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Ant rarity and vulnerability in Brazilian Atlantic Forest fragments

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ABSTRACT

The rarity of organisms is related either to a natural origin or human-induced impacts, and rare species are more susceptible to extinction. The Atlantic Forest is an endangered biome with a diverse ant fauna. This study focuses on identifying forms of rarity in ant species recorded in the leaf litter in fragments of the Brazilian Atlantic Forest, as a more acute knowledge of rare species can support more appropriate conservation strategies. To do so, we applied the Rabinowitz method to leaf litter ants, considering data on geographical distribution, habitat specificity, and local occurrence to classify them into "forms of rarity". We then investigated the variation in the composition of forms between phytophysiognomies, and whether environmental variables predict the richness of rare species or not. We also analyzed the degree to which each species is endangered using lists of fauna threatened with extinction from two databases on ants in the Atlantic Forest. In total, we analyzed 242 ant species collected in the forest leaf litter, with 50.4 % classified as "Common", and the remaining 49.6 % presenting some "form of rarity". In general, phytophysiognomies have a similar composition of forms. Environmental predictors influence each form differently. Among all species analyzed (rare and common), seven presented some degree of threat (global, national and state lists). Therefore, conservation strategies must aim at the inclusion of rare ants to ensure their diversity.

1. Introduction

Rare species can be defined from a set of characteristics such as low local abundance, restricted distribution, narrow environmental tolerance (Brown, 1984), habitat specificity, low temporal persistence, a high degree of endemism, and low gene flow (Gaston, 1994, 1997). The causes of rarity may stem from natural factors, such as pathogens and exclusive mutualistic relationships, or from human interference (e.g., loss and/or degradation of habitat and introduction of exotic species) (Rabinowitz, 1981; Flather and Sieg, 2007), which make the phenomenon complex and difficult to quantify (Maciel and Martins, 2019). Rabinowitz (1981) proposed a method for classifying the rarity of organisms based on the combination of three parameters: geographic range, habitat specificity, and local population size. This approach enables the analysis of biological characteristics simultaneously (Borges, 2006) and has been consistently applied on data from diverse groups, including trees (Pitman et al., 1999; Caiafa and Martins, 2010), birds, mammals, amphibians (Yu and Dobson, 2000; Sykes et al., 2020), and bees (Harrison et al., 2017).

Knowledge about rare species is important (Myers et al., 2000; Marques et al., 2021), as these species play a fundamental role in maintaining habitat biodiversity (Flather and Sieg, 2007; Richardson et al., 2012), community dynamics and structure (Bracken and Low, 2012; Jain et al., 2014). For instance, sometimes rare species establish

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barriers to the entry of exotic species (Lyons and Schwartz, 2001) or play unique functional roles that cannot be performed by other species (Mouillot et al., 2013; Leitão et al., 2016; Violle et al., 2017), highlighting their fundamental role in directing conservation strategies (Flather and Sieg, 2007; Maciel and Martins, 2019). The analysis of the mechanisms that enable the combination of knowledge about rare and threatened species [e.g., Red List of the International Union for the Conservation of Nature - IUCN (Mehlman et al., 2004; Maciel and Eisenlohr, 2016)] is a necessary approach for biomes that harbor a high percentage of threatened species, such as the Atlantic Forest (ICMBio, 2018a; Myers et al., 2000; Marques et al., 2021). This is one of the most biodiverse forests in the world, featuring flora and fauna with comparatively high levels of endemism (Mittermeier et al., 2011; Figueiredo et al., 2021), and serving as a center of rarity (Kass et al., 2022).

In Atlantic Forest, ants have been the subject of extensive research (Divieso et al., 2020; Schmidt et al., 2022; Silva et al., 2022b), particularly with regard to the diversity of leaf litter communities (Delabie et al., 2007; Silva et al., 2022b), which harbor a high taxonomic, functional, and morphological diversity of ants (Silva and Brandão, 2010, 2014; Koch et al., 2019, 2021; Silva et al., 2022b). A recent study demonstrated that 1114 species and 2235 coded morphospecies have already been recorded in the biome (Silva et al., 2022b); with up to 30 species occurring in 1 m^2 of leaf litter (Silva and Brandão, 2010). Hypogeic and subterranean ants are generally considered rare because their habitat makes sampling operations and logistics challenging (Schmidt and Solar, 2010; Wong and Guénard, 2017; Delabie et al., 2021).

Although regional inventories may reveal a high richness of rare ants, rarity can be attributed to "undersampling" (e.g., low sampling due to the techniques used) or "locally rare", species considered common in other regions (Longino et al., 2002). Only a small percentage of ants are truly rare, characterized by low abundance and restricted geographical range (Longino et al., 2002; King and Porter, 2005). The imprecision in assessing rarity in ants is due to a lack of knowledge about their biology, the absence of data on distribution, and the difficulty and inadequacy of sampling techniques in some circumstances (Espadaler and López-Soria, 1991; Delabie and Reis, 2000; Brandão et al., 2008; Guénard et al., 2013; Delabie et al., 2021). These species are often classified as data deficient and are therefore underestimated in conservation strategies (Bland et al., 2015; Roberts et al., 2016). Rabinowitz's approach can help address this issue by providing a framework for assessing and prioritizing conservation efforts for these species (Toledo et al., 2014; Maciel and Martins, 2021).

The main objective of this study was to identify the forms of rarity in leaf litter ants in the Brazilian Atlantic Forest, using the Rabinowitz rarity classification method. In addition, we asked whether a set of environmental variables may influence the distribution of richness in rare species, and evaluated the threat category of ant species stated in the official lists of threatened fauna in Brazil at both the national and state levels. Considering the high level of endemism observed in the Atlantic Forest (Mittermeier et al., 2011; Marques and Grelle, 2021), as well as the asymmetric distribution of ants which may result in local rarity (Longino et al., 2002; Brandão et al., 2008; Dunn et al., 2009; Jenkins et al., 2011), we expected a high occurrence of rare species. Yet, we expected that all forms of rarity proposed by Rabinowitz would occur in the Atlantic Forest since the region is home to spatially restricted species (Campiolo et al., 2015), habitat specialists and locally scarce species in terms of occurrence and abundance (Suguituru et al., 2015).

Furthermore, recognizing that each phytophysiognomy has a unique set of characteristics, which can influence the diversity and distribution of ant species (Silva et al., 2011; Lasmar et al., 2020), such as differences in vegetation composition and abiotic factors (Veloso, 1992), we expect distinct composition of forms in each phytophysiognomy. It is well known that abiotic factors [e.g., habitat heterogeneity, precipitation, and temperature (Harrison et al., 2008, Liu et al., 2019)] explain the rarity of different taxa [e.g., bats (Churchill, 1991); herbaceous and woody plants (Harrison et al., 2008, Liu et al., 2019)]. In ants, the richness and distribution are influenced by environmental variables (Queiroz et al., 2013; Silva and Brandão, 2014), such as humidity [tending to have a positive relationship with increasing humidity (Levings, 1983; Kaspari, 1993; Kaspari and Weiser, 2000)], temperature [tending to have a positive relationship with increasing temperature, except for high temperatures (Brühl et al., 1999; Longino and Colwell, 2011)], and altitude [tending to increase richness with increasing altitude, showing a drop at high altitudes (Longino and Colwell, 2011; Silva and Brandão, 2014; Joseph et al., 2019)], we expect that these abiotic factors are also determinants for rare ants. Considering that rare and endangered species are of urgent interest for biodiversity conservation (Lambeck, 1997; Kricsfalusy and Trevisan, 2014; Maciel et al., 2016), rare ants as determined in our approach, would also be found in the official lists of threatened species in Brazil.

2. Materials and methods

2.1. Database

The data used to compose our database comes from (1) BIOTA-FAPESP, Virtual Institute of Biodiversity program (Silva and Brandão, 2014); (2) "DataAntTieteLeafLitter" database, associated with the ant sampling "Silvia Sayuri Suguituru", from the Myrmecology Laboratory of Alto Tietê (Souza-Campana et al., 2020), we only used information derived from publications (articles, undergraduate theses, dissertations, and theses), between 2011 and 2020 in our analyses. We selected publications that met the following criteria: (1) studies conducted in the Brazilian Atlantic Forest; (2) sampling from leaf litter and/or soil; and (3) with geographical coordinates. In cases where publications resulted from the same sampling (i.e., overlapped data), we only counted the species per sampling point once and considered only the maximum occurrence value. The resultant database comprised 242 ant species (exotic species ($n = 6$) and morphospecies ($n = 109$) were not included in the analysis), from 11 publications, totaling 3985 sampling points (Table A1), distributed across 77 locations and 9 states (Fig. 1; Table A2).

2.2. Forms of rarity

The forms of rarity were identified through Rabinowitz's classification (Rabinowitz, 1981), which consists of the combination of three dichotomous parameters: Geographic range (Wide or Restricted), Habitat specificity (Various or Single), and Local population size (Large or Small). The combination of these parameters results in eight forms, one being considered "Common" and the other seven rare to varying degrees (Form 1 to Form 7) (Fig. 2). In addition, this classification expresses a gradient of rarity, where Form 7 is classified as the "rarest", representing local endemism (Rabinowitz, 1981; Caiafa and Martins, 2010).

2.2.1. Geographic range

Given the wide geographic distribution of some ant species and the focus of this study on the Atlantic Forest, we assumed that species that occur exclusively in this biome are geographically restricted ("Restricted geographic range"), while those occurring also outside it were considered widely distributed ("Wide geographic range"). This definition was implemented to ensure that endemic species of the Atlantic Forest are accounted for in the classification of rarity (Fattorini, 2010).

To include information from other regions (Brazil and other countries) and to obtain a more comprehensive characterization of the geographic distribution of species (i.e., those whose distribution extends beyond the Atlantic Forest, avoiding bias in the rarity classification), we added the coordinates from the Global Biodiversity Information Facility (GBIF) (https://www.gbif.org/) and AntWeb (https://www.antweb.org/), both of which were accessed in March 2021. Based on the list

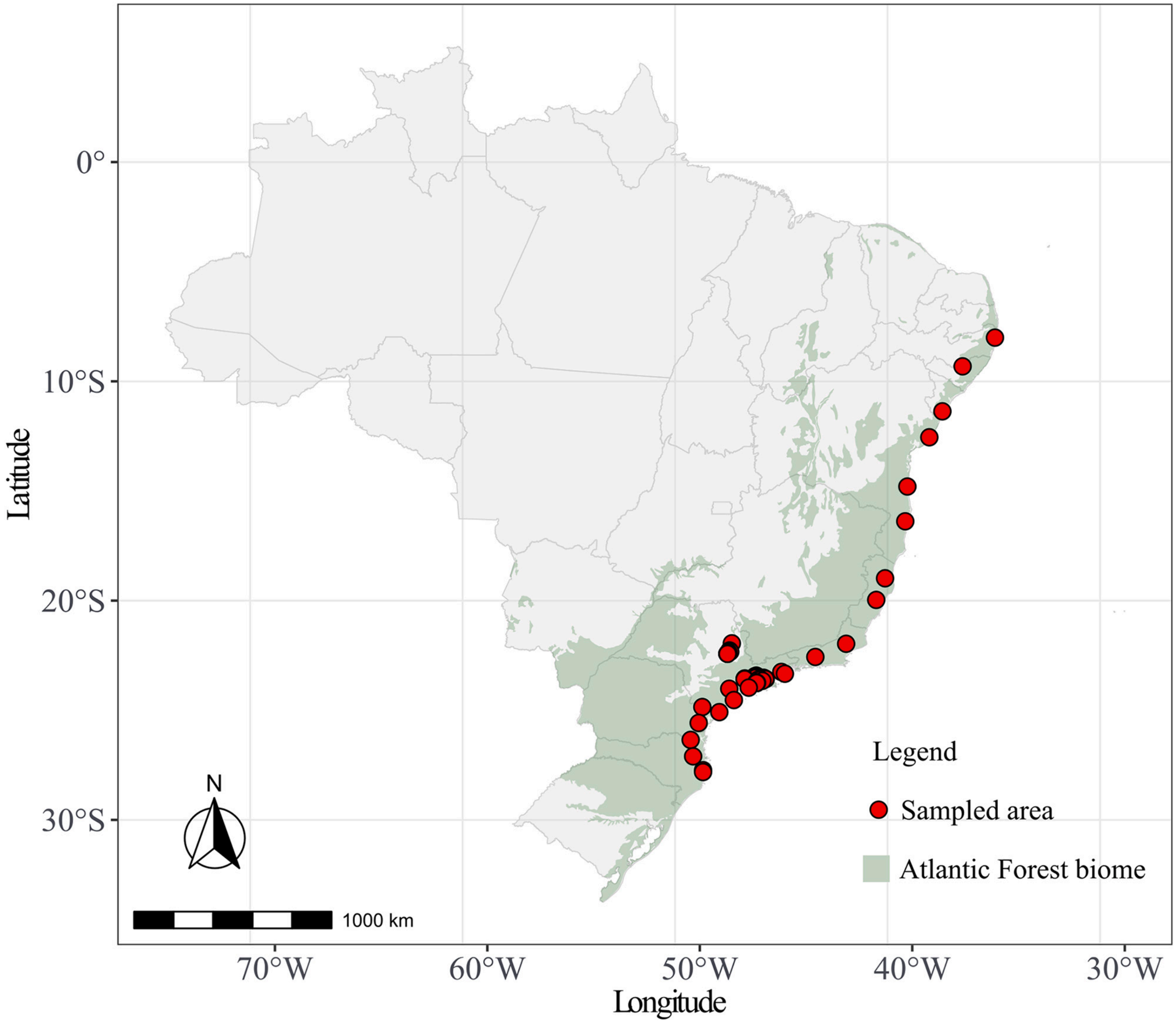

Fig. 1. Geographical distribution of sampling areas ($n = 77$ locations) of ant species collected in leaf litter in the Brazilian Atlantic Forest (in green; limits according to "Instituto Brasileiro de Geografia e Estatística" - IBGE). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

of species in our database (242 species), the following were considered in the searches: (1) the name of each species; (2) the existence of vouchers; and (3) geographic coordinates. The initial searches were performed on GBIF, which provided a downloadable Formicidae species list, followed by a programmatic selection of target data using a custom bash script (Script A1). For species not found on GBIF, additional searches were conducted on the AntWeb database, and each species was individually inspected following the three criteria mentioned above. The data obtained underwent manual validation, and occurrences in dubious locations (e.g., outside the known geographic distribution of the species) were removed.

After this procedure, data were organized into a matrix with the identification of the species and their respective coordinates (database of the present study, GBIF, and AntWeb). A vector data layer was created using ArcGIS (Esri, 2011), and the occurrence information for the respective geographic coordinates was extracted using a layer of the Atlantic Forest matrix data from Veloso et al. (1991) (Fig. 3A). It is important to note that the external coordinates (GBIF and AntWeb) were used solely to define the parameter "Geographic range".

2.2.2. *Habitat specificity*

The phytophysiognomies of sampled localities (Table A2) were considered in the habitat designation since the vegetation differs among them (Veloso, 1992) and influences the diversity and distribution of species (Silva et al., 2011; Lasmar et al., 2020). Thus, "Single" defined species occurring in only one phytophysionomy and "Various" those recorded in two or more phytophysiognomies (Fig. 3B).

The classification of phytophysionomy and their respective forest formations, which are determined by altitude and latitude, follows the definitions of the "Instituto Brasileiro de Geografia e Estatística - IBGE" (Veloso et al., 1991; IBGE, 2012). Thus, we used the latitudes reported in the studies and their respective altitude was obtained through the "rgbif" package (Chamberlain et al., 2021) on the R environment (RStudio, version 4.0.3; R Core Team, 2022). According to the classification, ants were recorded in six phytophysiognomies: Pioneer Formations; Lowlands Rainforest; Submontane Rainforest; Montane Rainforest; Submontane Semideciduous Forest; Montane Semideciduous Forest (Table A2).

2.2.3. *Local population size*

Ants are highly abundant insects (Majer, 1983) and the colonies of

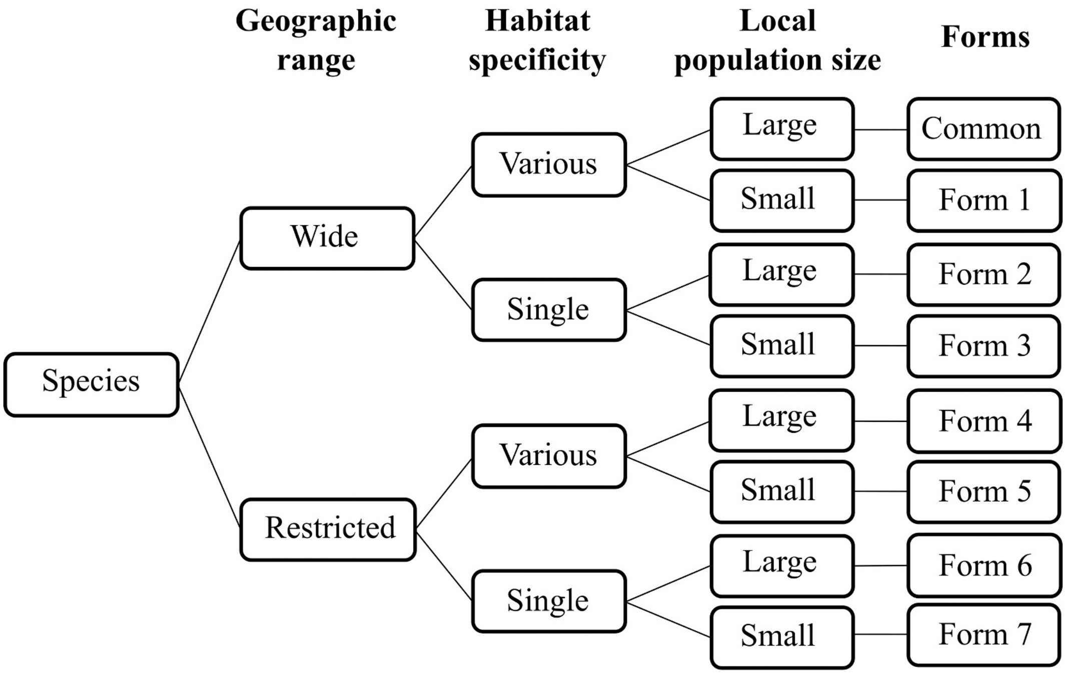

Fig. 2. Scheme of parameters (Geographic range, Habitat specificity and Local population size) and forms of Rabinowitz's classification (Rabinowitz, 1981). According to the combination of the three dichotomous parameters, eight forms are determined, one common and seven rare.

some genera (e.g., *Atta* Fabricius, 1804, *Azteca* Forel, 1878, *Eciton* Latreille, 1804 and *Solenopsis* Westwood, 1840) can reach thousands of individuals in number (Beckers et al., 1989). Therefore, using abundance (number of specimens) as a parameter in the classification of rarity of ants could cause biases; so, we chose to replace abundance by occurrence (Romero and Jaffe, 1989; Longino, 2000; Delabie et al., 2021). We considered 'occurrence' as the presence of given species at a sampling point. Given that the number of unique/duplicate and singleton/doubleton are high in arthropods surveys (Coddington et al., 2009; Reyes- González et al., 2022), we considered the maximum occurrence of the species at the sampling point per collection. To include the concept of rarity based on "unique" (species collected in only one sample) and "duplicate" (species collected in two samples) (Reyes-González et al., 2022), we considered uniques and duplicates per locality as "Small occurrence"; those with greater than or equal to three occurrences as "Large occurrence" (Fig. 3C) (modified from Caiafa and Martins, 2010).

2.3. Data analysis

2.3.1. Beta diversity

Beta diversity (βsor) and its components [turnover (βsim) and nestedness (βsne)], were calculated for phytophysiognomies using rarity forms, as a substitute of species. Considering that each rarity form groups together species with common characteristics (such as geographic distribution, habitat specificity and occurrence), we used form richness by phytophysiognomies. The analysis was carried out on two levels: (1) "All forms" – considering common and rare forms; (2) "Rare forms" - only the seven rarity forms. We used the "betapart" package (Baselga et al., 2023) based on Sorensen dissimilarity in beta diversity analyses (Vilela, 2021). The sum of the turnover and nestedness components results in beta diversity, with values varying between 0 and 1 (Silva et al., 2022a).

2.3.2. Effect of the environmental prediction on species richness

We defined as response variables the number of rare species per sampled area ($n = 77$ locations). For predictors, we selected five environmental variables that influence ant diversity: altitude (Longino and Colwell, 2011; Joseph et al., 2019), average annual rainfall (Sanders et al., 2003), annual potential evapotranspiration (proxy for productivity; Silva and Brandão, 2014), annual mean temperature (Sanders et al., 2007; Jenkins et al., 2011), and annual thermal amplitude (Dunn et al., 2009). All variables (but altitude, see "Section 2.2.2 Habitat specificity") were obtained from WorldClim (climate data for 1970–2000) at a resolution of 30 arc-seconds (Hijmans et al., 2005).

We first evaluated multicollinearity among variables, using the Variance Inflation Factor (VIF), where "annual potential evapotranspiration" was removed from further analyses due to high correlation (VIF > 5). VIF values were calculated using the "car" R package (Fox and Weisberg, 2019). Then, we explored graphically the relationships between rarity and our four remaining predictors. Finally, given nonlinear trends in these relationships, we used Generalized Additive Models (GAM) with different error families (Zuur et al., 2014; Hayden et al., 2019; Pedersen et al., 2019). In GAM models we fitted all four explanatory variables using the non-parametric smoother. Additionally, considering the high frequency of zero, we explored Zero-Inflated Poisson and Hurdle models (zero-truncated negative binomial model; Zuur et al., 2014). We kept the model simple and only used an intercept in the logistic link function in zero-inflated and zero-altered models. We further used a negative binomial model for model comparisons (as the best candidate among GLM distributions).

We applied a binomial GLM to two forms of rarity (Form 5 and Form 6) characterized uniquely by 0 or 1 values (i.e., presence or absence) and applied a forward selection procedure using the R *step* function. We ran a model with only an intercept and on the other hand, we used a model which contained all covariates and selected 2-way interactions (between precipitation vs. other predictors).

The best model was determined by the lowest AIC criterion among the different models tested. We checked for overdispersion or underdispersion in the models. Model validation verified for normality, homogeneity, and influential observations by extracting the residuals of the model and plotting these against fitted values, against each covariate in the model and covariate not in the model (Zuur et al., 2014). Statistical models were done at two composition levels of rarity: (1) "All rare" - all seven rare forms combined (Form 1 to Form 7); (2) "Forms" - each rarity form analyzed individually (Script A2). Plots were created using

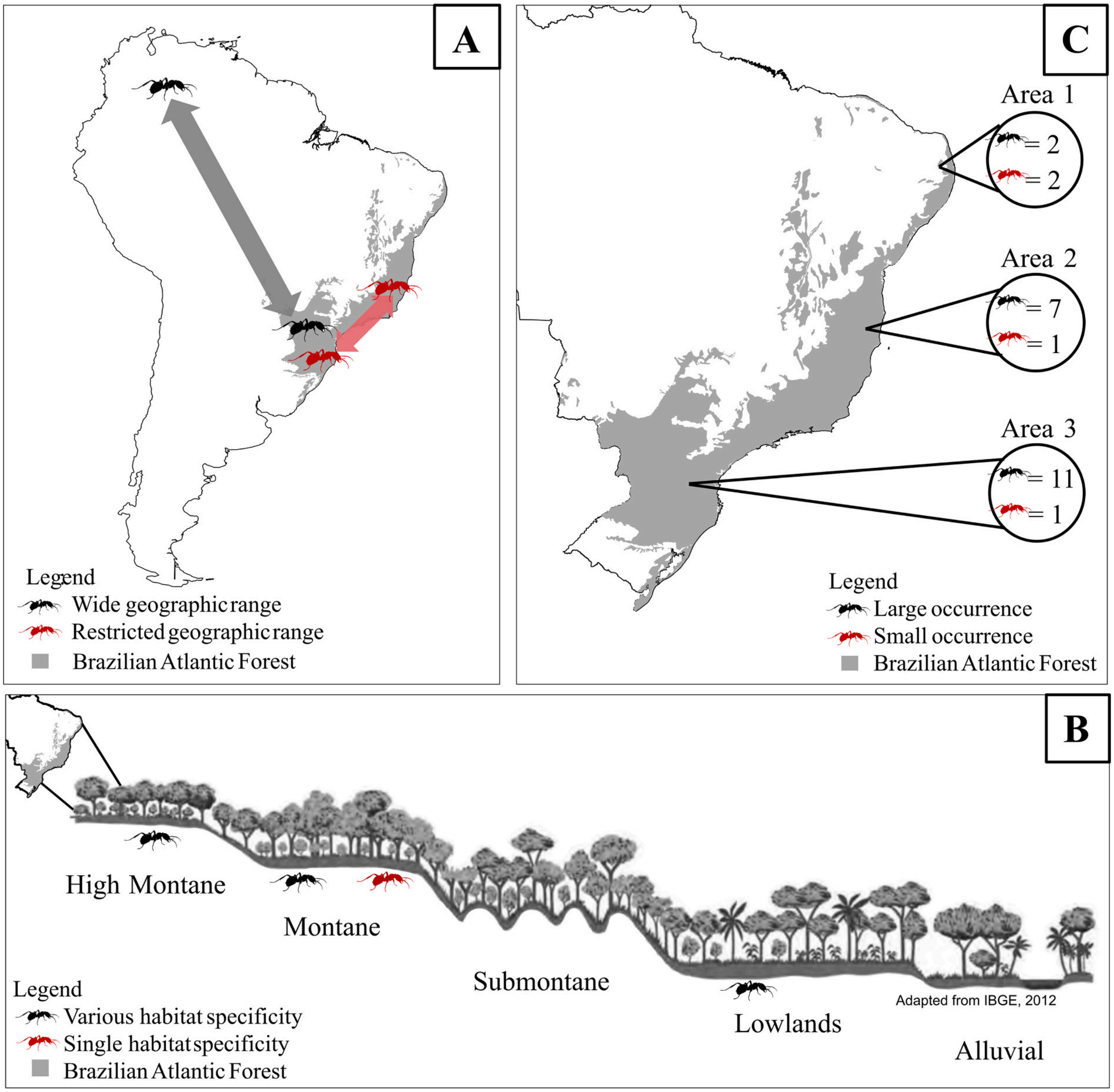

Fig. 3. Criteria selected in the definition of the parameters used for the classification of rarity in ant species collected in the leaf litter of the Brazilian Atlantic Forest, based on Rabinowitz (1981). A) Geographic range: Wide, species that occur inside and outside the Atlantic Forest; Restricted, those that occur exclusively within the Atlantic Forest. B) Habitat specificity: Various, species that occur in different phytophysiognomies; Single, those that occur in a single phytophysiognomy. C) Occurrence: Large, species with local occurrence greater than or equal to three; Small, those with local occurrence less than or equal to two.

the “ggplot2” package (Wickham, 2016). All analyses were performed on the R environment (RStudio, version 4.0.3; R Core Team, 2022). We used the R packages “mgcv” (Wood, 2017) for GAM models, “pscl” (Jackman, 2020) for zero-inflated models, and “MASS” (Venables and Ripley, 2002) for GLM with a negative binomial structure.

2.4. The endangered category

The endangered category of rare and common species was verified from the consultation of taxa in publications at the global, national and state scope (Toledo et al., 2014), using a previous survey. Global data was obtained from the Red List of Threatened Species of IUCN, in Social Insects Specialist Group (IUCN, 1996), available on its official website. The national list was obtained from the publication “List of Brazilian Fauna Threatened with Extinction”, available on the official website of the Chico Mendes Institute for Biodiversity Conservation (ICMBio) (Table A3). At the Brazilian state level, the search was carried out on the official websites of each state government, using the words: “Red List”, “endangered fauna”, “extinction”, and “endangered species” as a query in the site’s search fields. For the states that did not present lists, the same survey was carried out on the website of the state environment office or the official body responsible for this topic (Table A3). To complement the survey, we used the state lists mentioned in Silva (2018). We considered the most updated list data for each Brazilian state.

The selected lists follow the criteria defined by the IUCN, which establishes nine categories: “Extinct”, “Extinct in the Wild”, “Critically Endangered”, “Endangered”, “Vulnerable”, “Near Threatened”, “Least Concern”, “Data Deficient” and “Not Evaluated”; which are defined through five criteria: A. Population size reduction; B. Geographic range; C. Small population size and decline; D. Very small or restricted population; and E. Quantitative Analysis (IUCN, 2012).

3. Results

3.1. Forms of rarity

We identified the eight forms defined by Rabinowitz, classifying 122 ant species (50.41 %) as Common (Table 1). Moreover, 120 species (49.59 %) were classified into rarity categories in the following proportions: Form 1, with 10 % of the species, Form 2 with 14 %, Form 3 with 14 %, Form 4 with 4 %, Form 5 with 2 %, Form 6 with 2 % and Form 7 with 4 % (Table 2; Fig. A1).

Species with "Distribution geographic wide", that is, that also occurred outside the Atlantic Forest, represent 214 species (88.43 %), while those with "Distribution geographic restricted", occurring only in the Atlantic Forest, add up to 28 species (11.57 %). In "habitat specificity", 159 species (65.70 %) had no specificity ("Various") and 83 (34.30 %) had specificity ("Single"). As for occurrence, ants with "Large occurrence" correspond to 170 species (70.25 %) and those with "Small occurrence" represent 72 species (29.75 %) (Fig. 4).

Regarding phytophysiognomies, Form 1 and Common are present in all of them. Form 3, species with habitat specificity, presented species that are exclusive to each phytophysionomy, so this form occurred in all analyzed habitats. Meanwhile, Form 5 and Form 7 appear only in the phytophysiognomies Submontane and Montane Rainforest (Fig. 5). Among the rare ants (120 species), 3 of the species (2.50 %) occurred in up to three phytophysiognomies, 34 (28.33 %) in two phytophysiognomies, and 83 (69.17 %) only in one phytophysiognomy (Table A4). Among the ants that occur only in one phytophysiognomy, most of them were in the Montane Rainforest (55 species; 66.27 %), while Lowland Rainforest had the lowest group of unique species (two species; 2.41 %) (Table A4).

3.2. Beta diversity

We observed, for the "All forms" (common and rare) and "Rare forms" (without common forms) levels, that there is a similar pattern of beta diversity, nestedness, and turnover (Fig. A2). The beta diversity index shows that both analyzed levels have a similar composition of rarity forms ($\beta\text{sor} = 0.33$). Although the values of nestedness and turnover are relatively low, nestedness explains most of the diversity of forms found among the physiognomies ($\beta\text{sne} = 0.33$). This indicates that rarity forms represent subsets among the physiognomies. However, "Pioneer Formations" had a higher turnover component ($\beta\text{sim} = 0.25$), indicating that in this habitat, the composition of forms is related to the replacement of forms in the community, rather than being a subset among other physiognomies (Fig. A2).

3.3. Effect of the environmental prediction on species richness

Altitude, average annual rainfall, annual mean temperature or annual thermal amplitude had no effect on total richness of all combined forms of rarity. However, when analyzed individually, we detected significant relationships between environment and rarity. For example, Form 1 had significant smoothers of altitude ($F = 4.56$, $p < 0.01$) and average temperature ($F = 6.46$, $p = 0.01$). Predicted richness of Form 1 was highly variable along the altitude gradient (suggests a non-linear pattern) but showed a gradual increase along the gradient of average temperature (Deviance explained = 74 %). We did not find a relationship between Form 2 of rarity and environmental predictors. Form 3 had a significant smoother of altitude ($F = 4.22$, $p < 0.01$), accumulating higher predicted richness of Form 3 at ½ of the gradient. Form 4 had a significant smoother of altitude ($F = 3.62$, $p < 0.01$) and precipitation ($F = 4.26$, $p < 0.01$), and temperature range ($F = 12.99$, $p < 0.01$). Predicted richness of Form 4 increased at higher altitudes (> 800 m) or higher values of temperature range, but showed strong variation along gradient of precipitation (suggesting a non-linear pattern). The binomial GLM model for Form 5 had increased probability of presence with

Table 1
Rarity forms and subfamilies of ant species collected in leaf litter from the Brazilian Atlantic Forest.

Forms	Subfamily	Species
Common	Amblyoponinae	*Fulakora armigera* (Mayr, 1887)
		Fulakora elongata (Santschi, 1912)
		Prionopelta antillana Forel, 1909
		Prionopelta punctulata Mayr, 1866
	Dolichoderinae	*Dolichoderus imitator* Emery, 1894
		Linepithema iniquum (Mayr, 1870)
		Linepithema neotropicum Wild, 2007
	Dorylinae	*Eciton burchellii* (Westwood, 1842)
		Labidus coecus (Latreille, 1802)
		Labidus praedator (Smith, 1858)
		Neocerapachys splendens (Borgmeier, 1957)
	Ectatomminae	*Ectatomma edentatum* Roger, 1863
		Ectatomma opaciventre (Roger, 1861)
		Gnamptogenys acuminata (Emery, 1896)
		Gnamptogenys continua (Mayr, 1887)
		Gnamptogenys horni (Santschi, 1929)
		Heteroponera dentinodis (Mayr, 1887)
		Heteroponera dolo (Roger, 1860)
		Heteroponera mayri Kempf, 1962
		Bazboltonia microps (Borgmeier, 1957)
		Holcoponera striatula (Mayr, 1884)
		Poneracantha mediatrix (Brown, 1958)
		Poneracantha rastrata (Mayr, 1866)
		Typhlomyrmex major Santschi, 1923
		Typhlomyrmex pusillus Emery, 1894
	Formicinae	*Acropyga decedens* (Mayr, 1887)
		Acropyga fuhrmanni (Forel, 1914)
		Acropyga goeldii Forel, 1893
		Acropyga smithii Forel, 1893
		Brachymyrmex admotus Mayr, 1887
		Brachymyrmex cordemoyi Forel, 1895
		Brachymyrmex heeri Forel, 1874
		Camponotus alboannulatus Mayr, 1887
		Camponotus balzani Emery, 1894
		Camponotus novogranadensis Mayr, 1870
		Camponotus rufipes (Fabricius, 1775)
		Camponotus sericeiventris (Guérin-Méneville, 1838)
	Myrmicinae	*Acanthognathus brevicornis* Smith, 1944
		Acanthognathus lentus Mann, 1922
		Acanthognathus ocellatus Mayr, 1887
		Acanthognathus rudis Brown & Kempf, 1969
		Acromyrmex aspersus (Smith, 1858)
		Acromyrmex crassispinus (Forel, 1909)
		Acromyrmex disciger (Mayr, 1887)
		Acromyrmex niger (Smith, 1858)
		Atta sexdens (Linnaeus, 1758)
		Basiceros disciger (Mayr, 1887)
		Carebara brevipilosa Fernández, 2004
		Carebara urichi (Wheeler, 1922)
		Cephalotes pusillus (Klug, 1824)
		Crematogaster chodati Forel, 1921
		Cryptomyrmex boltoni (Fernández, 2003)
		Cyphomyrmex rimosus (Spinola, 1851)
		Eurhopalothrix spectabilis Kempf, 1962
		Hylomyrma balzani (Emery, 1894)
		Hylomyrma immanis Kempf, 1973
		Hylomyrma reitteri (Mayr, 1887)
		Lachnomyrmex plaumanni Borgmeier, 1957
		Megalomyrmex drifti Kempf, 1961
		Megalomyrmex goeldii Forel, 1912
		Megalomyrmex silvestrii Wheeler, 1909
		Mycetophylax strigatus (Mayr, 1887)
		Octostruma iheringi (Emery, 1888)
		Octostruma petiolata (Mayr, 1887)
		Octostruma rugifera (Mayr, 1887)
		Octostruma stenognatha Brown & Kempf, 1960
		Oxyepoecus myops Albuquerque & Brandão, 2009
		Oxyepoecus punctifrons (Borgmeier, 1927)
		Oxyepoecus rastratus (Mayr, 1887)
		Oxyepoecus rosai Albuquerque & Brandão, 2009
		Pheidole alpinensis Forel, 1912
		Pheidole flavens Roger, 1863

(continued on next page)

Table 1 (*continued*)

Forms	Subfamily	Species
		Pheidole gertrudae Forel, 1886
		Pheidole oxyops Forel, 1908
		Pheidole radoszkowskii Mayr, 1884
		Pheidole sarcina Forel, 1912
		Pheidole sigillata Wilson, 2003
		Pheidole sospes Forel, 1908
		Pheidole triconstricta Forel, 1886
		Sericomyrmex parvulus Forel, 1912
		Solenopsis saevissima (Smith, 1855)
		Solenopsis subterranea MacKay & Vinson, 1989
		Stegomyrmex vizottoi Diniz, 1990
		Strumigenys appretiata (Borgmeier, 1954)
		Strumigenys cosmostela Kempf, 1975
		Strumigenys crassicornis Mayr, 1887
		Strumigenys denticulata Mayr, 1887
		Strumigenys eggersi Emery, 1890
		Strumigenys elongata Roger, 1863
		Strumigenys louisianae Roger, 1863
		Strumigenys rugithorax (Kempf, 1959)
		Strumigenys saliens Mayr, 1887
		Strumigenys schmalzi Emery, 1906
		Strumigenys subedentata Mayr, 1887
		Strumigenys tanymastax (Brown, 1964)
		Strumigenys trinidadensis Wheeler, 1922
		Strumigenys urrhobia (Bolton, 2000)
		Strumigenys villiersi (Perrault, 1986)
		Wasmannia affinis Santschi, 1929
		Wasmannia auropunctata (Roger, 1863)
		Wasmannia lutzi Forel, 1908
	Ponerinae	*Anochetus altisquamis* Mayr, 1887
		Anochetus mayri Emery, 1884
		Anochetus neglectus Emery, 1894
		Anochetus simoni Emery, 1890
		Hypoponera foreli (Mayr, 1887)
		Leptogenys crudelis (Smith, 1858)
		Mayaponera constricta (Mayr, 1884)
		Neoponera bucki (Borgmeier, 1927)
		Neoponera crenata (Roger, 1861)
		Neoponera venusta Forel, 1912
		Odontomachus affinis Guérin-Méneville, 1844
		Odontomachus brunneus (Patton, 1894)
		Odontomachus chelifer (Latreille, 1802)
		Odontomachus meinerti Forel, 1905
		Pachycondyla harpax (Fabricius, 1804)
		Pachycondyla lenis Kempf, 1961
		Pachycondyla striata Smith, 1858
		Rasopone ferruginea (Smith, 1858)
	Proceratiinae	*Discothyrea neotropica* Bruch, 1919
		Discothyrea sexarticulata Borgmeier, 1954
		Proceratium brasiliense Borgmeier, 1959
Form 1	Dorylinae	*Neivamyrmex punctaticeps* (Emery, 1894)
	Ectatomminae	*Acanthoponera mucronata* (Roger, 1860)
		Alfaria minuta Emery, 1896
		Ectatomma tuberculatum (Olivier, 1792)
	Formicinae	*Acropyga guianensis* Weber, 1944
		Brachymyrmex coactus Mayr, 1887
		Camponotus trapezoideus Mayr, 1870
	Myrmicinae	*Eurhopalothrix bruchi* (Santschi, 1922)
		Megalomyrmex incisus Smith, 1947
		Oxyepoecus longicephalus Albuquerque & Brandão, 2004
		Oxyepoecus reticulatus Kempf, 1974
		Procryptocerus convergens (Mayr, 1887)
		Strumigenys cultrigera Mayr, 1887
		Strumigenys gytha Bolton, 2000
		Strumigenys precava Brown, 1954
		Strumigenys schulzi Emery, 1894
		Strumigenys smithii Forel, 1886
		Wasmannia scrobifera Kempf, 1961
	Ponerinae	*Leptogenys unistimulosa* Roger, 1863
		Mayaponera arhuaca (Forel, 1901)
		Pseudoponera gilberti (Kempf, 1960)
		Pseudoponera stigma (Fabricius, 1804)
		Thaumatomyrmex atrox Weber, 1939
	Pseudomyrmecinae	*Pseudomyrmex tenuis* (Fabricius, 1804)
Form 2	Dolichoderinae	*Dorymyrmex brunneus* Forel, 1908
		Linepithema leucomelas (Emery, 1894)
		Linepithema micans (Forel, 1908)
	Dorylinae	*Neivamyrmex pseudops* (Forel, 1909)
	Ectatomminae	*Typhlomyrmex rogenhoferi* Mayr, 1862
	Formicinae	*Camponotus atriceps* (Smith, 1858)
		Camponotus blandus (Smith, 1858)
		Camponotus crassus Mayr, 1862
		Camponotus lespesii Forel, 1886
		Camponotus senex (Smith, 1858)
		Myrmelachista arthuri Forel, 1903
		Myrmelachista catharinae Mayr, 1887
		Myrmelachista ruzskyi Forel, 1903
	Myrmicinae	*Apterostigma acre* Lattke, 1997
		Crematogaster arata Emery, 1906
		Crematogaster rochai Forel, 1903
		Cyphomyrmex major Forel, 1901
		Mycocepurus goeldii (Forel, 1893)
		Mycocepurus smithii (Forel, 1893)
		Ochetomyrmex semipolitus Mayr, 1878
		Octostruma balzani (Emery, 1894)
		Oxyepoecus plaumanni Kempf, 1974
		Pheidole aberrans Mayr, 1868
		Pheidole fimbriata Roger, 1863
		Pheidole obscurithorax Naves, 1985
		Pheidole subarmata Mayr, 1884
		Pogonomyrmex naegelii Emery, 1878
		Solenopsis geminata (Fabricius, 1804)
		Wasmannia rochai Forel, 1912
	Ponerinae	*Hypoponera distinguenda* (Emery, 1890)
		Thaumatomyrmex mutilatus Mayr, 1887
	Pseudomyrmecinae	*Pseudomyrmex gracilis* (Fabricius, 1804)
		Pseudomyrmex phyllophilus (Smith, 1858)
		Pseudomyrmex schuppi (Forel, 1901)
Form 3	Dolichoderinae	*Linepithema pulex* Wild, 2007
	Dorylinae	*Cylindromyrmex brasiliensis* Emery, 1901
		Eciton quadriglume (Haliday, 1836)
		Labidus mars (Forel, 1912)
	Ectatomminae	*Ectatomma brunneum* Smith, 1858
		Ectatomma permagnum Forel, 1908
		Gnamptogenys haenschi (Emery, 1902)
		Gnamptogenys interrupta (Mayr, 1887)
		Gnamptogenys sulcata (Smith, 1858)
		Holcoponera pleurodon (Emery, 1896)
	Formicinae	*Acropyga exsanguis* (Wheeler, 1909)
		Acropyga panamensis Weber, 1944
		Brachymyrmex patagonicus Mayr, 1868
		Camponotus canescens Mayr, 1870
	Myrmicinae	*Basiceros convexiceps* (Mayr, 1887)
		Cephalotes angustus (Mayr, 1862)
		Crematogaster corticicola Mayr, 1887
		Cyphomyrmex transversus Emery, 1894
		Eurhopalothrix gravis (Mann, 1922)
		Mycetarotes carinatus Mayhé-Nunes, 1995
		Mycetarotes parallelus (Emery, 1906)
		Mycetomoellerius urichii (Forel, 1893)
		Mycetophylax olitor (Forel, 1893)
		Nesomyrmex echinatinodis (Forel, 1886)
		Oxyepoecus bruchi Santschi, 1926
		Oxyepoecus vezenyii (Forel, 1907)
		Procryptocerus regularis Emery, 1888
		Rogeria subarmata (Kempf, 1961)
		Strumigenys carinithorax Borgmeier, 1934
		Strumigenys epelys Bolton, 2000
		Strumigenys fridericimuelleri Forel, 1886
	Ponerinae	*Neoponera unidentata* (Mayr, 1862)
		Rasopone lunaris (Emery, 1896)
	Pseudomyrmecinae	*Pseudomyrmex oculatus* (Smith, 1855)
Form 4	Ectatomminae	*Heteroponera inermis* (Emery, 1894)
		Typhlomyrmex reichenspergeri (Santschi, 1929)
	Formicinae	*Brachymyrmex feitosai* Ortiz & Fernández, 2014
	Myrmicinae	*Lachnomyrmex victori* Feitosa & Brandão, 2008
		Megalomyrmex iheringi Forel, 1911
		Megalomyrmex myops Santschi, 1925
		Mycetophylax plaumanni (Kempf, 1962)
		Oxyepoecus crassinodus Kempf, 1974
		Strumigenys splendens (Borgmeier, 1954)

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Table 1 (*continued*)

Forms	Subfamily	Species
Form 5	Ectatomminae	*Poneracantha lucaris* (Kempf, 1968)
	Myrmicinae	*Phalacromyrmex fugax* Kempf, 1960
		Strumigenys dapsilis (Bolton, 2000)
		Strumigenys reticeps (Kempf, 1969)
Form 6	Dorylinae	*Sphinctomyrmex stali* Mayr, 1866
	Myrmicinae	*Lachnomyrmex nordestinus* Feitosa & Brandão, 2008
		Megalomyrmex pusillus Forel, 1912
		Oxyepoecus browni Albuquerque & Brandão, 2004
		Strumigenys sanctipauli Kempf, 1958
Form 7	Formicinae	*Brachymyrmex micromegas* Santschi, 1923
		Camponotus tripartitus Mayr, 1887
	Ectatomminae	*Heteroponera robusta* Kempf, 1962
	Myrmicinae	*Diaphoromyrma sofiae* Fernández et al., 2009
		Eurhopalothrix speciosa Brown & Kempf, 1960
		Mycetarotes senticosus Kempf, 1960
		Mycetophylax auritus (Mayr, 1887)
		Strumigenys dentinasis (Kempf, 1960)
		Strumigenys substricta (Kempf, 1964)
	Ponerinae	*Neoponera metanotalis* (Luederwaldt, 1918)

Table 2
Richness of ant species, collected in the leaf litter of the Brazilian Atlantic Forest, for each Rabinowitz's (1981) form of rarity.

	Geographic range	Wide		Restricted	
	Habitat specificity	Various	Single	Various	Single
Occurrence	Large	122 Common	34 Form 2	09 Form 4	05 Form 6
	Small	24 Form 1	34 Form 3	04 Form 5	10 Form 7

increasing temperature range, although the best model explained only 10 % of that probability (Table A5). We did not find any relationships between environment and Form 6 of rarity (binomial GLM). Form 7 had a significant smoother of altitude (Chi-square = 15.72, $p < 0.01$), with increasing predicted rarity of Form 7 along the gradient of altitude (Fig. 6; Table A5).

3.4. *The endangered category*

On the global list, only one species, *Oxyepoecus bruchi* (Form 3) in the category "Vulnerable". At the national level, a total of 15 species were recorded on the list of endangered fauna. Among these, seven were classified as Common (e.g., *Acromyrmex crassispinus* (Forel, 1909), category "Least Concern"), and eight feature some form of rarity. Only *Brachymyrmex micromegas* Santschi, 1923 and *Diaphoromyrma sofiae* Fernández et al., 2009 are in the category "Endangered", and *Lachnomyrmex nordestinus* Feitosa & Brandão, 2008, appears as "Vulnerable", the others were classified as "Least Concern".

At the regional level, state lists were found for 10 states (Alagoas, Bahia, Espírito Santo, Minas Gerais, Paraná, Pernambuco, Rio de Janeiro, Rio Grande do Sul, Santa Catarina, and São Paulo) out of the 17 that comprise the Atlantic Forest. Only four states (Bahia, Espírito Santo, Santa Catarina, and São Paulo) possess Formicidae. The state of Bahia presented one (Form 7) of the 242 species we analyzed; while São Paulo counted 22 species (5 Common and 17 rare); Espírito Santo and Santa Catarina presented none of our species (Table 3).

4. Discussion

This study revealed that nearly half of the ant species ($n = 120$ species) in the Brazilian Atlantic Forest are classified in some form of rarity according to Rabinowitz's method, confirming the expected high richness of rare ant species and all forms of rarity. Further, we found that environmental predictors determine the richness of most forms of rarity. In terms of conservation, we highlight that 85 % of species (of these, 53 % are common and 47 % rare) are not on the official lists of endangered species from Brazil.

4.1. *Forms of rarity*

The forms of rarity, their richness proportions, and the number of species classified as rare support our hypothesis in the Atlantic Forest to find all forms of rarity proposed by Rabinowitz. These results reflect Rabinowitz's dichotomous classification, which attributes to a species 50 % chance to be rare in each of the three parameters used (Fattorini et al., 2013). Studies using the Rabinowitz's classification showed a similar distribution of common and rare species in several groups, such as birds (Goerck, 1997), trees (Caiafa and Martins, 2010; Oliveira et al., 2019), arthropods (e.g., arachnids, Coleoptera and Lepidoptera) (Fattorini et al., 2012), and anurans (Toledo et al., 2014).

Most of the ants analyzed are characterized by wide geographic distribution, occurring also in other Brazilian biomes [e.g., Caatinga, Cerrado, Amazon rainforest, Pantanal and Pampa (Dröse et al., 2017; Jory and Feitosa, 2020; Lasmar et al., 2021)]. This is the case of many *Linepithema* and *Solenopsis* species, which in addition to their wide geographic distribution, are abundant in different habitats, and include generalist species concerning foraging and feeding (Baccaro et al., 2015). The presence of species with these characteristics in our results may be the main point responsible for the high richness of species with wide geographic distribution (Common, Form 1, Form 2 and Form 3), also of those without habitat specificity (Common, Form 1, Form 4 and

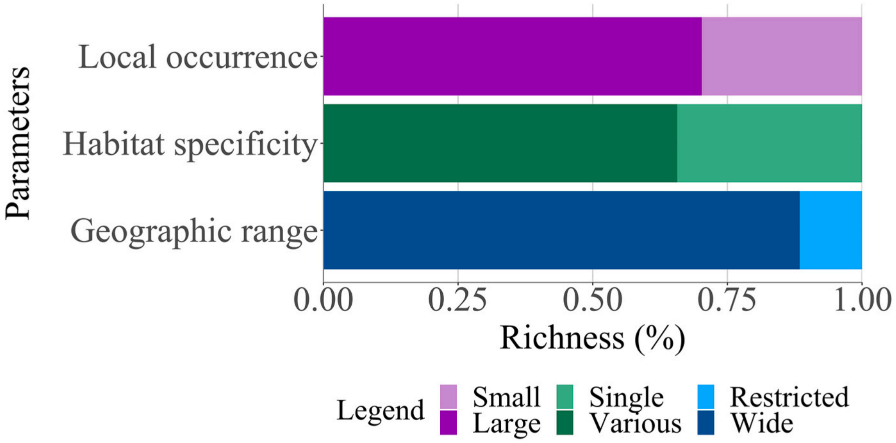

Fig. 4. Richness of ant species, collected in leaf litter from the Brazilian Atlantic Forest, for each Rabinowitz's (1981) rarity parameter.

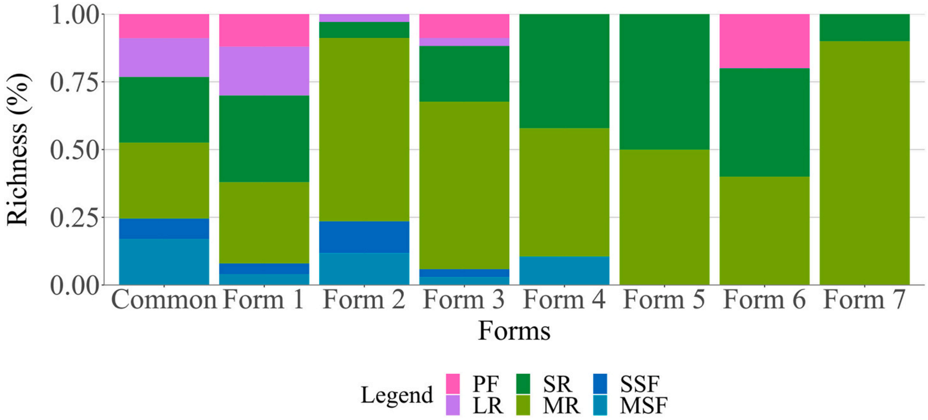

Fig. 5. Percentage of species richness of ants, collected in the leaf litter of the Brazilian Atlantic Forest, of the forms of Rabinowitz (1981) in each phytophysiognomy (habitat) sampled. (PF - Pioneer Formations; LR - Lowlands Rainforest; SR - Submontane Rainforest; MR - Montane Rainforest; SSF - Submontane Semideciduous Forest; MSF - Montane Semideciduous Forest).

Form 5), or high occurrence in the sampled sites (Common, Form 2, Form 4 and Form 6) (Fig. 3, Table 2).

In our study, only 11.57 % of the species (Form 4, Form 5, Form 6 and Form 7) had restricted geographic distribution. Currently, three genera endemic to the Atlantic Forest have been identified: *Anillydris*, *Diaphoromyrma*, and *Phalacromyrmex* (Feitosa et al., 2021). The number of endemic species of ants in this biome is likely high (above average), though knowledge about them is still incipient (Feitosa et al., 2021). Although the species we listed may not represent “pure endemism” (Lima et al., 2020), our list can serve as a subsidy for further studies on endemism in the Atlantic Forest.

Regarding habitat specificity, 34.3 % of species (Form 2, Form 3, Form 6 and Form 7) occurred exclusively in one of the six phytophysiognomies analyzed. Ant species respond differently to distinct environmental complexity among phytophysiognomies (Guilherme et al., 2019) because differences in vegetation are related to (1) differences in availability of resources (e.g., nesting and foraging sites; Andersen, 1986), which contributes to ant diversity, not only those associated with vegetation (e.g. arboreal ants), but also leaf litter ants that forage in this stratum (Andersen, 1986; Delabie et al., 2000); and (2) the production of forest leaf litter (Lopes et al., 2012; Guilherme et al., 2019) determines the quality and heterogeneity of leaf litter, affecting ant richness (Silva et al., 2011; Queiroz et al., 2013), as it provides food and nesting sites to the myrmecofauna (Kaspari, 1996).

The species richness with the small occurrence was 29.75 % (Form 1, Form 3, Form 5 and Form 7). Even using the appropriate sampling techniques for sampling ants associated with leaf litter [e.g.,Winkler’s extractor and Berlese’s funnel (Bestelmeyer et al., 2000; Delabie et al., 2021)], we found “Small occurrence” species but that have a higher occurrence ($n > 2$) in other studies [e.g., *Brachymyrmex patagonicus* Mayr, 1868, *Cyphomyrmex transversus* Emery, 1894, *Strumigenys precava* Brown, 1954 (Oliveira et al., 2009; Santos et al., 2017)], indicating local rarity. We also found species considered “globally unique”, as some of them also had low occurrence in other places [e.g., *B. micromegas* (ICMBio, 2018b)]. Knowledge of locally rare species is important as they are more susceptible to extinction (Flather and Sieg, 2007; Maciel and Martins, 2019) and losing them can trigger an extinction cascade effect (Dunn, 2005).

4.2. Beta diversity

Our results demonstrate that the majority of the composition of rarity forms among physiognomies is due to a subset of physiognomies with higher richness of rarity forms. Although physiognomies exhibit unique biotic and abiotic characteristics (Veloso, 1992), which are factors that tend to influence ant diversity (Longino and Colwell, 2011; Silva et al., 2011; Lasmar et al., 2020), there are also shared characteristics among them, such as typical vegetation or temperature ranges. For example, rainforests are characterized by phanerophytes (woody plants of medium to tall stature), lianas, and epiphytes, with high and evenly distributed precipitation throughout the year, high temperatures, averaging 25 °C (Veloso, 1992; IBGE, 2012). In contrast, the Semideciduous Forest is characterized by both phanerophytes and deciduous trees (which can represent 20 to 50 % of these forests) (Veloso, 1992; IBGE, 2012). Thus, similar physiognomies such as “Submontane Rainforest”/“Montane Rainforest” ($\beta sor = 0$ and $\beta sne = 0$; Fig. A2) or “Submontane Semideciduous Forest”/“Montane Semideciduous Forest” ($\beta sor = 0.11$ and $\beta sne = 0.11$; Fig. A2) may exhibit a similar environmental gradient, consequently favoring the same group of rarity forms. This parallels the observations made by Guilherme et al. (2019) for ant communities in different physiognomies of the Amazon Basin.

The “Pioneer Formations” already have a set of forms different from other physiognomies. Thus, it is possible that our results are also related to environmental complexity. Ants tend to exhibit distinct diversity between more complex environments (e.g., rainforests) and less complex ones (e.g., savannas) (Guilherme et al., 2019). When compared to other physiognomies, “Pioneer Formations” represent a less complex environment, considering that they are characterized by a pioneer plant community associated with swamps, lagoons, and environments influenced by the marine influence (restingas) (IBGE, 2012).

Considering that funding for conservation tends to be scarce (Flather and Sieg, 2007), and beta diversity partitioning allows for different conservation measures (Baselga, 2010), these indices can aid in directing public conservation policies. For instance, higher values of nestedness indicate that less rich areas contain a subset of species from richer areas (Baselga, 2010; Silva et al., 2022a). This index suggests fewer target areas (i.e., only those with higher species richness) (Baselga, 2010). Conversely, a higher turnover demonstrates that the area has a set of species different from others, regardless of richness (Baselga, 2010; Silva et al., 2022a). Utilizing this index in conservation would imply selecting a greater number of target areas (i.e., including areas with species turnover) (Baselga, 2010).

4.3. Effect of the environmental prediction on species richness

The absence of the influence of environmental variables on the richness of rarity (“All rare” level) may be related to the fact that joining species in groups may mask the effect of environmental drivers (Leal et al., 2012). However, when analyzing each form individually, we found significant relationships (weak to moderate) between environment and forms of rarity, revealing positive relationships with altitude in most of models (but Form 2 and Form 6). Changes in abiotic factors

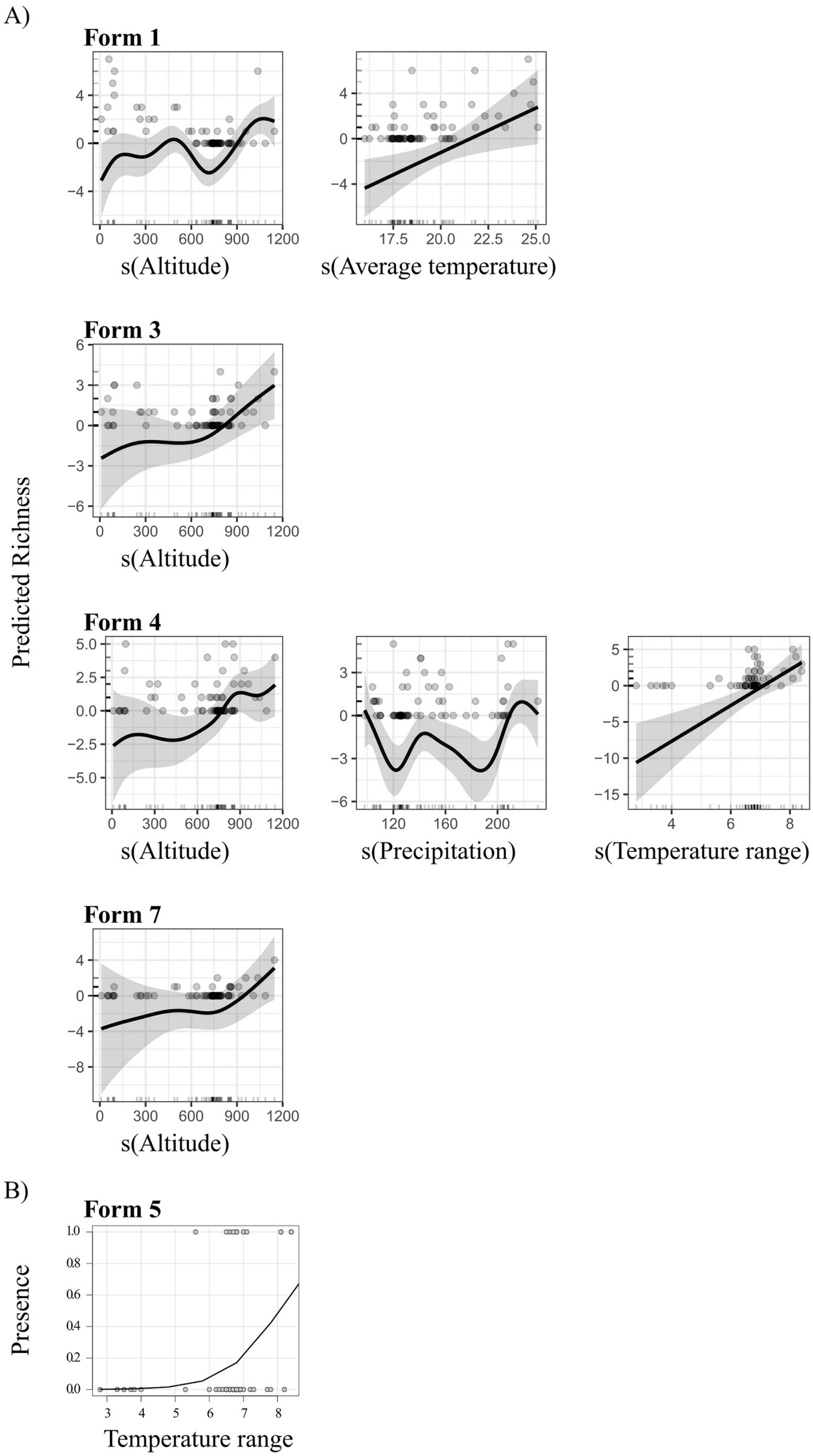

Fig. 6. Relationship between environmental variables and richness of rare ants. Solid lines and shading represent model relationships and confidence intervals, respectively. (A - GAM models; B - GLM model).

Table 3

Ant species in lists of endangered Brazilian fauna at national and state level, with endangered category on the lists and classification of rarity. (n - represents the number of ant species evaluated in the list).

List of endangered fauna	Species	Category	Forms
Global[a] ($n = 149$ species)	*Oxyepoecus bruchi*	Vulnerable	Form 3
National – Brazil[b] ($n = 95$ species)	*Brachymyrmex micromegas*	Endangered	Form 7
	Diaphoromyrma sofiae	Endangered	Form 7
	Lachnomyrmex nordestinus	Vulnerable	Form 6
	Acromyrmex crassispinus	Least concern	Common
	Neivamyrmex punctaticeps	Least concern	Form 1
	Neoponera bucki	Least concern	Common
	Neoponera crenata	Least concern	Common
	Neoponera metanotalis	Least concern	Form 7
	Pachycondyla harpax	Least concern	Common
	Pachycondyla lenis	Least concern	Common
	Pachycondyla striata	Least concern	Common
	Pseudoponera gilberti	Least concern	Form 1
	Pseudoponera stigma	Least concern	Form 1
	Rasopone ferruginea	Least concern	Common
	Thaumatomyrmex mutilatus	Least concern	Form 2
State - Bahia[c] ($n = 09$ species)	*Diaphoromyrma sofiae*	Endangered	Form 7
State - São Paulo[d] ($n = 98$ species)	*Apterostigma acre*	Vulnerable	Form 2
	Basiceros convexiceps	Vulnerable	Form 3
	Brachymyrmex micromegas	Vulnerable	Form 7
	Oxyepoecus longicephalus	Vulnerable	Form 1
	Acropyga decedens	Data deficient	Common
	Acropyga fuhrmanni	Data deficient	Common
	Acropyga guianensis	Data deficient	Form 1
	Acropyga smithii	Data deficient	Common
	Camponotus canescens	Data deficient	Form 3
	Eurhopalothrix gravis	Data deficient	Form 3
	Gnamptogenys haenschi	Data deficient	Form 3
	Gnamptogenys interrupta	Data deficient	Form 3
	Hypoponera foreli	Data deficient	Common
	Labidus mars	Data deficient	Form 3
	Linepithema pulex	Data deficient	Form 3
	Megalomyrmex myops	Data deficient	Form 4
	Mycetarotes carinatus	Data deficient	Form 3
	Poneracantha lucaris	Data deficient	Form 5
	Poneracantha mediatrix	Data deficient	Common
	Strumigenys dapsilis	Data deficient	Form 5
	Strumigenys dentinasis	Data deficient	Form 7
	Strumigenys sanctipauli	Data deficient	Form 6

[a] IUCN (1996).

[b] ICMBio (2018b).

[c] Bahia (2017).

[d] São Paulo (2018).

along the altitudinal gradient affect ant diversity (Brühl et al., 1999; Lessard et al., 2007; Longino and Colwell, 2011), with a decrease in richness starting from 1500 m (Longino and Colwell, 2011; Longino et al., 2014). The associations with other environmental variables may be related to the phytophysiognomies of the sampled environments, since they occur in certain altitudinal ranges, according to the latitude in which they are found; this implies distinct environmental characteristics, such as precipitation and temperature (Veloso, 1992).

Particularly, the ants classified in Form 2 and Form 6 did not have their richness influenced by abiotic factors analyzed (e.g., precipitation and temperature). Possibly, these species may be influenced by other abiotic characteristics of the phytophysiognomy not analyzed in the present study. Furthermore, species with locally abundant populations tend to occupy new locations, even if they have habitat specificity (Fattorini et al., 2012). These ants may show specificity with a given phytophysiognomy, but demonstrate tolerance to others.

In this study, we investigated environmental variables that are already known to influence ant richness ("Section 2.3.2 Effect of the environmental prediction on species richness"); but due to the weak association found for some forms of rarity, we suggest that new studies consider other environmental variables (Fernandes et al., 2019), interspecific relationships (Chick et al., 2020) and different spatial scales (Spiesman and Cumming, 2008) to broaden knowledge about rare ants.

4.4. *The endangered category*

We demonstrate that many species classified here as rare are not included in the lists of endangered fauna informed by IUCN and Brazilian state and federal agencies. The difference in our results for the aforementioned lists may be related to factors such as (1) endangered species classification parameters employed by official lists adopting the IUCN criterion (for more details see "Section 2.4 The endangered category") (ICMBio, 2018a); (2) endangered species may also be rare, but not necessarily a rare species is threatened with extinction (Flather and Sieg, 2007). For example, *Neoponera metanotalis* although this species belongs to Form 7, it is listed as Least Concern. Rare species that are not under significant threat may be included in this IUCN category (ICMBio, 2018a); (3) lists of endangered species most often do not cover locally rare species (Maciel et al., 2016). In addition, (4) it is recurrent that many rare species do not present sufficient data to be classified and therefore, are categorized as "insufficient data" and are not included in the analyses (Corlett, 2016).

Our study demonstrates that even the use of endangered species lists is not sufficient to uncover most of the rare species. In addition, some are not updated, for example the IUCN list of Formicidae is listed as "Needs updating", with 1996 being the last year of publication. Even though invertebrates are ecologically important, performing several essential ecosystem services (Diniz-Filho et al., 2010; Sánchez-Bayo and Wyckhuys, 2019); this group tends to be underrepresented in lists of threatened fauna, even though they are one of the taxa with the highest number of described species (Cowie et al., 2022). This is because there is a lack of knowledge about their species and/or there is a lack of experts to evaluate them (Diniz-Filho et al., 2010; Cardoso et al., 2011; Cowie et al., 2022). Thus, considering that rare species are prone to extinction (Flather and Sieg, 2007; Maciel and Martins, 2019), projects aimed at the conservation of Atlantic Forest fragments need to consider these species as part of the strategies to be implemented. This does not imply abandoning the IUCN criteria, but rather, combining different lists of endangered species and rare species in the decision-making.

The lack of state lists, as well as the insufficiency of data on the biology of the species, impair the assessment of the vulnerability condition and the decision-making on conservation (Brito, 2008). Although invertebrates can assist in conservation planning; in general, they tend to be neglected in conservation policies (Diniz-Filho et al., 2010; Cardoso et al., 2011). These facts are worrying, given that recent data suggest that there has been a global decrease in the richness and abundance of insects (Hallmann et al., 2017; Sánchez-Bayo and Wyckhuys, 2019; Cardoso et al., 2020; Van Klink et al., 2020).

4.5. *Conservation implications*

In our study we demonstrated that the Atlantic Forest leaf litter harbors 120 ant species with different degrees of rarity. However, this number should be even higher, considering that we analyzed only a portion of the myrmecofauna in this biome. Among the species analyzed, we highlight *B. micromegas*, classified as Form 7 for having a restricted geographic distribution (only in the Atlantic Forest), having habitat specificity (only in the Montane Rainforest), and for having a small occurrence (up to two occurrences per area). This information is crucial for the conservation of a species that is impaired by habitat quality (ICMBio, 2018b). *Brachymyrmex micromegas* is endemic to Brazil, being recorded only in areas of the Atlantic Forest in the state of São Paulo in leaf litter samples (Ortiz and Fernandez, 2014; ICMBio, 2018b).

These data are worrying, because the Brazilian Atlantic Forest is highly fragmented, and most of these fragments have up to 50 ha

(Ribeiro et al., 2009), and only 30 % of vegetation cover in protected areas (Rezende et al., 2018). Although the fragments harbor a subset of forest species, they have fewer rare species (Vasconcelos et al., 2006), as small fragments are more subject to the edge effect and have a lower variety of habitats (Laurance and Vasconcelos, 2009). Habitat loss and degradation are the main causes of rarity (Flather and Sieg, 2007), specifically, the loss of unique and specific microhabitats leads to local extinction (Murphy, 1997). Species that have become rare due to human interference may be more vulnerable to extinction as they have no history of living adapted to small populations (Flather and Sieg, 2007).

The scarcity of public policies for the conservation of invertebrate fauna and the absence of biological data for most species impair the elaboration of lists of endangered fauna and the establishment of regional or national conservation strategies (Brito, 2008). Increasing the knowledge of rare species becomes a crucial tool in the aid of subsidies for the increase of conservation areas. Considering that rare (Kricsfalusy and Trevisan, 2014; Maciel et al., 2016) and endangered species need urgent mobilization for their conservation and biodiversity in general (Lambeck, 1997), our approach may contribute to decision-making for the conservation of the myrmecofauna of the Atlantic Forest, as the distribution of ants and small vertebrates overlap, including in areas of rarity center (Kass et al., 2022). Therefore, the identification of such areas can help the preservation of these taxa (Kass et al., 2022). In addition, we addressed new knowledge on rarity patterns and the need to insert strategies that target rare species of ants into conservation policies, particularly in biomes that are under strong anthropogenic pressure.

CRediT authorship contribution statement

Nathalia S. Silva: Conceptualization, Writing – original draft, Writing – review & editing. **Everton A. Maciel:** Conceptualization, Writing – original draft, Writing – review & editing. **Lívia P. Prado:** Data curation, Writing – review & editing. **Otávio G.M. Silva:** Data curation, Writing – review & editing. **David Aciole Barbosa:** Software, Writing – review & editing. **Joudellys Andrade-Silva:** Formal analysis, Writing – review & editing. **Débora R. Souza-Campana:** Writing – review & editing. **Rogério R. Silva:** Formal analysis, Writing – original draft, Writing – review & editing. **Carlos R.F. Brandão:** Writing – review & editing. **Jacques H.C. Delabie:** Writing – review & editing. **Maria S.C. Morini:** Conceptualization, Writing – original draft, Writing – review & editing.

Declaration of competing interest

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

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2024.110640.

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