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A cobertura florestal e o tipo ambiental moldam a diversidade funcional de aves insetívoras dentro da Mata Atlântica do sudeste Brasileiro

São Carlos – SP

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A cobertura florestal e o tipo ambiental moldam a diversidade funcional de aves insetívoras na Mata Atlântica do sudeste Brasileiro

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A cobertura florestal e o tipo ambiental moldam a diversidade funcional de aves insetívoras na Mata Atlântica do sudeste Brasileiro

RESUMO

As aves que se alimentam de artrópodes são um grupo heterogêneo, com diferentes níveis de sensibilidade ambiental e diversas respostas à degradação do habitat. Neste trabalho, testamos os efeitos da paisagem sobre a diversidade funcional de aves insetívoras na Mata Atlântica brasileira. Prevemos que (I) a composição das espécies e a diversidade funcional são moldadas pelo *turnover* e aninhamento em diferentes habitats, e (II) o gradiente da cobertura florestal tem um efeito positivo na composição das espécies de aves e na diversidade funcional. Foram utilizados dados de 22 paisagens de Mata Atlântica na região da Cantareira-Mantiqueira (Brasil), dentro de buffers de raio de 1 km, sobrescrevendo três tipos de ambientes (ou seja, florestas, pastagens e pântanos). Os componentes da diversidade β-funcional foram calculados utilizando-se o par beta e beta multifuncional para cada tipo de ambiente, e os efeitos do gradiente de cobertura florestal e do tipo de ambiente foram testados utilizando modelos lineares e GLMM, respectivamente. Nossos resultados mostraram que o gradiente de cobertura florestal e o tipo de ambiente tiveram um efeito negativo sobre os índices de diversidade funcional, contrariando nossas expectativas. Pastagens e pântanos foram suscetíveis à rotatividade e nidificação, respectivamente. A diversidade beta das florestas foi influenciada tanto pela nidificação quanto pela rotatividade das espécies. Os fragmentos florestais nativos regionais são geralmente de pequeno porte e em estágios iniciais de sucessão, o que poderia explicar os padrões que encontramos. A presença de florestas secundárias pode ter afetado o padrão esperado de diversidade funcional, portanto, é preciso cautela ao interpretá-la, uma vez que a forma como a dinâmica compensatória pode não envolver uma compensação funcional real.

Palavras-chave: Aves insetívoras, Cobertura florestal, Diversidade funcional beta, Diversidade funcional, Mudança na paisagem.

Forest cover and environmental type shape functional diversity of insectivorous birds in Atlantic Forest of southeastern Brazil

ABSTRACT

Arthropod-eating birds are a heterogeneous group, with different levels of environmental sensitivity and diverse responses to habitat degradation. In this paper, we tested the effects of landscape on the functional diversity of insectivorous birds within the Brazilian Atlantic Forest. We predict that (I) species composition and functional diversity are shaped by turnover and nestedness across different habitats, and (II) the gradient of forest cover has a positive effect on bird species composition and functional diversity. We used data from 22 landscapes of the Atlantic Forest in the Cantareira-Mantiqueira region (Brazil), within buffers of 1 km radius, surrogating three types of environments (i.e., forests, pastures, and marshes). The components of β-functional diversity were calculated using the beta pair and beta multi-function for each type of environment, and the effects of the forest cover gradient and environment type were tested using linear models and GLMM, respectively. Our results showed that the forest cover gradient and the type of environment had a negative effect on the indices of functional diversity, contrary to our expectations. Pasturelands and marshes were susceptible to turnover and nestedness, respectively. The beta diversity of forests was influenced by both species nestedness and turnover. The regional native forest fragments are generally small-sized, and in early successional stages, which could explain the patterns we found. The presence of secondary forests may have affected the expected pattern of functional diversity, therefore, caution is needed when interpreting this, since the way in which compensatory dynamics may not involve real functional compensation.

Key words: Beta functional diversity, Forest cover, Functional diversity, Insectivorous birds, Landscape change.

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SUMÁRIO

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1. INTRODUCTION

Occupying 8% of all South America, the Atlantic Forest extends along the entire Brazilian coastline, including the restinga and inland regions, occurring from Pernanbuco to Rio Grande do Sul (SICK; BARRUEL, 1984; TABARELLI et al., 2005). The Atlantic Forest is home to 60% of the Brazilian fauna and flora threatened with extinction. This biome provides shelter for several species, especially birds, with nearly 900 species (~30% of the Neotropical avifauna). The region boasts an almost incomparable species richness (REZENDE et al., 2018; STOTZ et al., 1996). Despite enormous richness, only 28% of the original vegetation of the biome remained standing, most of it in the southern region. However, only a third of the remaining vegetation is legally protected; the remaining vegetation is small and isolated fragments (ORME et al., 2019; et al., 2018; RIBEIRO et al., 2009).

Agroecosystems, urban sprawl, and human needs for natural resources have converted pristine ecosystems into fragmented and anthropogenic landscapes (JOHNSON et al., 2017). In the Atlantic Forest the predominant commodity crops are sugarcane (~5.2 Mha), eucalyptus (~5.8 Mha) and soy, corn, and coffee (~14.4 Mha together). Their recent expansion over pastures may have shifted these activities to steeper regions, eagerly for deforestation as well (ROSA et al., 2023). Indeed, one of the main components driving forest loss across the Earth is deforestation for commodity extraction, silviculture, shifting agriculture (i.e., conversion of forest lands to agriculture, that may later be abandoned followed by subsequent forest regrowth) and forest fires (CURTIS et al., 2018; DINIZ et al., 2022).

Environmental changes have led to a reduction in the size and connectivity of native vegetation, boosting edge effects and isolation between patches (FAHRIG, 2003). This ultimately a result in both local extinctions and communities declines, mainly for the most sensitive species, leading to biodiversity losses, environmental homogenization (CHACE; WALSH, 2006; GREEN et al., 2005; TILMAN, 2001), depletion in the maintenance and integrity of ecological functions (GRIMM et al., 2008; TYLIANAKIS; TSCHARNTKE; LEWIS, 2007; ULRICH et al., 2016) and the provision of ecosystem services (DE COSTER; BANKS-LEITE; METZGER, 2015; DUARTE et al., 2018).

The landscape mosaics are composed mainly by anthropogenic matrix (i.e., pasture, agriculture, planted forest, etc.) and native forest remnants, which can be unique refuges for biodiversity (ŞEKERCIOĞLU et al., 2002). Shape, size, and location of these native habitats,

and the structure and composition of the surrounding land cover (HAILA, 2002; KUPFER; MALANSON; FRANKLIN, 2006), are central for defining the structure and composition of biological composition. Studies on how habitat reduction and fragmentation have been affecting the arrangement of biological communities (ecological drift) and species responses (environmental filtering) have become increasingly common (ADORNO et al., 2021; BOESING; NICHOLS; METZGER, 2017; MORANTE-FILHO et al., 2015; PARDINI; NICHOLS; PÜTTKER, 2017). However, the role of anthropogenic landscape matrix as a modifying agent of community assemblies still unclear, and the results of habitat loss in communities composition, ecological functions, and ecosystem services provision are barely known (BARROS et al., 2019a; KUPFER; MALANSON; FRANKLIN, 2006; BOESING et al., 2022; MEDEIROS et al., 2019; PARDINI; NICHOLS; PÜTTKER, 2017). A landscape perspective is required to understand the effects of agriculture land use on the biodiversity and ecological processes (e.g., arthropod predation; DE SOUZA LEITE et al., 2022; TSCHARNTKE et al., 2005; TURNER; DONATO; ROMME, 2013).

Intensification of agricultural practices has led to the homogenization of the landscapes (DUDLEY; ALEXANDER, 2017), and it is assigned as one of the main factors leading to the decline of arthropods (SÁNCHEZ-BAYO; WYCKHUYS, 2019). This is a result derived from the loss of natural habitats and/or use of toxic pesticides (defined as the concentrations of polyunsaturated fatty acids) that modify the abundance, availability, and quality of aerial insects (ATTWOOD et al., 2008; BELLAVANCE et al., 2018; GÉNIER et al., 2021; PAQUETTE et al., 2013; TWINING; SHIPLEY; WINKLER, 2018). The decline in the availability of nutritious aquatic insects can negatively affect both birds' nestling growth, and fledging success (TWINING et al., 2016; TWINING; SHIPLEY; WINKLER, 2018).

Since bird communities are highly susceptible to modifications in agroecosystems (BERG, 2002; CATARINO et al., 2016; HERRERA et al., 2016), it is to be expected that modifications to the landscape will alter the composition of the local fauna and flora. These modifications result in either turnovers in species composition (i.e., dissimilarity among species composition across an environmental gradient) ;(BASELGA, 2010), or in nestedness (i.e., loss or gain of species, creating a subgroup of the original community); (BASELGA; BONTHOUX; BALENT, 2015; POLLOCK et al., 2020). In this sense, when one community is not identical to another, they can be described by both processes above, since the only requirement to generate them is the species replacement and the loss (or gain) of species.

Despite the importance of forests, another ecosystem globally degraded by agriculture are the marshes (REIS et al., 2017; Ramsar Convention on Wetlands 2018). These environments perform central functions such as regulating water flows and dampening floods; modifying and controlling water quality, controlling erosion and siltation; supplying of food and breeding sites for aquatic fauna, and refuge for terrestrial fauna (SALATI, 2000; REIS et al., 2017). More than half of wetlands had been affected in the last 60 years due to agricultural soil drainage and other processes (DAHL 2014; WATMOUGH et al., 2017) in the USA. A critically endangered Neotropical bird species (IUCN, 2022), the São Paulo Antwren (*Formicivora paludicola*), had severe feeding restrictions caused by the loss of quality of flooded environments, its exclusive habitats. The rapid-growth of the invasive species *Hedychium coronarium* interrupted the natural flow of water and, consequently, the maintenance of the marshes ((DEL-RIO et al., 2017).

 Landscape modifications usually tend to result in changes in ecological assemblages, modifying the composition of communities (NEWBOLD et al., 2015) leading to homogenization at any level of organization, whether genetic, taxonomic, or functional (OLDEN; ROONEY, 2006), as species diversity is reduced and replaced by widespread species (CLAVERO; BROTONS, 2010; GÁMEZ-VIRUÉS et al., 2015). Bird diversity is shaped by a range of human activities; however, the effect of changes in land use (e.g., decline in native forest cover) is arguably one of the more effective (FULLER; BURSLEM; PINARD, 2012). Studies at the landscape scale have found evidence for a threshold of forest cover; below this level, the response of communities and species changes dramatically (BETTS; FORBES; DIAMOND, 2007; MARON et al., 2012; MORANTE-FILHO et al., 2015, 2018; SWIFT; HANNON, 2010). Determining the impacts of shifts in forest cover is important because certain regions are home to many endemic species or species of high conservation interest (CORKERY et al., 2020).

Native forests are responsible for the provision of several ecosystem services (e.g., pest control, pollination, and seed dispersal) (DUARTE et al., 2018; WENNY et al., 2011), and the reduction of these vegetation can be critical within agroecosystems (TSCHARNTKE ET AL., 2016). Indeed, vegetation fitness is strongly dependent on the arthropod control provided by insectivorous vertebrates (e.g., birds and bats) due to the cascade effects (KARP; DAILY, 2014; MÄNTYLÄ; KLEMOLA; LAAKSONEN, 2011). Nearly 8-15% of world production of wheat, rice, potatoes, soybeans, cotton, and maize is damaged by arthropods, which would range from 9-37% without any biological control and pesticides (OERKE,

2006). There are estimates that the consumption of foliage-gleaning arthropods breaks ~13% of all potential crop production in the US (~US\$ 33 billion; PIMENTEL; ZUNIGA; MORRISON, 2005). Without the ecosystem services provided by native species that prey on these arthropods, the estimated damage would reach ~US\$ 4.5 billion higher (LOSEY, 2009).

The decline in species richness has been widely observed (CORRELL et al., 2019; JIGUET et al., 2010) and is often related with changes in land cover. Until the 1990s, ecological theory investigated which processes determined species abundance and richness in space and time (SILVA et al., 2022). However, species richness alone could not reveal the whole story about the biodiversity of an area; actually, this only provides an estimate of the species number (HAN et al., 2021). The more explicit use of species traits (i.e., morphological, physiological, and phenological characteristics, that may affect fitness, rates of growth, reproduction and survival; VIOLLE et al., 2007) as a central idea to explain their distribution and how they would affect the ecosystems, only started in the 2000s (DÍAZ; CABIDO, 2001; MCGILL et al., 2006); this shift in the focus of ecology became known as the "biodiversity revolution" (CERNANSKY, 2017). From then on, diversity measures started to be represented not only by differences in species number and quantity, yet also by differences and similarities of functional traits. Thus, the difference in the degree of expression of these functional traits across populations, communities, or ecosystems, is defined as functional diversity (GARNIER; NAVAS; GRIGULIS, 2016). Therefore, the trait-based approach assumes that changes in functional trait composition across different landscapes are more predictable than using species composition alone (FUKAMI et al., 2005).

Studies that combine the relationships between traits and the environment have been related to environmental or habitat filters (BELLO et al., 2021). This idea is based on "filtering" species from a regional pool into local communities according to their traits (DÍAZ; CABIDO; CASANOVES, 1998; KEDDY, 1992; MACARTHUER; WILSON, 1967). In short, within a geographically defined space (i.e., either communities or assemblages), a series of hierarchical filters determine the traits that provide the best performance within the specific ecological conditions; therefore, which species are most likely to coexist within that space. Focusing only on taxonomic and phylogenetic diversity may pose a risk to biodiversity conservation, since these strategies may not ensure high functionality (MAZEL et al., 2018).

Distinct patterns of taxonomic and functional diversity had been described in response to environmental changes (PRESCOTT et al., 2016). Although many studies focus on the effects of anthropogenic changes on biodiversity, they are still limited to patterns found on either

species richness (GIBSON et al., 2011) or taxonomic diversity metrics (NAEEM et al., 2012). Because the structuring of bird guilds and their species composition varies spatially (HOLMES; BONNEY JR.; PACALA, 1979; HOLMES; RECHER, 1986), as they prefer to live in heterogeneous landscapes to better suit nesting, roosting, and foraging (AGGARWAL; SAHI; WANI, 2008; BERG, 2002; VEECH; SMALL; BACCUS, 2011). Knowledge related to the habitat preferences of avian species is vital for analyzing their responses to habitat changes and their conservation policies (LAWTON et al., 1998; SEKERCIOGLU, 2006). Furthermore, the association of birds with environmental heterogeneity helps to decipher the influence of biotic interactions on the distribution of bird species (JANKOWSKI et al., 2013) and functional traits (SPAKE et al., 2020).

In this paper, we tested the effects of landscape on the functional diversity of insectivorous birds within the Brazilian Atlantic Forest. We investigate whether there would be a correlation between the environmental variables of the type of environments (i.e., pasture, native forest, and marsh) and forest cover and the indices of bird functional diversity and species composition. We hypothesize that the environment type and native forest cover gradient filter the functional traits and - thereby - the functional diversity of insectivorous birds in the context of the Atlantic Forest. We predict that (1) species composition and functional diversity are shaped by species turnover and nestedness across different types of environments. Environments under the influence of human disturbance as pasturelands, dominance of generalist species having increased dispersion ability, and greater nestedness effect are expected, arising in a reduced biodiversity due to homogenized landscape mosaics (KARP et al., 2012). The species turnover effect would be more associated with heterogeneous environment characteristics with different successional backgrounds (ARROYO-RODRÍGUEZ et al., 2013). We also predict that (2) the gradient of percentage of relict native vegetation cover has significant and positive effects on the composition of insectivorous bird assemblages and on functional diversity. Areas having higher forest cover would support greater functional diversity, which may also be related to a greater complexity of the forest habitats (e.g., vertical structure; MORELLI et al., 2018).

2. METHODS
2.1. Study site
The study was conducted in the ecological corridor of Cantareira-Mantiqueira (Fig. 1), which is located ~50 km far from the metropolitan region of São Paulo, and where long-term ecological research (LTER CCM) has been conducted since 2014. The Corridor of Cantareira-

Mantiqueira is in the southeastern of the Atlantic Forest (dense rain rainforest), in an area of ~700,000 ha, with elevation ranging from 700 to 1,700 m. a.s.l, connecting two large forest blocks, the Cantareira State Park and the Serra da Mantiqueira (BOSCOLO et al., 2017). The Atlantic Forest has key interest for biological conservation, and is considered as a biodiversity hotspot mainly for birds, due to the high species richness and endemic species (620 species; MYERS et al., 2000).
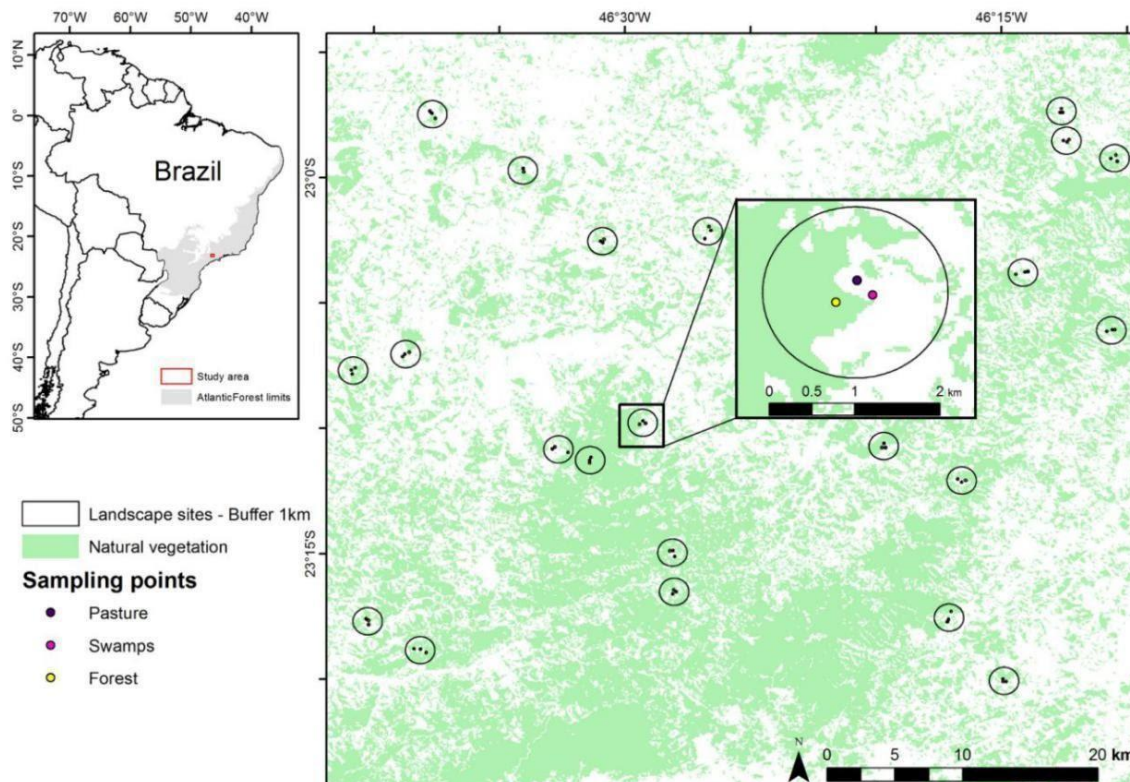
Fig. 1 Landscapes where soundscape data were collected using autonomous audio recorders within the Long-Term Ecological Research of Ecological Corridor Cantareira-Mantiqueira (LTER CCM or PELD CCM), São Paulo, Brazil between October 2016 and January 2017 (Gaspar 2021)

The region comprises landscape mosaics having a wide gradient of forest losses and large heterogeneity of land use, and most of the forest remnants are small (i.e., <100 ha) and isolated fragments, composed by second-growth forests in early to medium stages of succession (METZGER et al., 2009; RIBEIRO et al., 2009). These forest remnants are surrounded by multiple land use systems, including several agroecosystems, such as pasture, small scale agriculture, forestry, regenerating forests, and urban areas (BARROS et al., 2019b). Köeppen climate classification for this region is Cwa, that is, humid subtropical with dry winters and hot summers (ALCARDE ALVARES et al., 2013).

2.2.   Selection of landscapes

We used data derived from 22 landscapes sites that were selected in the LTER CCM region (Fig. 1). Forest cover data for each landscape consisted of buffers at scales of 100m, 200m, 500m, 1km and 2km radius, arbitrarily chosen based on the theory of sound transmission in different environments (FARINA; PIERETTI; PICCIOLI, 2011; SCARPELLI; RIBEIRO; TEIXEIRA, 2021). For this study, we used only data from the 2 km radius scale, relying on previous evidence from multiscale analysis of bird responses to landscape structure (ADORNO et al., 2021; BARROS et al., 2019a). These landscapes represent a gradient of forest cover varying between 1% and 97%, in a radius of 1 km around the centroid of each landscape.

Within each landscape, three different types of habitats (~100 meters distant from each other) were sampled: forests, pastures, and marshes. The pastures were mostly for raising cattle, and marshes (i.e., defined as wetlands frequently or continually inundated with water) (KEDDY, 2010), were typical lower portions of the relief (GASPAR, 2021). The position of the forest sampling points were at least 50 meters away from any forest edge. The total data sampling time for all landscapes was 90 days, 30 days for each environment site and then switched to the next type of environment in the same landscape. Habitats were sampled between October 2016 and January 2017, starting with forest sites, sampled from October to November; then marshes, between November and December, and finally pastures, sampled between December and January. The breeding season for most birds in the southern hemisphere occurs during this time of year (DEVELEY; PERES, 2000).

2.3.   Sound records and bird data

Sound data were collected in three environments per landscape (66 sampling points) in each of the 22 landscapes sites. Data were collected using 22 Song Meter Digital Field Recorders (SM3; Wildlife Acoustics. Inc. Massachusetts) equipment. They were attached to tree trunks 1.5 m above the ground at the center of each landscape site. The recorders were equipped with two omnidirectional microphones (frequencies between 20 Hz and 20 kHz) and were configured for a sampling rate of 44.1 kHz, 16 bits and mono mode to save space and equipment battery (GASPAR, 2021).

We used a subset of the recordings that was organized by Gaspar (2021). They were organized by following four steps: (1) five 25-minutes files were selected in the periods of greater bird activity (05:00 am, 05:45 am, 06:30 am, 07:15 am, and 08:00 am) per day (9,151 files with 228,775 minutes); (2) two minutes were randomly extracted from each file, thus

totaling 18,594 minutes; (3) these minutes were grouped into nine random packages of 300 minutes each (2,700 minutes total), with 100 minutes for each landscape (forest, marsh and pasture) per package; (4) the nine packets were sent to bird experts, and the occurrence of species was cataloged every minute. Finally, 10,437 bird vocalizations were classified, 9,437 at the species level, 192 at the genus level and 808 unidentified (distant or doubtful calls), which were excluded. Each species was cataloged only once per minute, regardless of the number of times it vocalized in the recording.

2.4. Bird selection and traits

Bird species were classified according to seven traits (diet, biomass, bill and wing length, foraging environmental strata, migratory status, and habitat preference). Only bird species whose diet consisted mainly of invertebrates ($\geq$60%) were considered in this paper, according to the classification proposed by Wilman et. al. (2014). The wing length (mm) and bill size (mm) were extracted from Tobias et al (2022). Migratory status and habitat preference were based on a nationwide reference (SOMENZARI et al., 2018; IUCN 2022).

The total wing length is related to movement capacity and tolerance to habitat loss and fragmentation, foraging, seed dispersion, and nutrient cycling (RODRIGUES et al., 2019). The ability to perform long-distance movements and, consequently, the potential to colonize isolated habitats (BARBOSA et al., 2020) is associated with the trait of migratory strategies (SOMENZARI et al., 2018). Diet composition and foraging strata provide a deep understanding of how species occupy specific niches, retrieve food resources (Petchey and Gaston 2006), and the ecosystem functions they perform; in this case, arthropod population control (SEKERCIOGLU, 2012). Preference for a specific habitat is related to the bird's sensitivity and the liability of persisting in specific habitats, where the resource supply is adequate. The ability of these birds to capture their food and the use of habitats and microhabitats (LUCK et al., 2012) are also related to beak length (RODRIGUES et al., 2019). All traits can be checked on TABLE 1.

Table 1: Birds traits used to calculate functional diversity metrics (see WILMAN et al., 2014; MELO et al., 2021).

Trait	Range	Definition
Diet	0-100%	Corresponding to the percentage of each item in the diet (e.g., invertebrates, endothermic and ectothermic vertebrates, unknown vertebrates, fish, seeds, nectivores, plants, and fruits)
Biomass (g)	3-1200	The weight (g) of each species
Foraging strata	0-100%	Percentage of each level of forage stratum (in this case, water around the surface, soil, mid, canopy, and aerial) used by the species
Bill length (mm)	8-152	Beak size, in millimeters, of each bird species

Wing length (mm)	42-400	Wing size, in millimeters, of each bird species
Migratory status	0-1	Classification of species as non-migrant (0) and migrants (1)
Habitat preference	1-7	The habitat in which each bird species prevails, such as: 1 - Forest (tall trees-dominated vegetation, closed canopy, including palm forest); 2 - Wetland (wide range of freshwater aquatic habitats including lakes, marshes, marshes and reedbeds); 3 - Non Forest (includes Grassland, open dry to moist grass-dominated landscapes, at all elevations, Shrubland, low stature bushy habitats, included thorn scrub, thorny or arid savanna, caatinga, xerophytic shrubland and coastal scrub); and Human modified (urban landscapes, intensive agriculture, gardens); 4 - Forest + Wetland; 5 - Forest + Non Forest; 6 - Wetland + Non Forest; 7 - Forest + Wetland + Non Forest

2.5. Beta diversity and functional diversity indexes

To calculate the functional diversity indexes, we perform the following steps (LALIBERTÉ; LEGENDRE, 2010; MELO et al., 2021). First, the functional distance between each pair of species was continuous, according to their trait values using the method of Pavoine et al (2009), as we use functional traits with different natures (i.e., categorical, quantitative, and fuzzy variables). The generated distance matrix was then subjected to a Principal Coordinate Analysis (aka PCoA) to obtain a subset of PCoA axes, later used as new "traits" (Paradis and Schliep 2019). Finally, the new traits were used to calculate the functional diversity indices (functional richness, evenness, divergence and dispersion) using the 'dbFD' function of the FD package (LALIBERTÉ; LEGENDRE, 2010; LALIBERTÉ; LEGENDRE; SHIPLEY, 2014).

Values of functional richness (FRic) represent the volume of multidimensional space occupied by biological communities within the functional space and the number of unique traits; low indices indicate that several resources may not be used, while high indices suggest greater use of the available environmental resources (VILLÉGER et al., 2008). The functional divergence (FDiv) is a measurement of divergence in the distribution of species records in the volume of functional traits. It represents the degree of niche variation in biological communities, which increases as more species with unique functional traits emerge (i.e., specialized species). Finally, functional evenness (FEve), represents how regularly the abundance of functional traits is distributed within the multidimensional niche space (VILLÉGER et al., 2008). FEve values decrease when abundance is less evenly distributed or if functional distances between species are less regular (VILLÉGER et al., 2008). FDis is a multivariate measure of the dispersion of species in multidimensional niche space and reflects both the volume of occupied functional space and the distribution of species abundances within this space (LALIBERTÉ; LEGENDRE, 2010). It represents the mean distance of

individual species to the centroid of all species. Higher values of FDis show a greater potential for functional complementarity.

Beta functional diversity was also considered in the analysis. It represents a measure of comparison of composition and variation of species functional traits between two or more sites (SILVA et al., 2022). Therefore, we calculate (1) the total beta diversity of the functional traits and their partitions into (2) turnover, a measure of species and trait replacement between sites, and (3) nestedness, representing the loss of species and traits between sites along a gradient (BASELGA, 2010; VILLÉGER; GRENOUILLET; BROSSE, 2013). For this purpose, the functions "functional.beta.pair" and "functional.beta.multi" were used, available in the betapart package of R software (BASELGA; ORME, 2012; R CORE TEAM 2022).

2.6. Data analysis

To test the effect of the forest gradient on the components of functional diversity, we first calculated the Functional Divergence (FDiv), Functional Evenness (FEve), Functional Richness (FRic) and Functional Dispersion (FDis) matrices. Then we created the linear models to compare the effect of forest cover gradient on the matrices, as shown in the Appendix 1. Finally, we performed their diagnosis through an Analysis of Variance (ANOVA).

Then for our model analysis, we initially tested whether there was spatial autocorrelation within the components of functional diversity, to incorporate spatial components in the effects on response variables (FORTIN; DALE, 2005). For this, we used the function that computes the Moran's I autocorrelation index, available in the "ape" package. Posteriorly, we performed a Variance Inflation Factor (VIF) test to check for collinearity in our explanatory variables, available using the "usdm" package. After these steps we construct the candidate models. The generalized mixed models (GLMM; ZUUR et al., 2009) used the landscape ID as random factors. The response variables were the functional richness, functional divergence and functional evenness. The explanatory variables were forest cover (%) and type of environment (forest, pasture or marshes). We also used a model selection approach, with competing models (Appendix 2).

We start by testing the spatial correlation of the global model residuals with a latitude and longitude framework in those models with spatial autocorrelation (BROOKS et al., 2017). Next, we repeated Moram's I tests for the global models, followed by an ANOVA to verify the similarity between the models; when similar (p>0,05), we proceeded with the analyzes using the residuals.

Then, a list of competing models was evaluated for the explanatory variable (i.e., different Generalized Linear Mixed Models; GLMM) to explain the variation in functional diversity using the Akaike Information Criterion (AICc). A total of 12 models were composed to evaluate the random effect with the isolated effect of forest cover and environment type, and also the combined effect of forest cover with environment type. Models with ΔAICc < 2.0 were considered equally plausible to explain the patterns (BURNHAM; ANDERSON, 2004); however, the model average was calculated among all models assigned as equally plausible to determine which, among them, was the best. The weight of evidence (wAICc) for each competing model, which is the sum of the weights of the models in which the variable appears (BARBOSA et al., 2017; BURNHAM; ANDERSON, 2004), was also calculated. All analyzes were performed using the software RStudio (RSTUDIO TEAM, 2021).

3. RESULTS
3.1. Bird species and habitats

A total of 201 bird species were recorded within the landscapes, and 108 meet our criteria and were assigned as arthropod-consuming species; they represent 34 families and 11 orders. Some species were found exclusively in a given landscape (16 exclusives to pasture sites, 10 in forest, and 9 in marsh areas (Appendix 3).

3.2. β-Functional diversity

The PCoA revealed for groups. The first one grouped mostly species that use marsh sites; the second one is related to more generalist species, regarding the use of the environment; the last two clusters include forest- and non-forest species (Fig. 2). The results of the partition analysis (fun_beta_multi()) indicate that 54.6% (0.063 / 0.116) of the variation in beta diversity is explained by the substitution component, while 45.39% (0.052 / 0.116) by the nestedness component. The distance matrices from the pairwise analysis (fun_beta_pair()) stress the relationship between environmental gradients and functional beta diversity (Fig. 3).
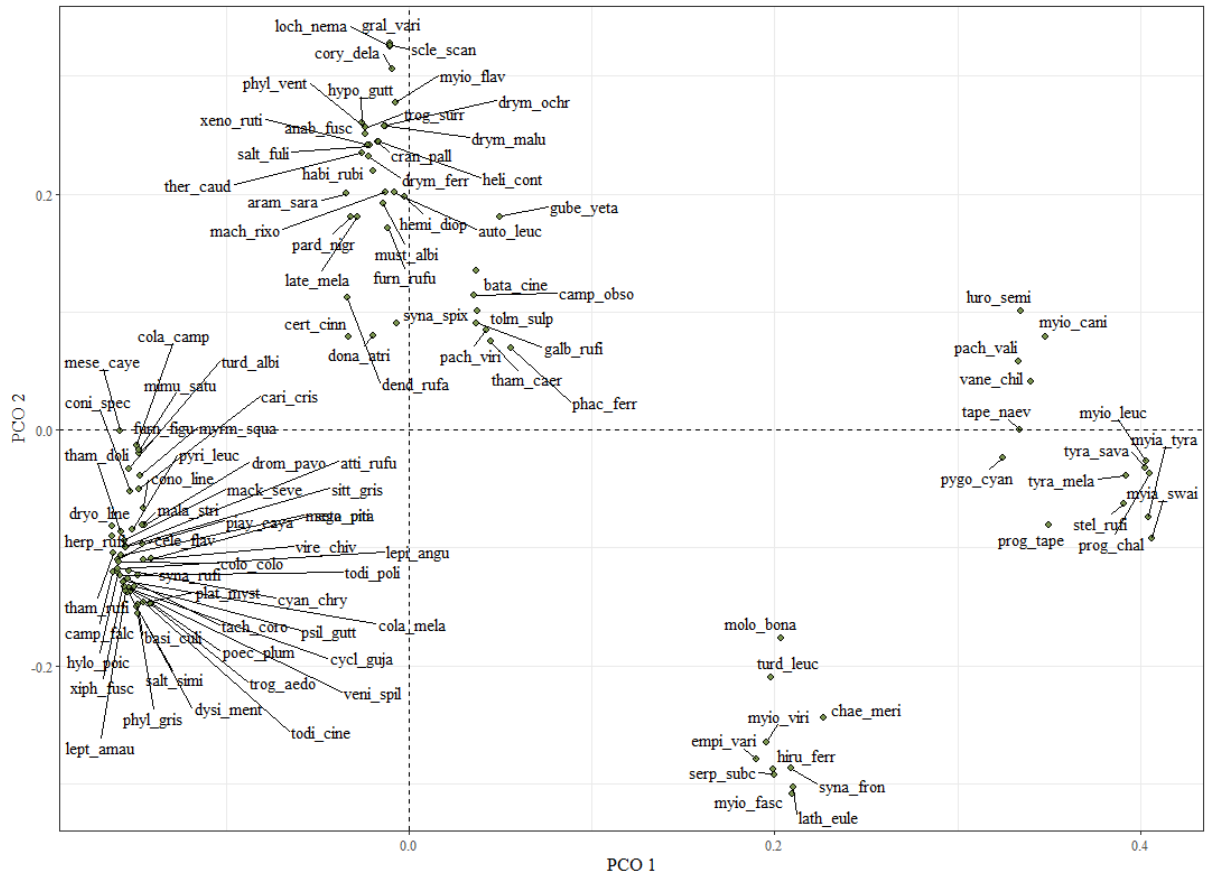
Fig. 2 PCoA for traits of bird species, where each dot represents a species in the trait space. Green dots represent the bird species within the functional trait space.
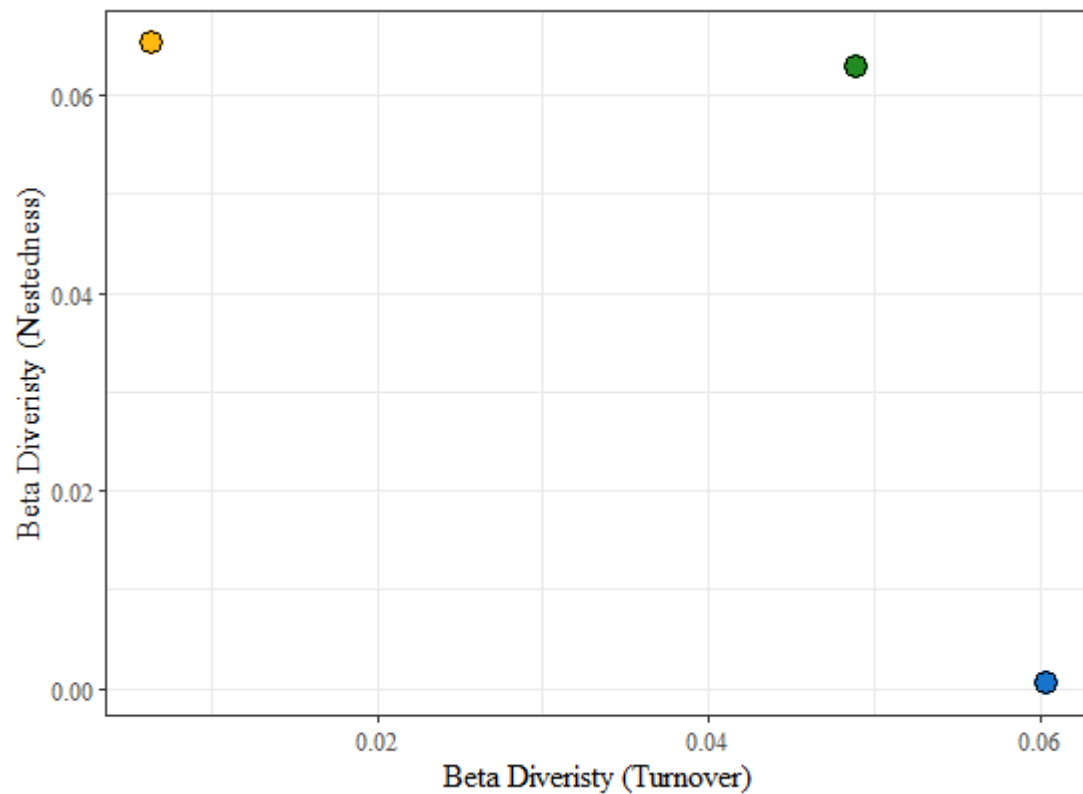
Fig. 3 Relationship between partition components of functional diversity (beta) in corridor Cantareira-Mantiqueira, where the yellow dot represents pasture areas, the green dot represents forest areas and the blue dot marsh areas

3.3.   Linear models and GLMM

The analyzes of the relationship between the functional composition and the forest cover gradient, adjusted by linear models with their diagnoses (Fig. 4), indicate that the forest cover gradient has no effect on the divergence and functional evenness ($F_{MOD1} = 0.1075$, $p_{MOD1} = 0.7441$; TABLE 2; $F_{MOD2} = 0.2503$, $p_{MOD2} = 0.6186$). However, forest cover has negatively affected the functional richness and functional dispersion ($F_{MOD3} = 8.0265$, $p_{MOD3} = 0.006184$; $F_{MOD4} = 8.9582$, $p_{MOD4} = 0.003942$). The forest cover gradient has a negative effect on functional richness and dispersion ($p_{MOD3} = 0.00618$; $p_{MOD4} = 0.003942$; TABLE 2).

Table 2: Analysis of Variance for the linear models for the effects of the forest cover gradient on the Functional Diversity indices, being a) ANOVA for Functional Richness; b) Functional Evenness; c) Functional Divergence and d) Functional Dispersion.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Functional Richness					
Forest Cover	1	8198	8198.4	8.0265	0.006184
Residuals	63	64349	1021.4		
Functional Evenness					
Forest Cover	1	0.000725	0.000725	0.2503	0.6186

Residuals	63	0.182473	0.002896		
Functional Divergence					
	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Forest Cover	1	0.000091	9.06E-05	0.1075	0.7441
Residuals	63	0.053065	8.42E-04		
Functional Dispersion					
	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Forest Cover	1	8198	8198.4	8.0265	0.006184
Residuals	63	64349	1021.4		
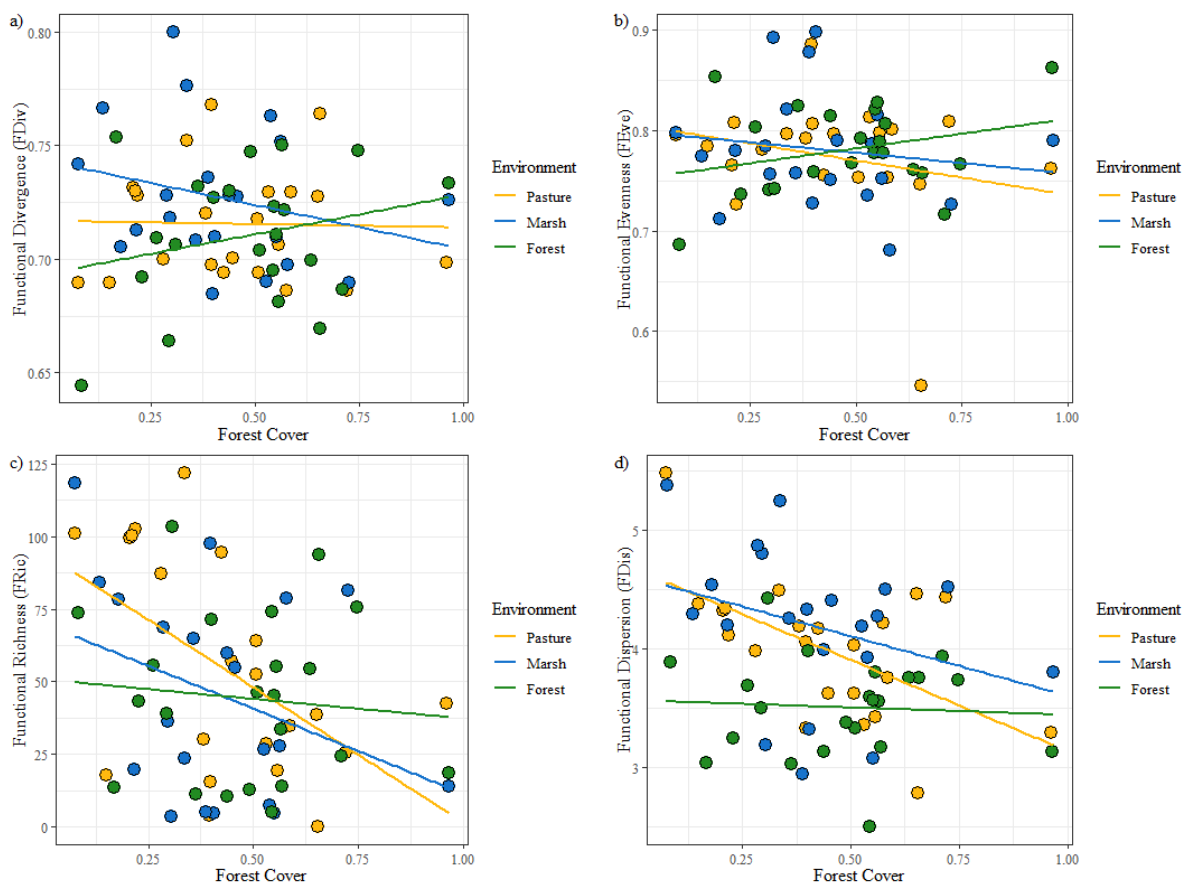
Fig. 4 Relationship between the functional composition and the forest cover gradient, adjusted by linear models with their diagnoses. The yellow dots represent pasture sites; the blue dots represent marsh sites, and the green dots, forest sites

The selection of models and the inference of multi models suggest that the forest cover (M1) is the predictor variable that best explains the values found for functional richness (ΔAIC = 0.00; wAIC = 0.35; AIC = -64.7; TABLE 3a). However, the Forest Cover + Environment Type (M3) and Environment Type (M2) models were also insightful as plausible to explain the patterns (ΔAIC = 0.2, wAIC = 0.32; ΔAIC = 1.3, wAIC = 0.18; TABLE 3a; respectively). In this last case, when performing the full model average, forest cover percentage is the only

variable to explain nonrandom variation of functional richness, with a negative relation (p_{M1} = 0.046087; TABLE 4a; Fig. 5).

Table 3: Most parsimonious Generalized Linear Mixed Models of insectivorous bird functional diversity and taxonomic diversity. For the best models (ΔAICc < 2.0), AICc – Akaike Information Criterion corrected for small sample sizes was used (Burnham and Anderson 2004), ΔAIC and weight of evidence (wAIC).

Response Variable		Model	AICc	ΔAICc	df	weight
a)	Functional Richness	~ Forest Cover - 2km	-64.7	**0**	5	0.35
		~ Forest Cover - 2km + Environment Type	-64.5	**0.2**	7	0.32
		~ Null	-63.4	**1.3**	4	0.18
		~ Environment Type	-62.9	**1.8**	6	0.14
b)	Functional Evenness	~ Null	-232.2	**0**	4	0.495
		~ Forest Cover - 2km	-230.7	**1.5**	5	0.238
		~ Environment Type	-230.1	2.1	6	0.177
		~ Forest Cover - 2km + Environment Type	-228.7	3.4	7	0.089
c)	Functional Divergence	~ Null	-255	**0**	3	0.583
		~ Forest Cover - 2km	-253	**2**	4	0.215
		~ Environment Type	-252.2	2.7	5	0.148
		~ Forest Cover - 2km + Environment Type	-250.2	4.7	6	0.054
d)	Functional Dispersion	~ Forest Cover - 2km + Environment Type	97	**0**	6	0.67
		~ Environment Type	98.4	**1.4**	5	0.33
		~ Forest Cover - 2km	118	21	4	<0.001
		~ Null	119.4	22.5	3	<0.001

Table 4: Full model-averaged parameter estimates and significance values for models of insectivorous birds' functional diversity with cumulative Akaike weight summed to 0.95, calculated by multiplying the estimates for individual models which contain parameters by their weights. Relative importance is the sum of the AICc weights across these models.

	Model Average				
		Estimate	Std. Error	Adjusted SE	z value	Pr(>|z|)
Functional Richness	cond((Int))	0.24808	0.06698	0.06786	3.656	0.000256
	cond(Flo_2km)	-0.25505	0.12527	0.12789	1.994	0.046113
	cond(envMarsh)	0.06848	0.03673	0.03751	1.826	0.067913
	cond(envPasture)	0.0548	0.03838	0.0392	1.398	0.162083
Functional Evenness	cond((Int))	0.82521	0.01216	0.01236	66.786	<2e-16
	cond(Flo_2km)	0.02782	0.03798	0.03876	0.718	0.473
Functional Divergence	cond((Int))	0.702281	0.006823	0.006955	100.979	<2e-16
	cond(Flo_2km)	0.000623	0.024432	0.024927	0.025	0.98
	cond(envMarsh)	0.010548	0.00982	0.010022	1.052	0.293
	cond(envPasture)	0.002277	0.009705	0.009905	0.23	0.818

	(Intercept)	4.301	0.1995	21.563	< 2e-16
Functional Dispersion	Flo_2km	-0.7878	0.4127	-1.909	0.0563
	envMarsh	0.7276	0.1305	5.575	2.48E-08
	envPasture	0.5289	0.1288	4.108	4.00E-05

The best model suggested by the GLMM for functional dispersion was the combined effects of forest cover and type of environment (ΔAIC = 0.0, wAIC = 0.67; TABLE 3d). On the other hand, the selection of models for them pointed to null (M0) and forest cover (M1) as plausible explanations for both functional evenness (for the M0, ΔAIC = 0.0, wAIC = 0.495; for the M1 ΔAIC = 1.5, wAIC = 0.238; TABLE 3b) and functional divergence (for the M0, ΔAIC = 0.0, wAIC = 0.583; for the M1, ΔAIC = 2, wAIC = 0.215; TABLE 3c). However, when performing the model average, referring to functional divergence and evenness, no significant variable was found to explain the data (p > 0.05; TABLE 4b and 4c). Finally, the best model for functional dispersion and functional richness were plotted and can be visualized in Fig. 5.
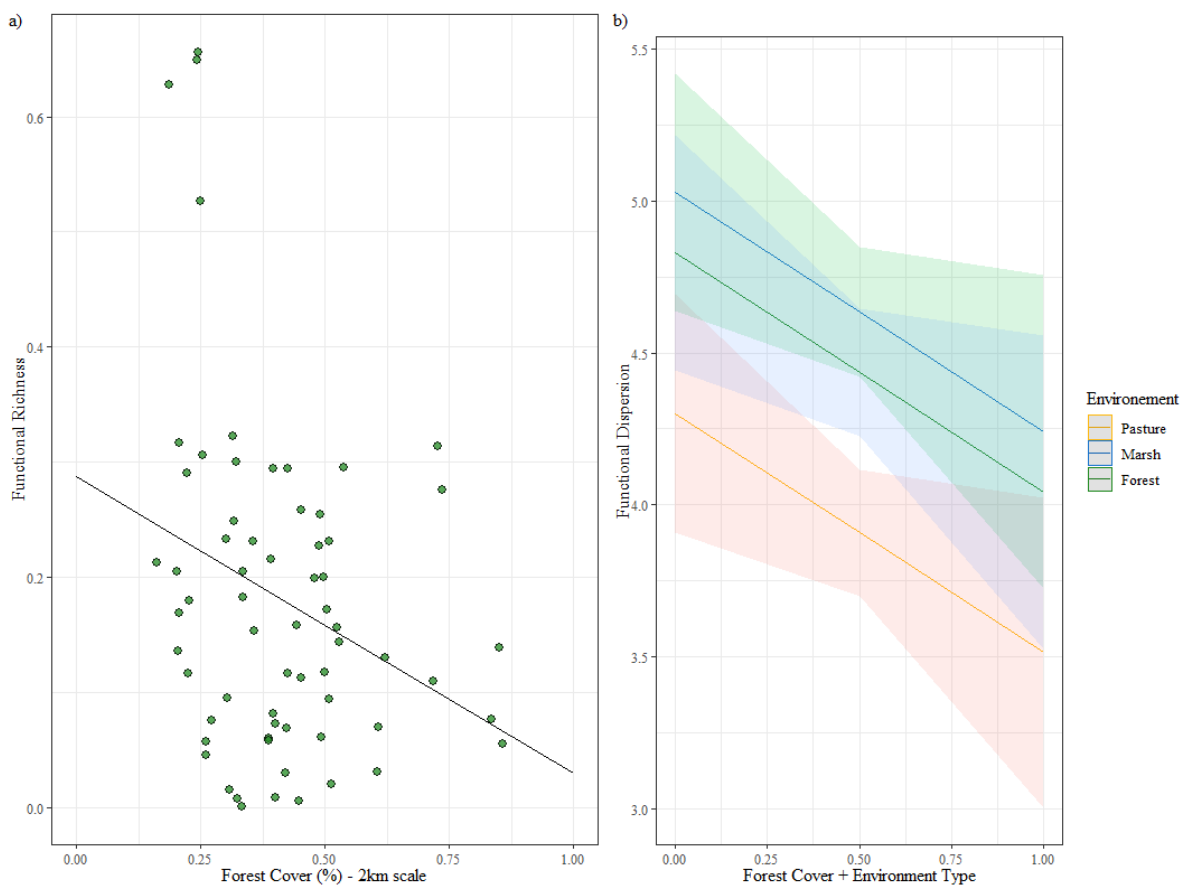

Fig. 5 Graphics generated for the best GLMM models. A) Influence of forest cover on functional richness; B) Influence of forest cover and environment type on functional dispersion

4. DISCUSSION

Our findings reveal an effect of the forest cover gradient on the components of functional diversity, although not related to the type of environment. Specifically, the GLMM showed that there was a marginal effect of forest cover on functional richness (TABLE 4a); however, contrary to our hypothesis, we found no effect of forest cover on functional divergence and functional evenness (TABLE 4b; TABLE 4c). Our data also support a turnover effect on the sampled communities; but there is also a nested effect associated with it (Fig. 3). Finally, contrary to what we had predicted, the percentage of forest cover has a negative effect on the functional richness (Fig. 4, Fig. 5, TABLE 4a).

4.1. Species configuration in the landscape - What does forest cover gradient tell us about functional diversity?

Functional traits represent environmental tolerance; thus, lower values of functional richness indicate that some specialists would be missing under specific conditions (i.e., habitat limitation for species with restrictive fundamental niche (MASON et al., 2005). This may lead to a decrease in the communities' tolerance levels to environmental fluctuations (TILMAN, 1996), affecting resistance to biological invasions, by creating gaps in the niche volume to be exploited by other species (DUKES, 2001).

The functional richness represents the volume of the multidimensional space occupied by a biological community within the functional space (VILLÉGER; MASON; MOUILLOT, 2008). Therefore, low values of functional richness indicate that part of the resources available to the community in each environment is wasted (Mason et al., 2005). This would lead to a loss of productivity (PETCHEY; GASTON, 2006). The relationship between the reduction in functional richness and the increase in forest cover (Fig. 4, Fig. 5) was previously reported (MATUOKA; BENCHIMOL; MORANTE-FILHO, 2020; MORANTE-FILHO et al., 2015, 2018). This is associated with the pattern of species composition; forest and non-forest species tend to respond differently to anthropogenic disturbances (BREGMAN et al., 2016) because they present different response patterns, distinct traits, and therefore, sensitivity to human disturbances (CLAVEL; JULLIARD; DEVICTOR, 2011; GARDNER et al., 2009). These patterns may be linked with a lower quality of resources available in second-growth forests in early to medium stages of succession, as our study area (METZGER et al., 2009; RIBEIRO et al., 2009). The nearby presence of cattle may also increase the proliferation of non-forest species (MORANTE-FILHO; ARROYO-RODRÍGUEZ; FARIA, 2016).

As previously mentioned, functional dispersion measures the dispersion of species in multidimensional niche space, which may represent the functional space occupied and the distribution of abundance within this space (LALIBERTÉ; LEGENDRE, 2010). Such species dispersion occurs from the average individual distance in relation to the centroid of all species. Higher values of functional dispersion indicate a greater potential for functional complementarity (i.e., larger range of traits that allow different ecological niches to be occupied; MELO et al., 2021; WONG; DOWD, 2021). This may increase the partition of resources, enabling the coexistence of species, culminating in an increase in the ecosystem functioning (LOREAU; HECTOR, 2001; TILMAN et al., 1997).

The groups of species that are furthest from the centroid of the functional space are composed by species of generalist habit with great dispersive capacity (see Fig. 2) (LALIBERTÉ; LEGENDRE, 2010), being related to the decrease of functional dispersion with the increase of forest cover (Fig. 4 and Fig. 5) since such species are not found in areas of dense forest.This expansion pattern of functional traits is probably caused by species with traits related to habitat preference and wing size, in this case species such *Myiarchus swainsoni*, *Stelgidopteryx ruficollis*, *Progne chalybea* and *Vanellus chilensis*. A clearer decrease in the values of functional dispersion in marsh and pasture environments is notable when compared to the forest ones (Fig. 4). This may be a consequence of a retention of some taxa with low dispersion capacity traits, while they also receive an influx of highly vagile taxa (BREGMAN et al., 2016). In short, these results suggest that the effects of forest cover on functional diversity are (I) specific to the different functional groups within the community; and (II) might have been impacted by the early succession stages in which the regional forest fragments are (JOHNSTONE et al., 2016; THORN et al., 2020).

4.2. Beta functional diversity: effects of turnover and nestedness

Our study revealed a distinct pattern of beta functional diversity for each type of environment (Fig. 3). Bird assemblies were more nested in the pasturelands, while a turnover effect was more notable in marsh sites, and both turnover and nesting effects were detected in the forest sites. The massive presence of second-growth forests in early to medium stages of succession may explain these forest results (METZGER et al., 2009; RIBEIRO et al., 2009). Bird assemblies are a set of an original species pool (i.e., derived from a set of species present in the original primary forest); as ecological succession advances, generalist species would be replaced by specialists, caused by directional turnover along secondary forest successions (BLAKE; LOISELLE, 2001; ROBINSON; TERBORGH, 1997). In addition, the age of the

secondary forests is also related to the recovery of specialist forest species (ACEVEDO-CHARRY; AIDE, 2019). The accelerated recovery of species composition and forest specialists among the different successional successes may be also related to their greater dispersal capacity (DOBROVOLSKI et al., 2012), characteristic intrinsically related to some traits we used in this study, such as wing size and migratory strategy.

We also found that communities of insectivorous birds in the pasturelands are more functionally nested because they were probably part of the native original forest pool in this region. These results contrast with what was described in Dias et al (2017) and Barros et al (2019b), given the functional traits addressed in their study and local habitat characteristics of the pastures sampled can decisively facilitate a wide spectrum of bird traits (mainly body size and social system), which likely led to an increase in functional diversity values in pastures based on turnover processes, comparable to those of adjacent forests. In this case, nestedness may be reflecting a non-random process of species loss (e.g., differences in species sensitivity to a widespread environmental disturbance), and also might be linked to the selection of functional traits, which may largely determine the functional metrics (PETCHEY; GASTON, 2006).

Our results also pointed to a greater turnover effect for the functional beta diversity of marsh environments, since the presence of water attracts specific birds to this type of habitat (e.g., *Aramides saracura, Theristicus caudatus, Donacobius atricapilla, Gubernetes yetapa, Mustelirallus albicollis*). In contrast, the results found by Li et al. (2022), Si et al. (2016), and Villéger et al. (2013) suggested that the turnover process is associated with taxonomic beta diversity where species are functionally redundant where different environmental conditions in marsh areas must be acting as an environmental filter, thus leading to a directional survival of the species, resulting in a functional convergence within the communities of these studies (LOGEZ; PONT; FERREIRA, 2010). Thus, our higher turnover values than nestedness for marsh areas suggests that the changes in the functional composition of marsh birds were caused by a functional substitution rather than by a loss of functional diversity.

5. CONCLUSIONS

Our study provides insights that evaluating multiple aspects of functional diversity, through different indices, leads to a more accurate understanding of the effects of the loss of forest cover on the functioning of the ecosystem performed by insectivorous birds – a key ecological

guild that plays an important ecological function, the control of invertebrate populations. We highlight two main implications to be considered in future studies.

First, we show that the greater species dispersion in the functional space (i.e., larger functional dispersion and functional richness) in deforested areas (in this case pasturelands) are not followed by increased functional divergence and functional evenness. Therefore, when considering only the dispersion and richness indexes, it is possible to an erroneous conclusion that functional diversity will be greater in deforested sites, and that the functioning of the ecosystem in these environments would be improved. Thus, we strongly emphasize the use of different functional indices in future studies to evaluate the effects of anthropogenic disturbances on biodiversity patterns.

The presence of secondary forests may have influenced the pattern of functional diversity we found. Hence, caution is needed with these findings, mainly because forest and non-forest bird species present different functional responses (MATUOKA et al 2020). For example, deforested landscapes should reduce the availability of niches for forest species, while increasing for non-forest species. Therefore, the behavior of forest communities in deforested environments can be severely affected, since compensatory dynamics may not involve real compensation within the functional perspective, as some specific functions will be lost or damaged (DE COSTER; BANKS-LEITE; METZGER, 2015; DOS ANJOS et al., 2019).

Finally, a possible limitation of our work is that we did not evaluate the specific abundance, since the data come from automatic recordings. Environmental disturbances cause distinct effects on the abundance of species (MAC NALLY, 2007), and those having higher ecological restrictions, and usually with low population density, may be extinct early, or have their abundance reduced in order to become functionally extinct (GALETTI et al., 2013; TOBIAS et al., 2013). We therefore suggest that these analyzes be incorporated into future studies.

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APPENDIX

Appendix 1: Models used for our linear model analysis

MOD1: FDiv ~ forest cover

MOD2: FEve ~ forest cover

MOD3: FRic ~ forest cover

MOD4: FDis ~ forest cover

Appendix 2: Models used for our GLMM analysis where "y" represents Functional Richness, Functional Evenness, Functional Divergence and Functional Dispersion.

M0: y ~ 1 | random (Landscape ID) = null model (no effect)

M1: y ~ Forest Cover | random (Landscape ID)

M2: y ~ Type of Environment | random (Landscape ID)

M3: y ~ Forest Cover + Type of Environment | random (Landscape ID)

Appendix 3: Bird species sampled and the number of records by type of environment.

Taxon	Environment		
	Pasture	Marsh	Forest
Pelecaniformes			
Threskiornithidae			
Mesembrinibis cayennensis	1	2	4
Theristicus caudatus	2	1	0
Gruiformes			
Rallidae			
Aramides saracura	1	5	8
Laterallus melanophaius	1	2	0
Mustelirallus albicollis	0	1	0
Pardirallus nigricans	0	3	0
Charadriiformes			
Charadriidae			
Vanellus chilensis	13	15	7
Cuculiformes			
Cuculidae			

Dromococcyx pavoninus	1	0	0
Piaya cayana	1	0	6
Tapera naevia	11	4	5
Caprimulgiformes			
Caprimulgidae			
Lurocalis semitorquatus	2	0	1
Apodiformes			
Apodidae			
Chaetura meridionalis	1	0	0
Trogoniformes			
Trogonidae			
Trogon surrucura	1	1	1
Galbuliformes			
Galbulidae			
Galbula ruficauda	2	0	0
Bucconidae			
Malacoptila striata	1	4	3
Piciformes			
Picidae			
Celeus flavescens	4	3	5
Colaptes campestris	17	9	7
Colaptes melanochloros	2	1	0
Dryocopus lineatus	1	0	2
Veniliornis spilogaster	1	0	4
Cariamiformes			
Cariamidae			
Cariama cristata	10	7	9
Passeriformes			
Thamnophilidae			
Batara cinerea	0	0	1
Drymophila ferruginea	0	1	2
Drymophila malura	1	0	0
Drymophila ochropyga	0	1	1
Dysithamnus mentalis	13	7	16
Herpsilochmus rufimarginatus	6	5	13
Hypoedaleus guttatus	6	5	7
Mackenziaena severa	1	0	1
Myrmoderus squamosus	0	0	7
Pyriglena leucoptera	5	3	12
Thamnophilus caerulescens	13	8	16
Thamnophilus doliatus	1	0	0
Thamnophilus ruficapillus	1	1	0
Conopophagidae			
Conopophaga lineata			

Grallariidae
Grallaria varia
Rhinocryptidae
Psilorhamphus guttatus	0	0	2

Scleruridae
Sclerurus scansor	0	0	2

Dendrocolaptidae
Campylorhamphus falcularius	1	0	0
Lepidocolaptes angustirostris	1	0	0
Sittasomus griseicapillus	5	3	7
Xiphorhynchus fuscus	0	0	2

Xenopidae
Xenops rutilans	2	0	7

Furnariidae
Anabazenops fuscus	1	0	0
Automolus leucophthalmus	4	1	9
Certhiaxis cinnamomeus	0	3	2
Cranioleuca pallida	5	5	3
Dendroma rufa	0	1	0
Furnarius figulus	0	0	1
Furnarius rufus	14	14	9
Heliobletus contaminatus	0	0	2
Lochmias nematura	5	3	6
Phacellodomus ferrugineigula	0	6	0
Synallaxis frontalis	2	1	1
Synallaxis ruficapilla	2	3	8
Synallaxis spixi	17	12	9

Tityridae
Pachyramphus validus	5	6	4
Pachyramphus viridis	0	1	0

Platyrinchidae
Platyrinchus mystaceus	3	1	11

Rhynchocyclidae
Corythopis delalandi	1	0	5
Hemitriccus diops	0	0	1
Leptopogon amaurocephalus	3	1	12
Phylloscartes ventralis	0	0	1
Poecilotriccus plumbeiceps	5	2	1
Todirostrum cinereum	4	1	0
Todirostrum poliocephalum	8	4	9
Tolmomyias sulphurescens	10	8	19

Tyrannidae
Attila rufus	0	0	2
Camptostoma obsoletum	13	14	11

Colonia colonus	3	2	0
Empidonomus varius	5	7	4
Gubernetes yetapa	0	1	0
Hirundinea ferruginea	1	0	0
Lathrotriccus euleri	3	1	13
Machetornis rixosa	1	4	0
Megarynchus pitangua	7	9	3
Myiarchus swainsoni	10	8	12
Myiarchus tyrannulus	7	7	3
Myiopagis caniceps	1	0	1
Myiopagis viridicata	1	0	2
Myiophobus fasciatus	11	10	1
Phyllomyias griseocapilla	1	0	0
Serpophaga subcristata	3	1	0
Tyrannus melancholicus	18	15	10
Tyrannus savana	2	0	0
Vireonidae			
Cyclarhis gujanensis	19	15	20
Hylophilus poicilotis	1	0	0
Vireo chivi	19	16	22
Corvidae			
Cyanocorax chrysops	7	3	6
Hirundinidae			
Progne chalybea	0	1	0
Progne tapera	2	0	0
Pygochelidon cyanoleuca	4	0	0
Stelgidopteryx ruficollis	3	0	0
Troglodytidae			
Troglodytes aedon	19	16	7
Donacobiidae			
Donacobius atricapilla	0	1	0
Turdidae			
Turdus albicollis	7	2	12
Turdus leucomelas	18	12	17
Mimidae			
Mimus saturninus	3	3	0
Parulidae			
Basileuterus culicivorus	16	12	22
Myiothlypis flaveola	1	1	2
Myiothlypis leucoblephara	7	4	19
Setophaga pitiayumi	11	5	11
Icteridae			
Molothrus bonariensis	0	2	0
Thraupidae			

Conirostrum speciosum	6	4	10
Saltator fuliginosus	1	0	0
Saltator similis	9	5	11
Tachyphonus coronatus	12	12	14
Cardinalidae			
Habia rubica	2	1	7