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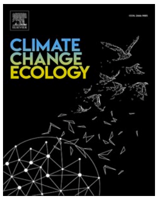

Genetic viability and habitat suitability of the critically endangered southern muriqui (*Brachyteles arachnoides*) in the Atlantic Forest's fragmented landscapes under land use and climate change scenarios

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ABSTRACT

The joint effects of climate change and landscape fragmentation to the genetic viability of isolated populations has barely been addressed for the Atlantic Forest fauna. Therefore, this work explored the potential habitat suitability for the southern muriqui (*Brachyteles arachnoides*), by modeling climate change, landscape fragmentation, and genetic diversity loss of the species. Maxent was used to model its potential distribution in 2050, with two climate change scenarios. A land use and land cover change model was applied to describe current and future forest fragmentation patterns, and a Population and Habitat Viability Analysis (PHVA) was used to describe the retention of genetic diversity of the southern muriqui. Although PHVA modeling provided a low risk of extinction of the southern muriqui, climate change and fragmentation could result in the loss of >65% of the suitable forest patches, and reduce the habitat suitability to only 11% of the potential distribution area, which could lead to future genetic diversity loss and decreased capacity of self-sustained populations. In both climate change scenarios, the suitable areas for the southern muriqui in Paraná and Rio de Janeiro states will decrease more drastically. Areas where the primate occurs in the interior of São Paulo and Rio de Janeiro states will disappear or be climatically disconnected from the core potential habitat. Alike preventing further deforestation, Atlantic Forest restoration actions are needed to connect the viable populations for compensating the projected land use and climate change impacts to the long term persistence of the southern muriqui.

1. Introduction

Given the landscape complexity of the Brazilian Atlantic Forest, this region is considered one of the global hotspots for biodiversity conservation. Its environmental diversity harbors a unique number of endemic species, under low levels of protection [1] and high levels of fragmentation [2]. Endemic populations are profoundly affected by landscape modifications caused by human activities, e.g. deforestation for agriculture, silviculture, mining, and urban expansion. These activities strongly affect the probability of population persistence due to the loss of genetic diversity caused by a reduction of gene flux through the landscape [3,4].

Especially in the Atlantic Forest, vegetation loss is a major issue for biodiversity conservation. The region has been exploited for centuries since the colonization in the XVIth Century, resulting in a large number of species facing extinction nowadays. Because of the historical changes in the Atlantic Forest, around 60% of the endemic plant species [5], and 593 endemic vertebrates [6], are estimated to be threatened. Historical deforestation resulted in only 12% of remaining forest cover, and a highly fragmented landscape [2]. Along with hunting, infrastructure and disease spread, fragmentation had already triggered a large-scale defaunation of the Atlantic Forest, which has cascading ecological consequences for the ecosystem functioning, from reducing plant diversity due to the loss of seed dispersal, to reduced overall carbon storage [7].

As a consequence of landscape fragmentation, the isolated endemic population tends to present lower genetic diversity followed by lower heterozygosities [8,9]. Endemic species are usually structured, which means the lack of gene and allele flux between populations. Consequently, the isolation of populations in fragmented landscapes increases

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the private alleles and the inbreeding process [10,8], leading to microevolution, local adaptation, and biodiversity loss [10,11]. Forest degradation at the landscape scale, such as deforestation, fires, and mining activities, strongly structure endemic populations, drastically decreasing individuals' movement and persistence. Tthus, degradation decreases the occurrence and distribution patterns of endemic species, which potentially leads to local extinctions [12].

Nevertheless, not only past, and possibly future, deforestation, and consequent genetic isolation of populations, are a threat to the Atlantic Forest's biodiversity, but also the expected impacts of climate change should be considered in conservation planning. While Atlantic Forest plant diversity is projected to be more impacted by land cover than climate change [13], diverging responses of different animal groups are reported in the literature [14,15,16,17], in some cases favoring the habitat expansion of invasive species [18]. In association with land use, climate change could lead to a "savannization" of the Atlantic Forest fauna [16], profoundly changing the forest ecosystems in unpredictable ways, given the changes in the composition of animal communities.

In this sense, predicting where suitable habitats will persist and accommodate viable populations of a species is essential for targeting proper conservation actions [19]. Primates are amongst the most threatened animals by climate change because they already live closer to their thermal tolerances [20], being sensitive to even small changes in temperature [21]. Moreover, forest fragmentation could prevent the migration of primates towards landscapes with climatic suitable habitats [21], suggesting that they should rely on behavioral flexibility to cope with climate changes [22]. In the Atlantic Forest, climate change may reduce the primate richness over space and time, due to the reduction of the climatic suitable areas for most species [15]. However, the combined impacts of climate change, landscape fragmentation, and consequent loss of genetic diversity for endemic and threatened primate species have been scarcely explored [23].

Out of the 26 primate species occurring in the Atlantic Forest, 19 are endemic and 16 are considered threatened by extinction [24], which is the case of the largest extant non-human primate in the Americas: the muriqui (Fig. 1). In Tupi-Guarani language, muriqui means "gentle people of the forest", which describes the calm behavior of the animals. In fact, the term muriqui refers generally to the two Atelidae species of the genus *Brachyteles,* endemic from the Atlantic Forest: *B. hypoxanthus* and *B. arachnoides*. Until recently, both species were named *B. arachnoides*, while *B. hypoxanthus* was commonly referred as the subspecies *B. arachnoides hypoxanthus*. But morphological and phylogeographic evidence support two reciprocally monophyletic groups corresponding to the northern (*B. hypoxanthus*) and the southern (*B. arachnoides*) muriquis, separated by an average 12.7% genetic distance [25]. There is no evidence of co-occurrence between the northern and southern muriqui, even with a potential habitat overlap, predicted by the Species Distribution Modeling (SDM) with Maxent [26].

Despite both muriqui species are now classified as Critically Endangered [27,28], greater attention has been devoted to the *B. hypoxanthus* because the northern muriqui populations have been considered even more threatened than *B. arachnoides* (Mendes et al. 2005; [29,30]). This is related to the fact that the southern specie occurs mainly in the largest portion of well preserved and protected Atlantic Forest remnants [26,31]. At least twenty southern muriqui populations are known to occur in both private and public protected areas [31]. The largest population of the southern muriqui is found in the Carlos Botelho state park, southwestern São Paulo state, where most research about *B arachnoides* has been conducted [32]. Recently, six small populations were discovered in unprotected private forests of the highly fragmented landscapes in Paraná state, including the first report of the southern muriqui in a forestry plantation [33].

Nevertheless, poaching and habitat loss are the major threats to the southern muriqui [28], despite climate change has not been considered yet. Especially in regions with low richness of primates and other seed dispersers, local extinctions of a single species, such as the southern muriqui, could severely affect the ecosystem as whole [15]. *B. arachnoides* has the most diversified known fruit diet, with observed frugivory interactions with 137 plant species (Bello et al., 2017). The southern muriqui thus acts as a "forest gardener", by dispersing and pollinating several species. This way these animals shape the biodiversity and ecosystem functioning of the forest patches they inhabit (Assumpção, 1981; [34]).

Therefore, the persistence of southern muriqui populations is of especial concern for the maintenance of ecosystem services in the relatively well-preserved large remnants of the Atlantic Forest. In light of that, this work aimed at modeling the potential habitat suitability for the southern muriqui by addressing the joint effects of climate change, landscape fragmentation and genetic diversity loss on the species. The resulting maps of the modeling approach are expected to provide useful information on priority areas that could support viable populations of the southern muriqui in the medium term and, thus, to contribute to the

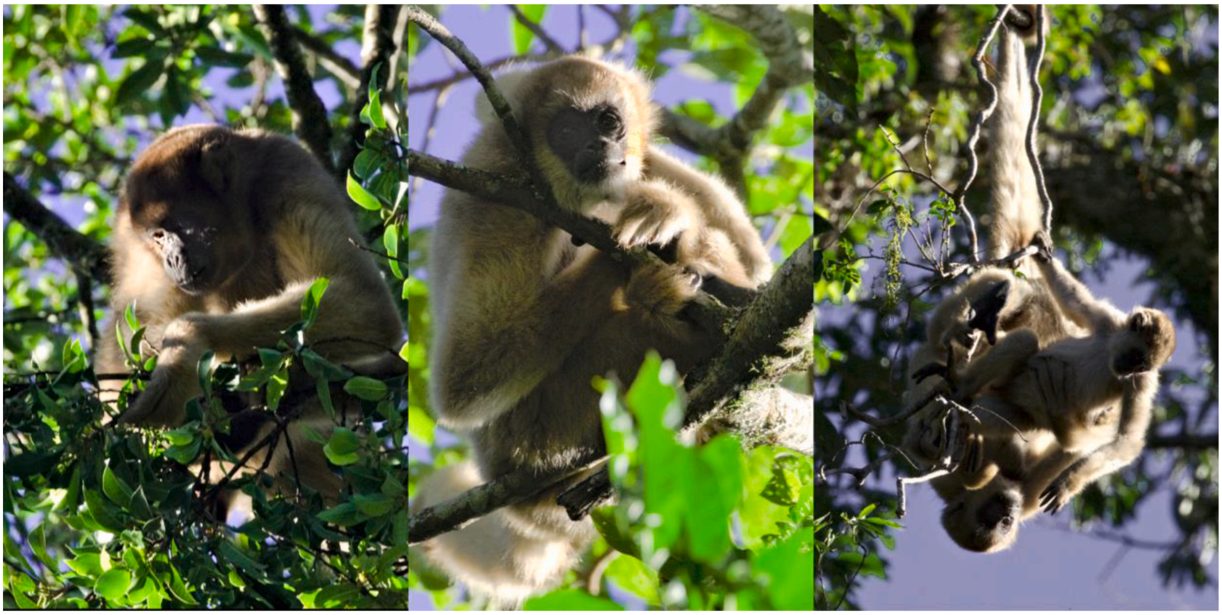

Fig. 1. Southern muriqui (*Brachyteles arachnoides*) behaviors for foraging (left), resting (middle) and a female with young (right). Photography: João Pompeu.

conservation of both this Critically Endangered primate and, consequently, to the remaining Atlantic Forestecosystems.

2. Study area

The southern muriqui is endemic to the Atlantic Forest, with known occurrences in the Brazilian states of Paraná, São Paulo, and Rio de Janeiro (Fig. 2). The historical distribution is likely constrained by large rivers and high mountains in the interior of Paraná, São Paulo, and Minas Gerais states. Most of the remnant habitat is more concentrated in the coastal areas of preserved forests [26], where the steeper slopes are less suitable for agricultural land use [2]. IUCN's geographic range of the southern muriqui reflects this pattern [28], but with limited ranges in the states of Rio de Janeiro and Paraná, as shown in Fig. 2. Thus, to consider most of the already estimated suitable climatic areas, and to also include the known occurrences of the primate beyond the limits of IUCN's range, a 2° buffer from the IUCN polygon was drawn to delimit the area for modeling the muriqui's distribution in future climatic and land use change scenarios. This region is of great importance for the maintenance of the ecosystem services provided by the preserved Atlantic Forest (such as water availability and clean air), once more than 15% of the Brazilian population is found in the defined study area.

3. Material and methods

There are three major steps for modeling the landscape suitability for the southern muriqui, divided into the SDM, land use and land cover modeling and population viability analysis (PVA). The approaches are described in detail below and the flowchart in Fig. 3 summarizes the main steps.

3.1. Occurrence records

One of the most critical procedures in presence-only species distribution models (SDM) is the collection of reliable records, once sampling bias can impact the potential distribution in several ways, from the calibration to the final thresholding of the distribution maps. Boria et al. [35] demonstrated that SDM with filtered data sets showed overall lower overfitting and better performance. However, records of species like the southern muriqui tend to be spatially autocorrelated because of the difficult access to the locations the animals occur [26]. Moreover, unreliable occurrences of the species are found in the literature and, therefore, should be avoided [36]. Calibration and cross-validation of the potential distribution maps were performed with 34 southern muriqui occurrences (shown in Fig. 2), validated and spatially filtered by Ingberman et al. [26], to minimize the sampling bias in the modeling results.

3.2. Environmental variables

Following Ingberman et al. [26] and Lima et al. [15], altitude and 19 bioclimatic variables were first considered for modeling the spatial distribution of the southern muriqui. These variables were downloaded from the WorldClim v. 2.1 [37] at the spatial resolution of 30″ (nearly 1 km in the Equator). Historical bioclimatic variables are calculated based on the 1970 to 2000 period ("baseline" climate scenario = 1985). The

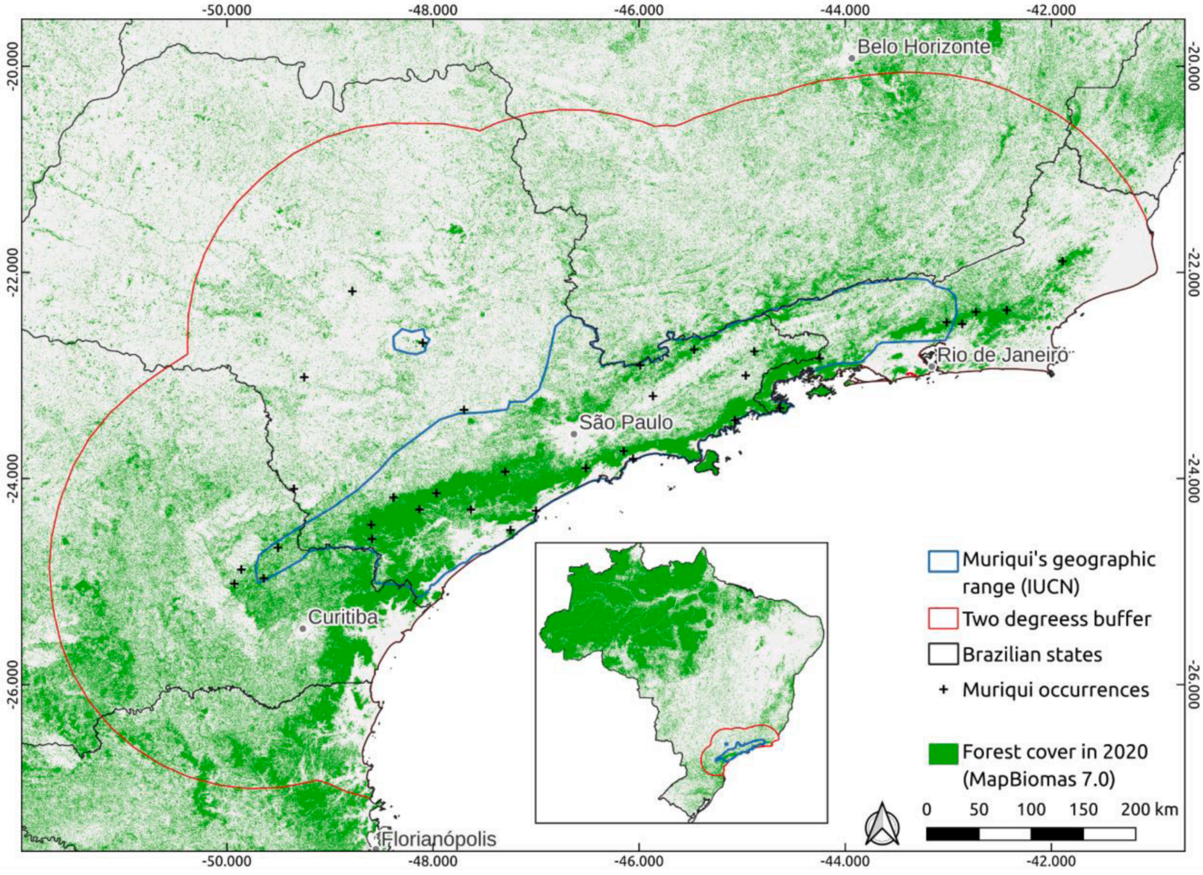

Fig. 2. Study area for modeling the southern muriqui distribution. Blue polygon is the southern muriqui's geographic range from the IUCN; red polygon is a 2° buffer from the IUCN limits used for climate modeling; black lines are the Brazilian states limits; black crosses are the southern muriqui occurrences used for habitat suitability modeling. Forest cover in 2020, from the MapBiomas project, is shown in green. Gray dots indicate the capitals of the following states: Florianṕolis is the capital of Santa Catarina, Curitiba is the capital of Paraná, São Paulo is the capital of São Paulo state, Rio de Janeiro is the capital of Rio de Janeiro and Belo Horizonte is the capital of Minas Gerais.

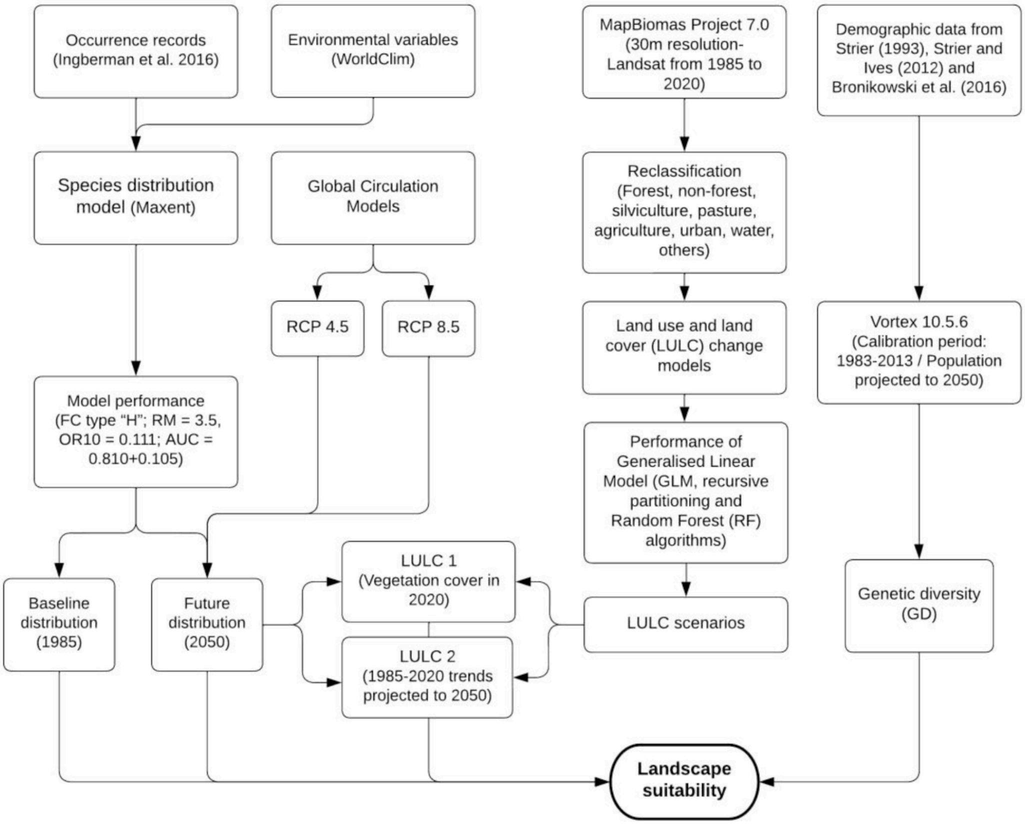

Fig. 3. Flowchart summarizing the methodological steps involved in the modeling approach.

future data considers the period of 2041 to 2060 (future climate scenario = 2050).

Here, two climate change scenarios, RCP 4.5 and RCP 8.5, were used to compare the southern muriqui distribution under different climatic conditions. RCP 4.5 and RCP 8.5 assume, respectively, a more likely climate change scenario given the current policies with weak mitigation efforts and a more extreme though unlikely worst-case no policy scenario [38]. This comparison of the RCP 4.5 and RCP 8.5 is useful when dealing with conservation issues, as it provides practical insights for a range of uncertainty of Greenhouse Gas (GHG) pathways [39], allowing to evaluate the possibilities between a most plausible and a worst-case scenario. To account for the variability in the scenarios, as in Lima et al. [15], the following eight Global Circulation Models (GCM) were considered in the analysis: BCC—CSM1–1, CCSM4, GISS-E2-R, HadGEM2-AO, HadGEM2-ES, IPSL-CM5A-LR, MRI-CGCM3, and NorESM1-M.

As observed by Ingberman et al. [26], the altitude and climate extremes, for example, the maximum or minimum temperature of the warmest or coldest month, rather than mean temperature of the warmest quarter, are more biologically meaningful for the muriqui. To minimize the autocorrelation of the environmental data, preference was given to the variables used by Ingberman et al. [26] to model the historical distribution of the southern muriqui: annual mean temperature (Bio 1), mean diurnal range (Bio 2), isothermality (Bio 3), temperature seasonality (Bio 4), temperature annual range (Bio 7), annual precipitation (Bio 12), precipitation of wettest month (Bio 13), precipitation of driest month (Bio 14) and altitude. Pearson's correlation of the variables is shown in Table 1.

A previous variance inflation factor (VIF) analysis, with 10,000 random observations and threshold of three variables, was performed following Lima et al. [15]. The analysis suggested the use of five bioclimatic variables: Bio 3, Bio 7, Bio 8, Bio 18 and Bio 19. However, due to the remaining correlation between them (>0.6) and the lack of known biological importance for the southern muriqui, the more meaningful variables from Ingberman et al. [26] were preferred instead, despite resulting in a higher number of variables and the strong correlation of Bio 1 with altitude and Bio 4 with Bio 14 (>0.8).

3.3. Maxent modeling

Maxent is one of the most widely used machine learning algorithms

Table 1
Pearson's correlation between the variables used for modeling the muriqui distribution under baseline and future climates.

	Bio 1	Bio 2	Bio 3	Bio 4	Bio 7	Bio 12	Bio 13	Bio 14
Bio 1	–							
Bio 2	−0.035	–						
Bio 3	0.292	0.767	–					
Bio 4	−0.502	−0.135	−0.679	–				
Bio 7	−0.351	0.793	0.222	0.442	–			
Bio 12	−0.387	−0.362	−0.465	0.226	−0.128	–		
Bio 13	0.065	0.024	0.242	−0.571	−0.210	0.477	–	
Bio 14	−0.484	−0.374	−0.704	0.822	0.099	0.487	−0.500	–
Altitude	−0.803	0.383	0.244	0.012	0.369	0.245	0.294	−0.023

for modeling species distribution, especially when only presence data is available, with overall robust results when trained with a small number of occurrences [40,41]. Additionally, Maxent was previously used for modeling the historical distribution of both muriqui species [26], as well as for studying the effects of climate change on the Atlantic Forest's primate communities [15].

Here, the *R* package ENMeval [42] was used to run Maxent with 10, 000 background points and different combinations of parameters. The package was chosen because of its unique approach to perform model tuning to reach optimal species distribution. As in Lima et al. [15], 60 models were run by combining 10 regularization multiplier (RM) values (from 0.5 to 5, with a step of 0.5) with six types of feature class (FC): L, LQ, H, LQH, LQHP and LQHPT, where L = linear, Q = quadratic, H = hinge, P = product and T = threshold.

Previous approaches (e.g. [15]) relied on the corrected Akaike Information Criterion (AICc) to choose the most suitable primate distribution model among a set of models with different parameters. However, the use of spatial cross-validation is recommended when the model transferability to other environmental conditions is performed [42,43]. Thus, a four-fold spatial partitions block method, delineated by longitude and latitude positioned to balance the number of localities in each fold was used to assess the performance of the sixty models [44].

The optimal model was selected based both on the lowest average test omission rate using the 10-percentile training presence (OR10) and the highest average test area under the curve of the receiving operator characteristic (AUC), as recommended by Kass et al. [44]. This way, the optimal Maxent parameters to map the distribution of the southern muriqui were FC type "H" and RM = 3.5, with OR10 = 0.111 and AUC = 0.810 ± 0.105. Finally, this model was compared with null SDMs, using 999 replications and the spatial partitions method developed by Kass et al. [44]. The average AUC for null SDMs was 0.637±0.055, indicating that the tuned Maxent produces a statistically better representation of

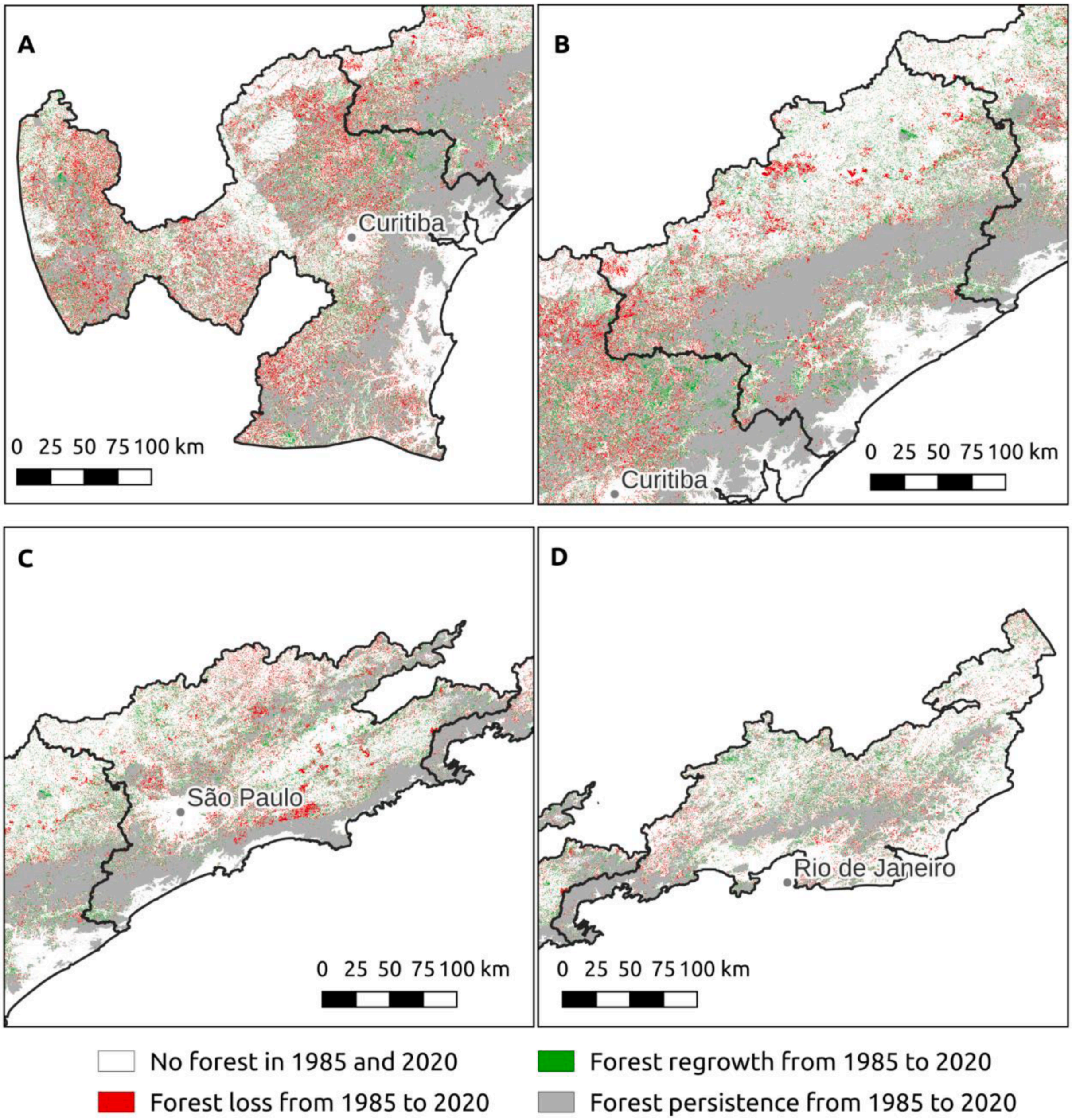

Fig. 4. Subdivisions of the study area for optimizing LULC modeling. (A) Paraná and Santa Catarina states; (B) Southwestern São Paulo state; (C) São Paulo city and surroundings, Paraíba River Valley and Mantiqueira mountains; (D) Rio de Janeiro state. Forest cover is derived from MapBiomas 7.0.

the muriqui distribution than a random model ($p = 0.0009$).

Future distribution of the southern muriqui is based on the projection of the climatic conditions under the different GHG emission scenarios, using the better Maxent model with the bioclimatic variables predicted by each of the GCM. The modeled suitability surfaces were converted into binary maps using the 10-percentile training presence threshold [45]. Furthermore, the final projected distributions of the southern muriqui in each RCP scenario is the consensus ensemble between the resulting maps using each of the eight different GCMs.

3.4. Landscape change modeling

To account for the landscape patterns in the potential southern muriqui distribution and genetic viability, a land use and land cover (LULC) change model was performed with the "lulccR" package [46]. The LULC model was constrained in the study area to the continuous patch resulting from the union of the climatically suitable muriqui habitat in the baseline and future climate scenarios. This approach leaves apart the LULC dynamics which are not representative of the potential southern muriqui habitat [47] that, thus, could affect the modeling results in the areas actually occupied by the primate. A 5-km buffer was added to the unified area, resulting in a 181,435.27 km^2 landscape (Supplementary Table 1) along the states of Paraná, São Paulo, Minas Gerais, and Rio de Janeiro. The landscape was then subdivided into four areas for LULC modeling (Fig. 4) to better capture the LULC trends in each region, once the entire region shows contrasting LULC dynamics, e.g. deforestation in the surroundings of Curitiba, the Paraná's capital [48], forest conservation in the Ribeira river valley in the southwestern São Paulo state [2], and forest transition in the Paraíba river valley in São Paulo and Rio de Janeiro states [49,50].

The LULC maps used in the modeling approach were obtained from the MapBiomas Project collection 7.0. MapBiomas is a platform that uses machine learning to produce annual LULC over the Brazilian territory with 31 different classes, at 30 m of spatial resolution, using all the available Landsat imagery since 1985 [51]. To perform the landscape change model, the years 1985 and 2020 were selected because they represent the larger period (35 years) of available data and are balanced with the projected period from 2020 to 2050 (Vliet et al., 2017).

In order to retain only the most relevant LULC for the muriqui dynamics, the MapBiomas maps were reclassified to the following eight general classes, that are mostly observed in the studied landscape: (1) Forest; (2) Non-forest natural formations (including mangrove and sandbank vegetation); (3) Silviculture (mainly plantations of *Eucalyptus* spp. and *Pinus* spp.); (4) Pasture; (5) Agriculture (including temporary and perennial crops); (6) Urban areas; (7) Water and; (8) Other land uses. Indeed, forest is the only class of biological interest for muriqui conservation, however, the other classes were retained for a better representation of the LULC transitions over time.

By the analysis of the transition matrices in the whole region and in the subdivided areas (Supplementary Tables 1 to 5), the distances to agriculture, silviculture and pastures were retained as explanatory variables for LULC modeling, along with the slope and distance to protected areas. The slope was retrieved from SRTM at 30 m of spatial resolution provided by EarthData and downloaded with the "SRTM downloader" plugin for QGIS. The protected areas shapefile was obtained from the National Water Agency webpage (https://metadados.snirh.gov.br/geonetwork/srv/api/records/9407d38f-84d2-48ea-97dd-ee152c493043). Only the strictly protected areas were considered, once less restrictive protected areas allow agricultural land uses that are, thus, prone to deforestation. The polygons of the protected areas were clipped to the bounding box of the study area in QGIS, to also consider the distances outside the 2 km buffer. Moreover, distance calculations were performed with GDAL's proximity tool due to its better time performance in computing raster distances when compared with *R* packages. The resulting explanatory variables are shown in Supplementary Figs. 1 to 5.

The performances of the Generalized Linear Model (GLM), recursive partitioning (rpart), and Random Forest (RF) algorithms, available from the lulccR package, were compared in each of the four subdivided areas. The models were fed with a stratified random sampling of 150,000 samples [52], divided into training (67%) and testing partitions (33%). They were evaluated by the analysis of the area under the ROC curves (AUC). In all of the four cases, Random Forest produced the overall better results (Supplementary Figs. 6 to 9) and, thus, was the chosen algorithm for the LULC modeling.

Two future LULC scenarios for 2050 were evaluated along with the climatic projections [53]. The first scenario (LULC1) assumes the no further Atlantic Forest conversion, thus considering no landscape changes after 2020 [53]; the second scenario (LULC2) assumes that the historical trend observed during 1985 to 2020 will continue into the future, by projecting the changes until 2050, using the same annual transition rates from the past period [54].

Following Gomes et al. [55], LULC2 allocation was based on the ordered method [56], due to its lower computational requirements and higher stability, in comparison with the CLUE-S allocation method [46]. The modeled LULC maps were validated with the reclassification of the MapBiomas in 2020, using the method proposed by Pontius and Millones [57] and implemented in the *R* package "diffeR". In general, the models performed well, with higher errors in the agriculture class, as shown in the Supplementary Figures 10 to 13. Regarding the forest class, the best performance of the model was in Rio de Janeiro state (Supplementary Figure 13), and the worst in São Paulo surroundings, Mantiqueira and Paraiba valley (Supplementary Figure 12), despite still acceptable (11.2%). Quantity errors of the forest class were predominant in Santa Catarina and Paraná (Supplementary Figure 10) and Rio de Janeiro states (Supplementary Figure 12), while exchange errors were more important in the other two regions. To reduce the propagation of the quantity and exchange errors, the 2020 MapBiomas reclassified map was used for projecting LULC to 2050, instead of the modeled map for this year.

Finally, for considering the joint climate and land use potential suitable habitat for the conservation of the southern muriqui populations, landscape patterns of LULC1 (forest in 2020) were analyzed in conjunction with the climate suitability area projected resulting from the RCP 4.5 Maxent models, while LULC2 (past LULC trends projected to 2050) was analyzed with the suitability maps from RCP 8.5. Thus, the remaining forest patches for maintaining the genetic viability of the southern muriqui are analyzed in two contrasting scenarios of landscape and climate changes: one in which less pronounced changes are expected in the future (LULC1 + RCP4.5) and another more dynamic one (LULC2 + RCP 8.5). The landscape structure was analyzed with the *R* packages "raster" and "terra". All the maps were elaborated with QGIS.

3.5. Genetically viable populations

For determining the minimum habitat for maintaining a genetically viable population in the 65 years from 1985 to 2050, a Population and Habitat Viability Analysis (PHVA) was conducted with the package Vortex 10.5.6 [58].

Obtaining detailed demographic data of the southern muriqui for feeding PHVA models is complex due to its canopy habitat in dense forests, and limited budget for adequately monitoring of the known populations [31]. Given the lack of up-to-date and publicly available demographic knowledge for the southern muriqui, the PHVA here assumed the same population structure of a well studied population of the northern muriqui at the private reserve "Feliciano Miguel Abdala". This population is isolated in a 957 ha forest fragment and its field study initiated in 1983 [59]. After 30 years of population monitoring, a detailed life-table of the northern muriqui is provided by Bronikowski et al. [60]. Such long-term monitoring effort ensures accurate population knowledge, essential for calibrating the PHVA. Although limited, the approach of considering data from other species from the same genus, when unavailable for the targeted species, is also implemented in other PHVA studies of threatened primates from Brazil [23].

To calibrate the PVHA analysis, the maximum age of survival, sex ratio at birth, annual mortality and the female age distribution were retrieved from the life-table provided by Bronikowski et al. [60], which summarizes 30 years of fieldwork. The other parameters were taken from Strier [61], also used by Rylands et al. [62] and Brito and Grelle [63], as shown in the Supplementary Table 6. Vortex was first run for a period of 30 years to compare the modeled population growth with the observed by Strier [64]. Considering an initial population size of 60 individuals [59], the final population after 30 years was 335.16 ± 94.87 (Supplementary Fig. 13). Despite a different shape of the growing curve, the final number of individuals observed by Strier [64] is ~340. Therefore, the calibrated model was considered satisfactory to represent the muriqui demography in the absence of catastrophes, and was used to project the populations to 2050, as explained below.

An important caveat, however, is observed by Strier [61] regarding the carrying capacity (K) assumed in her study ($K = 240$), which could be subjected to doubt because the forest fragment is also occupied by other large primates. Another approach for estimating K is to consider that the simulated initial populations are actually at their carrying capacity ($N = K$), as in Barreto et al. [23], but this can be misleading once a growing population could be constrained by an artificial factor in the PHVA. In this sense, the carrying capacity was calculated here based on Paccagnella [65], who led the first population survey of the southern muriqui in the Carlos Botelho state park, in 1985 [32]. Her survey found 7.3 ind/km^2, in an area of 241.52 km^2, which results in an estimate of 1763 individuals [66]. Despite a quite large number, even higher than what is estimated for the total current muriqui distribution [28], this park conserves the most genetically diverse population of the southern muriqui [31] and the period of the survey is compatible with the historical climatic and LULC data used here. Thus, the PHVA simulations assumed that the southern muriqui populations are at an equilibrium with the environment when $K = 1763$ and the habitat is sufficiently large.

Generally, the standard average minimum retention of genetic diversity (heterozygosity) in PHVA studies is 95%, but the analyses are usually ran for a period longer than 65 years. To adopt a more conservative estimate and minimize an artificial higher genetic diversity (GD) resulting from the short period of time in the model, here, the minimum size of a genetically viable population in 2050 is calculated as the population whose retained average GD minus the standard deviation is higher than 95% (GD - SD > 95%). To find this minimum population size, 10 PHVA simulations with 1000 interactions were ran with initial populations of 10 individuals, increasing by 10 until 100 individuals.

4. Results

4.1. PHVA

In order to retain at least 95% of the heterozygosity by 2050 (GD - SD), the southern muriqui populations in 1985 would require at least 50 individuals (Table 2). With a constant density of 7.3 individuals/km^2, forest habitats larger than 6.849 km^2 would sustain the optimal population of at least 50 individuals in equilibrium with the environment. Extinction of the southern muriqui is unlikely (PE = 0) in all simulated populations but that started with 10 and 20 individuals in 1985, which had a 4.8% and 0.01% chance of extinction until 2050 (Supplementary Table 7).

4.2. Climate and LULC changes

Climatically suitable habitat for the southern muriqui in 1985 was 199,671 km^2, and it is expected to decrease, according to the climate change scenario in 2050, to 145,661 km^2 and 131,566 km^2 in the RCP 4.5 and RCP 8.5 scenarios, respectively (Fig. 5). However, these numbers are much lower when land use is considered. Forest habitat in the climatic suitable habitat in 1985 was 78,837.63 km^2, of which 62,204.77 km^2 is the summed area of all the forest fragments considered to support a genetically viable population until 2050 (0.12% of the total fragments in the landscape). In the LULC1 + RCP 4.5 scenario, the forest area in 2050 is projected to 61,076.40 km^2, which 49,144.88 km^2 could support the genetically viable muriqui populations, while in the LULC2 + RCP 8.5 scenario, forest cover is, respectively, projected to 53,422.12 km^2 and 42,274.06 km^2.

The largest continuous forest patch possibly occupied by the southern muriqui in 1985 had 36,556.70 km^2 and is part of the mosaic of preserved Atlantic Forest in the coastal mountains of Paraná, São Paulo and Rio de Janeiro states. In 2050, this patch is projected to shrink to 16,904.66 km^2 and 14,49.67 km^2 in the LULC1 (equivalent to the forest cover in 2020) and LULC2 scenarios, respectively. The number and mean area of the forest fragments in the scenarios is shown in Table 3.

5. Discussion

Its diverse diet provides the southern muriqui a great plasticity to cope with variable climatic conditions [67] and to survive in degraded environments [33]. However, climate change could reduce the potential habitat of the southern muriqui from 28% to 35% in 2050, with an overall similar pattern of change in both RCP 4.5 and 8.5 scenarios. As evidenced in the Fig. 5, the most dramatic reduction in the climatically suitable habitat for the primate is in the interior of Paraná state, while habitat suitability is also projected to decline at a lower extension in the northern Rio de Janeiro, in the Mantiqueira mountains (the conjunction of Rio de Janeiro, São Paulo and Minas Gerais states), and disappear from the interior of São Paulo. In both climate change scenarios, but more pronounced in the RCP 8.5, the suitable areas in the interior of Paraná and Rio de Janeiro are disconnected from the core habitat of the southern muriqui in the coastal São Paulo mountains.

The specific isolated population in the interior of São Paulo state is considered a high priority for demographic monitoring due to its current isolation and consequent expected genetic uniqueness [31], So, the climatic unsuitability projected for the area this population occurs, in both RCP 4.5 and 8.5 scenarios, has practical ecological and conservation implications, once this population is already inhabiting isolated fragments, far from the core habitat of the southern muriqui and with limited dispersal capacity, and that are potentially outside the optimal climatic conditions for the species. This evidence reinforces the importance of improving the efforts for monitoring such isolated populations, mainly to investigate whether these muriquis will physiologically cope with new climate conditions in the short period of time, despite their dietary plasticity [67]. Moreover, monitoring this specific population could shed light on whether the Paraná and Rio de Janeiro populations could migrate or adapt if the climatic isolation from the core habitat is realized in the future.

Table 2
% of the retained Genetic Diversity (GD), standard deviation of GD (SD) and the threshold for the minimum genetically diverse population (GD - SD) in 2050, per simulated initial number of individuals (N) in the population.

N	10	20	30	40	50	60	70	80	90	100
GD (%)	70.56	87.48	92.60	94.56	95.70	96.41	96.90	97.31	97.58	97.81
SD (%)	23.10	10.17	1.93	1.10	0.70	0.53	0.41	0.34	0.29	0.24
GD - SD (%)	47.15	77.31	90.67	93.46	95.00	95.88	96.49	96.97	97.29	97.57

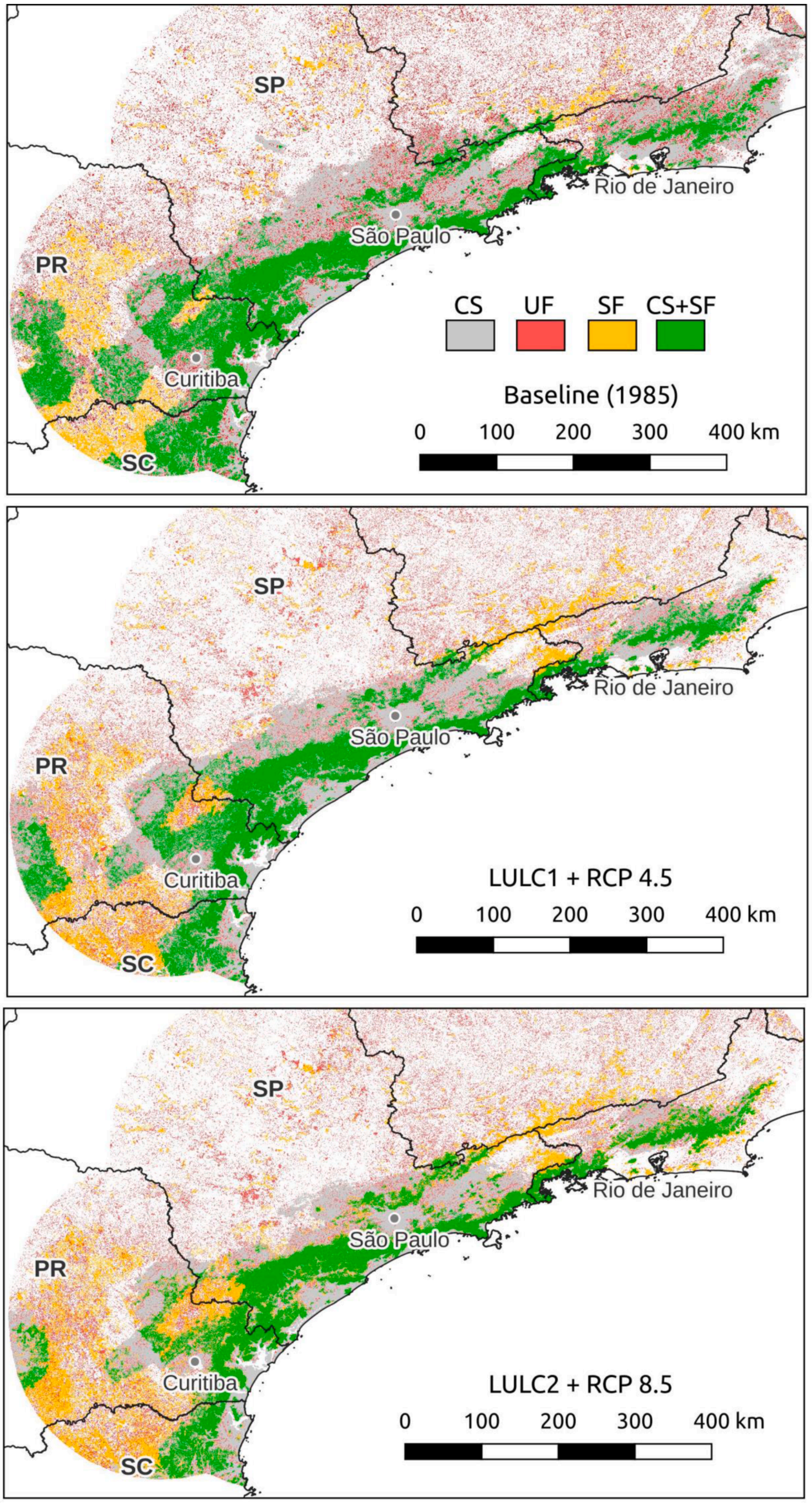

Fig. 5. Climatically suitable habitats for the southern muriqui. CS = Climatically suitable areas; UF = Unsuitable forests ($<$6.849 km^2); SF = suitable forests ($>$6.849 km^2); CS+SF = suitable forests overlapping with the climatically suitable areas. UF and SF in LULC2 + RCP8.5 outside the modeled regions (Section 3.4) are correspondent to the LULC 1 + RCP 4.5 (forests in 2020).

In this sense, the combined effects of landscape fragmentation and climate change could reduce the suitable habitat for the southern muriqui to only 21% of its potential distribution (42,274.06 km^2). Even when considering no further deforestation, the remaining suitable habitat for retaining the genetic diversity in 2050 is still far lower than the distribution projected with Maxent (Table 3). It highlights that forest loss is a major issue for the muriqui conservation, not only in the past, but also in the next decades. Only ceasing deforestation is not enough to avoid the shrinking of the potential habitat that could support viable muriqui populations. In both evaluated scenarios, the number of suitable fragments in 2050 are very similar, while ~32% lower than in the baseline scenario. The increased mean size of the suitable fragments in

Table 3
Landscape structure in the baseline and climate and land LULC change scenarios. All the numbers refer to forest land cover. “Suitable” refers only to those fragments larger than 6.849 km^2 and “All” takes all of the forest fragments into account.

		Baseline (1985)	LULC 1 + RCP 4.5	LULC2 + RCP 8.5
Number of forest fragments	All	361,660	283,369	303,989
	Suitable	441	300	308
Forest area (km^2)	All	78,837.63	61,076.40	53,422.12
	Suitable	62,204.77	49,144.88	42,274.06
Mean fragment size (km^2)	All	0.21 (±61.75)	0.21 (±43.82)	0.17 (±34.80)
	Suitable	141.05 (±1764)	163.63 (±1339)	137.25 (±1086)

2050, despite being larger than 115 km^2, the threshold for long term genetic viability of the northern muriqui [63], is mainly caused by the numeric reduction of the suitable patches due to land clearing or division of larger fragments into smaller patches. Thus, Atlantic Forest restoration actions aiming at planting forest corridors that connect the populations are needed, especially for compensating the projected climatic isolation of the Rio de Janeiro and Paraná populations. Moreover, the enhancement of the agricultural matrix with forested systems (e.g. agroforestry) could provide habitat connectivity for the muriqui and human wellbeing as an agricultural adaptation strategy to cope with climate change [68].

With this respect, the most expressive LULC changes between 1985 and 2020 reveals that 94% of the forest gain in the period occurred over agriculture (63.4%) and pasture (30.6%) lands (Supplementary Table 1). This forest transition pattern, more pronounced in São Paulo and Rio de Janeiro states (Supplementary Tables 4 and 5) has also been observed in the region by other authors, using other mapping techniques, as a result of land abandonment especially in areas with steeper slopes and closer to urban centers [49]. On the other hand, 96% of the forest conversion was to agriculture (53.6%), silviculture (30.6%) and pasture (11.8%), offsetting the vegetation recovery by 2938.34 km^2. This highlights that promoting a sustainable agriculture, more oriented to forested systems (Assad et al., 2022) and to food production rather than export commodities [69] could enhance the landscape matrix to the southern muriqui, while benefiting society in this part of the Atlantic Forest, that concentrates more than 15% of the Brazilian population.

However, the projections emphasize the continued trend of landscape fragmentation, which in this case could affect the maintenance of self-sustained populations and gene flux in the medium and large terms [12,70,61], decreasing the probability of population survival for a reasonable period of time. Previous studies have already analyzed the viability of the northern muriqui, showing that a high number of individuals are necessary to maintain the stability of the populations in the long run [63,62,61]. The maintenance of population viability is a fundamental goal of conservation biology and habitat fragmentation scenarios should be considered for conservation interventions, especially in the case of threatened primates [70]. Isolated populations of muriquis could face future genetic diversity loss and decreased capacity of self-sustained populations following the impacts of climate change scenarios.

Strier [61] showed that the population growth of the northern muriqui was insensitive to the simulated catastrophes because of the long interbirth intervals. However, population declines of the northern muriqui after El Niño and extreme drought events suggest that large-scale climatic variation intensified by climate change pose additional threats to the persistence of the muriquis [64,71]. Also, demographic changes in primate communities are reported after yellow fever outbreak [72,64]. As climate change exacerbates the extreme weather events in the Atlantic Forest [17], potentially increasing the risk of new outbreaks, further investigation should explore to which extent the more frequent extreme events attributed to climate change could impact the mortality rates and the reproductive success of the populations. In this sense, climate change could also impact the demography of the southern muriqui through extreme events, thus impacting its genetic viability in the long term.

As expected, the potential distribution of the southern muriqui found here is in line with Ingberman et al. [26] once the same predictor variables and occurrences were used to feed the Maxent model. They report a potential area of distribution 5% lower than found in the baseline scenario, which could be attributed to the higher spatial resolution of the climatic data in this study (30 arc-seconds) than in hers (2.5 arc-minutes). However, the authors reported that only 20,611 km^2 are suitable forest habitats to the southern muriqui, while here this number is more than three times higher in the baseline and at least twice higher in the future scenarios (Table 3). The reason for this discrepancy is that they used a suitability threshold for the forest fragments of 115 km^2 (against ~6.8 km^2 here), which is based on Brito and Grelle [63], who estimated a minimum population of 700 animals to maintain the genetic viability of the northern muriqui for a thousand years. While this approach is sound for predicting the long-term viability of a species, it can be less meaningful for short-term actions once conservation priorities could also be focused on smaller fragments potentially occupied by the species.N These smaller fragmentscould be relevant for the long-term persistence of the populations by allowing the migration and genetic flux in the landscape, as evidenced by the occurrence of individuals in small patches (10 ha) of the highly fragmented landscapes with forestry plantation matrix [33]. Moreover, the larger Atlantic Forest fragments are already protected, despite the projected reduction of their area. Thus, focusing on the preservation of the smallest potentially suitable habitat for the southern muriqui could be a proactive conservation measure to reduce the habitat loss pressure on the species.

Not only the quantity of habitat but also the quality matters for supporting a viable population in the long run. Differently from previous PHVA analysis, a much larger carrying capacity was assumed here and even the smallest initial population sizes in the simulations tend to a demographic increase (Supplementary Table 6), as also reported by Strier [61], despite the heterozygosity decrease. However, the fact that most southern muriqui populations nowadays are smaller than 50 individuals [33,26] might reflect that not only fragmentation and poaching pressure the population growth [29], but also the carrying capacity of the current habitats could be close to the upper limit in some cases. Recently, in June 2021, southern muriqui individuals were seen for the first time in Minas Gerais (Colas-Rosas, unpublished), where they were not expected to occur before, but the maps provided here indicate the suitability of the site in all the evaluated scenarios. In this case, the population found in the Mantiqueira mountains in São Paulo could have reached the carrying capacity of the habitat, and individuals had to move for foraging. This situation also evidences that certain limitations of the current PHVA, such as the lack of a spatial explicit mode for evaluating dispersion, should be addressed in future investigations.

On the other hand, Landis [66] suggests that the population in the Carlos Botelho state park is increasing, where the habitat is large enough and, thus, the carrying capacity is far from the current population size. These cases suggest that the proper estimation of K is critical for more reliable assessments and should be evaluated for each individual group of animals. In the case of the muriquis, this is currently impractical due to personal and budget allocation [31], which implies that intensifying the scientific research on all the known populations is urgent for a better understanding on how these primates can cope with climate change and habitat loss, informing conservation actions with updated data.

For better understanding of the genetic history of muriqui, especially in small populations [29], future investigations could explore the genotyping-by-sequencing (GBS) approach to describe the real genetic distribution of muriquis and the relations between genetic structure and landscape heterogeneity [73]. It will open new perspectives to muriqui conservation in light of allele fluctuations in time and space, showing short-term actions of genetics and environment losses, overcoming the well-known limitations of classic PHVA in conservation planning. Not only strictly academic research is needed for this purpose, but also involving different stakeholders and considering citizen science data has proven as essential tasks in promoting the muriqui conservation and future landscape design to cope with climate change [33,74,30]

6. Conclusions

For the first time, the joint impacts of climate change, landscape fragmentation and loss of genetic diversity are modeled to map the suitable remaining habitat for the southern muriqui, a Critically Endangered primate endemic from the Atlantic Forest. The results indicate a pronounced decrease in habitat suitability, even though large patches of protected forests are projected to remain in 2050. However, some populations are projected to be isolated by climate and landscape changes, which could have substantial implications for the genetic diversity of the southern muriquis in the short and long terms.

Despite exploratory and with intrinsic limitations, the results provided here point to some important conservation measures for the viability of the southern muriqui under climate and land use scenarios: (1) increasing the demographic and genetic monitoring efforts of the southern muriqui populations is imperative to understand whether they could cope to climate change; (2) habitat suitability will decrease in all the land use and climate change scenarios and; (3) ceasing the Atlantic Forest deforestation alone is not enough, therefore both the restoration and the enhancement the agricultural matrices are necessary for promoting connectivity and gene flux across the extant populations for maintaining long term genetic diversity.

Finally, there are already actions for the northern muriqui populations to ensure species conservation by several stakeholders; however, this action for southern muriqui still needs improvement. The southern muriqui is found in protected and unprotected, public and private, and large and small forest patches. Therefore, investing in the long-term conservation of the southern muriqui action is essential for the proper maintenance of the Atlantic Forest's ecosystems and, thus, for promoting key ecosystem services in its remaining suitable habitat, a region inhabited by more than 15% of the Brazilian population.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

All the data used is published and freely available for public used.

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Supplementary materials

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