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BIOLOGICAL SCIENCES

Improvement of vegetation structure enhances bird functional traits and habitat resilience in an area of ongoing restoration in the Atlantic Forest

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Abstract: Ecological restoration is a traditional option for recovering biodiversity and ecosystem functions. Birds perform pollination, seed dispersal, and pest-control services, which catalyze increases in habitat structure. Habitat complexity changes bird composition, but there is little evidence of its effects on bird functional diversity in Neotropical restorations. We tested whether bird functional diversity and composition respond to increased habitat complexity. Point-counts were performed (January-December 2015) in an area undergoing restoration (536 ha) in the Atlantic Forest of southeastern Brazil, in restorations with less and more structured vegetation and pastures and forest-fragments. The functional bird traits considered were diet, habitat, biomass, environmental sensitivity, and foraging strata. Increased habitat complexity was evaluated using plant characteristics (exotic grass, canopy, herbaceous cover, and diameter at breast height). A total of 172 bird species (5% endemic; 12% migratory) were recorded. Increased vegetation structure in both restored sites and forest-fragments drove a reorganization and addition of functional bird traits, which positively influenced functional richness, dispersion, and evenness. Shifts in plant-characteristics rearranged bird functional traits (diet-forest-dependence and diet-strata-foraging). The rapid development of vegetation structure is a key factor for restoration because it provides additional habitat for semi-dependent forest birds and enhances resilience and sustainability in new man-made forests.

Key words: active restoration, avian assemblages, bird guilds, ecosystem functions, functional diversity.

INTRODUCTION

The expansion of human activities and the development of agriculture, livestock, and urbanization are responsible for the collapse of pristine tropical forests worldwide (Houghton 1994, Myers et al. 2000, Laurance et al. 2014). Therefore, the restoration of more than two billion hectares of former native vegetation is now a global priority (Minnermayer et al. 2011, Crouzeilles et al. 2016). Ecological restoration aims to recover degraded lands (SER 2004, Brancalion et al. 2013) and rescue a set of their biodiversity, ecological interactions, and ecosystem services (Chazdon et al. 2009, Hobbs et al. 2009, Rey-Benayas et al. 2009), and has been a widely-adopted strategy by ecologists and decision-makers (Brancalion et al. 2013).

Restoration success can be evaluated by the ability to improve biodiversity and ecosystem functions (Sullivan et al. 2018, Batisteli et al. 2018). The restoration of animal communities has long remained in the background, following the idea that fauna would be passively rescued by only recreating suitable conditions (Palmer et al. 1997). Nonetheless, the restoration of faunal assemblages is highly complex in the tropics due to the awesome amount of biodiversity and ecological interactions involved (da Silva et al. 2015). Birds possess characteristics that make them good models for evaluating whether restorations are reaching their goals. These vertebrates are highly diverse (Del Hoyo et al. 2019), extremely vagile (usually the first re-colonizers of restored sites) (Munro et al. 2011), and perform vital ecosystem functions (e.g., pollination, seed dispersal, and pest control) (Medellin & Gaona 1999, Morrison & Lindell 2012). The ecosystem functions provided by birds are essential for habitat maintenance and are strictly connected to their multiple ecological traits (Mason et al. 2005). Functional traits are individual morphological, physiological and/or phenological attributes (Laliberté & Legendre 2010) that have been used to calculate functional diversity (FD) (Laliberté et al. 2014) and to understand how birds interact in an ecosystem (Violle et al. 2007). Positive responses of bird FD to vegetation diversity can be modulated by multiple associations between animal traits and vegetation structure (Sitters et al. 2016). Likewise, FD metrics are sensitive to vegetation structure of restored sites (Batisteli et al. 2018) and have been considered better metrics for evaluating restoration success than taxonomic composition (Brancalion & Holl 2016). The relationship between FD and habitat resilience is linked to the maintenance of a high number of species with similar functions yet distinct responses to disturbance (Arruda Almeida et al. 2018).

The Atlantic Forest is considered a global biodiversity hotspot (Myers et al. 2000). Currently highly fragmented, the Atlantic Forest persists as small-isolated remnants surrounded by a matrix of pastures and croplands (Ribeiro et al. 2009, Calaboni et al. 2018). This scenario makes the coexistence of bird conservation and agriculture production in this biome a great challenge (Uezu et al. 2005, Uezu & Metzger 2016, Piratelli et al. 2019). On the other hand, the Atlantic Forest offers great opportunities for habitat restoration (Minnermayer et al. 2011), and active restoration has become a central strategy for reducing the effects of forest fragmentation and to avoid local extinctions of forest birds (Uezu & Metzger 2016).

The effects that vegetation structure has on bird FD has been studied in ecoregions across the world. In general, bird FD metrics increase with increasing vegetation structure in temperate forests in North America, Europe and Asia (Bae et al. 2018). However, distinct responses have been found in tropical zones. In Australia, FD indices were found to be positively related to vertical vegetation diversity in humid forests, yet inversely related to vertical vegetation in dry forests (Sitters et al. 2016). A similar pattern was also found in savannahs in Namibia (Seymour et al. 2015). These results illustrate that tropical ecosystems may have different responses than temperate habitats, and extrapolations based on FD indices found in distinct ecoregions can lead to unsuccessful conservation strategies for the megadiversity of the Neotropics (Freitas & Mantovani 2018). Nonetheless, there is a large knowledge gap regarding how bird assemblages and FD respond to the increased vegetation structure from active restoration process in Neotropical ecosystems, which limits the assessment of the efficacy of restoration actions (Ortega-Alvárez & Lindig-Cisneros 2012). Several local-scale active restorations have been undertaken in the Brazilian Atlantic Forest (Rodrigues et al. 2011), but there is little evidence regarding the effects of the development of vegetation structure on bird taxonomic composition and the conservation of their functional traits in these systems.

Here we address how a recent (i.e., less than 10 years old; Twedt et al. 2002) active restoration program with high-diversity plantation may drive the taxonomic and functional diversity of birds, compared to pasture and small native forest fragments. Specifically, we tested whether increased vegetation structure of restored areas changes the arrangement of bird assemblages. Thus, we evaluated whether bird species richness (SR) and FD indexes (based on bird traits regarding diet, biomass, forest dependence, foraging strata, and environmental sensitivity) differ between restored and non-restored habitats due to non-random environmental changes linked to increased vegetation structure. These non-restored habitats were represented by pasture (as a degraded reference) and small native forest fragments (as meta reference). Although from a restoration ecology perspective the restored habitats are young (< 10 years old post-planting) (Twedt et al. 2002), we still expected to find differences in vegetation structure because they were first visually checked and then confirmed as different by comparing the proportion of grass and canopy cover, diameter at breast height and tree morphorichness). Increased vegetation structure in new man-made forests might be a central tool for recovering native bird species and their essential functional traits to increase ecosystem resilience and sustainability. We predicted the following:

Less structured restorations, dominated by exotic grass and with little canopy cover and low tree morphorichness (Melo et al. 2007), should maintain bird SR and FD similar to that of pasture, but different from more-structured restorations and small native forest fragments. Degraded habitats dominated by exotic grass cover sustain simplified bird assemblages composed of omnivorous, granivorous, forest-independent and low sensitivity species (Becker et al. 2013, Casas et al. 2016);

More structured restorations with higher tree morphorichness, more canopy cover, and less exotic grass cover, should provide more microhabitats, niches, and resources for birds. Thus, they are likely to maintain levels of bird SR and FD above that of pasture and less-structured restored habitats — both dominated by exotic grass — yet below that of small native forest fragments. Active restorations add vegetation structure (e.g., herbaceous and tree traits), which provides habitats for several functional groups of birds (e.g., frugivores, nectarivores and insectivores) (Becker et al. 2013, Batisteli et al. 2018).

MATERIALS AND METHODS

Study area

This study was carried out at "*Centro de Experimentos Florestais*", an area of 526 ha in eastern São Paulo State, southeastern Brazil (23°14'15.18" S, 47°24'3.29" W; 580 m a.s.l). The climate is characterized by dry winters and hot summers, with average monthly precipitation of 56 mm and 160 mm, respectively (Alvares et al. 2013). The vegetation is semideciduous seasonal forest, one of the phytophysiognomies of the Atlantic Forest (Veloso et al. 1991).

The native forest fragments in the area are of different ages and were historically deforested and converted to coffee (*Coffea arabica* L.) plantations in the early 20th century (César et al. 2013). Prior to restoration actions, the coffee plantations were abandoned and converted to pastures dominated by invasive exotic grass (*Urochloa* spp.) for raising cattle by intensive system (Amazonas et al. 2018). These land uses drastically affected the native vegetation arising in the highly fragmented landscape, with few small and isolated secondary forest remnants (Amazonas et al. 2018, Andrade et al. 2018). In this context, a forest restoration program was initiated in 2007 with the aim of restoring a set of the native vegetation, fauna and ecosystem functions and services (Gagetti et al. 2016). A high diversity planting, using ~720,000 seedlings from more than 100 native tree species, was performed randomly with 3 x 2 m spacing, composed of pioneer and secondary species (see Gagetti et al. 2016). The restored area encompasses nearly 400 ha, with planting age ranging from four to 11 years. This area is currently a restored island in a highly fragmented landscape of Atlantic Forest, surrounded by pastures with exotic grass (*Urochloa* spp.) for cattle ranching, and croplands. Bodies of water (e.g., artificial lakes and swamps) are also found throughout the area.

Vegetation structure

Tree traits, such as canopy cover, diameter at breast height, tree height and increase in biomass following the age of plantings, have been used as indicators of the structural development of vegetation during forest restoration (Melo et al. 2007, Crouzeilles et al. 2016). Herein, we assume that habitat types with greater exotic grass and lower values for tree traits (e.g., canopy cover, diameter at breast height, and tree morphorichness) have less vegetation structural development (hereafter, VSD), while habitat types with higher values for these tree traits and less exotic grass cover have higher VSD. We measured plant characteristics (below) for each of 39 fixed-point bird-count sites to acquire VSD. Fixed-point counting is a commonly used method for evaluating bird assemblages by which researchers consider only birds recorded during a limited sampling time and/or in a defined area (Bibby et al. 2000; more details below). The measured plant characteristics were: (i) herbaceous plants (*Herb*) - visually estimated percentage of ground covered by herbaceous plants in 20-m radius plots; (ii) exotic grasses (*Grass*) - visually estimated percentage of ground covered by exotic grasses in 20-m radius plots; (iii) canopy cover (*Canopy*) – mean of four estimates, one in each cardinal direction (N, S, E, and W) at 10-m from the center of each point, made using percentage of spherodensiometer squares occupied by light passing through the foliage; (iv) diameter at breast height (cm) (*DBH*) - estimated from tree basal area; (v) tree morphorichness (*Ric.tree*) - morphologically distinct arboreal tree specimens were classified as tree morphospecies and counted at each point locations; and (vi) tree height (cm) (*Tree. height*) - measured from the ground to the top of tree foliage (Table I).

Even though the two restored habitats were of similar age, we visually verified *in loco* that they had distinct characteristics of VSD. This was confirmed by subjecting plant traits (grass cover, canopy cover, herbaceous cover, DBH and tree morphorichness) to a one-way ANOVA followed by Tukey's *pos-hoc test p* <0.05). The two restoration habitats were subsequently considered as distinct areas, and form here on referred to as the (1) less structured restored habitat and the (2) more structured restored habitat.

Bird samplings, functional traits, and other arrangements

Birds were surveyed twice a day (at 05:30–09:30 and 16:30-18:30) from January to December 2015. A total of 39 point-count sites (Bibby et al. 2000) with a limited radius of 60 m (Rolo et al. 2017) were established such that they were separated by at least 200 m to avoid repeated counts (Vielliard et al. 2010). Each point-count involved recording the number of individuals of all species heard and/or seen (8x42 mm binoculars) for 10 min (Becker et al. 2013, Rolo et al. 2017). Birds flying over the area without any observed resource/substrate use were excluded

Table I. Sites, samples and vegetation characteristics of the four studied habitats: PA, pasture; LS, less structured restoration; MS, more structured restoration; and FF, forest fragments. Mean values of vegetation characteristics collected on 10x20 m plots from the center of each point-count.

Sites, samples and vegetation characteristics	PA	LS	MS	FF
Number of point-counts	9	13	12	5
Size of area (ha)	52	112.5	60	0.9-23
Age of vegetation (years)	< 0.5	4-5	6-7	> 30
Ric.Tree (mean)	1.7^{a}	7.3^{b}	11.8^{c}	14.6^{c}
DBH (cm)	22.5^{a}	37.4^{a}	40.2^{a}	45.8^{a}
Tree height (m)	1.7^{a}	3.2^{ac}	4.2^{bc}	6.5^{b}
Canopy cover (%)	0^{a}	26.3^{a}	45.3^{b}	83.7^{c}
Grass cover (%)	100^{a}	97.5^{a}	38.7^{b}	0^{c}
Herbaceous cover (%)	0^{a}	2.6^{a}	0^{a}	80^{b}

DBH = diameter at breast height; Ric.Tree = tree morphorichness.
PA = pasture; LS = less structured restoration; MS = more structured restoration; FF = forest fragments.
Distinct overwritten letters indicate significant differences between the habitats (ANOVA and Tukey *post hoc* p<0.05).

from the analysis (Roels et al. 2019). Rainy and windy days were avoided for performing point-counts (Rolo et al. 2017, Roels et al. 2019). Point-counts were performed monthly in a random order among sites during campaigns of three consecutive days (total of 468 samplings) (Vielliard et al. 2010).

Bird species were classified according to 13 traits related to their ability to occupy and explore habitats and resources: (a) *Diet* is represented by the percentage of each of the following items (Wilman et al. 2014) — invertebrates, endotherms, ectotherms, fish, other vertebrates, carrion, fruits, nectar, seeds, and plants; (b) *Foraging stratum* is represented by the percentage of use of each level (Wilman et al. 2014) — below and around water surface, ground, understory, mid-height, canopy, and aerial; (c) *Body mass* (Wilman et al. 2014); (d) *Forest dependence* (Parker III et al. 1996) as — independent (I) for species recorded mainly in grasslands, pastures, and marshes; semi-dependent (S) for species observed mainly at forest edges and also using open habitats; and dependent (D) for species recorded mainly in forest habitats; (e) *Environmental sensitivity* (Parker III et al. 1996) S: low (L), medium (M) and high (H) sensitivity to disturbed and degraded lands. Generalists are defined here as those species having high ecological plasticity (diet and/or environmental) and whose populations tend to grow in simplified habitats such as pastures and degraded/open-habitats (e.g., granivores, omnivores, and insectivores, here also considered as forest independent and having low environmental sensitivity). Similarly, specialists are defined as those species with some restrictions in their requirements, either for forest habitats or feeding strategies (forest dependent, and/or high sensitivity or insectivorous and frugivorous forest birds).

The conservation status of bird species was assessed using official regional (São Paulo 2018) and global (IUCN 2019) red lists. Endemic birds of the Atlantic Forest followed Vale et al. (2018). Migratory birds followed Somenzari et al. (2018) as: (a) migratory (MGT) - species with populations that regularly and seasonally move away from their breeding sites and return every breeding season; and (b) partially migratory (MPR) - species with populations that are partially migratory; and (c) resident (RE), species that occupy the same area throughout the year, including nomadic birds, with minor variation in population structure. Nomenclature followed the Brazilian Ornithological Records Committee (Piacentini et al. 2015).

Statistical analysis

Bird assemblages of the four habitats were first evaluated using the iNEXT function of the homonym package (Hsieh et al. 2016). Individual-based rarefaction curves were plotted against a given number of individuals chosen randomly from observed samples until all individuals had been accumulated, whereas extrapolation curves were plotted to double the degraded reference habitat (Colwell 2012), which in the present case was pasture. Pasture was chosen as a reference because it is a regional habitat that existed before the restoration program. A total of 999 bootstrap replicates were used to estimate 95% confidence intervals, with non-overlapping confidence intervals among the habitats being assumed to reflect significant differences.

Functional distances between pairs of species were then calculated using Gower's distance metric (Gower 1966), which is suitable for calculating both categorical and continuous traits with missing trait values (Legendre & Legendre 1998, Podani 1999). Species richness (SR) and functional diversity (FD) parameters were computed, the latter as functional richness (FRic), functional divergence (FDiv), functional evenness (FEve), functional dispersion (FDis), and Rao's quadratic entropy (Rao's Q) for each point-count site using the *dbFD* function of the *FD* package (Laliberté & Legendre 2010, Laliberté et al. 2014).

Functional richness (FRic) is the volume of multidimensional space occupied by a biological community within functional space (Villéger et al. 2008). Low functional richness occurs when some of the available resources are unused. Similarly, more efficient use of available resources is translated into higher values of functional richness (Mason et al. 2005). Functional divergence (FDiv) measures divergence in the distribution of abundance in the trait volume. It represents the degree of niche differentiation in a biological assemblage and increases with the number of species that have unique functional trait values. Functional evenness (FEve) represents the regularity of the abundance distribution of the functional traits in multidimensional niche space (Mouillot et al. 2005, Villéger et al. 2008). Values of FEve decrease either when abundance is less evenly distributed among species or when functional distances among species are less regular (Villéger et al. 2008). FDis and Rao's Q are multivariate measures of the dispersion of species in multidimensional niche space and reflect both the volume of occupied functional space and the distribution of species abundances within this space (Laliberté & Legendre 2010). The difference between these two parameters is that FDis represents the mean distance of individual species to the centroid of all species, while Rao's Q is the mean distance between each pair of these species. Higher values of FDis indicate a greater potential for functional complementarity among species. Different from FRic, which is monotonically related to SR, FDis and Rao's Q are influenced only by species abundances (Laliberté & Legendre 2010). Moreover, the *vif* function in the *usdm* package (Naimi et al. 2014) was used to calculate the variance inflation factor (VIF) for the vegetation variables and excluded *Tree.height* because of a problem with multi-collinearity (VIF > 0.4). Moran's I test was then used to test for spatial autocorrelation, which was not found for SR (Moran's I: -0.02, *p-value*: 0.85) or FD parameters (all *p-value*: >0.1).

Whether vegetation structural development (VSD) shaped bird predictors as SR and FD measures in restored and non-restored (pasture and forest fragments) habitats was then tested. The dimensionality of the vegetation characteristics was reduced using principal component analysis (PCA), with each of the first two axes (1^{st} and 2^{nd} PCs) being used to frame a vegetation structure gradient (VSD 1 and 2) (Batisteli et al. 2018). Multiple regressions models were then applied to test whether VSD values (predictor variables) significantly influenced bird predictors ($p < 0.05$).

Finally, since the habitats were spatially close (10 to 1200 m), we assumed that birds have the same chance of occurring in all areas, except for their specific habitat requirements, here translated as VSD. Thus, the influence that VSD had on the composition of bird guilds in the four studied habitats was tested. To do this, bird traits were combined to transform them into categorical functional bird groups: (a) *diet-forest dependence*, which was composed of species with a combination of diet and forest dependence, such as fruit-nectar forest independent (Fn.I), semi-dependent (Fn.S) and dependent (Fn.D), insectivores (In.I, In.S and In.D), omnivores (Om.I, Om.S, and Om.D), granivores (Gf.I, Gf.S, Gf.D), and vertebrate-fish-scavengers (Vfs.I, Vfs.S); and (b) *diet-foraging stratum*, which comprised frugivores-nectarivores of the canopy (Fc.C), mid-height (Fn.M), generalist (Fn.Mix), understory (Fn.U), insectivores (In.C, In.M, In.Mix, In.U), omnivores (Om.C, Om.M, Om.Mix, Om.U, including Om.G as ground omnivores), granivores (Gf.C, Gf.G, Gf.Mix, Gf.U), and vertebrate-fish-scavengers (Vfs.C, Vsf.G, Vsf.Mix). This was done by evaluating the correlation among species abundance and vegetation characteristics in restored and non-restored habitats, assuming a null hypothesis of the absence of correlation.

A non-metric multidimensional scaling (NMDS) analysis with Bray-Curtis distance index was conducted to evaluate the composition of each bird functional group weighted by species abundances. The stress values of the best ordination solution arrived at after 20 tries was examined and the number of dimensions increased to achieve solutions with stress values of < 20.0, due to the acceptable representation of multivariate relationships (McCune & Grace 2002). The same number of dimensions was adopted across all ordinations to allow comparisons. Thus, the *vectorfit* function in the Vegan package (Oksanen et al. 2019) was implemented to regress each variable on scores for the NMDS axes, calculate the strength of the association (R^2), and determine the significance of this R^2 using a permutation test with 1000 simulations.

For graphical representation, only significant variables (*p-value* < 0.05) were added to NMDS ordination plots as vectors with directions weighted by the regression coefficient with each axis, and the length of the vector weighted by the R^2 value. This procedure was able to determine which bird functional groups were associated with the vegetation characteristics presented in the restored and non-restored habitats. All analyses and graphics were performed in R software v.3.5.2 (R Core Team 2019).

RESULTS

Vegetation structure

Vegetation structure differed between restored and non-restored habitats (Table I; Figure 1). The first axis of the PCA (Vegetation axis 1) explained 56.7% of the variation and was positively related to tree morphorichness (*Ric.Tree*) and canopy cover (*Canopy*), and negatively associated with grass cover (*Grass*). The second axis (Vegetation axis 2) explained 18.4% of the variation, with diameter at breast height (*DBH*) and herbaceous cover (*Herb*) being positively and negatively related, respectively. Our prediction that the vegetation (VSD) of the two restored habitats, even having the same post-planting age, would be structurally distinct was confirmed. Vegetation structure also differed among these and the reference habitats (pasture and forest fragments). Thus, the sampling habitats will hereinafter be referred to as restoration with more structured and developed vegetation (MS); restoration with less structured and developed vegetation (LS); pasture (PA); and fragments of native vegetation (FF).

Thus, the axes of the PCA created a vegetation structure gradient with forest-fragments (FF) and more structured restoration (MS) being dominated by a higher prevalence of *Ric.Tree*, *Canopy* and *DBH* (with the exception of MS1, MS9, MS11, MS12, and MS13 point-count sites). On the other hand, less structured restoration (LS) and pasture (PA) habitats were dominated by high grass cover (Figure 1; with the exception of LS3, LS 4, LS7 and LS10 point-count sites).

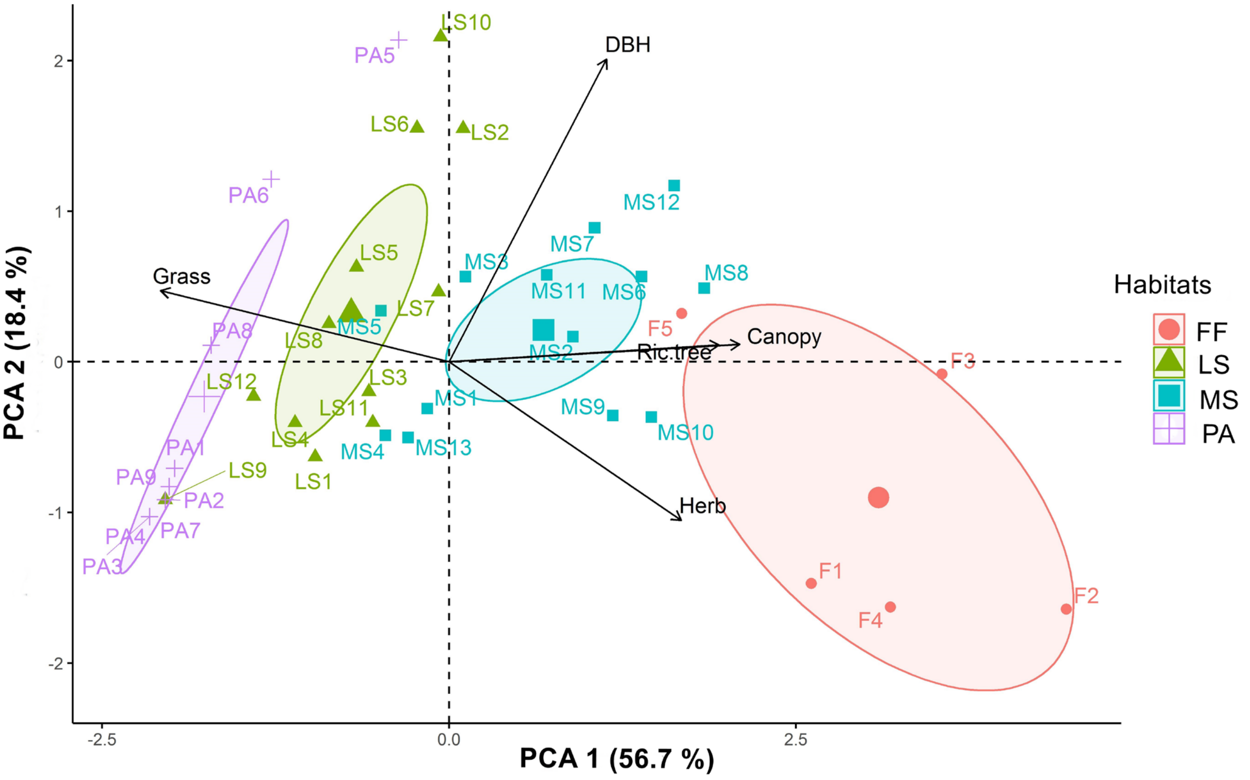

Figure 1. Influence of vegetation traits (arrows) on the four habitat-types represented by results of principal component analysis (PCA) in 39 point-counts at less (LS1: LS12) and more (MS1: MS13) structured restorations, pasture (P1: P9) and forest fragments (F1: F5).

Birds

A total of 9,163 records representing 172 bird species (20 Orders and 44 Families) were sampled (Table SI - Supplementary Material). The observed species richness (SR) corresponded to 89% and 92% of the richness estimated by *Jacknnife1* (192.9) and *Chao1* (187.7) respectively. Rarefaction curves suggest stabilization only for forest-fragments (Figure 2). Less structured restoration (LS) and pasture (PA) habitats had higher SR than more structured restoration (MS) and forest-fragments (FF), while restorations (both LS and MS) had the greatest bird abundance (Figure 2), although significantly different only between LS and FF (Figure 2).

Nine of the sampled species (5%) were endemics of the Atlantic Forest (Vale et al. 2018) (Table SI), and were recorded mainly in FF. Some endemic birds were only recorded in FF, such as the Whited-eye Foliage-gleaner (*Automolus leucophthalmus*), whereas the Crescent-chested Puffbird (*Malacoptila striata*) and Orange-breasted Thornbird (*Phacellodomus ferrugineigula*) were recorded in FF and in both restoration habitats. Records of the Brazilian Tanager (*Ramphocelus bresilius*) were exclusively from the restored habitats. Other endemic birds (e.g., Pallid Spinetail [*Cranioleuca pallida*], Rufous-capped Spinetail [*Synallaxis ruficapilla*], and Ochre-collared Piculet [*Picumnus temminckii*]) occurred in both forest fragments and the restored habitats. The Red-winged Tinamou (*Rhynchotus rufescens*), Rusty-margined Guan (*Penelope superciliaris*), and Turquoise-fronted Amazon (*Amazona aestiva*) are regionally near-threatened species (São Paulo 2018); they were recorded in both PA and LS, and *A. aestiva* also in MS. The Common Waxbill (*Estrilda astrild*) was the only exotic introduced species (Sick 1997) (Table SI). Most species (151 species; 88%) were classified as residents, while

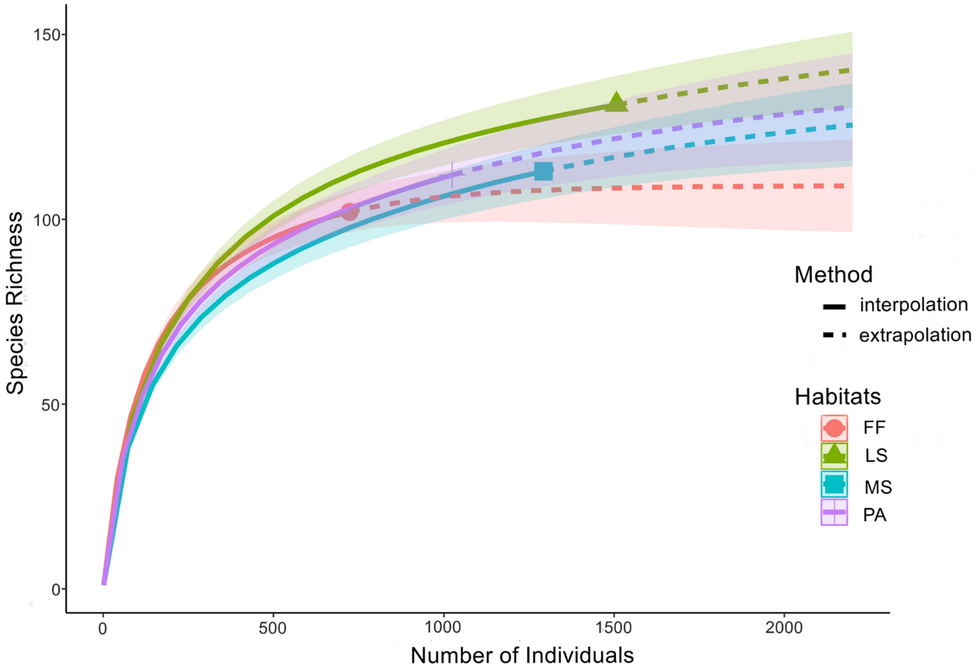

Figure 2. Sample-based rarefaction (solid line) and extrapolation (dashed line) for bird species richness in less (LS) and more (MS) structured restorations and pasture (PA) and (FF) forest fragment as references sites. Solid and dashed lines are, respectively, rarefaction and extrapolation (up to double the degraded habitat reference site, pasture), and 95% confidence intervals were obtained by a bootstrap method based on 999 replications.

21 (12%) were classified as migrants (Somenzari et al. 2018). Twenty of these migrants are partially migratory (e.g., Plumbeous Kite *Ictinia plumbea*, Streaked Flycatcher *Myiodynastes maculatus*, and Swainson's Flycatcher *Myiarchus swainsoni*), and one fully migratory (Sick's Swift *Chaetura meridionalis*) (Somenzari et al. 2018), which was recorded only in the rainy season.

Bird functional traits and composition in relation to VSD

Only LS and FF differed significantly in accumulated SR, due to non-overlapping confidence interval curves (Figure 2). Vegetation structural development (PCA axis 1) did not affect SR ($p > 0.05$) or functional divergence (FDiv, $p > 0.05$), but positively affected functional richness (FRic, $p = 0.008$), functional dispersion (FDis; $p < 0.001$), functional evenness (FEve; $p = 0.01$), and Rao's quadratic entropy (Rao's Q, $p < 0.001$) (Figure 3a-d). Point-counts in MS and FF were more related (Figure 3a-d). However, contrary to our expectation, restoration point-count sites showed two-way results for FRic: (1) low FRic with higher VSD, and (2) high FRic with low VSD (Figure 3a). Plant traits induced non-aleatory effects on bird assemblages, while bird functional groups were significantly related to VSD (Tables II and III). Ordination by NMDS revealed a trend for segregating bird composition between restored and non-restored habitats. Point-count sites of both pasture (PA) and forest-fragments (FF) were

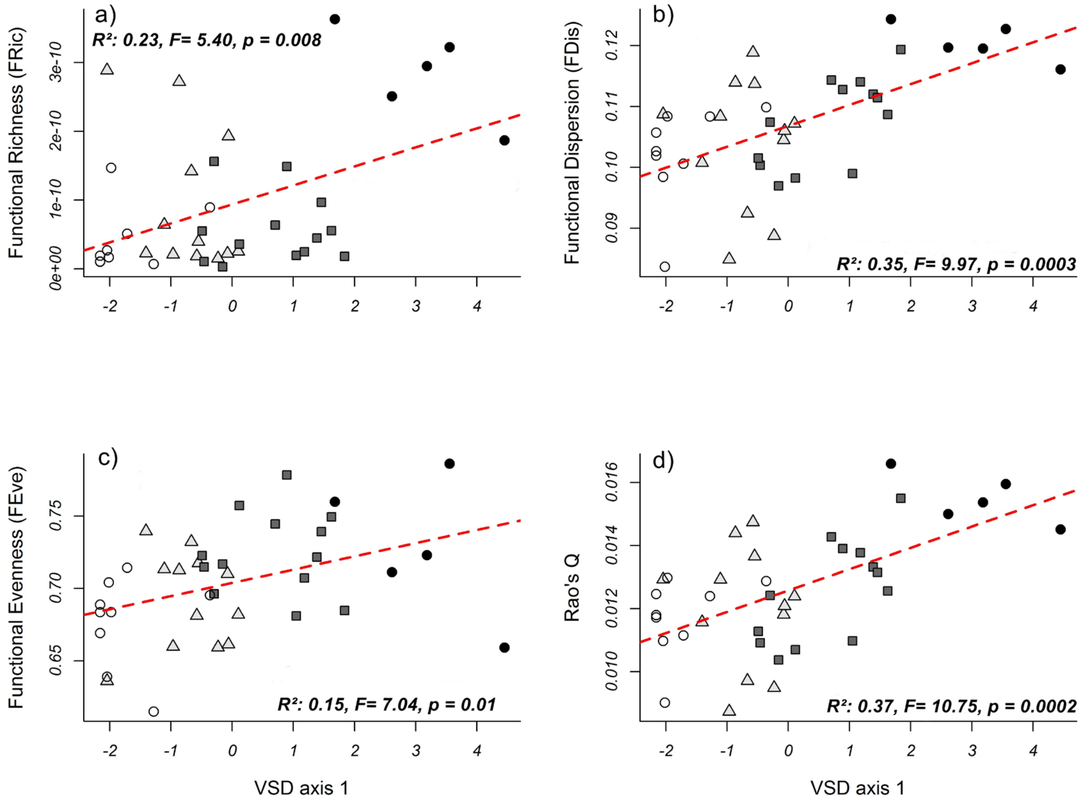

Figure 3. The influence of vegetation structure development (VSD) on bird functional diversity parameters: a) functional richness (FRic); b) functional dispersion (FDis); c) functional evenness; and d) Rao's quadratic entropy and its relationships at each habitat-types. Legend: triangles, less structured restoration; squares, more structured restoration; white circles, pasture; and black circles, forest fragment. Red dashed lines indicate significative multiple linear regression models ($p \leq 0.01$). Species richness (SR) and functional divergence (FDiv) were non-significantly related to VSD and not showed.

located at the extremes of the NMDS axes, while those of both LS and MS were located in the middle.

Canopy, Ric.tree, and *DBH* were strongly correlated with NMDS axis 1, in the same direction as *diet-strata foraging*, while *Grass* was correlated in the opposite direction; *Herb* was correlated with NMDS axis 2. Thus, the high predominance of exotic grass in PA, LS, and some point-count sites in MS retained bird assemblages typical of degraded sites, such as non-forest birds represented by ground-foraging granivores, omnivores, and insectivores (Table II). The relative increase in the values for plant characteristics (*Ric.tree*, *DBH*, and *Canopy*) in restored habitats was translated into better-structured diet-strata bird groups (insectivores, granivores, omnivores and

Table II. Effects of vegetation traits on diet-strata foraging of birds following NMDS analysis ($p < 0.05$). See methods for abbreviations of the vegetation traits and bird functional groups.

Vegetation	**NMDS1**	**NMDS2**	**R²**	***p***
Ric.Tree	- 0.92	- 0.38	0.53	<0.001
DBH	- 0.85	- 0.51	0.25	<0.01
Grass	0.97	0.20	0.34	<0.001
Herb	- 0.50	- 0.86	0.29	0.001
Canopy	- 0.99	- 0.09	0.63	<0.001
Functional group				
Fn.C	-0.32	-0.94	0.22	<0.01
Fn.M	-0.99	-0.04	0.58	0.001
Fn.Mix	-0.83	-0.55	0.30	<0.01
Fn.U	-0.45	0.89	0.65	0.001
In.C	-0.88	0.45	0.40	0.001
In.G	0.83	0.54	0.65	0.001
In.M	-0.95	-0.31	0.43	0.001
In.Mix	0.99	-0.08	0.08	>0.05
In.U	-0.49	-0.87	0.16	<0.05
Om.C	-0.36	-0.93	0.04	>0.05
Om.G	0.97	0.23	0.43	0.001
Om.M	-0.15	0.98	0.23	0.01
Om.Mix	1.00	-0.00	0.00	>0.05
Om.U	0.58	-0.81	0.21	<0.01
Gf.C	0.33	0.94	0.33	<0.01
Gf.G	0.99	-0.06	0.44	0.001
Gf.Mix	0.99	-0.14	0.49	0.001
Gf.U	0.39	-0.91	0.17	<0.01

frugivores-nectarivores), which were mostly generalists foraging from the understory to the canopy. Only the increase in vegetation structure observed in FF and some point-count sites in MS could allow mid-story insectivores and frugivores-nectarivores (Table II, Figure 4). For *diet-forest* dependents, however, *Ric.tree*, *DBH*, and *Herb* were associated with NMDS axis 1 in the same direction, and *Grass* in the opposite direction; *Canopy* was related to NMDS axis 2 (Table III). Therefore, non-forest insectivores, omnivores, granivores, and carnivores were more correlated with the massive presence of *Grass* cover in PA, LS, and in some point-count sites in MS (Table III). Restored habitats added important plant structure (*Ric.tree*, *DBH*, *Herb*, and *Canopy*), supporting insectivores, frugivores-nectarivores, and forest semi-dependent granivores. Nevertheless, only forest fragments supported forest-dependent (insectivores, frugivores-nectarivores and omnivores), and forest-semi dependent (omnivores) species (Table III, Figure 5).

Table III. Results of NMDS analysis for the effects of vegetation structure on diet-forest dependence of birds (p < 0.05). See methods for abbreviations of the vegetation and functional group.

Vegetation	**NMDS1**	**NMDS2**	**R²**	***p***
Ric.Tree	0.30	0.95	0.25	<0.01
DBH	0.16	0.98	0.23	<0.01
Grass	- 0.92	- 0.37	0.34	0.001
Herb	0.98	0.14	0.44	<0.001
Canopy	0.84	0.53	0.20	<0.05
Functional group				
Fn.D	-0.979	0.205	0.314	<0.01
Fn.I	-0.723	-0.691	0.451	0.001
Fn.S	-0.562	0.827	0.372	0.001
In.D	-0.97	0.241	0.719	0.001
In.I	0.509	-0.861	0.553	0.001
In.S	-0.899	0.438	0.628	0.001
Om.D	-0.94	0.341	0.227	0.01
Om.I	0.812	-0.583	0.075	>0.05
Om.S	-0.961	-0.277	0.562	0.001
Gf.D	-0.54	-0.842	0.528	0.001
Gf.I	0.671	-0.742	0.445	0.001
Gf.S	-0.963	-0.271	0.559	0.001
Vfs.I	0.472	-0.882	0.117	>0.05
Vfs.S	-0.251	-0.968	0.357	0.001

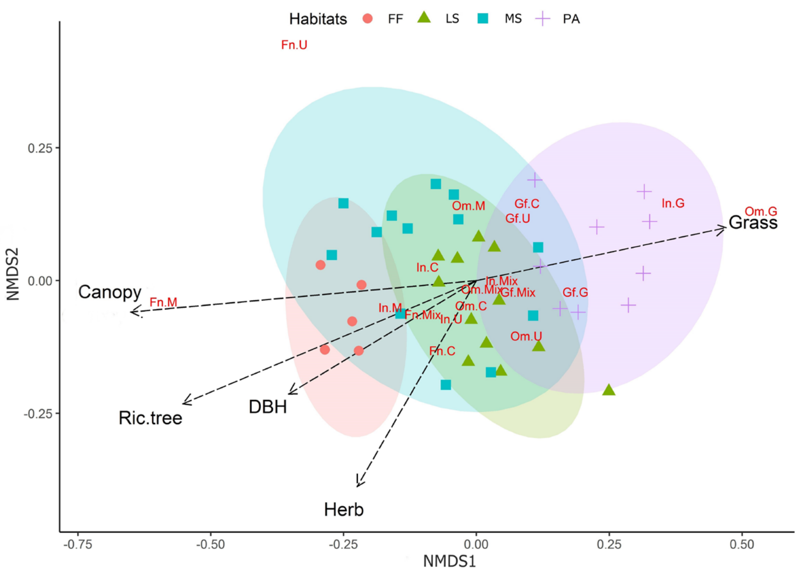

Figure 4. NMDS ordination plot of bird community data from four (restored and non-restored) habitats, including the vectors of the explanatory variables, *Canopy*, *Ric.tree*, *Herb*, *DBH*, and *Grass* that the various functional groups were related to. Final stress from two-dimensional solution = 0.17. Ellipses = 95 % confidence level in each habitat type. Legend. *Habitats:* red circles, forest fragment (FF); green triangles, less structured restoration (LS); blue squares, more structured restoration (MS); purple plus, pasture (PA). *Diet-foraging stratum*: frugivores-nectarivores (Fc.C) canopy, (Fn.M) mid-high, (Fn.Mix) generalist, (Fn.U) understory; following the same nomenclature for insectivores (In.C, In.M, In.Mix, In.U), omnivores (Om.C, Om.M, Om.Mix, Om.U, included Om.G as ground omnivores), and granivores (Gf.C, Gf.G, Gf.Mix, Gf.U).

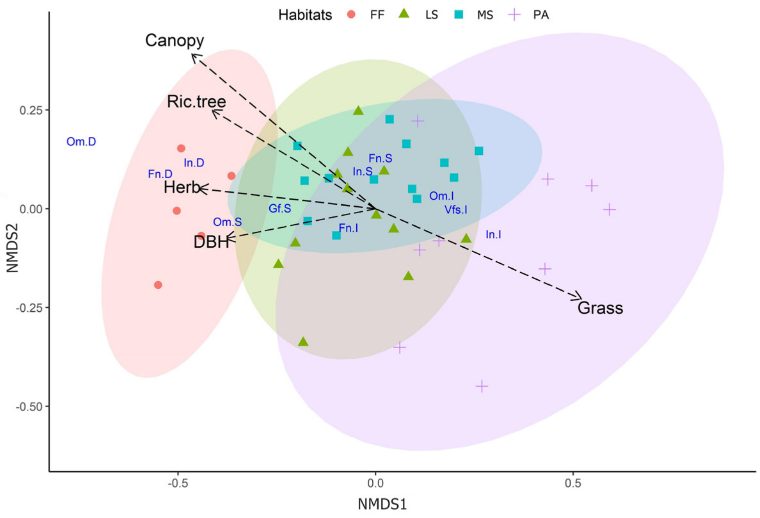

Figure 5. NMDS ordination plot of bird assemblages from restored and non-restored habitats, including the vectors of the explanatory variables, *Canopy*, *Ric.tree*, *Herb*, *DBH*, and *Grass* that influenced bird composition of diet-forest dependence. Final stress from two-dimensional solution = 0.13. Ellipses = 95% confidence level in each habitat type. Habitats: red circles, forest fragments (FF); green triangles, less structured restoration (LS); blue squares, more structured restoration (MS); purple plus, pasture (PA). Bird diet-forest dependence: frugivores-nectarivores forest independent (Fn.I), frugivores-nectarivores forest semidependent (Fn.S) and frugivores-nectarivores forest-dependent (Fn.D); following same nomenclature to insectivores (In.I, In.S and In.D); omnivores (Om.I, Om.S, and Om.D); granivores (Gf.I, Gf.S, Gf.D); and vertebrate-fish-scavengers (Vfs.I) classified as carnivores.

DISCUSSION

Increases in bird functional richness (FRic), functional dispersion (FDis), functional evenness (FEve) and Rao's quadratic entropy (Rao'Q) were found to be related to the vegetation structure gradient, with no effects on bird species richness (SR) and functional divergence (FDiv). Previous studies have also reported positive correlations between functional diversity (FD) measures and vegetation structure for butterflies (Aguirre-Gutiérrez et al. 2017), lizards (Berriozabal-Islas et al. 2017), birds (Hidasi-Neto et al. 2012, Sitters et al. 2016) and mammals (Sukma et al. 2019); yet there are few data on the responses of FD indexes for birds in Neotropical restored habitats (but see Batisteli et al. 2018). The present results add evidence that active restored habitats in the Atlantic Forest need more attention with planning to shade exotic grasses (Parrotta et al. 1997, Melo et al. 2007), since this may increase vegetation structural complexity and thus favor birds (Munro et al. 2011, Becker et al. 2013, Batisteli et al. 2018). Overall, the present study demonstrated that habitats with more structured vegetation had higher values for bird FRic, FDis, FEve, and Rao's Q compared to lesser-structured habitats (Figure 3a-d); however, SR and FDiv were not affected. This study also contributes evidence that FD may be a better metric than taxonomic diversity for evaluating how birds respond to environmental changes in restored (Batisteli et al. 2018) and reference (Anjos et al. 2019) habitats in tropical forests, adding important insights into ecosystem functioning (Ernst et al. 2006). Similar results were obtained by a previous study conducted in active restored riparian habitats in the Atlantic Forest (Batisteli et al. 2018). This occurs because increases in vegetation structure improve habitat and resource availability in a vertical layer (MacArthur & MacArthur 1961, Gould & Mackey 2015, Becker et al. 2013). Here, increases in vegetation structure represented replacement of grass cover by tree morphorichness and canopy cover. Indeed, increased habitat structure allows niche diversification because it offers greater resource partitioning and species coexistence by reducing niche overlap (Sitters et al. 2016), which leads to more diversified bird functional traits (Mason et al. 2005, Batisteli et al. 2018).

The present study found components of FD (FDiv excepted) to be related to the higher vegetation structural development (VSD) of the forest fragments and the more structured restored sites, compared to pasture and the less structured restoration sites. As SR was unaffected by the VSD gradient, an increase in FD indexes suggests a more parsimonious distribution of functional traits at most point-count sites in restoration habitats and forest fragments, both having more structured vegetation (e.g., canopy cover and tree morphorichness). This was reinforced by significant results for FRic as a function of positive VSD, with these plant characteristics being important for creating a greater amount of niche space in young restorations. This, in turn, catalyzes the ability of restored habitats to become occupied by more diversified traits of birds, independent of any SR effect. For instance, as FRic is monotonically related to SR (Laliberté & Legendre 2010), shifts in FRic without significative alterations in SR suggests that habitats with higher VSD increased functional space for the regional bird species pool, reflecting the amount of niche space efficiently used by birds (Mason et al. 2005). Previous studies have also found a similar correlation (Batisteli et al. 2018, Sitters et al. 2016, but see Oliveira et al. 2019).

The present study demonstrated that the effects that canopy cover and tree morphorichness have on bird FRic were strong only in the forest fragments (Figure 3a). Although tree traits, such as DBH and canopy cover, have been considered central characteristics for augmenting the amount of niche space for birds (Batisteli et al. 2018), increased VSD in the present study area was not able to increase the occurrence of birds with unique functional traits. Instead, restorations presented contradictory FRic values in relation to VSD (Figure 3a). For example, low FRic was seen with high VSD and high FRic with low VSD. The former reflects the presence of resources (alpha niches) not completely used by the bird community while the latter reflects better use of niche space (Mason et al. 2005). The first case is expected to occur due to asynchronous timing between habitat provision and bird species occupation (Catterall et al. 2012, Santos-Junior et al. 2016). Forest-dependent bird species slowly colonize restoration areas (Twedt et al. 2002, Catterall et al. 2012). This delay in niche occupation is likely to result in a low occurrence of forest specialist birds, leading to vague or underutilized niches. On the other hand, it suggests potential for the occupation of additional birds (generalists first - Gould & Mackey 2015, Becker et al. 2013, Santos-Junior et al. 2016). On the other hand, to explain high FRic with low VSD, we suspect that the presence of water-bodies at some of the point-count sites may have added some environmental heterogeneity and increased habitat diversification for varied functional traits. A similar effect, but in an inverse habitat order, was found to be related to the presence of vegetation surrounding bodies of water, which increased FD metrics of waterbirds in the Atlantic Forest (Arruda Almeida et al. 2018). Habitats in which vegetation structure was spatially variable was found to support the largest number of bird functional traits in Australia (Sitters et al. 2016). However, in the Amazon Forest, FRic for understory birds was found to be weakly affected by the distance of streams (Oliveira et al. 2019), while traits of generalist birds were favored in an active restored riparian forest in the Atlantic Forest (Batisteli et al. 2018), and in passively regenerated forests (Dias et al. 2015), as observed here. Environmental heterogeneity should have also added birds linked to bodies of water (e.g., Masked Yellowthroat [*Geothlypis aequinoctialis*], Chestnut-capped Blackbird [*Chrysomus ruficapillus*], Yellow-chinned Spinetail [*Certhiaxis cinnamomeus*], etc.) with varied unique traits, thus inflating FRic.

Increases in FDis (which is independent of SR) may be related to a decay in the abundance and/or local extinction of species having more central trait values (Laliberté & Legendre 2010). In fragmented landscapes of the Atlantic Forest, FDis of specialist birds has been strongly linked to continuous forest, whereas that of generalists has been linked to small forest fragments (Anjos et al. 2019). The data of the present study showed that even generalist birds were favored by increased VSD in both the restored sites and forest fragments, giving rise to increased niche complementarity (Mason et al. 2013). Thus, canopy cover and tree morphorichness were responsible for gains in FDis and Rao’s Q. Canopy cover was also an important tree trait for increases in FDis and Rao’s Q for birds in a restored riparian forest (Batisteli et al. 2018). Shifts in FDis are likely linked to turnover in abundance between open-area and forest semi-dependent species, related to shifts in the vegetation structure. This turnover of generalist *versus* specialist functional traits was also observed in active restored riparian forests (Batisteli et al. 2018) and in passively regenerated forests (Dias et al. 2015) in the Atlantic Forest, confirming what had previously been found for taxonomic diversity in this biome (Becker et al. 2013, Vogel et al. 2015, Santos-Junior et al. 2016). Moreover, the present results give more evidence that VSD of young restorations affects the abundance and distribution of bird traits. High FEve indicates a better distribution of biomass in niche space, which represents the effective use of resources and increasing resilience against biological invasions due to the occupancy of niches (Mason et al. 2005). Thus, habitats with more structured vegetation (e.g., MS and FF) assemble birds with diversified functional traits related to sensitivity, biomass, diet feeding, and diet-foraging strata. Thus, bird species composition in restored habitats may gradually become similar to that of older native forest remnants (Gardali et al. 2006, Munro et al. 2011, Catterall et al. 2012), despite the absence of forest specialized species in early restored systems (Casas et al. 2016, Santos-Junior et al. 2016).

We agree with Batisteli et al. (2018) that FDiv is not a good indicator of vegetation development in restored Atlantic Forest habitats because the turnover of species with similar traits results in ecological redundancy (Jarzyna & Jetz 2018) from intra-guild competition (Lindenmayer et al. 2015) among generalist species (Maure et al. 2018). The shifts in avian composition found in the preset study reflect better grouping of more diverse functional traits from the regional species pool. Indeed, restored and reference habitats were unable to attract rarer/endemic and forest-dependent species. The absence of suitable microhabitats can act as a local biological filter for specialist forest birds (Santos-Junior et al. 2016). The establishment of additional forest bird species may be limited because the small native forest fragments are highly isolated, surrounded by pasturelands and croplands, with more than 5 km from the nearest large forest fragment. This scenario is highly unfavorable for bird conservation (Baum et al. 2004, Martensen et al. 2012, Barbosa et al. 2017), but it is the reality of the greater part of this biome (Ribeiro et al. 2009). Endemic Atlantic Forest birds are unable to disperse long distances across a deforested matrix, which restricts their ability to colonize isolated remnants (Uezu et al. 2005, Martensen et al. 2012). There is evidence that a minimum of 30% native vegetation may increase the occurrence of forest specialist birds (Banks-Leite et al. 2014, Boscolo & Metzger 2011).

The present study provided additional evidence that specialized functional groups are dispersed according to vegetation structure in restored sites (see also Batisteli et al. 2018). Overall, independent forest birds represented by either diet-generalists (omnivores, granivores and insectivores) that forage on the ground of open areas, or foraging strata generalists, were related to habitats with a dominance of exotic grass cover. On the other hand, semi-dependent and dependent forest birds with some diet-foraging strata specialization (mainly insectivores and frugivores-nectarivores that forage in the canopy, mid-height or understory), were positively influenced by tree traits (e.g., *DBH*, *Rich.tree*, *Canopy* and *Herb*), which increased linearly from restorations to forest fragments, thus representing a gradient of vegetation structure. Previous studies on both taxonomic (Twedt et al. 2002, Becker et al. 2013, Casas et al. 2016) and functional diversity (Batisteli et al. 2018) have also reported that generalist functional groups were positively related to the dominance of exotic grass cover or weeds, and birds with some habitat or food specialization were immediately recruited to restored sites (Santos-Junior et al. 2016). This recruitment occurs when the dominance of exotic grass is broken by shade provided by canopy cover and other tree traits (Melo et al. 2007), which offer additional microhabitats, food resources, and sites for perching and nesting (Catterall et al. 2012, Gould & Mackey 2015, Santos-Junior et al. 2016, Batisteli et al. 2018), and leads to a rapid increase in the abundance of birds with some diet, habitat or foraging specialization.

Habitats with more structured tree traits than pasture and/or open agroecosystems provide multiple and varied microhabitats and resources for insectivorous and frugivorous species (Becker et al. 2013, Godoi et al. 2016, Sekercioglu 2012). Accordingly, pasturelands with more tree and shrub cover increase the occurrence of several forest bird species, including insectivores and frugivores (Godoi et al. 2017). Indeed, the return of insectivorous and frugivorous-nectarivorous birds is fundamental to increasing important ecosystem functions provided by birds. Insectivorous birds exert intensive biological control of herbivorous insect populations (Nyffeler et al. 2018), and thus reduce leaf damage and favor plant growth (Marquis & Whelan 1994). Frugivorous-nectarivorous species act as seed dispersers and pollinators (Sekercioglu 2012), both of which are fundamental mechanisms to ensure plant reproduction and to conduct shifts in patterns of diversity and density of plant communities in restored sites (Viani et al. 2015, Casas et al. 2016, Carlo & Morales 2016), mainly those plants with fleshy fruits (Gagetti et al. 2016). Increased bird biomass augments excrement production, which in turn benefits restoration sites by inputting nitrogen into the system (Slavin & Shisler 1983).

Our findings validate our predictions. Habitats dominated by exotic grass sustain simplified functional bird assemblages, similar to that of pasture habitats. However, the addition of canopy cover and other tree attributes in restoration sites produced: (a) vertical structuration of habitats and environmental heterogeneity; (b) additional habitats and resources responsible for increases in bird functional groups with some forest specialization, in accordance with the habitat complexity hypothesis (MacArthur & MacArthur 1961); (c) better arrangement of bird functional traits (FEve and FDis, same without changes in SR) from the existent regional pool; and (d) the attraction of frugivorous-nectarivorous and insectivorous birds that might catalyze ecological succession (Viani et al. 2015) and thus assuring ecosystem sustainability and resilience (Sekercioglu 2006, Mouchet et al. 2010, Maure et al. 2018). The increase of tree traits in restored sites is also an important biological tool for reducing biological invasions of exotic grass cover (mainly canopy cover; Melo et al. 2007) and recovering central ecosystem services provide by native bird groups.

Therefore, we advocate that the rapid development of vegetation structural complexity in restored sites a key factor for provisioning planned additional habitat for birds with some specialization in diet, foraging and/or habitat resource (here called semi-specialist forest birds). To accelerating this process we recommend that restoration procedures should initially focus in the suppression of exotic grass cover. Rapid suppression of exotic grass can be achieved by introducing native tree species with larger and fast-growing canopies to promote more shaded habitats, with the addition of integrating shrub (Roels et al. 2019) and herbaceous plant species to build structurally diverse vertical vegetation. To more rapidly supply habitat and food resources (Santos-Junior et al. 2016, Batisteli et al. 2018), and increase ecological interactions between birds and trees in young restorations (Lindell et al. 2012), we encourage restoration engineers to insert animal-dispersed pioneer trees (Viani et al. 2015) that provide black and red fleshy fruits (Gagetti et al. 2016), with consideration of their reproductive phenological features (Viani et al. 2015). We highly indicate these management measures for several degraded lands dominated by exotic grass in the Brazilian Atlantic Forest, but particularly those that are distant from large native forest fragments and thus with reduced plant recruitment. Thus, in this way, forest restoration can contribute to the conservation of native birds and their respective ecosystem services.

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SUPPLEMENTARY MATERIAL

Table SI.

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