



Natural forest regeneration on anthropized landscapes could overcome climate change effects on the endangered maned sloth (*Bradypus torquatus*, Illiger 1811)

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Climate change and habitat loss have been identified as the main causes of species extinction. Forest regeneration and protected areas are essential to buffer climate change impacts and to ensure quality habitats for threatened species. We assessed the current and future environmental suitability for the maned sloth, *Bradypus torquatus*, under both future climate and forest restoration scenarios, using ecological niche modeling. We compared environmental suitability for two Evolutionarily Significant Units (ESUnorth and ESUsouth) using two climate change scenarios for 2070, and three potential forest regeneration scenarios. Likewise, we evaluated the protection degree of the suitable areas resulting from the models, according to Brazilian law: PA—Protected Areas; PPA—Permanent Protection Areas (environmentally sensitive areas in private properties); and LR—Legal Reserves (natural vegetation areas in private properties). Finally, we calculated the deficit of PPA and LR in each ESU, considering the current forest cover. Forest regeneration might mitigate the deleterious effects of climate change by maintaining and increasing environmental suitability in future scenarios. The ESUnorth contains more suitable areas (21,570 km²) than the ESUsouth (12,386 km²), with an increase in all future scenarios (up to 45,648 km² of new suitable areas), while ESUsouth might have a significant decrease (up to 7,546 km² less). Suitable areas are mostly unprotected (ESUnorth—65.5% and ESUsouth—58.3%). Therefore, PPA and PA can maintain only a small portion of current and future suitable areas. Both ESUs present a high deficit of PPA and LR, highlighting the necessity to act in the recovery of these areas to accomplish a large-scale restoration, mitigate climate change effects, and achieve, at least, a minimum forested area to safeguard the species. Notwithstanding, a long-term conservation of *B. torquatus* will benefit from forest regeneration besides those minimum requirements, allied to the protection of forest areas.

Key words: Atlantic Forest, climate change, conservation, forest regeneration, landscape ecology, Pilosa, Xenarthra

Mudanças climáticas e perda de habitat são comumente identificadas como as principais causas de extinção de espécies. A regeneração florestal e as áreas protegidas são essenciais para amortecer os efeitos das mudanças climáticas e garantir habitat de qualidade para espécies ameaçadas. Avaliamos a adequabilidade ambiental atual e futura para preguiça-de-juba, *Bradypus torquatus*, tanto sob mudanças climáticas quanto florestais. Comparamos a adequabilidade ambiental em duas unidades evolutivas significativas (UES norte e sul) usando dois cenários de mudança climática para 2070 e três cenários de regeneração florestal potencial. Avaliamos os modelos resultantes quanto ao seu grau de proteção, conforme a legislação brasileira: Áreas Protegidas (AP); Áreas de Proteção Permanente (APP—áreas ambientalmente sensíveis em propriedades privadas); e Reserva Legal (RL—áreas de vegetação natural em propriedades privadas). Por fim, calculamos o déficit de APP e RL em cada UES, considerando a cobertura florestal atual. A regeneração florestal poderá mitigar os efeitos perversos das mudanças climáticas, mantendo e aumentando a futura adequabilidade ambiental. O UESnorte concentra áreas mais adequadas (21.570 km²; UESSul = 12.386 km²), com aumento em todos os cenários futuros (até 45.648 km² de novas áreas adequadas). Por outro lado, UESSul pode ter uma queda elevada em áreas adequadas (até 7.546 km² a menos). As áreas adequadas são, em sua maioria, desprotegidas (UESnorte—65,5% e UESSul—58,3%). Ainda assim, APP e AP protegem apenas uma pequena parte de áreas adequadas atuais e futuras. Ambas as UES apresentam alto déficit de APP e RL, evidenciando a necessidade de atuar na recuperação dessas áreas para realizar restaurações em larga escala, mitigar os efeitos das mudanças climáticas e atingir, ao menos, uma área mínima de floresta para preservar a espécie. Contudo, uma conservação de longo prazo de *B. torquatus* se beneficiará da regeneração florestal além dos requerimentos mínimos, aliada à proteção de áreas florestais.

Palavras-chave: Conservação, ecologia da paisagem, Mata Atlântica, mudanças climáticas, Pilosa, regeneração florestal, Xenarthra

Human-induced climate and land cover change are undoubtedly the two main current threats to biodiversity (IPCC 2021). Extensive regions are vulnerable to novel and disappearing climates (Williams et al. 2007), resulting in discernible shifts in species richness (Prieto-Torres et al. 2020) and distribution (Jose and Nameer 2020), and loss of suitable areas for viable populations (Zhang et al. 2020). The expansion of anthropogenic areas is the primary driver of habitat loss and fragmentation (Fahrig 2003; Leblois et al. 2017), hampering several ecological functions and processes that are vital to long-term conservation (Haddad et al. 2015; Moraes et al. 2018). Land cover change is responsible for 23% of global greenhouse gas emissions (IPCC 2021), stressing the existence of synergistic effects between the two factors, with unprecedented consequences for biodiversity (Sales et al. 2020; Oshima et al. 2021). Therefore, the status of species and populations in the future will depend on the interplay between current human activities, their effects on land use and climate, as well as how species will respond to such changes.

Forested areas play a fundamental role in regulating and mitigating the effects caused by climate change, guaranteeing a more sustainable future (Prevedello et al. 2019). The establishment of protected areas is of utmost importance to safeguard biodiversity; yet their spatially static location—even covering larger areas—may jeopardize their future effectiveness under climate change (Lovejoy 2006; Loarie et al. 2009; D'Aloia et al. 2019). Thus, effective long-term conservation ought to include goals that mitigate global warming such as restoration of degraded habitats, which has become a global conservation strategy, as stated by a number of international agreements and programs (e.g., Paris Conference on Climate Change, Union4Restoration, Aichi Biodiversity targets, Bonn Challenge, United Nations Decade on

Restoration), due to the rate and magnitude of climate change over the past decades. Natural regeneration is a cost-effective, gradual process that aims to restore the structural properties of degraded habitat to pre-disturbance levels (Chazdon and Guariguata 2016). Global analyses show that naturally restored tropical forests might take less than 25 years to achieve old-forest conditions in terms of soil and plant conditions (Poorter et al. 2021), about 50 years to sustain tree species comparable to old-growth forests (Rozendaal et al. 2019) and have higher biodiversity than actively planted forests (Crouzeilles et al. 2017). Additionally, it may be an affordable way to increase environmental quality for endangered species (Ferraz et al. 2021; Ramalho et al. 2021), and to contribute to restoration goals (Crouzeilles et al. 2020).

The Brazilian Atlantic Forest covers part of Brazil's east coast, extending to more inland areas in its southern distribution (Muylaert et al. 2018). The biome has been reduced to just over 28% of its original extent (Rezende et al. 2018), with only about 4% of its territory covered by protected areas (Silva et al. 2021). The deforestation rate of the Atlantic Forest increased 27% between 2018 and 2019 (Fundação SOS Mata Atlântica 2020), with only a few regions reporting an increase in forest cover (Baptista and Rudel 2006; Rezende et al. 2018). Due to its high level of disturbance, the region is highly vulnerable to overall global change (Bellard et al. 2014; Sales et al. 2020), with several impacts to its fauna (Souza et al. 2011; Ramalho et al. 2021; Tourinho et al. 2022) and flora (Zwiener et al. 2018). The combined effects of climate and land-use change might have unprecedented impacts on, at least, 67% of fauna species (Tonetti et al. 2022). Notwithstanding, the Atlantic Forest harbors an impressive biodiversity, composed of more than 20,000 species, from which about 40% are endemic (CEPF 2001), being considered a biodiversity hotspot (Myers et al. 2000).

The maned three-toed sloth (*Bradypus torquatus*: Bradypodidae) is endemic to the Brazilian Atlantic Forest (Hirsch and Chiarello 2012). As with all six species of extant sloths, *B. torquatus* is a forest-dependent species, exclusive folivore, with a strictly arboreal habitat, depending on trees for feeding, sheltering, moving, and resting (Chiarello 1998a), as well as for thermoregulatory behavior (Giné et al. 2015). This thermoregulation is an essential aspect, owing to its labile body temperature, that oscillates responding to environmental temperature (Giné et al. 2015). Thus, forest loss, apart from diminishing habitat availability and quality, may expose it to nonanalog (novel) climates, exceeding its thermal tolerances. Additionally, climate change may affect the structure, coverage, and composition of natural areas (Prevedello et al. 2019), by, for example, increasing drought periods and the incidences of wildfire (Pivello et al. 2021), further impacting the conditions and the supply of resources (Santos et al. 2016, 2019b). Because of these biological and ecological particularities, allied to its restricted distribution and decreasing population trend, the species is listed as Vulnerable in the IUCN red list, mainly due to habitat loss and climate change, combined with a restricted distribution in Atlantic Forest remnants of only four Brazilian states (Chiarello and Moraes-Barros 2014). The species is one of the top-priority species for conservation in Brazil (ICMbio Ordinance No. 702/2018), as it is urgent to understand how this threatened, range-restricted, forest specialist species may respond to prominent environmental pressures.

Using ecological niche modeling, this paper aims to: (1) evaluate current and future environmental suitability for *B. torquatus* throughout its distributional range, using natural forest regeneration and climate change scenarios; and (2) analyze the resulting scenarios according to current Brazilian environmental legislation by assessing the proportion of areas legally protected and their deficits. Hence, we aim to identify if the current protected areas in the Atlantic Forest, under climate change, may be adequate to safeguard suitable areas for the species. In this paper, we focused on an optimistic outlook to demonstrate the importance of forest cover to improve the future environmental suitability for this species, facing climate change, by contrasting one pessimistic scenario with two optimistic scenarios, in terms of different levels of forest regeneration. Specifically, we explored the combined effects of natural regeneration in pasture lands and climate change on environmental suitability by combining habitat and climatic suitability (Ramalho et al. 2021) for *B. torquatus*. Given its physiological and ecological characteristics described above (Chiarello 1998a; Giné et al. 2015; Santos et al. 2019b) and the Atlantic Forest regeneration potential (Crouzeilles et al. 2020), we hypothesize that natural regeneration could mitigate, at least partially, the deleterious effects of climate change by providing more suitable areas for the species.

MATERIALS AND METHODS

Study system and geographical space.—*Bradypus torquatus* has a restricted and fragmented distribution in the

Atlantic Coast Forest (Hirsch and Chiarello 2012; Santos et al. 2019a). Throughout its extent, the Atlantic Forest encompasses different vegetation types, and the ombrophilous (i.e., high rainfall tolerant) formations—preferred by *B. torquatus*—are located nearer coastal areas (Hirsch and Chiarello 2012). Overall, populations of *B. torquatus* are genetically structured: the northern lineages (Sergipe and Bahia states) diverged from those to the south (Espírito Santo and Rio de Janeiro states) to the point of being considered two distinct Evolutionarily Significant Units (ESUs; Schetino et al. 2017). This diversification probably occurred during the Miocene–Pliocene transition (Schetino et al. 2017), and the current natural boundaries between the two lineages are in northern Espírito Santo state. Consequently, from a conservation perspective it is crucial to treat these two lineages as if they were different species (Moreira et al. 2014; Schetino et al. 2017).

Considering the differences in evolutionary processes for both lineages, we opted to model current and future suitable areas separately for each *B. torquatus* ESU, as we assumed that the environmental conditions of each area could predict the units differently (Fig. 1). One of the key inputs in ecological niche modeling is the definition of the geographic space, that is, the space where one considers a species distributed (Soberon and Peterson 2005). We delimited it by selecting eight terrestrial ecoregions from the WWF data set—Alto Paraná Atlantic Forests, Atlantic Coast Restingas, Bahia Coastal Forest, Pernambuco Coastal Forest, Bahia Interior Forests, Pernambuco Interior Forests, Southern Atlantic Brazilian Mangroves, and Serra do Mar Coastal Forests (<https://ecoregions.appspot.com/>; Olson et al. 2001)—matching *B. torquatus* vegetation preference and nearby areas (Hirsch and Chiarello 2012) to avoid overprediction of the models (Peterson et al. 2011). We also included ecoregions from the most northerly areas since there are some historic and unconfirmed reports of species occurrence there (Hirsch and Chiarello 2012). The total geographic space covers coastal regions in eight Brazilian states and consists of perennial vegetation, sandbanks, and mangroves. ESUnorth (123,516 km²) encompasses the northern populations of the Atlantic Forest Biome, located in Sergipe (SE), Bahia (BA), and nearby states, while ESUsouth (114,420 km²) encompasses the southern populations, located in Espírito Santo (ES) and Rio de Janeiro (RJ), as shown in Fig. 1.

Presence data and sampling bias.—We compiled 638 presence records of *B. torquatus* from the Neotropical Xenarthrans data paper (Santos et al. 2019a; https://github.com/LEEClab/Neotropical_Xenarthra), which includes data from species-Link, GBIF, and other important data sets. To avoid uncertainties, we performed a three-step filter selection: (1) exclusion of records with coordinate accuracy above 100 m, as the data paper included information about coordinate precision, in meters, allowing us to select only location points and not localities; (2) exclusion of apprehensions, interviews, road kills, and indirect vestiges records (species trace elements that

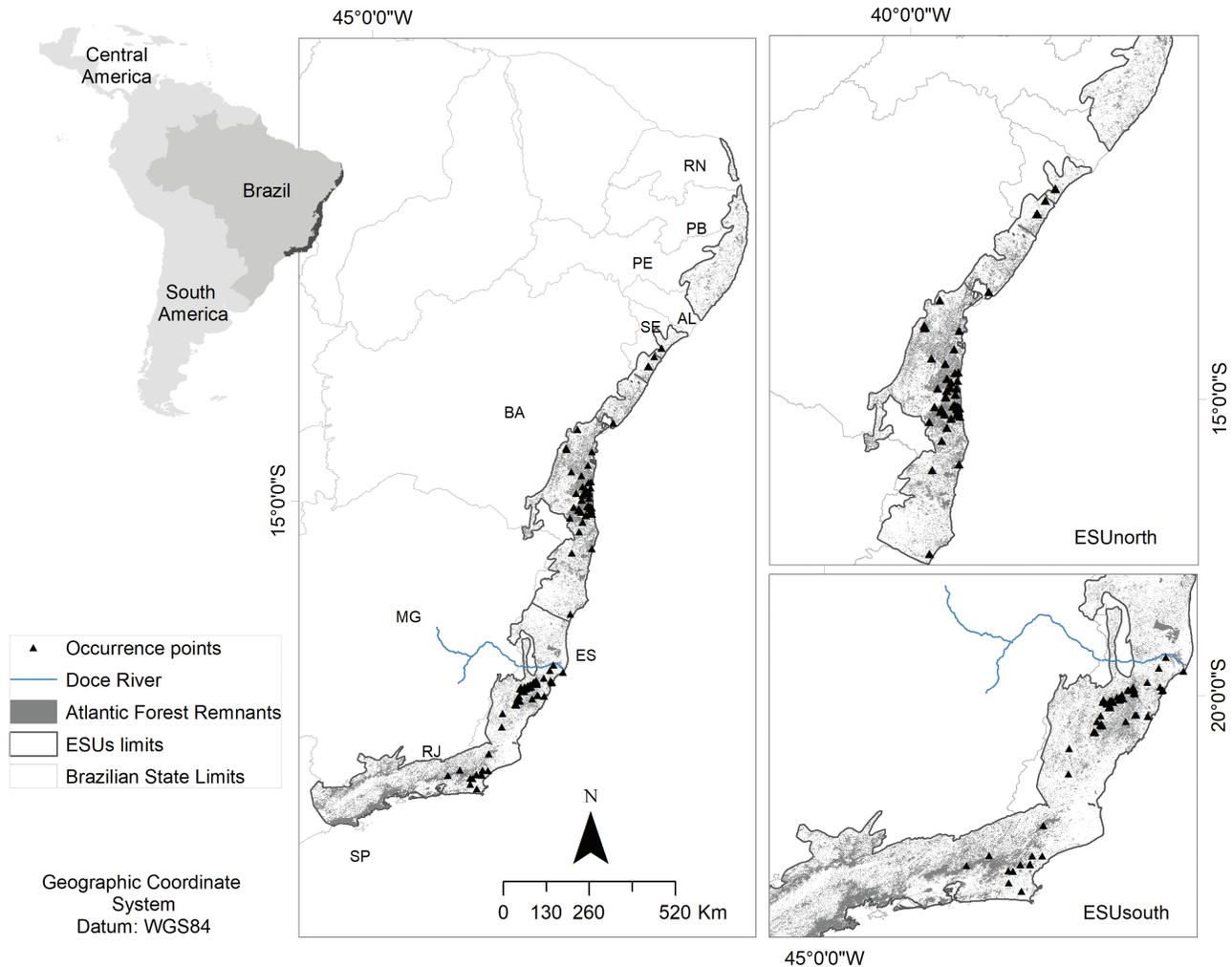


Fig. 1.—Geographical space for each of the Evolutionarily Significant Units (ESUs) of *B. torquatus* in the Atlantic Forest, Brazil. Letters indicate Brazilian states. RN—Rio Grande do Norte; PB—Paraíba; PE—Pernambuco; AL—Alagoas; SE—Sergipe; BA—Bahia; MG—Minas Gerais; ES—Espírito Santo; RJ—Rio de Janeiro.

cannot be reliably identified) since these might not be accurate regarding species identification and geographic location; and (3) selection of data obtained from 2009 to the present, to be temporally consistent with the environmental data used. We kept records without precision information to check the data origin, since they may integrate reliable data set (Hirsch and Chiarello 2012).

Before establishing the final data set of confirmed presences, we checked if all records were in forest fragments, resulting in 176 independent points: 99 from ESUnorth and 77 from ESUsouth (Fig. 1). Next, we developed a sampling probability surface to reduce the sampling bias in areas more intensely sampled than others by decreasing the weight of these locations (Phillips et al. 2009). The bias grid was created by calculating the Gaussian Kernel density of the sampling locations within 30 km of distance. This value best represents the two large clusters of occurrence records—in the south of Bahia and the mountain region of Espírito Santo.

Environmental predictors and climate scenarios.—To fit the environmental suitability models, we used elevation and

climate variables for both current and future climate change scenarios, and two landscape variables that changed according to the forest regeneration scenarios.

We obtained the elevation data (30 arc-seconds) through USGS (United States Geological Service; [Supplementary Data SD1](#)). To assess current and projected climatic conditions, we used 19 bioclimatic variables from WorldClim V1.4 (Hijmans et al. 2005), as this older version contains climate projection with high resolution (0.0083 arc-seconds). We performed a Principal Component Analysis (PCA) with the current climate data set, based on a correlation matrix, to reduce multicollinearity and avoid the subjectivity of selecting an arbitrary random variable set. In the geographic space of each ESU, we used the first six principal components (PCs)—which explained 95% of the variance from the original data set (De Marco and Nóbrega 2018)—to create current models and generate projections on future climate data ([Supplementary Data SD2](#)). Therefore, we maintained the proportion of variation and importance of each variable constant for both the present and the future scenarios, through the “PCA” and “PCAprojection” functions, in the

ENMGadgets R package (<https://github.com/narayanibarve/ENMGadgets>).

We used the climatic projections of the fifth assessment report from the Intergovernmental Panel on Climate Change (IPCC 2014) and considered two different greenhouse gas emissions for 2070 (mean for the period from 2061 and 2080). The Representative Concentration Pathway (RCP) 4.5 represents a mid-range emission scenario, while the RCP 8.5 constitutes a high emission scenario (van Vuuren et al. 2011). For each RCP, we considered three of the best Global Climate Models (GCMs) for the Atlantic Forest—ACCESS1-0, HadGEM2-ES, and MIROC-ESM (Vale et al. 2009).

The two landscape variables chosen for modeling were proportion of forest cover and proportion of pasture lands (Supplementary Data SD1), previously identified as important predictors of *B. torquatus* occupancy (Santos et al. 2019b). We calculated forest and pasture cover (in percentage, in a 1-km buffer) in current and future through the software GRASS-GIS 7.4.4 (Neteler et al. 2012).

Atlantic Forest regeneration scenarios.—We used a map of natural regeneration potential in pasture areas with pixels ranging from 0 to 100, where higher values stood for the greater potential for regeneration (Tonetti et al. 2022; see Supplementary Data SD3 for a detailed description of regeneration modeling approach; see also the online database from Niebuhr et al. 2021; <https://osf.io/xcasm/>). This map considered the landscape structure (fragment size and connectivity; Fig. 2) and the movement of the seed-dispersing fauna (Chazdon

2012; Markl et al. 2012; Côrtes and Uriarte 2013; Fuzessy et al. 2017) to predict natural regeneration based on the chance of seed dispersal from forests to the surrounding nonforest matrix. In this map, areas with large and nearby fragments—which theoretically correspond to higher diversity areas—have a higher potential of natural regeneration, since their surrounding matrix is more susceptible to receive a higher load of seeds (Fig. 2).

From this map, we created two scenarios of potential future natural regeneration by combining the present landscape structure with thresholds of natural regeneration potential. They consisted of a minimum and a maximum regeneration scenario. These scenarios considered that all pixels with natural regeneration potential value higher than a given threshold would likely become forest in the future. In the minimum regeneration scenario, we aimed to achieve a minimum amount of forest cover in the landscapes that would guarantee the occurrence of maned sloths. This value is 35% of forest cover, based on forest requirements of maned sloths (Santos et al. 2019b). We first calculated the minimum area that would need to be regenerated in geographic space for each ESU. Secondly, we selected pixels higher than a certain regeneration potential threshold, so that the accumulated area (km²) reached 35% of forest cover (Supplementary Data SD4).

In the scenario with maximum regeneration, we designed a landscape that attained the maximum possible regeneration, by assuming all pixels with regeneration potential higher than one would likely become forests in the future. Given these future scenarios, the landscape variables described in the previous

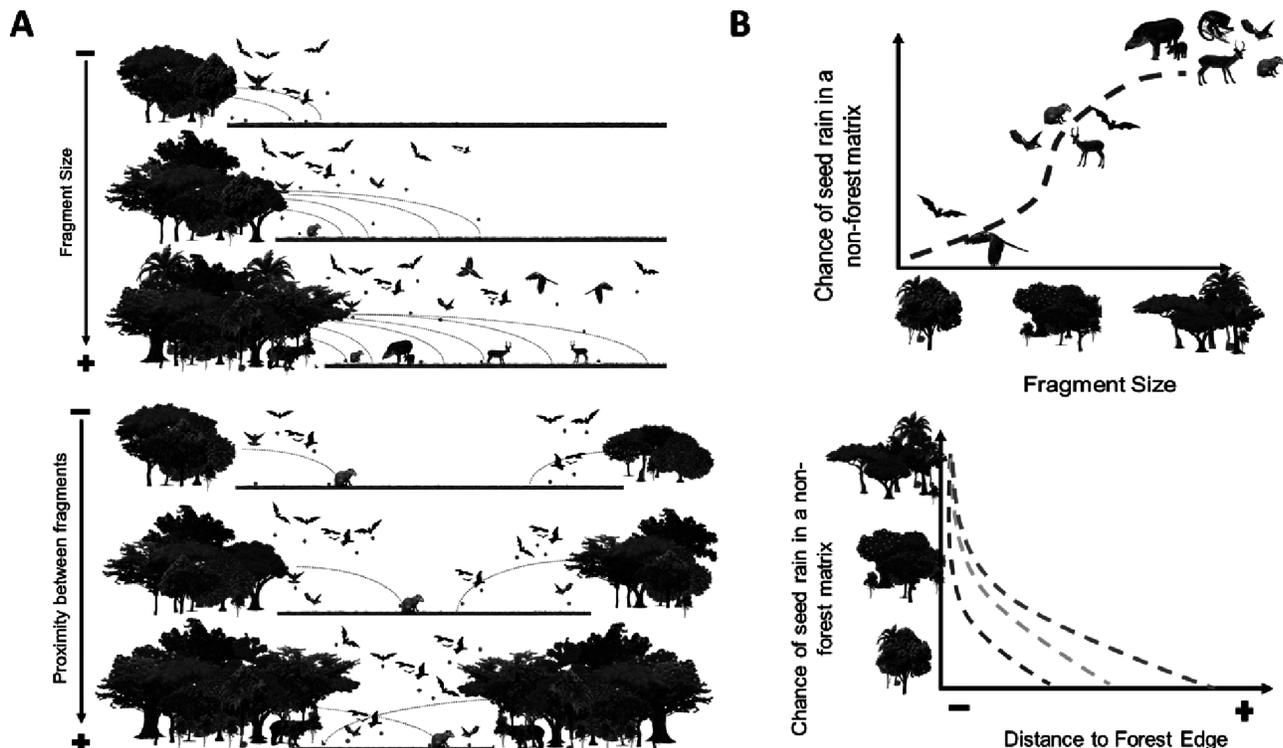


Fig. 2.—Graphical representation of the regeneration potential map construction. (A) Graphical hypothesis; (B) assumptions of the theoretical model of regeneration based on the chance of seed dispersion, considering the spatial structure of the landscape. “+” = increase; “–” = decrease.

section were recalculated to be used as input for the prediction of the environmental suitability maps.

Next, we developed future environmental suitability models from these landscape, climate, and elevation variables (Fig. 3). The first scenario of future suitability (FS), FS_REGzero, projects future climate without forest regeneration, analyzing the losses/gains of suitable areas only from a climatic perspective, being considered a more pessimistic and destructive scenario. The second scenario, FS_REGmin, projects future climate and a moderate landscape change, implementing a minimum regeneration, from the perspective of the species requirements (Fig. 3). Finally, the third scenario, FS_REGmax, projects future climate and more substantial changes in the landscape through the implementation of a maximum regeneration (Fig. 3). Hence, we were able to compare different perspectives on forest regeneration importance, contrasting one pessimistic scenario (FS_REGzero) and two optimistic scenarios (FS_REGmin and FS_REGmax). All the environmental variables were resampled to a spatial resolution of ~1 km (0.0083 arc-seconds geographic and WGS84 Datum) for the modeling.

Ecological niche modeling.—We generated the ecological niche modeling through the Maximum Entropy algorithm

(Phillips et al. 2017), a modeling technique with high accuracy and performance, highly adequate for our data (Roura-Pascual et al. 2009). Current environmental space was extrapolated into novel environmental combinations in future scenarios by assigning the option “projection layer directory file” (Barry and Elith 2006) in the Maxent version 3.4.3 (http://biodiversityinformatics.amnh.org/open_source/maxent; Phillips et al. 2017). We calibrated the current models using bootstrapping methods with 10 random partitions, with 70% of the presence points for training, and 30% for testing. All models were generated with a convergence threshold of 10^{-5} with 500 interactions, 0.5 of prevalence, 10,000 background points, using the regularization multiplier default from Maxent (=1), output models = Cloglog, and the generated bias file to minimize model overfitting. To evaluate the performance of the resulting test models, we calculated the Area Under the Curve (AUC) of the Receiving Operator Characteristic, and the True Statistical Skills (TSS) of the average of the 10 random partitions. We considered successful models with an excellent discriminatory capacity between generated and random models when $AUC > 0.7$ and $TSS > 0.5$ (Allouche et al. 2006; Elith et al. 2006). Finally, we used a jackknife test to measure the relative importance of each variable in model performance.

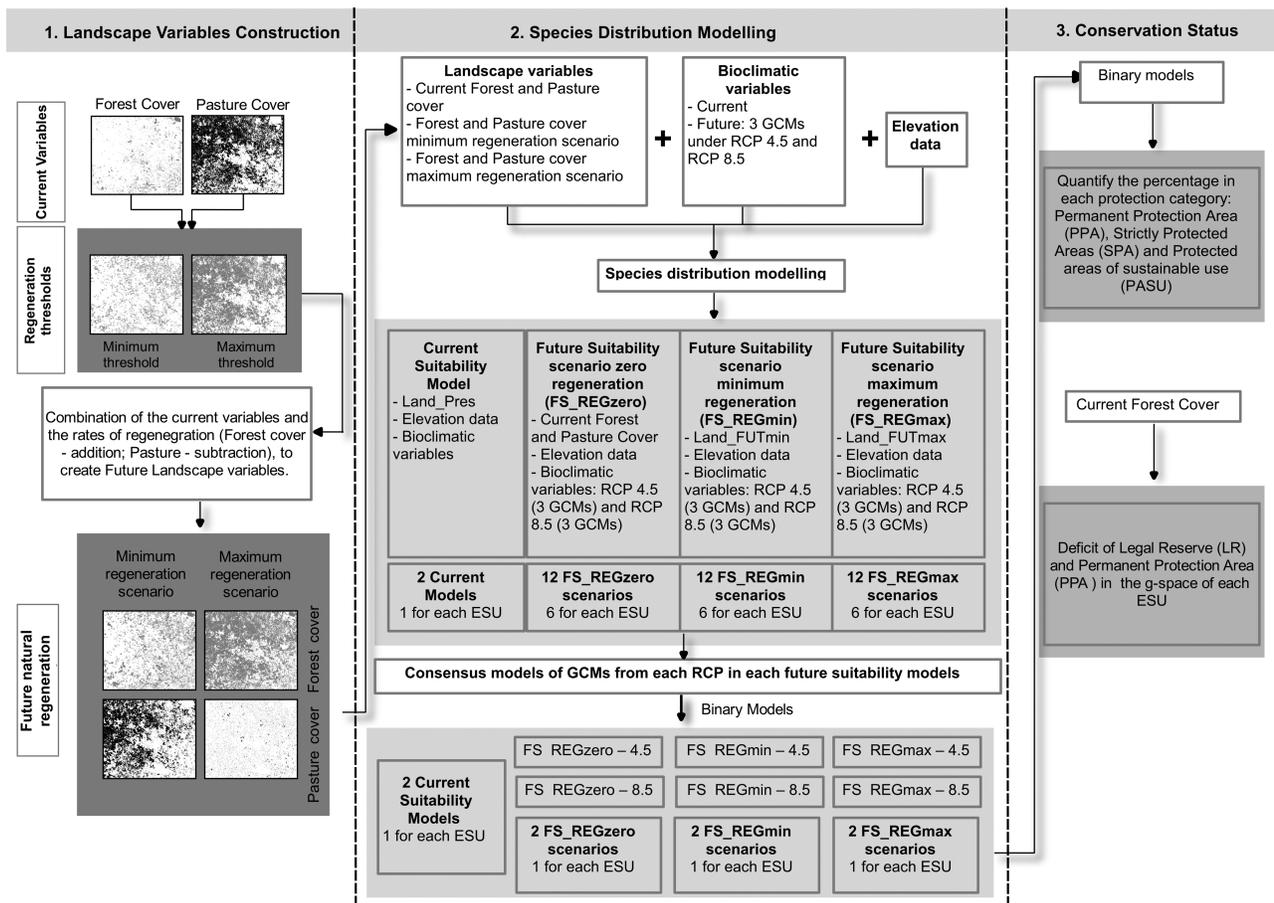


Fig. 3.—Workflow of the main steps used for building current and future species distribution models for the *Bradypus torquatus* within Atlantic Forest, Brazil. Both Evolutionarily Significant Units (ESUs) pass through the same process. FS_REGzero—no regeneration scenarios; FS_REGmin—minimum potential regeneration scenarios; FS_REGmax—maximum potential of regeneration scenarios.

After model fitting, we had a total of 38 models (1 current model (landscape + climate) + 3 different regeneration scenarios * 2 climate change scenarios (* 3 Global Climate Models) = 19 * 2 ESUs = 38 models; Fig. 3). These models were converted into binary maps to discriminate between suitable and unsuitable areas, applying an average threshold rule which maximizes the sum of the model sensitivity and specificity (ESUnorth = 0.2897; ESUsouth = 0.271; Liu et al. 2013, 2016). Binomial probability and omission error were also evaluated. We produced consensus models by adding all the Global Climate Models resulting from each RCP to the final maps containing only the pixels predicted simultaneously in the three RCPs, reducing to 12 (six for each ESU) models (Fig. 3), through the extension BioDinamica (Oliveira et al. 2019), from DinamicaEgo software (Soares-Filho et al. 2009).

Conservation status of suitable areas.—In Brazil, different areas might be classified within different conservation criteria. The National System of Conservation Units (SNUC, Law 9985/2000) establish the types and functions of protected areas in Brazil, from different jurisdictions levels (federal, state, and municipal). They are classified as Strictly Protected Areas (SPA, IUCN Protected Areas Categories I–II; Dudley 2008) or as Protected Areas of Sustainable Use (PASU, IUCN Protected Areas Categories III–VI). Another current law in Brazil is the Brazilian Native Vegetation Protection Law (LPVN, Law 12727/2012), which establishes different protection categories in areas not covered by the National System of Conservation Units: Permanent Protection Area (PPA), that require landowners should preserve riparian forests in river springs, riverbanks, lakes, lagoons, hilltops, and steep slopes (Supplementary Data SD1); and Legal Reserves (LR), to preserve natural vegetation areas in private areas (20% of property in the Atlantic Forest).

We used the current and future maps of species distribution to assess the conservation status of the suitable areas. We divided the study area into polygons corresponding to areas with different conservation enforcement (or status) and quantified the percentage (%) of area suitable to the maned sloth in these polygons, within four categories: (1) PPA; (2) SPA; (3) PASU; and (4) regions Outside Protected Areas (OPA). Lastly, for an environmental balance overview, we calculated the deficit of LR and PPA in the geographic space of each ESU, proportional to the current forest cover within LR and PPA. Further information about databases accessed are in Supplementary Data SD1.

RESULTS

The current distribution models for the maned sloth performed well for both ESUs (ESUnorth: TSS = 0.774, AUC = 0.922 ± 0.018, omission = 5.3%, $P < 0.001$; ESUsouth: TSS = 0.825, AUC = 0.952 ± 0.011, omission = 3.3%, $P < 0.001$). The models predicted suitable areas for *B. torquatus* of 21,570 km² in the ESUnorth (with proportionally more suitable areas), and 12,386 km² in the ESUsouth, corresponding to 17.5% and 10.8% of the total geographic space, respectively. Overall, two

areas of the *B. torquatus* range stand out for their high suitability: South Bahia and Center-South Espírito Santo states (Fig. 4). Most of the variation in the environmental suitability was associated with forest cover for both ESUs (Forest contribution in ESUnorth = 81.1%, Forest contribution in ESUsouth = 58.5%; Supplementary Data SD5).

ESUnorth and ESUsouth presented different patterns of suitable areas, for current models and future scenarios. ESUnorth will gain suitable areas in all climate and regeneration scenarios (Fig. 4). Specifically, under the scenario of no regeneration (FS_REGzero), suitable areas will slightly increase, reaching 15,558 km² in gains by 2070, with more substantial gains under FS_REGmin and FS_REGmax (up to 45,648 km² in gains; Supplementary Data SD6). Conversely, ESUsouth presented a different pattern (Fig. 4). Considering a zero or a minimum regeneration, combined with most pessimistic emission predictions, this region will suffer a decrease in suitable areas (Fig. 4). An increase in suitable areas will only occur in the best climate scenario with some regeneration (FS_REGmin-RCP 4.5) or in the maximum regeneration scenarios (FS_REGmax-RCP 4.5 and FS_REGmax-RCP 8.5).

Both ESUs also differ concerning current and future suitable area locations and dynamics. Currently, ESUnorth concentrates suitable areas on the Atlantic Coast, while future increments are more likely to occur further inland (Fig. 4). Suitability loss is located mainly inland, near the western limits of the geographic distribution of the maned sloth (Fig. 4). Conversely, suitability gains will most likely take place near the Atlantic Coast on ESUsouth (Fig. 4).

Most of the suitable areas in both ESUs are currently outside of legally protected areas (PPA, SPA, or PASU; ESUnorth—65.5% and ESUsouth—58.3%; Fig. 5). PASU encompasses more suitable areas in ESUnorth (21.8%), followed by PPA (7.1%) and SPA (5.6%). For ESUsouth, the three conservation categories cover the suitable areas almost in the same proportion (15.8%, 14.1%, and 11.8%, respectively; Fig. 5). The same trend for both ESUs remains throughout the future scenarios: even though in some scenarios there will be a gain in suitable areas, most new suitable areas are likely to be unprotected (Fig. 5). The ESUnorth presents a stability tendency, with all three categories of legally protected areas guaranteeing healthy environments, while the ESUsouth presents a slight loss of suitability in protected areas in all future scenarios. Nevertheless, the most significant loss is outside protected areas, which is expected anyway since most of the forest (and current suitable areas) is outside legally protected areas (Fig. 5).

The two ESUs present a high deficit in PPA and LR areas (Table 1). The LR deficit in ESUnorth is higher than the PPA deficit, and the joint values (PPA+LR deficit) almost reach the minimum area necessary to achieve the *B. torquatus* minimum forest requirements (Table 1). Conversely, PPA+LR deficit in ESUsouth is higher, with the PPA deficit three times higher than the LR deficit, overcoming the minimum area necessary to achieve the *B. torquatus* forest requirements (Table 1).

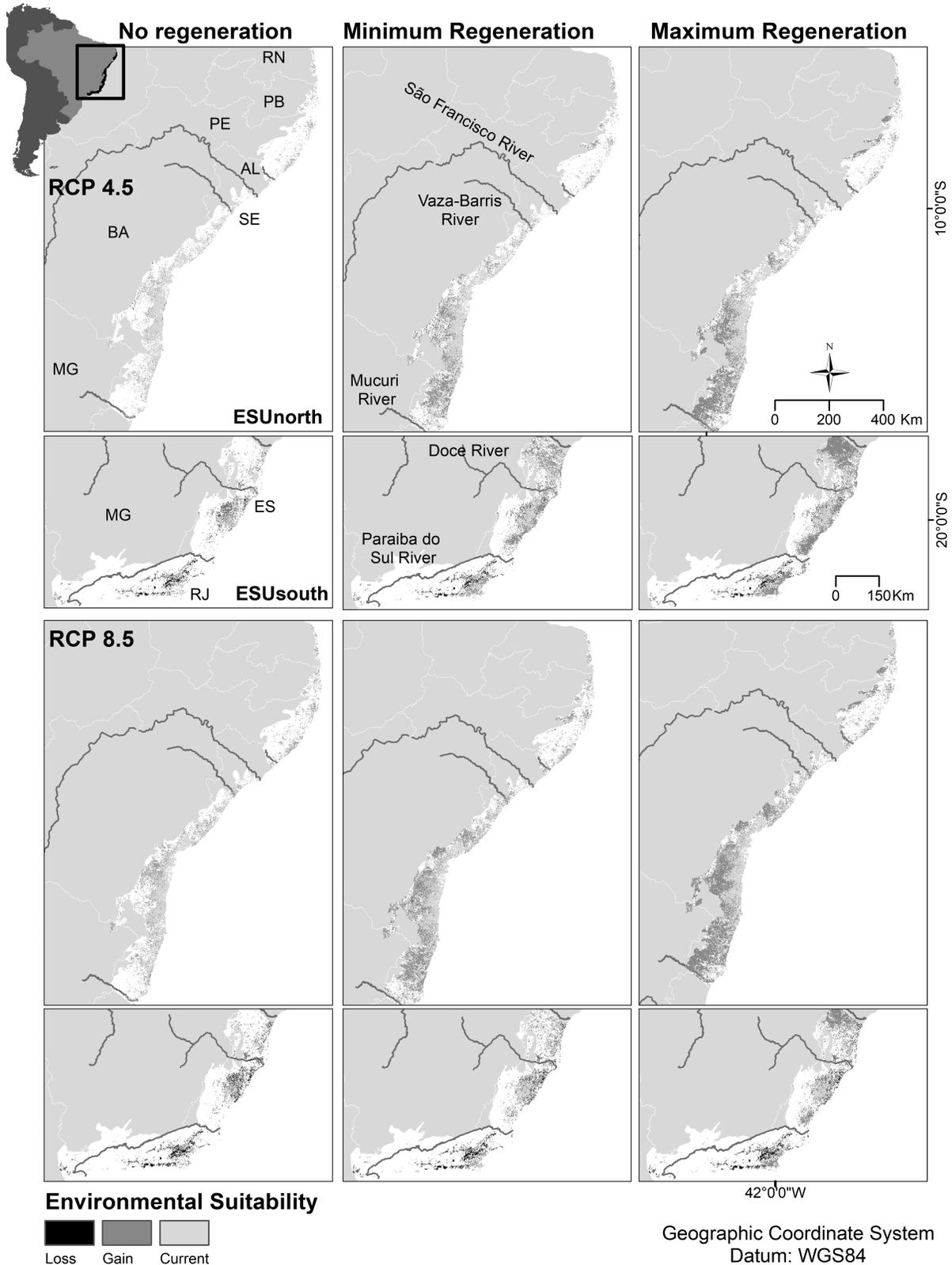


Fig. 4.—Changes on suitable areas relating to current environmental suitability for *B. torquatus* both evolutionary units, ESUnorth and ESUsouth, considering different scenarios of regeneration and climate changes (Representative Concentration Pathway [RCP] 4.5 and 8.5). The scenario with no regeneration consists in the current landscape + climate changes; the scenario with minimum regeneration consist in the future landscape with a minimum forest regeneration + climate changes; the scenario with maximum regeneration consist in the future landscape with a maximum forest regeneration + climate changes; RN—Rio Grande do Norte; PB—Paraíba; PE—Pernambuco; AL—Alagoas; SE—Sergipe; BA—Bahia; MG—Minas Gerais; ES—Espírito Santo; RJ—Rio de Janeiro states.

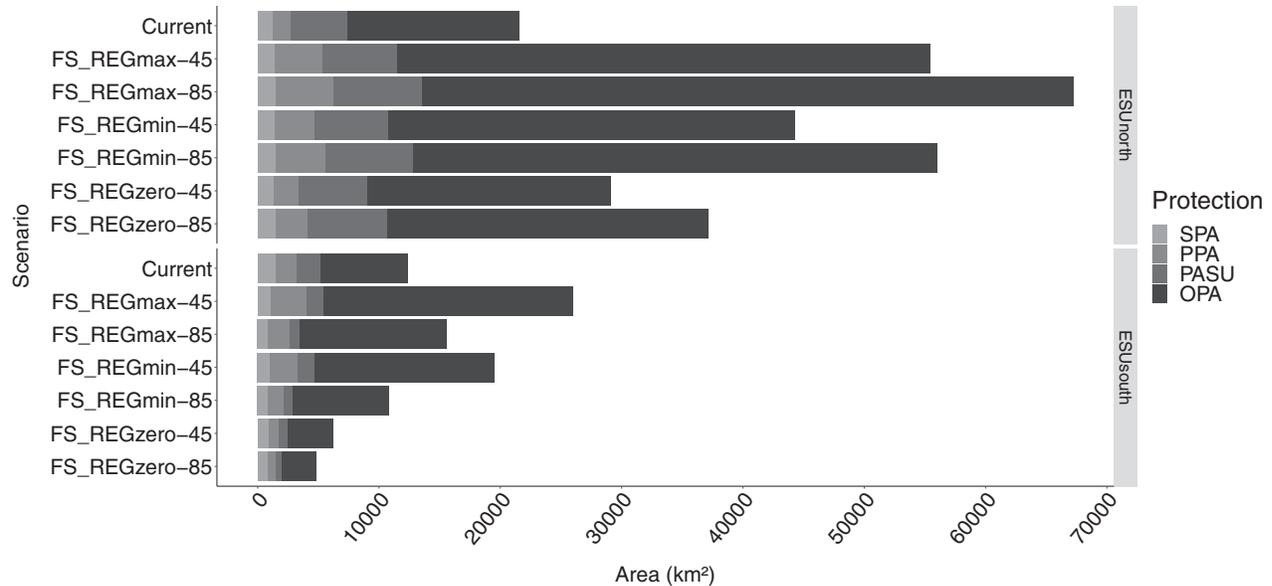


Fig. 5.—Suitable areas (km²) for *B. torquatus* in both evolutionary units (ESU) in the different scenarios and the distribution of Suitable Area Outside Protected Area (OPA) and in different conservation categories. PPA—Permanent Protection Area; PASU—Protected Areas of Sustainable Use; SPA—Strictly Protected Area. FS_REGzero—no regeneration scenario; FS_REGmin—minimum potential regeneration scenario; FS_REGmax—maximum potential regeneration scenario.

Table 1.—Deficit in PPA and LR areas in both evolutionary units (ESUs), and the minimum area required to achieve the *B. torquatus* forest requirements (FS_REGmin). Where: PPA—Permanent Protection Areas; LR—Legal Reserves.

	Deficit PPA (km ²)	Deficit LR (km ²)	Total (km ²)	Minimum area to regenerate (km ²)
ESUnorth	2,497	8,289	10,786	13,217
ESUsouth	19,185	5,556	24,741	10,607

DISCUSSION

Overview of environmental suitability models.—Natural forest regeneration, particularly outside protected areas, has a great potential to mitigate the negative influence of climate change on *B. torquatus* by maintaining and increasing the environment suitability in future scenarios. These results follow the pattern found in other studies, demonstrating that future environmental suitability will benefit from forest regeneration (Prevedello et al. 2019; Ramalho et al. 2021; Tonetti et al. 2022).

The increase in forest cover directly benefits forest specialist species by providing suitable conditions and resources (Santos et al. 2019b). With climate change, species dispersal to novel suitable areas are more likely in landscapes having higher forest cover and connectivity (Damschen et al. 2006). Overall, both ESUnorth and, to a lesser extent, ESUsouth present large and continuous forest patches (Ribeiro et al. 2009), with both areas being regions with medium-sized fragments and functionally connected areas (Ribeiro et al. 2009; Rezende et al. 2018). This high level of connectivity, combined with existing pasture lands, creates ideal conditions for natural regeneration (Crouzeilles et al. 2020), since they may cover a greater diversity of species that disperse seeds (Wunderle 1997)—increasing

the exposure of anthropogenic matrices to seed rain (Chazdon 2012).

Notwithstanding this convergence, the two geographic spaces differ in the current availability of suitable areas and respond distinctively to future climate and landscape changes (Fig. 4). The ESUsouth encompasses important forest areas, but some are less suitable for *B. torquatus*. In that case, the forest cover does not solely indicate a suitable environment for the species: climatic and elevation conditions may drive the environmental suitability in the region. Most current (particularly on ESUnorth) and future suitable areas are near coastal areas, while the more substantial losses are in south and hinterland areas. The Atlantic Forest naturally presents increasing climate seasonality from east to west, with coastal areas presenting abundant and evenly distributed rainfall throughout the year due to humidity from the ocean, favoring the occurrence of dense ombrophilous forests (Oliveira-Filho and Fontes 2000). The constant rainfall also benefits the increase in production of young leaves (Oliveira-Filho and Fontes 2000), a preferred food item for *B. torquatus* due to its high palatability (Chiarello 1998a).

Although *B. torquatus* can find and consume young leaves throughout the year, despite the seasonal variation, typically strongest in the ESUsouth region (Chiarello 1998b), this flexibility might be compromised with the expected increase in seasonality, as possible adaptations in the physiology of the species may not keep pace with climatic changes (Schloss et al. 2012). Further, present and future suitable areas in the ESUsouth have a greater proportion of hilly areas that might not constitute adequate habitats for *B. torquatus*, particularly those located higher than 1,000 m of altitude given the poor ability of the species to endure cold (Chiarello 2008; Giné et al. 2015).

Future climate change may impose several nonanalog (novel) conditions to *B. torquatus*, particularly to ESUsouth populations. The overall tendency indicates extreme climate and climatic events to become more frequent, for example, increasing in seasonality, and consequently, result in prolonged droughts (IPCC 2021). The arid climate may augment the chances for wildfires (Pivello et al. 2021), implying a decrease in forest fragment quality through simplification of tree species and structure, thus reducing the chance of seed dispersal and the natural regeneration of pasture lands (Pivello et al. 2021). This dramatic and novel condition will hamper long-term species conservation, with a likely decrease in suitable areas for *B. torquatus*.

Our models correctly predicted the current low environmental suitability of already known gaps in *B. torquatus* distribution (Fig. 4). These areas present low forest cover, which may be reducing environmental suitability. Yet, we believe that other undetected influences related to the discontinuities of the dense ombrophilous forests exist. Due to epeirogenic and forest shrinkage–expansion events, mainly in the Late Quaternary period (Carnaval and Moritz 2008), these gap regions are distinct from the rest of the ombrophilous Atlantic Forest, with higher seasonality and the presence of a semi-deciduous forest (Jesus and Rolim 2005). Similarly, previous studies carried out in the north of Rio de Janeiro state highlight the low tree diversity of the semi-deciduous forests there, which is linked to a strong seasonal climate and a cold ocean upwelling (Oliveira-Filho and Fontes 2000), which likely acts as a limiting factor for the presence of strictly folivorous species.

These climatic events helped shape much of the biodiversity currently known by forming biodiversity refugia (Porto et al. 2013; Carnaval et al. 2014). Thus, these two gaps are directly related to the division of separate populations of the species into two ESUs more than 5 million years ago (Schetino et al. 2017). Additionally, most of the suitable areas, and specifically, most (if not all) of the known records for the species, are in climatically stable areas (e.g., Bahia and Pernambuco Refugia; Carnaval et al. 2009; Sobral-Souza et al. 2018), with less potential for vegetation shifts (Costa et al. 2018), resulting from this complex climatic history of the Atlantic Forest domain. This long and stable history may explain, for instance, the outstanding effect of forest cover mainly in the ESUnorth models, while climate variables contribute significantly to the ESUsouth models, which is less stable and more subject to novel climate conditions. The rate of climate change in these refugia areas might be reduced due to extensive and continuous forest areas and mountainous regions, serving as safe shelters for the species (Loarie et al. 2009). For a dispersal-limited species, climate refugia formation might be of paramount importance (Pearson 2006; Schloss et al. 2012).

Conservation of suitable areas.—Consistent with overall Atlantic Forest patterns (Rezende et al. 2018), few suitable areas are legally protected in both ESUs (Fig. 5), with a possible decrease with climate changes, especially in the FS_REGzero scenario. Therefore, protected areas might guarantee only a small portion of current and future suitable environments for this species. This is quite worrying since most of the

losses may likely occur in areas outside any protection. Parts of these unprotected areas are somewhat protected by the Atlantic Forest Law (Law 11.428/2006), which prohibits the suppression of primary and late secondary forest. However, early secondary areas and areas in the initial stage of regeneration are legally amenable to forest clearance, threatening the incidence of natural regeneration in an area and limiting the potential regeneration-mediated gains in environmentally suitable areas.

Other areas lying outside the aforementioned conservation categories may belong to LR areas. If the law is followed, its restoration—along with PPA areas, might nearly be sufficient to increase forest cover, at least for the minimum habitat requirements to maintain the species (Table 1). Among other decisions, the Brazilian Native Vegetation Protection Law—since it was instituted in 2012 and results in debt forgiving of small landowners who deforested their LR areas before 2008, may have resulted in the regeneration of thousands of hectares (Soares-Filho et al. 2014; Brancalion et al. 2016). LR composes essential parts of the landscape in Brazilian territory (137 Mha), and along with PPAs and PAs, may assist in the incremental increase of regional forest areas, facilitation of organism movements, and climate regulation (Damschen et al. 2006; Metzger et al. 2019).

Implications for conservation.—Natural regeneration is an increasing reality in the Atlantic Forest (Baptista and Rudel 2006; Santos et al. 2012; Rezende et al. 2015), and it can mitigate local effects from climate change on environmental suitability for a forest-dependent species. The biome presents a sound opportunity for large-scale forest recovery (Crouzeilles et al. 2020), especially if an associated monetary return exists (Brancalion et al. 2012; Banks-Leite et al. 2014) without compromising agriculture expansion (Brancalion et al. 2012) through agriculture and cattle-ranching intensification (Brancalion et al. 2012; Strassburg et al. 2014). Encouraging natural regeneration may also contribute to policies such as the National Policy for the Recovery of Native vegetation (Planaveg, Decree n° 8.972/2017)—which aims to recover up to 12 million hectares of native vegetation by 2030. These policies may also assist the Decade on Ecosystem Restoration (2021–2030), instituted by the United Nations, whose objective is to halt ecosystem degradation and restore natural environments to achieve global goals (<https://www.decadeonrestoration.org/>).

We must highlight another important aspect when we consider forest regeneration. The Atlantic Forest will likely require over 100 years to fully recover naturally after a disturbance, to both secure a high diversity of species and to provide a complex habitat (Liebsch et al. 2008). The quality and complexity of forest habitats, including canopy height and openness, might be crucial for *B. torquatus* occurrence in a certain area (Santos et al. 2016), as these habitats are of utmost importance to maintain a healthy population (Falconi et al. 2015; Santos et al. 2016). Still, these regeneration areas might assist with long-term conservation since the species can use and select disturbed habitats—depending on the spatial context in which these habitats are restored (Cassano et al. 2011; Falconi et al. 2015). Additionally, these young forests may decrease the contrast between the forest and the nonhabitat matrix, acting as a

buffer zone (Derhé et al. 2018). Still, even relying solely on natural regeneration might require active management from government, institutions, and landowners, such as fencing of areas to avoid soil trampling by cattle.

It is imperative to ensure the maintenance of areas already protected by decreasing external pressures (Rosa et al. 2021). Southern Bahia, a vital area for species conservation, suffered an increase in forest loss, resulting in an increase in forest isolation throughout the years (Fundação SOS Mata Atlântica 2020; Rosa et al. 2021). Additionally, there is a concern about increasing the management intensity of cocoa agroforestry located in this region, constantly used by *B. torquatus* (Cassano et al. 2011; Falconi et al. 2015). This intensification may decrease the quality of these areas by, for example, reducing the density of native trees and canopy connectivity (Schroth et al. 2011). The regions in the northernmost portion of the species distribution present flat terrain prone to high deforestation rates (Rosa et al. 2021). Simultaneously, they include suitable yet isolated areas that threaten this unique population (Schettino et al. 2017). Guaranteeing an assisted natural regeneration may be one of the key conservation measures to ensure forest cover.

Overall, throughout the geographic range of *B. torquatus*, it is necessary to collaborate for forest protection, minimize regrowth suppression, and monitor the successional stages of the forests—interfering, when necessary, to increase their quality. Our research highlights the importance of creating and maintaining a network of connected forests, including different types of protected and nonprotected areas, which may be a key to safeguard the species in nonanalog climate conditions. Promoting compliance with environmental law is essential to preserve both young and old-growth forests, to ensure suitable environments and long-term *B. torquatus* conservation.

CONFLICT OF INTEREST

The authors declare there are no Conflict of Interest.

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SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Characteristics and descriptions of environmental variables used to delineate environmental suitability for *Bradypus torquatus* in Atlantic Forest, Brazil.

Supplementary Data SD2.—Main values of the Principal Component Analysis (PCA).

Supplementary Data SD3.—Regeneration potential map.

Supplementary Data SD4.—Accumulated pixel area in the regeneration map for both ESUs.

Supplementary Data SD5.—Results in percentage for the jackknife test for environmental variables in the development of MaxEnt model.

Supplementary Data SD6.—Suitable areas in km² for the two populations in the different scenarios.

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