reality, climate change will affect species simultaneously with many other drivers of change. We accounted for one additional driver: land use change; and showed that it has a much larger negative impact on plant habitat than climate change. This result confirms previous studies showing that land use change has a much larger importance than climate change as a driver of biodiversity loss in tropical forest regions (de Chazal & Rounsevell 2009; Jetz et al. 2007; Sala et al. 2000). Changes in climate tend to be less pronounced in the tropics, as compared to high latitudes, and land use change tend to be more intense. The larger number of rare and narrowly adapted species, makes tropical regions vulnerable to lose large amounts of biodiversity. The intensification of land use in the Atlantic Forest region tend to cause more severe losses in plant habitat and threaten more species than in ecosystems at high latitudes. Projected land use change causes essentially loss of plant habitat for all species, while climate change may increase habitat availability for many species, thus pushing the mean effect of climate to be more positive.

Finally, the combined effects of climate and land use changes were predominantly detrimental to the habitat suitability of plants. The two scenarios for future climate and land use include substantial losses to plant habitat, but the BAU scenario (RCP8.5 SSP5) is clearly much more detrimental than mitigation scenario (RCP4.5 SSP2), as exemplified by its ability to reverse any positive trends observed under mitigation. Because land use

had the most important negative effect, decisions related to land use rather than the concentration of greenhouse gases in the atmosphere will tend to have higher relevance to the persistence of plant species in the region (at least in the next several decades).

### *Ecological groups*

Two ecological groups stand out by having the consistent negative response (epiphytes) and positive response (aquatic) to projected changes. Not coincidentally, epiphytes and aquatic have respectively the smallest and largest observed range size (Leão & Reich 2018). However, both groups (aquatic plants in particular) showed independent association with change in potential area of occupancy after controlling for observed area of occupancy. Growth form gained importance when all relevant predictors were controlled for; trees were associated with the most negative average response and herbs the least negative average response to climate and land use changes. We focus the discussion on epiphytes and aquatics, which had most consistent and extreme responses.

The high sensitivity of epiphytes to climate change may be largely due to (1) small range size and (2) dependence on a narrow range of environmental conditions. Range size accounted for around 50% of the sensitivity of epiphytes to projected climate change (calculated as the ratio of effect sizes when including or not observed area of occupancy as covariate). Thus, similar reasons for the sensitivity of small-ranged species applies to epiphytes, and more broadly to lineages of epiphytes (see Leão & Reich 2018). Second, epiphytes have a particularly tight dependence on local climate, especially atmospheric humidity and distribution of rainfall (Benzing 1998; Gradstein 2008). For

that reason, Benzing (1998) hypothesized that epiphytes are the floristic components of humid tropical forests most sensitive to climate warming, and expected to be among the first to disappear in cloud forests that are getting drier, warmer and more seasonal. In addition, epiphytes face further challenges, not captured by our models, due to their often dependence on late successional communities (e.g. old growth forests), dependence on other species (e.g. phorophytes), and slow recovery from disturbances such as from forest clearing (Gradstein 2008; Schmidt & Zotz 2002). The predicted high sensitivity of epiphytes reinforces the pattern of epiphytes as the ecological group with the highest vulnerability to species extinction among Atlantic Forest plants (Leão et al. 2014; Leão & Reich 2018).

On the other side of the spectrum, aquatic species tend to have broad climatic tolerances and large geographic range size (Santamaría 2002), thereby less vulnerable to climate change. In fact, aquatic species have largest average range size among the habitat groups in the Atlantic Forest region (Leão & Reich 2018). However, range size did not explain much of the change in potential range size, contrasting with epiphytes and suggesting that large niche breadth are particularly important to understand the response of aquatic plants to climate change. In addition, aquatic plants often have the ability to long distance dispersal with the assistance of waterbirds, which gives them the capacity to migrate fast and likely to keep up with climate change (Viana 2017). Thus, on average, aquatic species tend to particularly resilient to climate change and under relatively lower threat of losing suitable habitat.

### *Caveats*

Our results have important sources of uncertainty. The range of environmental conditions observed in occupied sites might not accurately reflect environmental tolerances (Spicer & Gaston 1999). Species tolerance usually goes beyond the environmental conditions observed in their current area of occupancy, limiting the accuracy of habitat suitability modelling techniques to predict impacts of climate change (Malhi et al. 2014; Vetaas 2002). In particular, the predicted area of suitable habitat for range-restricted species are distinctly uncertain (Schwartz et al. 2006). Species with small range size typically occur on a narrow range of environmental conditions, causing the models to estimate a small area of suitable habitat. If the species do not occur beyond its observed range due to dispersal limitation or biotic interactions rather than environmental tolerance, then the suitability model may underestimate its area of suitable habitat (Guisan et al. 2017). To aggravate this problem, biotic interactions may be particularly important to determining species' geographic range in the species-rich and complex tropical ecosystems (MacArthur 1972; Malhi et al. 2014).

Our results do not indicate gains or losses in actual geographic range size. It attempts to show changes in habitat suitability and potential range size, which are quite different. We expect that changes in potential range size indicate some of the pressures (positive or negative) that climate and land use may exert on the species; whether the species' range size will change accordingly to these pressures is beyond the scope of this study (and critical to conservation). Species may withstand environmental changes and persist in their current area of occupancy despite apparent decreasing suitability (Spicer

& Gaston 1999). 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. On the other side of the spectrum, projected gains in area of suitable habitat that are far away from current populations may be virtually impossible to be colonized without assisted migration. We tried to minimize this problem by considering for ‘potential area of occupancy’ only areas within a certain distance of observed occurrences – under the assumption that these areas might already be colonized.

In addition, our projections do not take into account that some ecosystems on which species may depend may not exist under projected climate change. For instance, humid forest ecosystems are projected to retract in many parts of South America (Zelazowski et al. 2011). This may have severe implications for the occurrence of late successional species that depends on well-developed humid forest plant communities to exist. The facilitation provided by other species and the local microclimate provided by the humid forests are critical for many species (e.g. shade tolerant and slow growing trees, and many epiphytes). Unfortunately, our models do not account for that.

Mean temperatures in some areas are projected to be higher than anywhere in the observed ranges for many species. This brings the problem of fitting habitat suitability models on climates beyond the training range (i.e. non-analog conditions). Projections over non-analog conditions are particularly uncertain, which is a problem hard to avoid (Guisan et al. 2017), particularly in the tropics (Hannah et al. 2011; Malhi et al. 2014).

## *Conclusion*

Projected climate and land use changes are likely to reduce the area of suitable habitat for many species ('losers') and substantially increase it for fewer species ('winners').

Whether a species loses or gain suitable habitat depends substantially on current range size, ecological characteristics and emissions scenario. We expect that small-ranged and epiphytic species to be particularly vulnerable to lose area of suitable habitat, while widespread and aquatic species are more resistant and may often benefit from climate change. Even though both projected scenarios incur average loss of suitable habitat for plants, the high emissions and most intense land use scenario (BAU) clearly incur on much larger losses of suitable habitat than the mitigation scenario, particularly due to the impacts of land use change.

Overall, we can expect that the combined effects of climate and land use change will impoverish plant communities the Atlantic Forest region. As the habitat suitability decreases for most but increases for a few species, plant communities may reassemble to reflect those changes (mediated by changes in fitness and competitive ability at a particular location). Eventually, species with diminishing suitability may lose relative abundance, at the same time that other species (particularly those with increasing suitability) increase relative abundance. This seems to support evidences of increasing similarity among plant assemblages through time (Lôbo et al. 2011; Zwiener et al. 2018), likely aggravating the undergoing homogenization of plant communities in the Atlantic Forest region (Tabarelli et al. 2012).

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## Appendix

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1. Herbário ALCB, Instituto de Biologia, UFBA
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13. Herbário CPAP da Embrapa Pantanal
14. Herbário Pe. Dr. Raulino Reitz - CRI ([herbario@unesp.net](mailto:herbario@unesp.net))
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19. Herbário Prof. Jayme Coelho de Moraes, EAN
20. Herbário Escola de Florestas Curitiba, EFC
21. Herbário da Escola Superior de Agricultura Luiz de Queiroz, USP - [www.lcb.esalq.usp.br](http://www.lcb.esalq.usp.br)
22. The Field Museum of Natural History. <http://fieldmuseum.org/about/copyright-information>
23. Herbário Friburguense, FCAB
24. Herbário FLOR, Universidade Federal de Santa Catarina
25. Fundación Puerto Rastrojo - Colombia
26. Herbário da Universidade Estadual de Londrina (<http://www.uel.br/ccb/bav/herbario>)
27. Herbário Dr. Roberto Miguel Klein, FURB
28. Herbário Alarich R.H. Schultz, do Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul (HAS/MCN/FZBRS)([www.fzb.rs.gov.br](http://www.fzb.rs.gov.br))
29. Herbário do Instituto de Estudos Costeiros da UFPA-Bragança (HBRA)
30. Herbário Virtual Flora Brasiliensis, Projeto Re flora
31. Herbário Caririense Dárdano de Andrade-Lima, HCDAL, URCA
32. Herbário da Universidade Tecnológica Federal do Paraná Campus Campo Mourão – HCF
33. Jardim Botânico de Brasília, Herbário HEPH
34. Herbário da Amazônia Meridional – HERBAM

35. Herbário Dr. Ary Tupinambá Penna Pinheiro – HFSL
36. Herbário Jataiense Prof. Germano Guarim Neto, HJ
37. Herbário Montes Claros (HMC)
38. HPAN – Herbário do Pantanal “Vali Joana Pott”, UNEMAT, Cáceres, MT
39. Herbário Padre Balduino Rambo, HPBR
40. Herbário Instituto Plantarum de Estudos da Flora Ltda.
41. Herbário Rioclarense (HRCB), Instituto de Biociências, UNESP campus de Rio Claro
42. Herbário de São José do Rio Preto, SJRP
43. HST - Herbário Sérgio Tavares
44. Herbário da Universidade Católica de Pernambuco (HUCPE)
45. Herbário da Universidade de Caxias do Sul
46. HUEFS - Herbario da Universidade Estadual de Feira de Santana
47. Herbário da Universidade Estadual de Goiás, HUEG
48. Herbário da Universidade Estadual de Maringá, UEM
49. Herbário da Universidade Estadual do Sudoeste da Bahia, HUESB  
([huesbjequie@gmail.com](mailto:huesbjequie@gmail.com))
50. Herbário da Universidade Federal de São João del-Rei, HUFSJ.
51. Herbário HUFU (<http://www.portal.ib.ufu.br/node/73>)
52. Herbarium Mogiense (HUMC) da Universidade de Mogi das Cruzes (Acesso:  
<http://www.umc.br/herbario>)
53. Herbário HUTO da Universidade do Tocantins

54. Herbário Vale do São Francisco – HVASF
55. Herbário do Instituto Agronômico de Campinas - IAC (Instituto Agronômico)
56. Herbário ICN, UFRGS (<http://icnbio.ufrgs.br/icn/>)
57. Coleção do Herbário de Rio Verde (RV) - Instituto Federal Goiano - Câmpus Rio Verde
58. Herbário INPA
59. Herbário - IPA Dárdano de Andrade Lima
60. Herbário IRAI (Parque da Ciência Newton Freire Maia - SEED/PR)
61. Herbário Joinvillea, UNIVILLE
62. Herbario da Universidade Federal da Paraíba, JPB
63. Coleção Botânica do LABEV - Universidade Federal do Acre
64. Herbário Lages da Universidade do Estado de Santa Catarina, LUSC
65. MAC- herbário do Instituto do Meio Ambiente de Alagoas ([www.mac.org.br](http://www.mac.org.br))
66. Herbário MAR - Universidade Federal do Maranhão
67. Herbário do Museu Botânico Municipal de Curitiba, MBM
68. Herbário Mello Leitão, Museu de Biologia Professor Mello Leitão, MBML
69. Herbário Prof<sup>a</sup>. Dr<sup>a</sup>. Marlene Freitas da Silva - Herbário MFS
70. MIRR - Herbário do Museu Integrado de Roraima
71. MNHN - Herbário Virtual A. de Saint-Hilaire
72. Herbário Dárdano de Andrade Lima - MOSS
73. Herbário do Museu de Ciências e Tecnologia da PUCRS, MPUC

74. Smithsonian Department of Botany - Brazilian records
75. Herbário NX, UNEMAT, campus de-Nova Xavantina-MT
76. The New York Botanical Garden Virtual Herbarium  
(<http://sciweb.nybg.org/science2/VirtualHerbarium.asp>)
77. Herbário Professor José Badini – OUPR
78. Herbário PEUFR (DB/UFRPE)
79. Herbário do Museu Nacional - Centro de referência da biodiversidade brasileira
80. Instituto de Pesquisas Jardim Botânico do Rio de Janeiro (JBRJ). Jabot - Banco de Dados da Flora Brasileira. Disponível em: (<http://www.jbrj.gov.br/jabot>)
81. Herbário Rondoniense – RON
82. Sistema de Informação do Programa Biota/Fapesp
83. Herbário de São José do Rio Preto, SJRP
84. Herbário Rosa Mochel, SLUI
85. Herbário do Estado "Maria Eneyda P. Kaufmann Fidalgo" - Instituto de Botânica, IBT
86. Herbário da Universidade de São Paulo, USP
87. Herbário Dom Bento José Pickel, Instituto Florestal, IF
88. Herbário Tangará, Universidade do Estado de Mato Grosso
89. TEPB - Herbário Graziela Barroso
90. Herbário da Universidade de Brasília, UB
91. Herbário da Universidade Estadual de Campinas, UNICAMP
92. Herbário Universidade Estadual de Santa Cruz, HUESC

93. UFACPZ - Herbário da Universidade Federal do Acre
94. Unidade de Conservação/PRPPG/UFG - Herbário UFG
95. Herbário UFMT
96. Herbário UFP - Geraldo Mariz
97. Herbário UFRN
98. Herbário da Universidade Federal de Roraima, UFRR
99. Herbário da Universidade Estadual do Oeste do Paraná, UNOP
100. Herbário do Departamento de Botânica, Universidade Federal do Paraná, UFPR
101. Herbário Central da Universidade Federal do Espírito Santo VIES