Journal of Biogeography

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Journal of Biogeography

RESEARCH ARTICLE OPEN ACCESS

Bat Distribution and Habitat Protection Degree Along an Elevational Gradient in the Brazilian Atlantic Forest

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Received: 11 December 2024 | **Revised:** 8 May 2025 | **Accepted:** 9 July 2025

Keywords: Chiroptera | fuzzy models | hotspot conservation | mountain range | Serra da Mantiqueira | species distribution modelling

ABSTRACT

Aim: We aim to identify areas with greater favourability for bat occurrence in the Serra da Mantiqueira, southeastern Brazil, analyse gaps in bat distribution and evaluate the level of protection of areas with the greatest bat diversity.

Location: Serra da Mantiqueira, Atlantic Forest, Brazil.

Taxon: Bats.

Methods: We compiled data from 115 bat inventories carried out there for 25 years. Based on the presence/absence of 61 bat species and 47 explanatory variables, we used the favourability function as a modelling algorithm to predict species richness and distribution. We also calculated an Insecurity Index to estimate the degree of protection of favourable Atlantic Forest areas for each species and the overall richness of bat species.

Results: Models were obtained for 50 species based on the 10 best variables, of which the top five were the proportion of savanna formation (41.2%), spatial component (39.2%), the extension of roads (39.2%), proportion of forest formation (33.3%) and proportion of rocky outcrop (27.5%). We found that 37% of the area with 10 or more species has more than 70% of their surface protected, while ~74% are either not protected or have < 10% protected. However, ~22% of the most favourable areas still lack legal protection.

Main Conclusions: The highlands of the Serra da Mantiqueira are a hotspot for bat species richness and diversity in the Atlantic Forest, and our results facilitate more local discussions oriented to supporting the creation, improvement and implementation

of tools focused on the conservation of species and ecosystems in Brazil in this changing world. In this sense, in our study area, ecological corridors coupled with ecological restoration, in addition to improvements in the effectiveness of existing protected areas already implemented throughout the entire region, are extremely necessary.

1 | Introduction

Understanding how natural and anthropogenic factors determine species distribution, occupation and diversity in a given area is one of the key issues in ecology and biogeography (McGill et al. 2006; Lomolino et al. 2016). Different studies have tried to explain how elevation, latitude, temperature, precipitation and anthropogenic factors—like human population density and land use change—drive current species distribution patterns (e.g., Waltari et al. 2014; Coelho, Romero, et al. 2018; Aguiar et al. 2020). Globally, studies considering environmental and anthropogenic variables have been carried out with plants, amphibians, birds, medium and large-sized terrestrial mammals, and bats (see Milanovich et al. 2012; Aximoff et al. 2020; Delgado-Jaramillo et al. 2020; Sales et al. 2020; Tehrani et al. 2021). However, fewer studies have pooled these variables together, seeking to understand whether the current distribution of species is driven by recent changes in land use or by natural factors along elevational gradients (e.g., Real et al. 2013; Scherrer et al. 2019; Aximoff et al. 2020), and how these drivers may affect regional species conservation.

Studies on how different drivers of species distribution act along elevational gradients require a very evident environmental gradient (e.g., Mateo et al. 2012; Scherrer et al. 2019). The Serra da Mantiqueira, located in southeastern Brazil, is such an area, presenting a sharp elevational variation (from 500 to 2798 m a.s.l.), which leads to a very apparent variation in temperature, precipitation and vegetation structure and complexity (Ururahy et al. 1983; Veloso et al. 1991). Specifically, the vegetation of this region is classified as a tropical moist broadleaf forest, also known as Atlantic Forest and subdivided into lower montane forest (ca. 50–500 m a.s.l.), montane forest (ca. 501–1500 m a.s.l.), upper montane forest (ca. 1501–2000 m a.s.l.) and high-elevation fields (above 2000 m a.s.l.). This subdivision is due to the climatic variation that occurs mainly due to the difference in elevation, with the lower lands presenting average temperatures that vary between ~17°C (coldest months) and ~24°C (warmest months—Ururahy et al. 1983; Veloso et al. 1991; Pompeu et al. 2018). On the other hand, at higher elevations, the average temperatures vary from ~10°C (coldest months) to ~14°C (warmest months—Ururahy et al. 1983; Veloso et al. 1991). This same pattern is also observed for precipitation, where in the lowlands there is an average annual rainfall between ~800 mm and ~1600 mm and in the highlands between ~1200 mm and ~2400 mm (Ururahy et al. 1983; Veloso et al. 1991; Pompeu et al. 2018). This area still concentrates large remnants of the Atlantic Forest, a highly threatened biodiversity hotspot with many endemic species and is a priority area for conservation (Myers et al. 2000; Weber et al. 2007; Le Saout et al. 2013). Different studies have been carried out in the Serra da Mantiqueira to determine whether natural and/or anthropogenic factors may drive the distribution of species (Martins et al. 2015; Pompeu et al. 2018; Carvalho, Martins, Esbérard, and Palmeirim 2019; Gonzaga et al. 2019; Aximoff et al. 2020). However, few studies have considered current threats to local biodiversity, such as small hydroelectric power plants, power transmission lines, roads and land use changes (Aximoff et al. 2020; da Silva, Dupas, et al. 2021). For example, Aximoff et al. (2020) found that the distribution of the maned wolf *Chrysocyon brachyurus* is affected by both natural (elevation) and anthropogenic factors (agriculture fields), which are both extremely important for the management of the species and its habitat in the long term in the Serra da Mantiqueira. Furthermore, there is a large gap in the distribution of endemic Cactaceae species in the Serra da Mantiqueira, all of which are strongly threatened by the environmental degradation caused mainly by crop cultivation, cattle grazing, forest fires and disordered tourism (Gonzaga et al. 2019).

Besides considering wide environmental gradients, studies on species distribution patterns also need to carefully consider the chosen taxonomic groups, because the ideal taxa must respond well to the environmental gradient (Holt and Miller 2011). Bats are a useful group for such studies, as they are locally abundant and ecologically very diverse—with many different trophic guilds (Kalko et al. 1996; Kunz and Parsons 2009). For example, in the tropics and after rodents, bats are the most species-rich and locally abundant mammalian group (Medellín et al. 2000), with Brazil having 250 species of rodents followed by 186 species of bats (Abreu et al. 2024). In addition, bat species occupy different trophic guilds, including open- and closed-space insectivores, piscivores, gleaners, frugivores, sanguinivores and nectarivores (Kunz et al. 2011). Furthermore, they include species with both broad (e.g., *Carollia perspicillata*) and restricted (e.g., *Lonchophylla peracchii*) distributions. Some of those species and guilds have been documented to respond to natural and anthropogenic changes in a clear or predictable way (Gorresen and Willig 2004; Carvalho, Fluck, et al. 2023). In addition, their conservation is critical due to their key role in seed dispersal, pollination and insect suppression, with clear consequences for forest dynamics and maintenance (Kunz et al. 2011). Therefore, studies on the role that different environmental and anthropogenic drivers may play in the occurrence of bat species are useful not only for the conservation of bats per se but also for the other species they interact with and for the habitats and ecosystems in which they occur.

The southeastern region of Brazil has a high concentration of bat inventories (Delgado-Jaramillo et al. 2020) with at least 50 bat species occurring along the Serra da Mantiqueira (Nobre, Mello, et al. 2013; Martins et al. 2015; Mello et al. 2016; Esbérard et al. 2017; Xavier et al. 2018; Carvalho, Martins, Esbérard, and Palmeirim 2019; Mancini et al. 2022; Vela-Ulian et al. 2023). Recent studies have addressed the factors involving bat species distribution in Brazil (Aguiar et al. 2020; Delgado-Jaramillo et al. 2020), and the elevation in the Serra da Mantiqueira may negatively affect such distribution, reducing its taxonomic diversity, total abundance, and abundance of frugivorous and omnivorous bats (Moras et al. 2013; Martins et al. 2015; Carvalho, Martins, Esbérard, and Palmeirim 2019). Locally, this pattern is related to decreased food availability and cold tolerance, which do not appear to affect insectivorous and sanguinivorous bats (Martins et al. 2015; Carvalho, Martins, Esbérard, and Palmeirim 2019). But besides natural drivers, the number of small hydroelectric plants, paved roads, mining requisitions and the suppression of local vegetation has greatly increased in the Serra da Mantiqueira in the last 20 years (e.g., Carvalho et al. 2015; Xavier et al. 2018; Zucarelli and Zhouri 2023). This is particularly alarming considering that the Serra da Mantiqueira harbours the headwaters of the main rivers that supply dozens of cities in the largest urban centres in Brazil. Therefore, anthropogenic variables must be considered and included when predicting the future fate of the region and its biodiversity.

Using the favourability function, an algorithm based on the properties of fuzzy logic, we (1) modelled the bat species distribution for the Serra da Mantiqueira to find environmental favourability values based on the probability of the presence of bat species obtained from species distribution models (SDMs). Furthermore, Insecurity Index metrics were employed to (2) analyse gaps in the distribution of the entire species pool and each species under investigation. This methodology allowed us to (3) identify areas with greater favourability for bat occurrence, that is, the ecologically sensitive regions for bats in the Serra da Mantiqueira. From the results of the modelling and gap analysis of the distribution of bat species, and by crossing our outputs with maps of Brazilian protected areas, we were able to (4) evaluate the level of protection for the most ecologically sensitive regions and (5) propose potential areas for future conservation management efforts.

2 | Methods

2.1 | Study Area

The Serra da Mantiqueira (Figure 1), placed in southeastern Brazil, extends over ~500 km across the most populated Brazilian region, along the states of Espírito Santo, Minas Gerais, Rio de Janeiro and São Paulo (Pompeu et al. 2018; Gonzaga et al. 2019). Serra da Mantiqueira covers one of the most representative areas of the Brazilian Atlantic Forest, with altitudes from 500 to 2892 m a.s.l. (Simas et al. 2005; Barreto et al. 2013; ICMBio 2015). Moreover, this extensive mountain range is recognised as a biodiversity hotspot and a conservation priority within Brazil (Myers et al. 2000; Becker et al. 2013; Le Saout et al. 2013; Gonzaga and Menini Neto 2017).

The area of the Serra da Mantiqueira has been delimited in several ways by various authors after different administrative or geographical boundaries (e.g., Machado-Filho et al. 1983; Radam Brasil 1983; Pelissari and Neto 2013; Pompeu et al. 2018; Gonzaga et al. 2019). Here, we follow Pereira et al. (2021), whose proposed limits comprise 399 municipalities and around 135,000 km^2, with the largest part in Minas Gerais state (Figure 1).

For our analyses, the study area was divided into 1564 hexagons of approximately 6 km apothem (about 100 km^2) using QGIS software version 3.16 (QGIS Development Team 2021).

2.2 | Species Data Collection

We searched for previous peer-reviewed studies on bats in the Scientific Electronic Library Online—Scielo (http://www.scielo.org), Web of Science database—WoS (http://www.webofknowledge.com) and Google Scholar (https://scholar.google.com.br/), using a combination of the following keywords: bat, bats, *morcego*, *morcegos*, Mantiqueira Mountains and Serra da Mantiqueira. This search covered 20 studies published up to 2023 (Nobre et al. 1998, 2009; Barros et al. 2006; Carvalho et al. 2013; Luz et al. 2013; Moras et al. 2013; Nobre, Mello, et al. 2013; Nobre, Manhães, et al. 2013; Mello et al. 2014, 2016; Dias et al. 2015; Martins et al. 2015; Esbérard et al. 2017; Xavier et al. 2018; Carvalho, Martins, Esbérard, and Palmeirim 2019; Carvalho, Martins, Dias, et al. 2019; Mancini et al. 2019, 2022; Vela-Ulian et al. 2023). In addition, we searched additional records from the databases of the Sistema de Avaliação do Risco de Extinção da Biodiversidade (SALVE) of Instituto Chico Mendes de Conservação da Biodiversidade (SALVE/ICMBio—https://salve.icmbio.gov.br/). Additional non-published records from 18 locations sampled by the *Laboratório de Diversidade de Morcegos* (LADIM) from the *Universidade Federal Rural do Rio de Janeiro*

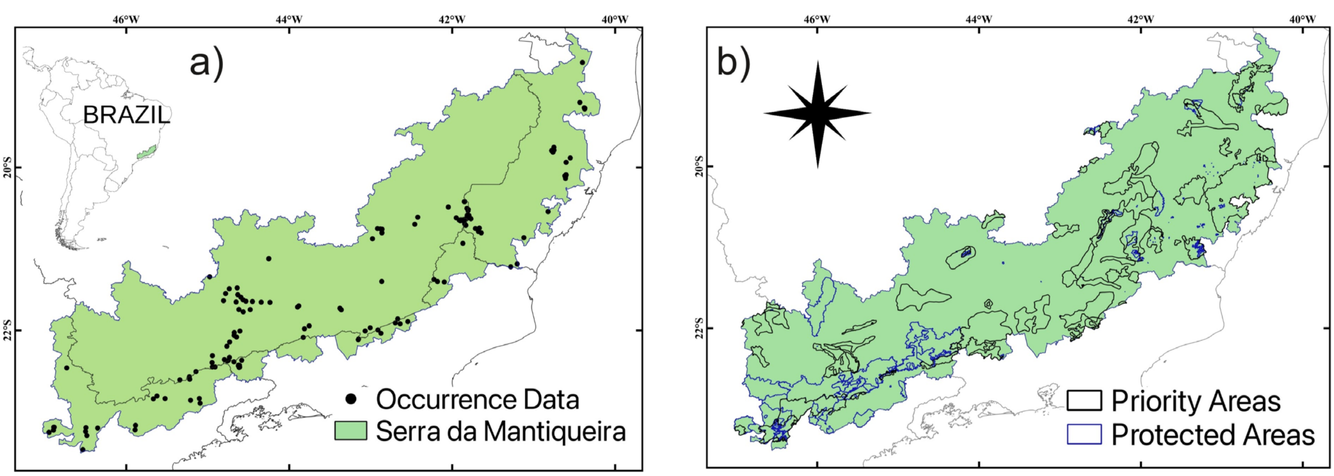

FIGURE 1 | Map of the study context. (a) Sites with the occurrence of bats detected in the Serra da Mantiqueira, southeastern Brazil and (b) the limits of the territory with priority and protected areas.

(UFRRJ), the *Coleção de Mamíferos* from the *Universidade Federal de Lavras* (UFLA), the *Laboratório de Estudos de Quirópteros* (LabEQ) from the *Universidade Federal do Espírito Santo* (UFES), and from samplings by Pedro Henrique Nobre from the *Universidade Federal de Juiz de Fora* (UFJF) were also considered. We compiled 1029 occurrences of 61 bat species in an elevational gradient from 6 to 1954 m a.s.l. (Table S1). The presence/absence matrix was elaborated using QGIS software version 3.16 (QGIS Development Team 2021). If at least one observed record of a given species was inside the hexagon, that species was classified as present. It was considered absent if the species was not observed (Lobo et al. 2010).

2.3 | Environmental and Anthropogenic Variables

The 47 predictors we employed to characterise the environment already have been evidenced as affecting bat distribution (e.g., Carvalho, Martins, Esbérard, and Palmeirim 2019; Delgado-Jaramillo et al. 2020; Carvalho, Rosalino, et al. 2023): spatial trends, topography, hydrology, climate (temperature and precipitation), population density, land use (e.g., forest and savanna formation, pasture amount, rocky outcrop, semi-perennial crop amount), energy developments, length of roads and mining operation (see variables and factors in Table S2). We assigned a value or category for each environmental or anthropogenic predictor to each hexagonal grid cell using QGIS tools.

To account for broad-scale spatial structure not captured by environmental variables, we incorporated a polynomial trend surface derived from geographic coordinates—latitude (La) and longitude (Lo). This approach enables the detection of purely spatial trends potentially related to spatial dynamics (Legendre 1993; Barbosa et al. 2010). Following Legendre and Legendre (1998), we computed a set of spatial predictors including the linear, quadratic, and cubic terms of La and Lo, as well as their interactions: La, La^2, La^3, Lo, Lo^2, Lo^3, La·Lo, La^2·Lo and La·Lo^2. Purely linear or uncombined geographic predictors rarely capture the full spatial complexity of species distributions. In contrast, polynomial combinations derived from trend surface analysis allow for the modelling of both linear and nonlinear spatial patterns—including quadratic, cubic, and interaction terms—thus offering a more flexible and spatially informed representation (Legendre and Legendre 1998). We first performed a logistic regression of species presence/absence against this full set of nine spatial terms as part of the trend-surface analysis. The resulting multifactorial spatial combination (hereafter, spatial logit) was then included in the modelling process alongside the environmental predictors. This spatial term enables the identification of whether each bat species' distribution is better explained by underlying geographic trends—potentially associated with historical factors or recent population dynamics—rather than by the environmental conditions of the habitats they currently occupy (Barbosa et al. 2010; Legendre 1993). The average elevation was extracted based on data from Danielson and Gesch (2011). Climatic variables (BIO1 to BIO19) from CHELSA (Karger et al. 2017), ETP Seasonal, ETP Annual, Climatic Moisture Index, Growing Degree Days greater than 0°C (GD00) and Growing Degree Days greater than 5°C (GDD5) were obtained from the Environmental Raster for Ecological Modelling https://envirem.github.io. The variables referring to hydrology (Total of river lines and distance to rivers) were extracted from https://www.hydrosheds.org/page/hydrorivers. The land use data were extracted from *Projeto Map Biomas* (Projeto MapBiomas 2022). Finally, we considered mining (both in operation and requested licences), extracted from https://geo.anm.gov.br/portal/apps/webappviewer/index.html?id=6a8f5ccc4b6a4c2bba79759aa952d908, and population density and length of roads, extracted from https://sedac.ciesin.columbia.edu/data/set/gpw-v4-data-quality-indicators-rev11/data-download#close, as anthropogenic variables.

2.4 | Procedure and Favourability Algorithm Analysis of Species Distribution Models (SDMs)

We used SDMs to relate bat species occurrences to environmental variables and to predict their potential distributions, as other authors have already applied to improve decision-making on its conservation (Razgour et al. 2016). Specifically, we applied the favourability function (Real et al. 2006), which adjusts the logistic regression probability to account for species prevalence, making the resulting favourability values comparable across species. This comparability enables the integration of multiple species (Romero et al. 2016; Romero, Olivero, Real, and Guerrero 2019) in joint analyses and supports the application of fuzzy logic operations in subsequent steps (Zadeh 1965; Salski and Kandzia 1996; Acevedo and Real 2012; Romero et al. 2023).

In the modelling process, and for each species of bats, prior to running logistic regression and to reduce redundancy among predictors, we assessed pairwise correlations using the commonly accepted threshold in biogeography of $r > 0.8$ (Mateo et al. 2013; Romero, Olivero, and Real 2019; Aximoff et al. 2020; Choi and Lee 2022), which allows detection of problematic collinearity while retaining explanatory variables that are ecologically meaningful. Pearson's correlation coefficient ($r > 0.8$) was applied using the *corSelet* function in R to retain non-collinear variables (Barbosa 2024). From the correlated pair of variables, this function iteratively eliminates variables based on their variance inflation factor (VIF; Marquardt 1970) and significance (*p* values) with the response variable, always retaining the variable with the greatest explanatory support and most strongly associated with bat species distributions. Then, according to the resulting set of variables that passed this filter and the occurrences of presence/absence, we performed a forward-backward stepwise logistic regression function (Hastie and Pregibon 1992) as SDMs for each bat species. Stepwise variable selection is a widely used method to choose a significant subset of variables in a model (e.g., Muñoz et al. 2005; Real et al. 2013; Estrada and Real 2018; Romero, Olivero, and Real 2019; Romero, Olivero, Real, and Guerrero 2019). This function runs a stepwise regression, selecting and/or excluding variables based on significance (*p*-value), where the threshold value for a variable to enter the model is $p = 0.05$ and for a variable to be dropped from the model is $p = 0.1$. Therefore, at each step, only one variable with a significant additional contribution to the model is added. This procedure evaluates the explanatory contribution of each variable set at each step, allowing the addition of new variables only if a significant proportion of variation in the presence/absence data remains unexplained. Importantly, the algorithm can also remove previously included variables if they no longer improve the model's overall performance. This iterative mechanism avoids overfitting and ensures that only variables that significantly contribute to the model are retained. The 'fuzzySim' package (Barbosa 2024) was used to automatise this run modelling routine. For this purpose, the *multGLM* function was applied, which allows the entire procedure to be performed sequentially through a script (for more information, see: https://modtools.wordpress.com). Variables with non-significant coefficients in the model (Chi-square test, $p < 0.05$) were eliminated with the *trim* function to obtain a model with all the coefficients significantly different from zero according to Crawley's procedure (Crawley 2007). Finally, we evaluated the relative weight of each variable included in the models through the Wald parameter (Wald 1943) and checked multicollinearity problems according to the inflation values or VIF (Montgomery and Peck 1992).

From the probability generated by the logistic regression for each bat species, we obtained favourability values according to the F Function (FF) formula (Real et al. 2006; Acevedo and Real 2012):

$$F = [P/(1 - P)] / [(n1/n0) + (P/[1 - P])]$$

where F is the environmental favourability (ranging between 0 and 1), P is the probability of occurrence obtained from the multivariate logistic regression performed for each explanatory variable, n1 is the number of presences, and n0 is the number of absences in each case. The favourability values represent the contribution to the probability of occurrence of the species response to the local environmental conditions and its particular history and population dynamics. Note that local probability depends on local favourability and the overall prevalence of the species in the dataset. Thus, favourability is a commensurate unit that allows us to compare and combine models of species differing in prevalence.

2.5 | Performance of the Models

The discrimination and classification ability of the models was evaluated according to Zurell et al. (2020). The discrimination ability of the models was assessed by the receiver operating characteristic (ROC) curve and area under the ROC curve (AUC), which is independent of any favourability threshold (Hanley and McNeil 1982; Dodd and Pepe 2003; Guisan et al. 2017). The classification ability of the models was evaluated using four threshold-dependent indices: sensitivity, specificity, correct classification rate (CCR) and true skill statistic (TSS) (Liu et al. 2009). These classification indexes vary from 0 to 1, and the prevalence value was used as the classification threshold. However, the TSS index is found by subtracting true positive and false positive rates without considering the prevalence. It varies between −1 and +1, where TSS = 1 indicates a perfect match, and a value of TSS = 0 would indicate a performance worse than random (Allouche et al. 2006).

2.6 | Assessing Richness Versus Accumulative Favourability

The summary of the known richness was obtained from the observed presence of each bat species in each hexagon unit. Then, according to the fuzzy logic tools and the commensurable characteristic of the favourability function, we summed and obtained the cumulative favourability in each hexagon as a potential richness measure.

2.7 | Insecurity Index Metrics

An Insecurity Index was calculated for each analysed bat species and for total richness. The Insecurity Index, ranging from values between 0 and 1, is based on species distribution modelling and fuzzy logic, representing how much of the fuzzy set of favourable areas for a species or a group of species is not contained in protected areas (Estrada and Real 2018; Díaz-Gómez et al. 2013). The closer to 1, the greater the extension of the favourable areas not covered by the protected areas. We obtained two metrics of the Insecurity Index for each species:

1) The Insecurity Index for each hexagon (pixel) (I_{ij}), according to the equation:

$$I_{ij} = F_{ij} - \left(F_{ij} \times P_j\right)$$

where I_{ij} is the Insecurity Index of species i in cell j, F_{ij} is the favourability for species i in cell j, and P_j is the extent of a hexagon that is covered by a protected area as a quantitative measure of the percentage of hexagons that it is protected (Sánchez-Fernández and Abellán 2015; Estrada and Real 2018). Then, from the Insecurity Index for each species in each hexagon unit, we obtained the sum of the Insecurity Index for bats in each hexagon unit. Therefore, mapping the sum of the Insecurity Index for hexagon units identified 'insecure areas', or areas with high environmental favourability to bats but not protected, proportioning an objective criterion to establish spatial conservation priorities.

2) The Overall Insecurity Index of each species (I_i):

$$I_i = \frac{\sum_{j=1}^{n} I_{ij}}{\sum_{j=1}^{n} F_{ij}}$$

where I_{ij} is the Insecurity Index of the species i in cell j, F_{ij} is the favourability for the species i in cell j, and n is the total number of cells in the study area. This gives a value of overall insecurity for each species. Then, from the Overall Insecurity Index, we calculated the complementary *i (Si)* or the Overall Security Index as I_i ($Si = 1 - I_i$) for each species. The Overall Security Index represents how much of the fuzzy set of a species' favourable areas are included in protected areas. This is equivalent to calculating the proportion of favourable areas covered by the Brazilian protected areas network and priority areas for conservation. A bat species was correctly represented by the current protected areas network when the proportion of favourable areas covered by the network was higher than the proportion of the total area of the Serra da Mantiqueira covered by the network (10.98%, 21.88% and 29.03% all together). To obtain the representativeness of the species in the network, we divided the Overall Security Index for each species by the proportion of the study area in the Serra da Mantiqueira covered by the network. Values above 1 imply that the percentage of favourable areas covered by the protected areas network for a given species is higher than the percentage of the Serra da Mantiqueira covered by the network and, thus, higher than expected by chance.

We used the World Database on Protected Areas (https://www.iucn.org/theme/protected-areas/our-work/world-database-protected-areas) and the database of Brazilian protected areas provided by Brazil's *Ministério do Meio Ambiente* (http://mapas.mma.gov.br/i3geo/datadownload.htm) to overlay the maps resulting from the SDMs with local protected areas. In addition to protected areas, we also use the map for priority areas for biodiversity conservation, provided by the Brazilian Environment Ministry (https://www.gov.br/mma/pt-br/assuntos/biodiversidade-e-ecossistemas/ecossistemas/conservacao-1/areas-prioritarias/2a-atualizacao-das-areas-prioritarias-para-conservacao-da-biodiversidade-2018). Priority areas are not yet protected areas but are defined as important areas for taking actions, formulating and implementing public policies, programmes, projects and activities aimed at conserving biodiversity, such as the implementation of protected areas (see Brasil 2018). The entire Serra da Mantiqueira area has 11% protected areas and 22% priority areas for conservation (see Figure 1b). We used QGIS software (QGIS Development Team 2021) to calculate the percentage of protected and priority areas in each hexagon.

3 | Results

Based on 1029 occurrences detected, 61 species of bats occur along the Serra da Mantiqueira, distributed in the families Phyllostomidae (34 species), Molossidae (13 species), Vespertilionidae (13 species) and Emballonuridae (one species). Of these species, the phyllostomids *Sturnira lilium* (118 occurrences), *Carollia perspicillata* (108 occurrences), *Desmodus rotundus* (99 occurrences) and *Artibeus lituratus* (86 occurrences) were more widespread. Vespertilionids (*Eptesicus diminutus*, *Lasiurus cinereus* and *Myotis levis*) and Molossids (*Molossus aztecus, Eumops auripendulus* and *Molossops neglectus*) presented fewer occurrences (Tables S1 and S3).

3.1 | Species Distribution Models and Factors That Determine the Distribution of Bats

Since for 10 bat species the number of occupied hexagons was not sufficient to generate a model (less than five occurrences), species distribution models were obtained only for 50 bat species (82% of our compiled species pool), including 28 species of Phyllostomidae, 13 species of Vespertilionidae, eight species of Molossidae and one species of Emballonuridae (Table S4). The generated favourability models had a high discrimination capacity [AUC >0.9 (0.559–0.999)—Hosmer and Lemeshow 2000], plus a high classification capacity in terms of presences or sensitivity 0.864 (0.500–1), absence or specificity 0.846 (0.664–1), and general classification measure or CCR 0.846 (0.666–0.977). The minimum cumulative favourability value (CF) for the Serra da Mantiqueira was 4.78, with a nucleus in favourability in the distribution of bat species in its central corridor (CF ≥ 10), which had the greatest coverage of Atlantic Forest and the highest elevations for the region (> 500 m a.s.l.—Figure 2a,b). This nucleus in favourability also strongly coincided with the cells that presented the highest observed species richness (Figure 2c).

Thirty variables were included in at least one species model, with five appearing in 15 or more models. The number of variables contributing to the models ranged from one to seven (see Table S4). Specifically, the environmental predictors that most often entered in models were the proportion of savanna formation (positive contribution in 41.2%, $n=21$), spatial component (positive contribution in 39.2%, $n=20$) presence and extension of roads (positive contribution in 39.2% of models, $n=20$ species), the proportion of forest formation (positive contribution in 33.3%, $n=17$), and the proportion of rocky outcrop (positive contribution in 27.4%, $n=14$—Table S4).

3.2 | Coverage of Protected Areas for Hotspots of Bat Diversity in the Serra da Mantiqueira

Overall, we found that 23.27% of the 1564 hexagons were covered by protected areas, while 43.09% were covered by priority areas for conservation. We found that only 26.67% of the hexagons with 10 or more species had more than 70% of their surface within protected areas (Figure 2). However, 76.68% of the hexagons were either not protected or had < 10% protected. For the cumulative favourability, 309 (28.74%) out of 1075 hexagons with ≥ 10 of cumulative favourability were within protected areas that correspond to the areas of higher favourability and the highest areas of this mountain range. However, of these 293 hexagons, 84 (27.39%) were within sustainable use areas designated as *Área de Proteção Ambiental* (APA—Environmental Protection Areas), an IUCN category V protected area with the lowest level of protection under Brazilian legislation. That included APA Serra da Mantiqueira and APA Fernão Dias. We obtained the Insecurity Index metrics, representing the cartographic values obtained by the sum of bat species in relation to the location of protected territories (see Figure 3; Table S5). In general, the sum of the Insecurity Index indicated that priority areas covered less favourable territories for bats, and for those with the highest insecurity values, especially focused on the southwestern part of the region, in areas with the highest accumulation of favourability values (Figures 2b and 3b). On the other hand, the sum of the Insecurity Index for protected areas was highest only in a few hexagons next to the limits of the protected areas (Figures 2a and 3a).

4 | Discussion

We compiled data from 125 bat inventories over 25 years (1998–2023) in the Serra da Mantiqueira, which resulted in at least 61 bat species for the area. Our analysis evidenced that the central corridor of the Serra da Mantiqueira with higher elevations has greater bat species richness and diversity. This region is already relatively well protected by a network of protected areas and 27% of the areas with 10 or more species have more than 70% of their surface protected. However, our more local analysis with diffuse logic attention highlighted that many bat species could still be unprotected, as 76.73% of the region is not protected at all and 7.7% has < 10% protection. Moreover, we detected that despite the large network

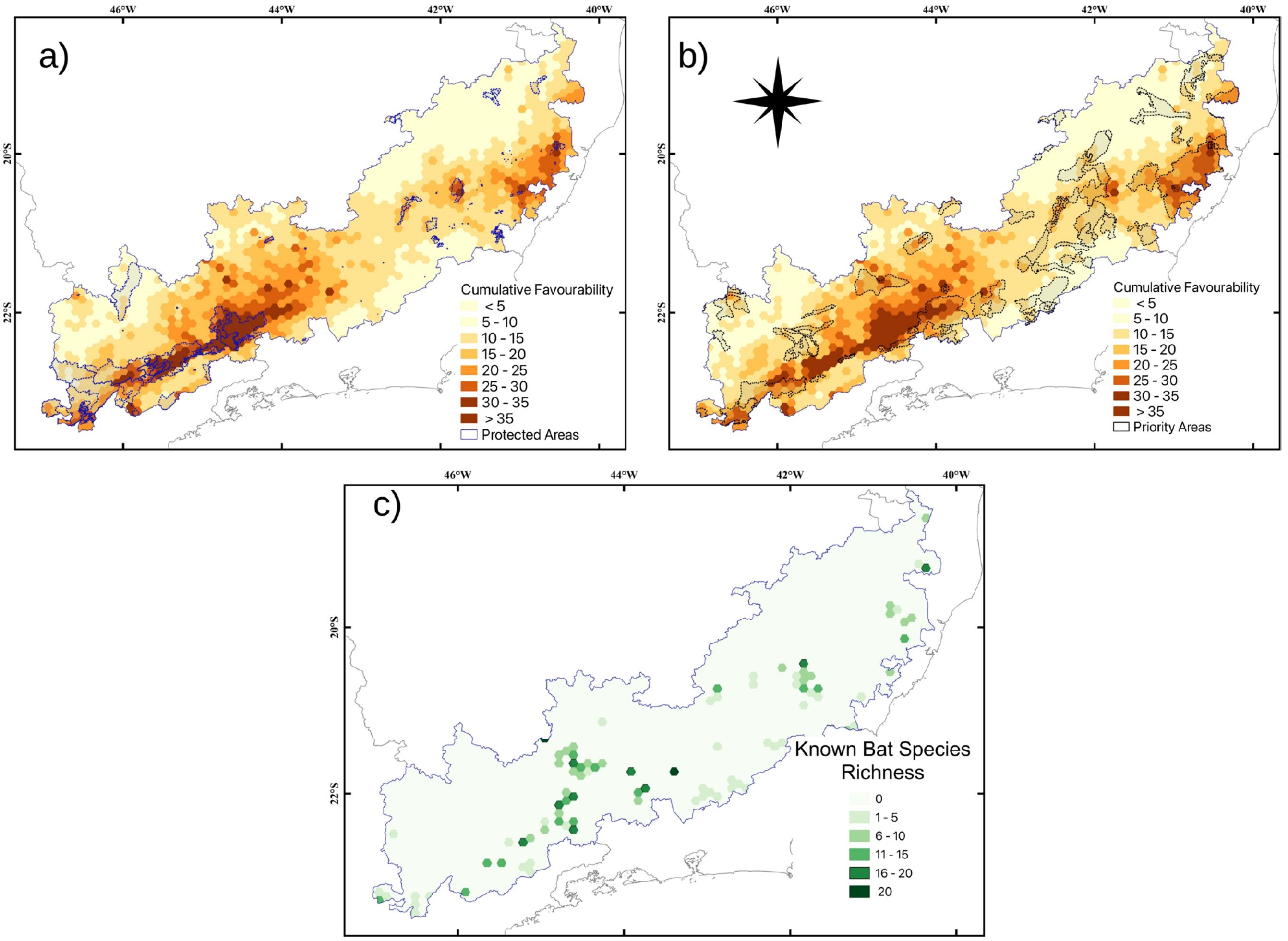

FIGURE 2 | Cumulative favourability maps for bat species in the Serra da Mantiqueira (a and b), southeastern Brazil, with values ranging from < 5 (favourable areas to fewer bat species) to > 35 (favourable areas to most bat species). Blue polygons are limits of protected areas (a); black polygons are priority areas for biodiversity conservation (b). Know bat species richness (c).

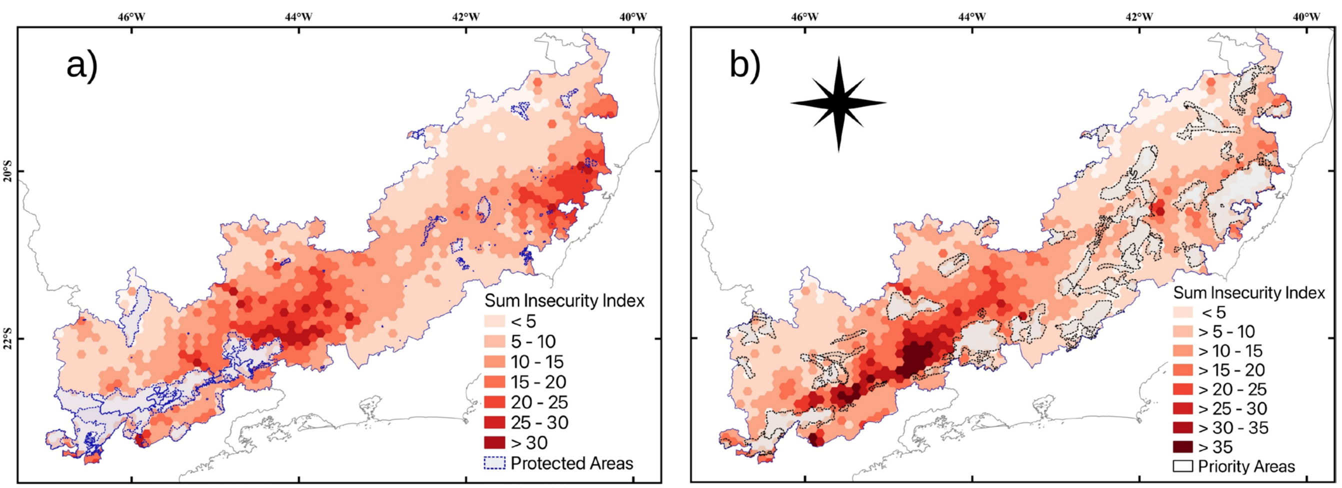

FIGURE 3 | Insecurity Index for 50 bat species in the Serra da Mantiqueira, southeastern Brazil. Values range from < 5 (for few bat species) to > 35 (for most bat species). Blue polygons are the limits of protected areas (a), and black polygons are priority areas for biodiversity conservation (b).

of protected areas along the Serra da Mantiqueira, bats are mainly affected by the presence and extension of roads in the landscape, which are denser in the lowlands (< 1000 m a.s.l.). Therefore, considering the overall landscape, the highlands of the Serra da Mantiqueira could be considered a hotspot for bat species richness and diversity.

4.1 | Current Species Richness

The richness in the Serra da Mantiqueira represents ~62% of the species already reported for the entire Atlantic Forest ($n = 98$ species, Muylaert et al. 2017) and ~33% of the overall species richness for Brazil ($n = 186$ species, Garbino et al. 2024). Of the 61 bats recorded in the Serra da Mantiqueira, Phyllostomidae bats were more widespread, while Emballonuridae, Molossidae and Vespertilionidae were less widespread. This is a clear sampling bias since most studies in Brazil use mist nets, which are the most efficient method for capturing phyllostomid bats but are frequently unequal for other bat families (Mancini et al. 2022). In fact, of the studies we compiled, only two used acoustic recorders in at least 14 locations in the Serra da Mantiqueira (see Mancini et al. 2022; Vela-Ulian et al. 2023). Therefore, once interested in accessing species richness, priority should be given to studies that employ acoustic sampling and capture bats near daytime roosts, canopy or water bodies to increase the sampling of non-phyllostomid bats (Xavier et al. 2018; Gregorin et al. 2022; Costa et al. 2023).

Despite the limitations inherent to the occurrence data, such as the absence of detailed information on sampling effort, our observed species richness (Figure 2c) shows notable mismatches to the accumulated favourability map (Figure 2a). In particular, vast areas in the southwestern portion of the study region display high accumulated favourability (yellow to red hexagons) yet very low or no observed richness. These discrepancies suggest that such regions may host more species than currently recorded, either due to under-sampling or the lack of systematic survey efforts. As such, these areas may represent hidden conservation opportunities—regions of ecological potential that remain undocumented. This pattern aligns with our insecurity index analysis, which also highlighted that many of these potentially suitable but data-deficient areas are not covered by protected areas or are underprotected, emphasising the need for increased survey efforts and strategic conservation planning in those regions.

Among the species in the Serra da Mantiqueira, *Sturnira lilium* was more abundant in higher-elevation forests (Martins et al. 2015; Carvalho, Martins, Esbérard, and Palmeirim 2019). In addition, species such as *Histiotus montanus* and *Myotis levis* were less frequent in inventories in the lowlands of the Atlantic Forest, because they seem to prefer the higher and colder regions of South America, like those in Serra da Mantiqueira (Carvalho et al. 2013; Martins et al. 2015; Mancini et al. 2019; Gregorin et al. 2020). No species endemic to high elevation, as occurs in the Andes for example, was detected in Serra da Mantiqueira, and species richness there was lower compared with mountain ranges with a greater elevational gradient, such as the Andes (e.g., Cisneros et al. 2014—between 500 and 3500 m a.s.l.). This can be explained by greater elevational variation that occurs in the Andes (up to almost 7000 m a.s.l.), with the formation of plateaus, which has led to this mountain chain being a centre of endemism for different genera, such as *Sturnira* (e.g., Velazco and Patterson 2013). Nevertheless, the richness in Serra da Mantiqueira is higher than that in other elevational gradients of Brazil, such as Reserva Biológica do Tinguá in the state of Rio de Janeiro, with an elevational variation of 65–1270 m a.s.l. (see Dias and Peracchi 2008), and Parque Estadual do Rio Preto in the state of Minas Gerais, with an elevational variation of 750–1760 m a.s.l. (see Coelho, Paglia, et al. 2018).

4.2 | Drivers of Bat Species Presence

Our distribution modelling for 50 bat species indicated a higher favourability for species occurrence and richness in the central corridor of Serra da Mantiqueira, precisely where the largest forest remnants occur, and where there is a greater proportion of protected areas (Costa et al. 1998; Valor Natural 2005; Rezende et al. 2018; see Figure 1). This is likely a result of the modelling approach, which was affected mainly by the positive effect of the proportion of savanna and forest formation. Furthermore, the distribution of most species was positively influenced by the spatial component, the proportion of rocky outcrop and the proportion of presence and extension of roads.

Natural formations, whether forest or savanna, positively influenced most of our models. Both types of habitats are globally described as determining factors for an increase in bat abundance and diversity, regardless of the trophic guild or family within Chiroptera (e.g., Shapiro et al. 2020; Carvalho, Fluck, et al. 2023). More specifically, in Neotropical forests, forest-dwelling bats, like most of the ones we analysed, are positively influenced by the amount of forest in the landscape (Carvalho, Rosalino, et al. 2023; Pedroso-Santos et al. 2024). Also, in areas with savannas in the Neotropics, which can vary from more forested to more open, bats use them mainly to feed and move around the landscape, which is more permeable than agricultural systems or urban areas, for example (e.g., Loayza and Loiselle 2009; Bernard and Fenton 2003; Sousa et al. 2013). On the other hand, a few analysed species, including *Cynomops planirostris*, *Molossus fluminensis*, *M. molossus* and *Myotis nigricans* (all aerial insectivorous), had their distribution positively affected by the proportion of urban infrastructure in the landscape. Globally, species of Molossidae and Vespertilionidae are known for increasing their abundance and diversity in urban environments, either by taking advantage of human constructions or by artificial light and artificial water bodies to nest and establish (e.g., Biavatti et al. 2015; Lopez-Baucells et al. 2017; Ávila-Flores et al. 2023).

The spatial component, that is, the geographic trend in species distribution, exhibited a major positive influence on species distribution. This non-random distribution pattern for bats in the Serra da Mantiqueira may be due to the vicarious barriers for different high-altitude species created by its unique geological formation and its separation from the nearby Serra do Mar, due to the formation of broad valleys, such as the Paraíba River Valley (Chaves et al. 2015; Silva et al. 2018; Guedes et al. 2020). Indeed, several vertebrate species, including amphibians and birds, are endemic to the Serra da Mantiqueira (Chaves et al. 2015; Silva et al. 2018). The spatiotemporal component may lead some species to be more frequent in the highlands of the Serra da Mantiqueira, because this mountain range contains species that have adapted to survive in highlands and in extreme cold, such as *Histiotus montanus*, *Myotis levis* and *Sturnira lilium* (Carvalho et al. 2013; Martins et al. 2015; Carvalho, Martins, Esbérard, and Palmeirim 2019). For instance, these bat species exhibit longer and denser pelage and use rock shelters, a behaviour that assists in regulating their body temperature (Audet and Thomas 1997; Carvalho et al. 2013; Carvalho, Martins, Esbérard, and Palmeirim 2019). However, the history of occupation and land use changes in the Atlantic Forest of southeastern Brazil in the last 500 years may also explain this spatial component. In southeastern Brazil, the conversion of natural to agricultural landscapes occurred mainly in areas below 500–1000 m a.s.l., with large forest remnants being maintained in highlands, especially in the Serra da Mantiqueira and the Serra do Mar (Joly et al. 2014; Projeto MapBiomas 2022). Combining these factors with the extensive interconnection within the network of protected areas in the Serra da Mantiqueira (Costa et al. 1998; Valor Natural 2005) that provides some ecological integrity of this region, the spatial component ends up having greater importance in predicting the distribution of the analysed species.

The positive effect of rocky outcrops for ~27% ($n = 14$) of the species analysed may be directly linked to the occurrence of natural shelters in those outcrops, whether large caves or even cracks in rocks. For example, of the species we analysed, *Anoura geoffroyi*, *Desmodus rotundus*, *M. molossus* and *Carollia perspicillata* are described as occasional or principal cave-dwelling species in Brazil (Barros and Bernard 2023). In addition, *H. montanus* has been found sheltering under a rock in high-elevational fields in the Serra da Mantiqueira (Carvalho et al. 2013; Gregorin et al. 2020). Considering that the use of rocky outcrops is one of the main functional traits that lead bat species to colonise forests with higher elevations in southeastern Brazil (Carvalho, Martins, Esbérard, and Palmeirim 2019), our results reinforce the importance of this type of habitat for bats. Therefore, different conservation strategies applied along the mountain ranges of southeastern Brazil must consider the preservation of rocky outcrops, not only for the conservation of bats but also for the conservation of their entire associated cave ecosystem (Meierhofer et al. 2024).

The positive effect associated with road extension may seem counterintuitive, especially considering the extensive literature reporting the negative impact that roads may have on forest cover maintenance and habitat conversion (Chomitz and Gray 1996; Locklin and Haack 2003). However, in our case, this is more related to a sampling bias: researchers tend to sample locations that have greater accessibility, such as areas closer to roads, highways and rivers (Kadmon et al. 2004; Delgado-Jaramillo et al. 2020; Johnston et al. 2022). Similar patterns have been observed for insufficiently sampled animal groups worldwide (Carvalho, Resende, et al. 2023; Romero et al. 2023).

We expected that an increase in elevation, in addition to a decrease in temperature and precipitation (climate) would have a negative effect on species richness, as these are factors known to negatively affect bat fauna globally (Presley et al. 2012; Guo et al. 2013; Vogeler et al. 2022; Pedroso-Santos et al. 2024), including previous studies in the Serra da Mantiqueira (see Martins et al. 2015; Carvalho, Martins, Esbérard, and Palmeirim 2019). However, this may have been due to the greater number of phyllostomid bat species in our data, which appear to be more negatively affected by elevation (Fleming 1986; Soriano et al. 1999; McCain 2007). Also, our data can be biased towards the lowlands of the Serra da Mantiqueira (mainly < 1500 m a.s.l.—97 sampled locations) and the lack of more data from higher areas may have influenced our result (only 19 sampled locations are above 1500 m a.s.l.). To remove such bias effect, researchers should be financially and logistically encouraged to carry out studies in more remote areas and with different methods (i.e., mist nets and acoustic records), especially far from large research centres, mainly in highlands, which could improve our current knowledge about the occurrence and distribution of different species and, consequently, refine our analyses of SDMs (Kadmon et al. 2004; Brito et al. 2009; Johnston et al. 2022).

4.3 | In Situ Protection: Current Status and Gaps in the Serra da Mantiqueira

We detected that ~8.63% (~135) of the 1564 hexagons with 1 or more species and only 30 hexagons with 10 or more species had more than 70% of their surface protected. Even though ~77% of the studied area has no protection or has < 10% protection, we consider that the current protected areas network in the Serra da Mantiqueira sufficiently protects the proportion of the area with higher favourability. Specifically, the adopted Insecurity Index highlighted that only a few territories of high favourability were not protected (1.6% of the area with Insecurity Index value higher than 30—see Figure 3). Although ~13% of the areas with higher favourability are still lacking protection, these areas are mainly found in the central highlands of the Serra da Mantiqueira, where the use of intensive agriculture, a main driver for species loss, is difficult (Williams-Guillén et al. 2016). Nevertheless, the potential impact of the recent expansion of small hydroelectric power plants in the region must be considered (see GESTA 2022), even when located in lowland areas (below 500 m a.s.l.) that already have presented some degree of degradation. Considering the amount of area with higher bat diversity currently protected, the mosaic of protected areas in the Serra da Mantiqueira seems to fulfil its role in reducing the impact of anthropogenic actions in the region. Our results may help the network of protected areas to increase in the region, especially considering the overlap between the already known priority areas for conservation and the areas we detected with high Insecurity Index. Some of these areas are inserted in the central corridor and to the northeast in the Serra da Mantiqueira (Figure 3b).

The extension and coverage of Brazilian protected areas has managed to halt the largest amount of deforestation in the country, mainly in the Atlantic Forest (Cazalis et al. 2020). However, Brazil has not spent enough resources on managing its protected areas, making it difficult to measure the real scope of the objectives of these areas (Bernard et al. 2014; SAMGe 2022). Data from the protected areas that are in and around the Serra da Mantiqueira provide a snapshot of the current state of the entire network of protected areas in Brazil, with a lack of investment, technicians and rangers, and low–medium effectiveness (SAMGe 2022). Considering that ~20% (~308) of the 1564 hexagons with favourability > 10 are within protected areas with the lowest level of protection under Brazilian legislation (e.g., *Áreas de Proteção Ambiental*), we are concerned about the quality of protection of the areas with higher diversity in the Serra da Mantiqueira. More financial resources and better participatory management are necessary to improve the effective management of the mosaic of protected areas in the Serra da

Mantiqueira, thus increasing the conservation of these bat biodiversity hotspots (Bernard et al. 2014; Barnes et al. 2018; Dawson et al. 2023). Initiatives aimed at participatory management have already taken place, such as in the *Parque Estadual da Serra do Papagaio* (PESP), located in the highest portions of the Serra da Mantiqueira (between 1100 and 2400 m a.s.l.), where most of the area exhibited greater favourability (> 25) and lower insecurity (< 5). The limit of this state park was adjusted with forest areas added and agricultural areas removed, based on the indications of residents who live in and around it (Menegassi 2021). Thus, this park gained ~13% in area (from 22,917 to 25,888 ha), reducing the environmental conflicts that involve its complete land tenure regularisation (Menegassi 2021).

As already noted for the major mountain ranges of the planet, mountain regions will need specific actions to enhance the conservation of ecosystem diversity if global land protection goals are to be met (Theobald et al. 2024). Despite the overall lower exposure to climate and land-use changes faced by South American mountains, including Serra da Mantiqueira (Dragonetti et al. 2024), our results support and direct the implementation of conservation tools in these ecosystems. Regarding the relevance of lowlands for the maintenance of bat populations (Carvalho, Martins, Dias, et al. 2019), we highlight that the areas with higher values of the Insecurity Index detected southwest of the Sierra (see Figure 3b) could be used in restoration projects, leading to recolonisation by different bat species and favouring the maintenance of ecosystem services (e.g., seed dispersal). This type of intervention could also help reduce the vulnerability of this mountain range to climate change, which would facilitate dispersal and vertical movement of bats for foraging or reproduction (La Sorte and Jetz 2010; Carvalho, Martins, Dias, et al. 2019).

The Serra da Mantiqueira is already recognised as having great potential for forest restoration projects within the Atlantic Forest (Strassburg et al. 2020). In addition, private protected areas could be expanded in the Serra da Mantiqueira (see da Silva, Pinto, et al. 2021), which would allow, together with forest restoration, the creation and more effective maintenance of ecological corridors along the lowlands. Our study highlights key environmental and spatial variables shaping the distribution of bat species in the Atlantic Forest, with savanna formations, spatial gradients, road networks, forest cover and rocky outcrops emerging as the most relevant predictors. We found that a significant portion (63%) of areas with high bat species richness remain poorly protected, and about 22% of the most favourable areas still lack legal protection entirely. The highlands of the Serra da Mantiqueira stand out as a hotspot of richness and conservation priority. These findings provide a robust spatial basis for identifying gaps in current conservation planning and emphasise the urgent need to enhance the effectiveness of protected areas, implement ecological corridors and prioritise ecological restoration strategies in this biodiverse and threatened region. Importantly, most Priority Conservation Areas fall outside existing protected boundaries. Integrating these areas into the current conservation framework would considerably increase the spatial coverage of suitable habitats for bats across the study region. This expansion would not only enhance protection in key areas currently unprotected but also promote ecological connectivity and resilience—both essential for the long-term conservation of bat assemblages under ongoing environmental change.

Author Contributions

William D. Carvalho: writing – review and editing, writing – original draft, visualisation, methodology, formal analysis, data curation, conceptualisation. **José C. Guerrero:** writing – review and editing, writing – original draft, visualisation, methodology, formal analysis, data curation, conceptualisation. **Enrico Bernard:** conceptualisation, writing – review. **Carlos E. L. Esbérard:** data curation, conceptualisation, writing – review. **Albert D. Ditchfield:** writing – review. **Renato Gregorin:** data curation, conceptualisation, writing – review. **Rafael S. Laurindo:** writing – review. **Matheus C. S. Mancini:** writing – review. **Mayara A. Martins:** conceptualisation, writing – review. **Pedro H. Nobre:** data curation, conceptualisation, writing – review. **Ana C. Srbek-Araujo:** conceptualisation, writing – review. **Carina M. Vela-Ulian:** data curation, conceptualisation, writing – review. **Bruna S. Xavier:** conceptualisation, writing – review. **David Romero:** writing – review and editing, writing – original draft, visualisation, methodology, formal analysis, data curation, conceptualisation.

Acknowledgements

William Douglas Carvalho is supported by 'Ayudas Maria Zambrano' (CA3/RSUE/2021-00197) funded by the Spanish Ministry of Universities, and by "Ayudas para contratos Ramón y Cajal (RYC) 2023" {RYC2023-045231-I}, financed by MCIU/AEI/https://doi.org/10.13039/501100011033 and by the FSE+. Romero David is supported by the incorporation Doctor programme of the University of Malaga, UMA-2022/REGSED-64576. José Carlos Guerrero acknowledges support for PEDECIBA—Programa para el desarrollo de las Ciencias Básicas and Sistema Nacional de Investigadores (SNI-ANII). Renato Gregorin is partially funded by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq - process 301946/2022-1) and Fundação de Amparo à Pesquisa do Estado de Minas Gerais (FAPEMIG)- PPM 00203/18). Matheus Camargo Silva Mancini is partially funded by the Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP - process 2023/10302-6. Ana C. Srbek-Araujo thanks the Fundação de Amparo à Pesquisa e Inovação do Espírito Santo (FAPES for the research funding—FAPES 180/2019) and for the productivity fellowship (Bolsa Pesquisador Capixaba—FAPES 404/2022). Carina M. Vela-Ulian thanks the 'Coordenação de Aperfeiçoamento de Pessoal de Nível Superior' (CAPES) for the doctoral scholarship awarded (Financial Code 001). Bruna Silva Xavier is supported by CAPES (88882.424975/2019-01). The studies carried out by LADIM, *Coleção de Mamíferos*—UFLA, LabEQ and Pedro H. Nobre were authorised by the Ministry of the Environment (MMA) through the Chico Mendes Institute for Biodiversity Conservation (ICMBio), under permits SISBIO 65730-1, SISBIO 65730-2, SISBIO 62847, SISBIO 50363-2 and SISBIO 18932-4, and by the Brazilian Institute of Environment and Renewable Natural Resources (IBAMA) under authorization numbers 10356-1, 10767-1, 275281-1 and 10767-2. The *Instituto Estadual de Florestas* (IEF-MG) granted permission to carry out sampling under permits number 78/11 and 151/11.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All the data relevant generated or analysed during this study are included in this published article and its Supporting Information.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1.** Occurrence data for bat species occurring along the elevational gradient of the Serra da Mantiqueira, Atlantic Forest, Southeastern Brazil. **Table S2.** Variables and factors analysed during the modelling procedure in this study. **Table S3.** Total occurrences and captures for bat species in Serra da Mantiqueira, Brazil. **Table S4.** Variables that contributed to the models obtained for 51 species of bats that occur in the Serra da Mantiqueira, Brazil. The variables are arranged in order of entry in the model. The Estimate is the coefficient multiplying the variable values in the logit of the multivariate logistic regression, and the positive or negative sign indicates the relationship between the variable and the model. Std. Error: Standard Error. Wald value is the relative contribution of that variable to the model. Sig: Level of significance. Exp(B) represents the ratio change in the odds of the event of interest for a one-unit change in the predictor. See Table S2 for variable information. **Table S5.** Security and insecurity index metrics inside and outside protected areas and priority areas for conservation for each bat species that were modelled and occur within the Serra da Mantiqueira area, Brazil.