Matrix type and landscape attributes modulate avian taxonomic and functional spillover across habitat boundaries in the Brazilian Atlantic Forest

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Abstract

Land use intensification drives biodiversity loss worldwide. In heterogeneous landscape mosaics, both overall forest area and anthropogenic matrix structure induce changes in biological communities in primary habitat remnants. However, community changes via cross-habitat spillover processes along forest-matrix interfaces remain poorly understood. Moreover, information on how landscape attributes affect spillover processes across habitat boundaries are embryonic. Here, we quantify avian ☐ and β-diversity (as proxies of spillover rates) across two dominant types of forest-matrix interfaces (forest-pasture and forest-eucalyptus plantation) within the Atlantic Forest biodiversity hotspot in southeast Brazil. We also assess the effects of anthropogenic matrix type and landscape attributes (forest cover, edge density and land-use diversity) on bird taxonomic and functional β-diversity across forest-matrix boundaries. Alpha taxonomic richness was higher in forest edges than within both matrix types, but between matrix types, it was higher in pastures than in eucalyptus plantations. Although significantly higher in forests edges than in the adjacent eucalyptus, bird functional richness did not differ between forest edges and adjacent pastures. Community changes (β-diversity) related to species and functional replacements (turnover component) were higher across forest-pasture boundaries, whereas changes related to species and functional loss (nested component) were higher across forest-eucalyptus boundaries. Forest edges adjacent to eucalyptus had significant higher species and functional replacements than forest edges adjacent to pastures. Forest cover negatively influenced functional β-diversity across both forest-pasture and forest-eucalyptus interfaces. We show the importance of matrix type and the structure of surrounding landscapes (mainly forest cover) on rates of bird assemblage spillover across forest-matrix boundaries, which has profound implications to biological fluxes, ecosystem functioning and land-use management in human-modified landscapes.

Keywords: functional diversity, alpha and beta-diversity, functional traits, edge effects, fragmented landscapes, ecosystem functioning, pasture, eucalyptus plantation

1. Introduction

Land use intensification and the resulting fragmentation of primary habitats remnants are leading drivers of biodiversity loss worldwide (Haddad et al. 2015). This is a prominent process in tropical regions because high levels of species diversity, often favoured by geoclimatic stability over millions of years, are coupled with high rates of contemporary deforestation and co-occurring human pressure (Peres et al. 2010). Apart from reducing overall native habitat amount, tropical deforestation also reduces habitat quality — through a combination of edge, habitat area, and isolation effects — elevating biodiversity loss in forest remnants throughout fragmented tropical forest landscapes (Pfeifer et al. 2017). In the Atlantic Forest biodiversity hotspot, for instance, fragmentation and habitat loss are particularly critical because over 80% of the original forest cover was lost in the last four centuries, and almost half of the ~1.1 million km^2 of remaining forest area currently experiences edge effects (Ribeiro et al. 2009). As a consequence, forest remnants are exposed to the direct influence of anthropogenic matrix habitats, thereby becoming more vulnerable to the synergistic detrimental effects of coexisting threats and biodiversity declines (Peres 2001, Tabarelli et al. 2008).

The boundaries between native forest remnants and adjacent agroecosystems often induce many ecological constraints to biotic and abiotic fluxes in anthropogenic landscape mosaics. Abrupt qualitative changes in vegetation structure across forest-matrix interfaces yield particular ecological conditions that — depending on the dominant matrix type — ensure cross-habitat spillover by some, but not all, species (Boesing et al. 2018a). Given the differential conditions in both vegetation structure and ecological niches, losses and replacements of species and ecological functions across adjacent habitats can reveal important insights on the biotic fluxes across contrasting habitat boundaries (Blitzer et al. 2012, Tscharntke et al. 2012). Thus, changes in both taxonomic and functional community composition across interfaces between natural and

anthropogenic habitats can reveal key ecological mechanisms linked to edge effects, matrix permeability, species flows and therefore overall biodiversity levels that can be sustained by human-modified landscapes (Tscharntke et al. 2012).

The amount of landscape-wide forest cover, particularly old-growth forests (Kormann et al. 2018), is often considered to be the most important factor modulating biodiversity persistence in tropical landscapes (Watson et al. 2018). However, the quality and composition of matrix habitats at the landscape level (e.g. land-use diversity), have received increasing research attention due to their interplay with overall forest amount in maintaining native biodiversity (Driscoll et al. 2013) and promoting land-use multifunctionality (van der Plas et al. 2019). In fragmented forest landscapes, for instance, avian extinction thresholds depend on the predominant matrix type (Boesing et al. 2018b), which may induce selective filtering of species traits (Kennedy et al. 2010, 2017). Some recent studies argue that matrix effects should be a key factor compensating for potentially negative landscape level effects of fragmentation *per se* (i.e. independently of the effect of habitat amount, Fahrig et al. 2019). These landscape level processes, in turn, are often underpinned by ecological mechanisms operating at smaller spatial scales, such as the cross-habitat spillover processes by species (Tscharntke et al. 2012, Boesing et al. 2018a). Assessing the ecological interplay across forest-matrix habitat boundaries at smaller spatial scales may therefore reveal key ecological mechanisms related to species fluxes operating in fragmented landscapes (Tscharntke et al. 2012, Jeltsh et al. 2013). This information may also provide pragmatic knowledge for designing biodiversity-friendly landscapes (Tscharntke et al. 2012, Melo et al. 2013), thereby adding valuable insights into current theoretical debates on fragmentation ecology (Fletcher et al. 2018, Fahrig et al. 2019).

The ecological mechanisms underpinning the biotic permeability across habitat boundaries (i.e. cross-habitat spillover processes) are still not well understood.

Available studies focusing on spillover processes primarily address plants (Dodonov et al. 2013, Alignier et al. 2014) and insects (Martello et al. 2016), and mainly in annual croplands (Blitzer et al. 2012, Tscharntke et al. 2012). Regarding forest-matrix boundaries, some experimental studies on bird spillover movements have been conducted using playbacks (Awade & Metzger 2008, Tomasevic & Estades 2008, Giubbina et al. 2018) and radiotelemetry (translocation experiments, Biz et al. 2017, Cornelius et al. 2017). Other observational studies have also assessed spillover processes in vertebrate assemblages by measuring and comparing species occupancy across adjacent habitats (Hodgson et al. 2007, Hurst et al. 2013, Craig et al. 2015, Boesing et al. 2018a, Barros et al. 2019). Nevertheless, mechanistic changes in species composition and ecological functions across habitat boundaries remain largely unknown. Furthermore, even less information is available on the role of surrounding landscape structure affecting cross-habitat spillover processes (Ries et al. 2017).

Cattle pastures and eucalyptus plantations are dominant matrix types surrounding forest remnants in Atlantic Forest landscapes. Given that almost half the current area of forest cover in this biome occurs within ~100 m of the nearest adjacent man-made matrix edge (Ribeiro et al. 2009), forest habitats interfacing either pastures or eucalyptus plantations represent a large and important supplementary extension of available habitat depending on spillover process. Considering that (1) open- (e.g. pastures) and closed-canopy matrix habitats (e.g. eucalyptus plantations) induce different changes in bird communities inhabiting forest remnants (Barbosa et al. 2017), and (2) landscape attributes (particularly forest cover) are widely known to drive the structure of avian assemblages in forest remnants, we seek to further understand these processes by asking three complementary questions. First, how do levels of avian taxonomic and functional α-diversity differ among forest-pasture and forest-eucalyptus habitat boundaries? Second, does matrix type influence taxonomic and functional β-

diversity differently across forest-pasture and forest-eucalyptus interfaces? And third, what is the relative importance of matrix type and landscape attributes (forest cover, edge density and land-use diversity) in bird community shifts across forest-matrix interfaces? We expect that natural habitats such as forest edges retain higher levels of functional and taxonomic richness than simplified habitats such as pastures and eucalyptus plantations, but that closed-canopy matrix habitats (eucalyptus) retain higher functional/taxonomic richness and facilitate higher spillover rates than the open-habitat matrix (pastures). Finally, higher levels of forest cover and landscape heterogeneity should boost bird spillover rates across both types of forest-matrix boundaries.

2. Material and Methods

2.1. Study area

Our study was conducted within highly heterogeneous landscapes embedded within a vast fragmented region of the Atlantic Forest domain in southeastern Brazil, which spans -3°S to -34°S in latitude and -58°W to -34.5^{o}W in longitude (Fig. 1; Muylaert et al. 2018; https://github.com/LEEClab/ATLANTIC-limits). The region has succumbed to intense human forest habitat conversion since the 17th century, resulting in high levels of habitat loss, patch size reduction, increased forest isolation, and highly disturbed forest remnants (Ribeiro et al. 2009). Pasture lands consisting of exotic grasses and eucalyptus monocultures comprise the predominant matrix habitat types across the region, which also include urban settlements and small fractions of sugar-cane plantations and other cropland such as maize, citrus, peach, and vineyards (MapBiomas 2017; http://mapbiomas.org). Forest remnants consist primarily of disturbed and secondary forests. Part of the region includes two of the largest patches of continuous Atlantic forests in the region (*Serra da Mantiqueira* and *Serra da Cantareira*), and an extensive ecological corridor between them, wherein landscapes with >50% forest cover

are often found (Ribeiro et al. 2009). Apart from forest environments, the natural vegetation is composed of wetlands and regeneration areas (abandoned lands undergoing early second-growth succession). Our study region spans elevations between 700 and 1700 masl (Oliveira and Fontes 2000) and experiences humid subtropical dry winters and hot summers, or a Cwa climate according to the Köpper classification.

2.2. Sampling design

We selected 32 study landscapes spaced apart by at least 2 km (Fig. 1), wherein bird assemblages were surveyed using pairwise point counts (Bibby et al. 2002). Each sampling landscape therefore consisted of two point-counts (PC), one inside and the other outside forest edges (the adjacent matrix). We sampled paired point-counts (PCs) along 16 forest-pasture interfaces and 16 forest-eucalyptus plantation interfaces, totalling 32 paired PCs (or 64 individual PCs). PCs were located at 70 to 100 m from the nearest edge in both forest fragments and matrix habitats (i.e. at least 140 m apart from each other, see Fig. 1). Each PC was sampled three times during two consecutive bird breeding seasons (September 2014 to January 2015, and October to December 2015). All birds sighted or heard within a 50-m fixed radius were recorded by one highly trained observer (FMB) during 10 min within 3 h post-sunrise. We also recorded birds during 30-min irregular transect walks along trails from habitat boundaries to each PC location, which were included to maximize species detections and sampling representation. Once transect walks were conducted in silence by a single observer (FMB) at very low speeds (~3 m/min), and we do not consider abundance data (only presence/absence, i.e. avoiding individual double-counting bias), we assumed that PCs and transects had equivalent detectability. For the statistical analysis, PCs and transects data were therefore merged as well as the three temporal sampling repeats.

The eucalyptus stands sampled were 5–12 m tall (~10 m on average, i.e. with a consistent canopy cover) and were highly managed for commercial purposes, including biocidal suppression of native understorey vegetation. In contrast, the pastures sampled were not grazed and contained trees, tall shrubs and sometimes neighbouring water bodies. We excluded grazed pastures from the study since (1) it often hosts overall low species richness and favour the presence of only ground or open-habitat specialists, and (2) we rarely found any bird species using grazed pastures adjacent to forest edges in our study area. To further isolate the effects of local habitat on bird assemblages along forest edges, we pre-selected only forest environments with a very similar vegetation structure between them (i.e. highly disturbed, but lacking water bodies and hyper-dominance of woody lianas and other plant species). Study landscapes had been pre-selected to include marked gradients of surrounding forest cover (range = 11% to 91%) and land-use diversity (Shannon index, 0.4 to 1.8) within a 1200-m circular buffer around each PC centroid. This buffer size was chosen based on previous random forest analysis (Bradter et al. 2013) wherein 1200m best explained bird richness and abundance compared to 300m, 600m and 900m distance radius.

2.3. Avian functional traits and assemblage metrics

To compute α and β-functional diversity of bird assemblages across forest-matrix interfaces, we considered six functional traits: (1) body mass, (2) clutch size, (3) diet, (4) foraging strata, and (5) social behaviour (Table 1). Information on bird diets (invertebrate, vertebrate, seed, fruit, floral nectar, and detritus) and foraging strata (ground, understorey, and canopy) were extracted from Wilman et al. (2014). Data on clutch size and social system were obtained from information available in the Handbook of Birds of the World (del Hoyo et al. 2016). We included bird social system (i.e. solitary, pairs, monospecific flocks and mixed-species flocks) as a functional trait

because it is known to affect interspecific interactions and community structure in birds (Maldonado-Coelho and Marini 2004, Goodale et al. 2010) and their capacity to traverse and/or use adjacent matrix habitats (Rodríguez et al. 2001).

As our main goal is to examine how abrupt ecological changes across forest-matrix interfaces can induce taxonomic and functional changes in β-diversity across adjacent assemblages, the traits selected were predominantly "response-traits" because they best ensure detection of bird responses to environmental change. Body mass and clutch size were log-transformed to avoid biases induced by species with extreme values (Bello et al. 2010). Dietary, foraging strata, and social behaviour are categorical traits that were transformed into a fuzzy variable (i.e. proportion variables relating to one unique trait, with Gower distance dissimilarities computed between communities; Pavoine et al. 2009). Functional richness (FR) represents the amount of functional trait space that each assemblage occupies and was considered as a proxy of overall functional diversity (Bello et al. 2010, Vandewalle et al. 2010). To calculate functional richness, a distance matrix with all predictors was constructed and a species-by-site matrix was run using the *FD* package in R (Laliberté et al. 2014).

We decomposed taxonomic and functional β-diversity into their four turnover and nested components (taxonomic turnover - TT, taxonomic nested - TN, functional turnover – FT, and functional nested – FN, Fig. 2). Whereas the turnover components provide an indication of the differences in composition (for both species and traits) between assemblages caused by species replacements, the nested components provide an indication of differences in composition caused by species losses (Baselga 2012). TT was estimated using the Simpson diversity index. TN was the difference between Sorensen diversity index (total β-diversity) and TT (Baselga 2012). Similarly to taxonomic β-diversity, the functional β-diversity between any two adjacent assemblages across forest-matrix interfaces was computed by the functional space that was not

shared divided by the total functional space filled (Villéger et al. 2011). Both

components of taxonomic and functional β-diversity were calculated using the *Betapart*

package in R (Baselga and Orme 2012). For each sampling site, we also define species

richness (or α taxonomic richness - TR) as the total number of species detected.

2.4. Landscape attributes

To quantify the landscapes attributes for each sampling landscape, we first mapped land

use within a 1.2 km radial buffer surrounding each forest sampling site using high-

resolution images (ArcGIS 10.3 basemap imagery, DigitalGlobe satellites 2010-2011;

mapping scale of 1:5,000). To do this, we considered 14 land cover types: forest,

pasture, eucalyptus plantation, regeneration areas, wetland, cropland (mainly maize),

sugar-cane, water bodies (lakes and reservoirs), urban areas, rural homesteads, urban

households (in suburban areas), paved roads, buildings, and bare soil. We further carried

out field validation at all sites for which images could not be properly interpreted.

For each landscape we computed three landscape metrics using Fragstats v.4

(McGarigal et al. 2012): Forest cover (%), Edge density (m/ha), and Shannon diversity

index of matrix types (i.e. in which forest patches were excluded). Edge density and

Shannon diversity were selected because they serve as two distinct proxies of landscape

heterogeneity, the first describing the amount of any type of habitat edge within the

landscape, and the second describing the land-use diversity. Given that birds are known

to respond to land-use diversity (Lee and Martin 2017), we included both of these

heterogeneity attributes to understand their relative importance in affecting changes in

bird β-diversity straddling forest-matrix interfaces.

2.5. Data analysis

α- and β-diversity across forest-matrix boundaries

To examine differences in TR and FR among the four types of habitat edges (i.e. forest adjacent to pasture, forest adjacent to eucalyptus, pasture adjacent to forest, and eucalyptus adjacent to forest), we first assessed the data distribution, performing Shapiro-Wilk tests on the residuals of linear regressions between each diversity metric and habitat type. To test for differences in α-diversity indices (taxonomic and functional) among habitats, we performed GLMM considering the sampling landscape as a random factor (Q1, Fig. 2). We then used a post-hoc tests, based on the Studentized range Tukey's HSD (Honest Significant Difference) using diversity metrics with a gaussian distribution. For indices that did not meet a normal distribution, we used a Kruskal-Wallis test followed by a non-parametric multiple comparison test. To examine differences in avian β-diversity (TN, TT, FN and FT) between forest-pasture and forest-eucalyptus interfaces, we performed Wilcoxon-Mann-Whitney tests (Q2, Fig. 2).

Matrix effect on avian β-diversity in forest edges

To test whether matrix type affects bird assemblage composition at forest edges, we selected only forest samples, and computed β-diversity for all comparisons between sampling sites located within forest sites adjacent to the same matrix type (either pasture or eucalyptus). We then calculated, for each forest sample, the average dissimilarity for the other 15 samples and performed Kruskal-Wallis tests to examine to what degree matrix type affects community similarity in forest sites adjacent to either pastures or eucalyptus stands (Q3, Fig. 2).

Landscape effects on avian β-diversity across forest-matrix boundaries

To investigate how landscape attributes and matrix type can affect taxonomic and functional pairwise similarities between bird assemblages in forest boundaries, we first calculated taxonomic and functional components of β-diversity between communities

located in forest and its adjacent matrix (Q2, Fig. 2). We then fitted a linear model with all landscape predictors using stepwise regression for each β-diversity component. We fitted the model with the best subset of predictors on the basis of AIC values. We also examined the estimated parameters of the selected models to assess which predictors were the main drivers, which were defined as those with slopes higher than 0.1 and significance levels lower than 0.05 (considerable), 0.01 (significant) and 0.001 (highly significant). All statistical analyses were performed within the R environment (R Development Core Team 2013).

3. Results

Avian α-diversity in forest-matrix boundaries

Bird taxonomic richness (TR) differed among habitat types (F=60.5, $p < 0.001$ GLMM, Fig. 3). Bird assemblages at forest edges had the highest TR, with no significant differences between forest edge adjacent to pasture (44.2 ± 9.8 SE) and those adjacent to eucalyptus (40.6 ± 8.4, Z=-1.30, $p = 0.56$). Pasture sites adjacent to forest had intermediate values (27.5 ± 3.3), whereas eucalyptus stands adjacent to forest consistently had the lowest values of TR (9.1 ± 3.2) (Fig. 3). Likewise, functional richness (FR) also differed among habitats (Kruskal Wallis $\chi^2 = 37.62$, $p < 0.001$). Bird assemblages at pasture edges, however, had FR values (10.21 ± 0.42) as high as those in either forest sites adjacent to pasture (9.15 ± 0.42) or forest sites adjacent to eucalyptus (8.68 ± 1.23). Again, bird assemblages at eucalyptus sites adjacent to forest exhibited the lowest FR values (3.18 ± 0.42; Fig. 3).

Matrix effect on avian β-diversity in forest edges

Comparing the compositional similarities among bird communities between forest and either adjacent pastures or adjacent eucalyptus plantations, we found significant

differences in the turnover components of both taxonomic (TT) and functional (FT) β-diversity (Kruskal-Wallis $\chi^2 = 6.00$, $p = 0.01$, and $\chi^2 = 45.04$, $p < 0.01$, respectively). However, both taxonomic (TN) and functional nested (FN) components of β-diversity did not differ between avian communities located in forest edges adjacent to either eucalyptus (Kruskal-Wallis, $\chi^2 = 0.05$, $p = 0.82$) or pastures ($\chi^2 = 1.19$, $p = 0.29$, Fig. 4).

Matrix and landscape effects on avian β-diversity across forest-matrix boundaries
Considering bird similarity across habitat interfaces, for TN and FN components of β-diversity, forest-eucalyptus interfaces had significantly higher values than those between forest and pasture (F = 50.61, $p < 0.001$ and F = 22.78, $p < 0.001$, respectively; Fig. 5). In contrast, forest-pasture interfaces had significantly higher values than those between forest and eucalyptus in terms of the turnover components of β-diversity (TT: F = 72.92, $p < 0.001$; FT: F=15.6, $p < 0.001$; Fig. 5).

Comparing bird communities across forest-matrix interfaces, we found that adjacent matrix type was the main driver of bird taxonomic and functional β-diversity, and the only predictor in selected models for both components of β-diversity (Table 2, Fig. 6). Edge density were significant predictor of both nested components (TN and FN), however the slopes were low (< 0.1). In contrast, Shannon diversity had significant slopes ($> 0,1$) but low statistical significance (p > 0.05) for both nested component (Table 2, Fig. 6). Functional turnover component (FT) was the only component of diversity for which the fitted model had two highly significant predictors: forest cover and matrix type (Table 2).

4. Discussion

Our findings show that both matrix habitat type and landscape attributes can alter the local taxonomic and functional richness as well as the cross-habitat spillover processes (here measured by β-diversity indices) by bird species across two contrasting types of forest-matrix boundaries in tropical landscapes. The higher TR values along forest edges compared to both matrix types (Fig. 3) were consistent with our expectations, and are probably linked to the higher structural complexity and heterogeneity of forest habitats compared to more simplified pastures and eucalyptus plantations (Tews et al. 2004). However, even closed-canopy habitats such as eucalyptus monocultures surprisingly contained lower α-diversity (in terms of both TR and FR) than open cattle pastures, suggesting that the former provide a narrower niche breadth for birds compared to the latter, at least near forest edges. Local habitat quality at our sampling sites is likely one of the main factors governing differences in TR between pasture and eucalyptus. The suitability of tree plantations in sustaining species-rich bird assemblages is often higher if they contain native regenerating woody plants (Deconchat et al. 2009, Najera & Simonetti 2010, Lopes et al. 2015, Millan et al. 2015). However, most eucalyptus sites in our study were commercial tree plantations where native trees and shrubs were either non-existent or rare. On the other hand, overgrazed pastures lacking scattered trees, water bodies and small wetlands may also reduce bird species richness and favour few terrestrial and open-habitat specialists (Mahood et al. 2012). However, our study did not consider such "clean" pastures typical of intensified farmland. The particularly low-diversity eucalyptus stands coupled with the high-diversity pastures considered in this study therefore amplified the differences in terms of both TR and FR between these two matrix types. Since matrix quality is highly dependent on local habitat features (Tomasevic and Estades 2008), caution should be exercised in interpreting these results.

Contrary to our expectations, functional richness of birds inhabiting cattle pastures was similar to that along forest edges, reflecting an equivalent niche breadth (or functional space) for birds in these two contrasting habitats. In addition, we observed significant species and functional turnover between pastures and forest edges (Fig. 5). Given the functional traits addressed in our study, local habitat characteristics of the pastures sampled (e.g. small wetlands, shrubs, scattered trees) can decisively facilitate a wide spectrum of bird traits (mainly body size and social system), which likely led to an increase in FR values in pastures, comparable to those of adjacent forests. Small-bodied passerines such as thrushes (*Turdus* spp.) and tanagers (*Tangara* spp.), for instance, can occur in sympatry with large-bodied species typical of open habitats (e.g. *Vanellus chilensis*, *Egretta thula*, *Cariama cristata*, *Mesembrinidis cayennensis*) within pastures, but this is not expected to occur within forest edges (FMB, pers. obs.). The similar functional richness found in bird communities across forest edges and pastures can therefore be explained by compensatory dynamics via high rates of functional turnover between these structurally contrasting habitats. This is also consistent with the higher levels of bird taxonomic and functional replacements found across forest-pastures interfaces (Fig. 5). These findings highlight the fact that comparing cross-habitat functional changes in biological communities requires special attention to the identity of which functional traits are used and their particular ecological implications, rather than the overall functional diversity *per se* (Luck et al. 2013).

In fragmented landscapes, some ecological functions linked to trophic interactions between species (e.g. insectivory) may increase with fragmentation (Hagen et al 2012, Barbaro et al. 2014). However, increasing some functions can lead to decreases of others, and land-use change may therefore induce replacements of particular ecological functions that help sustain overall community functionality (Newbold et al. 2013, De Coster et al. 2015). Likewise, the similar FR found in forest

edges and adjacent pastures combined with the higher levels of FT across forest-pastures interfaces, suggest that functional shifts in bird communities may also occur across habitat boundaries at local scales, reflecting the same mechanism operating at larger regional (Newbold et al. 2013, De Coster et al. 2015) or even global scales (Newbold et al 2016, see also Antão et al. 2019).

The high TN component values across forest-eucalyptus interfaces (Fig. 5) are in agreement with other bird community studies in natural forest patches and tree plantations (e.g. Wethered and Lawes 2005). The higher nestedness observed across forest-eucalyptus plantation boundaries resulted from selective species losses which may be explained, at least partially, by environmental filtering (Kraft et al. 2015). Although tree plantations often retain some ecological conditions similar to natural forests (e.g. closed canopy cover and limited light penetration), this itself is not enough to sustain food resources and structural features required by forest habitat specialists, particularly if intensively managed commercial tree plantations lack a regenerating understorey suppressed by herbicidal treatment. Moreover, the overall bird species composition of eucalyptus plantations was effectively a nested subset of species found in the neighbouring forests - e.g. *Turdus leucomelas*, *Cyclarhis gujanensis*, bird species typical of both eucalyptus and adjacent forest edges. Our findings suggest that commercial eucalyptus plantations near forest edges can therefore filter out most forest bird species, leading to severe reductions in both taxonomic and functional richness within such managed habitats.

Several factors are known to modulate the magnitude of edge effects in biological communities (Ries et al. 2017), mainly patch area (Phillips et al. 2018) and shape (Prevedello et al. 2013), and edge contrast (Pfeifer et al. 2017). Here we demonstrate further evidence of differential effects of the adjacent matrix type on both the taxonomic and functional β-diversity of bird communities inhabiting forest edges.

Although other potential ecological drivers such as patch size were not controlled for, the higher species and functional replacements among forest edges adjacent to eucalyptus plantations compared to forest edges adjacent to pastures (Fig. 4), suggest that the type of adjacent matrix (and likely edge contrast) can affects the magnitude of edge effects on bird communities. Although in some cases open matrix such as sugarcane monoculture can also limit local spillover movements by birds from forests (Giubbina et al. 2018), our observations on higher replacements of species and functions among forest edges with direct contact with eucalyptus stands may indirectly suggest a greater capacity of eucalyptus plantations to connect forest patches compared to pastures, facilitating inter-patch movement. Other studies indicate that landscapes containing matrix habitats dominated by tree plantations can minimize avian diversity loss (mainly forest species) within forest remnants (Zurita and Bellocq 2010, Lindenmayer et al. 2008, Ruffell et al. 2017, Barbosa et al. 2017). By a similar ecological mechanism (increased both connectivity and cross-habitat spillover), these authors suggest that the prevalence of a closed-canopy matrix can sustain higher bird species richness in forest fragments. Thus, while eucalyptus plantations can serve as a low-quality habitat for foraging forest birds (low functional and taxonomic richness, Fig. 3), they may also serve as high-quality habitats for gap-crossing and/or dispersing forest birds (higher β-diversity among forest edges adjacent to eucalyptus, Fig. 4) (see Ruffell et al. 2017). Given this assumption, the magnitude of both patterns is likely mediated by the amount of native regenerating understorey within tree plantations (Tomasevic and Estades 2008, Lopes et al. 2015).

Our results show that the functional space occupied by neighbouring bird assemblages across both forest-pasture and forest-eucalyptus boundaries become more similar with increasing amounts of surrounding forest cover (Fig. 6). This suggests that the ecological functions played by bird species in forest-matrix interfaces may become

increasingly homogeneous in more forested landscapes. This should likely reflect higher levels of functional permeability across forest-matrix interfaces, which has profound implications to ecosystem service delivery and functioning in disturbed landscapes. Should this be the case, lower levels of bird functional spillover (functional β-diversity) due to reduction of landscape-wide forest amount could severally affect landscape connectivity for many functionally important species, such as frugivorous species that deliver seed dispersal services (Bregman et al. 2016).

Although increasing surrounding landscape forest cover boosted spillover processes (via lower rates of FT component) in both forest-pastures and forest-eucalyptus boundaries, the magnitude of these processes was quite different. Compared to pastures, an eucalyptus-dominated landscape is expected to retain higher inter-patch connectivity to forest birds, and this pattern tend to be amplified within landscapes containing higher forest cover. At the other extreme, if pastures were the dominant matrix type, reductions in forest cover would severely limit inter-patch connectivity. Although our study did not control for the effect of fragmentation independently of the effect of forest amount, we believe that 'land sparing' strategy would be more appropriate to biodiversity maintenance in pasture-dominated landscapes (i.e. lower interpatch connectivity) whereas in eucalyptus-dominated landscapes (i.e. higher inter-patchy connectivity), a 'land sharing' strategy would be more appropriate (Kremen 2015). However, further studies are needed to better validate this hypothesis.

Our findings also show a significant effect of landscape edge density on both TN, FN and FT component across forest-matrix boundaries. However, the relationship with edge density was slightly weaker than with forest cover. Indeed, the relationship between landscape complexity (edge density) and taxonomic/functional β-diversity between neighbouring bird assemblages in forest-matrix boundaries is complex and lack direct causality - even strong relationships would not necessarily reveal clear ecological

mechanisms underpinning avian spillover and/or movement patterns in heterogeneous landscapes. This is likely because this metric disregards different types of edges (Ries et al. 2017) and little information is available on how different types of habitat boundaries, including both forest-matrix and matrix-matrix boundaries, can mediate organismal fluxes across landscapes. If our sampling landscapes exhibited overall low land-use diversity (i.e. predominance of a single matrix type across landscapes), positive effects of edge density covarying with forest cover in β-diversity indices could help support further evidence on the positive effect of landscape complexity or fragmentation *per se* (Fahrig et al. 2019). However, land-use diversity was not a significant driver of bird species spillover (Table 2, Fig. 6), indicating that somehow edge density (i.e. landscape complexity) may affect differently bird spillover across forest-matrix interfaces compared to land-use diversity. This probably occurs due to matrix identity and composition across the sampling landscapes we surveyed. Further studies should therefore focus on separating these complementary components to better understand ecological mechanisms underpinning biotic flow and persistence across heterogeneous landscapes.

Conclusions

Our results highlight how tropical bird assemblages can shift their taxonomic and functional properties across two ubiquitous and markedly contrasting habitat transitions (forest-pasture and forest-eucalyptus) in human-modified landscapes. Our findings therefore bring new insights on the nature of spillover processes across forest-matrix boundaries, here defined in terms of β-diversity indices. While forest-pasture interfaces induced compositional and functional changes, forest-eucalyptus interfaces induced selective filtering of both species and ecological functions. Our data revealed that forest cover can induce functional homogenization across neighbouring bird assemblages in

forest-matrix boundaries. This illustrates the role of landscape attributes (mainly forest cover and edge density) in mediating permeability of habitat boundaries to bird communities, which should have profound implications to biological fluxes and ecosystem functioning in fragmented and heterogeneous landscapes.

Although our sampling design did not account for direct observation on birds traversing habitat boundaries (Lees and Peres 2009), we believe that our proxy of spillovers (i.e. β-diversity metrics) contributed valuable insights to the overall spillover processes across forest-matrix interfaces. Given the properties of β-diversity metrics (turnover and nested) in reflecting the degree of permeability of habitat boundaries, we also argue that these metrics can be used as reference (or training) data to implement models and predictive maps of biodiversity transitions across broader spatial levels, thereby enhancing knowledge on biological fluxes and ecosystem functioning in human-modified landscapes. Once the permeability of different types of habitat boundaries are more accurately quantified in further studies, the amount and type of habitat edges could be tested as an important covariate modulating bird species persistence in fragmented forest landscapes. This could be particularly important in revealing key ecological mechanisms linking edge effects and inter-patch connectivity, thereby aiding further advances in both theoretical and applied issues in habitat fragmentation ecology.

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Figure Legends

Fig. 1. Study region in southeast Brazil showing the 32 sampling landscapes. Green and white backgrounds represent native forest cover and the non-forest matrix, respectively. Circles on the right illustrate the spatial design of paired point-counts sampled in either forest-eucalyptus plantations (A) or forest-pastures interfaces (B) under different landscape and land use contexts. Figure adapted from Barros et al. 2019.
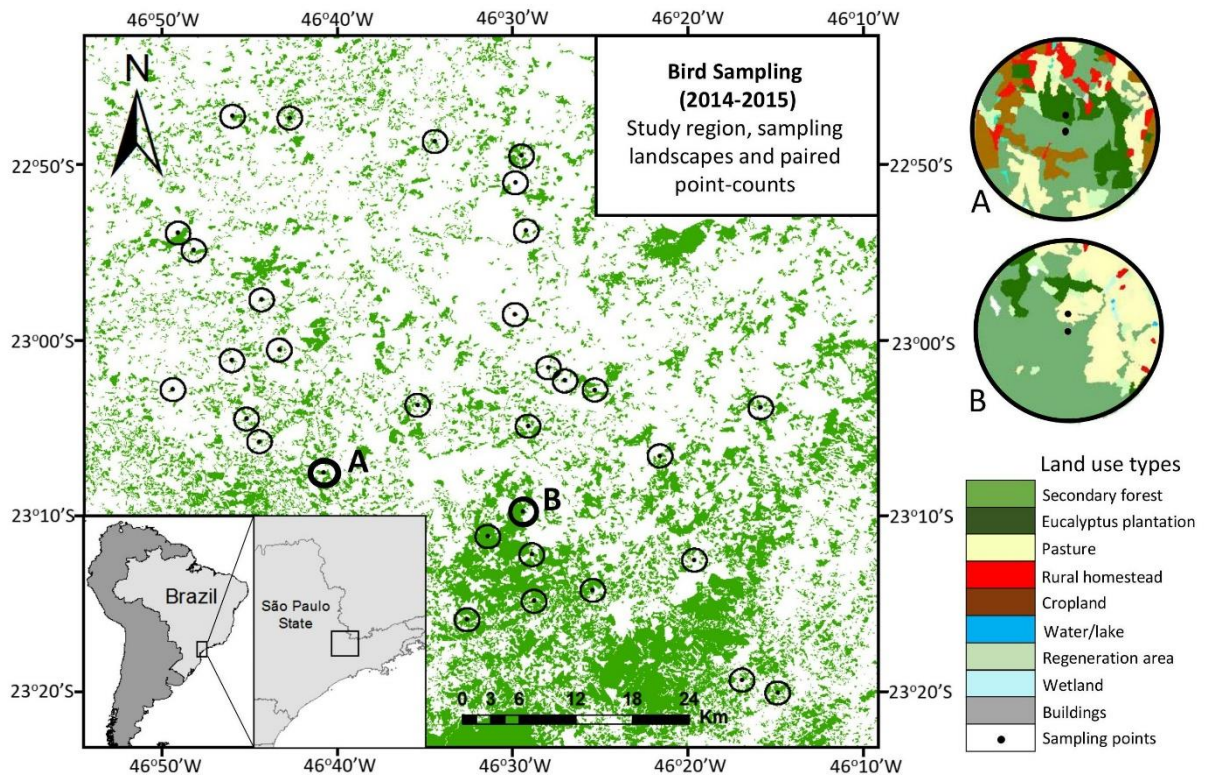
Fig. 2. Schematic illustration showing the experimental design with the three main questions addressed here (a) and their operational variables measured (b). Q1: How do levels of avian α-diversity differ between local habitats in forest-pasture (FP) and forest-eucalyptus (FE) interfaces? *Comparisons among local habitats [ForP (n=16), Pas (n=16), ForE (n=16) and Euc (n=16)]*. Q2: How do levels of avian β-diversity differ between FP and FE interfaces? How does landscape structure affect β-diversity in FP and FE interfaces? *Paired comparisons between adjacent habitats [ForP-Pas (n=16) and ForE-Euc (n=16)], where the landscape effects were assessed*. Q3: How do levels of avian β-diversity differ between forest edges adjacent to pastures (ForP) and forest edges adjacent to eucalyptus (ForE)? *All possible paired comparisons within each forest edge type [ForP-ForP (n=120) and ForE-ForE (n=120)], where mean values in relathion to each forest sample were considered*. See Methods section.

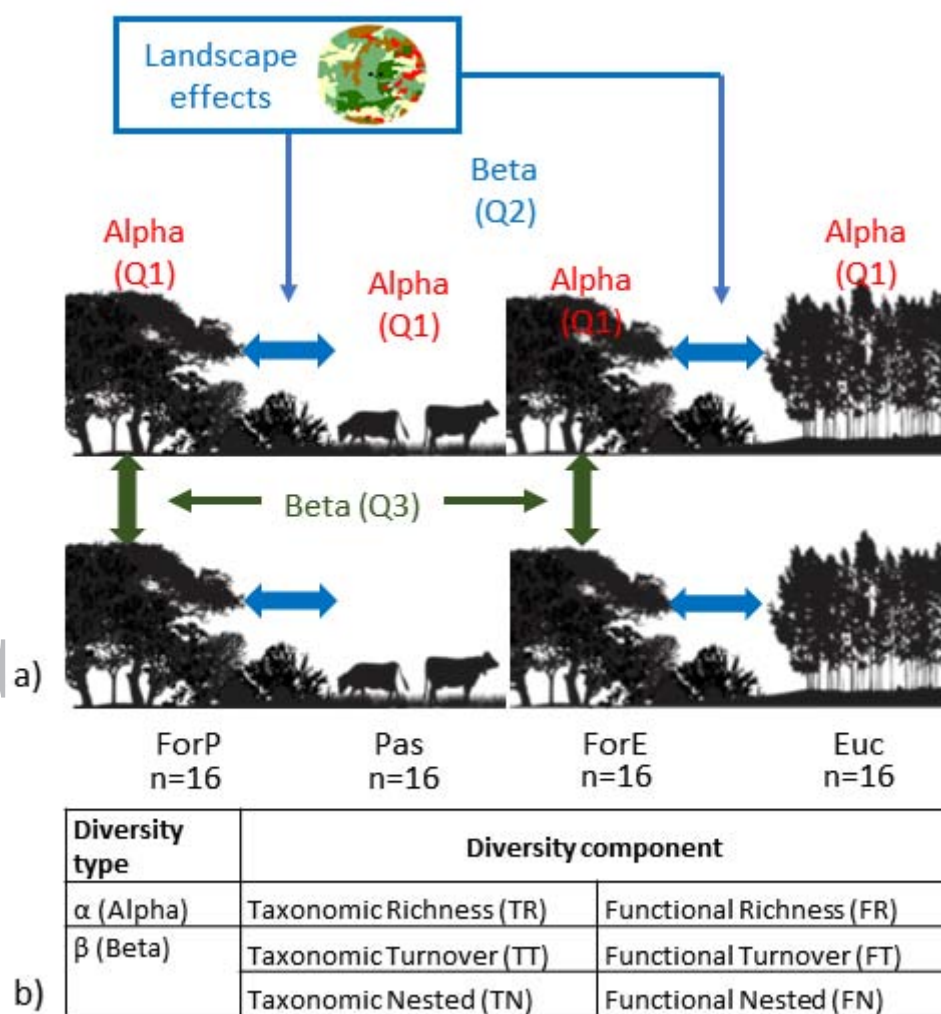| Diversity type	Diversity component	
α (Alpha)	Taxonomic Richness (TR)	Functional Richness (FR)
β (Beta)	Taxonomic Turnover (TT)	Functional Turnover (FT)
	Taxonomic Nested (TN)	Functional Nested (FN)

Fig. 3. Taxonomic and functional richness of birds inhabiting forest edges adjacent to either eucalyptus plantation (Forest-E) or pasture (Forest-P), and two types of matrix habitats adjacent to forest edges: eucalyptus plantation and pasture. Box-plots show mean and standard deviation.
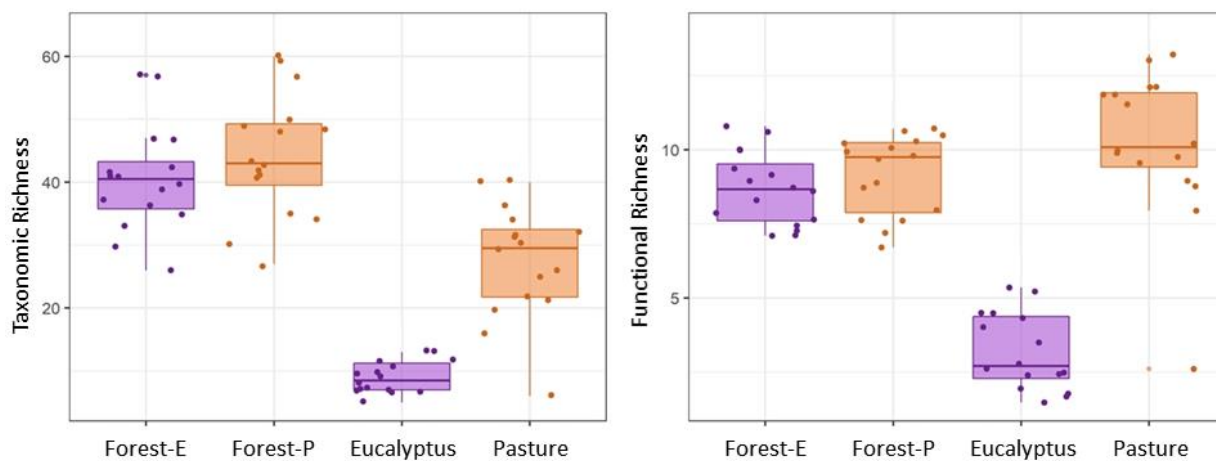
Fig. 4. Matrix effects on taxonomic and functional β-diversity (nested and turnover components) among avian assemblages inhabiting forest edges adjacent to either eucalyptus plantation (Forest-E) or pasture (Forest-P) in tropical forest landscapes. Solid dots represent mean values of β-diversity from 15 pairwise community comparisons related to each forest sample (n=16 in each treatment).
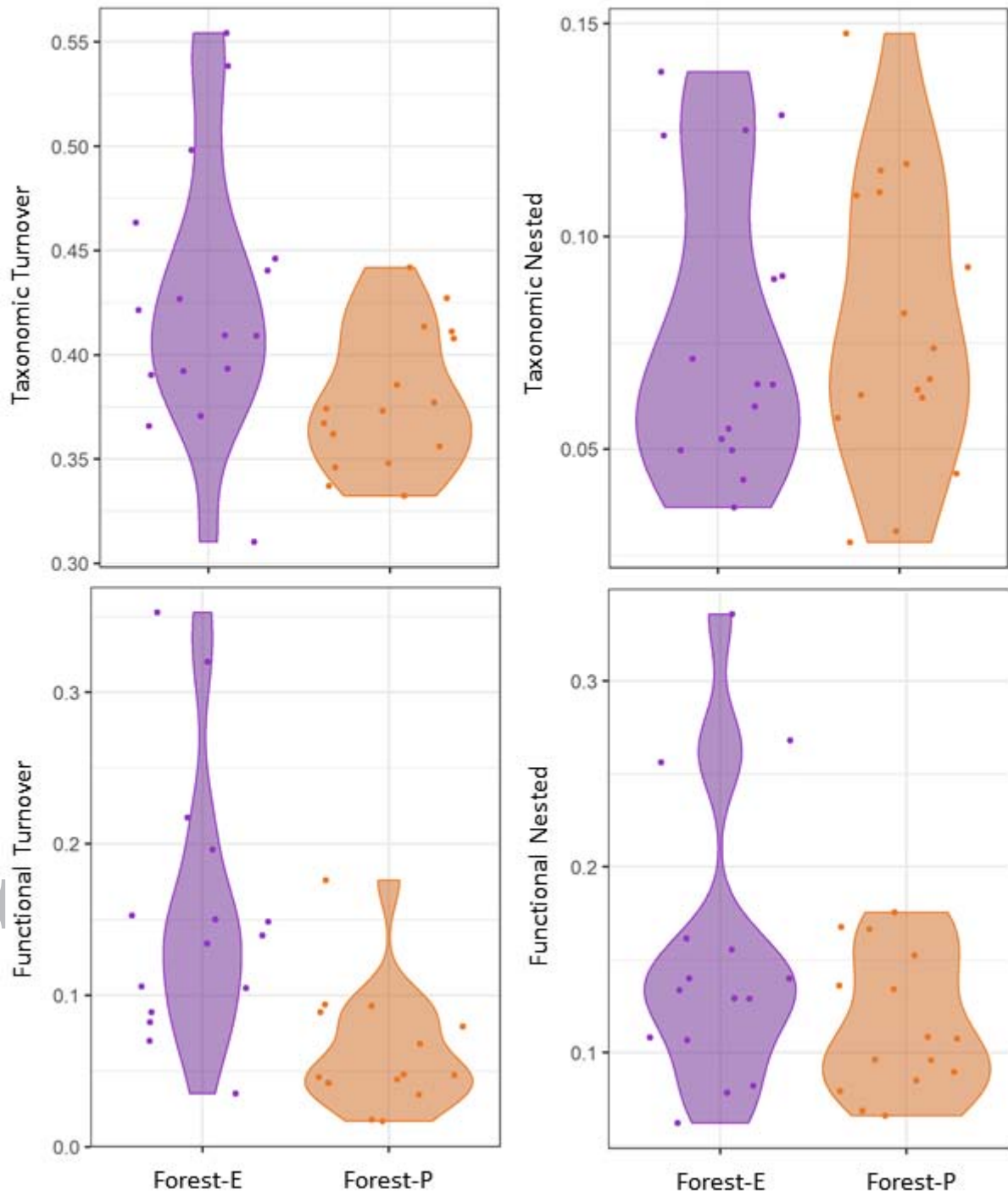
Fig. 5. Taxonomic and functional β-diversity of birds inhabiting two contrasting types of forest-matrix interfaces in fragmented tropical forest landscapes. Boxplots (mean and standard deviation) represent β-diversity values (nested and turnover) within forest-pasture and forest-eucalyptus interfaces.
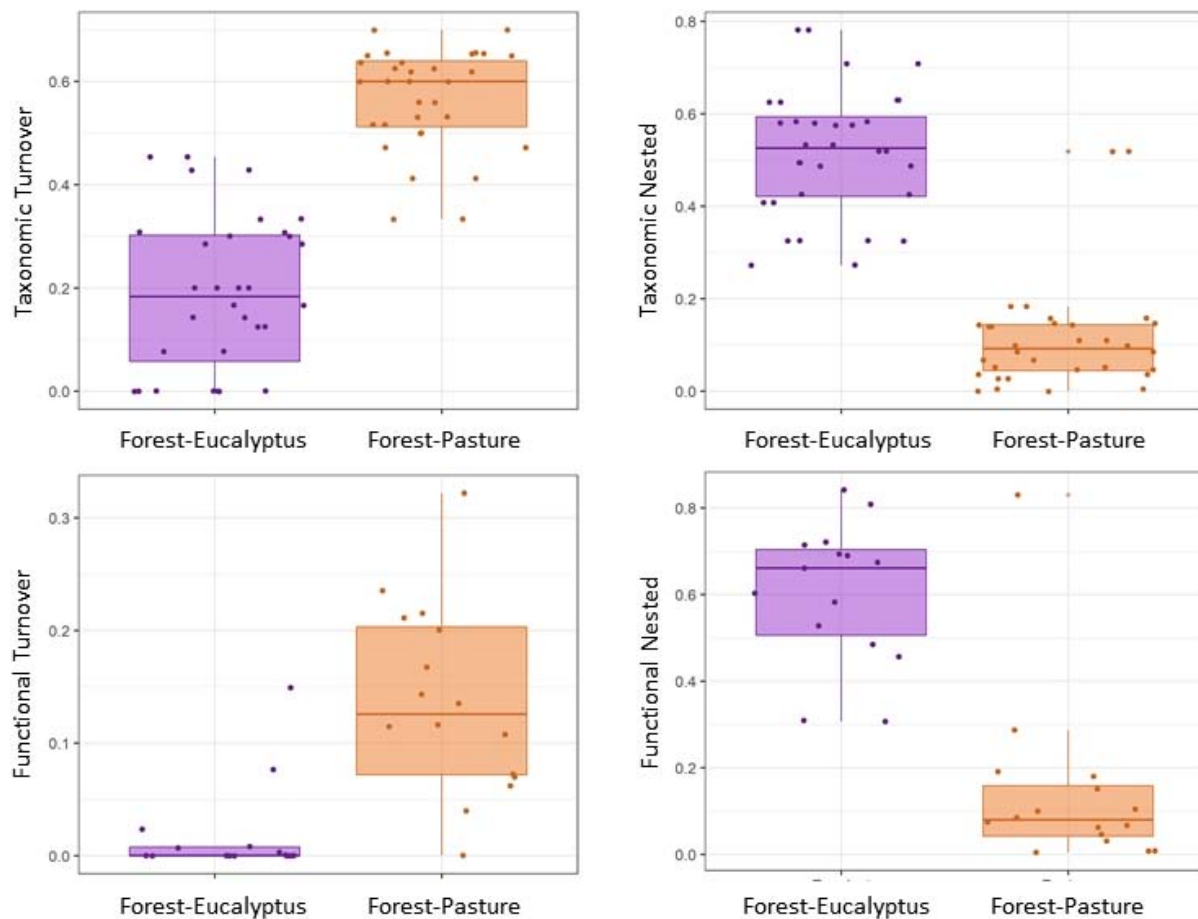
Fig. 6. Landscape effects (forest cover, land use diversity and edge density) on avian β-diversity (functional turnover, functional nested and taxonomic nested) within forest-pasture (orange) and forest-eucalyptus (purple) interfaces in tropical forest landscapes. The model with both *p*-value < 0.001 and slope >0.1 was highly significant (forest cover). The others models shown were only "considerable" models since they failed to reach both requirements (land-use diversity model had a slope >0.1, but p > 0.05, whereas edge density model had a p < 0.01, but slope <0.1).
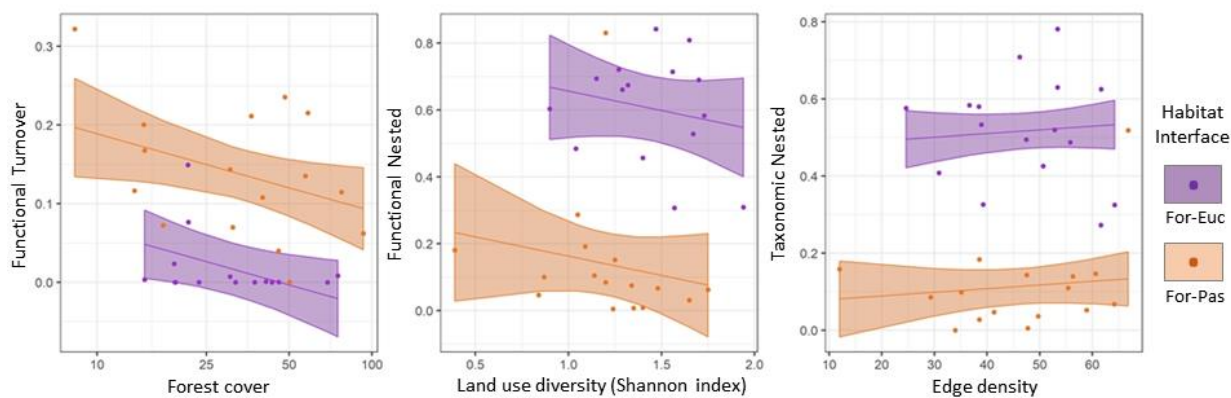
Table Legends

Table 1. Avian functional traits used to compute α and β-functional diversity indices.

Functional trait	Subdivision	Description	Source
Body mass		mean body mass	Wilman *et al*. (2014)
Clutch size		maximum clutch size	del Hoyo et al. (2016)
Diet	Invertebrates	proportion of invertebrates in diet	Wilman *et al*. (2014)
	Vertebrates	proportion of vertebrates in diet	
	Fruits	proportion of fruit in diet	
	Néctar	proportion of nectar in diet	
	Seed	proportion of seed in diet	
	Foliage	proportion of foliage in diet	
	Waste	proportion of carrion or necromass in diet	
Foraging strata	Ground	proportion of ground use	Wilman *et al*. (2014)
	Understorey	proportion of understory use	
	Canopy	proportion of canopy use	
Social behaviour	Alone	how much as solitary foragers	del Hoyo *et al*. (2016)
	Pair	how much foraging in pairs	
	Mixed-flocks	how much time in mixed-species flocks	
	Mono-flocks	how much time in mono-specific flocks	

Table 2. Selected models and slopes for matrix and landscape effects on taxonomic and functional β-diversity of birds inhabiting forest-matrix interfaces in tropical fragmented landscapes. Empty cells indicate that the corresponding predictor was excluded from the 'best' model. Selected models are shown in bold, wherein *, ** and *** indicate $p < 0.05$, $p < 0.01$ and $p < 0.001$, respectively.

β-diversity	Component	Forest cover	Shannon diversity	Edge density	Matrix type
Taxonomic	Nested	**0.077***	-0.156	**0.005**	**-0.438***
	Turnover	**-0.052***	--	--	**0.381***
Functional	Nested	-0.095	-0.265	**-0.007***	**-0.639***
	Turnover	**-0.177***	--	--	**0.420***