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RESEARCH ARTICLE

Environmental heterogeneity as a determinant of bee diversity patterns in the Atlantic Forest

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Abstract

The Atlantic Forest encompasses a wide range of environmental and geographical gradients with high endemism and species diversity among several taxonomic groups, including bees. Environmental heterogeneity is a determining factor for species diversity, as environments with greater heterogeneity tend to offer a greater variety of conditions, thus supporting higher species richness. However, bee richness patterns and their relationship with environmental heterogeneity in the Atlantic Forest remain underexplored. In this study, we aimed to describe the bee diversity patterns and investigate how different components of environmental heterogeneity—specifically temperature seasonality, topographic and geomorphic heterogeneity, and stream density—influence species richness, both for the entire biome and within each ecoregion. To do so, we modeled and estimated the distribution of 466 bee species. Relationships between bee species richness and environmental heterogeneity variables were analyzed using Generalized Linear Models, variable importance, and partial dependence curves. We found that the highest richness was in the southwestern regions of the Atlantic Forest, particularly in the Serra do Mar Coastal Forests and Araucaria Moist Forests. The most important variables positively related to species richness were temperature seasonality, followed by topographic and geomorphic heterogeneity, whereas stream density showed the lowest importance. At the ecoregion level, temperature seasonality was the most important variable for 9 of the 11 ecoregions, followed by topographic and geomorphic heterogeneity. In ecoregions with the highest bee richness, environmental heterogeneity showed a low explanatory power. Notably, the relationships between the environmental heterogeneity variables and species richness varied across ecoregions. Our findings highlight the significant role of environmental factors in shaping bee species richness in the Atlantic Forest at multiple scales. Furthermore, the distinct relationship observed between environmental heterogeneity and species richness across ecoregions reinforces the necessity of multi-scale diversity studies to elucidate the unique characteristics of each ecoregion.

Highlights

- Bee species richness in the Atlantic Forest is greatest in the south-west and southern regions.
- Seasonal temperature was the most important variable for predicting species richness, showing a positive effect in nine of the 11 ecoregions.
- Topographic and geomorphic heterogeneity contributed significantly to species richness in certain ecoregions.
- Relationship between species richness and environmental heterogeneity variables varied among ecoregions.
- Ecoregions with higher richness were poorly explained by environmental heterogeneity, suggesting other influencing factors.
- Multiscale analysis reveals that different regions may have unique species richness drivers, crucial to understanding species diversity in this biodiversity hotspot.

Keywords

Apoidea, Atlantic Forest, geomorphic heterogeneity, non-stationarity, richness pattern, seasonality, species distribution modeling, topographic heterogeneity

Introduction

The Atlantic Forest biome extends across eastern Brazil, northeastern Argentina, and eastern Paraguay. This region exhibits a wide range of latitudinal, altitudinal, and environmental gradients and comprises multiple ecoregions with distinctive environmental attributes (Olson et al. 2001; Batista et al. 2021; Carvalho et al. 2021). The Atlantic Forest is considered a biodiversity hotspot and is home to 2,200 vertebrate species (i.e., > 5% of the world's species; Myers et al. 2000), of which 334 are mammals (Souza et al. 2019). In addition, 35% of 20,000 native plant species (Faoro et al. 2015), 16% of 688 bird species, 31% of 200 reptile species, and 60% of 280 amphibian species are endemic to the Atlantic Forest (Mittermeier et al. 2005). This biome represents a region of high biological importance for arthropods, with 724 areas of endemism identified (Hoffmeister and Ferrari 2016). Recent studies based on DNA Barcoding have revealed a great diversity of arthropod species, many of which have not yet been cataloged (Bukowski et al. 2022). The region exhibits remarkably high biodiversity of eusocial insects, including bees, wasps, and termites (Feitosa et al. 2021), with high bee endemism, particularly in the genus *Euglossa* (Garraffoni et al. 2017).

The Anthophila clade comprises all bee species and represents a highly diverse group within Apoidea (Michener 2007), with > 20,000 species described globally, whose diversity is reflected in the wide variation in behavior, ecology, and distribution (Michener 2007). Bees provide important ecosystem services, the most important of which is pollination (Michener 2007; Rogers et al. 2014). This ecosystem service is essential for the sexual reproduction of plant species (Ollerton et al. 2011) and has a direct effect on the genetic diversity of plant seeds (Ramos and Schiestl 2019). In addition, crop pollination can be maintained exclusively by native bees, especially if natural habitats near plantations increase (Kremen et al. 2004; Ricketts et al. 2008).

Studying diversity patterns is fundamental for understanding the dynamics and structure of ecological communities, as well as for helping manage and conserve biodiversity (Rubene et al. 2015). These patterns are influenced by both evolutionary and ecological factors, biotic and abiotic, at different spatial scales (Ricklefs 2004). Bee diversity patterns have been studied because of their ecological importance and pollination services (Klein et al. 2006). Previous research has shown that bee species diversity is influenced by a variety of biotic and abiotic factors, including availability of floral resources, habitat, interactions with other species, and climatic variations (Potts et al. 2003; Classen et al. 2015; Escobedo-Kenefic et al. 2020). Recently, bee distribution has been mapped globally, showing a bimodal latitudinal gradient with a higher concentration of species at mid-latitudes than at low latitudes (Orr et al. 2021). Although there have been several studies on animal and plant diversity in the Atlantic Forest (Jenkins et al. 2015; Souza et al. 2019), there is still a gap in the diversity patterns of bees at broad scales and the environmental factors related to those patterns.

Environmental heterogeneity is defined as the variation in biotic (e.g., vegetation structure) and abiotic (e.g., topography) environmental characteristics within a given area (Maliniemi et al. 2024). Environmental heterogeneity plays a key role in shaping biodiversity patterns by promoting niche differentiation and reducing interspecific competition (Whalen et al. 2016; Xu et al. 2016; Tukiainen et al. 2017). Variations in land cover, vegetation, climate, soil, and topography strongly correlate with species richness across taxa and spatial scales (Dufour et al. 2006; Stein et al. 2014; Wan et al. 2023). Highly heterogeneous environments support greater species diversity and offer varied conditions and resources for different niches and refuges during environmental change (Stein and Kreft 2015). Furthermore, from an evolutionary perspective, heterogeneous environments can induce allopatric speciation, restrict gene flow, and foster local adaptation (Dool et al. 2022). Some studies in the Atlantic Forest have explored the relationship between different aspects of species diversity and environmental heterogeneity (Stevens 2013; Weber and Cáceres 2018; Delciellos et al. 2022). However, these studies primarily focused on vertebrates and plants using topographic heterogeneity as the main variable. As such, the influence of environmental heterogeneity on bee diversity remains to be evaluated, especially in particularly diverse regions such as the Atlantic Forest and considering multiple environmental variables.

Bees are sensitive to environmental changes and have specific requirements for foraging, gathering resources, and maintaining their nests (Klein et al. 2017; Burdine and McCluney 2019). Therefore, environmental heterogeneity is expected to have a positive relationship with bee diversity because of the variety of environments and resources, thus supporting greater species richness. In macroecological studies, environmental heterogeneity can be measured using multiple metrics (Stein and Kreft 2015). For example, heterogeneity in soil chemical properties (Xu et al. 2016), geomorphic heterogeneity, or water richness (Tukiainen et al. 2017). Due to the longitudinal, latitudinal, and climatic amplitudes of the Atlantic Forest, different metrics of environmental heterogeneity are expected to affect the patterns of bee species richness. Temperature seasonality indicates variations in average monthly temperatures yearly (O'Donnell and Ignizio 2012), which can affect plant phenology, resource availability timing, and bee thermal limits. Topographic heterogeneity refers to elevation variability; greater variation indicates greater topographic heterogeneity (Amatulli et al. 2020). Additionally, geomorphic heterogeneity refers to the variation of topographic features measured by classes of geomorphological forms

(Amatulli et al. 2020). High topographic and geomorphic heterogeneity creates diverse microclimates and environmental conditions. Areas with greater topographic heterogeneity are expected to have higher species richness, as such heterogeneity fosters different conditions for bees with different ecological requirements. Stream density represents the number of potential watercourses in an area and is associated with humidity and riparian habitats (Keeton et al. 2007). This variable is important for certain bee species because of the water needed for their survival and nest temperature control (Kühnholz and Seeley 1997). Thus, temperature seasonality, topographic and geomorphic heterogeneity, and stream density are expected to have a positive relationship with bee species richness.

The relationship between a response variable (e.g., species richness) and predictor variables (e.g., environmental heterogeneity) can vary significantly at different temporal or spatial scales, a phenomenon known as nonstationarity (Fortin and Dale 2005). Nonstationarity implies that ecological patterns and processes, and their relationships with different variables, are not constant over time or space (Rollinson et al. 2021). Because of the broad geographical and environmental extent of the Atlantic Forest, it is expected that there will be nonstationarity between bee richness and different components of environmental heterogeneity. In other words, these relationships could change between biome and different ecoregion scales, making it pertinent to explore these relationships at different levels separately (i.e., at the global level of the biome and within each ecoregion). In this study, we aimed to describe the patterns of native bee diversity in the Atlantic Forest and investigate how the different components of environmental heterogeneity influence bee richness in the Atlantic Forest on a global scale and in each ecoregion.

Material and methods

Study area

The Atlantic Forest extends along the entire eastern coast of Brazil, from Rio Grande do Norte to Rio Grande do Sul, and through the coastal and continental areas to southern Brazil, eastern Paraguay, and southwestern Argentina (Ribeiro et al. 2009; Muylaert et al. 2018). The Atlantic Forest is separated from the Amazon Rainforest by a corridor of seasonally dry forests and savannas such as semiarid Caatinga (northeastern Brazil), Cerrado (central Brazil), and Chaco (Paraguay, Argentina, and Bolivia) (Prado and Gibbs 1993). It contains a unique set of ecosystems that originally comprised > 1.5 million km² (Morellato and Haddad 2000). The biome has a wide latitude range (from 5°8'N to 33°8'S), an altitude between 0–2,200 m a.s.l., rainfall between 800–4,000 mm/year, and an average annual temperature ranging from 5–25 °C (Stehmann et al. 2009).

We used the integrative boundary of the Atlantic Forest (Muylaert et al. 2018) because it covers a more inclusive area, considering the transition regions with other biomes such as Cerrado and Caatinga, as well as representing portions of the Atlantic Forest for other countries, such as Argentina and Paraguay. We clipped the boundaries of the world's terrestrial ecoregions from the polygon as the integrating boundary of the Atlantic Forest (https://github.com/LEEClab/ATLANTIC-limits) (Dinerstein et al. 2017, https://ecoregions.appspot.com). Initially, 19 ecoregions were listed within the Atlantic Forest boundaries; however, many of them were represented marginally or with small extensions, which could make it difficult to analyze them separately (Suppl. material 1: table S1, fig. S1). Polygons of marginal ecoregions (i.e., < 3,000 km^2 equivalent to 120 cells) were joined to the largest and closest ecoregions. A total of 11 ecoregions were analyzed: Araucaria Moist Forests, Bahia Coastal Forests, Bahia Inland Forests, Brazilian Atlantic Dry Forests, Caatinga, Campos Rupestres Montane Savanna, Cerrado, Pernambuco Coastal Forests, Serra do Mar Coastal Forests, Upper Paraná Atlantic Forests, and Uruguayan Savanna.

Species list and occurrences

To construct the species list for the Atlantic Forest, we followed two stages. First, a list of species occurring in the Atlantic Forest was generated from occurrences sourced by Dorey et al. (2023). This occurrence dataset provides bees occurrences worldwide compiled, integrated, and cleaned from Atlas of Living Australia (ALA, https://www.ala.org.au), Global Biodiversity Information Facility (GBIF, https://www.gbif.org), Symbiota Collections of Arthropods Network (SCAN, https://scan-bugs.org/portal/), Integrated Digitized Biocollections (iDigBio, https://www.idigbio.org), and the United States Geological Survey (USGS, https://www.usgs.gov) (Dorey et al. 2023). We integrated the Dorey et al. (2023) database with SpeciesLink (https://specieslink.net), which is a biodiversity information portal from Brazil.

The species list included all bee species with at least one occurrence in the Atlantic Forest. We then removed species without distribution in the Atlantic Forest. We used the Taxonomic Catalog of Brazilian Fauna (https://fauna.jbrj.gov.br/) and the Taxonomic Catalog of Brazilian Fauna and Moure Catalog (https://moure.cria.org.br/) as species origin sources. The scientific names were revised according to the Taxonomic Catalog of Brazilian Fauna and Moure Catalog. The raw occurrence data listed 770 species names, but after scientific name correction and selection of those species native to the study area, 564 native bee species to the Atlantic Forest were listed. Species with only one occurrence (n = 74) were eliminated, leaving 490 species for distribution modeling.

We performed a spatial cleaning that consisted of removing occurrences with invalid coordinates, duplicated coordinates, and georeferenced in centroids of municipalities, provinces/states, and countries. For data integration and cleaning, we used the R packages *bdc* (Ribeiro et al. 2022) and *CoordinateCleaner* (Zizka et al. 2019). For each species, we checked whether the occurrences were within the species' natural distribution using the Moure Catalog as a source of species distribution. Occurrences georeferenced outside of the informed distribution were removed manually in a GIS environment using the program QGIS v. 3.38.0 (https://www.qgis.org/). Raw occurrence database contained 240,062 occurrences, which were reduced to 16,542 after cleaning.

Occurrences compiled from large databases generally have spatial bias, with a higher density of points close to human infrastructure (Stolar and Nielsen 2015). This bias can negatively affect the predictions of species distribution models (Baker et al. 2022). To correct sampling bias, we used environmental filtering (Varela et al. 2014). As this method is sensitive to the number of classes used to partition the environmental space (i.e., binds), for each species we tested 4, 6, 8, 10, and 12 classes and selected the filter with the lowest spatial autocorrelation (as measured by Moran's I) and the largest number of retained occurrence records (Velazco et al. 2021) 11,404 occurrences were retained after this process.

Species distribution models and species richness maps

Environmental variables

Variation in temperature, humidity, and precipitation patterns can directly influence species behavior and resource availability across an environment, thus shaping the geographic distribution of species (Cortopassi-Laurino et al. 2007). Species distribution models were built using bioclimatic variables from Chelsa v2.1 (https://chelsa-climate.org) (Karger et al. 2017) at 1 km. Of the 19 bioclimatic variables, we selected 11 that were ecologically related to bee distribution (Suppl. material 1: table S2). We also used the 1 km resolution elevation from SRTM (https://srtm.csi.cgiar.org). The extent of the variables ranged from the northern border of the United States to the southern extremes of Argentina and Chile. All variables were resampled to a resolution of 5 km. A Pearson's correlation matrix for the full range of environmental variables revealed significant collinearity among many of them (Suppl. material 1: fig. S2). To address multicollinearity and reduce the number of predictor variables used for modeling, we applied Principal Component Analysis (PCA) using raster cells from the training area of each species (see below). The PCAs were calculated based on a correlation matrix, and eigenvectors were used to predict principal components used as predictor variables in species distribution models. We selected a total of principal components that explained 95% of the total variance in the original environmental variables (De Marco and Nóbrega 2018). Thus, four, five, and six principal components were used for 282, 206, and two species, respectively.

Because the amount of occurrence data affects the performance of Species Distribution Models (SDM), and there are different techniques for dealing with lack of data, we defined three modeling protocols: one for species with ≥ 15 occurrences (n = 183 species), another for species with between 5 and 14 occurrences (n = 156), and another for those with between 2 and 4 occurrences (n = 151). Species with only one occurrence were not included in our analysis. For the first and second protocols, the SDM training area was defined as delimited by ecoregions where a species had at least one presence. We used Dinerstein et al. (2017; https://ecoregions.appspot.com) as the ecoregions polygon source for the 11 ecoregions. SDM were constructed using *flexsdm* R package (Velazco et al. 2022).

Modeling protocol for species with > 15 occurrences

No single algorithm can handle all modeling conditions, so we used the following seven algorithms: Artificial Neural Network (NET), Boosted Regression Trees (BRT), Generalized Additive Model (GAM), Generalized Linear Model (GLM), Maximum Entropy (MAXENT, hereafter MAX), Random Forest (RAF), Support Vector Machine (SVM), and Gaussian Process (GAU). The NET, BRT, MAX, RAF, and SVM algorithms have hyperparameters that can affect model performance and predicted suitability patterns (Fourcade 2021). Therefore, for these algorithms, we employed a hyperparameter optimization technique that selects the best combination of hyperparameters that maximizes the Sorensen performance metric (Suppl. material 1: table S3). The consensus was based on the median of the environmental suitability values because it is less sensitive to outliers (Rose et al. 2024).

Modeling protocol for species with 5–15 occurrences

For species with 5–15 occurrences, the Ensemble of Small Models (ESM) approach was used. This technique is suitable for building models for species with few occurrences and consists of creating bivariate models with a combination of all pairs of predictors and subsequent consensus between the bivariate models weighted by Somers'D metric ($D = 2 \times (AUC - 0.5)$), where AUC is the area under the curve (Breiner et al. 2015). The ESMs were constructed using the same algorithms as in the previous protocol, however, the default algorithm hyperparameters were used (Velazco et al. 2022). As with SDM, the final models consisted of a consensus model based on the median.

Modeling protocol for species with 2–4 occurrences

For species with 2–4 occurrences, distributions were estimated based on environmental similarity using Gower's distance for cells within a 50 km radius around the species occurrences (Carpenter et al. 1993; Andrella et al. 2023).

Model validation and modeling postprocessing

The SDM and ESM were validated using k-fold and repeated k-fold cross-validation techniques, respectively, with repetitions. Five partitions were used for SDM, and five partitions and five repetitions were used for ESM. We used the Inverse Mean Absolute Error –IMAE– (threshold-independent metric) and Sorensen (Leroy et al. 2018) as model performance metrics. Only those models with Sorensen ≥ 0.7 were used in the analyses. The 0.7 Sorensen value was employed as an acceptable threshold for model performance, as this value is widely recognized as a performance cutoff for other metrics such as Area Under the Curve (Swets 1988; Peterson et al. 2011).

When SDMs are projected over large geographical extents, models tend to predict high suitability areas outside the species' current range, potentially affecting diversity patterns (Velazco et al. 2020). To address this, we constrained model prediction to a region defined by a minimum convex polygon based on a species presence plus a buffer of 100 km buffer around it (Mendes et al. 2020).

Species richness map

We created a species richness map by stacking species semi-binary models. The semi-binary models consist of assigning zero to environmental suitability values that are below the threshold and keeping all values above it continuous (Domisch et al. 2019). This approach to building the richness map was adopted because it reduces over-prediction compared to the sum of binary models (Guillera-Arroita et al. 2015). We used the threshold that maximizes the sum of sensitivity and specificity to produce the semi-binary model outputs. This threshold was used because it is little affected by the relationship between presences and pseudo-absences (Liu et al. 2016).

Environmental heterogeneity variables and analyses

Four environmental heterogeneity variables were explored: topographic heterogeneity, geomorphic heterogeneity, temperature seasonality, precipitation seasonality, and stream density. Topographic heterogeneity was based on a 30 m resolution digital terrain model from the R *atlanticr* package (https://github.com/mauriciovancine/atlanticr) and was calculated using the standard deviation of the altitudinal variation of the 30 m cells contained in the 5 km resolution cells (i.e., equal to the resolution of the distribution models). For geomorphic heterogeneity, we calculated the Shannon diversity of the different geomorphological features (plane, peak or summit, ridge, shoulder, spur, slope, hollow, slope, valley, and depression) of the 90 m resolution cells contained in 5 km resolution cells. We used Geomorpho90m as the geomorphological feature source (Amatulli et al. 2020). Stream density was measured by adding the number of cells identified as potential watercourses in 5 km resolution cells. For this, we used Strahler stream order at a 90 m resolution and considered watercourses for cells with stream order > 3. Hydrography90m was used as a source of the Strahler stream order (Amatulli et al. 2022). The seasonality of temperature and precipitation were sourced from Chelsa. Due to the high correlation between temperature and precipitation seasonality (Pearson's correlation = -0.81), we selected the former variable for our analysis (Suppl. material 1: fig. S3).

The relationships between species richness and different environmental heterogeneity variables were analyzed for 12 regions: the Atlantic Forest as a whole and 11 ecoregions. For the extent of the Atlantic Forest, we also performed an analysis including ecoregions as a predictor variable together with environmental heterogeneity to evaluate the contribution of the ecoregion to explain the bee richness pattern. We used multiple regressions constructed using Generalized Linear Models (GLM) using the Poisson distribution family, which is suitable for discrete response variables (i.e., species richness). Assumptions of normality and homogeneity of the residuals were assessed visually. Moran's I correlograms were used to assess the spatial autocorrelation of the residuals. To correct it, we used a spatial filter method based on eigenvectors (Tiefelsdorf and Griffith 2007). The *SpatialFiltering* function from the R package *spatialreg* (Pebesma and Bivand 2023) selects eigenvectors in a semi-parametric spatial filtering approach to remove spatial dependence from linear models (Pebesma and Bivand 2023). These spatial filters were used as predictor variables in the GLMs. Because the creation of environmental filters can be time-consuming, we systematically sampled ~2200 cells while maintaining the original resolution (i.e., 5 km) by constructing GLMs using a sample of the cells for each analysis area. To explore the variable importance and partial response curves estimated by the GLMs, we used the R packages *spatialreg* and *vip* to construct Moran's I correlograms and spatial eigenvector filters, respectively (Greenwell and Boehmke 2020). *emmeans* package was used to calculate the variable importance and estimate the partial response curves (Lenth 2016). The method used to calculate variable importance is based on the absolute value of the *t*-statistic, which can vary from zero to infinity. For the response curves, we standardized the predictor variable scales to range between 0–1 and facilitate comparisons between different curves.

Temperature seasonality was used both to construct the SDMs and to analyze the relationship between richness and environmental heterogeneity, raising concerns about potential circularity—using the same variable in both modeling and explanatory analyses may artificially inflate the results. However, using one variable to model individual species distributions through SDMs is not the same as using this same variable to model the community-level pattern that emerges from stacking several individual modeled distributions (e.g., species richness; Ferrier and Guisan 2006). Indeed, the importance of such a variable in SDMs is more related to setting the geographical space potentially occupied by each species and thus its spatial limits, whereas the importance of this variable for species richness is more related to their spatial covariation (Ferrier and Guisan 2006; Guisan and Rahbek 2011). To assess potential circularity between predicted species richness and environmental heterogeneity, we examined correlations between individual species' suitability and the environmental heterogeneity variables. For those species with Pearson correlation > |0.7|, we generated a richness map to explore if those species were highly concentrated in some region of the study area. All analyses were performed in R v.4.4.0 (R Core Team 2024).

Results

Ensemble SDM models performed well, with IMAE and Sorensen values of 0.73 (± 0.05) and 0.74 (± 0.08), respectively. Similarly, the ESMs presented a good performance, with average IMAE and Sorensen values between the algorithms of 0.63 (± 0.06) and 0.74 (± 0.11) (Suppl. material 1: fig. S4). We excluded 24 species because of poor model performance (i.e., Sorensen < 0.7), thus, 466 out of the 490 modeled species were kept for further analysis. The highest species richness (> 75 species) was found in the southwestern and southern regions of the Atlantic Forest. These regions are characterized by high mountainous relief, such as the Serra do Mar Coastal Forests and eastern Araucaria Moist Forest, as well as in the southern region of the Upper Paraná Atlantic Forest (Fig. 1, Suppl. material 1). Species richness gradually decreases towards the east (Upper Paraná Atlantic Forest) and coastal regions of the northeast (Pernambuco Coastal Forests). The northeastern coastal strip showed lower richness (25–50 species). In addition to the northeastern coastal strip, parts of the interior, especially drier areas such as the Caatinga and inland forests of Bahia, also showed low richness (< 25 species; Fig. 1, Suppl. material 1).

Regarding the relationship between species richness and environmental heterogeneity, we found that the variable with the greatest importance (i.e., explained variance) for the Atlantic Forest was temperature seasonality (87.44), followed by topographic (25.7) and geomorphic (23.6) heterogeneity, which each demonstrated similar levels of importance. Stream density had low explanatory power (Fig. 2). Temperature seasonality, topographic heterogeneity, and geomorphic heterogeneity had a positive relationship with species richness, and this relationship was strongest for the first of these variables (Fig. 2, Suppl. material 1: fig. S5). When ecoregion is used in the model, it is the variable with the highest variable importance (56.9), followed by temperature seasonality and topographic and geomorphic heterogeneity (Suppl. material 1: fig. S6).

When we explored the relationship between environmental heterogeneity and bee richness separately for each ecoregion, we found that the influence of environmental heterogeneity on patterns of bee species richness varied among ecoregions. Thus, temperature seasonality was the most important variable in nine of the 11 ecoregions (Fig. 3), with the highest importance values emerging for the Cerrado (97.38), Uruguayan Savanna (92.17), and Campos Rupestres Montane Savanna (77.69). Topographic heterogeneity was a prominent predictor of bee species richness in the Uruguayan Savanna (39.09), Upper Paraná Atlantic Forest (33.87), and Bahia Coastal Forest ecoregions (29.93). Geomorphic heterogeneity and stream density were important variables in the Caatinga (16.29 and 24.30, respectively), Cerrado (41.96, 6.16), and Bahia Coastal Forests (11.21, 0.93). Interestingly, the Serra do Mar Coastal Forests was the ecoregion with the highest species richness, yet also the ecoregion in which the environmental heterogeneity variables explained the least variance in bee species richness (Figs 1, 3).

In addition to varying in relative importance, the direction of the relationship between different aspects of environmental heterogeneity and bee species richness varied among the ecoregions (Fig. 4; Suppl. material 1: fig. S7). While temperature seasonality demonstrated a positive relationship with bee species richness in 5 of the 11 ecoregions (Upper Paraná Atlantic Forests, Bahia Interior Forests, Brazilian Atlantic Dry Forests, Cerrado, and Campos Rupestres Montane Savanna) we observed a negative association between the two variables in 6 ecoregions (Araucaria Moist Forests, Caatinga, Pernambuco Coastal Forests, Serra do Mar Coastal Forests). Topographic heterogeneity and species richness had a positive relationship in 7 ecoregions (the Upper Paraná Atlantic Forest, Bahia Coastal Forests, Brazilian Atlantic Dry Forests, Caatinga, Cerrado, and the Uruguayan Savanna) and a negative relationship in the Campos Rupestres Montane Savanna and Serra do Mar Coastal Forests. Finally, we found that geomorphic heterogeneity showed a positive relationship with species richness in the Bahia Interior Forests, Caatinga, and Campos Rupestres Montane Savanna, but a negative association in the Araucaria Moist Forests, Bahia Coastal Forests, Pernambuco Coastal Forests, and Uruguayan Savanna (Fig. 4; Suppl. material 1: fig. S7). Our analysis of potential circularity between the richness map and the environmental heterogeneity variables revealed that only 27 (5.8%) species had a high correlation between species suitability and temperature seasonality (Suppl. material 1: fig. S8). The richness pattern of these particular species was slightly higher in the southwest region of the study area, but they represented only a small portion of the total richness in that region (Suppl. material 1: fig. S9). This further suggests that, if present, the potential circularity from using similar variables in the distribution and richness modeling should be minimal.

Discussion

In this study, we sought to describe the patterns of bee diversity in the Atlantic Forest and to investigate the influence of different environmental heterogeneity variables on species richness, both for the entire biome and each of its ecoregions. We found that bee richness was higher

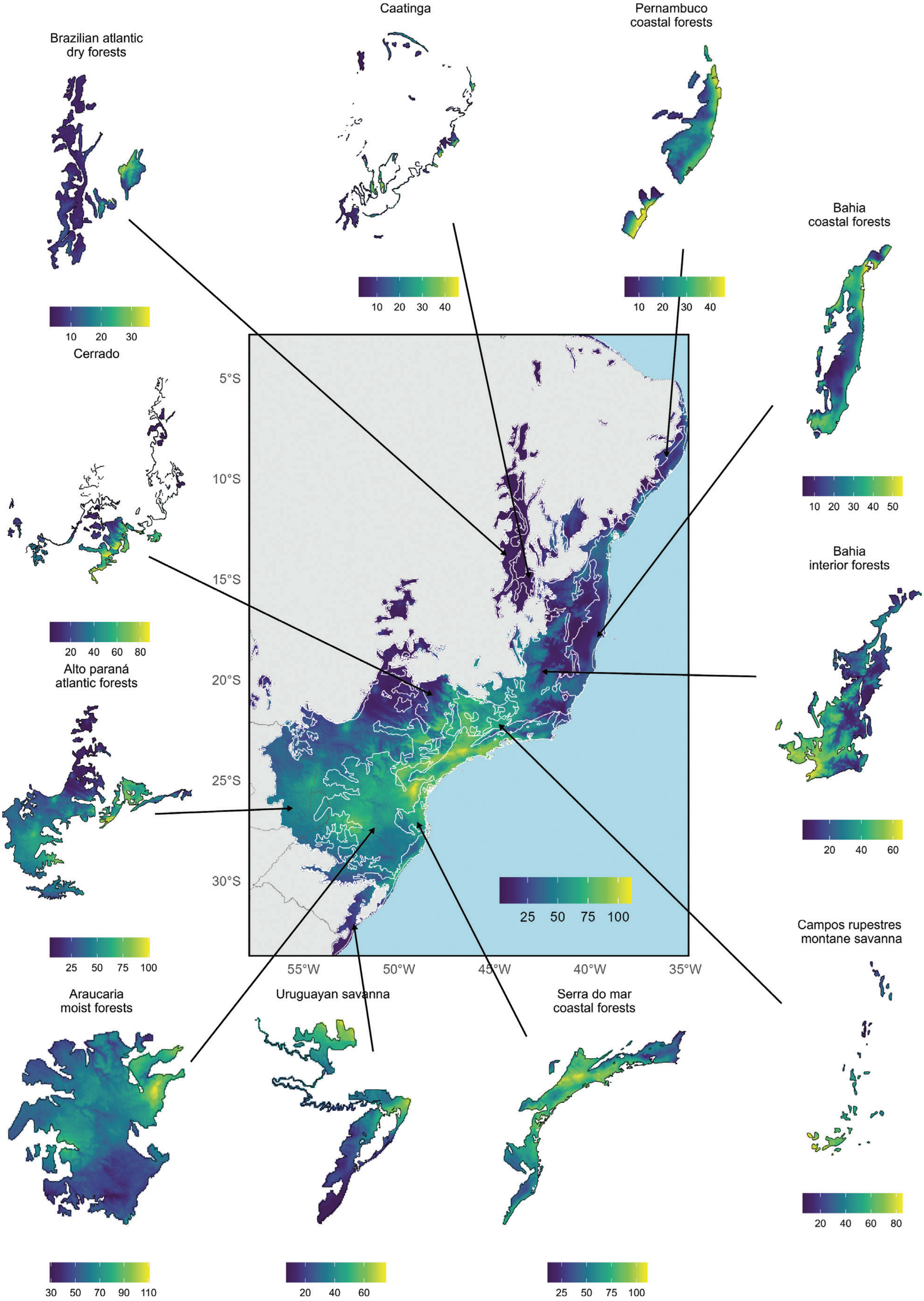

Figure 1. Species richness patterns of native Atlantic Forest bees throughout the biome and ecoregions. White lines denote the boundaries of the ecoregions.

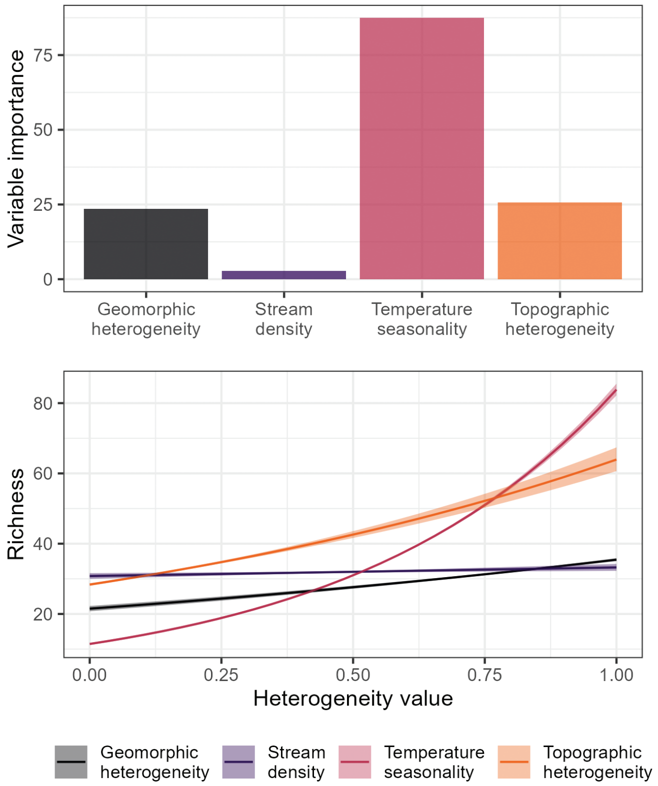

Figure 2. Importance of environmental heterogeneity variables in explaining bee species richness and the relationship between these variables and species richness of native bees in the Atlantic Forest. See Suppl. material 1: fig. S5 for results in original variable scales.

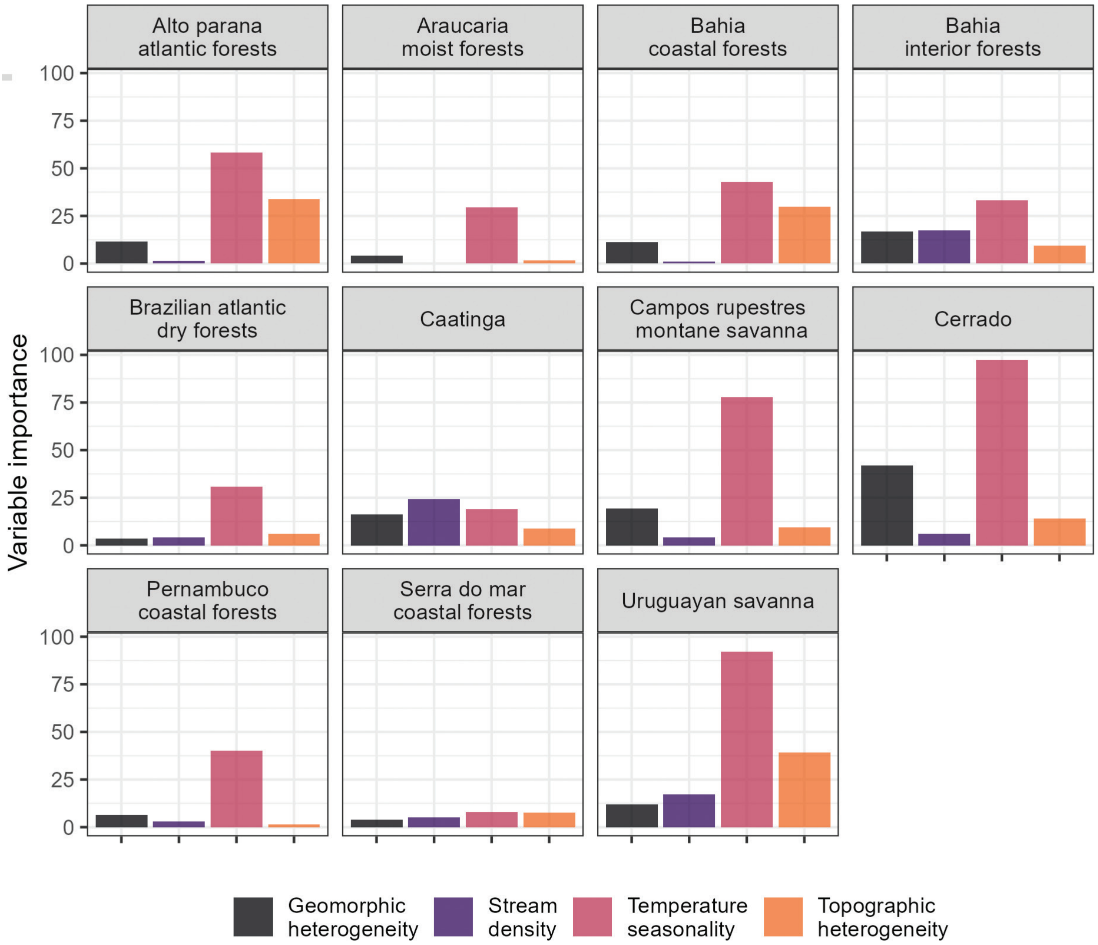

Figure 3. Importance of environmental heterogeneity variables in explaining bee richness in different ecoregions of the Atlantic Forest.

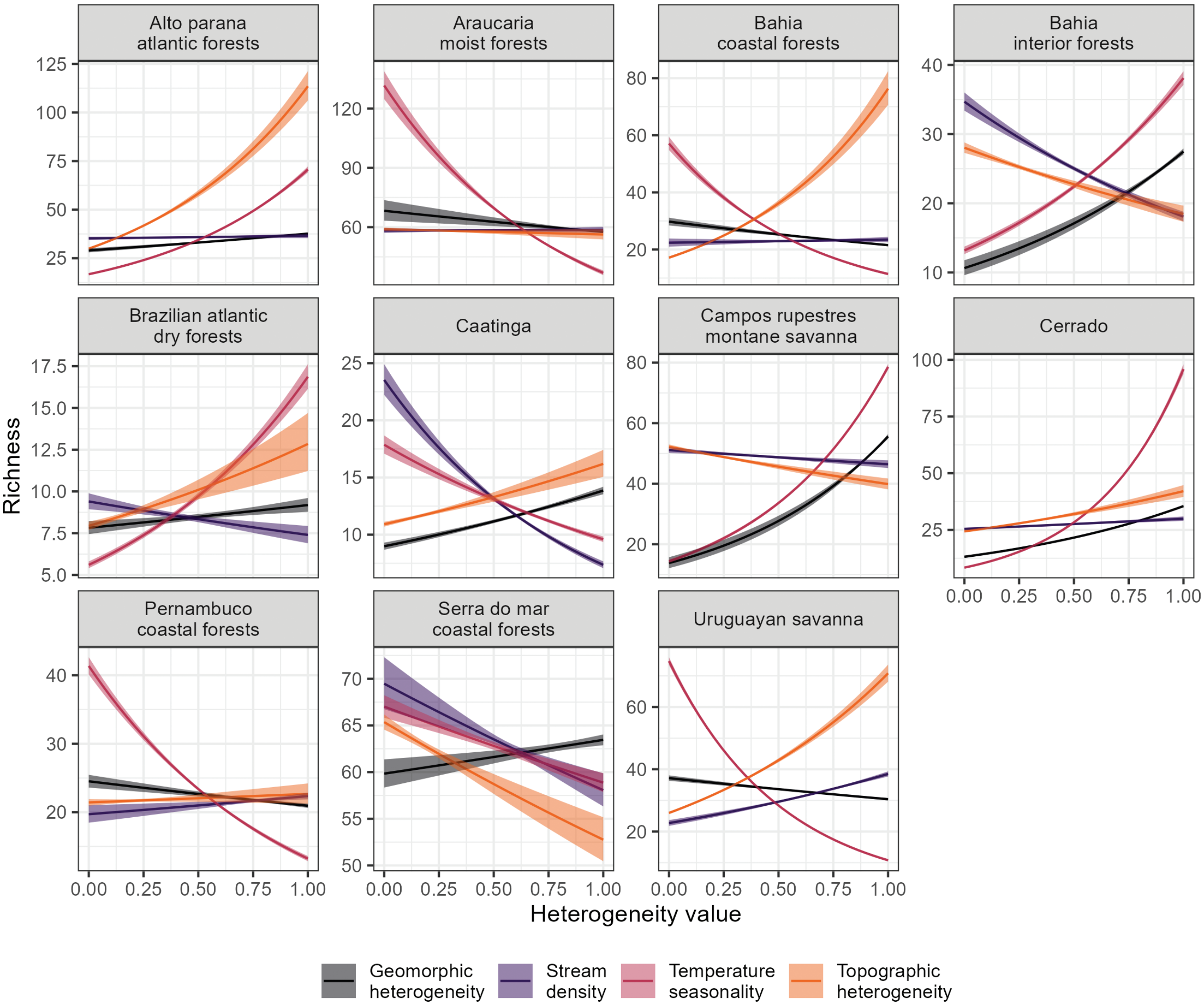

Figure 4. Relationship between environmental variables and species richness in Atlantic Forest ecoregions. See Suppl. material 1: fig. S7 for results in their original scales.

in the southern and southwestern regions of the Atlantic Forest and that temperature seasonality and topographic heterogeneity together partly explain these patterns. However, we found that the relationship between species richness and each of the features of environmental heterogeneity that we explored varied among ecoregions. This nonstationarity indicates that the relationship between environmental heterogeneity and bee richness is not spatially homogenous and that some environmental features may be more important for determining species richness in some regions than others (Foody 2004; Eme et al. 2015). Changes in the relationship between biodiversity features and predictor variables at different spatial scales are frequent in spatial ecology (Wang et al. 2012; Eme et al. 2015; Yeager et al. 2017). Understanding how biodiversity relates to the environment at different scales (e.g., biome, ecoregion, and sub-ecoregions) can reveal underlying mechanisms that drive biodiversity patterns in various landscapes. This reinforces the need to complement global analyses of species richness patterns with ecoregion- or landscape-specific assessments to understand richness patterns more deeply (Wang et al. 2012).

Patterns of estimated bee species richness were consistent with patterns observed for other taxonomic groups. For example, the regional hotspots of bee richness (i.e., the southwestern region of the Atlantic Forest) coincide with high concentrations of bird, mammal, and amphibian species (Jenkins et al. 2015); phylogenetic diversity of Opiliones (Arachnida) (Nogueira et al. 2019); and endemic species of amphibians, reptiles, birds, and mammals (Brown et al. 2020; Figueiredo et al. 2021). The general pattern of bee richness also coincides with that of woody plants (Lira-Noriega et al. 2017; Zwiener et al. 2017). Interpreting bee richness patterns demands consideration of the specific geographic and ecological context, especially in transitional zones. We found contrasting scenarios like disjunct Cerrado fragments within the Atlantic Forest (e.g., near to north Araucaria Moist Forest) supporting substantial bee richness, while Atlantic Forest within the Cerrado (e.g., upper portion of the Upper Paraná Atlantic Forest) showed reduced richness. These patterns suggest that geographic proximity to the Atlantic Forest core may influence local species composition. Nonetheless, richness pattern for the Cerrado and Caatinga ecoregions should be strictly limited to the context of this research. Extrapolation to the totality of these ecoregions is inappropriate because our analysis encompassed only portions of these vast areas that were merged with other smaller ecoregions within our study biome (Suppl. material 1: table S1).

We found that temperature seasonality was the most important feature of environmental heterogeneity for bee species richness across the Atlantic Forest biome and within some of its ecoregions. Surprisingly, for most ecoregions (7 of 11), temperature seasonality had a positive relationship with bee species richness. However, this relationship has not been commonly observed in other organisms. For bats and marsupials in the Atlantic Forest, temperature seasonality is negatively associated with species richness (Stevens 2013; Weber and Cáceres 2018; Delciellos et al. 2022), as well as endogenous fungi from Panama (Oita et al. 2021). Nevertheless, previous research has shown that global-scale plant richness is positively associated with temperature seasonality (Tietje et al. 2022). A probable explanation for the positive relationship between temperature seasonality and species richness is that sites with greater temperature seasonality throughout the year can avoid competitive exclusion and harbor a greater number of species niches in different seasons (Tonkin et al. 2017). Seasonal variation is directly linked to plant phenology, affecting flowering and, consequently, resource availability (Escobedo-Kenefic et al. 2020), which influences pollinator diversity.

Topographic and geomorphic heterogeneity showed positive relationships with bee species richness for the entire Atlantic Forest biome as well as several ecoregions in which these environmental features demonstrated high explanatory power. Topographic heterogeneity is important for maintaining biodiversity in the Atlantic Forest (Delciellos et al. 2022). Topographic and geomorphic heterogeneities are related to terrain complexity. As both variables increase, a diverse set of microclimates, vegetation types, and nesting and trophic opportunities for bees are expected (Tukiainen et al. 2019; Doherty et al. 2021; Cavigliasso et al. 2022; Pardee et al. 2023). Steep slopes, valleys, and varying elevations contribute to a mosaic of habitats, each supporting different plant communities, as is the case in the southwest Atlantic Forest, which has the greatest richness of tree species and significant changes in composition. (Zwiener et al. 2017; Rodrigues et al. 2019). Thus, a high diversity of plants can provide various essential food resources for bees (Cavigliasso et al. 2022; Dzekashu et al. 2022; Felderhoff et al. 2023). In addition, variations in microclimates created by topography can promote the coexistence of species with different environmental needs, resulting in greater ecological complexity in areas with more rugged terrain (Muscarella et al. 2020).

Stream density is a relatively understudied variable compared to other metrics of environmental heterogeneity, such as those related to topography or climate. Although water is a fundamental resource for bees (Rankin et al. 2020; Rosa-Fontana et al. 2020; McCune et al. 2021), we found a weak relationship between bee richness and stream density. One likely explanation is that, unlike other organisms, their main needs are the availability of floral resources (Vaudo et al. 2015) and nesting sites (Requier and Leonhardt 2020). However, certain species of bees use water to build nests or regulate temperature within their colonies (Stabentheiner et al. 2010; Stabentheiner et al. 2021). In tropical forests, such as the Atlantic Forest, humidity and high rainfall increase the abundance of floral resources, correlating with greater bee activity, indicating that humidity levels increase foraging opportunities (Silva et al. 2011; Marques et al. 2018). Another probable explanation for this finding is related to the nature of the stream density variable, as it represents potential watercourses, i.e., watercourses that may not exist permanently. Thus, these variables do not distinguish intermittent watercourses from permanent watercourses, especially in the drier regions of the Atlantic Forest (i.e., northeastern Brazil).

Despite the importance of seasonal temperature, topographic, and geomorphic heterogeneity in the Atlantic Forest biome and some ecoregions, these variables demonstrated relatively low explanatory power in ecoregions with the highest species richness, such as the Serra do Mar Coastal Forests and Araucaria Moist Forests. Previous research has shown that the distribution of species richness in areas characterized by especially high diversity cannot be explained by environmental heterogeneity alone (Chang et al. 2023). This finding emphasizes the importance of variables or mechanisms beyond those explained by environmental diversity in determining the diversity patterns of these ecoregions. For example, the Serra do Mar Coastal Forests and Araucaria Moist Forests may harbor high historical climatic stability, promoting favorable conditions for the survival of older species lineages and the emergence of new ones (speciation) (Carnaval et al. 2014; Brown et al. 2020). Globally, solar radiation and precipitation are important variables that explain bee diversity patterns (Orr et al. 2021), making them interesting to be explored at smaller spatial scales Another crucial factor could be the quality and availability of resources, such as floral sources for bees throughout the year, which are essential for maintaining bee diversity (Vaudo et al. 2015; Flo et al. 2018; Klaus et al. 2021). Given the high elevational gradient of the Serra do Mar coastal forest, the low explanatory power in this ecoregion could be related to the spatial resolution of SDM and variables, which may have been too coarse to capture the real variability of the region. Further studies are required to explore other drivers of bee species richness in these regions.

Environmental heterogeneity is increasingly being recognized as an important component in maintaining biodiversity (Knudson et al. 2018; Gordon et al. 2022). Conservation efforts in regions with high environmental heterogeneity have been emphasized to enhance biodiversity conservation because environmental heterogeneity can serve as a proxy for biodiversity (Beier and De Albuquerque 2015; Gordon et al. 2022; Maliniemi et al. 2024). Our results indicated that different components of environmental heterogeneity (temperature seasonality, topographic, and geomorphic heterogeneity) play important roles in determining bee species richness in the Atlantic Forest. Because the relationship between environmental heterogeneity and bee richness was specific to each ecoregion, and each ecoregion likely hosts different species compositions, ecoregion-specific conservation approaches may promote bee conservation throughout the Atlantic Forest. In regions where temperature seasonality was the most important predictor of richness, such as the Cerrado and the Uruguayan Savanna, promoting the conservation of bee habitats that capture climatic gradients may be fundamental for the persistence of local communities. Interestingly, the Serra do Mar Coastal Forests were one of the ecoregions with the highest biodiversity of bees. This ecoregion hosts one of the largest forest remnants of the Atlantic Forest and has been highlighted as a region to expand the current protected areas for amphibians, birds, and plants (Campos et al. 2017; Zwiener et al. 2017; Vale et al. 2018). Because of the large deforestation suffered in the Atlantic Forest, it is necessary to restore areas in ecoregions, such as the Araucaria Moist Forest, Upper Paraná Atlantic Forests, and Cerrado, which have a high biodiversity of bees and other organisms (Zwiener et al. 2017; Crouzeilles et al. 2020; Velazco et al. 2023). Further research could evaluate the contribution of anthropic land cover to the loss of species range and identify priority areas for bee conservation. The limitations of this study are largely related to the intrinsic complexity of the bee group and the ecological variation across bee species in the Atlantic Forest. These species cover a range of different life histories and habitat requirements, making the standardization of occurrence data and generalizability of results particularly challenging. Obtaining occurrence data for bees, and arthropods more broadly, is especially difficult in areas that are not easily accessible. The lack of data for these organisms makes the estimation of species distributions impossible in some cases, which may influence the resulting richness estimates.

Conclusion

Bee species richness was highest in the Serra do Mar Coastal Forests and Araucaria Moist Forest ecoregions, while the coastal regions of the northeast (e.g., the Pernambuco Coastal Forests) and drier inland areas (e.g., the Caatinga and Bahia Inland Forests) showed the lowest diversity. Temperature seasonality emerged as the most important variable explaining species richness, showing a positive relationship with bee richness in most ecoregions. Topographic and geomorphic heterogeneities also play an important role in determining bee richness patterns in some parts of the Atlantic Forest. Moreover, stream density was poorly correlated with richness patterns. We found that the relationship between environmental heterogeneity variables and bee species richness varied substantially between ecoregions. This finding reinforces the need to study diversity patterns at multiple spatial scales to highlight the nuanced drivers of species diversity within each ecoregion. Interestingly, in ecoregions with the highest bee species richness, aspects of environmental heterogeneity showed low explanatory power, suggesting that other factors are the primary determinants of local biodiversity.

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Author contributions

Conceptualization (AIA, SJEV), Methodology (AIA, SJEV), Formal analysis (AIA, ACOJ, SJEV), Data curation (AIA, SJEV), Writing – Original Draft (AIA, SJEV), Writing – Review & Editing (AIA, ACOJ, FV, SJEV).

Data accessibility statement

Species occurrence dataset and predictor variables used to construct species distribution, and raster with environmental heterogeneity variables can be accessed at: https://doi.org/10.6084/m9.figshare.28680413.

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Supplementary materials

Supplementary material 1

Figure S1: Map of Atlantic Forest ecoregions; Figure S2: Correlogram of the original predictor variables based on the Pearson correlation matrix; Figure S3: Geographical pattern of environmental heterogeneity variables used to relate with bee richness of the Atlantic Forest; Figure S4: Performance of ESM (esm_) and consensus models (median) based on Sorensen and IMAE metrics; Figure S5: Relationship between different environmental heterogeneity variables in their original scales and species richness of native bees in the Atlantic Forest; Figure S6: Importance of ecoregion and different environmental heterogeneity variables in explaining species richness of native bees in the Atlantic Forest; Figure S7: Relationship between environmental variables in their original scales and species richness in Atlantic Forest ecoregions; Figure S8: Pearson correlation between species suitability and predictor variables used to explore the relationship between species richness and environmental heterogeneity. Each point represents a species. Red-dashed lines represent correlation > |0.7|. 27 species presented correlation > |0.7|; Table S1: List of ecoregions analyzed and original ecoregion names. Ecoregions with small geographic expressions have been joined to larger and closer ecoregions; Table S2: Justification for the inclusion of predictor variables used in species distribution models; Table S3: Parameters and hyperparameters used in each algorithm, values, and number of hyperparameter combinations, and R codes used to generate the sequence of values (.docx)

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