



Planning for conservation and restoration under climate and land use change in the Brazilian Atlantic Forest

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Abstract

Aim: To propose and compare priority sites for conservation and restoration of woody plants under diverse climate and land use scenarios, considering socio-economic costs, presence of protected areas and distribution of forest remnants.

Location: The Atlantic Forest Biodiversity Hotspot, Brazil.

Methods: We used ecological niche modelling to estimate geographical distributions for 2,255 species under current and future climate scenarios, which we analysed in relation to spatially explicit land use projections, maps of forest remnants derived from remote sensing and socio-economic variables for each municipality within the Atlantic Forest region. We identified spatial priorities that complement the current network of protected areas under three different prioritization scenarios: (1) conservation of existing forest remnants only; (2) conservation of remnants followed by restoration of degraded habitat; and (3) unconstrained actions, in which management location is not defined a priori. We compared our results under different levels of land protection, with targets of 10%, 17% and 20% of the Atlantic Forest extent.

Results: Current forest remnants cover only 12% of the Atlantic Forest, so targets of 17% and 20% were achieved only through active restoration. Targets of 17% and 20% captured most species and represented on average 26%–34% of species' distributions. The spatial pattern of degraded habitats negatively affected representation of biodiversity and implied higher costs and reduced efficiency of planning. We did not observe major differences between conservation prioritizations based on contrasting climate change scenarios.

Main conclusions: Protection of forest remnants alone will not suffice to safeguard woody plant species under climate and land use changes; therefore, restoration actions are urgently needed in the Atlantic Forest. With integrated management actions and multicriterion nationwide planning, reaching the 17% of land protection of Aichi biodiversity targets will constitute an important step towards protecting Atlantic Forest biodiversity.

KEYWORDS

Aichi targets, climate change, ecological restoration, land use change, MAXENT, spatial conservation prioritization, species distribution modelling, ZONATION

1 | INTRODUCTION

Forests play fundamental roles in maintenance of global biodiversity and supporting human well-being through provision of ecosystem services (Cardinale et al., 2012; Gardner et al., 2009; MEA, 2005). Although vastly important for society, tropical forests rank among the most threatened ecosystems in the world owing mostly to human-driven deforestation and habitat fragmentation (Brooks et al., 2002; Wright, 2005). Climate change also constitutes an imminent threat to biodiversity: in synergy with land use change, it may increase extinction risk for many species (Pereira et al., 2010). Effective management actions considering both future climate and land use changes are thus needed to mitigate effects of global environmental change (Araújo, Alagador, Cabeza, Nogués-Bravo, & Thuiller, 2011; Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012; Faleiro, Machado, & Loyola, 2013; Thuiller et al., 2008).

Species may respond to climate change by acclimatization, evolutionary adaptation and/or distributional shifts to more suitable areas (Peterson et al., 2011). Tropical plants are thought to have low acclimation ability because they are adapted to limited seasonal variation in temperature (Corlett, 2011; Feeley, Rehm, & Machovina, 2012; Wright, Muller-Landau, & Schipper, 2009). Evolutionary adaptation is unlikely to buffer effects of climate change, given that long generation times constrain evolutionary rescue (Price & Kirkpatrick, 2009; Wright et al., 2009). Moreover, non-mobile edaphic factors, interspecific competition, forest fragmentation and loss of dispersal agents may further reduce colonization of otherwise suitable areas (Corlett, 2009; Price & Kirkpatrick, 2009). Although some species will likely retract to "climate refugia" within their current ranges, others may go extinct (Gavin et al., 2014; Keppel et al., 2012; Terribile et al., 2012; Thomas et al., 2004). Thus, assessing the effectiveness of current networks of protected areas for conservation of biodiversity under climate change, establishing new protected areas in climatically suitable areas, and restoring degraded habitats represent paramount steps towards reversing biodiversity decline (Araújo et al., 2011; Hannah et al., 2007; Thomson, Moilanen, Vesk, Bennett, & Mac Nally, 2009; Williams, Shoo, Isaac, Hoffmann, & Langham, 2008).

Many challenges are involved in effective conservation and management of biodiversity. In particular, knowing what fraction and which specific portions of the landscape need conservation intervention and management action is crucial to achieve conservation objectives (Brooks et al., 2006; Margules & Pressey, 2000; Wilson et al., 2007). From the perspective of biodiversity conservation, geographical distributions of species are the basic information required. Ecological niche modelling has emerged as an important tool by which to assess species' current and future potential distributions, allowing the dynamic conservation approach necessary to cope with climate change (Araújo & Peterson, 2012). Detailed data on other factors (benefits and costs) must be included in a multicriterion framework to improve chances of successful management, such as presence of remnant natural habitat and existing protected areas, land use type and changes, economic or opportunity costs, and political governance (Faleiro & Loyola, 2013; Margules & Pressey, 2000; O'Connor, Marvier, & Kareiva, 2003; Pressey & Cowling, 2001).

Addressing all species, communities or ecological systems for conservation is highly impractical and costly, making necessary the identification of clear conservation goals on which to focus planning and management efforts (Margules & Pressey, 2000). Systematic conservation planning techniques aim to make the best use of available resources to identify priority sites for management (Kukkala & Moilanen, 2013; Margules & Pressey, 2000; Wilson, Cabeza, & Klein, 2009). Planning for conservation of remaining habitat and restoration of degraded land differ essentially in that the latter considers locations that do not presently provide suitable habitat, but could potentially, given sufficient time and management effort (Noss, Nielsen, & Vance-Boland, 2009; Thomson et al., 2009). The extent to which these complementary management actions contribute to biodiversity conservation is largely unexplored and constitutes an important topic of research and debate for formulation of sound conservation policies (Possingham, Bode, & Klein, 2015; Wilson et al., 2007).

The Atlantic Forest constitutes a complex of ecosystems of great importance for the maintenance of biodiversity, originally extending across 1.5 million km² along the Brazilian coast and in the interior (Stehmann et al., 2009). The Atlantic Forest is considered a biodiversity hotspot, being one of the world's most species-rich biomes, with both high levels of endemism and high threat to its integrity (Mittermeier, Turner, Larsen, Brooks, & Gascon, 2011; Mittermeier et al., 2004). Given intense deforestation and human disturbance, only a small portion of the original Atlantic Forest cover still remains; remnant areas are distributed mostly in small fragments (Ribeiro, Metzger, Martensen, Ponzoni, & Hirota, 2009).

Here, we couple ecological niche modelling and spatial conservation prioritization to assess and identify priority sites for conservation and restoration of woody plant species under contrasting future climatic and socio-economic scenarios. More specifically, we explore the following questions: (1) Is the current network of protected areas in the Atlantic Forest sufficient to protect woody plant species in face of climate change? (2) How can complementary management actions contribute to current protected areas for protection of biodiversity? (3) How would complementary management actions affect representation of biodiversity in protected areas under different conservation goals?

2 | METHODS

2.1 | Focal species and occurrence records

The Atlantic Forest presents astonishing biodiversity, and plants are among the most diverse groups (Mittermeier et al., 2011); *ca.* 50% of plant species represented there are endemic to this biome (Forzza et al., 2012; Werneck, Sobral, Rocha, Landau, & Stehmann, 2011). Concordant spatial patterns between vegetation and other taxonomic groups have been reported in the region (Ferro & Melo, 2011; Vasconcelos, Prado, Silva, & Haddad, 2014). We opted to work with woody plants given both their elevated diversity and endemism, and their ecological importance for providing habitat to other taxonomic groups.

Focal plant species were selected from compiled checklists summarizing species' occurrences at 300 localities, comprising 2,948 woody plant species distributed across the Atlantic Forest (Lima et al., 2015). Occurrence records were obtained from field inventories and georeferenced data from speciesLink (<http://splink.cria.org.br>), an electronic database of Brazilian primary biodiversity data currently containing over five million georeferenced records from 377 herbaria and natural history museums.

We removed duplicate records documenting the same species at the same locality and compared the geographical location of occurrences with state-level checklists established by specialists (<http://floradobrasil.jbrj.gov.br>) to remove isolated records falling outside the species' natural range. We rarefied records for species so that no pair of points was closer than 20 km; this step reduced effects of sampling bias and spatial autocorrelation on model performance (Boria, Olson, Goodman, & Anderson, 2014; Hijmans, 2012). We chose this distance based on density and proximity of records. Hence, we retained 286,798 from the initial 673,096 georeferenced records for analysis of 2,948 species. We further considered only species with ≥ 15 unique locality records, which reduced the number to 2,255 plant species and 283,287 records.

2.2 | Environmental variables and climate change scenarios

We obtained environmental variables for current conditions and future climate projections from the WorldClim database (<http://www.worldclim.org>; Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) at a spatial resolution of 5'. These variables represent annual averages and variability of climatic factors (Hijmans et al., 2005). Future climate projections were based on the IPCC Fifth Assessment Report; we selected three general circulation models (CCSM4, GISS-E2-R and MIROC5) from two representative concentrations pathways (RCP2.6 and RCP8.5) for the year 2050 (average for 2,041–2,060) and 2070 (average for 2,061–2,080). Overall, RCP2.6 and RCP8.5 are associated with low and high intensities of climatic change, respectively (Appendix S1).

To reduce dimensionality and collinearity of environmental layers, we conducted a principal component analysis (PCA) based on a correlation matrix of standardized variables. PCA was done with all current 19 "bioclimatic" variables, and values were predicted to future climate projections. To characterize present and future environmental variation across the study region, we used the first six principal components, which collectively accounted for >95% of overall variation in climatic variables (Appendix S2).

2.3 | Ecological niche models

We used ecological niche models (ENMs) to derive estimates of species' potential distributions across the region based on climatic variables. ENMs have been used to estimate distributions of species in space and time, and represent an important tool in strategy development for protection of biodiversity (Araújo & Peterson, 2012; Elith & Leathwick, 2009; Guisan et al., 2013).

Several methods have been developed and explored for estimating species niches and related potential geographical distributions (Peterson et al., 2011). We chose the maximum entropy, "MAXENT," algorithm (Phillips, Anderson, & Schapire, 2006), given its high predictive ability for small samples and adequacy with presence-only data (Elith & Graham, 2009; Elith, Kearney, & Phillips, 2010; Wisz et al., 2008). We used five bootstrap replicates and raw output format; other settings were kept as default. Binary predictions were produced by applying a least training presence threshold over the mean estimate from the five bootstrap replicates, while discarding the 5% lowest values (i.e. admitting $E = 5\%$ omission "error," Peterson et al., 2011; Merow, Smith, & Silander, 2013). Because of the possibility of overly broad predictions, we chose a threshold such that presences of the species are restricted to sites at least as suitable as those of 95% of the sites at which the species has been observed. This approach is less sensitive to outliers: misleading records that were incorrectly identified, wrongly georeferenced or derived from sink populations (Peterson et al., 2011).

We approximated species' accessible areas as the area across which models would be calibrated (Barve et al., 2011; Peterson et al., 2011). These accessible areas ranged from the entire tropical and subtropical region east of the Andes for widely distributed species, to restricted areas of the Atlantic Forest for narrowly distributed endemic species, and were based on biogeographical interpretation of likely dispersal barriers for each species. See Appendix S3 for details.

Final ENM predictions for each species, projected to each different time period, climate model and emissions scenario, were obtained by overlaying thresholded projections from global climate models within the same RCP, and considering areas in which all three estimates coincided. Hence, we used a conservative estimate of potential distributions in the future.

2.4 | Land use change scenarios

We obtained spatially explicit data on areas identified as urban, cropland and pasture at present and forecasted for 2050 and 2070, from the Land-Use Harmonization Project (<http://luh.umd.edu>; Hurtt et al., 2011) at a spatial resolution of 30'. These data are based on historical reconstructions of land use, and smoothly connect with multiple alternative future scenarios developed by IAMs (i.e. IMAGE, MESSAGE). The data are provided as fraction of grid cell covered by each land use category estimated annually for the period 850–2,100 and different socio-economic trends. We used projections for the IMAGE and MESSAGE models that are consistent with RCP 2.6 and RCP 8.5, respectively.

2.5 | Land cost and political willingness to act

For each of the 3,096 municipalities within the Atlantic Forest extent, we obtained data on gross domestic product (GDP) in 2010 (<http://www.ibge.gov.br>). Based on municipal financial information (<http://www.stn.fazenda.gov.br>), we calculated average (2004–2010) percentage of GDP invested in environmental programmes. Percentage

invested in environmental programme was used as proxy for political “willingness to act” (Faleiro & Loyola, 2013). Land acquisition cost was obtained by summing values of agricultural, pasture and forested lands within each municipality from the purchase price of rural land in 2014 (Crouzeilles, Beyer, Mills, Grelle, & Possingham, 2015; Soares-Filho et al., 2016).

2.6 | Forest remnants and protected areas

We estimated the amount of forest remaining, based on Atlantic Forest fragment maps for 2012 (<http://mapas.sosma.org.br>), a product of collaborative work that constitutes the most comprehensive survey of Atlantic Forest remnants (SOS Mata Atlântica and Instituto Nacional de Pesquisas Espaciais, 2013). Data summarizing the current network of protected areas were retrieved from the Brazilian Ministry of Environment database (<http://mapas.mma.gov.br/i3geo/datadownload.htm>). We considered only strictly protected areas with a minimum size of 1,000 ha; we discarded other, smaller areas and areas with less effective protection. Results of prioritizations based on both types of protected areas are in the Supporting Information (Table S5).

2.7 | Spatial conservation prioritization

We used ZONATION (v.4.0; Moilanen, Kujala, & Leathwick, 2009; Di Minin, Veitch, Lehtomäki, Montesino-Pouzols, & Moilanen, 2014; Pouzols et al., 2014) to rank sites and obtain spatial priorities for conservation of woody plant species in the Atlantic Forest. Prioritizations were developed at a resolution of 5' (ca. 10 km) with the aim of reducing socio-economic conflicts (with urbanization, agriculture and livestock) and land cost, while maximizing political willingness to act, and accounting for effects of land use and climate change on species' distributions (hereafter “prioritization solution”). We set the additive benefit function (ABF) as the cell removal rule; ABF favours grid cells with higher species richness, and accounts for complementarity (details in Appendix S4).

Trade-offs between biodiversity, socio-economic, land cost and political features were defined by assigning positive weights to beneficial factors (features that should be maximized to increase conservation effectiveness and opportunity) and negative weights to constraint factors (features that should be minimized to avoid conservation conflicts). We assigned equal weights to each species at 1/1,683 (1/highest richness) and political willingness to act at 0.2, whereas land cost, forecasted urbanization, cropland and pasture area were each weighted at -0.3 . The sum of positive and negative weighted features was zero, allowing a balanced solution in the prioritization (Faleiro & Loyola, 2013; Moilanen et al., 2011). We did sensitivity analyses to investigate effects of these weights on our results (Moilanen et al., 2011); we systematically multiplied weights of each feature by five and measured the spatial overlap between original and weighted modified scenarios (see Tables S6–S9).

ZONATION also allows use of positive interactions within species from one site to another or from one time step to another (Carroll, Moilanen, & Dunk, 2010). Hence, we accounted for effects of climate

change by adding interactions (connectivity) between species' current distribution and future projections, making a conservative assumption of no dispersal, in which species' ranges can only retract, but not expand or colonize.

We sought to identify priority areas for extending the current network of protected areas in the Atlantic Forest. We achieved this objective by forcing inclusion of current protected areas via a mask layer, and looking at the top fraction of the study region, which included the protected areas plus the complementary areas. Because ZONATION does not plan for multiple objectives (e.g. both conservation and restoration actions) simultaneously in the same cell, we opted to compare conservation actions independently and the extent to which restoration actions complement conservation of woody plants. We generated three biodiversity management scenarios: (1) “conservation only,” in which we considered for prioritization only those cells with at least half of the area covered by forest; (2) “conservation prior to restoration,” in which forest remnant cells were forced into top priority fractions before cells with few or no remnants (this scenario represents a solution in which forest remnants would first be targeted for conservation, whereas sites that would require costly active restoration to maintain woody plant species populations would be targeted only second); and (3) “unconstrained” scenario, in which no management is defined a priori and cells are ranked solely according to distribution, weight and connectivity of features. All prioritization analyses were performed for the two climate change scenarios (RCP 2.6 and RCP 8.5) and two time periods (2050 and 2070), totalling 12 prioritization solutions. Prioritizations for 2050 and 2070, and for both RCPs, were highly correlated (0.98–0.99); hence, results for 2070 and low greenhouse gas emissions are in Supporting Information (S10–S17). To assess sensitivity of our results to using binary predictions from ENMs, we ran prioritizations using MAXENT raw output for present climate and projections to the three general circulation models under high emission scenarios for 2050 and measured the spatial overlap with the original prioritizations (see Table S18).

2.8 | Conservation targets and comparisons

To characterize and compare performance of prioritization solutions and management scenarios, we selected the top ranked cells at three different levels: 10%, 17% and 20%. These levels represent different conservation targets of coverage for the Atlantic Forest, with 10% representing a more restrictive target, 17% corresponding to the Aichi Biodiversity Target 11 (CBD, 2010) and 20% representing a more optimistic target.

Finally, we compared prioritization solutions in terms of the following measures: (1) number of species and average proportion of species' distributions remaining; (2) percentage lost or gained of feature representation obtained as the difference between the mean representation of features in the solutions; and (3) spatial correlation and overlap between rankings of cells from different solutions. We extracted cell rankings and spatial coordinates and correlated rankings from different solutions for each conservation target. We used Spearman's correlations and Dutilleul's (1993) method to estimate correct degrees of

freedom and assess statistical significance. Data processing and statistical analyses were performed with R (R Development Core Team, 2016); we used the package `DISMO` (Hijmans, Phillips, Leathwick, & Elith, 2012) to build ENMs (scripts available at: <https://github.com/narayanibarve/ENMGadgets>).

3 | RESULTS

Species richness obtained by stacking ENMs predictions was not evenly distributed, reaching 1,683 species per grid cell, with highest values concentrated in the middle to south-eastern portions of the Atlantic Forest (Figure 1). Of the 13,447 total grid cells, 12% held high proportions of forest (Figure 1). Protected areas covered ~7% of cells; only 4% of grid cells were both protected and with high proportion of forest.

Prioritization solutions regardless of management scenario and conservation target could not safeguard all woody plant species owing to potential climate-driven local extinctions. Protected areas represented less species in the “conservation only” scenario than “conservation prior to restoration” and “unconstrained” schemes for both low and high greenhouse gas emissions scenarios (Table 1).

Priority sites for the “conservation only” and “conservation prior to restoration” scenarios were concentrated in the southern south-eastern portions of the Atlantic Forest where more forest remnants are present, whereas priority sites for the “unconstrained” scenario shifted towards central and north-eastern regions (Figures 2 and 3). Correlations between “conservation prior to restoration” and “unconstrained” rankings of top priority sites were variable, generally decreasing with increasing percentage of the Atlantic Forest protected. Correlations ranged from 0.61 to 0.99, depending on conservation target and greenhouse gas emissions scenario (see Table S19). Spatial overlap between “conservation prior to restoration” and “unconstrained” for the top 10% of priority rankings was 58% under both emissions scenarios; for the top 17% of priority rankings, it was 43%

under low emission and 42% under high emission; finally, for the top 20% of priority rankings, it was 55% for both emissions scenarios.

Prioritization solutions for the 10% conservation target protected a high number of species and differed from conservation targets of 17% and 20% mostly in the proportion of species' distributions remaining and spatial configuration of top priority sites (Table 1, Figure 3). For a conservation area target of 10% under low and high greenhouse gas emissions scenarios, “conservation prior to restoration” covered smaller proportions of species' distributions, had increased probability of land use conflicts, encountered decreased political willingness to act and increased costs of protecting land compared to “unconstrained” scenarios. These differences increased for targets of 17% and 20% under the low emission and high emission scenarios (Figure 2, Table 2, Fig. S10). Both management scenarios reduced constraint factors at a relatively small expense to beneficial factors, when compared to a scenario in which only species' distributions were considered in prioritization (Tables S20 and S21).

Differences among prioritization solutions under low and high emissions were practically nil. Top priority rankings for the “conservation only” and “conservation prior to restoration” management scenarios under low greenhouse gas emissions were similar to prioritizations under high greenhouse gas emissions, with correlations of 0.99, whereas correlations for the “unconstrained” scenario were lower, ranging from 0.96 to 0.98 (Table S22). Spatial overlap between the top 10% of priority rankings for prioritizations under low and high greenhouse gas emissions scenarios was 94% in the “conservation only” and 96% in the “conservation prior to restoration” management scenarios, whereas for “unconstrained” it was 90%. For conservation targets of 17% and 20%, under low and high emissions scenarios, “conservation prior to restoration” had spatial overlaps of prioritization solutions of 95% and 93%, respectively, whereas “unconstrained” obtained 88% and 89% overlaps. Overall, low emission solutions had a slight tendency to represent smaller mean percentages of species' distributions (differences: -0.47% to 0.16%), having less political willingness to act (differences: -1.22% to -0.35%), and reducing land use conflicts and

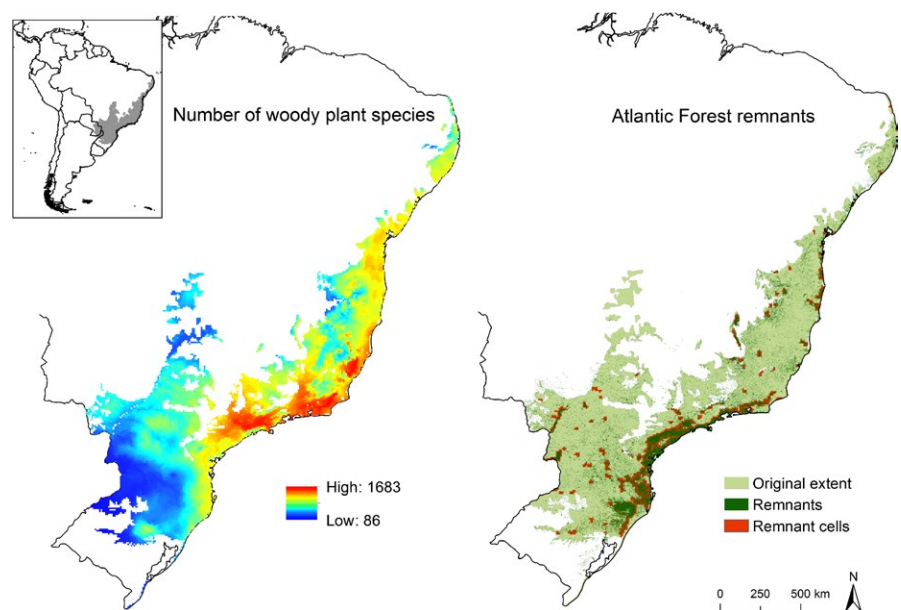


FIGURE 1 Woody plant species richness viewed in terms of summed results of ecological niche models, and geographical distribution of forest remnants in the Atlantic Forest. In the latter map, orange cells represent sites with high proportion of forest remnant considered in the biodiversity management scenarios

TABLE 1 Number of species and average proportion of species' distribution areas remaining, in parentheses, within top priority sites for different management scenarios. Comparisons are shown for priority sites within current protected areas (PAs) and for different conservation targets (10%, 17% and 20%), in the Atlantic Forest under low and high greenhouse gas emissions scenarios in 2050

Management scenarios	Low emission				High emission			
	PAs	10%	17%	20%	PAs	10%	17%	20%
Conservation only ^a	2,219 (0.37)	2,253 (0.85)	—	—	2,221 (0.37)	2,253 (0.86)	—	—
Conservation prior to restoration	2,250 (0.09)	2,253 (0.15)	2,254 (0.26)	2,254 (0.32)	2,251 (0.09)	2,253 (0.15)	2,254 (0.26)	2,254 (0.31)
Unconstrained	2,250 (0.09)	2,254 (0.17)	2,254 (0.30)	2,254 (0.34)	2,251 (0.09)	2,253 (0.17)	2,254 (0.30)	2,254 (0.34)

^aComparisons restricted to current forest remnants; comparisons of 17% and 20% top priority sites are not possible for the "conservation only" management scenario, given that only 12% of the Atlantic Forest original extent is available for conservation.

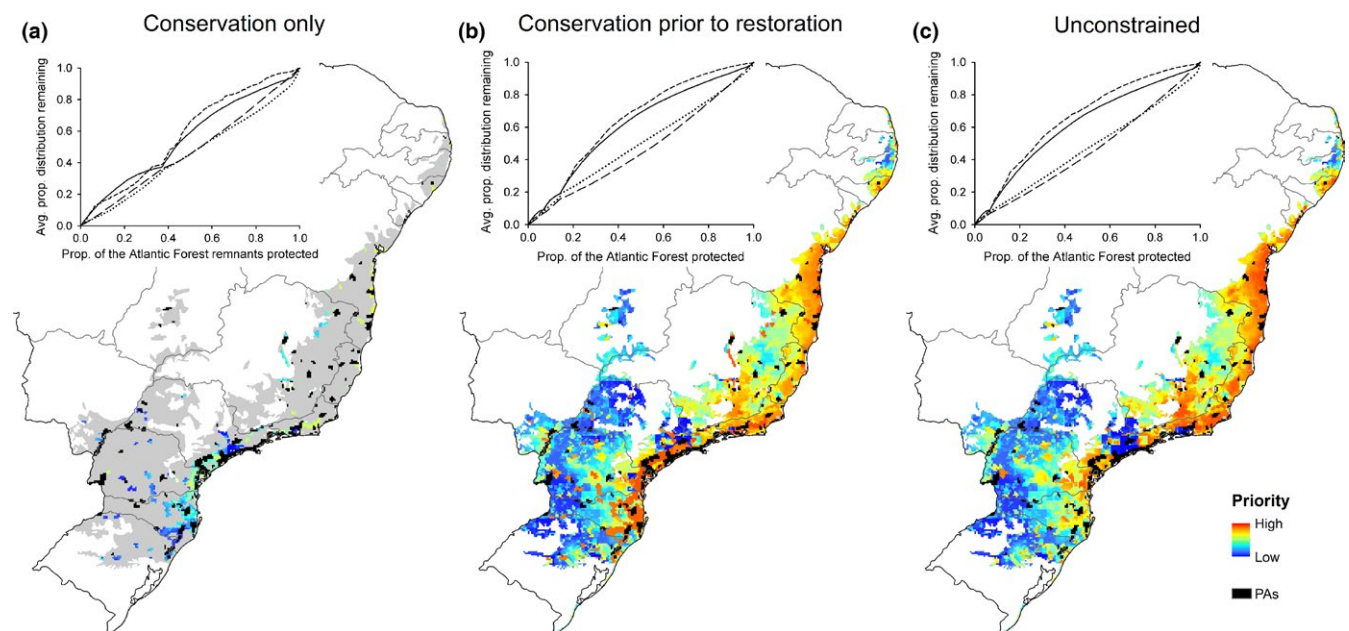


FIGURE 2 Nested hierarchical ranking of conservation priorities, current protected areas (PAs) and performance graphs for different management scenarios under high greenhouse gas emissions forecasted to 2050. Performance graphs indicate representation of each feature at a given proportion of the landscape protected. Graph legend: Woody plant species (solid line); forecasted land use (dotted line); political willingness to act (short-dashed line); land cost (long-dashed line)

economic costs (differences: -4.16% to 1.26% and -0.06% to 0.30% , respectively), depending on the conservation target (Table 3).

Prioritizations were robust to modification of feature weights and thresholding ENMs. Spatial overlap between the original prioritization and the 5-fold weighted modified prioritizations ranged from 83% to 93% in the "conservation only" scenario, 74% to 96% in the "conservation prior to restoration" scenario and 57% to 96% in the "unconstrained" scenario (Tables S6–S9). Spatial overlap between prioritizations with original and non-thresholded ENMs outputs ranged from 74% to 98% depending on the conservation target and management scenario (Table S18).

4 | DISCUSSION

Several conservation assessments and priority-setting initiatives have suggested conservation and restoration priorities within the Atlantic

Forest. Previous initiatives have varied greatly in terms of goals, taxonomic groups, data and methods used for identifying priorities (Paese et al., 2010). For instance, conservation and restoration priorities have been derived from present distributions and population estimates of various taxonomic groups (Crouzeilles et al., 2015; Galetti et al., 2009; Martins, Loyola, Messina, Avancini, & Martinelli, 2015; Murray-Smith et al., 2009; Trindade-Filho, Carvalho, Brito, & Loyola, 2012), centres of endemism (Silva, Sousa, & Castelletti, 2004), expert-based workshops (MMA, 2007), potential effects of climate change (Ferro, Lemes, Melo, & Loyola, 2014; Lemes & Loyola, 2013; Loyola, Lemes, Brum, Provete, & Duarte, 2014) and detailed descriptions of remaining forests (Rappaport, Tambosi, & Metzger, 2015; Ribeiro et al., 2009; Tambosi, Martensen, Ribeiro, & Metzger, 2014). Still lacking are initiatives that consider complementary management actions for conservation of comprehensive sets of species under different socio-economic, climatic and land use change scenarios, thus restricting applications of

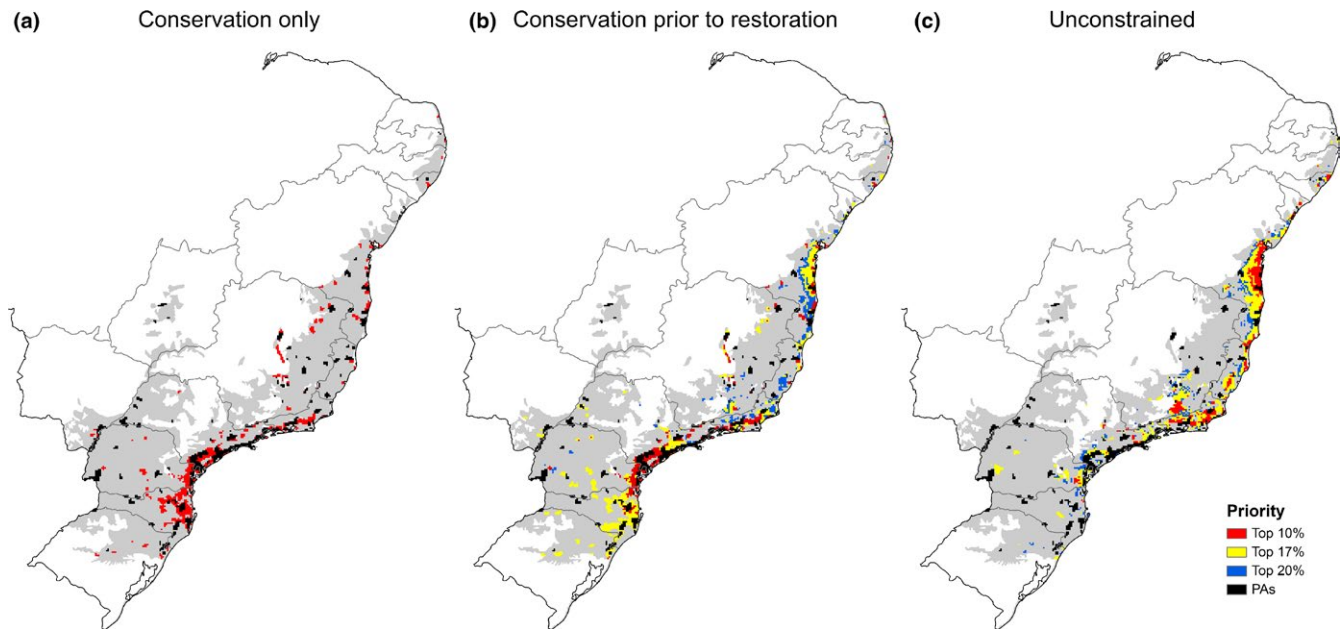


FIGURE 3 Spatial distribution of priorities for conservation targets of 10% (red), 17% (yellow) and 20% (blue) along with current protected areas (PAs) for different management scenarios under high greenhouse gas emissions forecasted to 2050

the dynamic sort of conservation strategy necessary to mitigate effects of global environmental changes and minimize conflicts and costs.

4.1 | Climate change and protected areas

Climate change and conversion of natural habitat to anthropogenic landscapes are considered the main threats to biodiversity in the Tropics (Asner, Loarie, & Heyder, 2010; Brodie, Post, & Laurance, 2012; Ferro et al., 2014; Lemes, Melo, & Loyola, 2013; Loyola et al., 2012). Protected areas have been shown to be essential for maintenance of biodiversity and mitigation of climate change effects (Araújo et al., 2011; Faleiro et al., 2013; Hannah et al., 2007). Even though the current network of protected areas in the Atlantic Forest is valuable in protecting woody plant diversity, our estimates show that it is insufficient to meet protection targets and mitigate effects of climate change. Two examples highlight the urgency of management actions. First, *Quiina paraensis* Pires, a tree species endemic to Brazil, also occurring in the Amazon Basin, could be extirpated from the Atlantic Forest by 2050 by shifting climate conditions. Second, *Pilocarpus microphyllus* Stapf ex Wardlew, an endangered medicinal plant used by both traditional communities and the pharmaceutical industry, could lose all natural populations to habitat reduction; as such, its long-term persistence depends on protection and restoration of natural habitats. The higher number of species inside protected areas in the scenario that considers restoration (“conservation prior to restoration”) stresses the importance and need for such efforts even inside protected areas (Ferretti & Britze, 2006).

The Atlantic Forest harbours striking numbers of plant species, with estimates ranging between 13,979 and 20,000 species (Forzza et al., 2012; Mittermeier et al., 2011). Because of the high dimensionality and complexity of its biodiversity, we selected a subset (woody

plant species) as surrogates to be used as an indicator group (Margules & Pressey, 2000). The extent to which woody plants are representative of other taxonomic groups is to our knowledge unknown. Nevertheless, our study represents the most comprehensive prioritization initiative in the Atlantic Forest in terms of number of species to date. While small decreases in species numbers in our comparisons do not seem much (or statistically significant), they may in fact signal hundreds or even thousands more species in other taxa, many still undocumented and undescribed (Forzza et al., 2012; Lewinsohn & Prado, 2005; Sobral & Stehmann, 2009). Our findings reinforce the potential of climate change and habitat reduction to drive extinctions of tropical plant species. Indeed, even if all current Atlantic Forest remnants are protected, species could still be lost without appropriate efforts towards management and restoration.

4.2 | Conservation targets and habitat management

Conservation targets are important in achieving goals in biodiversity conservation, yet they are rarely set and evaluated based on ecological knowledge (Soulé & Sanjayan, 1998; Tear et al., 2005). New protected areas are seldom established in a systematic manner, further endangering biodiversity (Venter et al., 2014). We found that, when a spatial conservation prioritization scheme was applied to maximize conservation outcomes, targets of 17% and 20% captured most species and represented on average 26%–34% of species' distributions. An alternative approach would be to set species-specific representation targets, based on area needs and population dynamics (Moilanen, 2007). However, such information is scarce for most tropical plants, greatly restricting its potential application. Given that forest remnants covered only 12% of the original Atlantic Forest extent considered here, conservation targets of 17% and 20% can only be achieved via

TABLE 2 Comparisons of representation of each feature between the management scenario of conservation of forest remnants prior to restoration of degraded habitat (“conservation prior to restoration”) and no a priori definition of action (“unconstrained”) within top priority sites for different conservation targets in the Atlantic Forest. Values represent the difference (loss is negative, gain is positive) in percentage of feature representation achieved by the conservation prior to restoration scenario under low and high greenhouse gas emissions scenarios in 2050

Features	Low emission			High emission		
	10%	17%	20%	10%	17%	20%
Biodiversity	-1.43	-3.90	-2.90	-1.39	-3.98	-3.08
Land use	0.97	6.48	6.34	1.19	4.23	3.94
Political willingness	-2.49	-7.38	-5.65	-2.74	-7.88	-5.12
Land cost	1.16	2.72	2.31	1.15	2.98	2.62

TABLE 3 Comparisons of representation of each feature between low and high greenhouse gas emissions scenarios within top priority sites for different management scenarios and conservation targets in the Atlantic Forest. Values represent the difference (loss is negative, gain is positive) in percentage of feature representation achieved by the low greenhouse gas emissions scenario in 2050

Features	Conservation only ^a			Conservation prior to restoration			Unconstrained		
	10%	17%	20%	10%	17%	20%	10%	17%	20%
Biodiversity	-0.47	–	–	-0.04	0.01	0.16	0.00	0.02	0.01
Land use	-4.16	–	–	-0.37	1.26	1.04	-0.15	-0.99	-1.37
Political willingness	-0.75	–	–	-0.35	-0.55	-1.22	-0.60	-1.05	-0.62
Land cost	-0.06	–	–	0.01	-0.02	0.00	0.00	0.24	0.30

^aComparisons restricted to current forest remnants; comparisons of 17% and 20% top priority sites are not possible for the “conservation only” management scenario, given that only 12% of the Atlantic Forest original extent is available for conservation.

restoration of degraded habitats. Identifying sites where conservation and restoration should take place is therefore urgent to implement effective management actions and enhance species' persistence.

Sites with high amounts of forest selected in the prioritizations represent candidate sites for efficient and low-cost conservation of biodiversity, in which establishing nature reserves, excluding anthropogenic impacts, and promoting forest regeneration would likely enable long-term persistence of woody plant species (Holl & Aide, 2011; Zwiener, Cardoso, Padiá, & Marques, 2014). These sites could be focus of payment for ecosystem services and habitat compensation, in which landowners receive financial support in return for setting aside private land (Banks-Leite et al., 2014). According to Brazil's Native Vegetation Protection Law, rural properties with native vegetation exceeding the minimum legal requirements may be used to offset a legal reserve debt on another property (Brancalion et al., 2016; Soares-Filho et al., 2014, 2016). Hence, forest remnant cells could be seen as primary targets for conservation; however, given the heterogeneous distribution of species, landscape factors (e.g. the spatial distribution of remnants, unforested matrix) and different quality of remnants (e.g. successional stage of forests and presence of exotic invasive species), they should be considered carefully. We advise strongly that forest remnant sites with potential for legal reserve compensation should also be selected based on clear environmental criteria, field assessments and in ecologically equivalent areas (Banks-Leite et al., 2014; Brancalion et al., 2016).

Although it would be desirable to have all sites with natural habitat included before selection of priority sites to expand a reserve network, such an ideal situation is, however, often unfeasible in much

of the Tropics. By comparing the “unconstrained” scenario with the “conservation prior to restoration” scenario, we could assess impacts of habitat reduction on prioritization solutions. Representation of beneficial factors (biodiversity and political willingness) and minimization of constraint factors (land use and cost) were clearly affected by availability of forest remnants. Neither biodiversity and political willingness are well represented, nor constraints are largely avoided, as the curves in Figure 2 are close to the 1:1 ratio. Ideally, one would see either curve approaching 1 on the y-axis much faster, which would reflect benefits for biodiversity protection, as well as working with the constraints. Our results demonstrate that meeting biodiversity targets within the constraints outlined here will be extremely difficult and that it is possible to reduce conflicts, but not avoid them altogether. In an ideal situation, the most effective prioritization solution would include top priority sites in regions where large forest remnants are no longer available for conservation. We found that the spatial pattern of habitat degradation has important implications for conservation planning, negatively affecting representation of biodiversity and implying higher cost and reduced efficiency.

4.3 | Climate change scenarios

Many factors must be considered when trying to anticipate how climate change will affect biodiversity (Thuiller et al., 2008). The intensity of changes is a key variable (Diniz-Filho et al., 2009). Considering different scenarios and understanding uncertainties is necessary to assess how robust different decisions or options may be under a wide range of possible futures (Moss et al., 2008). Prioritizations based on

the two climate change scenarios did not differ substantially in terms of the spatial configuration of top priority sites and representation of features, showing robustness of results in face of alternative futures. We reinforce, however, that using only species with ≥ 15 records, we excluded poorly sampled and highly endemic species (693), which may be the species most vulnerable to environmental changes (Moritz & Agudo, 2013). Exclusion of rare species may systematically underestimate certain important sites (Platts et al., 2014), possibly obscuring differences between climate change scenarios.

4.4 | Final considerations

Our main goal was to identify priority sites for complementing current protected areas, while accounting for different management actions, climate change scenarios, and socio-economic and political variables. To implement a comprehensive approach, we had to make assumptions that added uncertainty to results. For instance, we assumed that land costs and political willingness to act would remain constant over time; however, market fluctuations and governance instability may result in different patterns in the future (Soares-Filho et al., 2016; Strassburg et al., 2014). Prioritization solutions may also be affected by uncertainty associated with future scenarios and species' distributions (Lemes & Loyola, 2013; Merow et al., 2013; van Vuuren et al., 2011). Furthermore, we have considered forest remnant cells regardless of the quality and spatial distribution of remnants, when in fact most remnants are secondary and fragmented in the Atlantic Forest (Ribeiro et al., 2009). Habitat protection and restoration involve complex assessments and decisions; however, inclusion of all factors goes beyond the scope of this study, and as such, our results should be seen as indicative of the potential efficacy of future conservation and restoration efforts (Loyola, Kubota, da Fonseca, & Lewinsohn, 2009).

In this study, we explored the first stages of a multistage process, which aims at effective and systematic conservation of biodiversity. We show that, if a spatial conservation prioritization scheme considering complementary management actions is applied to the Atlantic Forest, reaching the 17% Aichi biodiversity target may constitute an important step towards protecting woody plant species. Most tropical forests face similar threats related to habitat reduction, fragmentation and climate change, so we believe that our results may represent patterns applicable in other threatened tropical forests. Expansion of protected areas will be necessary to compensate for altered species' distributions induced by climate change; however, additional efforts involving habitat restoration are urgently required to maintain Atlantic Forest biodiversity into the future.

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AUTHOR CONTRIBUTIONS

V.P.Z. collected and analysed the data; all authors conceived the ideas and wrote the manuscript.

DATA ACCESSIBILITY

Occurrence points and GIS files of accessible areas used to build niche models are available at <https://doi.org/10.17161/1808.23766>.

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BIOSKETCH

Victor P. Zwiener is a biologist with focus in plant ecology. His research interests cover various aspects of ecology, ranging from how different processes affect tropical plant diversity across multiple scales to applied ecology, providing ecological grounds for management actions.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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