Influence of forest type on the diversity, abundance, and naïve occupancy of the mammal assemblage in the southeastern Brazilian Atlantic Forest

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The Brazilian Atlantic Forest has the highest rate of native vegetation destruction, which is one of the principal drivers of mammal extinctions. Therefore, reducing information gaps regarding diversity patterns, abundance, and habitat use is crucial to understand mammal persistence in fragmented landscapes. Our objective was to establish the γ diversity and to assess the extent to which the α, and β diversity, the relative abundance, and naïve occupation of medium and large-sized mammal communities differ between seasonal and ombrophilous forests. Between January 2019 and March 2020, we placed 22 camera traps in the Atlantic Forest of Minas Gerais. We calculate Hill's numbers using iNEXT.4steps package, the β-diversity with the Betapart package, as well as the relative abundance index (RAI), and naïve occupancy (PAO). We used Kruskal-Wallis and Mann-Whitney statistical tests to compare the RAIs between different species and forest types. Finally, we calculated the correlation between the RAIs and PAOs. We found 32 species, principally from the orders Carnivora and Artiodactyla. The alpha diversity and evenness profiles were not different between the two forest types (seasonal $q0 = 0.91$, $q1 = 0.99$, $q2 = 1$, $J = 0.83$; ombrophilous $q0 = 0.96$, $q1 = 0.99$, $q2 = 1$, $J = 0.85$). The beta diversity was low ($\beta JAC = 0.37$) which was mostly associated with species turnover ($\beta JTU = 0.34$), while nestedness was almost non-existent ($\beta JNE = 0.02$). The RAIs varied among mammalian species ($H = 115.24$, $P = 0.000$), with the highest values for *Didelphis aurita* ($RAI = 4.55 \pm 7.66$) and *Cuniculus paca* ($RAI = 2.35 \pm 3.73$) and the minor values for *Speothos venaticus* ($RAI = 0.04 \pm 0.24$) and *Galictis cuja* ($RAI = 0.06 \pm 1.19$). The RAIs of species was not significantly different between forests ($U = 453.5$; $Z = 0.37$; $P = 0.70$), and only *Leopardus wiedii* showed significant differences between forests ($U = 84.5$; $P = 0.01$). Most of the mammalian species had restricted occupancy to a few localities ($< 50 \%$). The species *Eira barbara* and *Didelphis aurita* had the highest PAOs in both forests ($> 50 \%$), and the species *Tayassu pecari*, *Tamandua tetradactyla*, and *Speothos venaticus*, the lowest values (5%). We found a correlation of 75% between the average RAI and naïve occupancy. The γ diversity was representative and consistent with the species found in the Atlantic Forest, and the relative abundance and naïve occupancy reflected the rarity of most species in the area. Additionally, the only difference between the two forests corresponds to species turnover. Therefore, we must conserve native remnants of both forests to ensure the existence of native mammals, mainly the most threatened species, to prevent more dramatic scenarios of local extinction in Minas Gerais.

La Mata Atlántica Brasileña presenta la mayor tasa de destrucción de vegetación nativa, causa principal de la extinción de mamíferos. Por lo tanto, reducir las lagunas de información relacionadas con los patrones de diversidad α, β y γ, abundancia, ocupación y uso de hábitat es una prioridad, para comprender la persistencia de mamíferos en paisajes fragmentados. Nuestro objetivo fue establecer la diversidad γ, y evaluar en qué medida la diversidad α y β, la abundancia relativa y la ocupación naïve de las comunidades de mamíferos medianos y grandes, contrastan entre bosques estacionales y ombrófilos. Entre enero (2019) y marzo (2020), colocamos 22 cámaras trampa en el Bosque Atlántico de Minas Gerais. Calculamos los números de Hill utilizando el paquete iNEXT.4steps, la β-diversidad con el paquete Betapart, el índice de abundancia relativa (RAI) y la ocupación naïve (PAO). Utilizamos pruebas de Kruskal-Wallis y Mann-Whitney para comparar los RAI entre especies y bosques. Finalmente, calculamos la correlación entre los RAIs y PAOs. Registramos 32 especies, principalmente de los órdenes Carnivora y Artiodactyla. La diversidad alfa y los perfiles de uniformidad no difirieron entre bosques (estacional $q0 = 0.91$, $q1 = 0.99$, $q2 = 1$, $J = 0.83$; ombrófilo $q0 = 0.96$, $q1 = 0.99$, $q2 = 1$, $J = 0.85$). La beta-diversidad fue baja ($\beta JAC = 0.37$), correspondiente al recambio de especies ($\beta JTU = 0.34$), y a una anidación casi inexistente ($\beta JNE = 0.02$). Los RAIs difirieron entre especies ($H = 115.24$, $P = 0.000$), los valores más altos fueron para *Didelphis aurita* ($RAI = 4.55 \pm 7.66$) y *Cuniculus paca* ($RAI = 2.35 \pm 3.73$), y los valores más bajos para *Speothos venaticus* ($RAI = 0.04 \pm 0.24$) y *Galictis cuja* ($RAI = 0.06 \pm 1.19$). Los RAIs no difirieron entre bosques ($U = 453.5$; $Z = 0,37$; $P = 0.70$), y exclusivamente *Leopardus wiedii* mostró diferencias significativas entre bosques ($U = 84.5$; $P = 0.01$). La mayoría de las especies presentaron una ocupación restringida ($< 50 \%$). *Eira barbara* y *Didelphis aurita* presentaron los valores más altos en ambos bosques ($> 50 \%$), mientras que *Tayassu pecari*, *Tamandua tetradactyla* y *Speothos venaticus*, los valores más bajos (5%). Observamos una correlación del 75% entre los RAIs y PAOs. La diversidad γ fue representativa de la riqueza de especies reportada para la Mata Atlántica. Los RAIs y PAOs reflejaron la rareza de la mayoría de las especies. Adicionalmente, la única diferencia entre los dos bosques correspondió a la rotación de especies. Por lo tanto, debemos conservar los remanentes nativos de ambos bosques para asegurar la existencia de los mamíferos nativos, principalmente las especies más amenazadas, para evitar escenarios más dramáticos de extinción local en la Mata Atlántica de Minas Gerais.

Keywords: Biodiversity; Brazil; conservation; habitat use; mammals; relative abundance index.

Introduction

The Atlantic Forest is widely recognized as a biodiversity hotspot (Myers *et al.* 2000), yet it is also one of the most severely defaunated subregions on the planet, primarily due to anthropogenic drivers (Bogoni *et al.* 2020; Galetti *et al.* 2021). It harbors one of the world's most depleted mammal faunas, with an average historical loss of 62 % (Bogoni *et al.* 2020), primarily resulting from habitat loss, landscape fragmentation (Ribeiro *et al.* 2009; Haddad *et al.* 2015; Bogoni *et al.* 2018; Püttker *et al.* 2020), agricultural expansion, wildlife trafficking, urbanization, industrial development (Campanili and Schäffer 2010) and lack of protected areas (Bogoni *et al.* 2020).

Brazil is home to 770 mammal species, of which 384 are found in the Atlantic Forest (Abreu *et al.* 2021). Among these, 262 are terrestrial, and 109 are endemic to the region (Figueiredo *et al.* 2021). The state of Minas Gerais contains roughly 70 % of all mammal species found in the Brazilian Atlantic Forest, including nearly 60 endemic species (Campanili and Schäffer 2010). Unfortunately, Minas Gerais also harbors 45 species threatened with extinction, according to the List of Endangered Fauna Species in the State of Minas Gerais (COPAM 2010).

Mammals in the region are highly sensitive to changes in landscape structure (Regolin *et al.* 2020), floristic composition (Galetti *et al.* 2009), alterations in species abundance (Fahrig *et al.* 2019), changes in community composition (Beca *et al.* 2017), and the size of assemblages (Bogoni *et al.* 2020a). This vulnerability has resulted in the local extinctions of several mammal species (Bogoni *et al.* 2020), as well as alterations in ecological processes (Oliveira *et al.* 2020) and ecosystem services (Bogoni *et al.* 2020). The degree of threat faced by mammal species in Minas Gerais justifies the urgent need for conservation action in the region.

Insufficient data on population sizes, distribution, and occurrence of many threatened mammal species in Minas Gerais included in the Brazilian Red List pose challenges to understanding their conservation status (Corrêa *et al.* 2021). Particularly for rare species, data gaps occur mainly in the interior of forests, highlighting the need for increasing sampling efforts in the Atlantic Forest to identify priority areas for conservation (Corrêa *et al.* 2021; Figuereido *et al.* 2021). Among various monitoring methods, camera trapping has proven highly effective for medium to large mammals in neotropical forests (Srbek-Araujo and Chiarello 2005; Rovero and Spitale 2016), providing standardized data at regional or global scales (Wearn *et al.* 2019). This method can be especially useful for obtaining information about uncommon, rare, or cryptic species, supporting decision-making for biodiversity conservation in hotspots such as the Atlantic Forest (Trolliet *et al.* 2014).

Species richness, abundance, and distribution patterns are influenced by a variety of environmental and landscape factors, which can vary depending on the spatial scale (Bogoni *et al.* 2017). While forest type may have a greater impact on species response at smaller scales, larger-scale patterns remain poorly understood (Bogoni *et al.* 2016). Therefore, it is crucial to gather additional data (De Barros *et al.* 2021) on species abundance (Galetti *et al.* 2009; Bogoni *et al.* 2020), diversity, habitat use, species occurrence (Beselga *et al.* 2010; Vilas *et al.* 2022), and assemblage organization to better comprehend the ecological requirements of mammals across various habitat types (Regolin *et al.* 2020; De Barros *et al.* 2021; Vilas *et al.* 2022).

It is imperative to understand how native vegetation contributes to the persistence of many species in fragmented agricultural landscapes (Ikin *et al.* 2014). This includes identifying the α and β-diversity components to gain insight into the processes that drive differences in species assemblages (Regolin *et al.* 2020). Such knowledge can serve as a baseline for making comparisons between current, past, and future species richness, and for inferences about species distributions and differences across locations (Cooke *et al.* 2019; Steinbeiser *et al.* 2019). Additionally, it can contribute to the management of natural areas (Corrêa *et al.* 2021) and land-use decisions (Wearn *et al.* 2017), to expand and strengthen public policies and good agricultural practices. This, in turn, can support the implementation of Brazil's Vegetation Protection Law aimed at restoring native vegetation in the Atlantic Forest (Brancalion *et al.* 2016).

Our study aimed at estimating gamma diversity and comparing alpha and beta diversity, relative abundance, and naïve occupation of medium and large-sized mammals between seasonal and ombrophilous forests. Our specific objectives were: (a) analyzing the mammalian gamma diversity, abundance, and naïve occupation in the Atlantic Forest; (b) comparing mammal alpha diversity, abundance, and naïve occupation between seasonal and ombrophilous forests; and (c) assessing beta-diversity, species turnover and species nesting between the forests. We hypothesized that forest type would affect mammalian assemblages, resulting in significant differences between α-diversity, abundance, and occupancy, mainly due to differences in species' habitat use. Furthermore, we expected a high beta-diversity (>70 %) explained by the nestedness of species between forests.

Materials and methods

Mammal sampling. This study was conducted in 22 fragments located in the southeastern Brazilian Atlantic Forest, spanning 15 municipalities in Minas Gerais and one in Rio de Janeiro (-46° 0' W to -43° 0' W, -23° 0' S to -21° 0' S; Figure 1; Supplementary material 1), covering an area of approximately 22,049 km². Fragment selection was based on satellite images from Google Earth Pro software and updated maps of remaining forest fragments provided by the SOS Mata Atlântica Institute (2013/2014). The selection criteria included the presence of both seasonal and ombrophilous forest, with a minimum distance of 2.85 km between fragments.

To survey medium- and large-sized mammals (≥1 kg), we utilized one camera trap per sampling point (Bushnell® HD Bushnell Outdoor Products, California, USA) in each of the 22 fragments. The camera trap in each fragment operated continuously for an average of 130 days between January 2019 and March 2020, capturing images 24 hours per day. To ensure independence between pictures and avoid pseudo-replication, we implemented a 24-hour interval between pictures of the same species (Porfirio *et al.* 2014).

The study area consisted of a highly fragmented landscape surrounded by agricultural matrices and villages. The regional relief is rugged and occurs at elevations ranging from 887 to 2,087 masl. The lower elevations are predominantly characterized by a humid temperate climate with dry winters and hot summers (Cwa type), while the mountainous areas have dry winters and rainy and moderately hot summers (Cwb type), according to the classification by the Instituto Brasileiro de Geografia e Estatística (IBGE 2012).

We organize the data using the Wild.ID Program 0.9.31 (Conservation International 2018). We identified the spe-

Figure 1. Study area showing the location of the fragments sampled with the camera traps in the southeastern Brazilian Atlantic Forest of Minas Gerais.

cies at the lowest taxonomic level possible, grouping the records of *Mazama americana* and *Mazama gouazoubira*, as *Mazama* sp., due to the difficulty of differentiating between these two species.

Gamma, alpha, and beta diversity. We assessed the gamma diversity (Whitaker 1972) of the southeastern Brazilian Atlantic Forest using the TEAM library program 1.7.R for Windows (Rovero and Spitale 2016). To evaluate the sampling effectiveness and compare it with the richness of native species in other Atlantic Forest studies, we excluded domestic species. Accumulation curves were generated with the Vegan package (Oksanen *et al.* 2013) and used the non-parametric Jackknife 1 estimator from the Biodiversity R package (Kindt and Coe 2005), which is known for its precision in reducing bias of estimated values (Burnham and Overton 1979).

To compare the alpha diversity of seasonal and ombrophilous forests, we used the R package iNEXT.4steps online for rarefaction and extrapolation of species diversity with Hill numbers based on abundance data (Chao *et al.* 2020). We performed fifty bootstraps to calculate 95 % confidence intervals. Hill numbers included species richness ($q = 0$), Shannon diversity ($q = 1$), and Simpson diversity ($q = 2$; Chao *et al.* 2014; Hsieh *et al.* 2016). We followed a four-step procedure to assess each forest: (a) sample completeness profile, (b) size-based rarefaction/extrapolation, (c) asymptotic and empirical diversity profiles, (d) non-asymptotic coverage-based rarefaction and extrapolation analysis, and (e) evenness profile among species abundances (Pielou J), derived from the slopes of the diversity profile (Chao *et al.* 2020).

To compare species composition between seasonal and ombrophilous forests, we used the Partitioning Beta Diversity into Turnover and Nestedness Components package (betapart package; Baselga and Orme 2012; Baselga *et al.* 2021) in R v4.1.0 (R Core Team 2021). We computed the beta.JTU value of turnover, measured as the turnover fraction of Simpson's dissimilarity, the beta.JNE of the nesting component, measured as the resulting fraction of Simpson's dissimilarity nesting, and the beta.JAC value of overall beta diversity. We computed using a resampling procedure, taking 100 random samples. We performed this analysis by a) grouping native and non-native species and b) considering only native species.

Species abundance. We calculated the relative abundance index (RAI) for each species as follows: RAI ij = Nj/days j * 100 nights traps, where "Nj" is the number of independent records of the species, "i" is each species, and "j" is each landscape (Mandujano and Pérez 2019), throughout the study area and at each forest. We performed all analyses with the RAI.1 package (Mandujano and Pérez 2019). Finally, we used the Kruskal-Wallis and Mann-Whitney statistical tests to compare the RAIs between species and forests. To determine the magnitude of the differences obtained with the Kruskal Wallis test, we computed the epsilon squared (Tomczak and Tomczak 2014). In all the comparative analyses carried out, we used a significance level of $p < 0.05$.
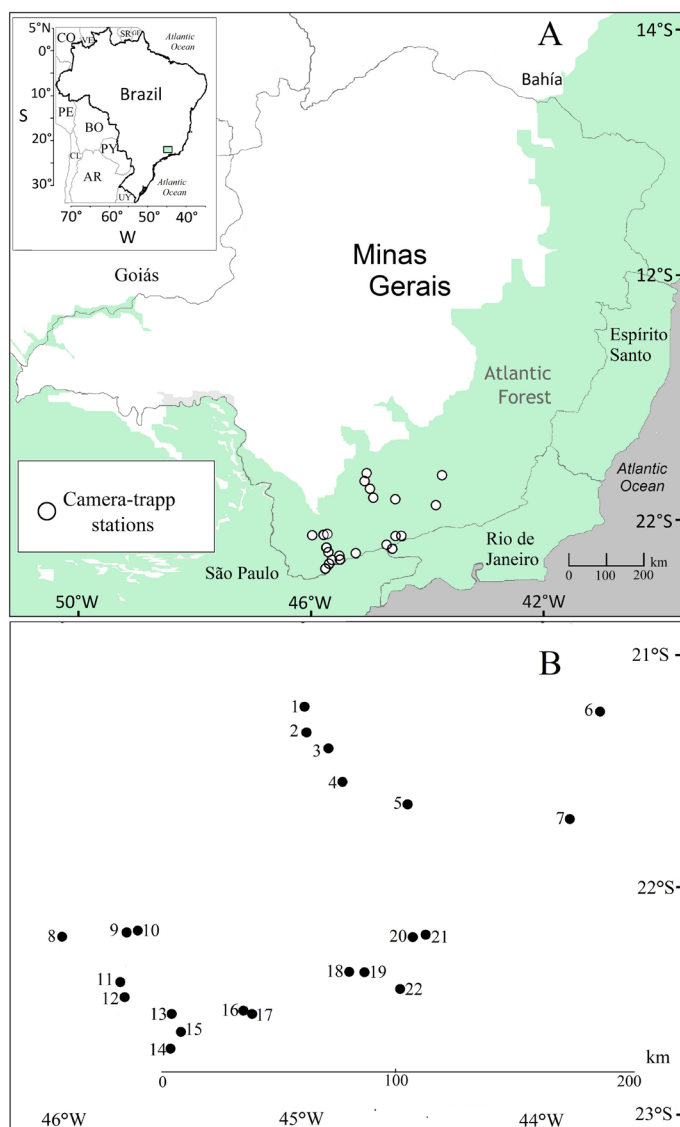
Species distribution in the study area. We calculated the naïve occupancy, also known as the Percent of Area Occupied (PAO; MacKenzie and Kendall 2002; sensu Kéry and Royle 2015), throughout the study area and at each type of forest. It was calculated as the number of camera trap sites occupied by each species divided by the total number of sites surveyed. The maximum occupancy value is 1, which indicates that a species occupies 100 % of the sites surveyed. Subsequently, to determine the influence of spatial distribution on species abundance, we calculated the correlation between the PAO and the RAI for each species (Mandujano and Pérez 2019). We performed all analyses using the R program 4.2.1 (R Core Team 2021).

Results

Estimation of mammal gamma, alpha and beta diversity. Based on 2,856 camera traps per day, we recorded 589 independent camera trap events of mammalian species in the entire region. The mammal richness in the study area was 32 species (Figures 2-3), distributed among 26 genera, 9 orders, and 17 families (Table 1). Native mammal species richness was 26, distributed among 22 genera, 8 orders, and 15 families (Table 1). The accumulation curve almost reached the asymptote, and according to the expected richness (Jackknife 1 = 29 ± 2 species) of mammalian species, the sampling effort was deemed sufficient. Therefore, we obtained a representative percentage (90 %) of the native species in the area.
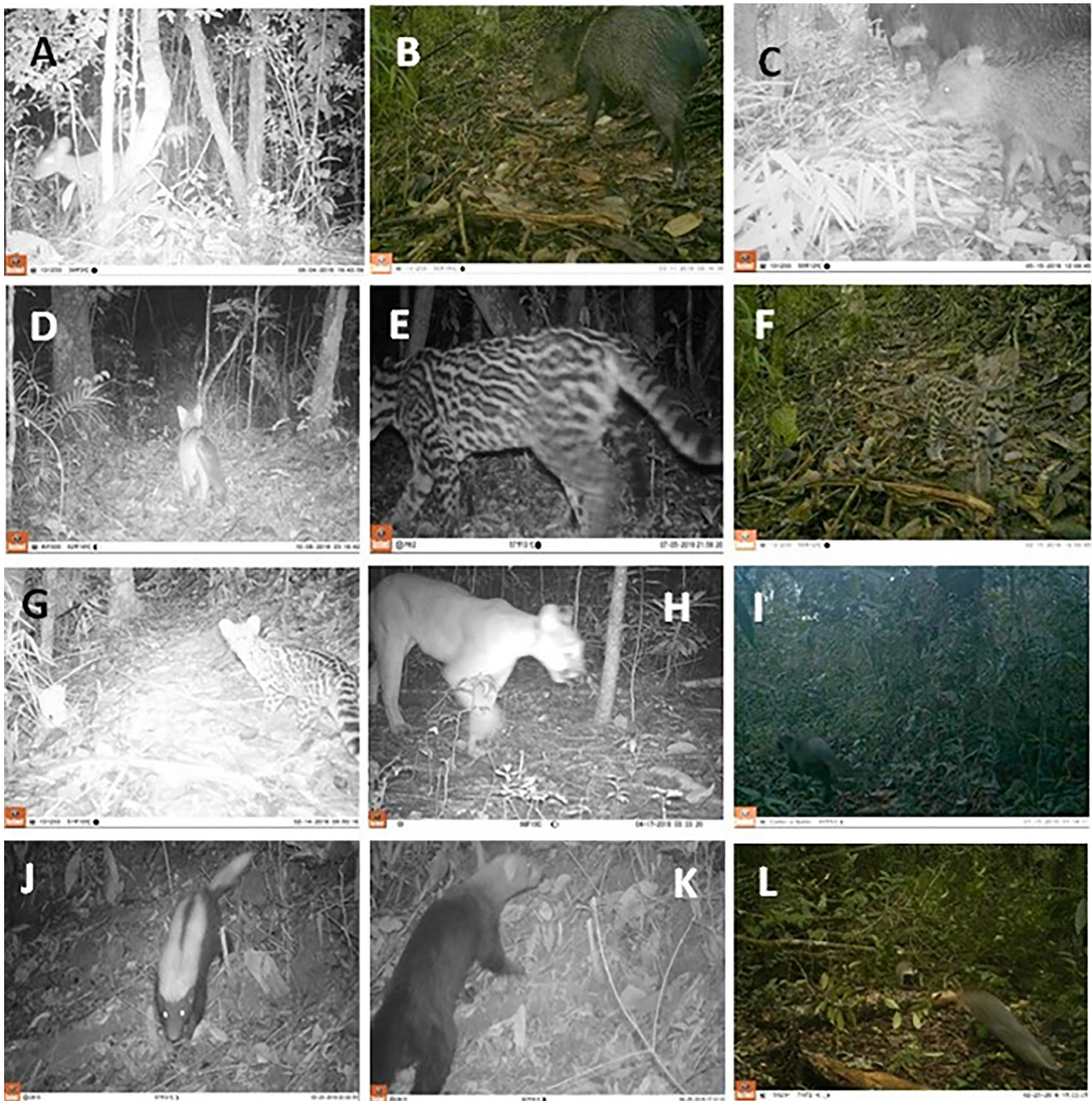

Figure 2. Mammal species recorded in the southeastern Brazilian Atlantic Forest of Minas Gerais. A) *Mazama* sp. B) *Tajacu pecari*. C) *Tayassu pecari*. D) *Cerdocyon thous*. E) *Leopardus pardalis*. F) *Leopardus guttulus*. G) *Leopardus wiedii*. H) *Puma concolor*. I) *Herpailurus yagouaroundi*. J) *Conepatus semistriatus*. K) *Eira barbara*. L) *Galictis cuja*.

The orders Carnivora and Artiodactyla were the most represented, with five and four families, respectively. The order Rodentia was represented by two families, while Cingulata, Didelphimorphia, Lagomorpha, Perissodactyla, Pilosa, and Primates were each represented by one family. Most of the recorded species were native to the Atlantic Forest (81 %), while 16 % were domestic and 3 % exotic (Table 1). Additionally, we recorded one new species in southeastern Minas Gerais, the bush dog *Speothos venaticus* (Soto-Werschitz *et al.* 2023).

There are some differences in the classification of threatened species at the global (International Union for the Conservation of Nature IUCN 2021), national (Instituto Chico Mendes de Conservação da Biodiversidade ICMBio 2018), and state levels (COPAM 2010). Among the species observed on the List of Endangered Species of Fauna in Minas Gerais state, the species *Leopardus pardalis* and *L. guttulus, Pecari tajacu, Puma concolor*, and *Tamandua tet-*

radactyla are classified as vulnerable; *L. wiedii* is classified as threatened and *Sapajus nigritus, Speothos venaticus*, and *Tayassu pecari* are classified as critically endangered (COPAM 2010; Table 1). The other species recorded in the study area are classified as Least Concern (IUCN 2021; ICMBio 2018) or are not included in the state list (COPAM 2010).

We collected a representative number of species in seasonal and ombrophilous forests (24 and 25 respectively), resulting in a sample completeness profile (seasonal $q0 = 0.91$, $q1 = 0.99$, $q2 = 1$; ombrophilous forest $q0 = 0.96$, $q1 = 0.99$, $q2 = 1$; Figures 4a, b, c; Supplementary material 2). Size-based rarefaction and extrapolation analysis and the asymptotic empirical diversity profiles suggest that our asymptotic diversity estimates for these forests are reliable to infer true diversities ($q = 1$ and $q = 2$; Figures 4b, c; Supplementary material 2). We calculated diversity and evenness measures up to a standardized coverage value of 99.8 % ($Cmax$). The alpha diversity ($q = 0$, $q = 1$, $q = 2$, and evenness

Table 1. Mammalian species richness, conservation status categories, and definition as non-native, native, or exotic species in the southeastern Brazilian Atlantic Forest of Minas Gerais (IUCN 2021; ICMBIO 2018; COPAM 2010).

Order	Family	Species	IUCN	ICMBIO	COPAM	Sp type
Artiodactyla	Bovidae	*Bos taurus*	NA	NA	NA	N-N
	Cervidae	*Mazama americana*	DD	DD	NA	N
		Mazama gouazoubira	LC	LC	NA	N
	Suidae	*Sus scrofa*	LC	NA	NA	E
	Tayassuidae	*Pecari tajacu*	LC	LC	VU	N
		Tayassu pecari	VU	VU	CR	N
Carnivora	Canidae	*Canis lupus familiaris*	NA	NA	NA	N-N
		Cerdocyon thous	LC	LC	NA	N
		Speothos venaticus	NT	VU	CR	N
	Felidae	*Felis silvestris*	NA	NA	NA	N-N
		Herpailurus yagouaroundi	LC	VU	NA	N
		Leopardus guttulus	VU	VU	VU	N
		Leopardus pardalis	LC	LC	VU	N
		Leopardus wiedii	NT	VU	EN	N
		Puma concolor	LC	VU	VU	N
	Mephitidae	*Conepatus semistriatus*	LC	LC	NA	N
	Mustelidae	*Eira barbara*	LC	LC	NA	N
		Galictis cuja	LC	LC	NA	N
	Procyonidae	*Nasua nasua*	LC	LC	NA	N
Cingulata	Dasypodidae	*Cabassous unicinctus*	LC	LC	NA	N
		Dasypus novemcinctus	LC	LC	NA	N
		Dasypus septemcinctus	LC	LC	NA	N
		Euphractus sexcinctus	LC	LC	NA	N
Didelphimorphia	Didelphidae	*Didelphis albiventris*	LC	LC	NA	N
		Didelphis aurita	LC	LC	NA	N
Lagomorphia	Leporidae	*Sylvilagus brasiliensis*	EN	LC	NA	N
Perissodactyla	Equidae	*Equus asinus*	NA	NA	NA	N-N
		Equus caballus	NA	NA	NA	N-N
Pilosa	Myrmecophagidae	*Tamandua tetradactyla*	LC	LC	VU	N
Primates	Cebidae	*Sapajus nigritus*	NT	NT	EN	N
Rodentia	Cuniculidae	*Cuniculus paca*	LC	LC	NA	N
	Sciuridae	*Sciurus aestuans*	LC	LC	NA	N

Not apply (NA), Insufficient Data-Know (DD), least concern (LC), vulnerable (VU), near threatened (NT), Endangered (EN) and critically endangered (CR). Non-native species (N-N). Native species (N). Exotic (E).

Figure 3. Mammal species recorded in the southeastern Brazilian Atlantic Forest of Minas Gerais. A) *Nasua nasua*. B) *Dasypus novemcinctus*. C) *Cabassous unicinctus*. D) *Euphractus sexcinctus*. E) *Dasypus septemcinctus*. F) *Didelphis aurita*. G) *Sylvilagus brasiliensis*. H) *Tamandua tetradactyla*. I) *Sapajus nigritus*. J) *Cuniculus paca*. K) *Sciurus aestuans*. L) *Sus scrofa*. M) *Canis lupus familiaris*. N) *Felis silvestris*.

profiles among species abundances) were similar between the two forests (Figures 4a, b, c, d, and e; Supplementary material 2). We observed that the profile curve decreased sharply in both vegetations, and the values of Pielou J index indicated an equal evenness among species abundances in each forest (seasonal $J = 0.83$; ombrophilous $J = 0.85$; Figure 4-e; Supplementary material 2).

We found that the overall beta diversity between sites was $\beta JAC = 0.37$, with a turnover of $\beta JTU = 0.34$ and species nestedness of $\beta JNE = 0.02$ (Figure 5a). When considering only the native species, the total beta diversity between sites was $\beta JAC = 0.28$, with a turnover of $\beta JTU = 0.25$ and species nestedness of $\beta JNE = 0.03$ (Figure 5b). In each forest, we observed a small number of species exclusive to it. Specifically, we found six species unique to the seasonal forest (*Dasypus septemcinctus*, *Didelphis albiventris*, *Speothos venaticus*, *Tamandua tetradactyla*, *Equus ferus*, and *Felis silvestris*), and seven species were unique to the ombrophilous forest (*Euphractus sexcinctus*, *Galictis cuja*, *Herpailurus yagouaroundi*, *Leopardus wiedii*, *Tayassu pecari*, *Bos taurus*, and *Equus africanus*). However, the overall beta diversity is primarily driven by turnover, while nestedness is almost absent.

Relative abundance. The Relative Abundance Indices (RAIs) between species were significantly different ($H = 115.24$, $d.f. = 30$, $P = 0.000$), but the effect size was not strong

(Epsilon-squared $\varepsilon^2 = 0.16$). Four species, *Didelphis aurita* ($RAI = 4.55 \pm 7.66$), *Cuniculus paca* ($RAI = 2.35 \pm 3.73$), *Pecari tajacu* ($RAI = 1.65 \pm 7.1$), *Eira barbara* ($RAI = 1.65 \pm 6.03$), had the highest RAIs, (Figure 6a; Supplementary material 3). In contrast, the species with the lowest abundance indices were *Speothos venaticus* ($RAI = 0.04 \pm 0.24$) and *Galictis cuja* ($RAI = 0.06 \pm 1.19$; Figure 6a; Supplementary material 3). Among the non-native species, *Canis lupus familiaris* ($RAI = 1.08 \pm 2.55$) had the highest relative abundance, while the *Sus scrofa* (RAI = 0.15 ± 0.56), and *Equus ferus* ($RAI = 0.04 \pm 0.18$), *Equus africanus* ($RAI = 0.04 \pm 0.62$), and *Bos taurus* ($RAI = 0.06 \pm 0.27$), the lowest values (Figure 6a; Supplementary material 3).

The relative abundance of species did not show significant differences between the two forests ($U = 453.5$; $Z = 0.37$; $P = 0.70$). However, the species *Leopardus wiedii* showed significant differences in relative abundance between forests ($U = 84.5$; $P = 0.01$; Figure 6b). In the seasonal forest, the species *Didelphis aurita* ($RAI = 4.70 \pm 8.28$), *Puma concolor* ($RAI = 2.40 \pm 7.55$), and *Sylvilagus brasiliensis* ($RAI = 2.38 \pm 8.91$) showed the highest abundance indices. On the other hand, *Speothos venaticus* ($RAI = 0.08 \pm 0.03$) and *Sus scrofa* (RAI = 0.08 ± 0.22) had the lowest abundance indices (Figure 6b; Supplementary material 3). In the ombrophilous forest, the species *Didelphis aurita* ($RAI = 4.28 \pm 6.97$), *Cuniculus paca* ($RAI = 3.26 \pm 5.3$), and *Leopardus guttulus* ($RAI = 2.23 \pm 2.16$)
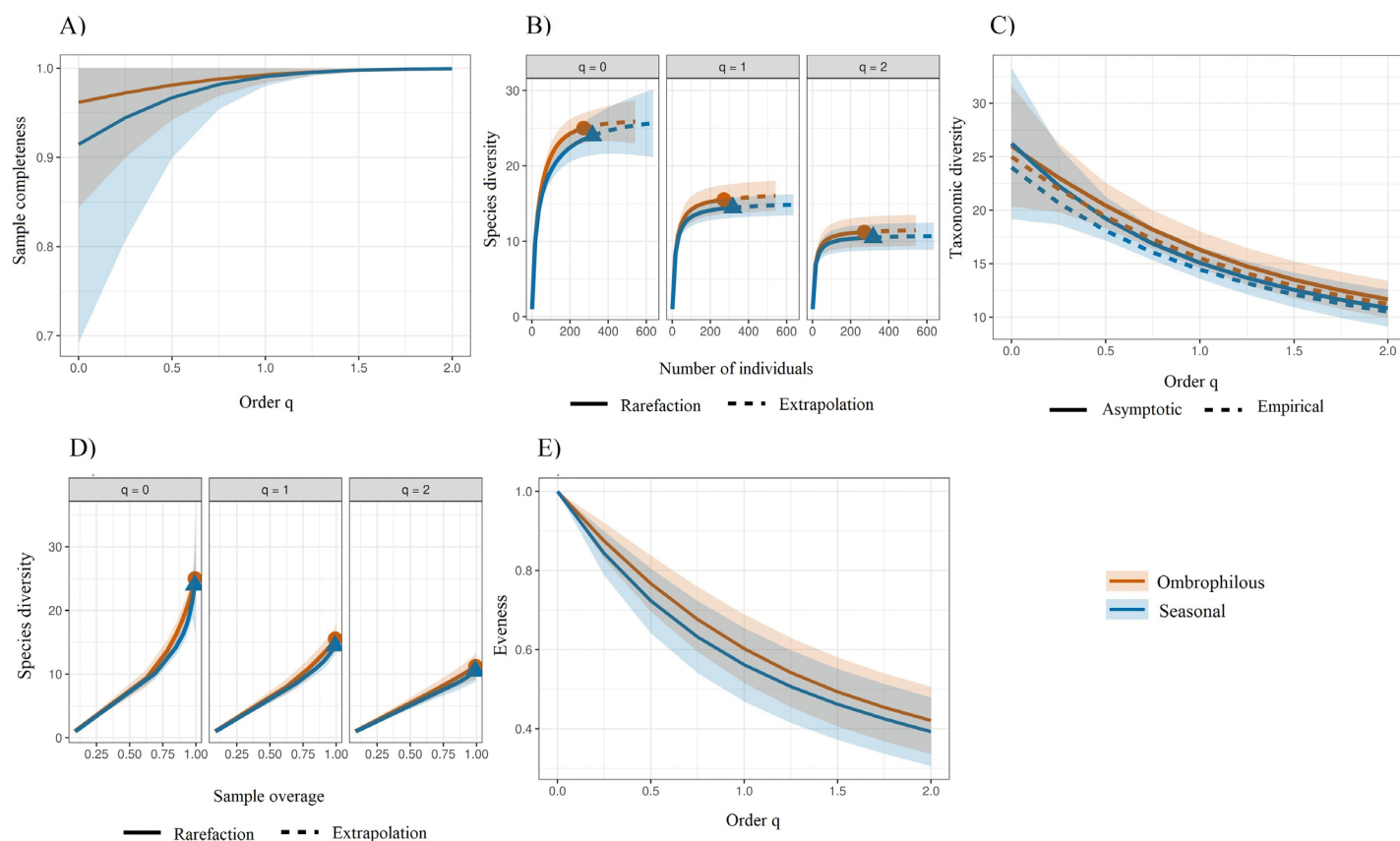

Figure 4. Diversity of mammal species assemblages in the southeastern Brazilian Atlantic Forest of Minas Gerais. A) Sample completeness profiles. B) Size-based rarefaction/extrapolation. C) Asymptotic and empirical diversity profiles. D) Non asymptotic coverage-based rarefaction and extrapolation analysis. E) Evenness among species abundances based on the normalized slope of Hill numbers. Size-based rarefaction is represented by solid curves, while extrapolation is represented by dashed curves.
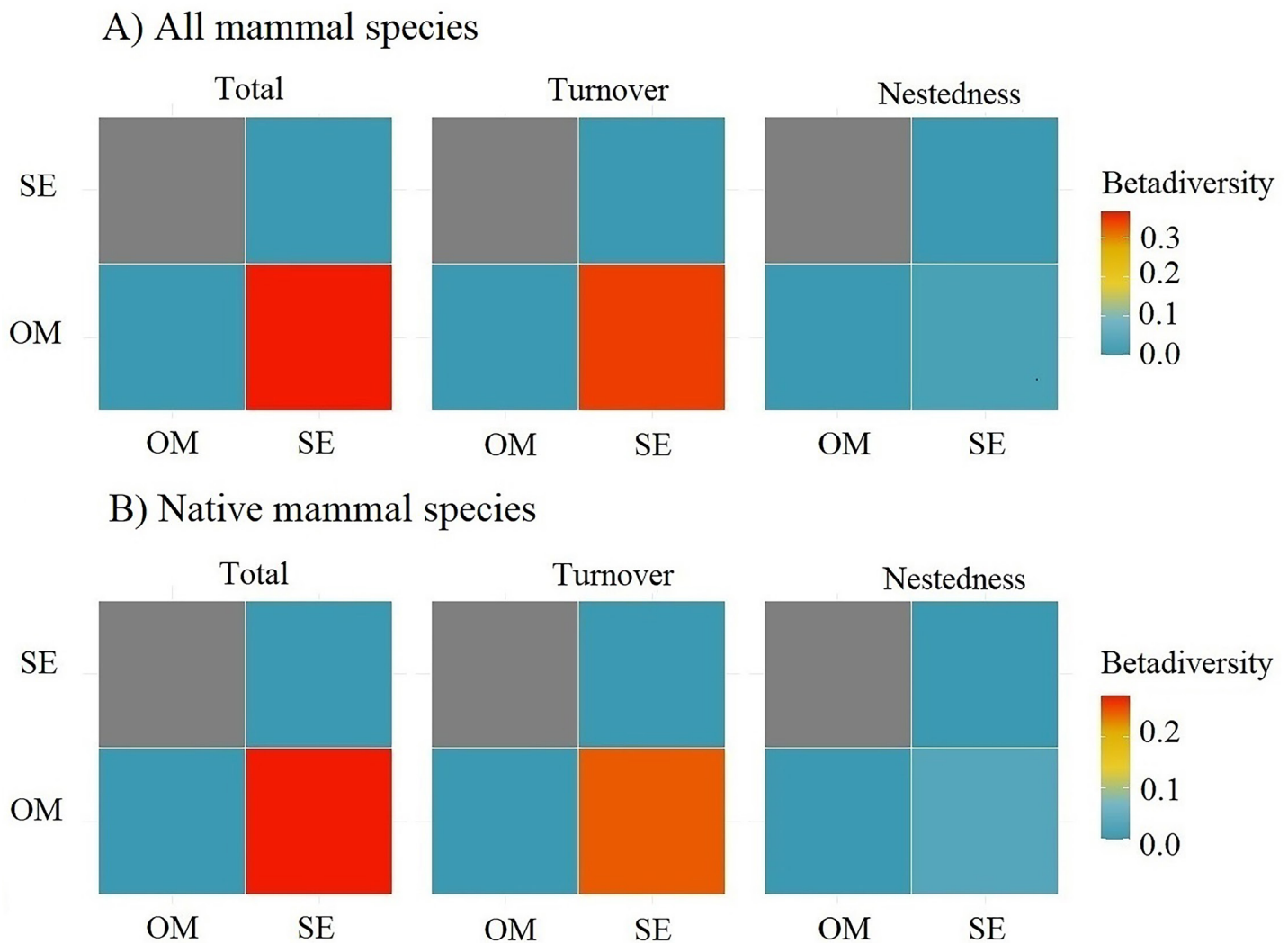
Figure 5. Beta-diversity components of mammal species between ombrophilous (OM) and seasonal (SE) forests in the southeastern Brazilian Atlantic Forest of Minas Gerais.

showed the highest abundance indices. Finally, the species *Cabassous unicinctus* (*RAI* = 0.08 ± 0.22) and *Sapajus nigritus* (*RAI* = 0.08 ± 0.22) showed the lowest indices of abundance (Figure 6-b; Supplementary material 3).

Distribution of species. The *naïve* occupancy of mammal species in the study area did not reach totality (naïve < 1; detection rate, min = 0, max = 0.68). Most of the mammalian species had restricted occupancy to a few localities and values lower than 50 % (Supplementary Material 3). The highest values were for the species *Eira barbara* (68 %), *Didelphis aurita* (55 %), *Cuniculus paca* (45 %), *Pecari tajacu* and *Puma concolor* (41 %), *Leopardus guttulus* and *Leopardus pardalis* (36 %). Instead, the species *Tayassu pecari*, *Tamandua tetradactyla*, and *Speothos venaticus* presented the lowest values (5 %). Regarding the non-native species, *Canis lupus familiaris* had the highest naïve occupancy values (32 %), whereas *Sus scrofa* (9 %), *Bos taurus*, *Equus ferus*, *Equus africanus*, and *Felis silvestris* had the lowest values (5 %; Supplementary Material 3).

In the seasonal forest, the naïve occupancy of the 24 mammal species ranged from 7 % to 57 %. The species with the highest values of naïve occupancy were *Eira barbara*

(57 %), *Didelphis aurita* (50 %), *Puma concolor*, and *Cuniculus paca* (43 %; Supplementary Material 3). In contrast, in the ombrophilous forest, the naïve occupancy of the 25 mammal species ranged from 12 % to 88 %. The species with the highest values were *Eira barbara* (88 %), *Didelphis aurita*, *Pecari tajacu*, and *Leopardus guttulus* (62 %; Supplementary Material 3). Finally, we found a correlation of 75 % between the average RAI and naïve occupancy (r² = 0.75). The species *Didelphis aurita*, *Cuniculus paca*, *Pecari tajacu* and *Eira barbara* showed the high occupancy and RAIs (Figure 7; Supplementary Material 3).

Discussion

The gamma diversity was 32 mammalian species, which accounts for approximately 12 % of the terrestrial non-flying mammal species recorded in the Brazilian Atlantic Forest (Figueiredo *et al.* 2021). The richness of species found in our study area was similar to the reported in other localities within the Atlantic Forest, which varies from 17 to 39 species (Bogoni *et al.* 2016, 2017, 2018; Souza *et al.* 2019; Ríos *et al.* 2021). Therefore, our results suggest that the study area is preserving a representative fraction of the original rich-
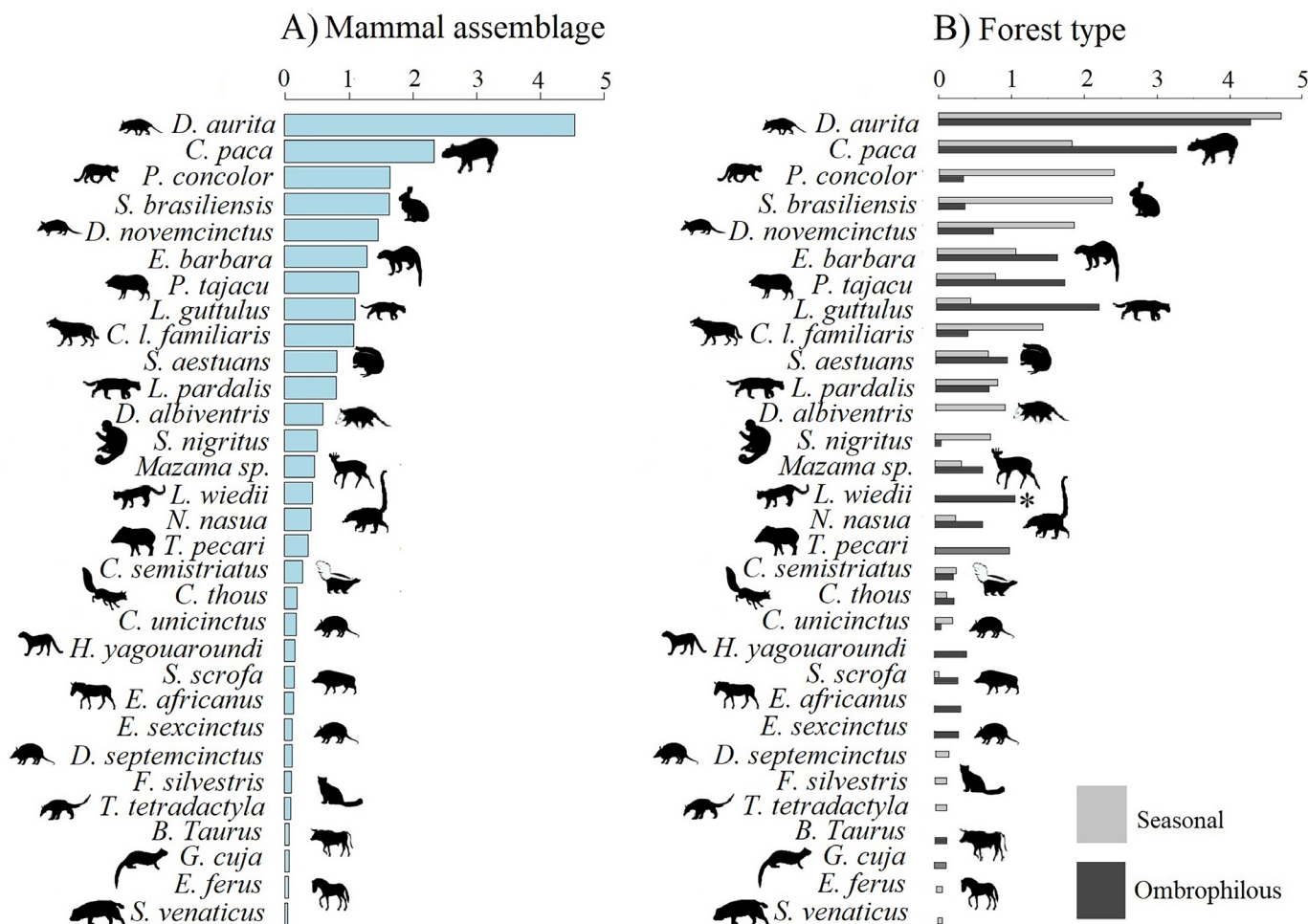
Figure 6. Differences in Relative Abundance Index (average RAIs) between mammals based on camera trap photographs in the southeastern Brazilian Atlantic Forest of Minas Gerais. *Leopardus wiedii* (*U* = 84.5; *P* = 0.011*).

ness of medium to large-sized in the Atlantic Forest. Furthermore, our study demonstrates that camera trapping is a suitable method to record rare, uncommon, and cryptic species (Figueiredo *et al.* 2021; Trolliet *et al.* 2014; Wearn *et al.* 2019), such as *Speothos venaticus*.

The order Carnivora exhibited the highest species richness, which is consistent with previous studies in the Atlantic Forest (Santos *et al.* 2016; Bogoni *et al.* 2018; Souza *et al.* 2019). Mesocarnivores accounted for the majority of the diversity (87 %), supporting the findings of Bogoni *et al.* (2018, 2020), Regolin et al. (2017), and the mesopredator release hypotheses (Crooks and Soulé 1999), which explains how the extirpation of apex predators benefits medium-sized carnivores. The detection of the puma, the only large mammal species in the area, is particularly noteworthy in the Atlantic Forest of Minas Gerais due to its crucial role in ecosystem structure, services, and functioning (Botelho *et al.* 2018).

Contrary to our expectations, we found no evidence for differences in alpha diversity or evenness profiles between the two forests, and the β-diversity values (<37 %), corresponded almost entirely to species turnover. Therefore, the expected degree of species homogenization in the Atlantic

Forest in Minas Gerais, was not found in the sampling area. The observed β-diversity could be due not only to differences between vegetation types but also likely to a mixture of factors such as body size (Bogoni *et al.* 2017), activity areas (Botelho *et al.* 2018), and habitat loss and fragmentation (Püttker *et al.* 2020).

Of the registered mammals, 35 % corresponded to species on the List of Endangered Species of Fauna in Minas Gerais, which explains their restricted distribution (naïve <0.5), and the low relative abundances (RAI <1). Our results confirm that variation in species abundance and occupancy of mammals in the Atlantic Forest (Souza *et al.* 2019), but in our case the species with the highest RAI were *Didelphis aurita* and *Cuniculus paca*. Additionally, our results confirm the high levels of defaunation present in the Atlantic Forest (Bogoni *et al.* 2016, 2018; Ríos *et al.* 2021), corresponding to 46 % (Galetti *et al.* 2021).

The only mammal species with the highest abundance indices and naïve occupancy in the seasonal and ombrophilous forest was *Didelphis aurita*. This didelphid exhibits strong plasticity in habitat, resource use, and higher matrix tolerance (Bogoni *et al.* 2016), which probably explains its presence in landscapes with agricultural matrices such as

those in this study. Furthermore, we must consider that species with small home ranges have a higher probability of detection (Santos *et al.* 2021). Therefore, it is likely that we overestimated their abundance by photographing the same individuals several times at some localities, because the cameras were placed in areas that covered their home range.

Surprisingly, the relative abundance and occupancy values of non-native species were not high in the sampled areas. The specie *Canis lupus familiaris* had a moderate abundance and a restricted distribution ($RAI = 1.8$; 32 % naïve occupancy), while *Sus scrofa* had one of the lowest values ($RAI = 0.15$; 9 % naïve occupancy). It is possible that they have not yet extended their population to the areas we sampled, or that we underestimated their abundance. Therefore, we should not ignore their presence as these species can cause increased disturbances to native fauna, predation, competition for resources, and transmission of diseases (Quintela *et al.* 2020). The wild boar continues to expand their distribution in the forest remnants (Galetti *et al.* 2021; Rosa *et al.* 2016). Therefore, we need planning management strategies to control their presence (De Assis Morais *et al.* 2020; Rosa *et al.* 2016).

Our study highlights the rarity of most species in the Atlantic Forest and provides valuable insights into the habitat use of mammals. Notably, while both forests exhibit similar species richness, their compositions differ. Therefore, we emphasize the importance of conserving all remaining native forest remnants, to favor particularly rare and threatened species (35 %) that are susceptible to local extinctions in the Minas Gerais Atlantic Forest (Ferreira *et al.* 2020).

Figure 7. Correlation between the Relative Abundance Index (average RAI) and the naïve occupancy (PA0) for the community of mammals in the southeastern Brazilian Atlantic Forest of Minas Gerais. 1. *D. aurita*. 2. *C. paca*. 3. *P. concolor*. 4. *S. brasiliensis*. 5. *D. novemcinctus*. 6. *E. Barbara*. 7. *P. tajacu*. 8. *L. guttulus*. 9. *C. l. familiaris*. 10. *S. aestuans*. 11. *L. pardalis*. 12. *D. albiventris*. 13. *S. nigritus*. 14. *Mazama sp.* 15. *L. wiedii*. 16. *N. nasua*. 17. *T. pecari*. 18. *C. semistriatus*. 19. *C. thous*. 20. *C. unicinctus*. 21. *H. yagouaroundi*. 22. *S. scrofa*. 23. *E. africanus*. 24. *E. sexcinctus*. 25. *D. septemcinctus*. 26. *F. silvestris*. 27. *T. tetradactyla*. 28. *B. Taurus*. 29. *G. cuja*. 30. *E. ferus*. 31. *S. venaticus*.

In conclusion, in order to prevent further extinctions and mitigate the risk of dramatic scenarios, it is crucial to understand the alpha and beta diversity of forest fragments in different landscapes (Bogoni *et al.* 2016). We need to prioritize restoration programs and establish functional connectivity between fragments to ensure species dispersal between the two forests and across landscapes (Beselga 2010; Bogoni *et al.* 2018).

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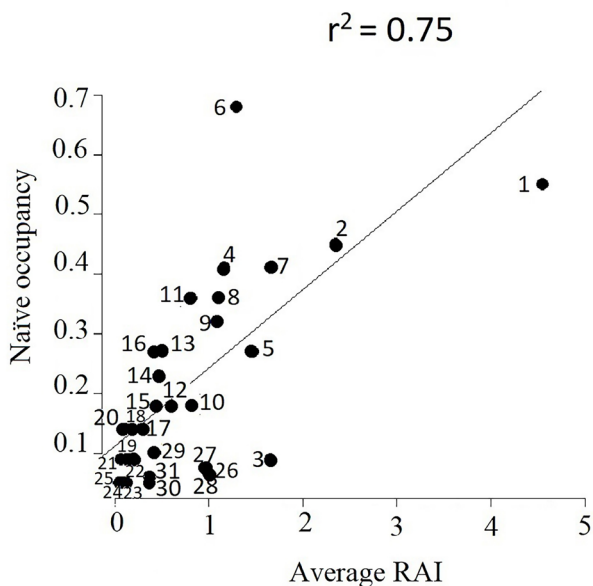
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Supplementary material 1

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