

Forest regeneration may reduce the negative impacts of climate change on the biodiversity of a tropical hotspot

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Abstract

Aim: Evaluate how large-scale forest regeneration based on a low-cost restoration method may mitigate the effects of habitat loss and fragmentation associated to future climate changes on the distribution of birds and arboreal mammals in a tropical biodiversity hotspot; find areas with different current and future potential species richness and assess how passive restoration can reduce the risk of species extinction.

Location: Brazilian Atlantic Forest (BAF).

Methods: We built a forest regeneration scenario via a model of seed dispersal based on the potential movement of frugivorous fauna and projected the potential distribution of 356 bird species and 21 arboreal mammals based on Species Distribution Models (SDM) which employed 79,462 occurrence records and four algorithms for different climate and landscape scenarios. SDM were based on climate and landscape predictors separately and the results were combined into maps of species richness. Finally, we assessed the species' risk of extinction based on the species-area relationship.

Results: Without considering the effects of climate change, the potential distribution area for each species increases on average by 72.5% (SD = 8%) in the scenario of potential regeneration. Climate change decreases the area of potential occurrence of 252 species, which may suffer a mean reduction of 74.4% (SD = 9.3%) in their current potential distribution areas. BAF regions with the largest amounts of forest had the greatest potential richness of species. In future climate scenario, 3.4% of species may become extinct, but we show that large-scale regeneration may prevent these extinctions.

Main conclusions: Despite the possible negative impacts of climate change on the distribution of 67% of the studied species, which would increase the risk of species extinction, our analysis indicated that promoting large-scale BAF restoration based on natural regeneration may prevent biodiversity loss.

KEYWORDS

Atlantic Forest, birds, ecological niche models, primates, seed dispersal, species distribution models

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1 | INTRODUCTION

The modification of natural habitats is one of the main causes of the current biodiversity loss (Newbold, 2018). This can be especially relevant in tropical forests, which combine high species richness and severe fragmentation and area reduction (Alroy, 2017; Haddad et al., 2015). In addition to the ongoing modification of natural habitats, climate changes are imposing a challenge to biodiversity (Scarano & Ceotto, 2015). The changes on Earth's climate induced by human activities may cause further reductions and/or shifts on species distributions (Lyra et al., 2017; Parmesan & Yohe, 2003). Therefore, it is of utmost importance to understand the effects of the interplay between habitat loss, fragmentation and climate change for the conservation of natural habitats (Tilman et al., 2017).

Due to the interlinkages of ecological processes, conservation measures that address different threats to biodiversity in an integrated manner may have a greater chance of being successful (Díaz et al., 2020). In this regard, forest restoration can be employed to mitigate the effects of climate changes by promoting at the same time the carbon sink and biodiversity conservation functions of forests (Matos et al., 2020; Poorter et al., 2021). An analysis involving secondary tropical forests spread across different continents showed that the time for the recovery to 90% of old-forest conditions is less than a decade for soil and less than 25 years for plant functioning (Poorter et al., 2021). Tropical forests growing ~50 years after land abandonment may sustain tree species richness comparable to old-growth forests (Rozendaal et al., 2019), which also results in a substantial carbon stock increment (Martin, Newton, et al., 2013). Richness and density of primates rise significantly in tropical forests regenerating from only 5 to 19 years (Chapman et al., 2020), and both species richness and phylogenetic diversity of birds may be high in these forests (Hughes et al., 2020).

Unsurprisingly, forest restoration is considered one of the 17 UN Global Goals that addresses the main development challenges on sustainable development (goal 15, 'Life on Land'; <https://sdgs.un.org/goals>). Other global initiatives also aim to restore natural environments. The Convention of Biological Diversity suggests the restoration of 15% of all degraded lands in the planet (Latawiec et al., 2015), and an association between the IUCN and the Government of Germany have launched a global goal to restore 350 million hectares of forests (the Bonn Challenge; <https://www.bonnchallenge.org/>). Furthermore, in the year of 2021 the UN has launched the decade for restoration, a call for the protection and revitalization of ecosystems around the world (<https://www.decadeonrestoration.org/>).

To minimize the costs of allocating land for forest restoration, areas with greater potential for crop production may be cultivated while areas with low agricultural aptitude should be designed for the conservation of biodiversity (Latawiec et al., 2015). In addition of being restored through 'active regeneration' – that is, when a series of human interventions promote forest growth (e.g. planting trees) – degraded areas can be recovered through passive restoration (or natural regeneration), which occurs when the prior anthropogenic disturbance is ceased and forests can naturally recover (Brancaion

et al., 2016; Holl, 2017a). In addition to having lower costs as compared to active restoration, a meta-analysis indicated that natural regeneration was more effective in promoting the diversity of birds, plants, and invertebrates (Crouzeilles et al., 2017).

Although there are many studies about the effects of natural regeneration on biodiversity, most of them are carried out at local scales and relatively few explored the potential of large scale natural regeneration in tropical forests (Crouzeilles et al., 2017). In addition to advancing the understanding of the effects of the interplay between habitat fragmentation and climate change, studies that aim to disentangle how the large scale restoration of forests based on low-cost methods might influence species occurrence and their risk of extinction can be useful for identifying priority areas for conservation and the design of conservation actions and policies. In this context, we present how natural regeneration based on a seed dispersal model may affect the occurrence and the risk of extinction of species in a highly fragmented tropical forest domain, the Brazilian Atlantic Forest (BAF). The seed rain promoted by frugivorous animals on anthropogenic matrixes favours natural regeneration and can be used as a strategy to recover areas in large scales at relatively low costs (Chazdon, 2017; Figure 1). This may be especially relevant in tropical environments, where most trees are dispersed by animals (Corlett, 2017).

Thus, our aims are (1) to evaluate how forest regeneration may affect the amount of area potentially available for species occurrence, estimating its potential in mitigating the effects of climate change; (2) to identify areas with higher species richness that should be prioritized for biodiversity conservation; and (3) to estimate the chance of species extinction due to climate change by considering current landscapes and a potential regeneration scenario. We expected that forest regeneration could reduce the chance of species extinction by increasing the amount of forest within landscapes.

2 | METHODS

2.1 | Natural forest regeneration models and scenarios of landscape restoration

We first employed a model of potential natural forest regeneration based on the seed dispersal from forest patches into the matrix promoted by the movement of frugivorous animals (Niebuhr, 2018; Figures 1 and 2). After that, we projected the potential distribution of a set of selected species of forest birds and arboreal mammals (primates and sloths) in four different scenarios that considered both current and potential future conditions of climate and landscape. The two climate conditions were (1) the current and (2) a future climate scenario based on the expected climate change, while the two landscapes were (a) the current configuration of the BAF native forest remnants and (b) our scenario of BAF regeneration. We choose the taxonomic groups for which we predicted distributions because they are considered good indicators of habitat quality and are of conservation concern in fragmented environments (Arroyo-Rodríguez &

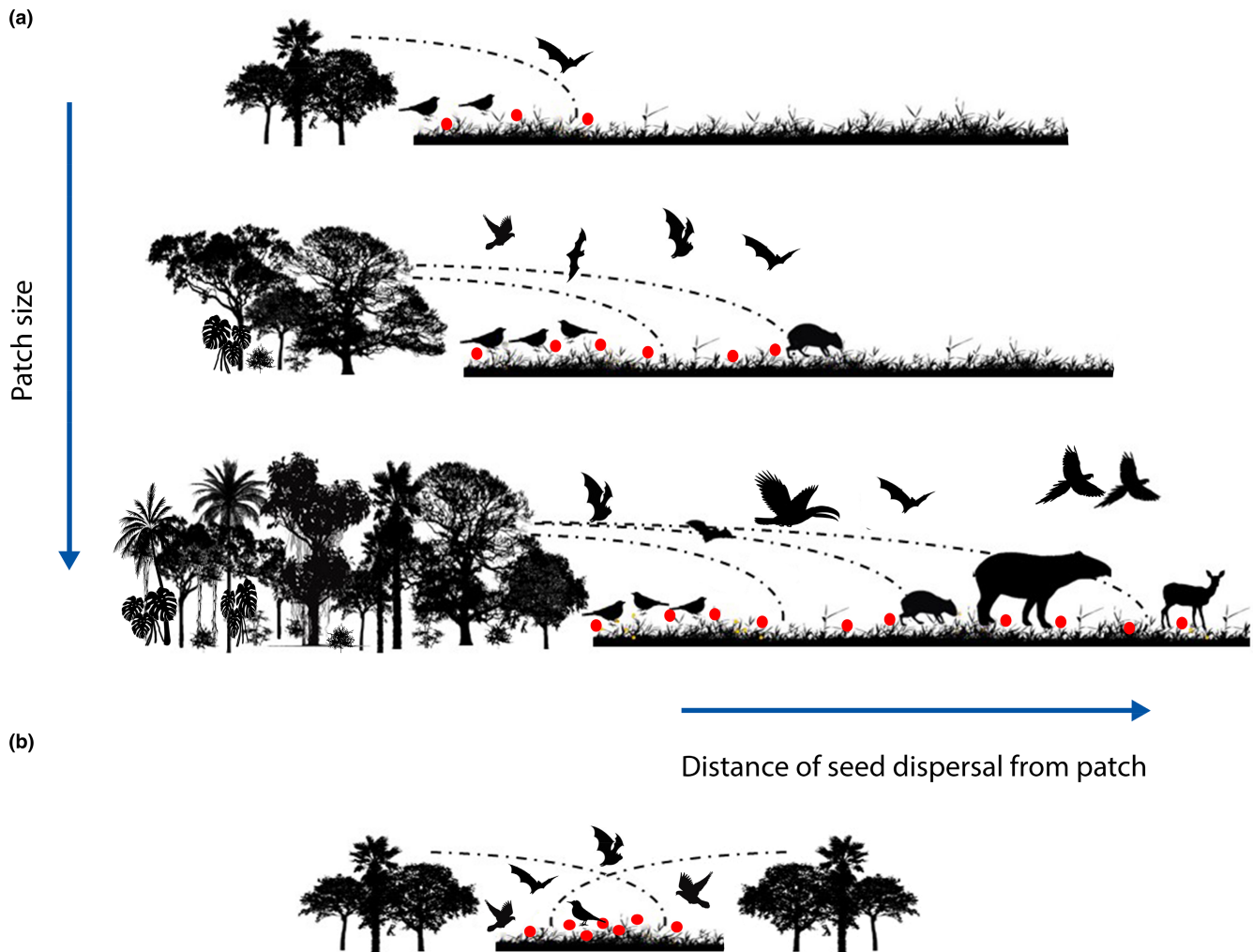


FIGURE 1 Scheme of the assumptions of our forest regeneration models. (a) Larger forest patches may sustain assemblages of frugivorous animals with greater species richness and abundances, increasing the rate of seed dispersal to the surrounding matrix and, consequently, the chance of natural forest regeneration. (b) As a consequence, the matrix in landscapes containing large amounts of forest fragments close to each other have greater natural regeneration. Seed dispersal (red dots) decreases as the distance from forest patches increases

Fahrig, 2014; Pizo & Tonetti, 2020), thus serving as environmental indicators of priority areas for biodiversity conservation.

The theoretical models of potential natural forest regeneration proposed here are based on three main ecologically rooted assumptions extracted from reviews and recent large-scale studies relating landscape ecology, seed dispersal, and natural regeneration. Our main assumption is that, since most of the seed dispersal is led by animals in the tropics (Corlett, 2017; Howe & Smallwood, 1982), places which receive a larger load of seed rain have the higher probability of natural regeneration, mainly degraded and open areas that are abandoned or subject to less intense human management (Molin et al., 2017; Silva et al., 2017). Second, we assume that the richness and abundance of the main frugivorous animals (e.g. bats, birds, non-flying mammals, reptiles and even invertebrates) increase within larger forest patches (Böhning-Gaese, 1997; Bovo et al., 2018; Kirika et al., 2008; Magioli et al., 2015; Figure 2). Accordingly, the higher the richness and abundance of frugivorous animals, the higher

the probability that they spread seeds around forest patches and for long distances (McConkey et al., 2012). Third, we assume that seed dispersal decreases as the distance of forest patches increases (Bullock et al., 2018; Camargo et al., 2020; Nathan & Muller-Landau, 2000; Figures 1 and 2). In combination, these assumptions mean that sites closer to larger forest patches have higher seed deposition, which leads to a higher potential for natural regeneration.

To operationalize these premises, we first classified BAF forest patches into five size classes, corresponding theoretically to different functional assemblages of seed dispersers (Table S1). The size classes were (1) up to 10 ha (<10), (2) between 11 and 25 ha, (3) between 26 and 50 ha, (4) between 51 and 250 ha, and (5) higher than 250 ha (Figure 2). Species abundance and diversity thresholds in tropical forests are generally assessed in terms of habitat amount in the landscape (e.g. Muylaert et al., 2016; Tambosi et al., 2014), but hardly using patch size and connectivity. In BAF, there is evidence that forest patches separated by size thresholds of 60 and 2050 ha

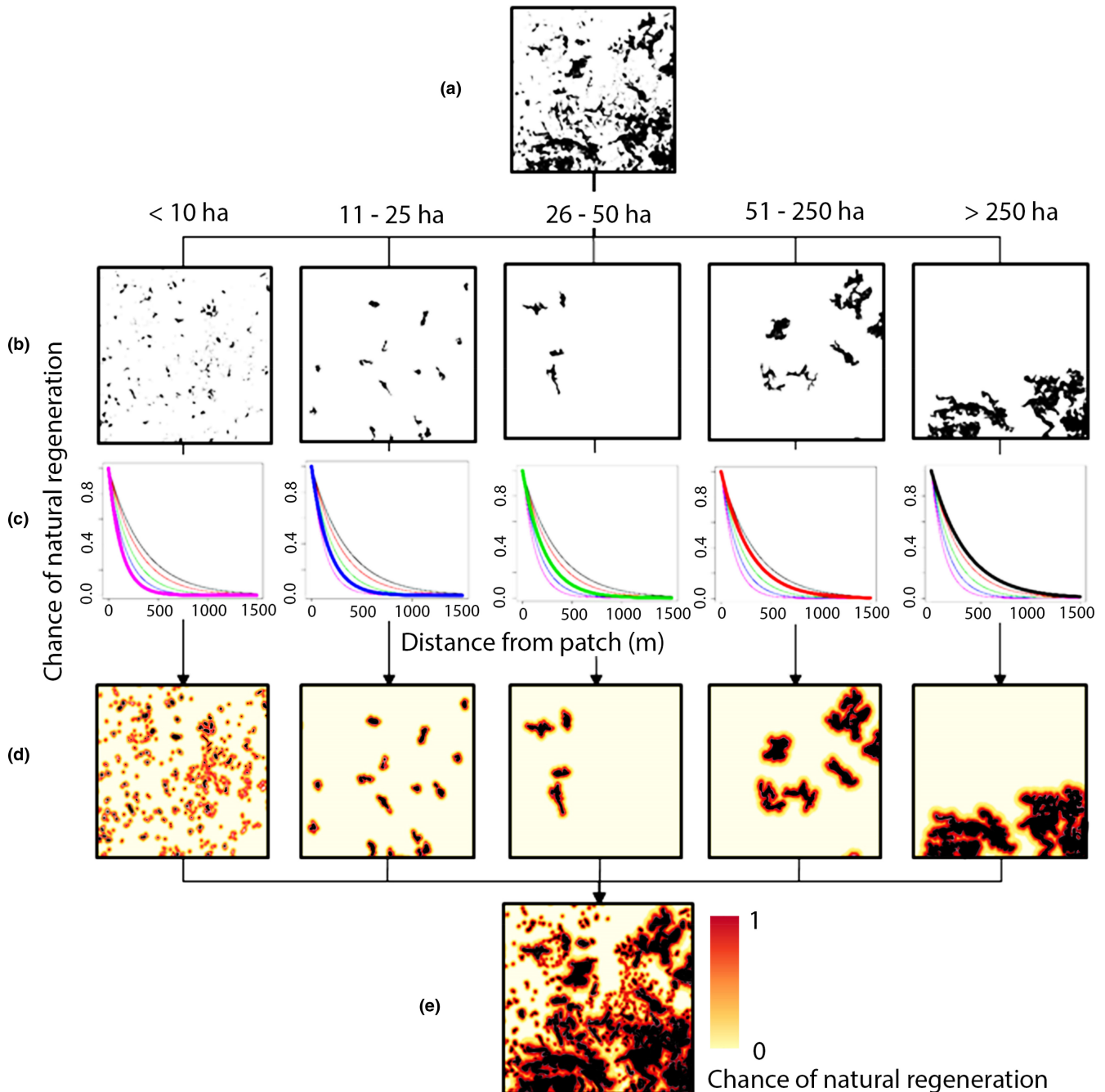


FIGURE 2 Flowchart for the elaboration of maps of potential of natural regeneration in the matrix. The forest remnants (in black) of a binary forest map (forest/non-forest; a) are classified into five patch size classes (b), and curves of forest regeneration potential are simulated for the fragments of each size class (c), so that individual maps (d) of forest regeneration potential of each fragment size class are created and summed into a final map of natural regeneration potential (e). The colour gradients in frames d and e indicate areas with different chances of regeneration, with red for higher chances and light yellow for lower

present different functional assemblages of mammals (Magioli et al., 2015).

We selected the above-mentioned patch size classes to allow for variation within the seed dispersal process derived from the smaller patches (<250 ha), which comprehend 95% of the forest patches in BAF (Ribeiro et al., 2009), and considering that a great part of the seed dispersal that leads to regeneration is driven by small bodied species (Galetti et al., 2013). We then created curves of potential

natural forest regeneration around these patches using an exponential function which assigns a decreasing chance of forest regeneration as one walks away from the edges of forest patches. The exponential distribution is defined by the scale parameter (λ), which determines the decreasing rate of the curves in relation to the distance of forest patches, varied among the different size classes of forest patches, according to an expected scale of mobility of the disperser animals (Table S1). Even though the decrease of these

curves alone is monotonic, when the curves of potential regeneration around multiple patches in different landscape arrangements are combined, complex spatial patterns of potential natural regeneration are created by our models (Figure 2).

Continuous values for the chance of seed dispersal (and consequently forest regeneration) were estimated for each pixel in the landscape, and they decrease as forest fragment distance increases (Figure 2). Although these values may be estimated for virtually any type of matrix, we established scenarios of forest regeneration only for pastures because BAF regeneration is more likely to occur in these areas (Latawiec et al., 2015). Pastures are more likely to be abandoned than other types of land use, allowing BAF and other tropical forests to regenerate (Rezende et al., 2015). Pasture map used in our analysis was developed by the Processing and Geoprocessing Lab (LAPIG; <https://www.lapig.iesa.ufg.br/lapig/>; Table S2; available in <https://pastagem.org>). Since this is an initiative to map Brazilian pastures, we considered only the Brazilian portion of Atlantic Forest. We established a threshold of 0.5 in the continuous values of forest regeneration to create a scenario of landscape restoration, that is, we assumed that all pixels with a potential natural regeneration of ≥ 0.5 would be converted to forests (Figures 1 and 2). Although arbitrary, with this threshold value our amount of forest regeneration is similar to the one proposed by the Atlantic Forest Restoration Pact. A chance of natural regeneration below 0.5 was considered too low for the analysis (see below; Cruzeilles et al., 2019; Melo et al., 2013).

2.2 | Study area

Extending from the Brazilian coast (from north-eastern to southern Brazil) to the inner southern parts of the continent, the Atlantic Forest is the second largest tropical forest domain in South America, and is mostly distributed in Brazil (99% of its area; Muylaert et al., 2018). Despite its high species richness and endemism, the Atlantic Forest was severely devastated in the last centuries, and only 28% of its native vegetation persist (Rezende et al., 2018; Figure 3). Moreover, most (80%) native forest patches are small (<50 ha) and distant from each other (1440 m in average; Ribeiro et al., 2009). The high latitudinal and altitudinal gradient of the Atlantic Forest causes great variation in climate and vegetation and its domain can be divided into different biogeographic regions (Figure 3). Due to limited availability of pasture data (see above), only the Brazilian portion of the Atlantic Forest was considered in our analyses (BAF; Figure 3).

High species richness and endemism associated with high devastation rates make the domain a priority region for biodiversity conservation (Myers et al., 2000; Pizo & Tonetti, 2020). Because forest remnants are fragmented and surrounded by different land cover types, BAF is an appropriate region for evaluating how natural forest regeneration may promote biodiversity in human-dominated environments. BAF delimitation and forest remnants considered in this study (Figure 3) were processed by the Spatial Ecology and Conservation Lab at the São Paulo State University, Brazil

(LEEC – UNESP) in an association with Agroicone, a Brazilian non-governmental organization (<https://www.agroicone.com.br/>) and are detailed in Table S2.

2.3 | Species distribution models

We projected the potential distribution of forest birds, primates, and sloths in BAF via SDM approach. SDM identifies areas with different suitability for the occurrence of species based on predictor variables (Guisan et al., 2017). We employed two categories of predictor variables – (1) climatic and (2) landscape. Species distribution at biogeographic scales (e.g. within a domain) is usually determined by climatic variables, while species occurrence at mesoscales, within a smaller regions, such as watersheds, are influenced by landscape ones (Peterson et al., 2011). We modelled species distribution separately based on climatic and landscape predictors and identified areas in which both predictors indicated suitability to species occurrence (Sobral-Souza et al., 2021; Figure 4).

Several SDM studies that predict species occurrence under future scenarios assume static conditions of landscapes, which may be unrealistic as land cover is usually dynamic (Martin, Van Dyck, et al., 2013). Some investigations have shown that considering different landscape scenarios in SDM may result in more accurate predictions (Regos et al., 2018; Visconti et al., 2016), probably because the different predictors (climate and landscape) that influence the distribution of species operate at different scales (Sobral-Souza et al., 2021).

To build the climate SDM we used the 19 WORLDCLIM 1.4 variables with 30-arc seconds resolution (~1 km). These variables are also known as 'bioclimatic' as they are biologically meaningful and derived from temperature and precipitation data collected in weather stations around the world (1960–1990 temporal range, <https://www.worldclim.org/data/v1.4/worldclim14.html>). We considered bioclimatic variables within BAF delimitation and, to avoid correlation among them, we applied a Variance Inflation Test (VIF) using the USD package in the R environment (Naimi et al., 2014). From the 19 variables, we eliminated those with VIF values ≥ 5 (Guisan et al., 2017), and used the remaining five, namely: mean diurnal range (bio 2); mean diurnal range/temperature annual range (bio 3); mean temperature of the wettest quarter (bio 8); precipitation of the wettest month (bio 13) and precipitation of the coldest quarter (bio 19).

In addition to the current climate, we projected the potential distribution of species for 2070 using the 6.0 representative concentration pathway (RCP). The emission of greenhouse gases is simulated by RCP scenarios according to different trends of human activity (IPCC, 2014). We opted for using an intermediated RCP scenario over the scenarios of highest (RCP = 8.5) and lowest gas emission (RCP = 2.6), as both are unlikely to occur and should not be used in environmental planning studies (Hausfather & Peters, 2020). To reduce the effect of uncertainty in the different general circulation models of the RCP scenario, we projected species distributions for three different models – MIROC ESM, HadGEM2-AO, and GFDL-ESM2G and averaged environmental suitability of these

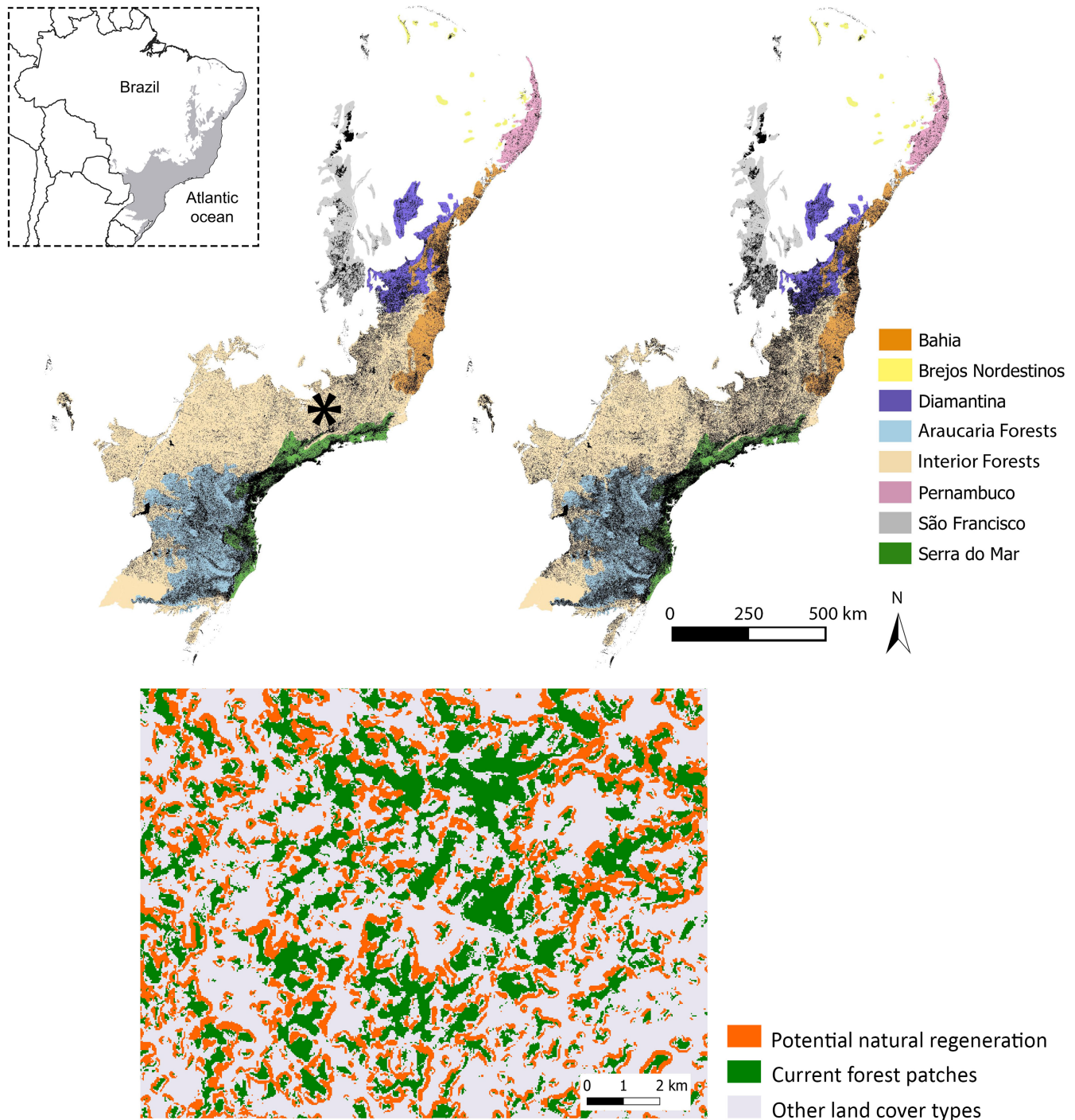


FIGURE 3 Biogeographical regions of the Brazilian Atlantic Forest (BAF) based on Silva and Casteleti (2003) and landscape scenarios used in our analysis. BAF forest remnants are in black. At the top left we show the current scenario of BAF landscape and, on the right, the scenario based on our potential forest regeneration model, with an increment of ~13 Mha of forests. At the bottom, a landscape is represented showing the current forest remnants in green and areas with natural regeneration potential on pastures in orange. Areas in orange are considered forest in our scenario of landscape restoration. The asterisk on the map at the top left indicates the location of the landscape

three models. We selected these models following Sanderson et al. (2015), that suggest choosing the models least related to each other.

To build the landscape SDM, we calculated the following landscape variables based on the BAF remnant map (30-m resolution): habitat amount, edge amount (edge depth = 30 m), functionally

connected area and patch size. The functionally connected area is the sum of the area of all patches closer than a gap-crossing distance – here we considered the value of 60 m. We used these variables because they are widely known to influence the occurrence of vertebrates (Baguette & Van Dyck, 2007; Fahrig, 2013; Pfeifer et al.,

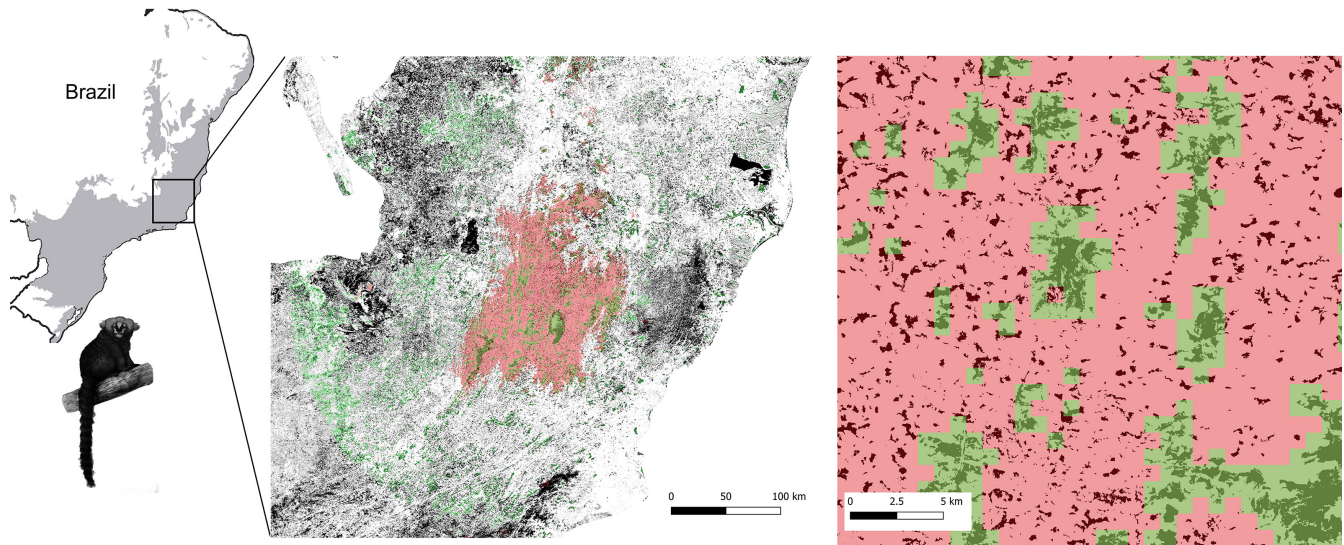


FIGURE 4 Results of species distribution models based on climate (in red) and on landscape predictors (in green) for one of the modelled species, the Buffy-headed Marmoset *Callithrix flaviceps*, in the scenario of current climate and current landscape. Note that there are areas where only either the climate or the landscape is suitable for the species occurrence. Only forest patches (in black) that presented both climatic and landscape suitability were considered to calculate the potential distribution area in the different scenarios

2017), and the value of edge depth and gap crossing were chosen based on the literature (Graham & Socha, 2019; Uezu et al., 2005). With the increase of forest amount in the regeneration scenario, it is expected that the values of the four landscape variables will also increase. Despite the relative value of edge amount in relation to habitat amount may diminish, its absolute value is also expected to increase (Figure S1). These variables were calculated for each landscape scenario (current and potential regeneration) with the aid of LSMetrics (Niebuhr, 2018; Niebuhr et al., 2020; https://github.com/LEEClab/LS_METRICS), a package designed to calculate landscape metrics in the GRASS GIS environment (Neteler et al., 2012).

For both habitat and edge amount, we considered a moving window of 2 km (i.e. for each central pixel we considered an average value of all pixels within a 2 km-distance). This distance was based on the scale at which the landscape may affect the occurrence of the studied species (Barros et al., 2019; Gestich et al., 2019). As elevation has proven to be an important variable in predicting species distribution (Guisan et al., 2017), we added this layer to the landscape variables and, after applying a VIF test (threshold value = 5), we removed edge amount to avoid high correlation among variables. After calculating landscape variables using 30-m pixel size, we resampled the data to the same resolution of bioclimatic variables (~1 km), a suitable resolution for SDM. We calibrated the SDM for the current landscape layers, in which species are currently distributed, and projected for both the current landscape and the potential regeneration scenario.

We downloaded species occurrence data with the aid of the spocc package in the R environment (Chamberlain, 2020) from the following databases: Global Biodiversity Information Facility (GBIF; <https://www.gbif.org>); iNaturalist (<https://www.inaturalist.org>); VertNet (<http://vertnet.org>); eBird (<https://ebird.org>) and Integrated Digitized Biocollections (iDigBio; <https://www.idigbio.org>). We

also considered primates and sloths occurrences in datasets of the Atlantic Forest region (Culot et al., 2019; Santos, Bocchiglieri, et al., 2019). We only considered primate and sloth data locations assigned as 'precise' or with a geographic accuracy of 1 km according to the authors (Culot et al., 2019; Santos, Bocchiglieri, et al., 2019). We excluded occurrence data recorded prior to 1980 to avoid mismatching between species presence and landscape features. The literature suggests that BAF forest remnants suffered no substantial changes in most of the domain from the 1980s onward (Ribeiro et al., 2009). Endemic birds considered in this study are listed in Vale, Souza, et al. (2018) and Vale, Tourinho, et al. (2018), non-endemic ones in Hasui et al. (2018), primates (endemic and non-endemic) in Reis et al. (2015), and sloths in Santos, Bocchiglieri, et al. (2019). We only considered species that have forest as main habitat type according to IUCN (<https://www.iucnredlist.org>) and included taxonomical synonyms in our searches.

To avoid spatial correlation and model overfitting, we spatially rarefied points keeping a distance of at least 10 km between them with the aid of the spThin package in R (Aiello-Lammens et al., 2015; Guisan et al., 2017; Peterson et al., 2011). To avoid potential location errors, we discarded species occurrence near biodiversity institutions, urban areas, state capitals and with zero decimal values for latitude and longitude with the aid of the package CoordinateCleaner in R (Zizka et al., 2019). Moreover, we plotted species occurrence and searched for potential outliers and records that failed to correspond to the expected distribution of the species based on our knowledge and on databases such as IUCN and Wiki Aves (<https://www.wikiaves.com/>). After these filtering procedures, we only modelled species with at least 10 occurrence points. We assumed this to be the minimum number of occurrences to sample a gradient of environmental variability adequate to estimate areas environmentally suitable for the species studied (Peterson et al., 2011).

As the study area in SDM should ideally consider the area accessible for the organisms (Barve et al., 2011), for each species we used a background region based on a minimum convex polygon of the occurrence points (comprising geographical extreme occurrences) and summed by a buffer of two coordinate degrees (~220 km). We then cropped variables for each species using the convex hull and sampled 5000 background points. We considered these types of backgrounds more adequate than using the entire BAF for all species, which could result in model overfitting and the overestimation of model evaluation (Barve et al., 2011; Guisan et al., 2017; Peterson et al., 2011). This approach is similar to other analyses employing SDM in BAF (Sales et al., 2021).

As there is no single best algorithm for use in SDM (Qiao et al., 2015), we combined the prediction of four different algorithms of presence-only data: bioclim, domain, random forest and maxent via the sdm package in R (Naimi & Araújo, 2016). For each species we ran 10 replicates of each algorithm assigning 70% of the occurrence points to training the models, and 30% to evaluate each run via bootstrapping (Peterson et al., 2011), resulting in 40 models per species for climate variables (four algorithms, 10 replicates) plus 40 models for landscape variables. Ensemble projections for the 10 replicates were performed via a weighted mean for the individual models based on a threshold that maximizes specificity +sensitivity considering the True Skill Statistic test (Allouche et al., 2006). We used the lowest presence-threshold in the raster of continuous values from the ensemble of the 40 individual models to create binary maps for each species (presence/absence; Liu et al., 2016). Then, we combined maps of climatic and landscape suitability and analysed regions where both landscape and climate were suitable for species occurrence (Figure 4).

After training the models for the current scenarios of climate and landscape, we projected the SDM for both current and future climate, current landscape configuration and future potential landscape regeneration. We added the binary maps of the potential distribution of species and identified areas with different potential species richness and suitable areas for the occurrence of species in the following scenarios: (1) current climate and current landscape, (2) current climate and future regenerated landscape, (3) future climate and current landscape and (4) future climate and future regenerated landscape. To calculate the area of occurrence of species in each scenario, we considered suitable areas only within forest patches. As forest patches may be small, to facilitate the visualization of species richness in different regions, we calculate the mean values of potential species richness considering only forest patches in hexagonal grids (~1000 km² hexagons, bottom line in Figure 5; see the potential species richness in forest fragments in Figure S2).

2.4 | Assessment of extinction risk

Based on the relation between geographical range and probability of extinction, we evaluated the percentage of species that would become extinct in the future in the two different BAF landscape

scenarios (current and with regeneration). We evaluated extinction risk assessment based on an equation developed by Thomas et al. (2004), which takes into account the average proportional loss of distribution area for each species: $E = 1 - \{(1/n) [\sum(A_{fut}/A_{original})]\}^z$ in which E is the proportion of extinct species, n , the number of species, A_{fut} , the future occupied area, $A_{original}$, the original occupied area and z , a constant that reflects the proportion of species overlap between areas (Tjørve & Tjørve, 2008). Based on the literature, we set $z = 0.25$ (Brooks & Balmford, 1996; Thomas et al., 2004).

3 | RESULTS

We identified ~34 million hectares (Mha) of native forest remnants in the BAF, while in our scenario of forest regeneration, the amount of regenerated forest sum 13 Mha (Figure 2). We predicted the potential distribution of 377 species in the four different scenarios (Figure 5): 356 of which are forest-dwelling birds and 21, arboreal mammals (19 primates and 2 sloths; Tables S3 and S4). We obtained 79,462 occurrence points (211 points per species on average; SD = 219; Figure S3) and 30,160 individual models were employed to predict distributions; half of them were based on climate and half on landscape predictors.

Without considering the effects of climate change, each species would have its potential distribution area increased by 72.5% on average (SD = 8%) in our scenario of forest regeneration (Figure 6, 'Current climate/regenerated landscape' bar; Table S5). Climate change alone may decrease the potential distribution of 67% of species, which represents a mean reduction of 74.4% (SD = 28.7%) in their potential distribution areas compared to the current landscape and climate scenario. For those species that may have their distribution areas reduced because of climate change, our regeneration scenario points to a mean increase of 75.3% (SD = 9.3%) in their future potential distribution areas ('future climate/regenerated landscape' scenario). In contrast, climate change may increase the potential distribution areas of 33% of species to an average increment of 10.5% (SD = 14.5%) of their current potential distribution ('future climate/current landscape' scenario). For these species, if our regeneration scenario also occurred, they would experience a mean increase of 54.6% (SD = 29.5%) of areas suitable to their occurrence.

Forest remnants that showed higher potential species richness concentrate mainly near the coast, in the Serra do Mar biogeographical region, the Araucaria region, in the central part of the state of Bahia and in the northern portion of Bahia interior forests (Figures 3 and 5). Brejos Nordestinos, Diamantina, São Francisco and Pernambuco regions presented lowest potential species richness. This pattern of species richness was consistent for all scenarios (Figure 5). In the future climate scenario, 3.4% of species may become extinct. When only species that may suffer reductions in their areas due to climate change effects are considered, 7.1% of them may disappear, a figure even higher if we consider endemic species (Table 1). Our regeneration scenario may zero the extinction

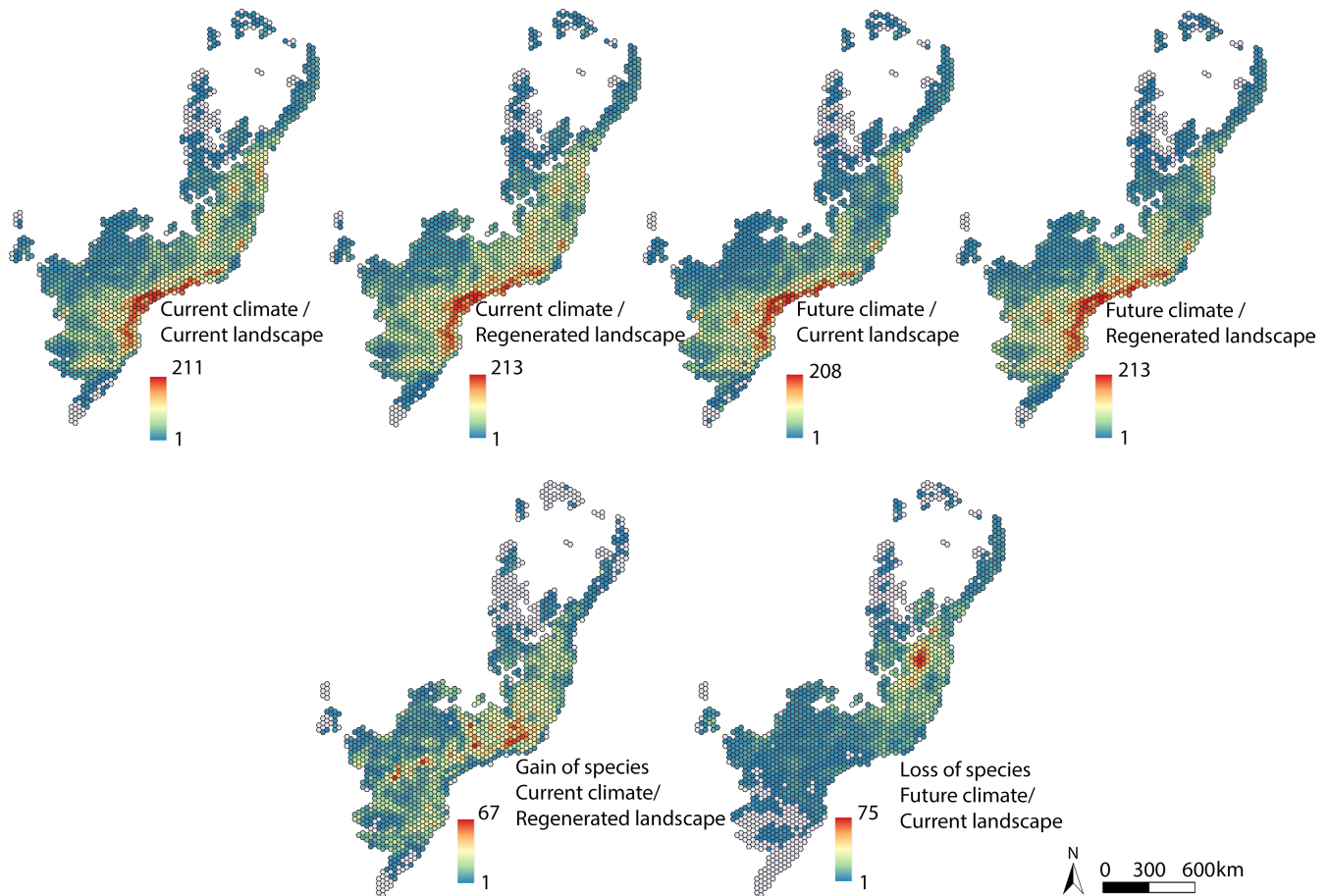


FIGURE 5 Potential species richness (maps at the top of the figure) of forest birds, primates, and sloths in the four different scenarios considering current/future climate (RCP 6.0) and current/regenerated landscapes. Maps at the bottom represent regions with different potential gains of species due to forest regeneration in the current climate and potential loss of species due to the effects of climate change in the current landscape. Species richness follows a colour gradient that varies from blue for lower values to red for higher. Areas in grey are those where the potential species richness is zero. To facilitate the visualization of potential species richness in different regions of the study area, maps represent the mean values of potential species richness considering only forest patches in a hexagonal grid (~1000-km² area)

probability of species, except for the endemic species that may suffer reductions in their distribution areas because of climate change, even with forest regeneration (Table 1).

4 | DISCUSSION

4.1 | Natural forest regeneration and biodiversity

Despite the possible negative impacts of climate change on the distribution of 67% of the studied species, our analysis indicated that, as expected, promoting natural forest regeneration at large scales may not only prevent biodiversity loss but also increase the potential distribution area of species that may be impacted by climate change in future scenarios. The 252 species that might be negatively impacted by climate change may suffer a reduction of 74.4% (SD = 28.7%) of their potential distribution area when considering future climate and current landscape scenarios. However, if our natural regeneration scenario is considered, these same species might increase their

potential distribution area by 75.3% (SD = 9.3%) in the future climate scenario (Figure 6). From these 252 species, except for six species that may zero their potential distribution areas with climate change regardless of the landscape scenario, the remaining species might increase their area of occurrence with forest regeneration. Several tropical forest species of birds and arboreal mammals, including endemic species, tolerate fragmented and secondary forests (Develey & Phalan, 2021; Pizo & Tonetti, 2020), which suggests that the regenerated environments could be used for many of the studied taxa (but see Santos, Bailey, et al., 2019).

Thus, as expected, with the increase of forest amount in the regeneration scenario as modelled here, it may be possible to reduce the proportion of species that would become extinct because of future climate change. In an assessment of the risk of extinction of Atlantic Forest birds due to deforestation, endemic species were the most vulnerable (Brooks & Balmford, 1996). Indeed, the potential loss of area of distribution due to climate change may also increase the extinction risk in different environments around the world, including other tropical forests (Thomas et al., 2004). Loss

FIGURE 6 Mean distribution area (in square kilometres) of the 377 species in each of the scenarios listed on the X axis. Lines represent the Standard Deviation, and numbers above the bars the percentage of area in relation to the current scenario

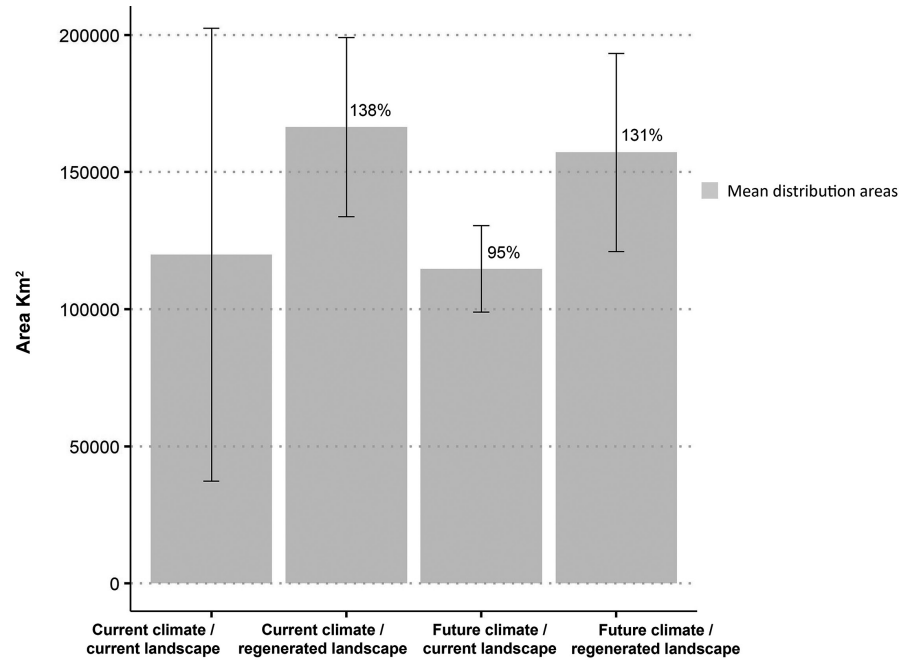


TABLE 1 Percentage of species that may become extinct under future climate conditions (RCP 6.0)

Species group	Future no-regeneration	Future regeneration
All spp (n = 377)	3.4	0
Endemics spp (n = 199)	4.9	0
All spp area reduced (n = 255)	7.1	0
Endemic area reduced (n = 136)	8.8	1.9

Note: *n* is the number of species in each group. *Future no-regeneration* corresponds to the scenario of future climate and current forest configuration in the Brazilian Atlantic Forest, and *Future regeneration* corresponds to the scenario of future climate associated with our regeneration scenario. *All spp* consider all species studied, *Endemic spp* refers to endemic species, *All spp area reduced* corresponds to the species that may suffer reductions in their distribution areas, and *Endemic area reduced* to the endemic species that may suffer reductions in their distribution areas.

of species may have deleterious cascading effects on biodiversity. Some studies have identified that endemic large-bodied birds (Vidal et al., 2014) and primates (Bufalo et al., 2016) are key elements involved in seed dispersal in tropical forests. Therefore, the loss of such large-bodied frugivores in BAF because of climate change may pledge seed dispersal systems with consequences for the dynamics of forest ecosystems (Sales et al., 2021).

Our models indicated that regions with higher forest amounts (such as Serra do Mar, Araucaria, and northern Bahia; Figures 3 and 5) have higher chances of natural regeneration and, thus, sustain a higher number of species, both in the present and future scenarios. Other studies found similar results (de Souza et al., 2011; Santos, Feltran-Barbieri, et al., 2020; Santos, Sobral-Souza, et al., 2020; Vale, Souza, et al., 2018; Vale, Tourinho, et al., 2018; Zwiener et al., 2017). When considering models based on landscape predictors only, species richness was higher in regions where landscapes have higher amounts of forest (Figure 4; Figure S4). These results were expected as the studied taxa are forest-dwelling species (Pizo & Tonetti, 2020; Reis et al., 2015; Santos, Bocchiglieri, et al., 2019).

Contrary to areas with high forest amount, regions where forest patches are small and distant to each other may show lower chance of forest regeneration and sustain lower potential species richness according to our models. Although some may presume that the higher the species richness the higher is the importance of an area for conservation, this must be interpreted with caution. In our study, some severely devastated regions that presented comparatively fewer potential species richness in all scenarios are relevant for the conservation of tropical biodiversity, as the Pernambuco Endemism Center in BAF (PEC; Figure 3). PEC is remarkable for its endemism of birds, mammals, and other groups, harbouring several species on the brink of extinction (Develey & Phalan, 2021; Garbino et al., 2018; Pizo & Tonetti, 2020). Therefore, when planning natural forest regeneration in large scales based on seed dispersal, it might be important to use restoration techniques beyond passive restoration to increase the amount of forest in landscapes with low amount of remaining forest (such as the PEC). These techniques may comprise the mixed restoration approach – that is, when less human input than used in active regeneration is employed. This has lower costs when compared to active regeneration and may increase the

chances of regeneration and decrease the time needed for new forest formations to be established (Brancalion et al., 2016).

4.2 | Forest restoration as an auxiliary measure of biodiversity conservation

Although secondary forests are relevant for the maintenance of species and ecological processes in human-dominated landscapes, older forests are crucial to preserve most of the original biodiversity and as sources of individuals that can establish populations in regenerated areas, especially in fragmented landscapes (Gibson et al., 2011). As in other tropical environments (e.g. Meyfroidt & Lambin, 2008; Smith et al., 2021), evidence shows a process of 'rejuvenation' of forests in BAF. Young forests increased at a rate of ~150,000 ha annually since 2000, however the loss of older forests occurred at rate of ~100,000–200,000 ha annually in the same period (Rosa et al., 2021). It is thus important that forest monitoring is carried out properly so that the allocation of areas for natural regeneration does not cause forest loss in other regions.

Regarding climate change, some of the imposed challenges to biodiversity may not be properly mitigated by increasing forest amount only. Population and community responses to altered climate may also drive complex changes on species interactions with consequences difficult to predict (Oliver & Morecroft, 2014), as for example, changes in phenology that can alter frugivory, seed dispersal, and pollination (Scranton & Amarasekare, 2017). With a more direct impact on forest regeneration, global warming is also expected to increase the frequency and intensity of fires in tropical forests, resulting in negative consequences to species persistence and to the growth of early forests (Herawati & Santoso, 2011). Added to the effects of fire, prolonged droughts caused by climate change may hinder seedling recruitment and survival, which may further compromise natural regeneration (Anderson-Teixeira et al., 2013). In sum, despite having several benefits, forest restoration should be seen as an auxiliary measure in the mitigation of the effects of climate change and landscape conversion and should be associated with policies that aim to drastically reduce carbon emissions and deforestation (Holl & Brancalion, 2020). Restoration policies that promote actions to enrich and accelerate the succession rate of secondary and regenerating forests might also be important, to account for the already increased loss of mature forests.

4.3 | Tropical forest regeneration and model limitations

The summed area of native forest remnants in our BAF map (~34 Mha; Figure 2) is similar to previous spatial analysis, which identified ~28–32 Mha of native forests in the domain (Rezende et al., 2018; Rosa et al., 2021). Our regeneration scenario indicated an addition of 13 Mha of forests in BAF (Figure 3), an area close to the 15 Mha of native forests that the Atlantic Forest Restoration Pact aims to

restore (Crouzeilles et al., 2019; Melo et al., 2013). The total area of pastures in BAF sum ~38 Mha. Therefore, for the amount of regenerated forests indicated in our study to be recovered (~13 Mha), 34% of current pastures need to be set aside for this purpose. Despite the area of regenerated forests in pastures indicated in our models seem excessive, studies suggest that the area of unproductive or underused pastures in BAF is also high – with the consequence that degraded pastures are often the land use class more prone to regenerate into forest (Silva et al., 2017). The cattle stocking rates in BAF are on average 1.17 animals per hectare, considered an extremely low production efficiency (Latawiec et al., 2015). It is estimated that 47% of pastures in Brazil could increase production by twice or even more (Santos, Feltran-Barbieri, et al., 2020; Santos, Sobral-Souza, et al., 2020). Thus, areas that could be allocated for conservation indicated in our regeneration model can be viable if productivity is increased in pastures that have low potential for forest regeneration.

Not all pastures that we identified as suitable to be converted into forests are unproductive and, thus, will not be destined for this purpose. Furthermore, although seed dispersal is one of the most important factors to promote forest regeneration, some other aspects may limit natural regeneration such as topography (Rezende et al., 2015; Silva et al., 2017), the past intensity of land use, and the amount of soil nutrient available (Crouzeilles et al., 2016; Mendes et al., 2019; but see Rozendaal et al., 2019). Socioeconomic factors such as the size of rural villages and the possibilities of farm credit might also influence how prone are landowners to convert their lands into crops, what might affect forest regeneration (Silva et al., 2017). Our model of forest regeneration is based on theoretical seed dispersal curves and their response to forest patch size and proximity and, although rooted in the literature, has limitations on its prediction of areas with higher potential of seed deposition and natural regeneration. Data-driven models that use seed dispersal data sampled at landscape-scale or natural regeneration data and take these aspects into account can generate more accurate results. For instance, Crouzeilles et al. (2020) developed a modelling approach based on machine learning algorithms to fit natural regeneration data from remote sensing to environmental and socioeconomic variables. Even though they used more complex models, they concluded that the most important variable to predict natural regeneration at large scales was the proximity to forest (Crouzeilles et al., 2020), which is the main assumption of our models. Therefore, we believe that data-driven approaches might have more reliable predictions locally and may be useful for driving location restoration planning, but do not change from our approach on a biogeographical scale.

Overall, most tropical forests have high potential for natural regeneration (Wright, 2010), which is also the case for the Atlantic Forest (Crouzeilles et al., 2019). There are evidences showing that even tropical regions where past land use intensity were high and forest cover low (~10%), the area of naturally regenerated forests was substantial (Baptista & Rudel, 2006; Brancalion et al., 2016; Crouzeilles et al., 2019; Lira et al., 2012; Mendes et al., 2019; Rezende et al., 2015). Moreover, the amount of degraded area is also large in other tropical regions (Lamb et al., 2005). This

suggests that our natural regeneration model may be a viable strategy to passively restore degraded areas in several tropical forest regions and pinpoint regions where natural regeneration may be more successful.

Regarding species distribution, although SDM is an adequate approach to predict species occurrence at large scales, some limitations should be considered. In addition to the intrinsic errors of models to detect all areas potentially suitable for a species indicating otherwise unsuitable areas (Guisan et al., 2017; Peterson et al., 2011), these models may not be adequate in predicting population parameters (Lee-Yaw et al., 2021). The risk of species extinction could be better estimated if variations of population size were assessed (<https://www.iucnredlist.org/assessment/process>). Moreover, despite considering the effects of landscape and climate on SDM may potentially improve predictions, some limitations need to be recognized, as the fact that climate and landscape might affect species disproportionately depending on the taxonomic group and the studied region (Betts et al., 2019; Newbold, 2018; Vermaat et al., 2017).

Finally, to be successful a landscape regeneration program must include multiple stakeholders, involve local communities, use democratic and inclusive approaches, and consider political issues, so that restoration is economically and socially viable (Díaz-García et al., 2020; Holl, 2017b). Summed to all factors expressed favouring tropical forest regeneration in our study area, the Atlantic Forest Law establishes that rural landowners are not allowed to suppress forest patches at intermediate and advanced stages of regeneration (http://www.planalto.gov.br/ccivil_03/_ato2004-2006/2006/lei/l11428.htm). This provides some protection to the recovering areas, increasing the chances of success of a large-scale regeneration program in the domain. Therefore, in sum, our study reinforces that the regeneration of a tropical forest domain can have high benefits for biodiversity, is feasible in economical and legislation terms, pending, however, the political will to effectively occur.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

All data (input, R and Python scripts, maps) used for the natural regeneration modelling is available in an Open Science Framework repository (<https://doi.org/10.17605/OSF.IO/XCASM>). Occurrence data were retrieved from publicly available data sources, as described in the Section 2.

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BIOSKETCH

All authors are broadly interested on spatial ecology and biodiversity conservation, especially in tropical environments. They conduct research that aim to guide the selection of priority areas for the conservation of biodiversity based on spatial modelling, on aspects of animal–plant interaction involving frugivory and seed dispersal, and on landscape and movement ecology.

Author contributions: All authors contributed to methodology design and reviewed the text. VT and BBN led data analysis. VT led the writing of the manuscript and the elaboration of figures. BBN contributed to major additions and revisions to the text.

SUPPORTING INFORMATION

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