



Research Paper

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Forest cover and environment type shape functional diversity of insectivorous birds within the Brazilian Atlantic Forest

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Summary

Tropical insectivorous birds comprise a diverse group that has a distinct response to habitat degradation. However, knowledge on birds' ecological functions and their large-scale functional responses to human impacts across various habitats is scarce. We sampled 22 1-km-radius buffer landscapes within the Cantareira-Mantiqueira region (south-east Brazil), including native forests, pastures and marshes, to assess how landscape and habitat characteristics might affect insectivorous birds within the Brazilian Atlantic Forest. We studied whether bird species and functional diversity might respond to habitat turnover and nestedness and to native forest cover using generalized linear mixed models. We found negative effects of increased native forest cover on functional diversity indices. Bird communities in pastures show more nestedness, whereas marsh areas exhibit higher turnover. Forest areas receive a balanced contribution from both nestedness and turnover. These results are attributable to the predominantly secondary growth and early successional stages of the native forest fragments in the region, emphasizing the connection between landscape characteristics, habitat types and bird functional diversity in the Brazilian Atlantic Forest.

Introduction

The Atlantic Forest hosts c. 60% of Brazil's biodiversity and nearly 30% of Neotropical bird species (Sick & Barruel 1984). Despite its rich biodiversity (Rezende et al. 2018), only 28% of the original vegetation remains. The ongoing deforestation is driven by commodities production, agriculture and forest fires (Diniz et al. 2022), leading to local population extinctions, biodiversity loss and negative impacts on ecological functions (Duarte et al. 2018).

Global declines of species, habitat loss and disruption of ecological functionality call for more precise ecological understanding. Functional traits of species offer better predictors of ecological patterns than classic diversity indexes (i.e., solely, richness, abundance and taxonomic diversity; Bello et al. 2021, Mariano-Neto & Santos 2023). Analysing species' unique characteristics can reveal their roles in ecosystem functioning (Carmona et al. 2017), aiding understanding of how the extinction of specific functional groups impacts the functionality of whole ecosystems (Mazel et al. 2018). Human modifications of landscapes lead to changes in species composition, yet there is no consensus on how functional diversity (FD) can persist in such settings (Riemann et al. 2017). Exploring relationships between habitat loss and FD can provide valuable insights into the mechanisms driving changes in FD that can impact ecosystem processes (Bello et al. 2021, Mariano-Neto & Santos 2023).

Several metrics of FD, including functional richness, evenness, divergence and dispersion, have been proposed to enhance our understanding of how environmental changes impact communities and ecosystem services (Mason et al. 2005, Laliberté & Legendre 2010). Both functional richness and functional evenness have been highlighted as potential indicators of biological control provided by birds (Barbaro et al. 2014). Evidence suggests that bird insectivory often rises with increasing functional richness and functional evenness, underscoring the complementarity of many functional traits (Barbaro et al. 2017).

Birds encompass a broad range of functional traits, including morphological, physiological and phenological characteristics that affect species' fitness, growth rates, reproduction and survival (Violle et al. 2007). These traits are sensitive to diverse environmental changes (Alexander et al. 2019), rendering birds as significant models for assessing changes in landscape, ecosystem functioning and FD (Bregman et al. 2016, Prescott et al. 2016). Moreover, birds



perform key ecological functions such as seed dispersal, pollination, nutrient cycling, soil formation and control of arthropod populations (Sekercioglu 2006).

In the mosaic of habitats that currently characterizes the Atlantic Forest, beta FD can provide insights into how functional traits change during transitions between habitats (Villéger *et al.* 2008). This variation results in both turnover processes, representing dissimilarity in species compositions along environmental gradients (Baselga 2010), and nestedness, which includes subsets of the original community (Pollock *et al.* 2020). Therefore, human-modified landscapes might reveal functionally nested communities and low redundancy, potentially increasing the susceptibility of persistence functions within these communities to rapid decline (Almeida-Gomes *et al.* 2019). A notable gap exists regarding comprehensive studies of bird beta FD, notably in terms of our understanding of ecological responses to human impacts and environmental changes. Addressing these knowledge gaps is essential for a better understanding of the ecological functions performed by tropical birds and for defining conservation and management strategies in tropical environments.

In this study, we investigated how landscape influences the FD of insectivorous birds in the Brazilian Atlantic Forest, exploring correlations between types of environments (pasture, native forest and marsh), forest cover and the FD and species composition of birds. Our hypothesis is that anthropogenic environments such as pastures together with the loss of native forest cover modify the filtering of functional characteristics amongst insectivorous birds within the Atlantic Forest. We predicted that FD would be influenced by species turnover and nestedness across different environment types. Disturbed environments may benefit generalists, leading to greater influences on nestedness and reduced biodiversity (Karp *et al.* 2012), whereas the contribution of turnover would be more pronounced in heterogeneous environments (Arroyo-Rodríguez *et al.* 2013). We also predicted that higher relict native vegetation cover would positively influence both insectivorous bird composition and FD due to increased habitat complexity (Morelli *et al.* 2018).

Methods

Study sites

The study was conducted within the ecological corridor of the Cantareira-Mantiqueira region (CMR; Fig. 1), where long-term ecological research has been conducted since 2014. The CMR is situated in the south-eastern part of the Atlantic Forest, characterized by dense rainforest that covers c. 700 000 ha. The elevation ranges from 700 to 1250 m above sea level (Tonetti *et al.* 2017), connecting two large blocks of rainforest: Cantareira State Park and Serra da Mantiqueira State Park (Boscolo *et al.* 2017).

The region comprises diverse landscape mosaics with a wide range of forest losses and great heterogeneity of land use. Most of the forest remnants are fewer than 100 ha in area and isolated, composed of second-growth forests in early to medium stages of succession (Ribeiro *et al.* 2009). These forest remnants are surrounded by multiple land-use systems, including several agroecosystems, such as pastures, small-scale agriculture, forestry, regenerating forests and urban areas (Barros *et al.* 2019a). The regional climate is classified as Cwa according to the Köppen classification, indicating a humid subtropical climate with dry winters and hot summers (Alcarde Alvares *et al.* 2013).

Selection of landscapes

We analysed data from 22 landscape sites within the CMR (Fig. 1). Forest cover data were at the 2-km diameter scale, following prior research on bird responses to landscape structure (Barros *et al.* 2019b, Adorno *et al.* 2021), and in these areas native forest cover ranged from 1% to 97% within a 1-km radius around each site's centroid. In each site, we sampled three habitat types (forests, pastures for cattle raising and marshes) located c. 100 m apart. Forest sampling points were at least 50 m away from the forest edge (Scarpelli *et al.* 2021, Gaspar *et al.* 2023).

Sound records and bird data

We collected sound data from all three environments across the 22 sites (65 sampling points) over a total of 90 days. Each environment was sampled for 30 days before transitioning to the next type within the same site. Sampling occurred from October 2016 to January 2017, with forests sampled in October–November, marshes sampled in November–December and pastures sampled in December–January, coinciding with the Southern Hemisphere's breeding season for most birds (Develey & Peres 2000). To reduce the effects of space and time inherent in such macroecological work, data were collected within a single reproductive season (*i.e.*, from October 2016 to January 2017), and the buffer scale was a 1-km radius.

We used 22 Song Meter Digital Field Recorders (SM3; Wildlife Acoustics, Inc., MA, USA), each with two omnidirectional microphones (20 Hz–20 kHz frequency range), configured at a 44.1-kHz sampling rate in 16-bit mono mode, attached 1.5 m above the ground at the landscape centre (Gaspar *et al.* 2023).

We selected recordings (Gaspar *et al.* 2023) as follows. First, we chose five 25-min files during peak bird activity (05.00–08.00) per day, totalling 9151 files containing 228 775 min of data. We then randomly extracted 2 min from each file, resulting in 18 594 min of data. These minutes were then divided into nine random 300-min packages (2700 min total), categorized by environment. After this, bird experts identified species occurrences every minute, resulting in 10 437 vocalizations: 9437 at the species level, 192 at the genus level and 808 distant or doubtful calls (excluded). Each species was catalogued once per minute, regardless of the number of vocalizations in the recording.

Bird selection and traits

Bird species were categorized based on traits of diet, biomass, bill and wing length, foraging environmental strata, migratory status and habitat preference (Table S1). We considered bird species the diets of which consisted of $\geq 60\%$ invertebrates (Wilman *et al.* 2014). Bird total wing length affects the ability to withstand habitat loss and fragmentation (Desrochers 2010, Rodrigues *et al.* 2019). Migratory strategies are closely linked to the potential for long-distance movements (Somenzari *et al.* 2018), thereby enabling the colonization of isolated habitats (Barbosa *et al.* 2020). Diet composition and foraging strata provide insights into species' niche occupancy and their approaches to resource acquisition (Petchey & Gaston 2006), including the specific ecosystem function of controlling arthropod populations (Sekercioglu 2012). Additionally, bill length is associated with the ability to capture food and utilize various habitats and microhabitats (Table 1; Rodrigues *et al.* 2019). Wing length (mm) and bill culmen length (mm) were obtained from Tobias *et al.* (2022), whereas migratory status and habitat preference were derived from Somenzari *et al.* (2018) and IUCN (2022).

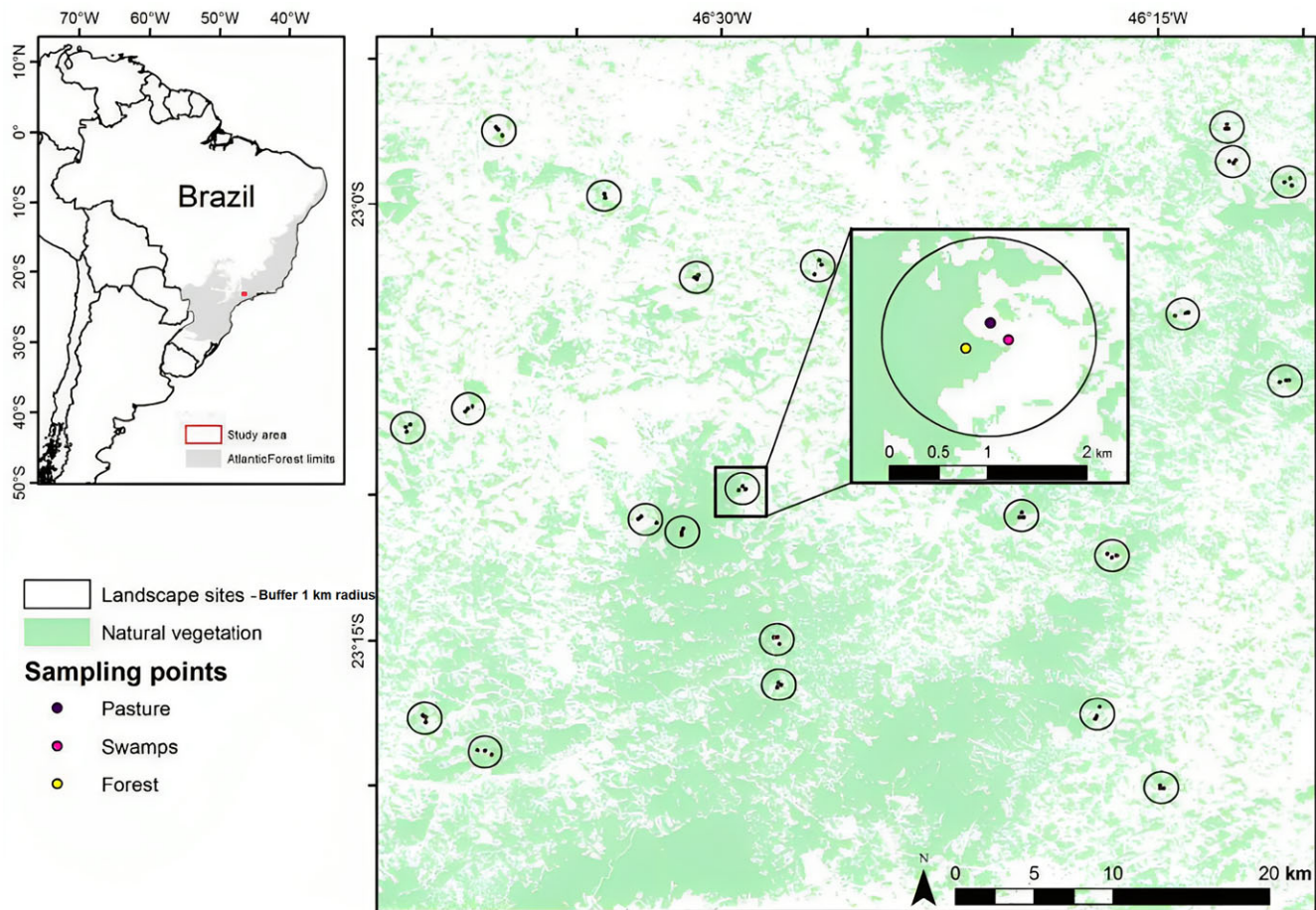


Figure 1. Landscapes where soundscape data were collected using autonomous audio recorders within the Long-Term Ecological Research of Ecological Corridor Cantareira-Mantiqueira (LTER CCM or PELD CCM), São Paulo, Brazil, between October 2016 and January 2017 (Gaspar et al. 2023).

Functional diversity and beta functional diversity

To address our first prediction, we first sum the records of each species obtained across all sites for each environment (i.e., 22 for grasslands, 21 for marshes and 22 for forests). This sum was then used to conduct an analysis of multisite beta FD across three different types of environments, considering the total presence/absence of species in each environment type (see Appendix S1). In the pairwise beta FD analysis, the total number of records was considered rather than the sum of all records per environment type. The Jaccard index was used, decomposing beta FD into two components: turnover and nestedness (Appendix S2). Turnover indicates the substitution of species and traits between sites, whereas nestedness represents differences in species and trait assemblages due to species filtering, creating subsamples from a regional species pool (Baselga & Orme 2012, Mouillot et al. 2013). To perform these calculations, we utilized two *betapart* package functions (*functional.beta.multi* and *functional.beta.pair*) in the R software (R Core Team 2022).

To test our second prediction, we used the following steps (Laliberté & Legendre 2010, Melo et al. 2022). We first determined the functional distance between each species pair using Gower’s distance (Appendix S2; Pavoine et al. 2009). The resulting matrix was subjected to a principal coordinate analysis (Figs S1 & S2; Paradis & Schliep 2019), as the construction of a functional space requires a dissimilarity matrix. Subsequently, the first three axes

were used to calculate the FD of the communities (i.e., functional richness, uniformity, divergence and dispersion; Melo et al. 2022), as the greatest total variation is explained by these axes (Table S2; Gower 1966, Legendre & Legendre 1998, Legendre & Birks 2012). The *dbFD* function in the *FD* package (Laliberté & Legendre 2010) was used to calculate FD.

After we calculated the four diversity indices and recognizing the importance of spatial considerations (Fortin & Dale 2005), we assessed spatial autocorrelation using the *ape* package and potential collinearity with a variance inflation factor test using the *usdm* package. We then formulated candidate models for further analysis and conducted model selection through a comparison of competing models (Appendix S3 & Table S3).

To account for spatial structure, we employed generalized linear mixed models (GLMM; Zuur et al. 2009), incorporating landscape ID as a random factor (Table S3). Our response variables included functional richness, functional divergence, functional evenness and functional dispersion, whereas our explanatory variables encompassed forest cover percentage, environmental type (i.e., forest, pasture, marsh) and their combinations (Table S5). When spatial autocorrelation was detected in the residuals of the global model, we introduced latitude and longitude as covariates (Brooks et al. 2017). Subsequently, we subjected the global models to Moran’s I tests and analysis of variance (ANOVA) to conduct a thorough evaluation

Table 1. Bird traits used to calculate functional diversity metrics (see Wilman et al. 2014, Melo et al. 2022).

Trait	Range	Definition
Diet	0–100%	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	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-level, canopy and aerial) used by the species
Bill culmen length (mm)	8–152	The distance from the tip of the upper mandible to the end of the culmen at its intersection with the cere, or forehead, in millimetres, of each bird species
Wing length (mm)	42–400	Wing size, in millimetres, of each bird species
Migratory status	0–1	Classification of species as non-migrant (0) or migrant (1)
Habitat preference	1–7	The habitat in which each bird species prevails: 1 = forest (tall tree-dominated vegetation, closed canopy, including palm forest); 2 = wetland (freshwater aquatic habitats including lakes, marshes and reedbeds); 3 = non-forest (includes grassland, open dry to moist grass-dominated landscapes, at all elevations), shrubland (low-stature bushy habitats, including thorn scrub, thorny or arid savannah, 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

of model similarities. If similarity was confirmed ($p > 0.05$), we proceeded with further analyses using the residuals.

The Akaike information criterion corrected for small samples (AICc) for model selection was used to understand the variation in FD. We created four comprehensive models for each FD index, assessing effects of forest cover, environment type and their interactions whilst accounting for the random effect. Models with $\Delta AICc < 2.0$ were considered equally plausible for explaining the observed patterns (Burnham & Anderson 2004). Additionally, we calculated model averages for equally plausible models to identify the best-fitting one. We also computed the weight of evidence (wAIC) for each competing model, representing the sum of weights amongst models in which the variable appears (Barbosa et al. 2017).

Results

A total of 201 bird species were recorded within the landscapes; 108 species representing 34 families and 11 orders were assigned as arthropod-consuming species. Some species were found within specific landscapes (16 exclusive to pastures, 10 exclusive to forests and 9 exclusive to marshes; see Table S4). The partition analysis for each environment type (i.e., the analysis that considered the sum of all sites within each environmental type – multiple-site functional dissimilarities) indicated that 54.6% (0.063/0.116) of the variation in beta FD was explained by the turnover component and 45.4% (0.052/0.116) of the variation in beta FD was explained by the nestedness component (Fig. 2a). The distance matrices from the pairwise analysis (pairwise functional dissimilarities) highlighted the relationship amongst all sites within each environmental type and functional beta FD (Fig. 2b & Appendix S4).

Forest Cover (M1) was the predictor variable that best explained the values found for functional richness (wAIC = 0.35; AIC = -64.7; Table 2). However, the Forest Cover + Environment Type (M3) and Environment Type (M2) models were also plausible in helping to explain the observed patterns (wAIC = 0.32 and 0.18; respectively; Table 2). When determining the full model average, forest cover percentage was the only variable to explain the non-random variation in functional richness, establishing a negative relationship ($p_{M1} = 0.046$; Fig. 3 & Table 3).

The best model suggested by the GLMMs for functional dispersion was the combined effects of native forest cover and type of environment (wAIC = 0.67; Table 2). The Null (M0) and Forest Cover (M1) models were plausible explanations for both functional

evenness (for M0, wAIC = 0.495; for M1, wAIC = 0.238; Table 2) and functional divergence (for M0, wAIC = 0.583; for M1, wAIC = 0.215; Table 2).

Discussion

Our data support the first prediction of the effects of environment type on beta FD; there was a nested effect within pastures and a turnover effect in marshes (Fig. 4). Moreover, both turnover (45.4%) and nestedness (54.6%) contributed in comparable proportions within forest communities (Fig. 2a). Contrary to our second prediction (Fig. 4), the percentage of native forest cover exhibited a negative relationship with functional richness and dispersion (Fig. 3 & Table 2). No effect of forest cover on functional divergence and functional evenness was detected ($p > 0.05$; Fig. 3 & Tables 2 & 3). Although some sites may have been small enough to have edge effects and thus influence neighbouring sites in our data, species typical of each studied environment were predominantly recorded in their characteristic habitat, so we consider that this limitation was minimized (e.g., Appendix S1).

Beta functional diversity: effects of turnover and nestedness

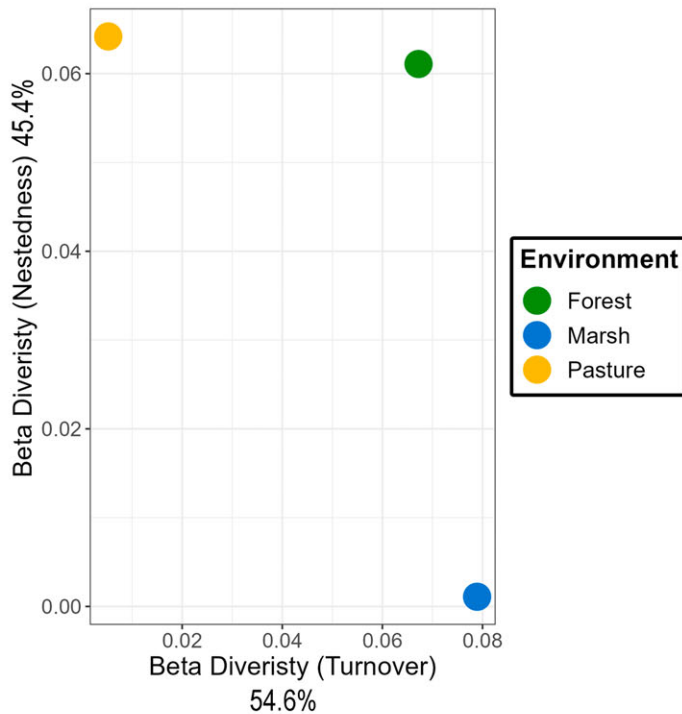
We found a specific pattern of beta FD in each environment type (Fig. 2). Bird communities were more nested in the pasturelands, whereas a more pronounced turnover effect was observed in marsh sites, and both turnover and nesting effects were detected in forested areas. The massive presence of second-growth forests in early to medium stages of succession could potentially explain these outcomes in forests (Ribeiro et al. 2009). As ecological succession advances, generalist species might be replaced by specialists through directional turnover (Blake & Loiselle 2001). Additionally, the age of secondary forests influences the recovery of specialist forest species (Acevedo-Charry & Aide 2019). The speed at which species composition recovers and the resurgence of forest specialists across diverse successional stages could also be related to their enhanced dispersal capacity (Dobrovolski et al. 2012). This ability is intrinsically linked to certain traits considered in our study, such as wing size and migratory strategy (Rodrigues et al. 2019).

The higher degree of functional nestedness observed in pastures can be attributed to a non-random process of species loss, potentially influenced by factors such as variations in species sensitivity to prevalent environmental disturbances. These

Table 2. Performance of generalized linear mixed models of insectivorous bird functional diversity using Akaike’s information criterion corrected for small sample sizes (AICc) on multiple regression. For the best models ($\Delta AICc < 2.0$; in bold), AICc was used (Burnham & Anderson 2004) as well as $\Delta AICc$ and weight of evidence (wAIC).

Response variable	Model	AICc	$\Delta AICc$	df	wAIC
Functional richness	Forest Cover – 2 km	–64.7	0	5	0.350
	Forest Cover – 2 km + Environment Type	–64.5	0.2	7	0.320
	Null	–63.4	1.3	4	0.180
	Environment Type	–62.9	1.8	6	0.140
Functional evenness	Null	–232.2	0	4	0.495
	Forest Cover – 2 km	–230.7	1.5	5	0.238
	Environment Type	–230.1	2.1	6	0.177
	Forest Cover – 2 km + Environment Type	–228.7	3.4	7	0.089
Functional divergence	Null	–255.0	0	3	0.583
	Forest Cover – 2 km	–253.0	2.0	4	0.215
	Environment Type	–252.2	2.7	5	0.148
	Forest Cover – 2 km + Environment Type	–250.2	4.7	6	0.054
Functional dispersion	Forest Cover – 2 km + Environment Type	97.0	0	6	0.670
	Environment Type	98.4	1.4	5	0.330
	Forest Cover – 2 km	118.0	21.0	4	<0.001
	Null	119.4	22.5	3	<0.001

(a) Multiple-site functional dissimilarities



(b) Pair-wise functional dissimilarities

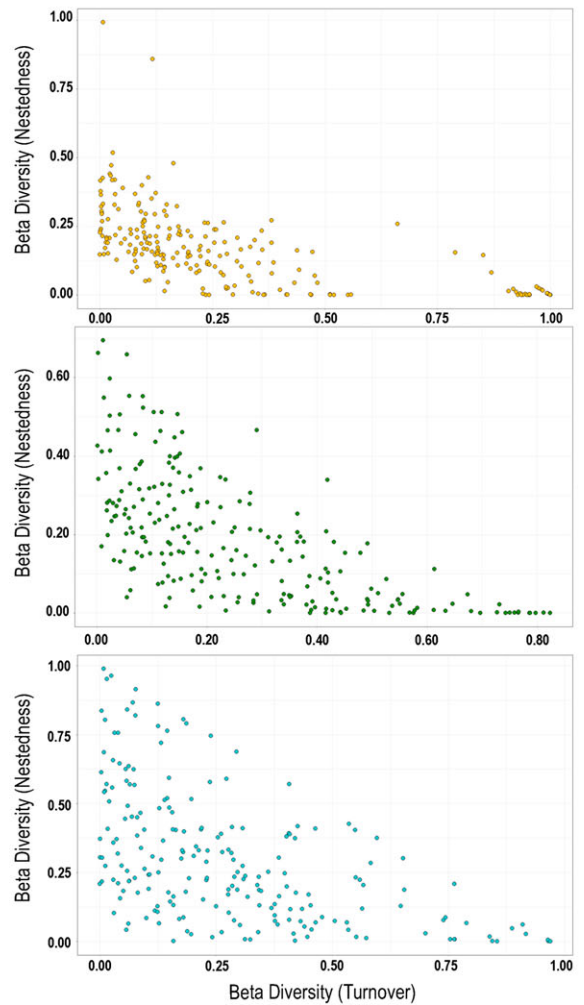


Figure 2. (a) Relationship between multiple-site functional dissimilarities in Ecological Corridor Cantareira-Mantiqueira, São Paulo, Brazil, considering pasturelands, marshes and forests. (b) Pairwise functional dissimilarities within each site in pastures, marshes and forests.

Table 3. Full model-averaged parameter estimates and significance values for models of insectivorous birds' functional diversity with cumulative Akaike information criterion corrected for small sample sizes (AICc) weights summed to 0.95, calculated by multiplying the estimates for individual models that contain parameters by their weights. Relative importance is the sum of the AICc weights across these models.

Response variable	Model	Estimate	SE	Adjusted SE	z value	Pr(> z)
Functional richness	cond((Int))	0.248	0.066	0.067	3.656	0.000
	cond(F_cover)	-0.255	0.125	0.127	1.994	0.046
	cond(envMarsh)	0.068	0.036	0.037	1.826	0.067
	cond(envPasture)	0.054	0.038	0.039	1.398	0.162
Functional evenness	cond((Int))	0.825	0.012	0.012	66.786	<2e ⁻¹⁶
	cond(F_cover)	0.027	0.037	0.038	0.718	0.473
Functional divergence	cond((Int))	0.702	0.006	0.006	100.979	<2e ⁻¹⁶
	cond(F_cover)	0.000	0.024	0.024	0.025	0.980
	cond(envMarsh)	0.010	0.009	0.010	1.052	0.293
	cond(envPasture)	0.002	0.009	0.009	0.230	0.818
Functional dispersion	(Intercept)	4.301	0.199	-	21.563	<2e ⁻¹⁶
	F_cover	-0.787	0.412	-	-1.909	0.056
	envMarsh	0.727	0.130	-	5.575	2.48e ⁻⁸
	envPasture	0.528	0.128	-	4.108	4.00e ⁻⁵

SE = standard error.

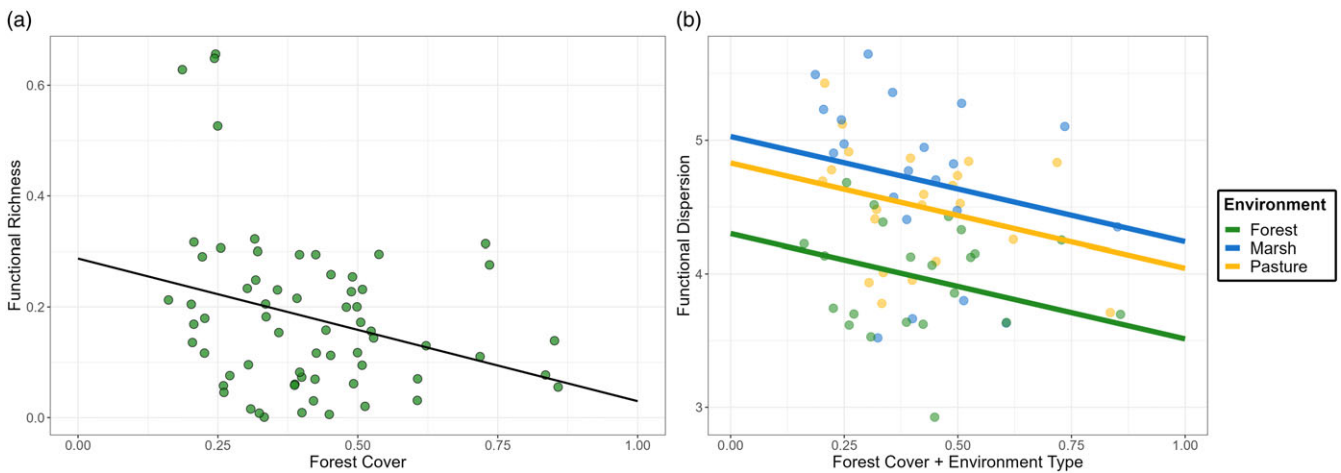


Figure 3. Graphs generated for the best generalized linear mixed models. (a) Influence of forest cover on functional richness. (b) Influence of forest cover and environment type on functional dispersion.

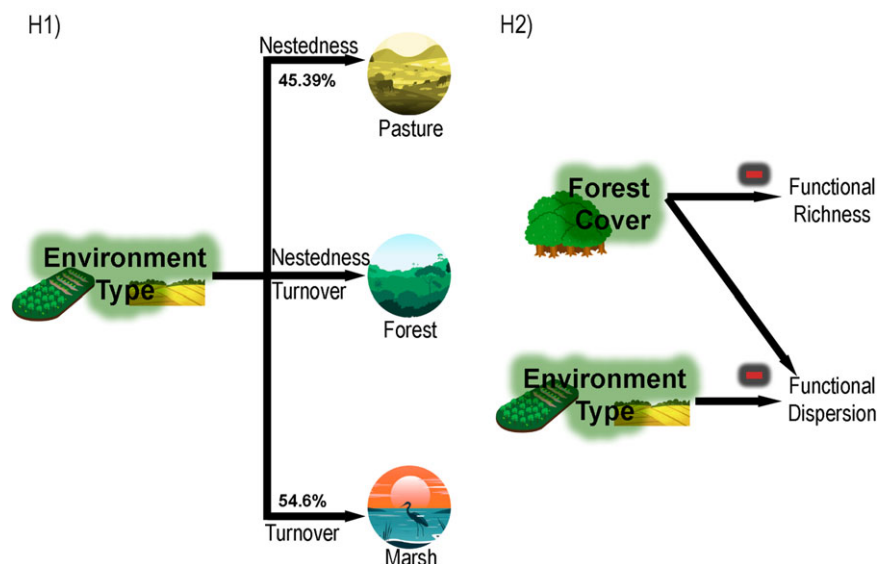


Figure 4. Main results in relation to our two hypotheses. (H1) The partitioning of beta functional diversity for the three types of environments. (H2) The effects of forest cover and type of environment on functional richness and functional dispersion.

outcomes are contrasted with previous findings (Dias et al. 2017, Barros et al. 2019a) and are probably related to the specific functional traits of social behaviour and clutch size addressed in those studies and to the local pastures differing in intensity of livestock disturbance. The selection of functional traits probably does play a central role in determining the functional metrics (Petchey & Gaston 2006).

Our results also indicated a pronounced turnover effect in the functional beta FD within marsh environments. Distinct environmental conditions potentially act as environmental filters in marshes, resulting in the selective survival of habitat-specialist species such as *Donacobius atricapilla*. Thus, the observed changes in the functional composition of marsh-dwelling birds are explicable by functional substitution rather than loss of FD. This process leads to functional convergence within the studied communities (Logez et al. 2010).

Forest cover percentage and functional diversity

Functional traits represent environmental tolerance; reduced values of functional richness suggest the absence of some specialists under specific conditions, such as habitat constraints on species with highly specific fundamental niches (i.e., the functional space used by a species in a theoretical framework without any competition or another limitation condition; Odum & Barrett 1971, Mason et al. 2005). Species characterized as specialists are more susceptible to population declines related to environmental changes (Moritz & Agudo 2013). This may lead to a reduction in communities' ability to tolerate environmental fluctuations due to compensatory interactions among co-occurring species (Tilman 1996). Lower values of functional richness also suggest that an amount of the available resources within each environment remains underutilized (Mason et al. 2005); this would lead to reduced nutrient cycling and productivity loss (Petchey & Gaston 2006).

The relationship between increase in forest cover and decline in functional richness (Fig. 3), which has been previously reported (Morante-Filho et al. 2015, Matuoka et al. 2020), is closely related to patterns of species composition; forest and non-forest species exhibit diverse responses to anthropogenic disturbances (Bregman et al. 2016) according to their distinct traits and sensitivities to human-induced disturbances (Gardner et al. 2009, Clavel et al. 2011). These patterns may be linked to the diminished number of resources in second-growth forests in early to medium stages of succession (Metzger et al. 2009), aligning with the characteristics of our study area. Furthermore, the adjacent pasturelands may also increase the proliferation of non-forest species (Morante-Filho et al. 2016).

We found that some generalist species with a greater ability to disperse to be located farther from the centroid of a specific functional space; this may indicate that these species have unique characteristics or distinct behaviours (Laliberté & Legendre 2010). This aligns with our observation of the reduction in functional dispersion with increased forest cover (Fig. 3). The evident decline in functional dispersion values observed in marsh and pasture environments compared to forests could be related to the retention of taxa with traits indicating low dispersion capacity coupled with an influx of highly vagile taxa (Bregman et al. 2016). Moreover, the presence of secondary forests may have influenced the observed patterns in FD.

Caution is warranted when interpreting these findings considering the diverse functional responses in forest and

non-forest birds (Matuoka et al. 2020). Furthermore, the autonomous recorders also have limitations, such as the inability to obtain information on species abundance. Although all data for this study were collected during the rainy season, sampling habitats in different months could have introduced some noise in the data related to the reduction in the intensity of reproductive activities such as courtship and territory defence, including vocalizations.

These findings imply that the influence of forest cover on FD is specific to the different functional groups within the community and could potentially be influenced by the early stages of succession characterizing these regional forest fragments (Johnstone et al. 2016, Thorn et al. 2020). Notably, the paucity of suitable microhabitats in these early stages can act as environmental filters for specialist forest birds (Santos Junior et al. 2016), delaying ecological succession. The arrival of insectivorous specialists would increase the population control of herbivorous arthropods, improving the quality of the environment through greater biomass input (Melo et al. 2020), thus ensuring the stability of key ecological interactions and ecosystem services (Sekercioglu 2012).

Conclusions

There are two significant implications of these results for future research. First, increased species dispersion within a functional space does not necessarily correlate with heightened functional divergence and evenness. Relying solely on functional dispersion and richness might lead to imprecise conclusions regarding higher FD in deforested sites and an assumed improvement in ecosystem functioning within these environments. Thus, we strongly advocate for the utilization of diverse functional indices in forthcoming studies, enabling a more comprehensive evaluation of the effects of anthropogenic disturbance on biodiversity.

Second, deforested landscapes may contain fewer available niches for forest species whilst providing new opportunities for non-forest species. Consequently, the behaviour of forest communities, vertical structuring of habitats and environmental heterogeneity in deforested settings (Melo et al. 2022) could be substantially disrupted, potentially leading to a lack of true compensatory dynamics within the functional framework (De Coster et al. 2015, dos Anjos et al. 2019). Furthermore, the intricate vertical structural complexity of habitats and the accessibility of resources could potentially be compromised due to the current stage of ecological succession observed in the studied sites.

Our data highlight the importance of considering habitat quality and ecological successional stages in conservation efforts. Human-impacted landscapes generally tend towards homogenization, massively suppressing continuous vegetation and/or restricting it to small second-growth fragments. Therefore, an appropriate conservation strategy is the protection of large old and well-connected patches of native vegetation, leading to maintenance of the FD of birds.

Investigation of the long-term dynamics of FD in response to environmental changes is desirable, and we also encourage comparative studies across different forest types from different successional stages.

Supplementary material. To view supplementary material for this article, please visit <https://doi.org/10.1017/S0376892924000080>.

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Competing interests. The authors declare none.

Ethical standards. None.

References

- Acevedo-Charry O, Aide TM (2019) Recovery of amphibian, reptile, bird and mammal diversity during secondary forest succession in the tropics. *Oikos* 128: 1065–1078.
- Adorno BFCB, Barros FM, Cezar Ribeiro M, da Silva VX, Hasui É (2021) Landscape heterogeneity shapes bird phylogenetic responses at forest-matrix interfaces in Atlantic Forest, Brazil. *Biotropica* 53: 409–421.
- Alcarde Alvares C, Stape J, Sentelhas P, Gonçalves J, Sparovek G (2013) Köppen's climate classification map for Brazil. *Meteorologische Zeitschrift* 22: 711–728.
- Alexander J, Ehlers Smith DA, Ehlers Smith YC, Downs CT (2019) Drivers of fine-scale avian functional diversity with changing land use: an assessment of the effects of eco-estate housing development and management. *Landscape Ecology* 34: 537–549.
- Almeida-Gomes M, Vieira MV, Rocha CFD, Melo AS (2019) Habitat amount drives the functional diversity and nestedness of anuran communities in an Atlantic Forest fragmented landscape. *Biotropica* 51: 874–884.
- Arroyo-Rodríguez V, Rös M, Escobar F, Melo FPL, Santos BA, Tabarelli M, et al. (2013) Plant β -diversity in fragmented rain forests: testing floristic homogenization and differentiation hypotheses. *Journal of Ecology* 101: 1449–1458.
- Barbaro L, Giffard B, Charbonnier Y, van Halder I, Brockerhoff EG (2014) Bird functional diversity enhances insectivory at forest edges: a transcontinental experiment. *Diversity and Distributions* 20: 149–159.
- Barbaro L, Rusch A, Muiruri EW, Gravelier B, Thiery D, Castagnayrol B (2017) Avian pest control in vineyards is driven by interactions between bird functional diversity and landscape heterogeneity. *Journal of Applied Ecology* 54: 500–508.
- Barbosa KV de C, Knogge C, Develey PF, Jenkins CN, Uezu A (2017) Use of small Atlantic Forest fragments by birds in southeast Brazil. *Perspectives in Ecology and Conservation* 15: 42–46.
- Barbosa KVdC, Rodewald AD, Ribeiro MC, Jahn AE (2020) Noise level and water distance drive resident and migratory bird species richness within a Neotropical megacity. *Landscape and Urban Planning* 197: 103769.
- Barros FM, Martello F, Peres CA, Pizo MA, Ribeiro MC (2019a) Matrix type and landscape attributes modulate avian taxonomic and functional spillover across habitat boundaries in the Brazilian Atlantic Forest. *Oikos* 128: 1600–1612.
- Barros FM, Peres C, Pizo M, Ribeiro M (2019b) Divergent flows of avian-mediated ecosystem services across forest-matrix interfaces in human-modified landscapes. *Landscape Ecology* 34: 879–894.
- Baselga A (2010) Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography* 19: 134–143.
- Baselga A, Orme CDL (2012) *betapart*: an R package for the study of beta diversity. *Methods in Ecology and Evolution* 3: 808–812.
- Bello FP, Carmona C, Dias A, Götzenberger L, Moretti M, Berg M (2021) *Handbook of Trait-Based Ecology: From Theory to R Tools*. Cambridge, UK: Cambridge University Press.
- Blake JG, Loiselle BA (2001) Bird assemblages in second-growth and old-growth forests, Costa Rica: perspectives from mist nets and point counts. *The Auk* 118: 304–326.
- Boscolo D, Tokumoto PM, Ferreira PA, Ribeiro JW, dos Santos JS (2017) Positive responses of flower visiting bees to landscape heterogeneity depend on functional connectivity levels. *Perspectives in Ecology and Conservation* 15: 18–24.
- Bregman TP, Lees AC, MacGregor HEA, Darski B, de Moura NG, Aleixo A, et al. (2016) Using avian functional traits to assess the impact of land-cover change on ecosystem processes linked to resilience in tropical forests. *Proceedings of the Royal Society B: Biological Sciences* 283: 20161289.
- Brooks M, Kristensen K, van Benthem K, Magnusson A, Berg CW, Nielsen A, et al. (2017) *glmmTMB* balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R Journal* 9: 378–400.
- Burnham KP, Anderson DR (2004) Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods & Research* 33: 261–304.
- Carmona CP, Guerrero I, Morales MB, Oñate JJ, Peco B (2017) Assessing vulnerability of functional diversity to species loss: a case study in Mediterranean agricultural systems. *Functional Ecology* 31: 427–435.
- Clavel J, Julliard R, Devictor V (2011) Worldwide decline of specialist species: toward a global functional homogenization? *Frontiers in Ecology and the Environment* 9: 222–228.
- De Coster G, Banks-Leite C, Metzger JP (2015) Atlantic forest bird communities provide different but not fewer functions after habitat loss. *Proceedings of the Royal Society B: Biological Sciences* 282: 20142844.
- Desrochers A (2010) Morphological response of songbirds to 100 years of landscape change in North America. *Ecology* 91: 1577–1582.
- Develey PF, Peres CA (2000) Resource seasonality and the structure of mixed species bird flocks in a coastal Atlantic forest of southeastern Brazil. *Journal of Tropical Ecology* 16: 33–53.
- Dias RA, Gianuca AT, Vizentin-Bugoni J, Gonçalves MSS, Bencke GA, Bastazini VAG (2017) Livestock disturbance in Brazilian grasslands influences avian species diversity via turnover. *Biodiversity and Conservation* 26: 2473–2490.
- Diniz MF, Coelho MTP, Sánchez-Cuervo AM, Loyola R (2022) How 30 years of land-use changes have affected habitat suitability and connectivity for Atlantic Forest species. *Biological Conservation* 274: 109737.
- Dobrowolski R, Melo AS, Casemiro FAS, Diniz-Filho JAF (2012) Climatic history and dispersal ability explain the relative importance of turnover and nestedness components of beta diversity. *Global Ecology and Biogeography* 21: 191–197.
- dos Anjos L, Bochio GM, Medeiros HR, Almeida B de A, Lindsey BRA, Calsavara LC, et al. (2019) Insights on the functional composition of specialist and generalist birds throughout continuous and fragmented forests. *Ecology and Evolution* 9: 6318–6328.
- Duarte GT, Santos PM, Cornelissen TG, Ribeiro MC, Paglia AP (2018) The effects of landscape patterns on ecosystem services: meta-analyses of landscape services. *Landscape Ecology* 33: 1247–1257.
- Fortin M-J, Dale MRT (2005) *Spatial Analysis: A Guide for Ecologists*. Cambridge, UK: Cambridge University Press.
- Gardner TA, Barlow J, Chazdon R, Ewers RM, Harvey CA, Peres CA, et al. (2009) Prospects for tropical forest biodiversity in a human-modified world. *Ecology Letters* 12: 561–582.
- Gaspar LP, Scarpelli MDA, Oliveira EG, Alves RS-C, Gomes AM, Wolf R, et al. (2023) Predicting bird diversity through acoustic indices within the Atlantic Forest biodiversity hotspot. *Frontiers in Remote Sensing* 4: 1283719.
- Gower JC (1966) Some distance properties of latent root and vector methods used in multivariate analysis. *Biometrika* 53: 325–338.
- IUCN (2022) The IUCN Red List of Threatened Species [www document]. URL <https://www.iucnredlist.org>
- Johnstone JF, Allen CD, Franklin JF, Frelich LE, Harvey BJ, Higuera PE, et al. (2016) Changing disturbance regimes, ecological memory, and forest resilience. *Frontiers in Ecology and the Environment* 14: 369–378.
- Karp DS, Rominger AJ, Zook J, Ranganathan J, Ehrlich PR, Daily GC (2012) Intensive agriculture erodes β -diversity at large scales. *Ecology Letters* 15: 963–970.
- Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91: 299–305.
- Legendre P, Birks HJB (2012) From classical to canonical ordination. In: HJB Birks, AF Lotter, S Juggins, JP Smol (eds), *Tracking Environmental Change*



- Using Lake Sediments: Data Handling and Numerical Techniques (pp. 201–248). Dordrecht, The Netherlands: Springer Netherlands.
- Legendre P, Legendre L (1998) *Numerical Ecology*, 2nd English edition. Amsterdam, The Netherlands: Elsevier.
- Logez M, Pont D, Ferreira MT (2010) Do Iberian and European fish faunas exhibit convergent functional structure along environmental gradients? *Journal of the North American Benthological Society* 29: 1310–1323.
- Mariano-Neto E, Santos RAS (2023) Changes in the functional diversity of birds due to habitat loss in the Brazil Atlantic Forest. *Frontiers in Forests and Global Change* 6: 1041268.
- Mason N, Mouillot D, Lee W, Wilson J (2005) Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos* 111: 112–118.
- Matuoka MA, Benchimol M, Morante-Filho JC (2020) Tropical forest loss drives divergent patterns in functional diversity of forest and non-forest birds. *Biotropica* 52: 738–748.
- Mazel F, Pennell MW, Cadotte MW, Diaz S, Dalla Riva GV, Grenyer R, et al. (2018) Prioritizing phylogenetic diversity captures functional diversity unreliably. *Nature Communications* 9: 2888.
- Melo MA, Sanches PM, Silva Filho DF, Piratelli AJ (2022) Influence of habitat type and distance from source area on bird taxonomic and functional diversity in a Neotropical megacity. *Urban Ecosystems* 25: 545–560.
- Melo MA, Silva MAGDA, Piratelli AJ (2020) Improvement of vegetation structure enhances bird functional traits and habitat resilience in an area of ongoing restoration in the Atlantic Forest. *Anais da Academia Brasileira de Ciências* 92: e20191241.
- Metzger J, Martensen A, Dixo M, Bernacci L, Ribeiro M, Teixeira A, et al. (2009) Time-lag in biological responses to landscape changes in a highly dynamic Atlantic Forest region. *Biological Conservation* 142: 1166–1177.
- Morante-Filho JC, Arroyo-Rodríguez V, Faria D (2016) Patterns and predictors of β -diversity in the fragmented Brazilian Atlantic forest: a multiscale analysis of forest specialist and generalist birds. *Journal of Animal Ecology* 85: 240–250.
- Morante-Filho JC, Faria D, Mariano-Neto E, Rhodes J (2015) Birds in anthropogenic landscapes: the responses of ecological groups to forest loss in the Brazilian Atlantic Forest. *PLoS ONE* 10: e0128923.
- Morelli F, Benedetti Y, Perna P, Santolini R (2018) Associations among taxonomic diversity, functional diversity and evolutionary distinctiveness vary among environments. *Ecological Indicators* 88: 8–16.
- Moritz C, Agudo R (2013) The future of species under climate change: resilience or decline? *Science* 341: 504–508.
- Mouillot D, Graham NAJ, Villéger S, Mason NWH, Bellwood DR (2013) A functional approach reveals community responses to disturbances. *Trends in Ecology & Evolution* 28: 167–177.
- Odum EP, Barret GW (1971) *Fundamentals of Ecology*, 3rd edition. Philadelphia, PA, USA: W.B. Saunders Co.
- Paradis E, Schliep K (2019) *ape* 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics* 35: 526–528.
- Pavoine S, Vallet J, Dufour A-B, Gachet S, Daniel H (2009) On the challenge of treating various types of variables: application for improving the measurement of functional diversity. *Oikos* 118: 391–402.
- Petchey OL, Gaston KJ (2006) Functional diversity: back to basics and looking forward. *Ecology Letters* 9: 741–758.
- Pollock HS, Jones TM, Tarwater CE, Nishikawa ET, Brawn JD (2020) Rapid colonization and turnover of birds in a tropical forest treefall gap. *Journal of Field Ornithology* 91: 107–117.
- Prescott GW, Gilroy JJ, Haugaasen T, Medina Uribe CA, Foster WA, Edwards DP (2016) Reducing the impacts of Neotropical oil palm development on functional diversity. *Biological Conservation* 197: 139–145.
- R Core Team (2022) *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Core Development Team.
- Rezende CL, Scarano FR, Assad ED, Joly CA, Metzger JP, Strassburg BBN, et al. (2018) From hotspot to hopespot: an opportunity for the Brazilian Atlantic Forest. *Perspectives in Ecology and Conservation* 16: 208–214.
- Ribeiro MC, Metzger JP, Martensen AC, Ponzoni FJ, Hirota MM (2009) The Brazilian Atlantic Forest: how much is left, and how is the remaining forest distributed? Implications for conservation. *Biological Conservation* 142: 1141–1153.
- Riemann JC, Ndriantsoa SH, Rödel M-O, Glos J (2017) Functional diversity in a fragmented landscape – habitat alterations affect functional trait composition of frog assemblages in Madagascar. *Global Ecology and Conservation* 10: 173–183.
- Rodrigues RC, Hasui É, Assis JC, Pena JCC, Muylaert RL, Tonetti VR, et al. (2019) ATLANTIC BIRD TRAITS: a data set of bird morphological traits from the Atlantic forests of South America. *Ecology* 100: e02647.
- Santos Junior PCA, Marques FC, Lima MR, dos Anjos L (2016) The importance of restoration areas to conserve bird species in a highly fragmented Atlantic Forest landscape. *Perspectives in Ecology and Conservation* 14: 1–7.
- Scarpelli MDA, Ribeiro MC, Teixeira CP (2021) What does Atlantic Forest soundscapes can tell us about landscape? *Ecological Indicators* 121: 107050.
- Sekercioglu CH (2006) *Ecological Significance of Bird Populations*. Cerdanyola del Vallès, Spain: Lynx Edicions.
- Sekercioglu CH (2012) Bird functional diversity and ecosystem services in tropical forests, agroforests and agricultural areas. *Journal of Ornithology* 153: 153–161.
- Sick H, Barruel P (1984) *Ornitologia brasileira*. Brasília, Brazil: Editora Universidade de Brasília.
- Somenzari M, do Amaral PP, Cueto VR, Guaraldo AdC, Jahn AE, Lima DM, et al. (2018) An overview of migratory birds in Brazil. *Papéis Avulsos de Zoologia* 58: e20185803.
- Thorn S, Chao A, Bernhardt-Römermann M, Chen Y-H, Georgiev KB, Heibl C, et al. (2020) Rare species, functional groups, and evolutionary lineages drive successional trajectories in disturbed forests. *Ecology* 101: e02949.
- Tilman D (1996) Biodiversity: population versus ecosystem stability. *Ecology* 77: 350–363.
- Tobias JA, Sheard C, Pigot AL, Devenish AJM, Yang J, Sayol F, et al. (2022) AVONET: morphological, ecological and geographical data for all birds. *Ecology Letters* 25: 581–597.
- Tonetti VR, Rego MA, De Luca AC, Devey PF, Schunck F, Silveira LF (2017) Historical knowledge, richness and relative representativeness of the avifauna of the largest native urban rainforest in the world. *Zoologia* 34: 1–18.
- Villéger S, Mason NWH, Mouillot D (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* 89: 2290–2301.
- Violle C, Navas M-L, Vile D, Kazakou E, Fortunel C, Hummel I, et al. (2007) Let the concept of trait be functional! *Oikos* 116: 882–892.
- Wilman H, Belmaker J, Simpson J, de la Rosa C, Rivadeneira MM, Jetz W (2014) *EltonTraits* 1.0: species-level foraging attributes of the world's birds and mammals. *Ecology* 95: 2027.
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) *Mixed Effects Models and Extensions in Ecology with R*. Berlin, Germany: Springer.