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From Hot to Cold Spots: Climate Change is Projected to Modify Diversity Patterns of Small Mammals in a Biodiversity Hotspot

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ABSTRACT

Aim: Climate change represents one of the main threats to global biodiversity, and such alterations are expected to induce shifts in distribution ranges and diversity patterns. We evaluate if protected areas and forest remnants in the Atlantic Forest in South America (AF) are projected to ensure the taxonomic diversity (TD) and phylogenetic diversity (PD) of non-volant small mammals under scenarios of future climate change.

Location: Atlantic Forest (AF), South America.

Methods: We used Species Distribution Modelling (SDMs) through an ensemble approach to assess the potential distribution of 101 species of small mammals using present (1979–2013) and future (2050 and 2070) climate scenarios. We consider optimistic and pessimistic greenhouse gas concentration scenarios (SSP370 and SSP585). We accessed TD through the sum of the suitable areas vs. areas of low or unknown suitability distribution maps for each species and PD using the sum of the branch lengths of a phylogenetic tree spatialised.

Results: Our models suggest that climate change is likely to reduce the suitable climatic areas for small mammals in the AF. The shrinkage in the potential distribution is projected to lead to high loss of TD and PD. The southeastern region of the Atlantic Forest is likely to experience the most pronounced decline in PD, while some small areas in the southern Atlantic Forest are projected to increase PD in the future.

Gabriela Alves-Ferreira and Maurício Humberto Vancine should be considered joint first author.

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Main Conclusions: Our models suggest a strong decline in TD and in PD from biodiversity hotspot regions in the AF under climate change scenarios. Since small mammals have low dispersal ability, and because most of the AF is highly fragmented, it is unlikely that this biome will sustain small mammal biodiversity in the future.

1 | Introduction

Climate change is expected to induce species range shifts and alter diversity and distribution patterns (Mota et al. 2022; Alves-Ferreira, Giné, et al. 2022; Biber et al. 2023). It is expected that up to 49% of insects, 44% of plants, and 26% of vertebrates will lose more than half of their historical geographical range (Wudu et al. 2023), potentially leading to a decline in future species richness and community impoverishment. While the number of species (Taxonomic Diversity; TD) is widely used to evaluate the impacts of climate change on biodiversity (e.g., Mota et al. 2022), it does not account for the evolutionary history among species. This highlights the importance of considering multiple facets of diversity, particularly when these facets diverge (Mendes et al. 2020).

The response to climate change differs among species, and some may be more vulnerable than others, suggesting that species loss due to climatic causes is not randomly distributed across phylogeny (Prinzing et al. 2001; Thuiller et al. 2005). In fact, species distribution responses to climate changes tend to be more similar between closely related species (Eiserhardt et al. 2015). Consequently, the contraction of distribution ranges among these species can result in the loss of distinct and irreplaceable clades, decreasing phylogenetic diversity (PD) (Thuiller et al. 2011). For instance, future projections indicate reductions in PD by 2.7%, 11.5%, and 9.6% for plants, birds, and mammals, respectively, and the prevalence of species losses may potentially lead to homogenisation of European communities (Thuiller et al. 2011). Furthermore, places with a high diversity of ancient lineages are projected to disappear or relocate due to the shrinking of their geographic ranges, thereby threatening entire clades on the phylogenetic tree (González-Orozco et al. 2016).

In particular, the Atlantic Forest (hereafter AF) is the second major rainforest of America, after the Amazonian domain, established between 60 and 65 million years ago [mya] (Pennington et al. 2006; Colombo and Joly 2010), but it is reduced (23% to 36%) and highly fragmented (~97% of fragments are less than 50 ha) (Vancine et al. 2024). The AF hosts one of the most important faunal diversities of the world (Myers et al. 2000) and is still suffering from degradation that threatens biodiversity. The maintenance of current protected areas and the creation of new ones are being pursued by many researchers as an alternative to conserve endangered species and reduce biodiversity decline (e.g., Vale et al. 2018; Mota et al. 2018). Regardless of the positive outcomes resulting from protected areas, mostly in preventing deforestation, they remain underrepresented (Geldmann et al. 2013; Françaço et al. 2015). For instance, a recent assessment of areas of endemism (i.e., regions with a high number of uniquely found species) within the AF for non-volant small mammals has shown that most of these areas are unprotected (Dalapiccola et al. 2021). Furthermore, the areas of high conservation value that hold distinct taxonomic and phylogenetic diversity of angiosperm trees in the AF also need attention (Saraiva et al. 2018). Unprotected areas that have been neglected

have great potential because these regions may harbour new species that are already threatened (Avigliano et al. 2019). While some protected areas may no longer be suitable for certain species due to climate change, there are other protected areas that are expected to maintain similar climatic conditions (Ferro et al. 2014). Moreover, unprotected stable areas could be considered for protection in the future when the opportunity arises (Vale et al. 2018), for the AF (Tonetti et al. 2024).

One measure of diversity that became popular at the beginning of the 21st century is phylogenetic diversity (hereafter referred to as PD; Faith 1992), which became widely employed using genetic information to recover phyletic relationships. PD conveys information regarding the evolutionary processes driving community structure (Dreiss et al. 2015; Safi et al. 2011). This is particularly useful for species with similar ecological niches (Kozak and Wiens 2006; Wiens and Graham 2005), as the phylogenetic structure of communities may offer insights into the evolutionary persistence of species and the biogeographic processes that shape community composition. Recognising species distribution patterns is the first step to conducting any biogeographical analysis since these patterns provide basic information to test hypothesised historical or ecological biogeographic processes (Myers and Giller 1988).

Species Distribution Models (SDMs) have been increasingly used to evaluate the impacts of climate change on species distribution (Loyola et al. 2014; Zwiener et al. 2018; de Lima et al. 2019), and to guide conservation measures (Vale et al. 2018). The modelling approach has shown continuous improvements, with good practices and guidelines available (e.g., Zurell et al. 2020; Sillero et al. 2021), as well as a very robust methodology to predict species distribution and community composition changes (e.g., Alves-Ferreira, Giné, et al. 2022; Alves-Ferreira, Talora, et al. 2022; Mota et al. 2022; de Oliveira-Silva et al. 2022). SDMs have already proven to be a useful tool in identifying key areas for species diversity protection (Bonfim et al. 2019). Despite the well-known historically stable areas located in the AF, in addition to its high levels of PD (Pugliesi and Rapini 2015; de Oliveira Bünger et al. 2016), the region still lacks information on how the tree of life will change in the future. Understanding whether areas relevant for conservation within one of the most threatened forests on the planet will serve as refuges for evolutionary history in the future is of utmost importance (Vale et al. 2021).

Here, we focus on small mammals (rodents and marsupials) of the AF to assess whether forest remnants and protected areas can sustain taxonomic diversity (TD) and phylogenetic diversity (PD) in the face of climate change. Given the expected contraction of climatically suitable habitats for these species, we hypothesise a significant decline in both TD and PD across the region. Small mammals were selected as a focal group due to their limited dispersal capacity (Bowman et al. 2002), which could hinder their ability to track shifting climatic conditions

and colonise newly suitable habitats (Fricke et al. 2022). This study thus enhances our understanding of the impacts of climate change on the TD and PD of small mammals, providing new insights into the potential resilience of this group within fragmented landscapes and the role of forest remnants and protected areas in conserving future biodiversity.

2 | Methods

2.1 | Study Site

The AF is characterised by a complex topography and a wide latitudinal distribution along the Brazilian coast (from 3° to 33°) and the interior of Argentina and Paraguay (Figure 1) (de Muylaert et al. 2018). The extensive latitudinal range

combined with altitudinal gradients resulted in a wide variety of floristic formations, including lowland and montane evergreen rainforests, deciduous and semi-deciduous forests, subtropical Araucaria forests, and 'brejos de altitudes' forests (Oliveira-Filho and Fontes 2000; da Silva et al. 2004; Joly et al. 2014). These forests provide essential ecosystem services (e.g., carbon sequestration, purification of water and maintenance of soil fertility) for one of the most populated areas of Brazil (Ditt et al. 2010). The forest used to cover more than 150 million hectares but currently only ~23% of the original forest area remains in a fragmented landscape dominated by anthropogenic areas (Vancine et al. 2024). Today, these forest remnants are under threat from illegal hunting (Galetti et al. 2009, 2017), logging (Chiarello 1999), and human-made infrastructure (e.g., pipelines, roads), all of which increase the occurrence of large mammal mortalities (Miotto

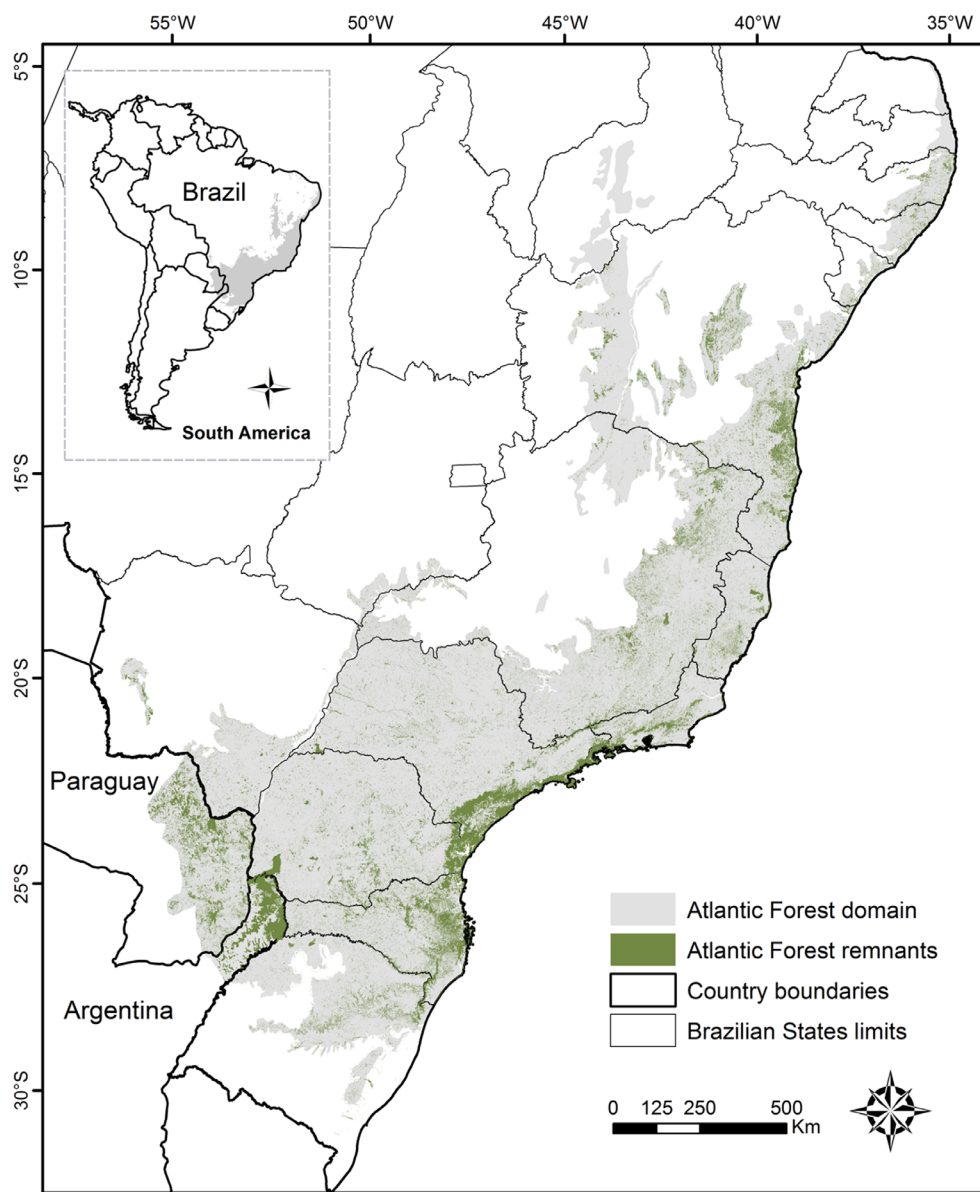


FIGURE 1 | Remnants of the Atlantic Forest present in Argentina, Paraguay, and Brazil. Brazilian states abbreviations: Alagoas—AL; Bahia—BA; Ceará—CE; Distrito Federal—DF; Espírito Santo—ES; Goiás—GO; Maranhão—MA; Mato Grosso—MT; Mato Grosso do Sul—MS; Minas Gerais—MG; Pará—PA; Paraíba—PB; Paraná—PR; Pernambuco—PE; Piauí—PI; Rio de Janeiro—RJ; Rio Grande do Norte—RN; Rio Grande do Sul—RS; Santa Catarina—SC; São Paulo—SP; Sergipe—SE; and Tocantins—TO.

et al. 2012; Galetti et al. 2017). In this region, we focus on terrestrial small mammals where around 30 species of marsupials (Didelphidae) and 97 species of small rodents (Caviidae, Cricetidae, Ctenomyidae, Echimyidae) (Bovendorp et al. 2017; Dalapicolla et al. 2021; Abreu et al. 2022).

2.2 | Occurrence Records and Bioclimatic Variables

We compiled occurrence records from the literature (Dalapicolla et al. 2021) and from the online platforms: GBIF (www.gbif.org, 2024), speciesLink (www.species-link.net, 2024), VertNet (<https://www.vertnet.org>), iDigBio (<https://www.idigbio.org>), Sistema da Informação sobre a Biodiversidade Brasileira (SiBBR) (www.sibbr.gov.br, 2024), iDigBio (www.idigbio.org/, 2024), and Portal da Biodiversidade-ICMBio (<https://portaldabiodiversidade.icmbio.gov.br/portal/>, 2024). The search returned 129,841 occurrences for 107 species. Afterward, we performed a quality control on the occurrences to eliminate duplicates, unlikely or impossible records, georeferenced in centroids of countries, states, and cities, or georeferenced in institutions (i.e., universities, zoos), filter only occurrences in South America spatial limit, and locate those over the ocean through the R package *CoordinateCleaner* (Zizka et al. 2019). We used occurrence records collected between 1970 and 2024. The taxonomic issues in species names were corrected by specialists in small mammals. We thinned occurrences to reduce spatial bias using 5 km filtering through the R package *spThin* (Aiello-Lammens et al. 2015). We also applied an environmental filter with the bioclimatic variables to eliminate occurrence records with the same value for the same environmental condition (using 12 classes) with the R package *flexsdm* (Velazco et al. 2022). Then, we selected species with more than 10 occurrence records to conduct further analysis. Our final database comprises 12,166 occurrence records for 101 species of small mammals (Table S1; Figure S1).

We obtained 19 bioclimatic variables (BIO01 to BIO19) from the CHELSA v.2.1 (Karger et al. 2017) database with a resolution of 2.5 arc-min resolution (~5 km²) for the spatial extent of South America. We used the present (1979–2013) and two future climate scenarios: 2050 and 2070. For each future scenario, we considered two Shared Socioeconomic Pathways (SSPs) representing optimistic (SSP370) and pessimistic (SSP585) greenhouse gas scenarios. We used all Global Circulation Models (GCM) available in CHELSA: GFDL-ESM4, MPI-ESM1-2-HR, MRI-ESM2-0, IPSL-CM6A-LR, and UKESM1-0-LL (Navarro-Racines et al. 2020; Cannon 2020) to minimise the uncertainty about the choice of just one GCM (Thuiller et al. 2019) and created mean rasters with the five GCMs for the two Shared Socioeconomic Pathways (SSPs).

2.3 | Species Distribution Modelling

We used Species Distribution Models (SDM) to model the climatically suitable areas of small mammals relating occurrences and a set of bioclimatic variables. We described the methodology for SDMs following the ODMAP (Overview, Data, Model,

Assessment and Prediction) standardised protocol (Zurell et al. 2020). Here, we include a summary of the ‘overview’ section, but detailed information about each step of the modelling can be found in [Supporting Information S2](#).

In this study, our goal was to project the TD and PD patterns of 101 species of small non-flying mammals for the present and under future climate change scenarios. To do so, we proceeded as follows: (1) we obtained occurrences for small mammals and a set of bioclimatic predictors; (2) we obtained multiple SDMs for each species generated with multiple algorithms and tuned with hyperparameters; (3) we derived an ensemble model for each species; (4) we stacked the suitable areas vs. areas of low or unknown suitability maps and calculated taxonomic and PD for each pixel. Our main study area is the AF in South America. However, we conduct the calibration and projection of the SDMs considering the entire extent of South America (Longitude −109.446 to −26.241, Latitude −58.498 to 12.590), since many species we are evaluating occur not only in the AF, but also in other biomes in South America. The community boundaries were defined as grid cells of 2.5 arc-min resolution (~5 km²). We adjusted bioclimatic variables for each species' calibration area using a buffer with a radius of ~300 km around species occurrences (Barve et al. 2011; Whitford et al. 2024) and selected a set of variables with the VIF lower than 2.0 (Dormann et al. 2013). The same variables were used to project the estimated niche for future scenarios of climate change.

We used SDMs for species with more than 20 occurrences (82 species, 81%) and Ensemble of Small Models (ESM) for species with less than 20 and more than 10 occurrences (19 species, 18%) (Breiner et al. 2015). For the calibration area of each species we randomly sampled background points (same number of presences) for Generalised Linear Models (GLM), Generalised Additive Models (GAM), Random Forest (RF), Support Vector Machines (SVM), Neural Networks Models (NNM), and Generalised Boosted Regression Models (GBM) algorithms, and randomly sampled background points (number of presences multiplied by 10; Whitford et al. 2024) for Gaussian Process Models (GPM) and MaxEnt algorithms throughout the area used for model fitting, because these algorithms need more information about environmental conditions. The models were fitted and evaluated using the R package *flexsdm* (Velazco et al. 2022) with the algorithms mentioned before, fitted without tuning: Generalised Linear Models (GLM, distribution family and poly = 2), Generalised Additive Models (GAM, binomial distribution family and thin plate regression spline as a smoothing basis), and Gaussian Process Models (GPM); and with hyperparameter tuning: Random Forest (RF; using *mtry* = (1, 2, 3, 4, 5, 6, 7), i.e., the number of variables to randomly sample as candidates at each split), Support Vector Machines (SVM; using *C* = (2, 4, 8, 16, 20), and *sigma* = (0.01, 0.1, 0.2, 0.3, 0.4)), MaxEnt (using regularisation multipliers = (0.5, 1, 1.5, 2, 2.5, 3, 3.5, 4), and feature classes = (l, lq, h, lqh, lqhp, lqhpt)), Neural Networks Models (NNM; using *size* = (2, 4, 6, 8, 10), and decay distance = (0.001, 0.05, 0.1, 1, 3, 4, 5, and 10)), and Generalised Boosted Regression Models (GBM; using *trees* = (20, 50, 100), *shrinkage* = (0.1, 0.5, 1), and *n.minobsinnode* = (1, 3, 5, 7, 9), i.e., the minimum number of observations in the terminal

nodes of the trees). We created SDMs with hyperparameters tuning because default hyperparameter values often do not return the best models (Fourcade 2021; Morales et al. 2017; Vignali et al. 2020).

We evaluated and calibrated the models using spatial block cross-validation with four partitions (Santini et al. 2021). The spatial block validation is considered a more robust approach for evaluating model transferability (Roberts et al. 2017). We partitioned the data using presence and background data using Spatial block cross-validation, which were used to partition the background data. First, we tried to partition to $k=4$ whenever possible; if the function returned an error, we decreased it and tried with $k=3$, and if the error persisted, we did it with $k=2$. For ESM, we used a random partition, with $k=3$ and 5 replicates due to few points of occurrences. We accessed the model performance by calculating the Boyce Index. We also reported other evaluation metrics to facilitate comparisons in the literature, such as Area Under Curve (AUC), Omission Rate (OR), FPB, and Sorensen Index.

We addressed algorithmic uncertainty by using an ensemble method that averaged the results from distinct algorithms (Araújo and New 2007). The ensemble models were computed as the weighted averages of the climatic suitability across all the algorithms, using the Boyce values as weight. We projected the models for the present, 2050, and 2070 in optimistic and pessimistic scenarios. We converted the final continuous models (present and future) into suitable areas vs. areas of low or unknown suitability maps (suitable areas=1 and areas of low or unknown suitability=0) using the threshold that maximises the sum of sensitivity and specificity (Max SSS) (Liu et al. 2013, but see Liu et al. 2016 for limits to that method). We chose this approach because our interest in this article was to analyse the composition of potential ecological communities (Stacked Species Distribution Modelling—S-SDM; Ferrier and Guisan 2006; Dubuis et al. 2011), and then calculate TD and PD for each potential community.

Lastly, we applied spatial constraints based on a posteriori method to reduce overprediction in suitable areas vs. areas of low or unknown suitability maps. We used the method “pres” (only occurrences-based restriction) to remove the overprediction, which only retains those pixels in suitability patches intercepting known occurrences records, for current and future scenarios (Mendes et al. 2020). All the analyses related to the modelling were conducted in the R package *flexsdm* (Velazco et al. 2022).

2.4 | Phylogenetic Analysis

For the phylogenetic analysis, we generated a molecular phylogeny through researching and compiling the Cytochrome B sequences for species present at the National Center for Biotechnology Information (NCBI; Bethesda, Maryland, USA). We excluded 30 species from the analyses that did not have Cytochrome B sequences. To perform the sequence alignment for species, we used Geneious (Biomatters Limited) (Kearse et al. 2012). To generate the AF small mammal tree, we imported species alignments to MEGA software and

generated pairwise distances for each species. We built the phylogenetic tree based on the Nei-Gojobori method, which is widely used to reconstruct mammalian phylogenies (Tobe et al. 2010). Thus, our phylogenetic tree for small mammals of AF had a strong degree of agreement with other phylogenies (Voss and Jansa 2009; Fabre et al. 2012; Jansa et al. 2014), and we used expert validation to ensure our phylogenetic tree had the most parsimonious taxonomic inference (Percequillo et al. 2011; Figure S2).

2.5 | Taxonomic and Phylogenetic Diversity

We estimated the TD as the number of species in each grid cell using the R package *divraster* (Mota et al. 2023), and calculated the PD based on the sum of the branch lengths (Faith 1992) for species in each grid cell using the R package *phyloraster* (Alves-Ferreira et al. 2024). The TD and PD were calculated for the present, 2050 SSP370, 2050 SSP585, 2070 SSP370, and 2070 SSP585. We overlapped the TD and PD rasters with protected areas from the World Database on Protected Areas (WDPA 2024) and forest remnants for the AF (ATLANTIC SPATIAL, Vancine et al. 2023).

As PD can be highly correlated with TD, we calculated the standardised effect size (SES) of PD using the R packages *SESraster* (Heming et al. 2023) and *phyloraster* (Alves-Ferreira et al. 2024). For this, we compared the observed values of the PD with randomised values of the metric generated with 999 randomisations. To generate the randomised communities, we used an algorithm that preserves the species richness for each grid cell and the number of sites occupied by each species, while randomising the location of the distribution of each species (Strona et al. 2014). Then, we calculated the SES using the following formula:

$$SES = \frac{\text{Metric}_{obs} - \text{Mean}(\text{Metric}_{null})}{SD(\text{Metric}_{null})}$$

where Metric_{obs} is the observed value for the metric, $\text{mean}(\text{Metric}_{rand})$ is the mean of the metric calculated based on 999 randomizations, and $SD(\text{Metric}_{rand})$ is the standard deviation of the 999 randomizations. Positive values of SES represent regions where the observed PD is higher than expected, and negative values of SES represent regions where the observed values are lower than expected randomly.

3 | Results

Ensemble models showed moderate to high predictive performance (median Boyce Index=0.910, SD=0.067; median Sorensen Index=0.667, SD=0.123; median AUC=0.698, SD=0.095; median TSS=0.434, SD=0.138; Median FPB=1.067, SD=0.259) (see Table S2). The models projected a decrease in the suitable area for many species (59 species, 57.84%) in response to future climate change. The three species projected to suffer the highest reduction in potential distribution are *Nectomys squamipes*, *Caluromys philander*, and *Thylamys velutinus*, while the species projected to

suffer the highest increase in suitability are *Calomys expul-sus*, *Caluromys lanatus*, and *Rhipidomys macrurus* (Table S3; Figure S3).

Our study estimates that many regions located within endemism centres of small mammals in the AF (Figure S4) are projected to lose TD in the future (Figure 2b–e). In the present, the models projected high TD in the southeastern region of the AF, including Brazilian states and regions of south Bahia (latitude –15), Espírito Santo (latitude –18 to –22), Rio de Janeiro (latitude –21 to –24), centre and northeastern São Paulo (latitude –21 to –25), southeast Minas Gerais (latitude –22), Paraná, and Santa Catarina (latitude –24 to –28) (Figure 2a).

However, the TD is projected to decline in the future, in both optimistic and pessimistic scenarios for 2050 (Figure 2b,c; Figure S5) and 2070 (Figure 2d,e; Figure S5). The regions projected to suffer the highest loss in TD are in the southeast of the AF, including various regions projected to have the highest richness in the present. Regions projected to have the higher increase in TD are in the south of AF, mainly in the Brazilian states of Rio Grande do Sul and Santa Catarina (latitude –27 to –34).

As the potential distribution area of the species slightly diminishes, there is also a reduction in the PD of small mammals (Figure 3b–e; Figure S6). Our models projected that regions with high TD in the present and in the future are congruent

with regions of high PD, as expected. High losses of PD are projected for the Brazilian states of south Bahia (latitude –13), Espírito Santo (latitude –17 to –21), Rio de Janeiro (latitude –21 to –23), southeast São Paulo (latitude –20 to –25), Minas Gerais (latitude –17 to –22), and Paraná (latitude –22 to –26) (Figure 3).

On the other hand, several regions of the AF are projected to increase the PD in the future, both in the optimistic and pessimistic scenarios and for the years 2050 and 2070. Models projected a gain of PD in the northern, central, and southern regions of the AF, including Bahia (latitude –10 to –15), north of Minas Gerais (latitude –15 to –18), Paraná, Santa Catarina, and Rio Grande do Sul (latitude –23 to –34; Figure 3). We also projected important areas for the conservation of small mammals (areas with high SES PD and high observed PD, Figure S7) in the centre, southeast, and northeast of the AF for the present and the future. Some of these critical areas for the conservation of PD of small mammals coincide spatially with regions projected to have an increase in TD in the future, such as the Brazilian states of South Bahia (Latitude –15 to –18), São Paulo (Latitude –20 to –25), Paraná, and Mato Grosso do Sul (Latitude –20 to –26, Figure S7 and Figure 2).

The decline in PD of small mammals is particularly concerning when focusing solely on the protected areas and forest remnants of the AF (Figure 4). Our models suggest that most of the protected areas along the central and northern region of AF are

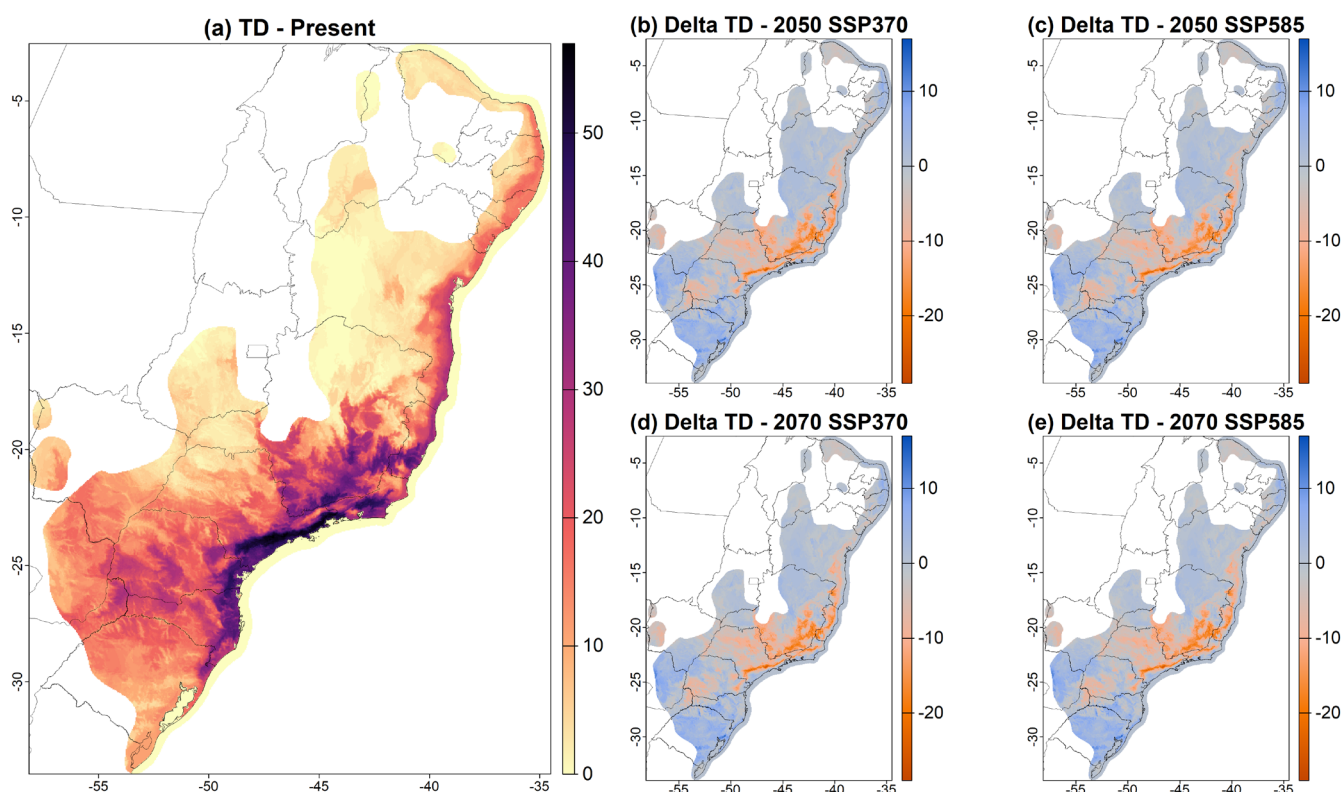


FIGURE 2 | Taxonomic diversity (TD) of small mammals in the Atlantic Forest. (a) TD for the present scenario, (b) differences in TD between present and the optimistic (SSP370) 2050 scenario, (c) differences in TD between present and the pessimistic (SSP585) 2050 scenario, (d) differences in TD between present and the optimistic (SSP370) 2070 scenario, and (e) differences in TD between present and the pessimistic (SSP585) 2070 scenario. Black and purple colours represent regions with high TD, and orange and yellow colours represent regions with low TD. Red colours represent losses in TD, grey colour represents areas where TD is not projected to change, and blue colour represents TD gains in the future.

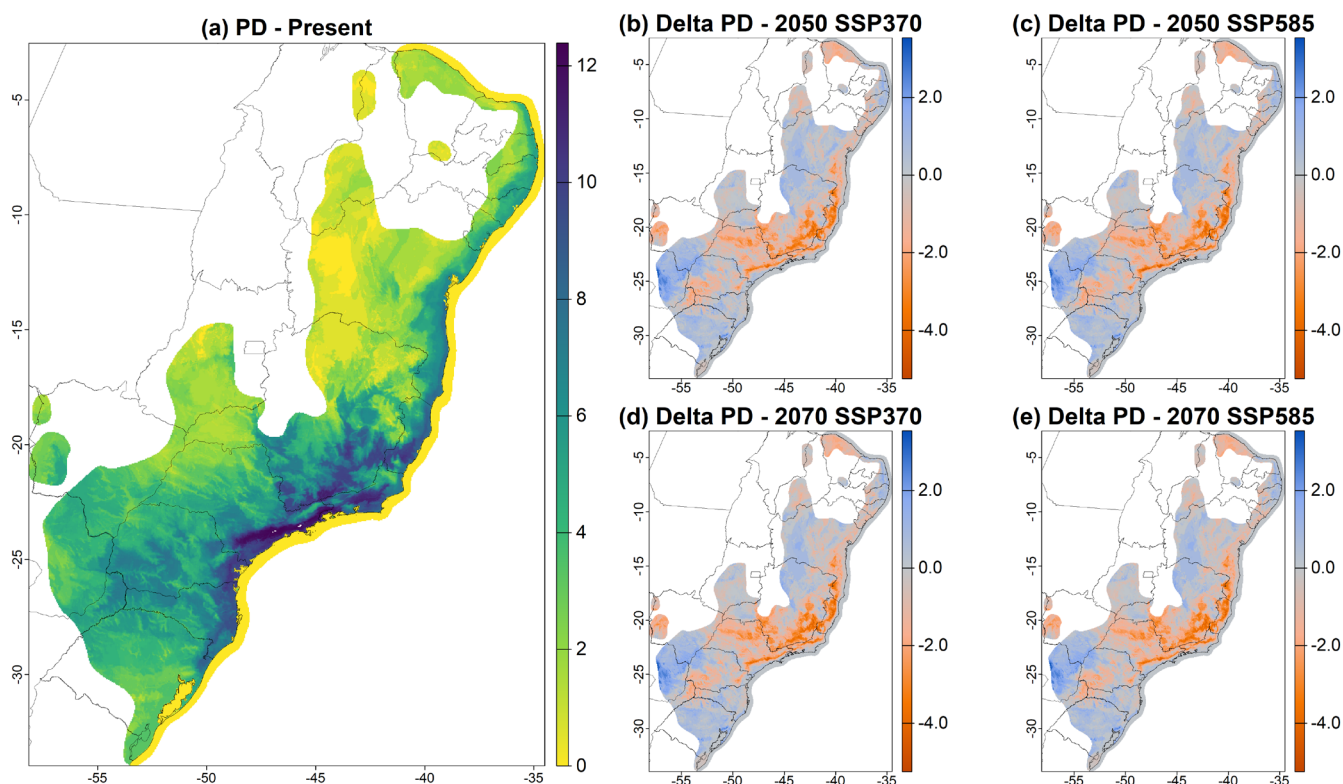


FIGURE 3 | Phylogenetic diversity of small mammals in the Atlantic Forest. (a) PD for the present scenario, (b) differences in PD between present and the optimistic (SSP370) 2050 scenario, (c) differences in PD between present and the pessimistic (SSP585) 2050 scenario, (d) differences in PD between present and the optimistic (SSP370) 2070 scenario, and (e) differences in PD between present and the pessimistic (SSP585) 2070 scenario. Dark green and purple colours represent regions with high PD, and light green and yellow colours represent regions with low PD. Red colours represent losses in PD, grey colour represents areas where PD is not projected to change, and blue colour represents PD gains in the future.

projected to suffer a loss in the PD of small mammals in 2070 in the pessimistic scenario, with few exceptions (Figure 4a). In the southern region of the AF, where the greatest increase in PD is expected, we observed some small and spatially distant protected areas (Figure 4a). On the other hand, regions with a high amount of native vegetation and a higher number of protected areas, such as Serra do Mar in the centre-south of the AF (latitude -22 to -26), present a pronounced loss in PD in the 2070 pessimistic scenario.

4 | Discussion

Our models suggest that changes in temperature and precipitation regimes measured by bioclimatic variables are likely to moderately reduce the taxonomic and PD of small mammals in several regions of the AF. Although some regions in the south of the AF are projected to gain PD in the future, most of these regions are in areas with few forest remnants and spatially isolated protected areas. To our knowledge, there is still no study evaluating the importance of forest remnants and protected areas for small mammals under climate change. Based on the results found here, we identify the regions projected to experience minimum to moderate losses in taxonomic and PD in the future. Even more importantly, our models projected areas of high stability (high SES PD, PD and TD) where diversity can be safeguarded and should be prioritised for conservation right now.

The projected patterns of TD observed for the present are congruent with other studies already carried out with mammals in South America, which have shown a high TD of small mammals along the south of the Brazilian state of Bahia, Espírito Santo, Rio de Janeiro, centre and northeast of São Paulo, northeast of Minas Gerais, and some regions in the north and centre of Paraná and Santa Catarina (Figure 1) (e.g., Maestri and Patterson 2016; da Silva et al. 2012; Costa et al. 2000). Additionally, these regions projected to present high TD spatially coincide with the Caparaó and Southeast endemism areas for non-volant small mammals in the AF (Dalapiccola et al. 2021). The projected high TD in these locations is also supported by other studies involving medium- and large-sized mammals, anurans, and birds (de Oliveira et al. 2023; Vale et al. 2018; Vasconcelos et al. 2018; Tonetti et al. 2022). In addition, these regions are home to unique species that cannot be found elsewhere, highlighting their importance as hotspots of endemism. Several of these regions currently harbour high levels of threatened species, mainly between the Paraná and São Paulo states (IUCN 2024), which are projected to be especially vulnerable to local extinctions. Furthermore, many species in these areas are understudied, potentially hiding even higher levels of threat and vulnerability (IUCN 2024; Lacher et al. 2020).

Our models suggest that many regions located within endemism centres are projected to lose TD in the future. Among these centres, the Bahia, Caparaó and Espinhaço endemism centres (see Figure S4) stand out due to a large loss in TD in 2050 and

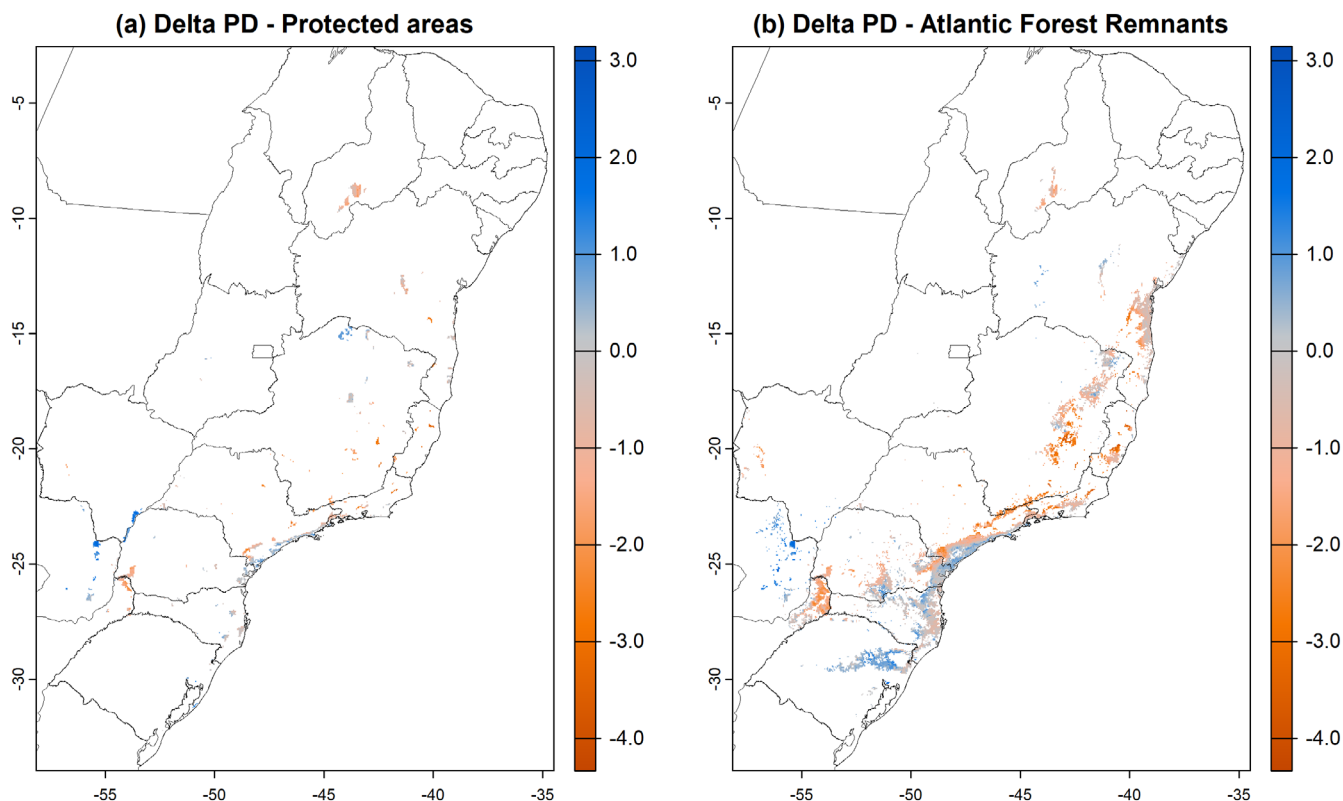


FIGURE 4 | Differences in phylogenetic diversity (PD) between present and the pessimistic 2070 scenario cropped by (a) protected areas and (b) forest remnants. Red colours represent losses in PD, grey colour represents areas where PD is not projected to change, and blue colour represents PD gains in the future.

2070. Significant changes in TD are also projected for the centre's Southeast (see Figure S4), located in the Coastal Mountain region in South-eastern Brazil. Although this region, delimited mainly by Serra do Mar, presents a large percentage of forest remnants and numerous protected areas, the projected changes in temperature and precipitation regimes are likely to lead to a strong reduction in the suitable climatic areas of small mammals in this region. The projected reduction in the potential distribution area of species in response to climate change has been recognised for other groups such as mammals (Levinsky et al. 2007; Maiorano et al. 2011; Schloss et al. 2012; Hidasi-Neto et al. 2019), anurans (Alves-Ferreira, Giné, et al. 2022; Alves-Ferreira, Talora, et al. 2022; Anunciação et al. 2023), reptiles (Biber et al. 2023), and birds (Mota et al. 2022; Tonetti et al. 2022).

The shrinking in the potential distribution of species can lead to a reduction or reallocation of mammal PD. In fact, climate change is projected to affect entire clades of the phylogenetic tree (González-Orozco et al. 2016). Our models suggest that PD of small mammals is projected to have a drastic decrease, mainly in the southeast of the AF. This region is projected to experience large increases in extreme events such as droughts, heavy rains, floods, and landslides (Magrin et al. 2014; Castellanos et al. 2022). As temperature determines the distributions of small mammals (Maestri and Patterson 2016), this climatic instability can lead to a decrease in taxonomic and PD of this group of vertebrates. Studies have shown that mammals with a low number of phylogenetically close relatives are more likely to be negatively impacted by climate change compared to species with a

high number of species in their genus and family (Russell and Schupp 1998; Purvis et al. 2000). This is because closely related species tend to share similar environmental needs and vulnerabilities to local threats (Jono and Pavoine 2012). However, having many similar species will not necessarily confirm more protection and/or less vulnerability, as some species show a genetic predisposition to local extinction and specific traits that increase their risk of extinction (Jono and Pavoine 2012).

The scenario gets worse when we consider that most protected areas and AF remnants cannot safeguard the projected PD of small mammals under climate change scenarios. Most of the remnants and protected areas are expected to experience a significant decline in PD in the future. For example, the endemism area in the southeast portion of the AF (see Figure S3) concentrates the highest loss of PD and deserves further attention. On the other hand, the eastern portion of Bahia state holds a significant amount of forest cover and is expected to hold PD in the future, thus representing a promising region to expand the protected areas network. This gain in PD is corroborated by a turnover pattern that has already been detected in the same region (Maestri and Patterson 2016). Parts of the south of the AF are also projected to have an increase in the PD.

Our models suggest yet that regions with fewer generic, tribal, and subfamily lineages, such as parts of the south and north-east, may experience future colonisation by phylogenetically distinct species, leading to an increase in PD. These areas can be used as a refuge for small mammals and are expected to concentrate high values of phylogenetic diversity in the future.

These places are of fundamental importance for conservation because they highlight regions that hold high evolutionary heritage (González-Orozco et al. 2016). Moreover, the stability of these areas aligns with historical patterns observed in the AF, where stable regions have acted as refuges, preserving endemic species and relict lineages (Keppel et al. 2012; Lourenço-de-Moraes et al. 2019). For example, the central AF served as a refuge for Neotropical species during the late Pleistocene (Carnaval et al. 2009), and high-elevation regions are expected to provide a similar refuge under future climate scenarios (Lemes and Loyola 2013; Struebig et al. 2015). Furthermore, unprotected areas with lower current diversity might serve as corridors for species migration to new suitable habitats (Littlefield et al. 2017, 2019). To ensure the persistence of small mammals and achieve long-term conservation objectives, it is essential to not only create new protected areas but also implement effective measures to reduce deforestation, fires, and species invasion in the south and northeast regions of the Atlantic Forest (Watson et al. 2013; Borges and Loyola 2020). Immediate action is needed to restore ecosystems, improve land management, and secure biodiversity while addressing private lands that do not comply with Brazilian legislation (Girardin et al. 2021; Rezende et al. 2018; Vancine et al. 2024).

We must consider that the potential distribution projected in this study contains some sources of uncertainty. For example, SDM models assume that species are at equilibrium with their environment, the niche is preserved over time, and species will not be able to adapt to climate change (Austin 2007). These assumptions disregard the species' capacity to persist through plasticity or shift their distribution to other regions when confronted with novel environmental conditions (Boutin and Lane 2014; Santos et al. 2017). Nonetheless, due to the ecological requirements and expected low plasticity of small mammals, especially those inhabiting anthropogenic-altered landscapes, distribution shifts and rapid adaptation are limited strategies for these species to effectively respond to swift climate changes (Boutin and Lane 2014). Furthermore, S-SDM are highly susceptible to criticism and may not represent species composition, often overestimating species composition (Calabrese et al. 2014; Zwiener et al. 2023). Despite this, our study is in line with other studies already published for several taxonomic groups that inferred the effects of climate change in the AF (e.g., Esser et al. 2019; Santos et al. 2020; Tonetti et al. 2022; Anunciação et al. 2023; Ribeiro-Souza et al. 2024). However, future studies may consider these limitations and apply more robust methods to estimate species composition (e.g., Guisan and Rahbek 2011; Calabrese et al. 2014).

In conclusion, our models suggest that climate change is likely to have a significant impact on small mammal communities in the AF. The proposed rise in greenhouse gas emissions, even if moderate, is expected to diminish the climatic suitability for small mammals across the entire AF, shrinking regions with high species richness. A substantial increase in average temperature would intensify the decline in areas conducive to climate for small mammals (this study), medium and large mammals even further (de Oliveira et al. 2023). Specifically, our models projected that the southeastern region of the AF is likely to experience the most pronounced decline in PD, while some areas in the south could serve as a climate refuge for these species.

However, the current protected areas and forest remnants are projected not to safeguard small mammal diversity under future climate change. Our study highlights the urgent need for action to mitigate the impact of climate change on small mammals and to protect their phylogenetic diversity. We recommend that conservation efforts consider the south of the AF as target regions, as these areas are projected to gain TD and PD in the future. These regions could be crucial for maintaining small mammals' evolutionary history. Addressing this issue could be the initial step toward protecting biodiversity and safeguarding the evolutionary history of the small mammals' community against the inevitable impacts of climate change (Bellard et al. 2012).

Author Contributions

R.S.B., C.B., M.H.V., T.S.-S., A.R.P., T.E.L., M.G.: designed the study. M.H.V., F.M.M.M., and G.A.-F.: conducted the analyses. R.S.B., G.A.-F., M.H.V., and F.M.M.M.: wrote the original draft. All authors reviewed and edited the manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All the scripts, raw data, and results are available on Dryad—digital object identifier (DOI): 0.5061/dryad.jdfn2z3m0.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.