

The distribution and conservation of areas with microendemic species in a biodiversity hotspot: a multi-taxa approach (#89090)

1

First submission

Guidance from your Editor

Please submit by **9 Sep 2023** for the benefit of the authors (and your token reward) .



Structure and Criteria

Please read the 'Structure and Criteria' page for general guidance.



Raw data check

Review the raw data.



Image check

Check that figures and images have not been inappropriately manipulated.

If this article is published your review will be made public. You can choose whether to sign your review. If uploading a PDF please remove any identifiable information (if you want to remain anonymous).

Files

Download and review all files from the [materials page](#).

3 Figure file(s)

2 Table file(s)

1 Raw data file(s)



Structure and Criteria

Structure your review

The review form is divided into 5 sections. Please consider these when composing your review:

1. **BASIC REPORTING**
2. **EXPERIMENTAL DESIGN**
3. **VALIDITY OF THE FINDINGS**
4. General comments
5. Confidential notes to the editor

 You can also annotate this PDF and upload it as part of your review

When ready [submit online](#).

Editorial Criteria

Use these criteria points to structure your review. The full detailed editorial criteria is on your [guidance page](#).

BASIC REPORTING

-  Clear, unambiguous, professional English language used throughout.
-  Intro & background to show context. Literature well referenced & relevant.
-  Structure conforms to [PeerJ standards](#), discipline norm, or improved for clarity.
-  Figures are relevant, high quality, well labelled & described.
-  Raw data supplied (see [PeerJ policy](#)).

EXPERIMENTAL DESIGN

-  Original primary research within [Scope of the journal](#).
-  Research question well defined, relevant & meaningful. It is stated how the research fills an identified knowledge gap.
-  Rigorous investigation performed to a high technical & ethical standard.
-  Methods described with sufficient detail & information to replicate.

VALIDITY OF THE FINDINGS

-  Impact and novelty not assessed. *Meaningful* replication encouraged where rationale & benefit to literature is clearly stated.
-  All underlying data have been provided; they are robust, statistically sound, & controlled.
-  Conclusions are well stated, linked to original research question & limited to supporting results.



The best reviewers use these techniques

Tip

Example

Support criticisms with evidence from the text or from other sources

Smith et al (J of Methodology, 2005, V3, pp 123) have shown that the analysis you use in Lines 241-250 is not the most appropriate for this situation. Please explain why you used this method.

Give specific suggestions on how to improve the manuscript

Your introduction needs more detail. I suggest that you improve the description at lines 57- 86 to provide more justification for your study (specifically, you should expand upon the knowledge gap being filled).

Comment on language and grammar issues

The English language should be improved to ensure that an international audience can clearly understand your text. Some examples where the language could be improved include lines 23, 77, 121, 128 – the current phrasing makes comprehension difficult. I suggest you have a colleague who is proficient in English and familiar with the subject matter review your manuscript, or contact a professional editing service.

Organize by importance of the issues, and number your points

1. Your most important issue
2. The next most important item
3. ...
4. The least important points

Please provide constructive criticism, and avoid personal opinions

I thank you for providing the raw data, however your supplemental files need more descriptive metadata identifiers to be useful to future readers. Although your results are compelling, the data analysis should be improved in the following ways: AA, BB, CC

Comment on strengths (as well as weaknesses) of the manuscript

I commend the authors for their extensive data set, compiled over many years of detailed fieldwork. In addition, the manuscript is clearly written in professional, unambiguous language. If there is a weakness, it is in the statistical analysis (as I have noted above) which should be improved upon before Acceptance.

The distribution and conservation of areas with microendemic species in a biodiversity hotspot: a multi-taxa approach

Helder F.P. Araujo¹, Célia C. C. Machado², José Maria C Silva^{Corresp. 3}

¹ Department of Biosciences, Federal University of Paraíba, Areias, Paraíba, Brazil

² Center of Applied Biological and Social Sciences, State University of Paraíba, João Pessoa, Paraíba, Brazil

³ Department of Geography and Sustainable Development, University of Miami, Coral Gables, Florida, United States of America

Corresponding Author: José Maria C Silva

Email address: jcsilva@miami.edu

Background. Microendemics are species with very small ranges. They are found in different regions worldwide and belong to different groups of organisms. The ranges of microendemics determine areas with microendemics (hereafter, “AMs”), representing the smallest spatial units containing at least one species not found elsewhere. AMs are expected not to be distributed randomly but associated with certain geographic factors. However, the nature of these factors and their level of influence are still unclear. We studied the distribution patterns of microendemic species within the Brazilian Atlantic Forest to (a) identify the region’s AMs; (b) evaluate the overlap between AMs and the region’s three large areas of endemism and transition sub-region; (c) test the hypotheses that the distribution of AMs is influenced by latitude, altitude, distance from the coastline, and climate stability; and (d) assess AMs conservation status.

Methods. We mapped the range of 1,345 microendemic species of three taxonomic groups (seed plants, freshwater fishes, and terrestrial vertebrates) to identify AMs. We used the Chi-Square test followed by Fischer exact test to test if AMs are concentrated in the region’s large areas of endemism. Spatial autoregressive logit regression models were used to assess if AMs are associated with latitude, altitude, distance from the coastline. Finally, we used the Kruskal-Wallis test to compare the conservation status of AMs and non-AMs.

Results. We identified 261 AMs for seed plants, 204 AMs for freshwater fishes, and 92 AMs for terrestrial vertebrates in the Brazilian Atlantic Forest. All combined, there are 468 AMs that cover 21% of the region. All four variables are associated with AMs; however, the direction and significance of these associations vary across taxonomic groups. AMs have more forests and are more formally protected than other areas. The Brazilian Atlantic Forest is a large and complex biogeographic mosaic where AMs represent islands or archipelagoes surrounded by transition areas with no microendemic species. Although these islands or archipelagoes are more frequent within the three previously recognized large areas of endemism, they are not restricted to them. AMs are associated with geographic variables, but a considerable variation in these associations among taxonomic groups exists. The 145 unprotected AMs with native vegetation should be priorities for conservation actions. This study provides insights into the biogeography of one of the most important global biodiversity hotspots and creates a foundation for comparative studies with other tropical forest hotspots.

**The distribution and conservation of areas with microendemic species
in a biodiversity hotspot: a multi-taxa approach**

Helder F. P. de Araujo¹, Célia C. C. Machado¹, José Maria Cardoso da Silva³,

^b Corresponding author

Author Affiliations

^a Department of Biosciences, Federal University of Paraíba, Campus II, Areia, Paraíba, Brazil.

^b Center of Applied Biological and Social Sciences, State University of Paraíba, João Pessoa, Paraíba, Brazil.

^c Department of Geography and Sustainable Development, University of Miami, 1300 Campo Sano, 33124-4401, Coral Gables, FL, USA, E-mail: jcsilva@miami.edu

Corresponding Author

^c Department of Geography and Sustainable Development, University of Miami, 1300 Campo Sano, 33124-4401, Coral Gables, FL, USA, E-mail: jcsilva@miami.edu

Abstract

Background. Microendemics are species with very small ranges. They are found in different regions worldwide and belong to different groups of organisms. The ranges of microendemics determine areas with microendemics (hereafter, “AMs”), representing the smallest spatial units containing at least one species not found elsewhere. AMs are expected not to be distributed randomly but associated with certain geographic factors. However, the nature of these factors and their level of influence are still unclear. We studied the distribution patterns of microendemic species within the Brazilian Atlantic Forest to (a) identify the region’s AMs; (b) evaluate the overlap between AMs and the region’s three large areas of endemism and transition sub-region; (c) test the hypotheses that the distribution of AMs is influenced by latitude, altitude, distance from the coastline, and climate stability; and (d) assess AMs conservation status.

Methods. We mapped the range of 1,345 microendemic species of three taxonomic groups (seed plants, freshwater fishes, and terrestrial vertebrates) to identify AMs. We used the Chi-Square test followed by Fischer exact test to test if AMs are concentrated in the region’s large areas of endemism. Spatial autoregressive logit regression models were used to assess if AMs are associated with latitude, altitude, distance from the coastline. Finally, we used the Kruskal-Wallis test to compare the conservation status of AMs and non-AMs.

Results. We identified 261 AMs for seed plants, 204 AMs for freshwater fishes, and 92 AMs for terrestrial vertebrates in the Brazilian Atlantic Forest. All combined, there are 468 AMs that cover 21% of the region. All four variables are associated with AMs; however, the direction and significance of these associations vary across taxonomic groups. AMs have more forests and are more formally protected than other areas. The Brazilian Atlantic Forest is a large and complex biogeographic mosaic where AMs represent islands or archipelagoes surrounded by transition areas with no microendemic species. Although these islands or archipelagoes are more frequent within the three previously recognized large areas of endemism, they are not restricted to them. AMs are associated with geographic variables, but a considerable variation in these associations among taxonomic groups exists. The 145 unprotected AMs with native vegetation should be priorities for conservation actions. This study provides insights into the biogeography of one of

the most important global biodiversity hotspots and creates a foundation for comparative studies with other tropical forest hotspots.

INTRODUCTION

Microendemics are species with very small ranges (Nogueira et al., 2010; Hobohm, 2013; Silva et al., 2019). They are found in different regions worldwide and belong to different groups of organisms (Kruckeberg & Rabinowitz, 1985; Wamelink, Goedhart & Frissel, 2014). Areas with microendemics (hereafter, “AMs”) represent the smallest spatial units containing at least one species not found elsewhere. Identifying these areas is relevant for biogeography and conservation. For biogeography, AMs are the fundamental focal areas for studying the intricate ecological and evolutionary mechanisms responsible for forming and maintaining modern biotas (Nattier et al., 2012; Weeks, Claramunt & Cracraft, 2016; e.g., Bertelli et al., 2017). For conservation, AMs represent unique places that should be prioritized for conservation efforts (e.g., Kruckeberg & Rabinowitz, 1985; Silva et al., 2019).

AMs can be both a "cradle" where young species have evolved and a "museum" for the survival of old species that have disappeared from other parts of their ranges (Kier et al., 2009; Albert, Petry & Reis, 2011; Rahbek et al., 2019). Because of this dual characteristic, AMs are expected not to be distributed randomly, but associated with certain geographic factors. However, the nature of these factors and their level of influence are still unclear (Hobohm, 2013). Four main geographic factors have been suggested as potential AM covariates: latitude, altitude, distance from the coastline, and long-term climatic stability. The probability of recognizing an AM is predicted to decline with latitude because low-latitude regions have more species with small ranges than high-latitude regions, primarily due to a combination of narrow species' ecological tolerance, high speciation rates, and long-term spatiotemporal variation in the precipitation regimes (Saupe et al., 2019). On the other hand, such probability is predicted to increase with altitude because areas with high altitudes typically have more complex topography, leading to sharp habitat changes in a relatively small area (Rahbek et al., 2019). These changes, in turn, lead to range fragmentation of ancestor species and the formation of more species with smaller ranges than in lowland habitats

(Körner, 2007). The probability of recognizing an AM is predicted to decrease with the distance from the coastline because coastal regions tend to be more heterogeneous, productive, and less seasonal compared to inland areas, which, over time, can lead to more opportunities for the formation and accumulation of microendemic species (Jenkins, Pimm & Joppa, 2013; Hobohm, 2013; Pimm et al., 2014; Acevedo & Sandel, 2021). Finally, more climatically stable areas are predicted to have a higher probability of being AMs than climatically unstable areas (Haffer, 1985; Fjeldså, Lambin & Mertens, 1999; Harrison & Noss, 2017), as they have served as refuges for populations of species affected multiple times by recurrent changes in climate in the past 3-4 million years (Ravelo et al., 2004). It is possible that these four factors work in synergy, so they should be evaluated simultaneously. In addition, different groups of organisms are expected to respond differently to these four factors because each clade has distinct traits and habitat requirements (Pacifi et al., 2017; Beissinger & Riddell, 2021; Green et al., 2022). As a result, assessing the association between these factors and AMs requires a multi-taxa approach.

The conservation status of AMs is still a large knowledge gap everywhere, as most studies focus on large regions, such as ecoregions or bioregions, and not on AMs within these regions (Silva, Rylands & Fonseca, 2005; e.g., Dinerstein et al., 2020). Regional conservation strategies can be proactive or reactive (Cunha, de Souza & Silva, 2019). A proactive strategy identifies priority conservation targets and sets aside protected areas to protect them before expanding human activities in a region. In contrast, a conservation strategy is reactive when protected areas are established as a late response to human expansion in a region (Cunha, de Souza & Silva, 2019). Only reactive strategies are possible in biodiversity hotspots, regions expected to have a high AM density and high levels of ecological transformation (Mittermeier et al., 2005). AMs within these regions are therefore expected to be mostly unprotected and degraded.

The Atlantic Forest is ideal for studying AMs, their distribution, association with geographic covariates, and conservation status because it harbors an unparalleled density of endemic species packed into a large and environmentally heterogeneous region (Tabarelli et al., 2005). As one of the largest South American biodiversity hotspots (Mittermeier et al., 2005), the Atlantic Forest covers around 1.4 million km². It occupies a large latitudinal extent (ca. 25 degrees) along the South American Atlantic coastline from the Rio Grande do Norte in northeastern Brazil to southern

Brazil (Galindo-Leal & Camara, 2003; Instituto Brasileiro. de Geografia e Estatística, 2019). Away from the coast, the Atlantic Forest extends to central Brazil, northeastern Argentina (Misiones), and southwestern Paraguay (Galindo-Leal & Camara, 2003). In addition, the region has a complex topography, with altitudes ranging from 0 to 2,892 m above sea level, forming ecological gradients that influence the distribution of species (Goerck, 1999; Silva, Sousa & Castelletti, 2004; da Silva, de A. Tozzi & Meireles, 2015). Because of these geographic factors, species in the region are rarely widespread but occupy only a small portion of it. Species restricted to the Atlantic Forest are concentrated into three major areas of endemism (Pernambuco, Central Bahia, and Serra do Mar) separated by transition regions (Silva & Casteleti, 2003; Peres et al., 2020; Barbo, Nogueira & Sawaya, 2021). Since areas of endemism are organized in levels, with small ones nested within large ones (Daru et al., 2020), it is expected that AMs will only be found within the three main areas of endemism (Silva, Sousa & Castelletti, 2004; Peres et al., 2020) because transition regions, by definition, do not contain any endemic species (Ferro & Morrone, 2014; Morrone, 2023).

This paper has four main goals. First, we identify the Atlantic Forest's AMs by analyzing the ranges of 1,345 microendemic species of three taxonomic groups (seed plants, freshwater fishes, and terrestrial vertebrates). Second, we test the hypothesis that AMs overlap exclusively with the region's three large areas of endemism. Third, we use spatial logistic regressions to simultaneously test the hypotheses that latitude, altitude, distance from the coastline, and climate stability are associated with AMs across all three taxonomic groups. Finally, we assess the conservation status of the AMs by evaluating two indicators (% of native vegetation and % within protected areas) and comparing these indicators to non-AMs. This study not only tests some general hypotheses on the distribution of microendemic species, but also generates new knowledge on the biogeography and conservation of a major global biodiversity hotspot. It lays the groundwork for future comparative research on other tropical forest hotspots.

METHODS

Study area

Our analysis is restricted to the Brazilian Atlantic Forest defined by Instituto Brasileiro de Geografia e Estatística (2019). The IBGE's limits differ from that of other studies (Silva & Casteleti, 2003; Silva, Sousa & Castelletti, 2004; e.g., Peres et al., 2020), as they exclude patches of humid forests and tropical dry forests found in the Caatinga and Cerrado regions (Araujo et al., 2022). We did not include other regions outside of Brazil (e.g., Argentina and Paraguay) because comparative data was unavailable. For analytical purposes, we divided the Brazilian Atlantic Forest into two groups of sub-regions: areas of endemism and a transition sub-region. There are three areas of endemism, as delimited by Peres (2020): Pernambuco, Coastal Bahia and Serra do Mar (including Paraná or Araucária). The transition sub-region encompasses all areas outside the three areas of endemism (Fig. 1).

Species datasets

We mapped the ranges of microendemic species (i.e., species with ranges smaller than 10,000 km²) of three taxonomic groups: seed plants, freshwater fishes, and terrestrial vertebrates (snakes, small mammals, and passerine birds). For seed plants and freshwater fishes, we used the databases provided by Silva et al. (2019) and Nogueira et al. (2010), respectively. For snakes and mammals, we selected the microendemic species from the dataset generated by Barbo et al. (2021) and Dalapicolla et al. (2021), respectively. For passerine birds, we first selected the microendemism from the list of Brazilian Atlantic Forest endemic species produced by Silva et al. (2004). Then we updated the species ranges using new information from Wikiaves (www.wikiaves.com.br) and the Global Biodiversity Information Facility (www.gbif.org). See Appendix 1 for all species and records used in the analysis.

Areas of microendemism and their overlap with sub-regions

We used QGIS to create a detailed map of all microendemic species within each taxonomic group in the Brazilian Atlantic Forest. Then, we superimposed these maps with a map dividing the region into 2,243 equal-sized hexagons (ca. 630 km²) and counted the microendemic species recorded within each. Any hexagon containing at least one microendemic species was designated as an AM.

Finally, we superimposed the AMs identified for each taxonomic group with a map of the four sub-regions to assess their overlap.

To test the hypothesis that the Brazilian Atlantic Forest's areas of endemism have more AMs than expected for their size, we compared the actual number of AMs in each area of endemism with the expected number of AMs based on each area of endemism's number of hexagons using Chi-Square. To calculate the expected number of AMs for each taxonomic group in each sub-region, we divided the number of hexagons of each sub-region (Pernambuco = 64; Coastal Bahia = 109; Serra do Mar = 388; and Transition Sub-Region = 1682) by the number total of hexagons in the Brazilian Atlantic Forest (2243), and multiplied by the number of AMs recorded within them. To assess where the difference within the contingency table is, we computed the exact p-value for each cell using Fisher's method as proposed by Shan and Gerstenberger (2017).

Predicting areas of microendemism using geographic variables

We assessed the association of four variables and AMs in the Brazilian Atlantic Forest: latitude, altitude, distance from the coastline, and climatic stability index. All these variables were collected from publicly available digital databases. Elevation represents the average elevation (in m) within the hexagon. This information came from the WorldClim 2.1 platform (Fick & Hijmans, 2017), with a resolution of 2.5 arc minutes or ca. 5 km² (<https://www.worldclim.org/>). We used the latitude (in degrees) of the hexagon's centroid to measure its distance from the equator. Distance from the hexagon to the nearest coast was calculated using a global database provided by NASA's Ocean Biology Processing Group (<https://oceancolor.gsfc.nasa.gov/docs/distfromcoast/>). Finally, the climate stability index (resolution of ca. 5 km) represents a hexagon's average climatic stability index since the Pliocene (Herrando-Moraira et al., 2022). The climatic stability index measures the variability of 14 bioclimatic variables using nine general circulation models of climate change over four periods available from WorldClim. The final CSI maps were obtained by summing the standard deviation of the variables selected and the normalized subsequent outputs. The climate stability index ranges from 0 (low climatic fluctuations) to 1 (high climatic fluctuations).

To test the hypotheses of associations between the four variables and AMs, we first coded all AMs as 1 and all hexagons without microendemics as 0. Then, we used a spatial logit regression using the non-linear two-stage least squares (N2SLS) estimator available in the spatbinary command for Stata (Spinelli, 2022). A contiguity weighting matrix that specifies neighbors as hexagons with shared boundaries or vertices (“queen”) was generated using the spmatrix command in Stata (StataCorp., 2017) and was added to the model to incorporate the spatial relations between hexagons. We ran the models separately for each one of the three taxonomic groups. To determine if nearby hexagons have a similar likelihood of having a positive outcome, the rho coefficient (a spatial autocorrelation parameter) was evaluated for each model. A positive coefficient indicates that the propensity is clustered, otherwise, it is dispersed in space. In addition, Hansen’s test for overidentification was used to assess if the number of explanatory variables is larger than the number of parameters to be estimated (Spinelli, 2022).

Conservation status of areas of microendemics

To assess the conservation status of the AMs and non-AMs within the Atlantic Forest, we measured the percentage of each hexagon covered by native vegetation and protected areas. To calculate the first indicator, we overlaid the general map of AMs and non-AMs with the most recent map of Annual Land Use and Land Cover Mapping Project produced by Mapbiomas (www.mapbiomas.org). To estimate the second indicator, we overlaid the general map of AMs and non-AMs with the most recent digital map of all protected areas in Brazil’s Protected Area National Register (cnuc.mma.gov.br). We used the Kruskal-Wallis rank test to evaluate if the two indicators differ between AMs and non-AMs.

RESULTS

Areas of microendemism

We identified 261 AMs for seed plants, 205 AMs for freshwater fishes, and 93 AMs for terrestrial vertebrates in the Brazilian Atlantic Forest (Fig. 2). These represent 11.6%, 7.8%, and 4.5% of the region’s total area, respectively. All combined, there are 468 AMs that cover 21% of the Brazilian Atlantic Forest. AMs cover 34.4% of Pernambuco, 46.8% of Coastal Bahia, 43.6% of Serra do Mar, and only 13.4% of the transition sub-region. The percentage of AMs in the transition sub-

region is 48.3% for seed plants, 49.3% for freshwater fishes, 25.8% for terrestrial vertebrates, and 48.3% for all taxonomic groups combined (Table 1).

The frequency of AMs by sub-regions of the Brazilian Atlantic Forest in all taxonomic groups differs from what is expected from their sizes: seed plants ($\chi^2=41.3$, $df=3$, $p=0.000$), freshwater fishes ($\chi^2=34.1$, $df=3$, $p=0.000$), terrestrial vertebrates ($\chi^2=46.5$, $df=3$, $p=0.000$), and all taxonomic groups combined ($\chi^2=70.0$, $df=3$, $p=0.000$). The number of AMs in Pernambuco is higher than expected in terrestrial vertebrates and not different from that expected in seed plants, freshwater fishes, and all taxonomic groups combined. In Coastal Bahia, the number of AMs is higher than expected for seed plants and all taxonomic groups combined, while for freshwater fishes and terrestrial vertebrates, it is not different from expected. The Serra do Mar region has more AMs than expected in all taxonomic groups, separated or combined. Finally, the number of AMs in the transition sub-region is lower than expected for all taxonomic groups, separated or combined (Table 1).

Association between geographic factors and areas of microendemism

Hansen's tests for all three spatial regression models were not significant (seed plants: $\chi^2=0.25$, $df=3$, $p=0.96$; freshwater fishes: $\chi^2=0.13$, $df=3$, $p=0.98$; terrestrial vertebrates: $\chi^2=0.31$, $df=3$, $p=0.96$), thus, all explanatory variables used in the models are valid (Table 2). The rho values for all three models were not significant for all groups of organisms (Table 2). Patterns of association between AMs and geographic factors differed across taxonomic groups. For seed plants, AM probability increases with climate stability, but decreases with the distance from the coastline. In contrast, the probability of AMs identified for freshwater fishes increases with latitude and climate stability, but decreases with the distance from the coastline. Finally, for terrestrial vertebrates, AM probability increases with altitude, but decreases with latitude, distance from the coastline, and climate stability.

Conservation status of areas with microendemisms

Although AMs and non-AMs showed a wide variation in the percentage of native vegetation cover (Fig. 3), AMs have a higher median (31.2) than non-AMs (18.1). This difference is significant (Kruskal-Wallis test, $\chi^2=136.1$, $p=0.0001$). Similarly, both have a wide variation regarding protected area cover (Fig. 3), but AMs have a larger median (3.7) than non-AMs (0). This difference is also significant (Kruskal-Wallis test; $\chi^2=181.1$, $p=0.0001$). Among the 468 AMs, 145 have native vegetation, but no protection. Only 3 AMs have no native vegetation, but all are within protected areas.

DISCUSSION

Mapping AMs shows that 21% of the Brazilian Atlantic Forest has microendemic species. This finding indicates a high regional biogeographic heterogeneity that has not been reported previously, although some studies have indicated that the region's biogeographic patterns are expected to be more complex than originally thought (Silva, Sousa & Castelletti, 2004; Nogueira et al., 2010; DaSilva, Pinto-da-Rocha & DeSouza, 2015; Silva et al., 2019). While the largest area of endemism (Serra do Mar) has more AMs than expected from its size in all groups of organisms separated or combined, the smallest areas of endemism (Coastal Bahia and Pernambuco) have more AMs than expected for some groups of organisms, but not for others. On the other hand, the transition sub-region, despite being the largest sub-region, had fewer AMs than expected from its size for all taxonomic groups, separated or combined. These results show that AMs are not uniformly distributed across the Brazilian Atlantic Forest's sub-regions and that the distribution patterns of these AMs differ across taxonomic groups.

The hypothesis that the three areas of endemism are the Atlantic Forest's main clusters of endemic species at any spatial level (see review by Peres et al., 2020) is partially supported by our analysis. However, we have also found that almost half of the AMs are outside these areas of endemism, indicating that microendemism is ubiquitous across the entire region. Therefore, the current framework used to describe the biogeographic patterns in the region is incomplete. For future biogeographical studies, the Brazilian Atlantic Forest should be envisioned as a large and complex biogeographic mosaic where AMs represent islands or archipelagoes surrounded by transition areas with no microendemic species. Although these islands or archipelagoes overlap more frequently with the three previously recognized large areas of endemism, they are not restricted to


them. Studies on microendemics in other biodiversity hotspots have also documented very complex mosaics of AMs and transition regions (Kruckeberg & Rabinowitz, 1985; Wilmé, Goodman & Ganzhorn, 2006; Hobohm, 2013; Wulff et al., 2013; Caesar, Grandcolas & Pellens, 2017). These similarities suggest that high internal biogeographical heterogeneity is a common attribute of all biodiversity hotspots.

This hypothesis that AM probability decreases with latitude and distance from the coastline, but increases with altitude and long-term climatic stability when all four predictors are evaluated simultaneously for all taxonomic groups was rejected. Instead, we found that AMs for each taxonomic group have distinctive associations with the four explanatory variables. Distance from the coastline showed negative relationships with AMs in all taxonomic groups. This is a relevant finding because distance from the coastline is not a geographic variable commonly used in macroecological studies to predict both species richness and endemism, even though all global maps produced so far show that, at least for some regions, coastal areas generally have a high density of species and endemic species in particular (Kier et al., 2009; Jenkins, Pimm & Joppa, 2013).

Latitude has a positive association with AMs for freshwater fishes, but a negative association with AMs for terrestrial vertebrates. The result with terrestrial vertebrates matches that expected from the model proposed by Saupe et al. (2019), in which species with narrow ranges are expected to decline with latitude because clades living in low-latitude areas have narrow ecological tolerance and high speciation rates due to temporal changes in precipitation regimes. However, Saupe's model does not explain the pattern observed for freshwater fishes. Patterns of species richness and endemism in Neotropical freshwater fishes follow the core-periphery pattern, characterized by high species richness at the continental core and high species endemism at the continental periphery (Albert, Petry & Reis, 2011). Thus, while fish species diversity decreases with latitude, endemism does not. For instance, the area with the highest concentrations of fish endemic species in the Atlantic Forest is in the southern Atlantic Forest (Albert, Tagliacollo & Dagosta, 2020), a pattern not found in other vertebrates (Peres et al., 2020).

Altitude has positive relationships with AMs only for terrestrial vertebrates, so this association cannot be generalized to other taxonomic groups. In contrast, as expected, long-term climate stability is positively associated with AMs for seed plants and freshwater fishes, but, against all expectations, it is negatively associated with AMs for terrestrial vertebrates. The result indicates that, for terrestrial vertebrates, climatically unstable areas are places where microendemics have originated and maintained. This pattern, although unexpected, is not to be restricted to Atlantic Forest. For instance, Silva (1997) reported that endemic species with small ranges within the Cerrado evolved in the region's most climatically unstable areas.

In general, our results show that AMs result from the interactions between the shared properties of the biological group under study and the shared properties of the areas where they occur. As none of these properties are stable over time, AMs are dynamic, as once widespread species can eventually become microendemics and microendemics can become widespread. Therefore, the imperfect matches in the boundaries of AMs and relationships between AMs and geographic covariates identified across different taxonomic groups should be considered the norm rather than the exceptions in biogeographic studies in the Atlantic Forest.

The  that AMs have more native vegetation and protected areas coverage than non-AMs indicates that despite the large conservation gap in the region, some level of conservation has been directed toward those areas harboring microendemic species. This can be the result of decades of efforts promoting and implementing science-based conservation across the region (Scarano, 2014; Silva et al., 2016; Pinto & Hirota, 2022), or the fact that at least a significant portion of AMs is inaccessible and therefore passively protected against human interventions. Regardless of the cause, the Brazilian Atlantic still has a huge conservation gap to be filled (Silva et al., 2016) and AMs should be prioritized for immediate conservation action. We suggest that zero deforestation policies should be adopted for all AMs with native vegetation, that AMs with no conservation should be considered priorities for establishing new protected areas, and that AMs with no native vegetation should be priorities for ecological restoration. The Brazilian private sector manages most of the Atlantic Forest (Freitas et al., 2018), thus, to guarantee the preservation of this region in the long term, it is essential to establish an extensive network of private reserves that are

meticulously planned and informed by the most reliable scientific data (Silva, Pinto & Scarano, 2021).

Conclusions

We studied the ranges of 1,345 microendemic species of three taxonomic groups (seed plants, freshwater fishes, and terrestrial vertebrates) in the Brazilian Atlantic Forest to map AMs, assess their overlap with previously identified areas of endemism, and evaluate their association with a set of geographic factors. Our results show that AMs are widespread across the region, that almost half of AMs are found outside large areas of endemism, and that all four geographic factors are associated with AMs, but the direction and significance of these associations vary across taxonomic groups. In addition, we demonstrated that despite the large variation within both AMs and non-AMs, AMs have more native vegetation and protected area coverage than non-AMs. We recognize that some AMs that we identified can be sampling artifacts because the knowledge of the Atlantic Forest's biota is still incomplete. However, the Atlantic Forest is Brazil's most well-sampled region because it harbors the country's highest density of scientists and organizations working on biodiversity (Silva et al., 2016). To mitigate the influence of incomplete knowledge, we used a conservative approach by considering only species records with documented and peer-reviewed evidence in our analyses. While it is possible that additional data may reveal larger ranges for some of the species included in our analysis, we believe that the general patterns described here are robust and interesting enough to both provide insights into the biogeography of one of the most important global biodiversity hotspots and create a foundation for comparative studies with other tropical forest regions.

Acknowledgments

We thank Luis Barbosa for helping us with maps and Julie Topf for reviewing the first draft of the manuscript.

References

- 389 Acevedo S, Sandel B. 2021. Phylogenetic endemism hotspots of north American birds are
390 associated with warm temperatures and long- and short-term climate stability. *Frontiers in*
391 *ecology and evolution* 9. DOI: 10.3389/fevo.2021.645396.
- 392 Albert JS, Petry P, Reis RE. 2011. Major Biogeographic and Phylogenetic Patterns. In: Albert JS,
393 Reis RE eds. *Historical Biogeography of Neotropical Freshwater Fishes*. Berkeley and
394 Los Angeles: University of California Press, 21–57.
- 395 Albert JS, Tagliacollo VA, Dagosta F. 2020. Diversification of Neotropical Freshwater Fishes.
396 *Annual review of ecology, evolution, and systematics* 51:27–53. DOI: 10.1146/annurev-
397 ecolsys-011620-031032.
- 398 Araujo HFP de, Garda AA, Girão e Silva WA de, Nascimento NFF do, Mariano E de F, Silva JMC
399 da. 2022. The Caatinga region is a system and not an aggregate. *Journal of arid*
400 *environments* 203:104778. DOI: 10.1016/j.jaridenv.2022.104778.
- 401 Barbo FE, Nogueira C de C, Sawaya RJ. 2021. Vicariance and regionalization patterns in snakes
402 of the South American Atlantic Forest megadiverse hotspot. *Journal of biogeography*
403 48:823–832. DOI: 10.1111/jbi.14040.
- 404 Beissinger SR, Riddell EA. 2021. Why Are Species’ Traits Weak Predictors of Range Shifts?
405 *Annual review of ecology, evolution, and systematics* 52:47–66. DOI: 10.1146/annurev-
406 ecolsys-012021-092849.
- 407 Bertelli S, Szumik C, Goloboff PA, Giannini NP, Navarro-Sigüenza AG, Peterson AT, Cracraft J.
408 2017. Mexican land birds reveal complexity in fine-scale patterns of endemism. *Journal of*
409 *biogeography* 44:1836–1846. DOI: 10.1111/jbi.12987.

410 Caesar M, Grandcolas P, Pellens R. 2017. Outstanding micro-endemism in New Caledonia: More
411 than one out of ten animal species have a very restricted distribution range. *PloS one*
412 12:e0181437. DOI: 10.1371/journal.pone.0181437.

413 Cunha HFA, de Souza AF, Silva JMC. 2019. Public support for protected areas in new forest
414 frontiers in the Brazilian Amazon. *Environmental Conservation* 46:278–284. DOI:
415 10.1017/S0376892919000262.

416 Dalapicolla J, Abreu EF, do Prado JR, de Almeida Chiquito E, de Oliveira Roth PR, de Góes
417 Brennand PG, Pavan ACD, Pereira A, Mendes FR, del Valle Alvarez MR, Rios ÉO,
418 Cassano CR, Miretzki M, Vélez F, da Paixão Sevá A, Percequillo AR, Bovendorp RS.
419 2021. Areas of endemism of small mammals are underprotected in the Atlantic Forest.
420 *Journal of mammalogy* 102:1390–1404. DOI: 10.1093/jmammal/gyab073.

421 Daru BH, Farooq H, Antonelli A, Faurby S. 2020. Endemism patterns are scale dependent. *Nature*
422 *communications* 11:2115. DOI: 10.1038/s41467-020-15921-6.

423 DaSilva MB, Pinto-da-Rocha R, DeSouza AM. 2015. A protocol for the delimitation of areas of
424 endemism and the historical regionalization of the Brazilian Atlantic Rain Forest using
425 harvestmen distribution data. *Cladistics* 31:692–705. DOI: 10.1111/cla.12121.

426 Dinerstein E, Joshi AR, Vynne C, Lee ATL, Pharand-Deschênes F, França M, Fernando S, Birch
427 T, Burkart K, Asner GP, Olson D. 2020. A “Global Safety Net” to reverse biodiversity loss
428 and stabilize Earth’s climate. *Science Advances* 6:eabb2824. DOI:
429 10.1126/sciadv.abb2824.

430 Ferro I, Morrone JJ. 2014. Biogeographical transition zones: a search for conceptual synthesis.
431 *Biological journal of the Linnean Society. Linnean Society of London* 113:1–12. DOI:
432 10.1111/bij.12333.

433 Fick SE, Hijmans RJ. 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global
434 land areas. *International Journal of Climatology* 37:4302–4315. DOI: 10.1002/joc.5086.

435 Fjeldsø J, Lambin E, Mertens B. 1999. Correlation between Endemism and Local Ecoclimatic
436 Stability Documented by Comparing Andean Bird Distributions and Remotely Sensed
437 Land Surface Data. *Ecography* 22:63–78.

438 Freitas FLM, Englund O, Sparovek G, Berndes G, Guidotti V, Pinto LFG, Mörtberg U. 2018. Who
439 owns the Brazilian carbon? *Global change biology* 24:2129–2142. DOI:
440 10.1111/gcb.14011.

441 Galindo-Leal C, Camara IG (eds.). 2003. *The Atlantic Forest of South America: Biodiversity*
442 *Status, Threats, and Outlook*. Island Press.

443 Goerck JM. 1999. Distribution of birds along an elevational gradient in the Atlantic forest of
444 Brazil: implications for the conservation of endemic and endangered species. *Bird*
445 *conservation international* 9:235–253. DOI: 10.1017/S0959270900003439.

446 Green SJ, Brookson CB, Hardy NA, Crowder LB. 2022. Trait-based approaches to global change
447 ecology: moving from description to prediction. *Proceedings. Biological sciences / The*
448 *Royal Society* 289:20220071. DOI: 10.1098/rspb.2022.0071.

449 Haffer J. 1985. Avian Zoogeography of the Neotropical Lowlands. *Ornithological Monographs*
450 36:113–146.

451 Harrison S, Noss R. 2017. Endemism hotspots are linked to stable climatic refugia. *Annals of*
452 *botany* 119:207–214. DOI: 10.1093/aob/mcw248.

453 Herrando-Moraira S, Nualart N, Galbany-Casals M, Garcia-Jacas N, Ohashi H, Matsui T, Susanna
454 A, Tang CQ, López-Pujol J. 2022. Climate Stability Index maps, a global high resolution

455 cartography of climate stability from Pliocene to 2100. *Scientific data* 9:48. DOI:
 456 10.1038/s41597-022-01144-5.

457 Hobohm C. 2013. *Endemism in Vascular Plants*. Dordrecht: Springer Netherlands.

458 Instituto Brasileiro. de Geografia e Estatística. 2019. *Biomass e Sistema Costeiro-Marinho do*
 459 *Brasil: compatível com a escala 1:250 000*. Rio de Janeiro: Instituto Brasileiro de
 460 Geografia e Estatística, Coordenação de Recursos Naturais e Estudos Ambientais.

461 Jenkins CN, Pimm SL, Joppa LN. 2013. Global patterns of terrestrial vertebrate diversity and
 462 conservation. *Proceedings of the National Academy of Sciences of the United States of*
 463 *America* 110:E2602-10. DOI: 10.1073/pnas.1302251110.

464 Kier G, Kreft H, Lee TM, Jetz W, Ibisch PL, Nowicki C, Mutke J, Barthlott W. 2009. A global
 465 assessment of endemism and species richness across island and mainland regions.
 466 *Proceedings of the National Academy of Sciences of the United States of America*
 467 106:9322–9327. DOI: 10.1073/pnas.0810306106.

468 Körner C. 2007. The use of “altitude” in ecological research. *Trends in ecology & evolution*
 469 22:569–574. DOI: 10.1016/j.tree.2007.09.006.

470 Kruckeberg AR, Rabinowitz D. 1985. Biological Aspects of Endemism in Higher Plants. *Annual*
 471 *review of ecology and systematics* 16:447–479. DOI:
 472 10.1146/annurev.es.16.110185.002311.

473 Mittermeier RA, Robles Gil P, Hoffman M, Pilgrim J, Brooks T, Mittermeier C, Lamoreux J,
 474 Fonseca GAB. 2005. *Hotspots revisited*. Agrupacion Sierra Madre.

475 Morrone JJ. 2023. Why biogeographical transition zones matter. *Journal of biogeography*. DOI:
 476 10.1111/jbi.14632.

- Nattier R, Grandcolas P, Elias M, Desutter-Grandcolas L, Jourdan H, Couloux A, Robillard T. 2012. Secondary sympatry caused by range expansion informs on the dynamics of microendemism in a biodiversity hotspot. *PloS one* 7:e48047. DOI: 10.1371/journal.pone.0048047.
- Nogueira C, Buckup PA, Menezes NA, Oyakawa OT, Kasecker TP, Ramos Neto MB, da Silva JMC. 2010. Restricted-Range Fishes and the Conservation of Brazilian Freshwaters. *PloS one* 5:e11390. DOI: 10.1371/journal.pone.0011390.
- Pacifici M, Visconti P, Butchart SHM, Watson JEM, Cassola FM, Rondinini C. 2017. Species' traits influenced their response to recent climate change. *Nature climate change* 7:205–208. DOI: 10.1038/nclimate3223.
- Peres EA, Pinto-da-Rocha R, Lohmann LG, Michelangeli FA, Miyaki CY, Carnaval AC. 2020. Patterns of Species and Lineage Diversity in the Atlantic Rainforest of Brazil. In: Rull V, Carnaval AC eds. *Neotropical Diversification: Patterns and Processes*. Cham: Springer International Publishing, 415–447. DOI: 10.1007/978-3-030-31167-4_16.
- Pimm SL, Jenkins CN, Abell R, Brooks TM, Gittleman JL, Joppa LN, Raven PH, Roberts CM, Sexton JO. 2014. The biodiversity of species and their rates of extinction, distribution, and protection. *Science* 344:1246752. DOI: 10.1126/science.1246752.
- Pinto LP, Hirota MM. 2022. *30 anos de Conservação do Hotspot de Biodiversidade da Mata Atlântica: desafios, avanços e um olhar para o futuro*. São Paulo: Fundação SOS Mata Atlântica.
- Rahbek C, Borregaard MK, Antonelli A, Colwell RK, Holt BG, Nogues-Bravo D, Rasmussen CMØ, Richardson K, Rosing MT, Whittaker RJ, Fjeldså J. 2019. Building mountain

499 biodiversity: Geological and evolutionary processes. *Science* 365:1114–1119. DOI:
500 10.1126/science.aax0151.

501 Ravelo AC, Andreasen DH, Lyle M, Olivarez Lyle A, Wara MW. 2004. Regional climate shifts
502 caused by gradual global cooling in the Pliocene epoch. *Nature* 429:263–267. DOI:
503 10.1038/nature02567.

504 Saupe EE, Myers CE, Townsend Peterson A, Soberón J, Singarayer J, Valdes P, Qiao H. 2019.
505 Spatio-temporal climate change contributes to latitudinal diversity gradients. *Nature*
506 *ecology & evolution* 3:1419–1429. DOI: 10.1038/s41559-019-0962-7.

507 Scarano FR. 2014. *Mata Atlântica: Uma história do futuro*. Rio de Janeiro: Conservação
508 Internacional.

509 Shan G, Gerstenberger S. 2017. Fisher’s exact approach for post hoc analysis of a chi-squared test.
510 *PloS one* 12:e0188709. DOI: 10.1371/journal.pone.0188709.

511 Silva JMC. 1997. Endemic bird species and conservation in the Cerrado Region, South America.
512 *Biodiversity and conservation* 6:435–450. DOI: 10.1023/A:1018368809116.

513 Silva JMC, Casteleti CHM. 2003. Status of the biodiversity of the Atlantic Forest of Brazil. In:
514 Galindo-Leal C, Gusmão Câmara I eds. *The Atlantic Forest of South America*. Washington
515 D.C.: Island Press, 43–59.

516 da Silva ED, de A. Tozzi AMG, Meireles LD. 2015. Distribution of Leguminosae tree species in
517 different altitudinal levels along the Atlantic Rain Forest in the Brazilian coast. *Journal of*
518 *systematics and evolution* 53:266–279. DOI: 10.1111/jse.12140.

519 Silva JMC, Pinto LP, Hirota M, Bedê L, Tabarelli M. 2016. Conservação da Mata Atlântica - um
520 balanço dos últimos dez anos. In: Cabral DC, Bustamante AG eds. *Metamorfoses*

Florestais: Culturas, ecologias e as transformações históricas da Mata Atlântica. Curitiba: Editora Prismas, 413–433.

Silva JMC, Pinto LP, Scarano FR. 2021. Toward integrating private conservation lands into national protected area systems: Lessons from a megadiversity country. *Conservation science and practice* 3. DOI: 10.1111/csp2.433.

Silva JMC, Rapini A, Barbosa LCF, Torres RR. 2019. Extinction risk of narrowly distributed species of seed plants in Brazil due to habitat loss and climate change. *PeerJ* 7:e7333. DOI: 10.7717/peerj.7333.

Silva JMC, Rylands AB, Fonseca GAB. 2005. The fate of the Amazonian areas of endemism. *Conservation biology* 19:689–694. DOI: 10.1111/j.1523-1739.2005.00705.x.

Silva JMC, Sousa MC, Castelletti CHM. 2004. Areas of endemism for passerine birds in the Atlantic forest, South America. *Global Ecology and Biogeography* 13:85–92. DOI: <https://doi.org/10.1111/j.1466-882X.2004.00077.x>.

Spinelli D. 2022. Fitting spatial autoregressive logit and probit models using Stata: The spatbinary command. *The Stata journal* 22:293–318. DOI: 10.1177/1536867X221106373.

StataCorp. 2017. *Stata Statistical Software, Release 15*. College Station, TX: StataCorp LLC.

Tabarelli M, Pinto LP, Silva JMC, Hirota M, Bede L. 2005. Challenges and opportunities for Biodiversity conservation in the Brazilian Atlantic forest. *Conservation biology* 19:695–700. DOI: 10.1111/j.1523-1739.2005.00694.x.

Wamelink GW, Goedhart PW, Frissel J. 2014. Why some plant species are rare. *PloS one* 9:e102674. DOI: 10.1371/journal.pone.0102674.

542 Weeks BC, Claramunt S, Cracraft J. 2016. Integrating systematics and biogeography to
543 disentangle the roles of history and ecology in biotic assembly. *Journal of biogeography*
544 43:1546–1559. DOI: 10.1111/jbi.12747.

545 Wilmé L, Goodman SM, Ganzhorn JU. 2006. Biogeographic evolution of Madagascar's
546 microendemic biota. *Science* 312:1063–1065. DOI: 10.1126/science.1122806.

547 Wulff AS, Hollingsworth PM, Ahrends A, Jaffré T, Veillon J-M, L'Huillier L, Fogliani B. 2013.
548 Conservation priorities in a biodiversity hotspot: analysis of narrow endemic plant species
549 in New Caledonia. *PloS one* 8:e73371. DOI: 10.1371/journal.pone.0073371.

Table 1(on next page)

Comparison of the actual and expected number of areas with microendemics by sub-regions and taxonomic groups in the Brazilian Atlantic Forest using the Fisher exact method for a post hoc test after a Chi-square test.

Table 1. Comparison of the actual and expected number of areas with microendemics by sub-regions and taxonomic groups in the Brazilian Atlantic Forest using the Fisher exact approach for post hoc test after a Chi-square test.

	Observed	Expected	Fisher's Exact Test
Seed Plants			
Pernambuco	7	7	1.000
Coastal Bahia	37	13	0.000
Serra do Mar	91	45	0.000
Transition Region	126	195	0.000
Freshwater Fishes			
Pernambuco	2	6	0.174
Coastal Bahia	21	10	0.060
Serra do Mar	81	35	0.000
Transition Region	101	153	0.000
Terrestrial Vertebrates			
Pernambuco	15	3	0.005
Coastal Bahia	4	4	1.000
Serra do Mar	50	16	0.000
Transition Region	24	69	0.000
All groups			
Pernambuco	22	13	0.167
Coastal Bahia	51	23	0.000
Serra do Mar	169	81	0.000
Transition Region	226	350	0.000

Table 2 (on next page)

Spatial logistic regression describing the relationship between latitude, altitude, distance from the coastline, climate stability, and the probability of an area harboring at least one microendemic species in the Brazilian Atlantic Forest.

Table 2. Spatial logistic regression describing the relationship between latitude, altitude, distance from the coastline, and climate stability index and the probability of an area harboring at least one microendemic species in the Brazilian Atlantic Forest, across various taxonomic groups.

Groups/Predictors	Coefficient	SE	P
Seed Plants			
Latitude	0.275	0.020	0.168
Altitude	0.0003	0.0002	0.158
Distance from coastline	-0.007	0.0008	0.000
Climate stability index	6.371	2.169	0.003
Constant	-3.040	0.692	0.000
Rho	-0.116	0.094	0.218
Freshwater Fishes			
Latitude	0.126	0.021	0.000
Altitude	-0.0003	0.00003	0.222
Distance from coastline	-0.005	0.0008	0.000
Climate stability index	5.167	2.327	0.026
Constant	-4.527	0.809	0.000
Rho	0.174	0.096	0.070
Terrestrial Vertebrates			
Latitude	-0.052	0.023	0.027
Altitude	0.001	0.0005	0.010
Distance from coastline	-0.010	0.003	0.001
Climate stability index	-4.450	2.076	0.000
Constant	0.356	0.670	0.595
Rho	0.078	0.089	0.380

Figure 1

Distribution of the Atlantic Forest hotspot and its sub-regions. Areas outside the areas of endemism were classified as one large transition sub-region.

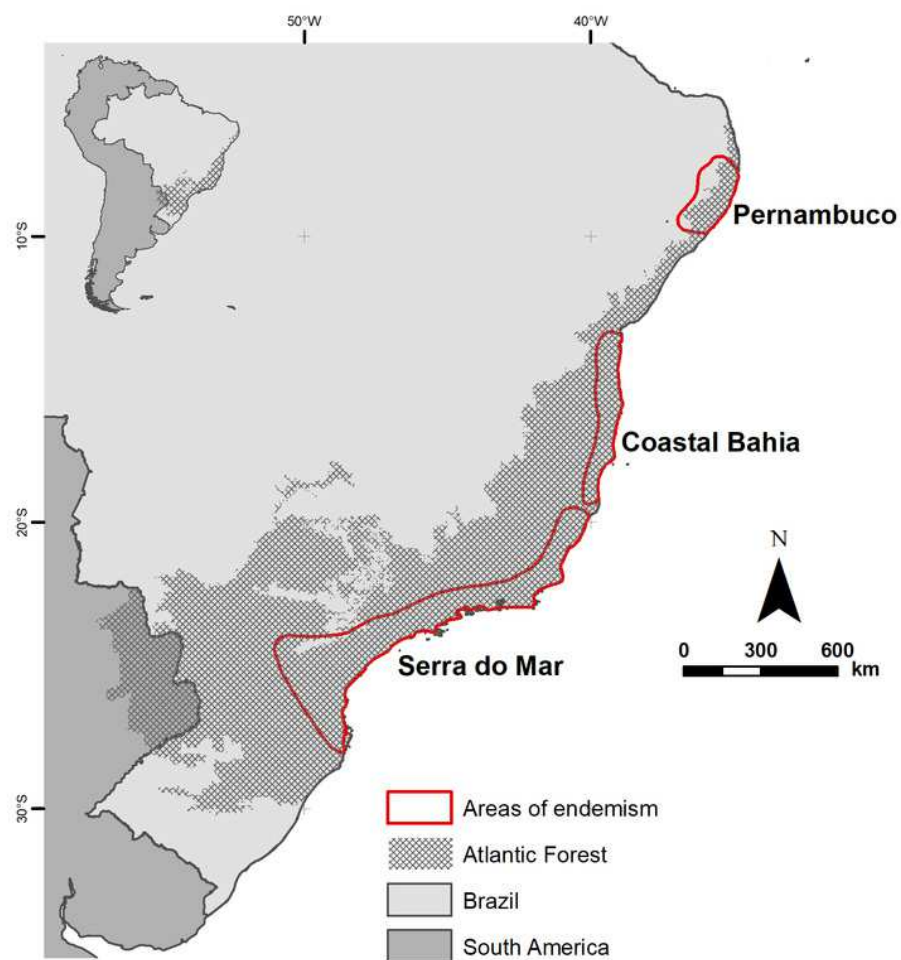


Figure 2

Distribution of the areas with microendemic species for seed plants, freshwater fishes, terrestrial vertebrates (snakes, birds, and small mammals) and all groups combined within the Brazilian Atlantic Forest.



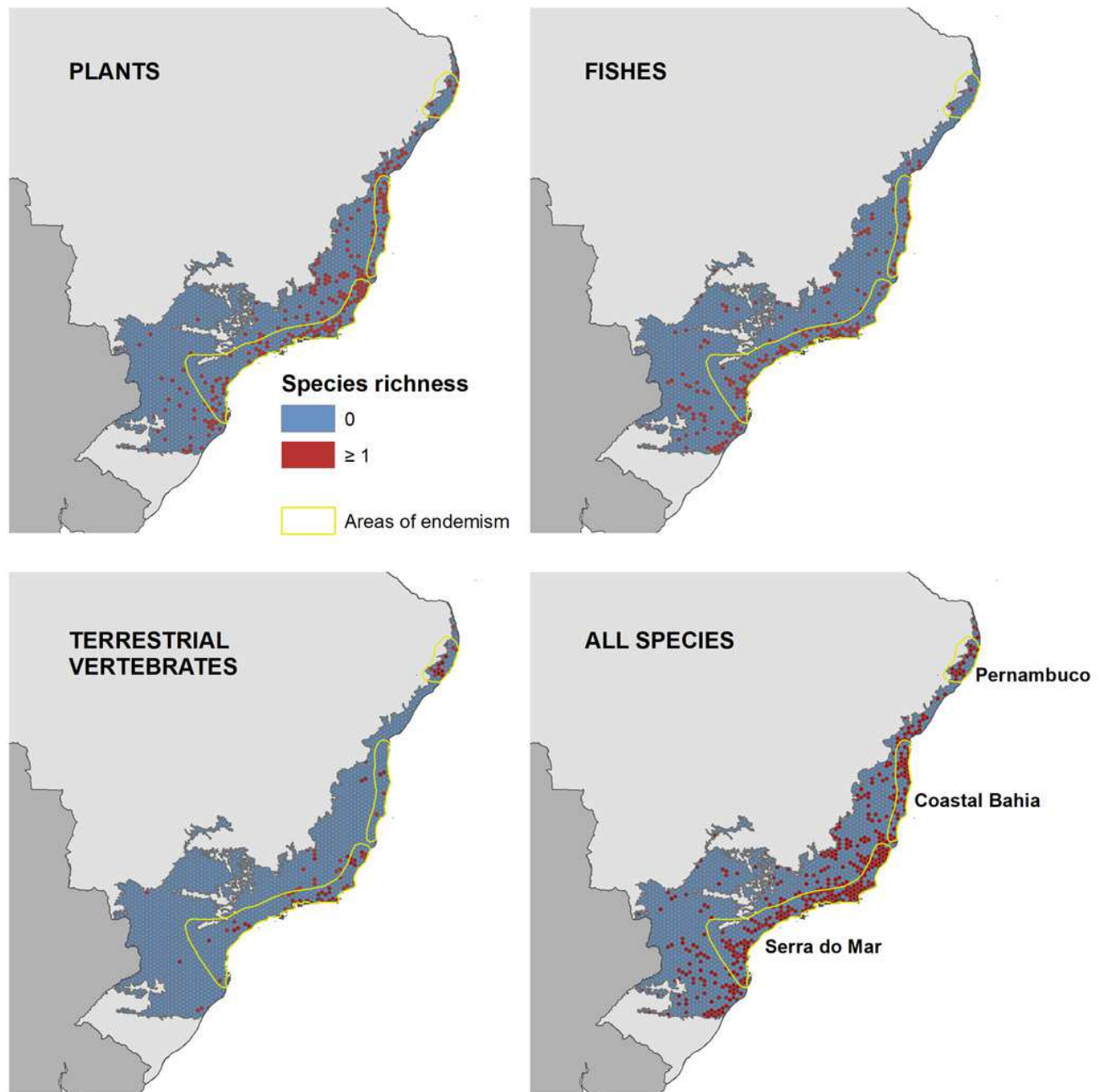


Figure 3

Comparison of two conservation indicators (% of native vegetation and % within protected areas) in areas with microendemic species (AMs) and those without (non-AMs) in the Brazilian Atlantic Forest.

