
RODRIGO SILVA DO CARMO

Influência da cobertura florestal e tipo de matriz na beta-
diversidade taxonômica e funcional de aves na Mata
Atlântica brasileira

Influence of forest cover and matrix type on bird taxonomic
and functional beta diversity in the Brazilian Atlantic forest

São Paulo

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Orientador: Jean Paul Metzger
Coorientadora: Andrea Larissa
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Prof(a). Dr(a).

Prof(a). Dr(a).

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Orientador

Dedication

Para Moacyr Gomes do Carmo
Por ter feito de tudo por mim e ter sido um pai
humilde com seu filho, muito mais do que mereci

Epigraph

“The distinction between the past, present and future is only a stubbornly
persistent illusion.”

Albert Einstein

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Resumo: A perda de habitat é um dos principais fatores afetando a mudança de comunidades biológicas e o funcionamento dos ecossistemas em paisagens fragmentadas. Entretanto, estes efeitos são geralmente avaliados isoladamente. Ademais, a qualidade da matriz desempenha um papel chave na persistência das espécies em paisagens fragmentadas, regulando a movimentação das espécies e, por consequência, a beta-diversidade. A princípio, quanto menor a movimentação (o que é esperado em paisagens mais desmatadas e com matrizes mais contrastantes), maior a beta-diversidade, em particular para espécies florestais. No caso das generalistas, que têm maior capacidade de movimentação pela paisagem, espera-se que os valores de beta-diversidade sejam menores em paisagens mais desmatadas. Neste trabalho, testamos como a beta-diversidade taxonômica ($T\beta$) e funcional ($F\beta$) de aves respondem à cobertura florestal e ao tipo de matriz na Mata Atlântica brasileira. Nós amostramos aves em pontos amostrais pareados (floresta-matriz; $N = 92$) imersos em matrizes de alto (pasto) ou baixo (café) contraste com o ambiente florestal. Selecionamos quatro características funcionais para calcular a $F\beta$, associadas com o uso de recursos (largura do bico, dieta) e propensão à extinção (massa corporal, e uma medida de extensão da asa relacionada à capacidade de dispersão, denominada “hand-wing”). Os padrões de beta-diversidade foram obtidos entre interfaces de floresta-matriz e entre manchas florestais, em duas escalas de análise (escala local e da paisagem). Nós encontramos que a cobertura florestal e o tipo de matriz são importantes variáveis explicativas da beta-diversidade e que a resposta muda entre as escalas e de acordo com a especificidade de habitat das aves. A $T\beta$ para generalistas entre interfaces floresta-matriz diminuiu com a perda de cobertura florestal na escala local, com valores menores em paisagens menos contrastantes, enquanto que na escala da paisagem essa variável foi explicada apenas pelo tipo de matriz. A $T\beta$ para aves dependentes de floresta aumentou com a perda de cobertura florestal na escala local, e também respondeu apenas à matriz na escala da paisagem, com uma beta-diversidade maior em matrizes mais contrastantes. $T\beta$ entre manchas florestais convergiu entre as escalas, sendo influenciada apenas pelo tipo de matriz, com maior beta-diversidade em matrizes mais contrastantes, independente da especificidade de habitat das espécies. Relações de $F\beta$ com características da paisagem ocorreram essencialmente para dependentes florestais. A $F\beta$ da dieta (na escala local), largura do bico e massa corporal (na escala da paisagem) aumentaram em paisagens mais desmatadas independente do tipo de matriz. A $F\beta$ para o hand-wing foi influenciada apenas pela matriz, sendo maior em matrizes mais contrastantes independente da especificidade de habitat. Paisagens com cobertura florestal intermediária imersa em matrizes de menor contraste foram as condições mais benéficas, tanto para a beta-diversidade taxonômica quanto para a funcional, o que sugere que estas condições sejam adequadas para a conservação de espécies e o funcionamento ecossistêmico em paisagens fragmentadas.

Palavras-chave: dispersão, complementação de recurso, funcionalidade do ecossistema, suplementação de recurso.

INFLUENCE OF FOREST COVER AND MATRIX TYPE ON BIRD TAXONOMIC E FUNCTIONAL BETA DIVERSITY IN THE BRAZILIAN ATLANTIC FOREST

Rodrigo Silva do Carmo*, Andrea Larissa Boesing, Jean Paul Metzger

Department of Ecology, Bioscience Institute, University of São Paulo, Rua do Matão 321, Travessa 14, 05509-900 São Paulo, SP, Brazil

Abstract: Habitat loss is one of the main drivers of biological communities change and ecosystem functioning in fragmented landscapes. However, these effects are often evaluated separately. Additionally, matrix quality plays a key role on species persistence in fragmented landscapes, regulating species movement and, consequently, beta diversity. At first, the lower the movement (which is expected in landscapes with less forest and more contrasting matrices), the higher the beta diversity, particularly for forest-associated species. In the case of forest-generalists, who have greater capacity to move across the landscape, beta diversity values are expected to be lower at more deforested landscapes. We tested how taxonomic ($T\beta$) and functional beta diversity ($F\beta$) of birds respond to forest cover and matrix type in the Brazilian Atlantic forest. We surveyed birds across paired sampling sites (forest-matrix; $N = 92$) embedded in high (pastures) or low (coffee) contrasting matrices. We selected four functional traits to calculate $F\beta$, associated with species resource use (bill width, diet) and propeness to extinction (body mass, and a proxy for dispersal capacity, named “hand-wing”). Beta diversity patterns were obtained across forest-matrix interfaces and across forest patches, across two scales of analysis (local and landscape scale). We found that both forest cover and matrix type are important drivers of beta diversity in fragmented landscapes and the pattern of response changes across scales and according to bird habitat specificity. Forest-generalists $T\beta$ across forest-matrix interfaces decreased with forest cover loss at local scale, with lower values at lower contrasting landscapes, while at landscape scale, this variable was explained only by matrix type. Forest-associated birds $T\beta$ increased with forest loss at local scale, and also responded only to matrix type at landscape scale, with higher beta diversity at high-contrasting matrices. $T\beta$ across forest patches converged across scales, being influenced only by matrix type, being higher at high-contrasting matrices, regardless species habitat specificity. Relationships of $F\beta$ with landscape structure arised mainly for forest-associated species. Diet $F\beta$ (at local scale), bill-width $F\beta$ and body mass $F\beta$ (at landscape scales) increased at more deforested landscapes regardless of matrix type. Hand-wing $F\beta$ was influenced only by matrix type, being higher at high-contrasting matrices regardless habitat specificity. Landscapes with intermediate forest cover embedded at lower contrasting matrices were most beneficial for both taxonomic and functional beta diversity, suggesting that these conditions are suitable for species conservation and ecosystem functioning in fragmented landscapes.

Keywords: dispersal, resource complementation, ecosystem functionality, resource supplementation.

1. INTRODUCTION

Conversion of native habitats into anthropogenic land uses is one of the main drivers of biodiversity loss (Haddad et al. 2015), leading to changes on biodiversity composition and abundance of biological communities, and also on ecosystem functioning (Haines-Young, 2009). One powerful approach to understand these relationships is through the understanding of variations between communities' composition following disturbance gradients, using beta diversity measures (Mori et al. 2018). Beta diversity has a multi-scale facet that takes into consideration both local and regional (alpha and gamma diversities) aspects of biodiversity (Legendre et al. 2005). Additionally, its partition into *nestedness* (i.e. the loss or gain of species/traits which ensures that the poorest site is a complete subset of the richest site) and *turnover* (i.e. species replacement which entails that the poorest site contains species/traits which are absent in the richest site) (Baselga, 2012) helps to disentangle the relative importance of different ecological processes assembling communities. Exploring beta diversity patterns may provide useful insights about how to appropriately make management decisions expected to mitigate biodiversity loss since it captures changes of both taxonomic and functional aspects (Socolar et al. 2016).

Beta diversity patterns are driven mostly by extinction and dispersal processes (Olden & Poff, 2004), where forest cover (Püttker et al. 2015) and matrix composition (Corbelli et al. 2015) play a key-role influencing both processes, but few studies have systematically tested matrix effects on beta diversity patterns (Barros et al. 2019, Jeliaskov et al. 2016, Karp et al. 2012). A less contrasting matrix determines extinction thresholds occurring at lower amounts of forest cover compared to inhospitable or high contrasting matrices (Boesing et al. 2018), directly affecting species composition in-patches (Hu et al. 2019). Furthermore, a high contrasting matrix can strengthen the negative consequences of forest cover loss (Reider et al. 2018). Therefore, a low contrasting matrix can offer shelter and food resources, counterbalancing the negative effects of patch isolation and patch size reduction, whereas a high contrasting matrix is usually avoided due to species' intolerance to its environmental conditions (Driscoll et al. 2013).

Moreover, species' dispersal events can differ across scales. Smaller scale movements reflect daily movements in search for different resources, such as food, shelter and nesting resources, whereas larger scale movements encompass dispersal among populations (i.e. meta population dynamics) (Cosgrove et al. 2017). A higher beta diversity could be expected when larger scales are evaluated simply due to sampling effect capturing distinct species as the increased distance between habitats is associated with environmental heterogeneity (Qian & Ricklefs, 2011) and reduced dispersal (Johst et al. 2002). However, although environmental heterogeneity might increase with geographical distances (Freestone & Inouye, 2006), if the majority of species are highly dispersive and tolerant of anthropic environments, communities would become homogenized despite habitat distances (Vellend et al. 2007). Extinction and immigration events or the lack of them are also more often detected when larger scales are evaluated, which affect local (alpha) and regional (gamma) diversity (Glenn & Collins, 1992), thereby affecting beta diversity.

Species differ in response due to landscape modification (Vallejos, Padiál & Vitule, 2016). Forest-associated species are known to be highly intolerant to human-modified environments (Magura, Lövei & Tóthmérész, 2017) but may be able to maintain immigration dynamics with high forest cover (Püttker et al. 2011) in low-contrasting matrices (Boesing et al. 2017). On the other hand, forest-generalist species use several kinds of non-forest environments (McIntyre, 2000), preferably low-contrasting ones that offer food resources (Kennedy et al. 2017). They have higher dispersal capacity (Dapporto & Dennis 2013) and are not dependent on forest cover as much as forest-associated species (Krauss et al. 2003). However, events of non-random extinction may lead to the gradual disappearance of species with certain ecological traits, whereas others can be favored and homogenize the communities (McKinney & Lockwood, 1999; Frishkoff & Karp, 2019).

In order to analyze taxonomic and functional beta diversity patterns generated by species' responses to changes in landscape structure, it is essential that the studied group of organisms has a great representability and enough known information to allow the functional characterization of environments. Birds compose a very well known taxon (Bonnet et al. 2002) that

presents great morphological, physiological and behavioral variation, allowing them to fill a large range of ecological niches (Brusatte et al. 2015), making them an excellent taxon to test environmental changes effects on both taxonomic and functional patterns (Newbold et al. 2013). They also contribute to ecosystem functioning at natural habitats and important ecosystem services in agricultural matrices such as pollination and pest control (Whelan et al. 2008).

Here, we propose to understand the effects of forest cover amount and matrix type on both taxonomic and functional beta diversity of bird communities. First, we hypothesize that forest cover changes beta diversity patterns distinctly according to species habitat specificity (forest-associated and forest-generalist) and matrix type (low- and high- contrast). We predict that forest loss will lead to a lower beta diversity of forest-generalists due to their high dispersal capacity and tolerance to matrix environments, with a higher contribution of nestedness. We expect an opposite pattern for forest-associated species, where beta diversity must increase (with an increase in turnover) at the most deforested landscapes due to increased isolation between patches, with a stronger effect in high-contrasting matrices, which may act as a barrier to forest-associated specie's movement.

Second, we hypothesize that the scale of analysis will affect beta diversity patterns. We expect similar responses of beta diversity patterns across spatial scales but the intensity of effect will be modulated by habitat specificity. We expect that larger scales will detect a lower beta diversity for forest-generalist species compared to smaller scales due to their high dispersal capacity to move across non-forest habitats. On the other hand, we expect a higher beta diversity for forest-associated species at larger scales due to their lower capacity of moving across non-forest habitats, thereby generating a higher beta diversity compared to smaller scales.

2. METHODS

2.1 STUDY REGION AND LANDSCAPE SELECTION

Study region

The study region is located between the Northeast São Paulo Atlantic Plateau and the South Minas Gerais region in southeastern Brazil along the

Atlantic Forest biome, considered a hotspot of biodiversity (Laurance, 2009; Ribeiro et al. 2011). It originally covered an area of 150 million ha (Ribeiro et al. 2009) and nowadays the Atlantic forest is reduced to 26% of its original extent (Rezende et al. 2018). A subtropical climate predominates over the whole study region (UNICAMP, 2016), with a mean temperature range between 11.3 °C (April-September) and 27.7 °C (October-March) during the cold and warm season respectively, and annual rainfall varying between 1,350 and 2,000 mm (Pompeu, Costa & Fontes, 2009). It has a mountainous relief with elevation between 700 and 1,700 m.a.s.l (Oliveira & Fontes, 2000).

Landscape selection

We selected 23 focal landscapes (2 km radius; 1,256ha) controlling for potential confounding factors including: elevation (between 800 and 1,300 m.a.s.l), soil type (ferric red latosol or argisol), absence of highways and water reservoirs, and the amount of eucalyptus plantations in the matrix (ideally <20%). Focal landscapes were far apart each other at least 6 km (from their centroids) in order to enhance spatial independence (Figure 1). Landscapes were embedded in two regions detaining similar biophysical characteristics and species pool, but the historical agricultural expansion led to different matrix composition. The northeast landscapes (N=10; hereafter *coffee-embedded landscapes*) were located between the South Minas Gerais and Mogiana regions, nowadays recognized as one of the most productive coffee regions in the world (CONAB, 2013). Coffee was introduced in the region in the 18th century but only after 1801 coffee production was established and expanded remarkably (Filetto, 2000; Vale et al. 2014). Before coffee expansion in the region, agricultural lands were destined to livestock production, cotton, sugarcane and tabbaco plantations (Filetto & Alencar, 2001). Landscapes located in the southeast area (N=13; hereafter *pasture-embedded landscapes*) currently detain an agricultural matrix composed majoritally by cattle pastures, but in the past, also composed by coffee plantations. The whole region experienced a transition from coffee to cotton plantation in the early 1930s, with significant clearing of forest areas for cotton crops due to the infertility of areas priorly dedicated to coffee (Por, 1992). Afterwards, cotton crops were replaced by pastureland and more recently (1980 – 1996) eucalyptus plantations advanced

in the region as well (Calaboni, 2017). More details about the matrix composition can be found in Boesing, Nichols & Metzger (2017b).

2.2 STUDY SITES SELECTION

In each focal landscape, we selected four independent forest fragments far apart (1.862 ± 716.3 m) in order to establish paired sampling sites (i.e. samplings in-forest patch and in- its adjacent matrix, either coffee plantations or unmanaged pastures). In order to survey fragments of different sizes, a stratified random selection (Ding et al. 1996) process based on the largest fragment size was performed. For example, if the largest fragment of the focal landscape detains 50% of forest cover, 50% of sampling sites ($N=2$) were randomly settled at that fragment, while the remaining 50% of sampling sites were randomly distributed across other fragments larger than 2.5 ha. Each paired sampling site (i.e. one sampling point inside the forest and one inside the adjacent matrix) were far apart (232.1 ± 46.1 m) and each sampling point was located at least 100 m far from forest edges. Only fragments with old secondary forests, clear vertical stratification, canopy structure and absence of cattle in the understory were considered. A total of 92 paired sampling sites were surveyed: 40 and 52 in-coffee and in-pasture embedded landscapes, respectively.

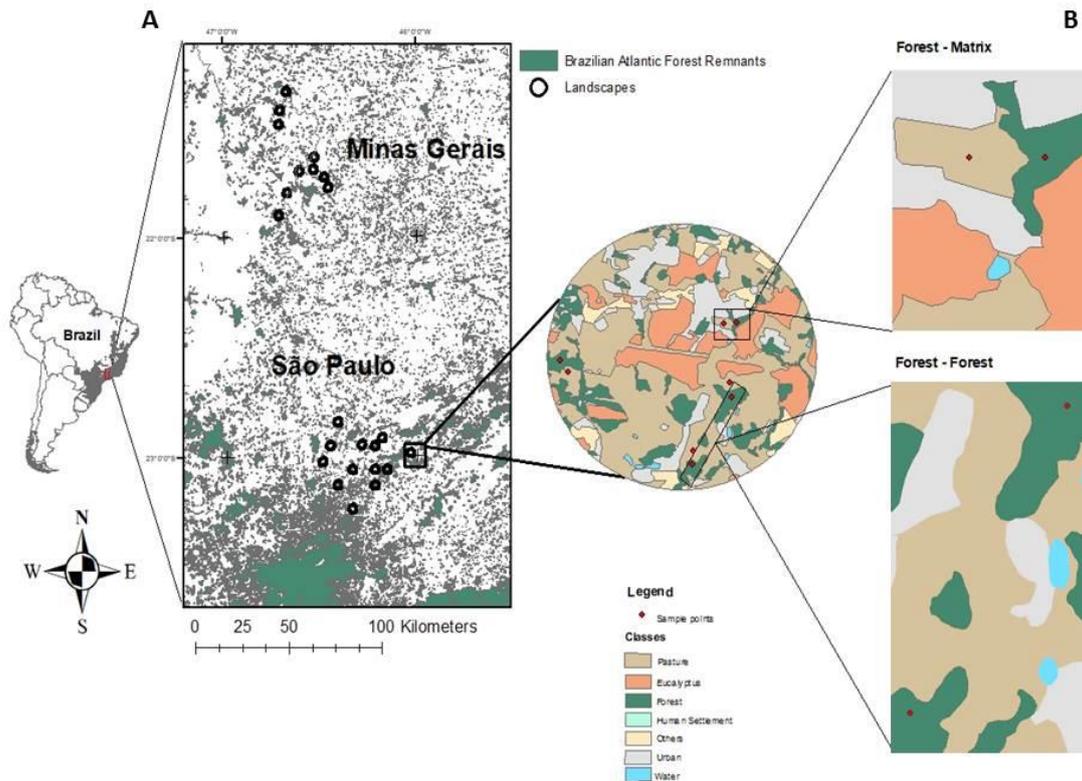


Figure 1: A. Study region and focal landscapes: 10 landscapes in the north (Minas Gerais state) with a low contrasting matrix composed mostly of sun coffee plantation and 13 landscapes in the south (São Paulo state) containing a high contrasting matrix composed mostly of pastures. B. Illustration of the paired sampling design (forest-matrix interfaces and between forest patches (forest-forest)).

2.3 BIRD DATA

We sampled birds using Point Counts, a well-recognized and widespread methodology to survey birds in the tropics (Blake, 2007). Point counts consist of systematic visual or aural detection of birds during a pre-established time period and a fixed radius of detection. Birds were detected during 15 minutes using a fixed 50-m radius of detection. Only species perched or active inside the sampling point radius were considered, and species flying above or across the radius were ignored. Each sampling point was surveyed four times across the year (2014), and a total of 736 point counts were performed. Further details about the methodology can be found in Boesing, Nichols & Metzger (2017b). In order to prevent biased results, punctual detections of birds of prey, water-associated and wetland birds were removed from our analysis. Bird species

were classified according to habitat association: forest-associated species (which require forest habitats for reproduction and survival; Sick, 1997; Del Hoyo et al. 2014) and forest-generalist species, which are able to use not only forest, but also several types of different environments (Morante-Filho et al. 2015). Finally, open-area associated species were not included in the analysis.

3. DATA ANALYSIS

We calculated two measures of beta diversity index: taxonomic beta diversity ($T\beta$; which corresponds to differences in species composition between communities) and functional beta diversity ($F\beta$; differences in ecological traits between communities) (Baselga, 2010). Moreover, we also calculated their associated components: nestedness (n_{es} ; the loss or gain of species/traits which ensures that the poorest site is a complete subset of the richest site) and turnover (t_{urn} ; species replacement which entails that the poorest site contains species/traits which are absent in the richest site) (Baselga, 2012). For $F\beta$, we considered species traits that better reflect species resource use and persistence in fragmented landscapes, including two resource use-based traits (diet and bill width) and two traits used as proxies for species persistence in fragmented landscapes (body mass and hand-wing index), see Table 1 for traits details.

We used bird presence-absence data to appropriately measure beta diversity as dissimilarity based on the Sorensen Family for both $T\beta$ and $F\beta$. Although abundance data provides an efficient way to estimate population size and thus it is able to inform when a species or trait is increasing or declining compared to presence-absence data (Joseph et al. 2006), the latter when performed more than once at the same site at multiple seasons in a short period of time is able to minimize the imperfect detection problem and therefore have a greater chance of generating unbiased results (MacKenzie, 2005). Since each sampling point was surveyed four times, we assumed that presence-absence data would provide genuine results.

Table 1: Ecological information about the selected bird functional traits that reflect resource use and persistence in fragmented landscapes.

Functional Trait	Description
Body Mass	Body size is associated with several life history characteristics of species (metabolic rate, extinction susceptibility, geographic distribution, territory range, movement capacity) which affect the functioning of the ecosystem by influencing in the flow of energy and matter between the ecosystem compartments and between different ecosystems (Owens & Bennett, 2000; Woodward et al. 2005).
Hand-Wing Index (proxy for dispersal capacity)	<p>The formula is composed of: $100 \times \frac{WL - SL}{WL}$</p> <p>Where WL refers to the standard length of the closed wing, reflecting wing extent and SL refers to the distance from the carpal joint to the tip of the first secondary feather, reflecting wing width. Higher values indicate higher dispersal capacity. Its related not only with maneuverability but also with natal dispersal, migratory behavior and flight performance (Claramunt et al. 2011; Lees et al. 2016).</p>
Diet	Provides information about the niche amplitude, energetic requirement and ecosystem function such as: seed dispersal, insect population control and pollination (Remsen & Robinson, 1990). Species were classified into four categories following Wilman et al. (2014): Invertebrate, frugivorous/nectarivorous, omnivorous and granivorous.
Bill Width	Bill morphology provides information which complement the feeding guild classification (Quiroga et al. 2018; Días, 1994). Bill morphology determines the food size a given species can forage on. Thus, wide and narrow billed species tend to forage on different items. For instance, although small seeds dispersal may not be correlated with bill width, large seeds can only be dispersed by species with wide bills (Wheelwright, 1985; Dehling et al. 2016, Pigot et al. 2016).

Both $T\beta$ and $F\beta$ and their associated nestedness and turnover were calculated in a two-step procedure. First, we calculated them across paired sampling sites (forest x matrix; forest x forest, Fig.1). Beta diversity between forest-matrix environments provides insights regarding species shared between native and agricultural lands, and importantly might be a proxy regarding ecosystem functionality and ecosystem services provision in crop lands. Beta diversity between forest-sites (forest-forest) detains information concerning species persistence in the native habitat following habitat loss, fragmentation and matrix intensification use. Second, $T\beta$ and $F\beta$ analysis were performed at two spatial scales: at the local scale (considering the best scale of response to habitat loss), considering each paired sampling site (forest-matrix; 4 $T\beta$ and $F\beta$ per focal landscape) and each forest-forest pair (forest-forest; 6 $T\beta$ and $F\beta$ per focal landscape), and at the 2 km radii landscape scale considering the accumulative species/traits across all sampling sites within each focal landscape (forest-matrix; 1 $T\beta$ and $F\beta$ per focal landscape, forest-forest; 1 $T\beta$ and $F\beta$ per focal landscape).

In order to test our first hypothesis that forest cover affects beta diversity patterns changes according to species habitat specificity and matrix type, $T\beta$ and $F\beta$ (between forest-matrix and forest-forest) for both forest-associated and forest-generalist species were modelled as a function of forest cover and matrix type. We built five competitive generalized linear mixed models (GLMMs) and we proceeded with a model selection based on the Akaike information criteria for small samples (AICc) (Burnham & Anderson, 2004) and the models with $\Delta AICc \leq 2$ were selected as the most parsimonious. Competing models encompassed models with unique predictors ($\beta \sim$ Matrix, $\beta \sim$ forest cover), models with additive effects ($\beta \sim$ forest cover + Matrix), models with interaction ($\beta \sim$ forest cover * Matrix) and a null model ($\beta \sim 1$) representing no significant changes generated by the predictive variables. We modelled our data (beta diversity and its components) using beta distribution, beta-one inflated distribution and beta-zero inflated distribution with a logit link function. A beta distribution was used when minimum and maximum values (zero and one, respectively) were not present in the data, while beta-one inflated was used to account for one inflated data (associated with either total turnover or no species presence in one habitat), and beta-zero inflated was used to account for zero

inflated data.

For $F\beta$ used in the models, we considered each selected trait (i.e. body size, hand-wing index, diet and bill width) individually in a single-trait $F\beta$ analysis. Single-trait analysis can better detect changes along an environmental gradient rather than multi-trait analysis, when traits are not highly correlated (Butterfield & Suding, 2012). Even though $F\beta$ provides information of functional homogenization or differentiation of communities along environmental gradients, it does not inform how exactly traits are changing following land use change. Thereby, in order to better explain changes in $F\beta$, we also fitted fourth corner models to communities inside the forest and inside the matrix, to provide additional information to our $F\beta$ results. Fourth corner models uses generalized linear models to make positive and negative correlations between environmental changes and species traits affecting their responses (Brown et al. 2014). For instance, it takes an ecological trait and compare it between intervals of an environmental gradient, generating three possible outcomes: a positive coefficient, a negative coefficient and a null response. A positive and a negative coefficient means an increase and a decrease on the ecological trait analyzed, respectively, while a null response represents a non-significant change. We used a LASSO (Least absolute shrinkage and selection operator) penalty in each fourth corner model, in order to appropriately perform variable selection and avoid overfitting (Tibshirani, 1996). We used forest cover as our main environmental variable, and proceeded with fourth corner analysis across matrix types and scales for our four selected functional traits. Forest cover was transformed into a categorical variable with the purpose to better capture changes in trait variation. The classification followed thresholds accepted in landscape ecology (Andr en, 1994; Fahrig, 2003). Thus, we created three forest cover categories as follows: high (>40%), intermediate ($\geq 21\%$ - $\leq 40\%$) and low (<21%).

To test our second hypothesis that the scale of analysis would change beta diversity patterns, we modelled $T\beta$ and $F\beta$ response to matrix type across a forest cover gradient at two spatial scales: at local level (i.e. at sampling site level, at the best scale of response) and at the focal landscape level (overall sampling sites within the focal landscape). For landscape level, we considered the focal landscape as sampling unit, thereby encompassing all 4 sampling

points of each landscape for $T\beta$ and $F\beta$, having the forest cover ranging between 7% and 55% at 2 km radii. Whereas, at local level, we tested multiple radii (400 m, 600 m, 800 m, 1200 m, 1600 m or 2000 m) from the centroid of each paired sampling site, keeping the focal landscape as random effect. The best local scales of response are displayed in Supplementary material (Table S1).

All analyses were conducted in the R environment 3.5.1 (R Development Core Team, 2018), functions in the 'betapart' (Baselga & Orme, 2012) package were used to calculate beta diversity, the statistical modelling was done with the 'gamlss' package (Rigby & Stasinopoulos, 2005) and the fourth corner models were fitted using the 'mvabund' package (Wang et al. 2012).

4. RESULTS

Overall 191 species were considered. We recorded 81 forest-generalists (22.1 ± 4.1 in-forest; 14.6 ± 3.7 in-matrix) and 70 forest-associated (25.4 ± 6.1 in-forest; 2.9 ± 1.5 in-matrix) at coffee-embedded landscapes, and 84 forest-generalists (17.5 ± 4.3 in-forest; 8.9 ± 4.7 in-matrix) and 85 forest-associated (19.9 ± 9.2 in-forest; 0.3 ± 0.7 in-matrix) at pasture-embedded landscapes (Fig.2). We recorded 68 forest-generalist and 61 forest-associated species shared between coffee and pasture-embedded landscapes. Forest-generalist and forest-associated species presented a similar set of traits between coffee and pasture-embedded landscapes as well (Figure S1).

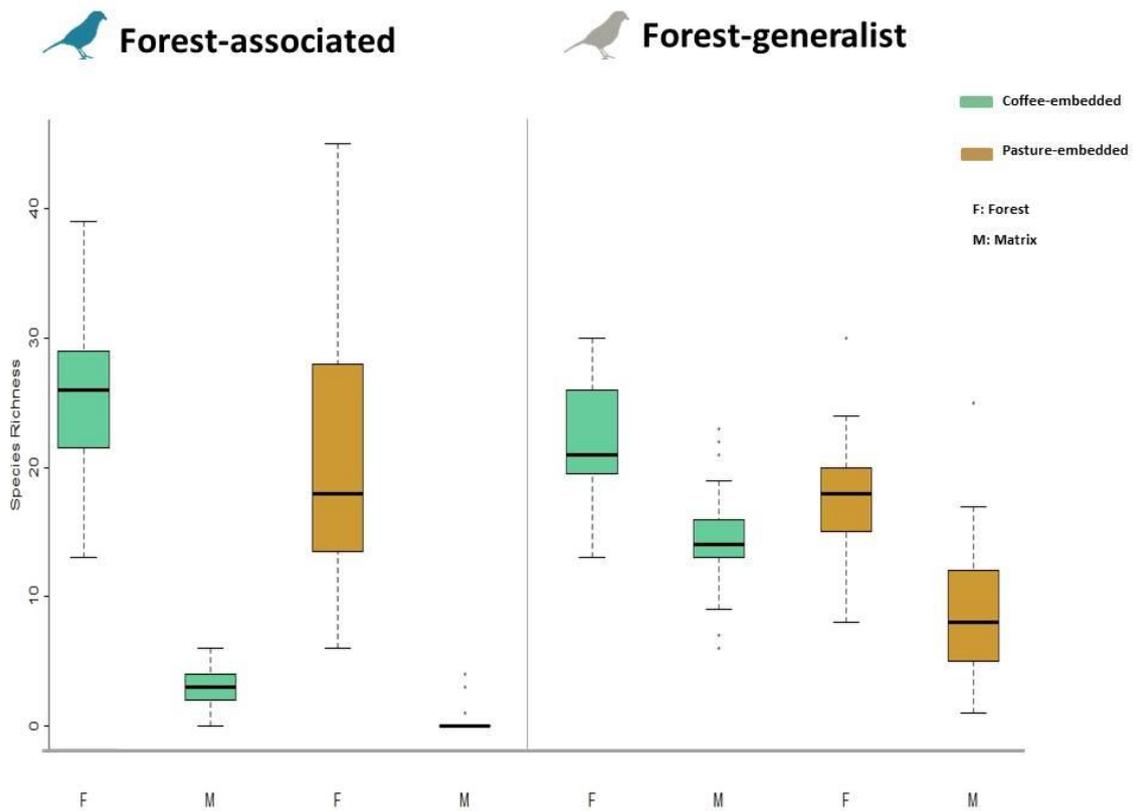


Figure 2: General patterns of species richness across sampling sites for forest-generalist and forest associated species in-forest patches and in-matrices at coffee-embedded and pasture-embedded landscapes.

Forest x Matrix

Both forest-generalist and forest-associated species showed different $T\beta$ responses to matrix type and forest cover and their responses differed across scales (Table S2). $T\beta$ of forest-generalist species was best explained by the additive model of forest cover and matrix type at local scale (Fig. 3a), and only by matrix type at landscape scale (Fig. 3b). At local scale, $T\beta$ of forest-generalists was higher at pasture-embedded landscapes compared to coffee-embedded landscapes, but both presented a pattern of increased $T\beta$ with forest cover (Fig. 3a). Thus, forest-generalist species are highly shared between forest-matrix at lower amounts of forest cover in both matrices. $T\beta$ components for forest-generalists showed a similar pattern across matrices but displayed diverging responses to forest cover: while nestedness decreased with forest cover loss (Fig. 3a.i), turnover increased (Fig. 3a.ii). At landscape scale, forest

cover did not contribute to $T\beta$ patterns of forest-generalists, but $T\beta$ was substantially higher at pasture-embedded landscapes compared to coffee-embedded landscapes (Fig. 3b), and when compared to the local scale, $T\beta$ was higher.

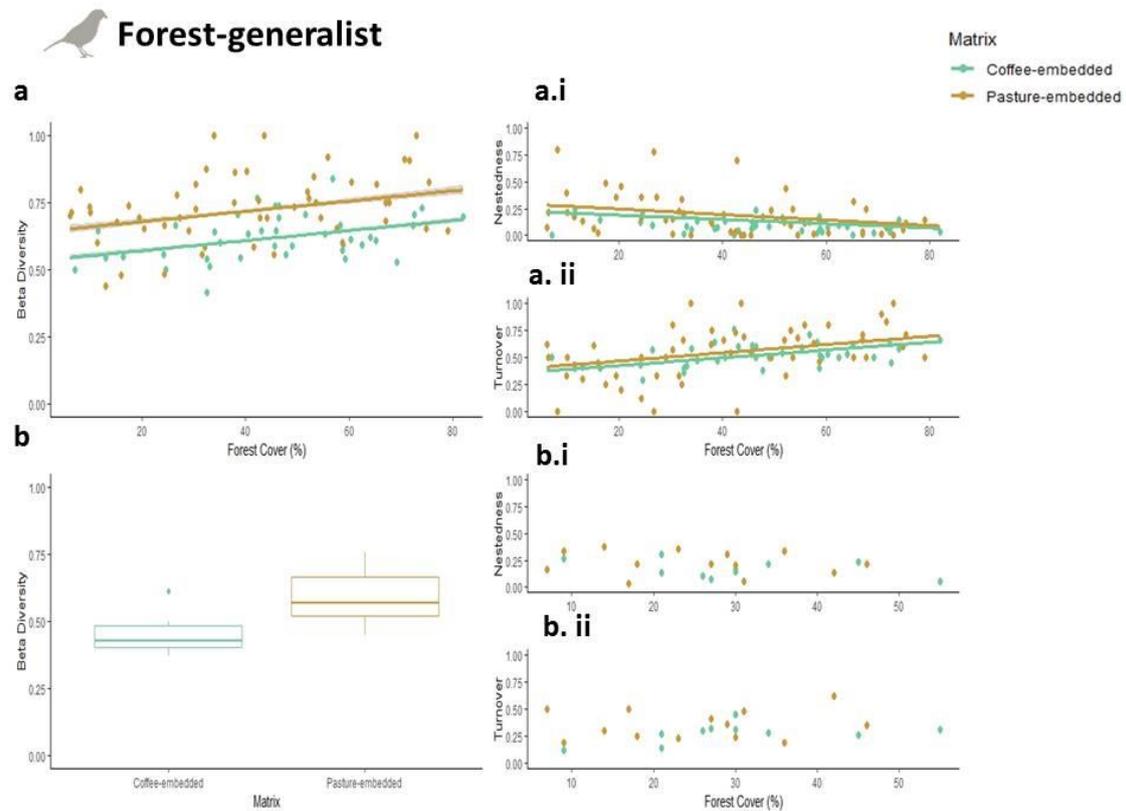


Figure 3: Local (a) and landscape (b) scales taxonomical beta diversity ($T\beta$) patterns and their associated components between paired sample points (Forest – Matrix) for forest-generalists.

The $T\beta$ of forest-associated species was best explained by the interaction between forest cover and matrix type at local (Fig. 4a) scale (unlike forest-generalists) and only by matrix type at landscape (Fig. 4b) scale (similar to forest-generalists). At local scale, $T\beta$ of forest-associated species decreased with forest cover at coffee-embedded landscapes, whereas it increased with forest cover at pasture-embedded landscapes (Figure 4a). Importantly, the unexpected decrease of $T\beta$ at forest-pasture matrix does not necessarily translate in a high occupancy of pastures by forest-associated species, because occurrences inside the pasture matrix were rare (10 unique occurrences).

Moreover, the null model was selected for $T\beta$ components (unlike for forest-generalists). At landscape level, $T\beta$ only responded to matrix type, being higher at pasture-embedded than coffee-embedded landscapes (Fig. 4b), and when compared to the local scale, $T\beta$ was higher (similar to forest-generalists).

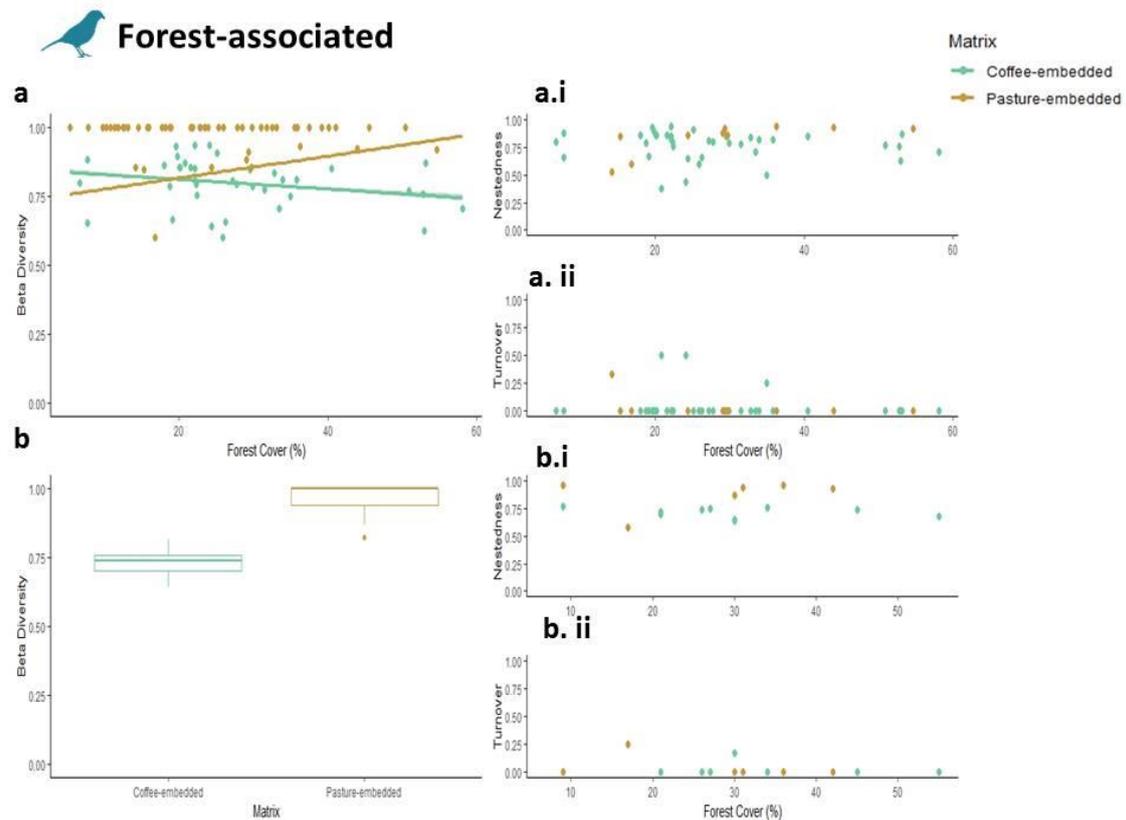


Figure 4: Local (a) and landscape (b) scale taxonomical beta diversity ($T\beta$) patterns and their associated components between paired sample points (Forest – Matrix) for forest-associated species.

No patterns were found regarding $F\beta$, of both forest-generalist and forest-associated species (Table S3). However, the fourth corner analysis revealed two main changes on functional diet composition inside coffee crops. First, there was an increase of forest-generalist granivorous species below 20% of forest cover at local scale, and an increase of forest-generalist insectivorous at intermediate forest cover (40%-21%) at landscape scale. Second, we detected an increase of forest-associated insectivorous species at both intermediate

(40%-21%) and high (>40%) forest cover, at local and landscape scale, respectively (See Figure S5).

Forest x Forest

Forest-generalist (Fig. 5a; Fig.5b) and forest-associated species (Fig. 6a; Fig. 6b) had similar $T\beta$ responses across scales. Both responded only to matrix type, but in general, with a higher $T\beta$ at landscape scale compared to local scale (Table S4). For both forest-generalist and forest-associated species, $T\beta$ was significantly higher at pasture-embedded than coffee-embedded landscapes, evidencing a higher number of species shared between forest patches in coffee-embedded landscapes. $T\beta$ components, on the other hand, showed divergent responses. Nestedness of both forest-generalists and forest-associated species was strongly determined by matrix type, often with a higher contribution to $T\beta$ at pasture-embedded patches (Fig. 5a.i & Fig. 5b.i; Fig. 6a.i & Fig. 6b.1). Turnover showed different patterns according to habitat association: forest-generalists demonstrated a pattern of decreased turnover at lower forest cover amounts at landscape scale (Fig. 5b.ii) and no change at local scale (Fig. 5a.ii). Forest-associated showed a strong effect of matrix type, only at local scale (Fig. 6a.ii). Interestingly, both local turnover and nestedness were higher at pasture-embedded landscapes for forest-associated species, indicating that some patches share several forest-associated species, while others rarely do.

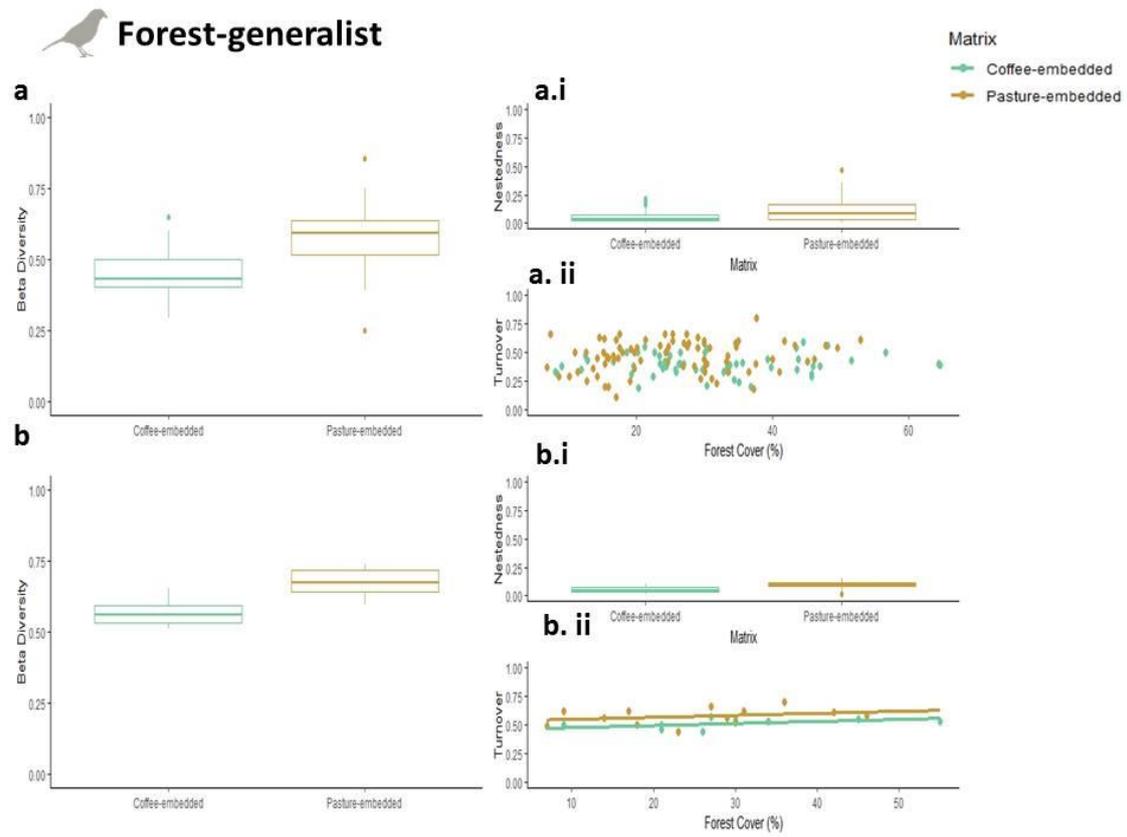


Figure 5: Local (a) and landscape (b) scales taxonomical beta diversity ($T\beta$) patterns and their associated components between forest patches (Forest-Forest) for forest-generalists.

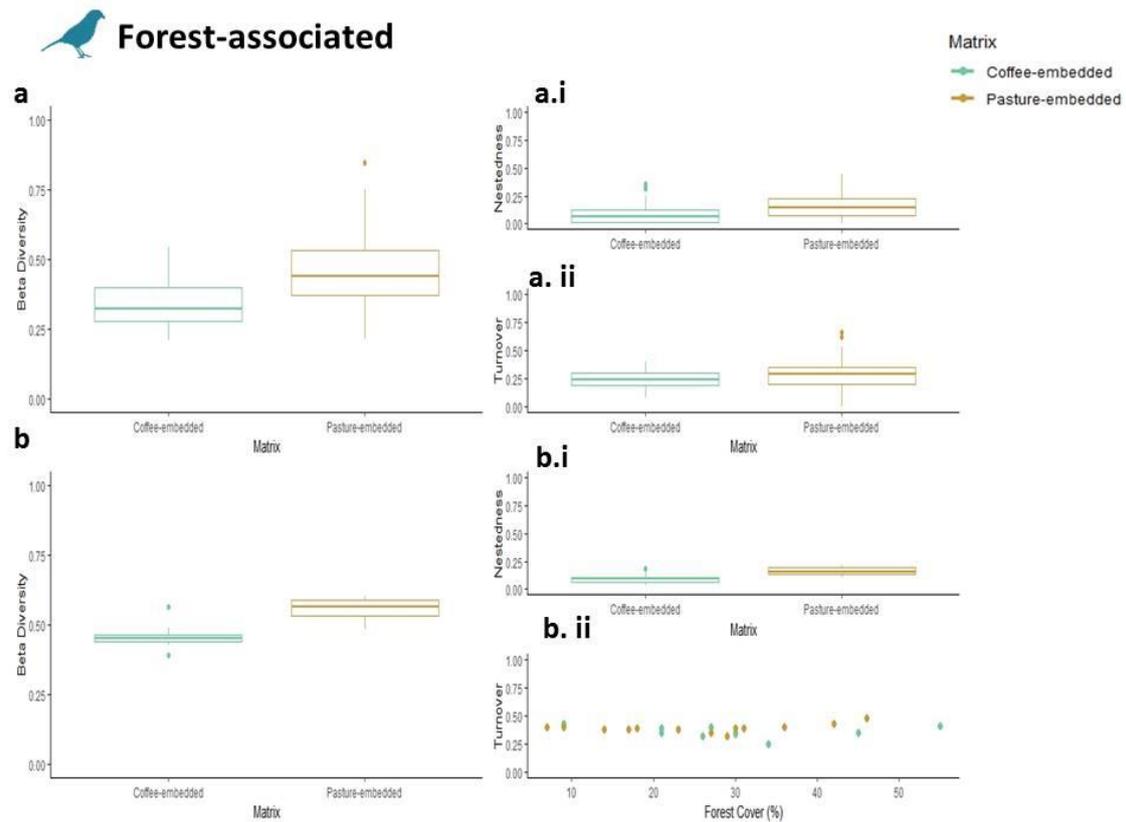


Figure 6: Local (a) and landscape (b) scale taxonomical beta diversity ($T\beta$) patterns and their associated components between forest patches (Forest-Forest) for forest-associated species.

We found evidence of landscape effects for $F\beta$ for all four ecological traits, but each trait had specific responses according to scale and specie's habitat specificity (Table S5). Most of the evidence of changes on $F\beta$ across traits were detected for forest-associated species. Forest-associated species displayed $F\beta$ patterns for hand-wing index and diet at local level (Fig. 7a, Fig.7b), and for hand-wing index, mass and bill width at landscape level (Fig. 8a; 8b; 8c), forest-generalist species only showed a $F\beta$ pattern for hand-wing index at landscape level. $F\beta$ for hand-wing index of forest associated species was best explained by matrix type (higher $F\beta$ at pasture-embedded landscapes) at local and landscape level, while $F\beta$ for diet decreased with forest cover (i.e. a higher diet similarity at higher amounts of forest cover regardless of matrix type) at local level. At landscape level, $F\beta$ for both mass and bill width of forest-associated species decreased with forest cover. Thus, forest-associated species presented similar mass and bill width at highly forested landscapes.

Forest-generalist species only showed response regarding $F\beta$ of hand-wing index at landscape level, which was explained only by matrix type, and being higher at pasture-embedded landscapes. Nevertheless, even though we found no support for $F\beta$ of diet regarding forest-generalists, the fourth corner analysis revealed that lower amounts of forest cover in pasture-embedded landscapes disfavor the occurrence of forest-generalist frugivorous, regardless of scale (See Figure S6).

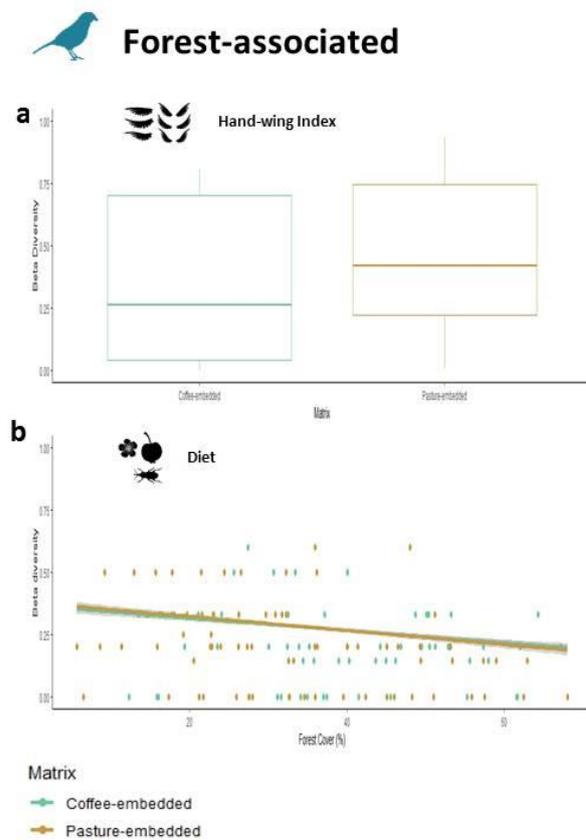


Figure 7: Local scale functional beta diversity ($F\beta$) patterns between forest patches (Forest-Forest) for hand-wing index (a) and diet (b) of forest-associated species.

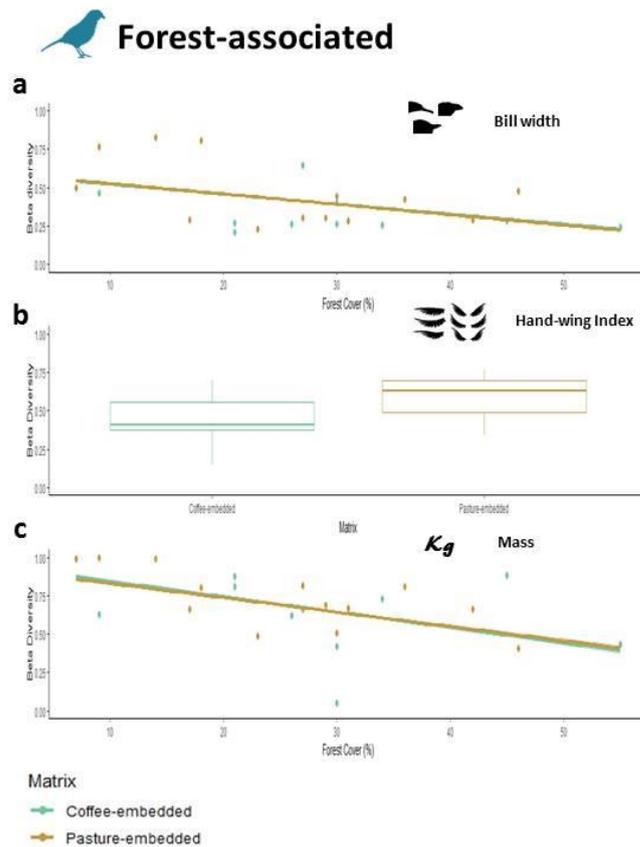


Figure 8: Landscape scale functional beta diversity ($F\beta$) patterns between forest patches (Forest-Forest) for bill width (a), mass (b) and hand-wing index (c) of forest-associated species.

5. DISCUSSION

Here, we provide novel evidence that $T\beta$ and $F\beta$ of bird communities respond differently to habitat loss and matrix type, and that responses change across scales. While $T\beta$ of both forest-associated and forest-generalist species clearly responded to landscape changes, only few patterns emerged for $F\beta$ (mainly for forest-associated species). Our work can be summarized in three main findings. First, $T\beta$ between the forest-matrix interface for forest-generalists and forest-associated species present opposing patterns across the forest cover gradient, while $T\beta$ of forest-generalists decreases with forest cover loss, $T\beta$ for forest-associated mainly increases at lower forest cover amounts. Meanwhile, matrix type plays the main role in generating $T\beta$ patterns for both forest-associated and forest-generalists in-forest patches. Second, $F\beta$ analysis revealed that ecological traits were either affected by forest cover or matrix

type, with most responses regarding forest-associated species. Finally, $T\beta$ and $F\beta$ for both forest-generalists and forest-associated species presented significant changes across scales. At the landscape scale, we usually observed higher $T\beta$ and $F\beta$ in-forest, and lower $T\beta$ across the forest-matrix interface, when compared to the local scale.

5.1 Opposing responses for $T\beta$ to forest loss and matrix type across scales

As expected forest-generalist and forest-associated species displayed opposing $T\beta$ patterns across the forest-matrix interface at local scale. While $T\beta$ of forest-generalists converged across matrices (increased beta diversity with increasing forest cover), forest-associated presented opposing responses (increased beta diversity with increasing forest cover at pasture-embedded landscapes, and decreasing beta diversity with increasing forest cover at coffee-embedded landscapes). These contrasting responses can be driven by two main mechanisms associated with specie's occupation across forest-matrix interfaces: boundary-response effects (Fahrig, 2007) and resource complementation (Dunning et al. 1992). Forest-associated species present a stronger boundary effect compared to forest-generalists, having crossing edges events (e.i spillover) inhibited when the matrix presents a high contrast (i.e.pastures; Kennedy et al. 2017) and facilitated once the edge contrast decreases (i.e. coffee plantations) (Boesing et al. 2018). This leads to a decreased $T\beta$, specially in more forested landscapes where isolation effects are reduced (Estavillo et al. 2013) and resource complementation outside forest patches may be facilitated (González et al. 2017). Forest-generalist species often present a lower boundary response to edges (Hansbauer et al. 2008). However, we found that matrix composition is an important driver of this movement across edges even for them, explaining the convergent trends on $T\beta$ across matrices. $T\beta$ of forest-generalists was also higher at pasture-embedded landscapes, indicating that coffee plantations might be an important source of complementary resources (Buechley et al. 2015), and reinforcing that pasture matrices are poor resource areas for biodiversity (Atkinson et al. 2004).

Although $T\beta$ of forest-associated and forest-generalists presented opposing responses to forest loss at coffee-embedded landscapes, at pasture-

embedded landscapes a common pattern arised. This pattern was especially evident in locations where forest-associated species declined inside forest patches (Figure S2), which might indicate that forest-generalists are replacing forest-associated species and thereby contributing to biotic homogenization in more deforested landscapes (Clavel et al. 2011). At highly deforested pasture-embedded landscapes, the remaining forest-associated species might encompass more tolerant species with lower boundary responses and a higher propensity to cross gaps and use scatarred trees in the matrix (Peh et al. 2006). Therefore, the lower TB of forest-associated species between forest and pastures at lower amounts of forest cover represents few crossing events of the same species across scaterred trees, which are important connectors in high-fragmented landscapes (Prevedello et al. 2017; Silva et al. 2020).

Contrary to our expectations, $T\beta$ of both forest-generalist and forest-associated species across forest patches only responded to matrix type. This finding highlights the importance of matrix permeability to facilitate species movement across fragmented landscapes and favor the maintenance of stable populations (Crone et al. 2019). Thus, our results show that dispersal is a key mechanism driving beta diversity patterns across patches, and that matrix permeability might be even more important than habitat amount for landscape connectivity (Bender & Fahrig, 2005) or that a high permeability can at least partially compensate for habitat loss. We found that forest-associated species persisting in-forest with increased deforestation are evenly distributed in terms of dispersal capacity compared to forest-associated species which disappear with forest loss at both coffee and pasture-embedded landscapes. This can explain the constant low $T\beta$ despite forest loss in two ways. First, a high rate of biotic homogenization can be maintained despite forest loss by forest-associated species emigrating from small degraded patches in search of suitable habitats (Centeno-Cuadros et al. 2011), possibly due to their high dispersal capacity. Second, forest patches that provide favorable conditions allow delays in extinction (Bull et al. 2006), possibly favouring low dispersive forest-associated species. Additionally, forest-associated species's richness peaked with intermediate forest cover embedded in coffee matrices, whereas it declined abruptly with forest loss at pasture-embedded landscapes (See Figure S4). Thus, matrix composition might attenuate habitat loss effects especially for

less dispersive species (Kupfer et al. 2006). The fact the $T\beta$ of forest-generalist species responded only to matrix type as well, reinforce the role of the matrix on dispersal of even forest-generalist species which in general are more dispersive and less sensitive to anthropogenic disturbances (Reinhardt et al. 2005; Thomas 2000).

5.2 Nestedness contributing most to beta diversity patterns across forest-matrix interfaces, and high turnover across forest patches

The contribution of nestedness and turnover to $T\beta$ changed when beta diversity patterns were evaluated between forest-matrix interfaces and between forest patches across scales. The clearest patterns across forest-matrix interfaces were recorded for forest-generalist species at local scale: while nestedness had a higher contribution at the most deforested landscapes, turnover generally took place in the most forested ones. This finding reinforces the role of deforestation in favouring biotic homogenization due to the spread of forest-generalists (Ibarra & Martin, 2015). On the other hand, the $T\beta$ patterns for both forest-generalist and forest-associated species across forest patches had a higher contribution from turnover regardless of forest cover amount. Additionally, a higher contribution of turnover was detected at pasture-embedded landscapes, further indicating the importance of matrix composition in driving communities to differentiate, where a high contrasting matrix favours a higher turnover of communities (Barros et al. 2019). Nevertheless, forest cover loss contributed to a slight decrease in turnover of forest-generalists at landscape scale, indicating that they might be further spreading through landscapes and leading to biotic homogenization. Moreover, nestedness patterns for both forest-generalist and forest-associated species converged across scales, mainly being determined by matrix type, whereas turnover had opposing responses: it decreased with forest loss for forest-generalists only at landscape scale, while it was mainly determined by matrix type for forest-associated species, only at local scale. Having a low nestedness indicates communities differentiate possibly due to dispersal inhibition, which can negatively affect small populations and favour local extinctions (Krauss et al. 2003).

5.3 Changes on traits's $F\beta$ in-patches more pronounced for forest-associated species

The evidence of $F\beta$ changes, mostly for forest-associated species between forest patches regardless of matrix type was unexpected. The main mechanism driving these changes might be related to specie's trait replacement (turnover) between highly forested and highly deforested landscapes. Species's trait replacement following forest loss is driven by species loss (Luck et al. 2013), which in turn causes functional diversity loss (Riemann et al. 2017, see Figure S3). The most remarkable differences were detected for foraging-related traits. We found that $F\beta$ changes for forest-associated species are due to a decline of frugivorous/nectarivorous and an increase of insectivorous at high-deforested pasture-embedded landscapes, whereas it is due to a decline of forest-associated granivorous at high-deforested coffee-embedded landscapes (See Figure S6). A similar pattern of increasing $F\beta$ at lower forest cover amounts was detected for body size of forest-associated species, which is related to loss of small species at pasture-embedded landscapes, whereas no association was found at coffee-embedded landscapes. Although no $F\beta$ changes of these traits were found for forest-generalists, we found that also at pasture-embedded landscapes, wide-billed frugivorous forest-generalist species decline with forest loss, while narrow-billed omnivorous increase, at local scale (See Figure S6). This indicates that ecological functions related to bird foraging might be disrupted in such deforested landscapes (Valiente-Banuet et al. 2014), suggesting that deforestation is leading to changes on the functional structure of bird communities in forest patches (Coster, Banks-Leite & Metzger, 2015) with important impacts for ecosystem functionality (Şekercioğlu et al. 2004).

We also found evidence of matrix type as the main driver of changes on $F\beta$ of hand-wing index, generating a similar trend of higher $F\beta$ at pasture-embedded compared to coffee-embedded landscapes for forest-associated and forest-generalist species. In the case of forest-generalist species, hand-wing index was the only trait that presented a response, and only at landscape scale. This finding further confirms the role of the matrix affecting specie's capacity to move across anthropogenic landscapes. Open matrices are recognized by inhibiting specie's dispersal (Kuefler et al. 2010), while more permeable

matrices facilitate it (Boesing et al. 2018), which might explain the higher value of hand-wing index at pasture-embedded compared to coffee-embedded landscapes, indicating the need for a higher dispersal capacity, for both forest-generalist and forest-associated species. Thus, even though forest-generalists might maintain dispersal through open matrices such as pastures (Pizo & Santos, 2010), they are also impacted. Moreover, $F\beta$ of hand-wing index was higher for forest-generalists compared to forest-associated species, further evidencing that the contrasting level of the matrix has a greater impact over forest-associated species' dispersal than over forest-generalist species' dispersal (Gobeil & Villard, 2002).

5.4 Intermediate forest cover embedded in lower contrasting matrices might benefit ecosystem functioning in fragmented landscapes

Given the structural differences between matrices, we would expect $F\beta$ changes between forest-matrix interfaces, but no pattern of change was detected. This might indicate that even though coffee and pasture matrices might differ in the occurrence of traits, the set of traits might be so limited and a nested subset found in-forest, that they are unable to cause any $F\beta$ changes. However, we found clear changes on species trait profile occupying different matrices in our fourth corner analysis. We found that the spillover of insectivorous species (both forest-associated and forest-generalist) was intensified into coffee plantations at intermediate amounts of forest cover. The presence of insectivorous birds in coffee plantations can decrease leaf loss of coffee plants due to predation of leaf miner (*Leucoptera coffeella*) (Librán-Embid et al. 2017), positively affecting plant biomass. Furthermore, insectivorous birds have demonstrated to decrease coffee-borer beetle (*Hypothenemus hampei*) infestations. Previous studies demonstrated that pest control service is enhanced with increases in forest cover amount, and that 99% of pest control provided by birds is provided at forest remnants surrounded by coffee plots (Karp et al. 2013).

Forest cover greatly affected $F\beta$ of forest-associated species across forest patches, generating a very pronounced difference: a low $F\beta$ at more forested landscapes and a high $F\beta$ at deforested landscapes. We detected that forest cover varying between 21% and 40% (i.e. intermediate forest cover)

favoured forest-associated frugivorous/nectarivorous to survive in-forest patches, further generating intermediate levels of differentiation between forest patches concerning size, diet and bill width, important traits related to ecosystem functioning. We can exemplify changes on ecosystem functionality taking frugivorous species into account. The presence of frugivorous birds is indispensable to seed dispersal of fruit trees and shrubs (Peña-Domene et al. 2014). The importance of maintaining a balanced distribution between large and small fruit dispersers at each forest patch is because the loss of large-bodied frugivorous reduce overall forest biomass (Peres et al. 2016) and the loss of small species make small trees and shrubs more prone to extinction (Emer et al. 2018). However, when they coexist, plants that need to deposit their seeds away from conspecifics in order to avoid high rates of seed predation and infectious diseases, and those that need to deposit seeds close to conspecifics, are benefited (Wotton & Kelly, 2012; Yamazaki et al. 2008; Fricke et al. 2014). Thus, we show that intermediate forest cover embedded in low-contrasting matrices ensures the distribution birds of different sizes, both wide-billed and narrow-billed frugivorous species across forest patches. This possibly allows seeds of several sizes to be dispersed and have the chance to establish either near or far from conspecifics, increasing the diversity of seeds that are dispersed and their dispersal's success.

5.5 Limitations of the study

It is important to acknowledge some limitations of our study, especially regarding the inconclusive patterns of response of $F\beta$ between forest-matrix interfaces. The lack of response of $F\beta$ between forest-matrix interfaces might be due to four main factors. First, deforestation might lead to the replacement of specialized ecological traits by more generalized traits (Coster et al. 2015). Thus, at higher forest cover amounts, species that spillover could present more specialized traits than at lower forest cover amounts. Regardless of the remaining forest cover (high or low), the set of traits might be so restricted and a limited subset of those found in-forest, being unable to cause any $F\beta$ changes across the forest cover gradient. Second, the use of other functional indices such as functional dispersion that measures species trait distribution weighted by abundance (Laliberté & Legendre, 2010), could have not only generated

patterns, but also provided a more complete knowledge about how functional traits vary between habitats. However, we wouldn't be able to explore beta diversity components which have been shown to present great importance to analyze beta diversity and generate conclusions (Baselga, 2010). Third, we analysed a subset of the species occupying matrices, not including open-area associated species. We chose to exclude them from our analysis mostly due to their lack of response to forest loss. Thus, our results display the functionality represented by species with some degree of dependency of natural areas to survive. Finally, the inclusion of other ecological traits could have led to different conclusions (Kennedy et al. 2010). At the same time, the traits used in this study are the ones most responsive to landscape change, and the lack of response copes with other studies such as Cannon et al. (2019).

6. CONCLUDING REMARKS

We showed that forest-associated and forest-generalist species present distinct responses to forest loss and matrix type. Forest-generalist species were less sensitive to deforestation and matrix type compared to forest-associated species, which is exemplified by the decrease in $T\beta$ (with a concomitant increase in nestedness) across forest-matrix interfaces at local scale and by a decrease in turnover across forest patches at landscape scale. Forest-associated species presented higher $T\beta$ across forest-matrix interfaces due to matrix avoidance (especially at high-contrasting matrices), and reduced movement across highly deforested landscapes embedded in lower contrasting matrices. Patterns for $F\beta$ mainly arised for forest-associated species's traits. We detected an increase in $F\beta$ in more deforested landscapes, which reinforces that forest cover loss and matrix contrast drive forest-associated communities to diverge in both taxonomic and functional composition. Finally, we detected lower $T\beta$ across forest patches for forest-associated compared to forest-generalist species, regardless of forest cover at both spatial scales, providing novel evidence that contradicts the notion of low beta diversity being associated with biodiversity impoverishment (Villéger & Brosse, 2012), since species richness in-patches was often higher at intermediate amounts of forest cover.

Our results highlight that matrix type can be more important to explain taxonomic beta diversity patterns than forest cover at large scales, generating a

lower and higher beta diversity between forest-matrix interfaces and across forest patches, respectively. This corroborates that the matrix can better explain community patterns than forest cover at large scales (Watling et al. 2011). Additionally, we found that forest-generalist species dominate fragmented landscapes, whereas a large proportion of forest-associated species are mostly inhibited to disperse, especially across a harsh matrix such as pasture. This corroborates with several studies that found that a higher contrasting matrix increases beta diversity by inhibiting species's dispersal (Karp et al. 2012) and that it also reduces forest-associated species's richness (Solar et al. 2015).

Finally, landscapes embedded in low-contrasting matrices with intermediate forest cover can also favour a greater ecosystem functionality in-forest and greater spillover of insectivorous birds into the matrix. Intermediate forest cover is recognized to favor patch connectivity, which in turn allows more immigration over extinction (Fahrig, 2003; Miyazono & Taylor 2013). Therefore, given that a lower patch connectivity increases beta diversity (Ehrlén, Eriksson, 2000) at the cost of lowering alpha diversity (Mouquet & Loreau, 2002) and the need to alleviate the agriculture-biodiversity conflict (Seppelt et al. 2016), we bring a practical management recommendation grounded in our results. We suggest that maintaining forest patches varying between 21% and 40% of forest cover embedded in a low contrasting agricultural matrix may be the best way to ensure biodiversity conservation and inhibit ecosystem functioning disruption, with the potential to also benefit surrounding agricultural crops through the provision of ecosystem services, such as pest control provided by insectivorous birds.

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Supplementary Material

Table S1: Best scale of response to forest cover with its associated forest cover range (%) at the local scale for $T\beta$ (taxonomic beta diversity) and $F\beta$ (functional beta diversity) according to species habitat specificity for forest-matrix and forest-forest analysis.

Habitat Specificity	β	Environment	Scale (m) (forest cover%)
Forest-generalist	$T\beta$	Forest-Matrix	400m (6.14% - 81.99%)
Forest-associated	$T\beta$	Forest-Matrix	2000m (5.43% - 58.10%)
Forest-generalist	$F\beta$	Forest-Matrix	800m (3.57% - 73.94%)
Forest-associated	$F\beta$	Forest-Matrix	2000m (5.43% - 58.10%)
Forest-generalist	$T\beta$	Forest-Forest	1200m (6.86% - 64.57%)
Forest-associated	$T\beta$	Forest-Forest	1200m (6.86% - 64.57%)
Forest-generalist	$F\beta$	Forest-Forest	1600m (6.86% - 60.33%)
Forest-associated	$F\beta$	Forest-Forest	600m (5.68% - 68.04%)

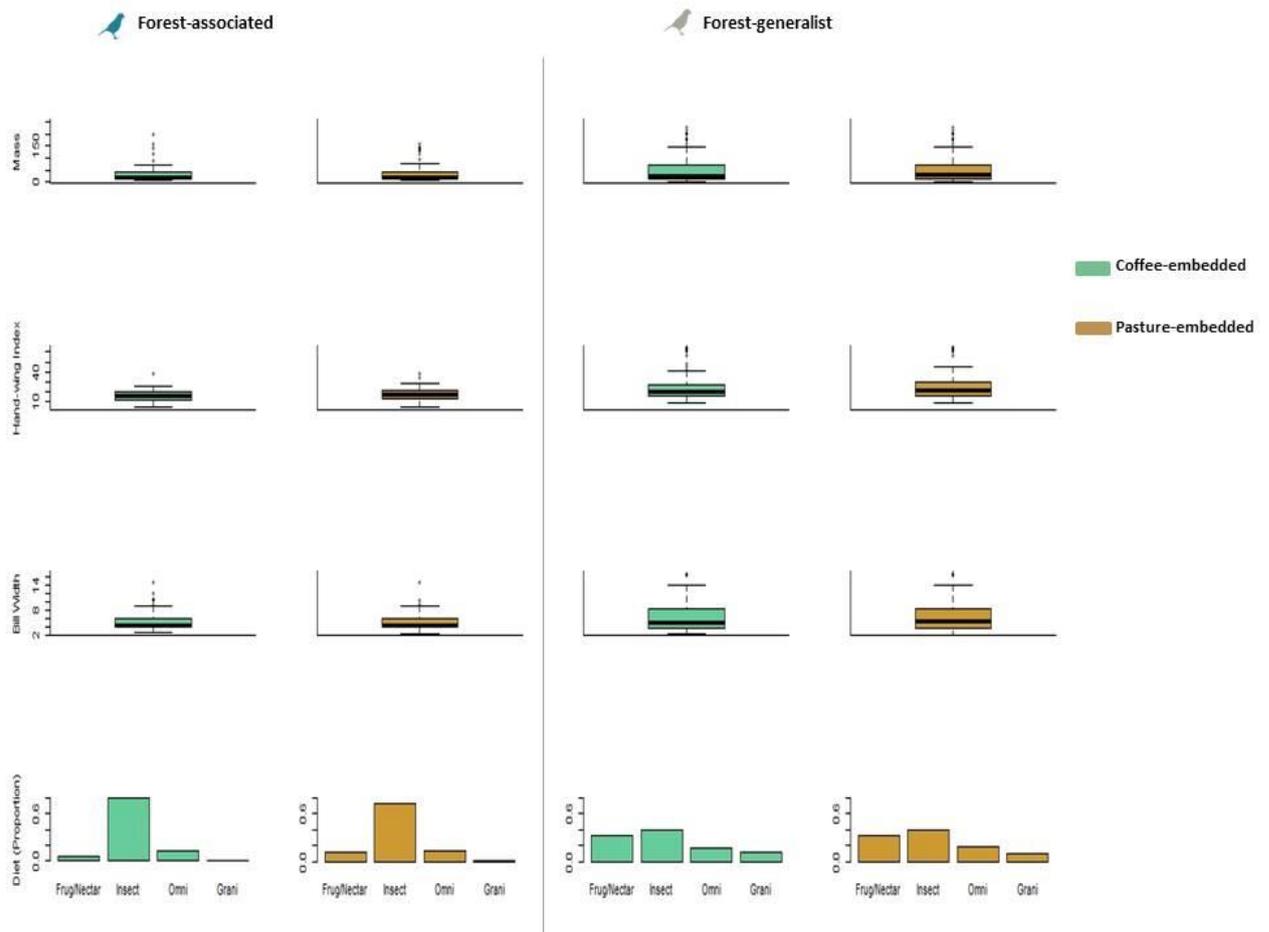


Figure S1: Ecological traits variation (Mass, Hand-wind Index, Bill width and Diet, respectively) between coffee-embedded landscapes for forest-associated (first column) and forest-generalist species (third column) and pasture-embedded landscapes for forest-associated (second column) and forest-generalist species (fourth column). Diet categories is described as follows: Frug/Nectar = Frugivorous/Nectarivorous; Insect = Insectivorous; Omni = Omnivorous; Grani = Grainivorous.

Table S2. Model's coefficients for T β (taxonomic beta diversity) of forest-generalist and forest-associated species between forest-matrix interfaces (Forest-Matrix), at local and landscape scale. Only models with $\Delta AICc < 2$ are presented.

Taxonomic beta diversity between forest-matrix	Estimate (sd)	p
Local scale		
Tβ of forest-generalist		
Selected model: Forest cover + Matrix ($\Delta AICc = 0$, weight = 0.785)		
Intercept	0.108 (0.112)	0.338
Forest Cover	0.008 (0.002)	0.000179 ***
Matrix	0.505 (0.083)	4.42e-08 ***
Tβ nestedness of forest-generalist		
Selected model 1: Forest cover + Matrix ($\Delta AICc = 0$, weight = 0.582)		
Intercept	-1.094 (0.242)	2.04e-05 ***
Forest cover	-0.016 (0.004)	0.000444 ***
Matrix	0.310 (0.183)	0.094188 .
Selected model 2: Forest cover ($\Delta AICc = 1.8$, weight = 0.236)		
Intercept	-0.867(0.198)	3.62e-05 ***
Forest cover	-0.017(0.004)	0.000162 ***
Tβ turnover of forest-generalist		
Selected model 1: Forest cover + Matrix ($\Delta AICc = 0$, weight = 0.350)		
Intercept	-0.614 (0.153)	0.00014 ***
Forest cover	0.015 (0.002)	9.78e-07 ***
Matrix	0.194 (0.111)	0.08536 .
Selected model 2: Forest cover ($\Delta AICc = 0$, weight = 0.350)		
Intercept	-0.481 (0.131)	0.000453 ***
Forest cover	0.014 (0.002)	1.6e-06 ***
Selected model 3: Forest cover * Matrix ($\Delta AICc = 0.3$, weight = 0.300)		
Intercept	-0.370 (0.219)	0.0963 .
Forest cover	0.009 (0.004)	0.0312 *
Matrix	-0.190 (0.275)	0.4910
Forest cover : Matrix	0.008 (0.005)	0.1310
Landscape scale		
Tβ of forest-generalist		
Selected model: Matrix ($\Delta AICc = 0$, weight = 0.757)		
Intercept	-0.205 (0.103)	0.060503 .
Matrix	0.537 (0.138)	0.000904 ***

Tβ nestedness of forest-generalist

Selected model 1: Null ($\Delta\text{AICC} = 0$, weight = 0.483)		
Intercept	-1.383 (0.137)	1.72e-09 ***
Selected model 2: Forest cover ($\Delta\text{AICC} = 1.4$, weight = 0.244)		
Intercept	-1.056 (0.311)	0.00289 **
Forest cover	-0.012 (0.010)	0.26720
Selected model 3: Matrix ($\Delta\text{AICC} = 1.9$, weight = 0.188)		
Intercept	-1.518 (0.207)	4.53e-07 ***
Matrix	0.233 (0.264)	0.388

Tβ turnover of forest-generalist

Selected model 1: Null ($\Delta\text{AICC} = 0$, weight = 0.33)		
Intercept	-0.744 (0.115)	2.06e-06 ***
Selected model 2: Matrix ($\Delta\text{AICC} = 0.3$, weight = 0.28)		
Intercept	-0.945 (0.171)	2.15e-05 ***
Matrix	0.346 (0.221)	0.134
Selected model 3: Forest cover + Matrix ($\Delta\text{AICC} = 1.2$, weight = 0.18)		
Intercept	-1.326 (0.307)	0.000373 ***
Forest cover	0.012 (0.008)	0.154893
Matrix	0.397 (0.215)	0.081282 .
Selected model 4: Forest cover ($\Delta\text{AICC} = 1.4$, weight = 0.16)		
Intercept	-1.026 (0.276)	0.00139 **
Forest cover	0.010 (0.009)	0.27489

Tβ of forest associated

Local scale

Selected model 1: Forest cover * Matrix ($\Delta\text{AICC} = 0$, weight = 0.765)		
Intercept	1.731 (0.192)	7.76e-14 ***
Forest cover	-0.012 (0.006)	0.04287 *
Matrix	-0.831 (0.477)	0.08574 .
Forest cover : Matrix	0.043 (0.016)	0.00931 **

Tβ nestedness of forest-associated

Selected model: Null ($\Delta\text{AICC} = 0$, weight = 0.863)		
Intercept	1.261 (0.084)	1.89e-15 ***

Tβ turnover of forest-associated

Selected model: Null ($\Delta\text{AICC} = 0$, weight = 0.907)		
Intercept	-0.456 (0.00006)	<2e-16 ***

Landscape scale

Tβ of forest-associated

Selected model: Matrix ($\Delta\text{AICC} = 0$, weight = 0.8)		
Intercept	0.979 (0.093)	2.44e-09 ***
Matrix	1.405 (0.209)	2.06e-06 ***

Tβ nestedness of forest-associated

Selected model: Matrix ($\Delta\text{AICC} = 0$, weight = 0.835)		
Intercept	0.864 (0.147)	5.46e-05 ***
Matrix	1.209 (0.298)	0.00137 **

Tβ turnover of forest-associated

Selected model: Null ($\Delta\text{AICC} = 0$, weight = 0.668)		
Intercept	-3.402 (0.365)	2.27e-07 ***

Table S3. Model's coefficients for $F\beta$ (functional beta diversity) of forest-generalist and forest-associated species between forest-matrix interfaces (Forest-Matrix), at local and landscape scale. Only models with $\Delta AICc < 2$ are presented.

Functional beta diversity between forest-matrix	Estimate (sd)	p
Local scale		
$F\beta$ of forest-generalist - Bill width		
Selected model: Forest cover ($\Delta AICC = 0$, weight = 0.516)		
Intercept	-0.205 (0.258)	0.4304
Forest cover	0.014 (0.007)	0.0522 .
$F\beta$ nestedness of forest-generalist - Bill width		
Selected model 1: Forest cover ($\Delta AICC = 0$, weight = 0.302)		
Intercept	-0.427 (0.272)	0.1203
Forest cover	0.012 (0.007)	0.0923 .
Selected model 2: Matrix ($\Delta AICC = 0.8$, weight = 0.207)		
Intercept	0.187 (0.186)	0.319
Matrix	-0.375 (0.254)	0.144
Selected model 3: Forest cover + Matrix ($\Delta AICC = 0.8$, weight = 0.206)		
Intercept	-0.208 (0.325)	0.523
Forest cover	0.011 (0.007)	0.143
Matrix	-0.310 (0.257)	0.231
Selected model 4: Null ($\Delta AICC = 1$, weight = 0.186)		
Intercept	-0.016 (0.126)	0.899
$F\beta$ turnover of forest-generalist - Bill width		
Selected model : Matrix ($\Delta AICC = 0$, weight = 0.608)		
Intercept	-2.891 (0.218)	< 2e-16 ***
Matrix	1.026 (0.234)	4.28e-05 ***
$F\beta$ of forest-associated - Bill width		
Selected model: Null ($\Delta AICC = 0$, weight = 1)		
Intercept	-1.895(0.210)	0.000843 ***
$F\beta$ nestedness of forest associated - Bill width		
Selected model 1: Null ($\Delta AICC = 0$, weight = 0.5)		
Intercept	3.490(0.185)	4.71e-05 ***
Selected model 2: Forest cover ($\Delta AICC = 0$, weight = 0.5)		
Intercept	3.490(0.185)	4.71e-05 ***
$F\beta$ of forest-generalist - Mass		
Selected model 1: Null ($\Delta AICC = 0$, weight = 0.509)		
Intercept	-0.340 (0.112)	0.00314 **
Selected model 2: Forest cover ($\Delta AICC = 1.8$, weight = 0.203)		
Intercept	-0.216 (0.236)	0.362
Forest cover	-0.003 (0.006)	0.554
$F\beta$ nestedness of forest-generalist - Mass		
Selected model 1: Null ($\Delta AICC = 0$, weight = 0.463)		

Intercept	-0.458 (0.116)	0.000161 ***
Selected model 2: Forest cover (ΔAICC = 1.5, weight = 0.22)		
Intercept	-0.272 (0.241)	0.263
Forest cover	-0.005 (0.006)	0.392
Fβ turnover of forest-generalist - Mass		
Selected model 1: Null (ΔAICC = 0, weight = 0.443)		
Intercept	-2.595 (0.186)	<2e-16 ***
Selected model 2: Matrix (ΔAICC = 0, weight = 0.375)		
Intercept	-2.760(0.225)	<2e-16 ***
Matrix	0.289(0.218)	0.189
Fβ of forest-associated - Mass		
Selected model: Null (ΔAICC = 0, weight = 0.997)		
Intercept	3.338 (0.243)	8.38e-08 ***
Fβ nestedness of forest-associated - Mass		
Selected model: Null (ΔAICC = 0, weight = 0.997)		
Intercept	3.306 (0.238)	7.36e-08 ***
Fβ turnover of forest-associated - Mass		
Selected model 1: Null (ΔAICC = 0, weight = 0.58)		
Intercept	-5.146 (0.051)	0.0000226 ***
Selected model 2: Forest cover (ΔAICC = 0.6, weight = 0.42)		
Intercept	-6.654(0.104)	0.000289 ***
Forest cover	0.0502(0.003)	0.000000134 ***
Fβ of forest-generalist - Hand-wing index		
Selected model 1: Matrix (ΔAICC = 0, weight = 0.372)		
Intercept	-0.286 (0.163)	0.0838 .
Matrix	0.375 (0.223)	0.0971 .
Selected model 2: Null (ΔAICC = 0, weight = 0.366)		
Intercept	-0.083 (0.110)	0.453
Fβ nestedness of forest-generalist - Hand-wing index		
Selected model: Matrix (ΔAICC = 0, weight = 0.591)		
Intercept	-0.769 (0.174)	0.0000308 ***
Matrix	0.638 (0.231)	0.00725 **
Fβ turnover of forest-generalist- Hand-wing index		
Selected model 1: Forest cover + Matrix (ΔAICC = 0, weight = 0.36)		
Intercept	-2.298 (0.301)	0.000000378 ***
Forest cover	0.011 (0.006)	0.0723 .
Matrix	-0.296 (0.220)	0.1823
Selected model 2: Matrix (ΔAICC = 1, weight = 0.22)		
Intercept	-1.878 (0.190)	0.000000114 ***
Matrix	-0.342 (0.220)	0.124
Selected model 3: Null (ΔAICC = 1.4, weight = 0.17)		
Intercept	-2.053 (0.158)	<0.00000002 ***
Fβ of forest-associated - Hand-wing index		

Selected model: Null (ΔAICC = 0, weight = 0.997)		
Intercept	1.814 (0.187)	0.00000215 ***
Fβ nestedness of forest-associated - Hand-wing index		
Selected model: Null (ΔAICC = 0, weight = 0.997)		
Intercept	1.810 (0.187)	0.0000022 ***
Fβ turnover of forest-associated - Hand-wing index		
Selected model: Null (ΔAICC = 0, weight = 0.998)		
Intercept	-5.204 (0.0001)	<0.00000002 ***
Fβ of forest-generalist - Diet		
Selected model: Null (ΔAICC = 0, weight = 0.544)		
Intercept	0.048 (0.074)	0.518
Fβ nestedness of forest-generalist - Diet		
Selected model: Null (ΔAICC = 0, weight = 0.534)		
Intercept	0.047 (0.074)	0.523
Fβ turnover of forest-generalist - Diet		
Selected model 1: Null (ΔAICC = 0, weight = 0.546)		
Intercept	-2.765 (0.192)	<0.0000002 ***
Selected model 2: Matrix (ΔAICC = 1.9, weight = 0.212)		
Intercept	-2.793 (0.231)	<0.0000002 ***
Matrix	0.048 (0.222)	0.827
Fβ of forest-associated - Diet		
Selected model: Null (ΔAICC = 0, weight = 0.85)		
Intercept	-0.179 (0.057)	0.00458 **
Fβ nestedness of forest-associated -Diet		
Selected model: Null (ΔAICC = 0, weight = 0.85)		
Intercept	-0.179 (0.057)	0.00458 **
Landscape scale		
Fβ of forest-generalist - Bill width		
Selected model 1: Null (ΔAICC = 0, weight = 0.329)		
Intercept	-0.283 (0.255)	0.28
Selected model 2: Forest cover (ΔAICC = 0, weight = 0.329)		
Intercept	-1.306 (0.688)	0.0722 .
Forest cover	0.036 (0.022)	0.1167
Selected model 3: Matrix (ΔAICC = 1.1, weight = 0.19)		
Intercept	0.076 (0.378)	0.842
Matrix	-0.643 (0.508)	0.220
Selected model 4: Forest cover + Matrix (ΔAICC = 1.9, weight = 0.126)		
Intercept	-0.915 (0.782)	0.256
Forest cover	0.032 (0.022)	0.161
Matrix	-0.513 (0.501)	0.318
Fβ nestedness of forest-generalist - Bill width		
Selected model 1: Null (ΔAICC = 0, weight = 0.344)		
Intercept	-0.297 (0.258)	0.263
Selected model 2: Forest cover (ΔAICC = 0.1, weight = 0.328)		
Intercept	-1.312 (0.694)	0.0733 .

Forest cover	0.035 (0.022)	0.1228
Selected model 3: Matrix (ΔAICC = 1.2, weight = 0.185)		
Intercept	0.049 (0.383)	0.899
Matrix	-0.620 (0.515)	0.242
Fβ turnover of forest-generalist - Bill width		
Selected model 1: Null (ΔAICC = 0, weight = 0.558)		
Intercept	-4.038 (0.172)	0.00000005 ***
Selected model 2: Matrix (ΔAICC = 1.6 weight = 0.252)		
Intercept	-4.367 (0.346)	0.000115 ***
Matrix	0.419 (0.373)	0.276
Fβ of forest-associated - Bill width		
Selected model: Null (ΔAICC = 0, weight = 0.83)		
Intercept	2.505 (0.389)	0.000202 ***
Fβ nestedness of forest-associated - Bill width		
Selected model: Null (ΔAICC = 0, weight = 0.83)		
Intercept	2.505 (0.389)	0.000202 ***
Fβ of forest-generalist - Mass		
Selected model 1: Null (ΔAICC = 0, weight = 0.542)		
Intercept	-0.713 (0.191)	0.00127 **
Selected model 2: Matrix (ΔAICC = 1.8, weight = 0.219)		
Intercept	-0.912 (0.289)	0.005 **
Matrix	0.344 (0.372)	0.366
Fβ nestedness of forest-generalist - Mass		
Selected model: Null (ΔAICC = 0, weight = 0.591)		
Intercept	-0.809 (0.205)	0.000741 ***
Fβ turnover of forest-generalist - Mass		
Selected model 1: Matrix (ΔAICC = 0, weight = 0.523)		
Intercept	-5.553 (0.431)	0.00000337 ***
Matrix	0.856 (0.417)	0.0561 .
Selected model 2: Null (ΔAICC = 1.1, weight = 0.306)		
Intercept	-4.997 (0.339)	0.0000177 ***
Fβ of forest-associated - Mass		
Selected model: Null (ΔAICC = 0, weight = 0.89)		
Intercept	4.117 (0.303)	0.000000827 ***
Fβ nestedness of forest-associated - Mass		
Selected model: Null (ΔAICC = 0, weight = 0.89)		
Intercept	4.117 (0.303)	0.000000827 ***
Fβ of forest-generalist - Hand-wing index		
Selected model 1: Null (ΔAICC = 0, weight = 0.406)		
Intercept	-0.901 (0.244)	0.00136 **
Selected model 2: Matrix (ΔAICC = 0.6, weight = 0.3)		
Intercept	-1.280 (0.359)	0.00195 **
Matrix	0.646 (0.446)	0.16324

Fβ nestedness of forest-generalist - Hand-wing index		
Selected model 1: Null (ΔAICC = 0, weight = 0.382)		
Intercept	-0.982 (0.263)	0.00123 **
Selected model 2: Matrix (ΔAICC = 0.2, weight = 0.338)		
Intercept	-1.412 (0.380)	0.00137 **
Matrix	0.731 (0.465)	0.13181
Fβ turnover of forest-generalist - Hand-wing index		
Selected model: Null (ΔAICC = 0, weight = 0.625)		
Intercept	-3.706 (0.282)	0.0000552 ***
Fβ of forest-associated - Hand-wing index		
Selected model: Null (ΔAICC = 0, weight = 0.76)		
Intercept	1.895 (0.223)	0.0000281 ***
Fβ nestedness of forest-associated - Hand-wing index		
Selected model: Null (ΔAICC = 0, weight = 0.77)		
Intercept	1.878 (0.224)	0.000032 ***
Fβ turnover of forest-associated - Hand-wing index		
Selected model: Null (ΔAICC = 0, weight = 0.89)		
Intercept	-5.019 (0.159)	0.000000112 ***
Fβ of forest-generalist - Diet		
Selected model 1: Forest cover (ΔAICC = 0, weight = 0.68)		
Intercept	0.098 (0.059)	0.11308
Forest cover	-0.009 (0.002)	0.00499 **
Selected model 2: Null (ΔAICC = 1.5, weight = 0.32)		
Intercept	-0.069 (0.056)	0.235
Fβ nestedness of forest-generalist - Diet		
Selected model 1: Forest cover (ΔAICC = 0, weight = 0.68)		
Intercept	0.098 (0.059)	0.11308
Forest cover	-0.009 (0.002)	0.00499 **
Selected model 2: Null (ΔAICC = 1.5, weight = 0.32)		
Intercept	-0.069 (0.056)	0.235
Fβ of forest-associated - Diet		
Selected model: Null (ΔAICC = 0, weight = 0.85)		
Intercept	-2.082 (0.098)	0.0000261 ***
Fβ nestedness of forest-associated- Diet		
Selected model: Null (ΔAICC = 0, weight = 0.85)		
Intercept	-2.082 (0.098)	0.0000261 ***

Table S4. Model's coefficients for T β (taxonomic beta diversity) of forest-generalist and forest-associated species between forest patches, at local and landscape scale. Only models with $\Delta AICc < 2$ are presented.

Taxonomic beta diversity between forest patches		
	Estimate (sd)	p
Local scale		
Tβ of forest-generalist		
Selected model: Matrix ($\Delta AICc = 0$, weight = 0.646)		
Intercept	-0.193 (0.038)	1.38e-06 ***
Matrix	0.509 (0.050)	< 2e-16 ***
Tβ nestedness of forest-generalist		
Selected model 1: Matrix ($\Delta AICc = 0$, weight = 0.495)		
Intercept	-2.598 (0.113)	< 2e-16 ***
Matrix	0.491 (0.133)	0.000329 ***
Selected model 2: Forest cover + Matrix ($\Delta AICc = 1.3$, weight = 0.259)		
Intercept	-2.390 (0.198)	< 2e-16 ***
Forest cover	-0.006 (0.005)	0.210528
Matrix	0.461 (0.134)	0.000825 ***
Tβ turnover of forest-generalist		
Selected model 1: Matrix ($\Delta AICc = 0$, weight = 0.373)		
Intercept	-0.408 (0.057)	8.49e-11 ***
Matrix	0.263 (0.075)	0.000704 ***
Selected model 2: Null ($\Delta AICc = 0.7$, weight = 0.269)		
Intercept	-0.259 (0.037)	1.74e-10 ***
Selected model 3: Forest cover + Matrix ($\Delta AICc = 1.5$, weight = 0.179)		
Intercept	-0.570 (0.115)	2.39e-06 ***
Forest cover	0.005 (0.003)	0.106368
Matrix	0.290 (0.077)	0.000288 ***
Landscape scale		
Tβ of forest-generalist		
Selected model 1: Matrix ($\Delta AICc = 0$, weight = 0.635)		
Intercept	0.265 (0.060)	0.000296 ***
Matrix	0.449 (0.082)	2.6e-05 ***
Selected model 2: Forest cover + Matrix ($\Delta AICc = 1.6$, weight = 0.291)		
Intercept	0.145 (0.116)	0.227
Forest cover	0.004 (0.003)	0.245
Matrix	0.468 (0.081)	1.65e-05 ***
Tβ nestedness of forest-generalist		
Selected model 1: Matrix ($\Delta AICc = 0$, weight = 0.568)		
Intercept	-2.864 (0.192)	2.73e-12 ***
Matrix	0.580 (0.228)	0.0194 *
Selected model 2: Forest cover * Matrix ($\Delta AICc = 1.6$, weight = 0.25)		
Intercept	-3.018 (0.449)	2.73e-06 ***
Forest cover	0.004 (0.013)	0.7718
Matrix	1.339 (0.529)	0.0209 *
Forest cover : Matrix	-0.028 (0.017)	0.1199
Tβ turnover of forest-generalist		

Selected model 1: Forest cover + Matrix ($\Delta AICC = 0$, weight = 0.41)

Intercept	-0.159 (0.137)	0.26186
Forest cover	0.007 (0.003)	0.08475 .
Matrix	0.290 (0.096)	0.00716 **

Selected model 2: Matrix ($\Delta AICC = 0.1$, weight = 0.381)

Intercept	0.055 (0.075)	0.4686
Matrix	0.257 (0.100)	0.0191 *

Local scale**T β of forest-associated****Selected model 1: Matrix ($\Delta AICC = 0$, weight = 0.567)**

Intercept	-0.660 (0.057)	< 2e-16 ***
Matrix	0.471 (0.074)	3.88e-09 ***

Selected model 2: Forest cover + Matrix ($\Delta AICC = 1.6$, weight = 0.251)

Intercept	-0.568 (0.112)	1.47e-06 ***
Forest cover	-0.002 (0.003)	0.349
Matrix	0.456 (0.076)	2.15e-08 ***

T β nestedness of forest-associated**Selected model 1: Matrix ($\Delta AICC = 0$, weight = 0.584)**

Intercept	-2.201 (0.115)	< 2e-16 ***
Matrix	0.534 (0.135)	0.000128 ***

Selected model 2: Forest cover + Matrix ($\Delta AICC = 1.5$, weight = 0.280)

Intercept	-2.067 (0.196)	< 2e-16 ***
Forest cover	-0.004 (0.005)	0.404627
Matrix	0.522 (0.136)	0.000189 ***

T β turnover of forest-associated**Selected model 1: Matrix ($\Delta AICC = 0$, weight = 0.439)**

Intercept	-1.073 (0.064)	<2e-16 ***
Matrix	0.207 (0.083)	0.0141 *

Selected model 2: Forest cover + Matrix ($\Delta AICC = 1$, weight = 0.27)

Intercept	-1.195 (0.129)	5.01e-16 ***
Forest cover	0.0039 (0.0036)	0.27482
Matrix	0.229 (0.086)	0.00848 **

Selected model 3: Forest cover * Matrix ($\Delta AICC = 1.9$, weight = 0.168)

Intercept	-1.073 (0.169)	3.53e-09 ***
Forest cover	-0.00005 (0.005)	0.992
Matrix	0.004 (0.220)	0.983
Forest cover : Matrix	0.008 (0.007)	0.270

Landscape scale**T β of forest-associated****Selected model: Matrix ($\Delta AICC = 0$, weight = 0.752)**

Intercept	-0.171 (0.050)	0.00274 **
Matrix	0.379 (0.066)	1.48e-05 ***

T β nestedness of forest-associated**Selected model 1: Matrix ($\Delta AICC = 0$, weight = 0.434)**

Intercept	-2.268 (0.134)	2.8e-13 ***
Matrix	0.620 (0.163)	0.0011 **

Selected model 2: Forest cover + Matrix ($\Delta AICC = 1.3$, weight = 0.308)

Intercept	-2.052 (0.209)	7.53e-09 ***
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Forest cover	-0.007 (0.005)	0.20907
Matrix	0.598 (0.158)	0.00131 **
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Tβ turnover of forest-associated		
Selected model 1: Matrix (ΔAICC = 0, weight = 0.436)		
Intercept	0.359 (0.013)	<2e-16 ***
Matrix	0.034 (0.018)	0.0732 .
Selected model 2: Null (ΔAICC = 0.7, weight = 0.315)		
Intercept	0.378 (0.009)	<2e-16 ***
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Table S5. Model's coefficients for $F\beta$ (functional beta diversity) of forest-generalist and forest-associated species between forest patches, at local and landscape scale. Only models with $\Delta AICc < 2$ are presented.

Functional beta diversity between forest patches	Estimate (sd)	p
Local scale		
<u>Fβ of forest-generalist - Bill width</u>		
Selected model 1: Null ($\Delta AICc = 0$, weight = 0.382)		
Intercept	-0.193 (0.095)	0.0449 *
Selected model 2: Forest cover ($\Delta AICc = 0.8$, weight = 0.258)		
Intercept	0.107 (0.241)	0.657
Forest cover	-0.011 (0.008)	0.177
Selected model 3: Matrix ($\Delta AICc = 1.6$, weight = 0.169)		
Intercept	-0.124 (0.144)	0.392
Matrix	-0.122 (0.192)	0.524
<u>Fβ nestedness of forest-generalist - Bill width</u>		
Selected model 1: Forest cover ($\Delta AICc = 0$, weight = 0.405)		
Intercept	-0.079 (0.245)	0.7476
Forest cover	-0.014 (0.008)	0.0888 .
Selected model 2: Null ($\Delta AICc = 0.7$, weight = 0.287)		
Intercept	-0.465 (0.100)	7.75e-06 ***
<u>Fβ turnover of forest-generalist Bill width</u>		
Selected model: Null ($\Delta AICc = 0$, weight = 0.598)		
Intercept	-2.638 (0.090)	<2e-16 ***
<u>Fβ of forest-associated - Bill width</u>		
Selected model 1: Forest cover ($\Delta AICc = 0$, weight = 0.457)		
Intercept	0.194 (0.211)	0.36
Forest cover	-0.024 (0.005)	4.06e-05 ***
Selected model 2: Forest cover + Matrix ($\Delta AICc = 1.5$, weight = 0.213)		
Intercept	-0.146 (0.254)	0.564081
Forest cover	-0.022 (0.005)	0.000171 ***
Matrix	0.493 (0.172)	0.005126 **
Selected model 3: Null ($\Delta AICc = 1.9$, weight = 0.173)		
Intercept	-0.666 (0.086)	4.4e-12 ***
<u>Fβ nestedness of forest-associated - Bill width</u>		
Selected model: Forest cover ($\Delta AICc = 0$, weight = 0.669)		
Intercept	-0.153 (0.210)	0.467
Forest cover	-0.024 (0.005)	4.79e-05 ***
<u>Fβ turnover of forest-associated - Bill width</u>		
Selected model 1: Null ($\Delta AICc = 0$, weight = 0.356)		
Intercept	-2.663 (0.089)	<2e-16 ***
Selected model 2: Forest cover * Matrix ($\Delta AICc = 0$, weight = 0.356)		
Intercept	-1.949 (0.307)	4.90e-09 ***
Forest cover	-0.030 (0.008)	0.000189 ***

Matrix	-1.184 (0.375)	0.002071 **
Forest cover : Matrix	0.053 (0.010)	5.52e-07 ***
Fβ of forest-generalist - Mass		
Selected model 1: Null (ΔAICC = 0, weight = 0.515)		
Intercept	-0.947 (0.084)	<2e-16 ***
Selected model 2: Matrix (ΔAICC = 1.5, weight = 0.244)		
Intercept	-0.805 (0.121)	8.98e-10 ***
Matrix	-0.252 (0.159)	0.117
Fβ nestedness of forest-generalist - Mass		
Selected model 1: Null (ΔAICC = 0, weight = 0.407)		
Intercept	-1.080 (0.090)	<2e-16 ***
Selected model 2: Matrix (ΔAICC = 0.4, weight = 0.335)		
Intercept	-0.892 (0.126)	9.94e-11 ***
Matrix	-0.337 (0.166)	0.0441 *
Fβ turnover of forest-generalist - Mass		
Selected model: Null (ΔAICC = 0, weight = 0.584)		
Intercept	-3.758 (0.089)	<2e-16 ***
Fβ of forest-associated - Mass		
Selected model 1: Matrix (ΔAICC = 0, weight = 0.304)		
Intercept	0.137 (0.156)	0.38177
Matrix	0.553 (0.210)	0.00965 **
Selected model 2: Forest cover + Matrix (ΔAICC = 0.1, weight = 0.286)		
Intercept	0.641 (0.309)	0.0403 *
Forest cover	-0.013 (0.006)	0.0623 .
Matrix	0.480 (0.213)	0.0261 *
Selected model 3: Forest cover (ΔAICC = 0.9, weight = 0.196)		
Intercept	1.013 (0.264)	0.000196 ***
Forest cover	-0.015 (0.006)	0.021127 *
Selected model 4: Null (ΔAICC = 1.7, weight = 0.128)		
Intercept	0.450 (0.106)	4.2e-05 ***
Fβ nestedness of forest-associated - Mass		
Selected model 1: Null (ΔAICC = 0, weight = 0.457)		
Intercept	0.139 (0.100)	0.168
Selected model 2: Forest cover (ΔAICC = 1.1, weight = 0.265)		
Intercept	0.522 (0.255)	0.0431 *
Forest cover	-0.010 (0.006)	0.1060
Fβ turnover of forest-associated - Mass		
Selected model 1: Matrix (ΔAICC = 0, weight = 0.42)		
Intercept	-2.719 (0.180)	< 2e-16 ***
Matrix	0.716 (0.184)	0.000159 ***
Selected model 2: Forest cover + Matrix (ΔAICC = 0.4, weight = 0.34)		
Intercept	-2.422 (0.285)	3.58e-14 ***
Forest cover	-0.008 (0.006)	0.185319
Matrix	0.705 (0.184)	0.000202 ***
Selected model 3: Forest cover * Matrix (ΔAICC = 1.1, weight = 0.24)		

Intercept	-2.790 (0.425)	1.17e-09 ***
Forest cover	0.001 (0.010)	0.9046
Matrix	1.269 (0.505)	0.0133 *
Forest cover : Matrix	-0.015 (0.012)	0.2295

F β of forest-generalist - Hand-wing index

Selected model 1: Null (Δ AICC = 0, weight = 0.274)

Intercept	-0.970 (0.086)	<2e-16 ***
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Selected model 2: Matrix (Δ AICC = 0,1 weight = 0.266)

Intercept	-1.179 (0.130)	2.41e-15 ***
Matrix	0.369 (0.164)	0.0266 *

Selected model 3: Forest cover (Δ AICC = 0,3 weight = 0.238)

Intercept	-0.591 (0.204)	0.00463 **
Forest cover	-0.014 (0.007)	0.04507 *

Selected model 4: Forest cover + Matrix (Δ AICC = 1 weight = 0.168)

Intercept	-0.848 (0.241)	0.000618 ***
Forest cover	-0.011 (0.007)	0.107678
Matrix	0.328 (0.165)	0.049976 *

F β nestedness of forest-generalist - Hand-wing index

Selected model 1: Matrix (Δ AICC = 0, weight = 0.32)

Intercept	-1.456 (0.145)	<2e-16 ***
Matrix	0.378 (0.176)	0.0344 *

Selected model 2: Forest cover + Matrix (Δ AICC = 0.8, weight = 0.219)

Intercept	-1.139 (0.266)	3.72e-05 ***
Forest cover	-0.010 (0.007)	0.1615
Matrix	0.338 (0.179)	0.0608 .

Selected model 3: Null (Δ AICC = 0.9, weight = 0.209)

Intercept	-1.240 (0.100)	<2e-16 ***
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Selected model 4: Forest cover (Δ AICC = 1.2, weight = 0.176)

Intercept	-0.879 (0.226)	0.000166 ***
Forest cover	-0.013 (0.007)	0.081646 .

F β turnover of forest-generalist - Hand-wing index

Selected model 1: Matrix (Δ AICC = 0, weight = 0.35)

Intercept	-3.223 (0.136)	<2e-16 ***
Matrix	0.289 (0.153)	0.061 .

Selected model 2: Null (Δ AICC = 0.4, weight = 0.28)

Intercept	-3.060 (0.099)	<2e-16 ***
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Selected model 3: Forest cover * Matrix (Δ AICC = 1.8, weight = 0.14)

Intercept	-3.057 (0.274)	<2e-16 ***
Forest cover	-0.005 (0.008)	0.488
Matrix	-0.220 (0.360)	0.541
Forest cover : Matrix	0.019 (0.011)	0.112

Selected model 4: Forest cover + Matrix (Δ AICC = 1.9, weight = 0.13)

Intercept	-3.314 (0.225)	<2e-16 ***
Forest cover	0.003 (0.005)	0.6034
Matrix	0.302 (0.156)	0.0552 .

F β of forest-associated – Hand-wing index

Selected model 1: Matrix (Δ AICC = 0 weight = 0.448)

Intercept	-0.665 (0.146)	1.22e-05 ***
Matrix	0.451 (0.190)	0.0193 *

Selected model 2: Forest cover + Matrix (Δ AICC = 0.9, weight = 0.281)

Intercept	-0.390 (0.287)	0.1767
Forest cover	-0.007 (0.006)	0.2707
Matrix	0.409 (0.194)	0.0367 *

F β nestedness of forest-associated – Hand-wing index

Selected model 1: Matrix (Δ AICC = 0 weight = 0.32)

Interface	-0.904 (0.147)	9.19e-09 ***
Matrix	0.274 (0.187)	0.147

Selected model 2: Null (Δ AICC = 0 weight = 0.32)

Intercept	-0.746 (0.099)	7.6e-12 ***
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Selected model 3: Forest cover (Δ AICC = 1.2, weight = 0.17)

Intercept	-0.537 (0.241)	0.0275 *
Forest cover	-0.005 (0.006)	0.3458

Selected model 4: Forest cover + Matrix (Δ AICC = 1.7, weight = 0.14)

Intercept	-0.738 (0.284)	0.0106 *
Forest cover	-0.004 (0.006)	0.4980
Matrix	0.249 (0.191)	0.1948

F β turnover of forest-associated – Hand-wing index

Selected model 1: Matrix (Δ AICC = 0 weight = 0.389)

Intercept	-2.545 (0.163)	< 2e-16 ***
Matrix	0.747 (0.183)	8.35e-05 ***

Selected model 2: Null (Δ AICC = 1 weight = 0.241)

Intercept	-2.140 (0.111)	<2e-16 ***
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Selected model 3: Forest cover + Matrix (Δ AICC = 1.6, weight = 0.177)

Intercept	-2.153 (0.281)	6.37e-12 ***
Forest cover	-0.010 (0.006)	0.101719
Matrix	0.683 (0.184)	0.000337 ***

Selected model 4: Forest cover (Δ AICC = 1.9, weight = 0.15)

Intercept	-1.660 (0.235)	1.43e-10 ***
Forest cover	-0.013 (0.006)	0.0268 *

F β of forest-generalist - Diet

Selected model 1: Null (Δ AICC = 0 weight = 0.549)

Intercept	-2.684 (0.132)	<2e-16 ***
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Selected model 2: Matrix (Δ AICC = 1.7 weight = 0.229)

Intercept	-2.787 (0.167)	<2e-16 ***
Matrix	0.183 (0.169)	0.281

F β nestedness of forest-generalist – Diet

Selected model 1: Null (Δ AICC = 0 weight = 0.549)

Intercept	-2.684 (0.132)	<2e-16 ***
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Selected model 2: Matrix (Δ AICC = 1.7 weight = 0.229)

Intercept	-2.787 (0.167)	<2e-16 ***
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Matrix	0.183 (0.169)	0.281
Fβ of forest-associated - Diet		
Selected model: Forest cover (ΔAICC = 0, weight = 0.588)		
Intercept	-0.551 (0.118)	8.36e-06 ***
Forest cover	-0.011 (0.003)	0.000443 ***
Fβ nestedness of forest-associated - Diet		
Selected model: Forest cover (ΔAICC = 0, weight = 0.687)		
Intercept	-0.611 (0.105)	6.13e-08 ***
Forest cover	-0.014 (0.002)	2.28e-06 ***
Fβ turnover of forest-associated - Diet		
Selected model 1: Null (ΔAICC = 0, weight = 0.376)		
Intercept	-3.003 (0.136)	<2e-16 ***
Selected model 2: Matrix (ΔAICC = 0.8, weight = 0.252)		
Intercept	-3.078 (0.168)	<2e-16 ***
Matrix	0.131 (0.167)	0.434
Selected model 3: Forest cover (ΔAICC = 1.1, weight = 0.214)		
Intercept	-2.924 (0.234)	<2e-16 ***
Forest cover	-0.002 (0.005)	0.684
Landscape scale		
Fβ of forest-generalist - Bill width		
Selected model: Null (ΔAICC = 0, weight = 0.608)		
Intercept	0.231 (0.138)	0.109
Fβ nestedness of forest-generalist - Bill width		
Selected model: Null (ΔAICC = 0, weight = 0.597)		
Intercept	-0.101 (0.134)	0.461
Fβ turnover of forest-generalist - Bill width		
Selected model: Null (ΔAICC = 0, weight = 0.608)		
Intercept	-2.390 (0.170)	4.04e-12 ***
Fβ of forest-associated - Bill width		
Selected model 1: Forest cover (ΔAICC = 0, weight = 0.397)		
Intercept	0.403 (0.350)	0.2629
Forest cover	-0.028 (0.012)	0.0315 *
Selected model 2: Forest cover + Matrix (ΔAICC = 0.8, weight = 0.27)		
Intercept	0.087 (0.396)	0.8275
Forest cover	-0.025 (0.011)	0.0445 *
Matrix	0.419 (0.277)	0.1471
Fβ nestedness of forest-associated - Bill width		
Selected model 1: Null (ΔAICC = 0, weight = 0.366)		
Intercept	-0.711 (0.129)	1.94e-05 ***
Selected model 2: Forest cover (ΔAICC = 0.1, weight = 0.351)		
Intercept	-0.250 (0.304)	0.420
Forest cover	-0.017 (0.010)	0.119
Selected model 3: Matrix (ΔAICC = 1.7, weight = 0.154)		
Intercept	-0.855 (0.196)	0.000309 ***

Matrix	0.249 (0.255)	0.340984
Fβ turnover of forest-associated - Bill width		
Selected model 1: Forest cover + Matrix (ΔAICC = 0 weight = 0.389)		
Intercept	-2.261 (0.415)	3e-05 ***
Forest cover	-0.026 (0.012)	0.0569 .
Matrix	0.645 (0.296)	0.0424 *
Selected model 2: Matrix (ΔAICC = 0.9 weight = 0.249)		
Intercept	-2.937 (0.273)	9.26e-10 ***
Matrix	0.676 (0.312)	0.0427 *
Selected model 3: Forest cover (ΔAICC = 1.6 weight = 0.171)		
Intercept	-1.786 (0.380)	0.000138 ***
Forest cover	-0.028 (0.014)	0.059995 .
Fβ of forest-generalist - Mass		
Selected model 1: Null (ΔAICC = 0 weight = 0.555)		
Intercept	-0.471 (0.125)	0.00117 **
Selected model 2: Matrix (ΔAICC = 1.8 weight = 0.231)		
Intercept	-0.338 (0.184)	0.0812 .
Matrix	-0.238 (0.247)	0.3471
Fβ nestedness of forest-generalist - Mass		
Selected model 1: Null (ΔAICC = 0 weight = 0.484)		
Intercept	-0.639 (0.130)	7.37e-05 ***
Selected model 2: Matrix (ΔAICC = 1 weight = 0.298)		
Intercept	-0.454 (0.185)	0.0237 *
Matrix	-0.333 (0.251)	0.1987
Fβ turnover of forest-generalist - Mass		
Selected model 1: Null (ΔAICC = 0 weight = 0.538)		
Intercept	-3.186 (0.195)	2.12e-13 ***
Selected model 2: Matrix (ΔAICC = 1.6 weight = 0.244)		
Intercept	-3.389 (0.281)	1.27e-10 ***
Matrix	0.337 (0.325)	0.312
Fβ of forest-associated - Mass		
Selected model 1: Forest cover (ΔAICC = 0 weight = 0.461)		
Intercept	1.975 (0.478)	0.000526 ***
Forest cover	-0.044 (0.015)	0.010218 *
Selected model 2: Forest cover + Matrix (ΔAICC = 1.4 weight = 0.225)		
Intercept	1.553 (0.576)	0.0143 *
Forest cover	-0.040 (0.016)	0.0227 *
Matrix	0.518 (0.410)	0.2223
Selected model 3: Forest cover * Matrix (ΔAICC = 1.5 weight = 0.216)		
Intercept	0.620 (0.715)	0.3971
Forest cover	-0.008 (0.022)	0.6942
Matrix	2.101 (0.931)	0.0367 *
Forest cover : Matrix	-0.0564 (0.0303)	0.0794 .
Fβ nestedness of forest-associated - Mass		
Selected model: Forest cover (ΔAICC = 0 weight = 0.544)		

Intercept	1.276 (0.428)	0.00738 **
Forest cover	-0.032 (0.014)	0.03660 *
Fβ turnover of forest-associated - Mass		
Selected model: Matrix (ΔAICC = 0 weight = 0.752)		
Intercept	-3.375 (0.331)	2.28e-09 ***
Forest cover	1.110 (0.355)	0.00536 **
Fβ of forest-generalist - Hand-wing index		
Selected model: Matrix (ΔAICC = 0 weight = 0.671)		
Intercept	-1.041 (0.199)	4.17e-05 ***
Matrix	0.678 (0.253)	0.0145 *
Fβ nestedness of forest-generalist - Hand-wing index		
Selected model 1: Matrix (ΔAICC = 0 weight = 0.503)		
Intercept	-1.407 (0.252)	1.85e-05 ***
Matrix	0.701 (0.312)	0.0365 *
Fβ turnover of forest-generalist - Hand-wing index		
Selected model 1: Null (ΔAICC = 0, weight = 0.32)		
Intercept	-2.594 (0.099)	<2e-16 ***
Selected model 2: Forest cover + Matrix (ΔAICC = 0.8, weight = 0.21)		
Intercept	-3.161 (0.275)	5.48e-10 ***
Forest cover	0.013 (0.007)	0.0848 .
Matrix	0.338 (0.184)	0.0818 .
Selected model 3: Matrix (ΔAICC = 0.9, weight = 0.21)		
Intercept	-2.743 (0.150)	6.19e-14 ***
Matrix	0.251 (0.188)	0.197
Selected model 4: Forest cover (ΔAICC = 1.1, weight = 0.19)		
Intercept	-2.858 (0.231)	8.28e-11 ***
Forest cover	0.009 (0.007)	0.215
Fβ of forest-associated - Hand-wing index		
Selected model: Matrix (ΔAICC = 0, weight = 0.574)		
Intercept	-0.231 (0.177)	0.208
Matrix	0.613 (0.237)	0.018 *
Fβ nestedness of forest-associated - Hand-wing index		
Selected model: Null (ΔAICC = 0, weight = 0.521)		
Intercept	-0.366 (0.130)	0.0105 *
Fβ turnover of forest-associated - Hand-wing index		
Selected model 1: Null (ΔAICC = 0, weight = 0.48)		
Intercept	-1.969 (0.235)	3.87e-08 ***
Selected model 2: Matrix (ΔAICC = 1.2, weight = 0.268)		
Intercept	-2.253 (0.333)	1.44e-06 ***
Matrix	0.469 (0.383)	0.235
Fβ of forest-generalist - Diet		

Selected model: Null ($\Delta\text{AICC} = 0$, weight = 0.594)		
Intercept	-2.544 (0.328)	1.38e-07 ***
Fβ nestedness of forest-generalist - Diet		
Selected model: Null ($\Delta\text{AICC} = 0$, weight = 0.8)		
Intercept	-0.815 (0.027)	<2e-16 ***
Fβ of forest-associated - Diet		
Selected model 1: Null ($\Delta\text{AICC} = 0$, weight = 0.460)		
Intercept	-1.887 (0.211)	2.12e-08 ***
Selected model 2: Forest cover ($\Delta\text{AICC} = 1$, weight = 0.279)		
Intercept	-1.441 (0.358)	0.000725 ***
Forest cover	-0.018 (0.013)	0.178120
Selected model 3: Matrix ($\Delta\text{AICC} = 1.7$, weight = 0.192)		
Intercept	-2.168 (0.334)	3.24e-06 ***
Matrix	0.440 (0.398)	0.283
Fβ nestedness of forest-associated - Diet		
Selected model: Forest cover ($\Delta\text{AICC} = 0$, weight = 0.750)		
Intercept	-1.910 (0.090)	1.25e-14 ***
Forest cover	-0.013 (0.003)	0.000886 ***
Fβ turnover of forest-associated - Diet		
Selected model: Null ($\Delta\text{AICC} = 0$, weight = 0.601)		
Intercept	-3.890 (0.285)	6.6e-12 ***

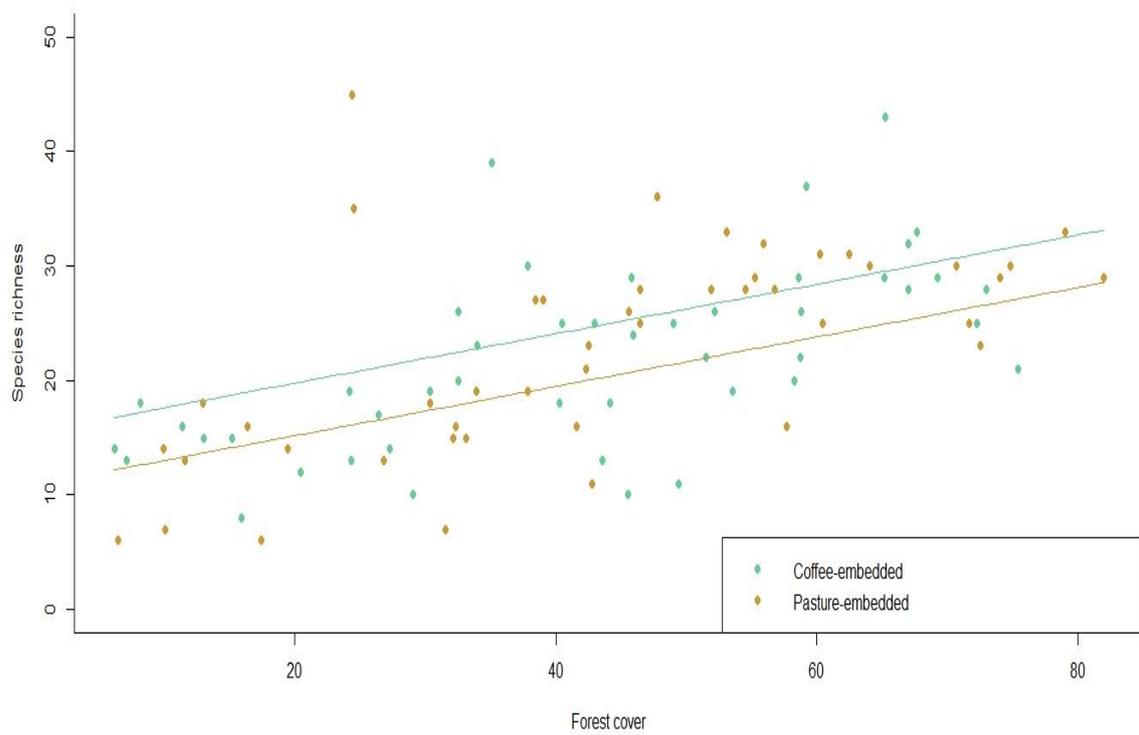


Figure S2: Local scale forest-associated species richness at coffee-embedded and pasture-embedded landscapes across a forest cover gradient.

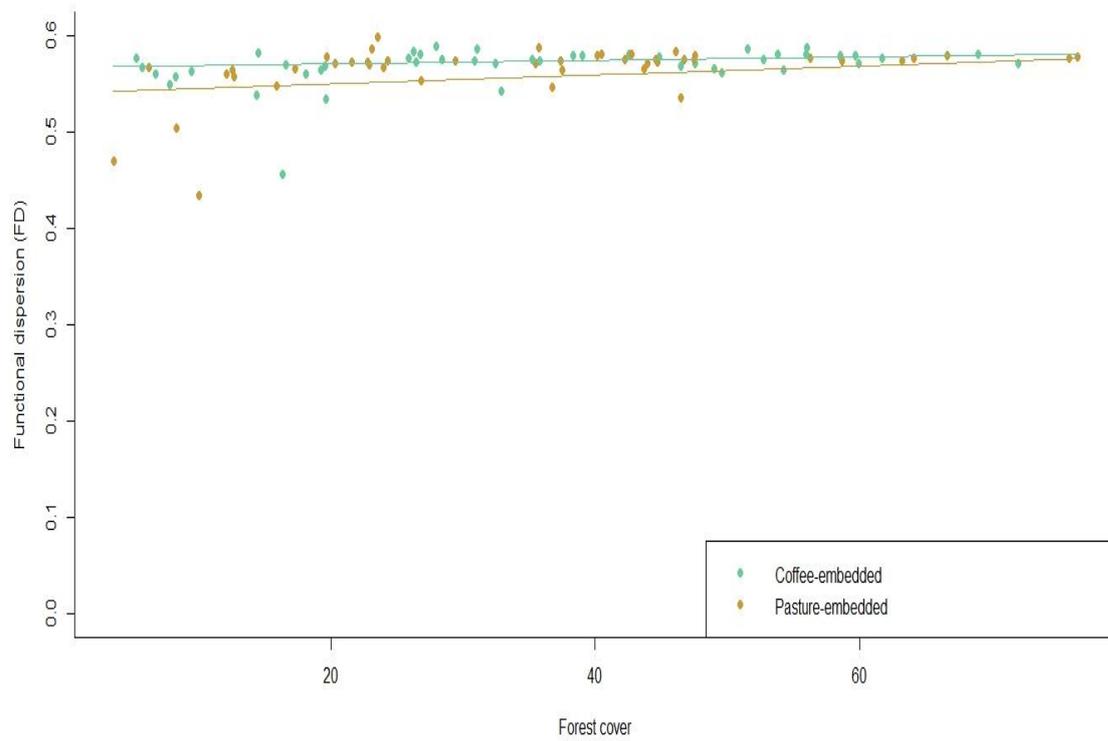


Figure S3: Functional dispersion of forest-associated species at coffee-embedded and pasture-embedded landscapes across a forest cover gradient.

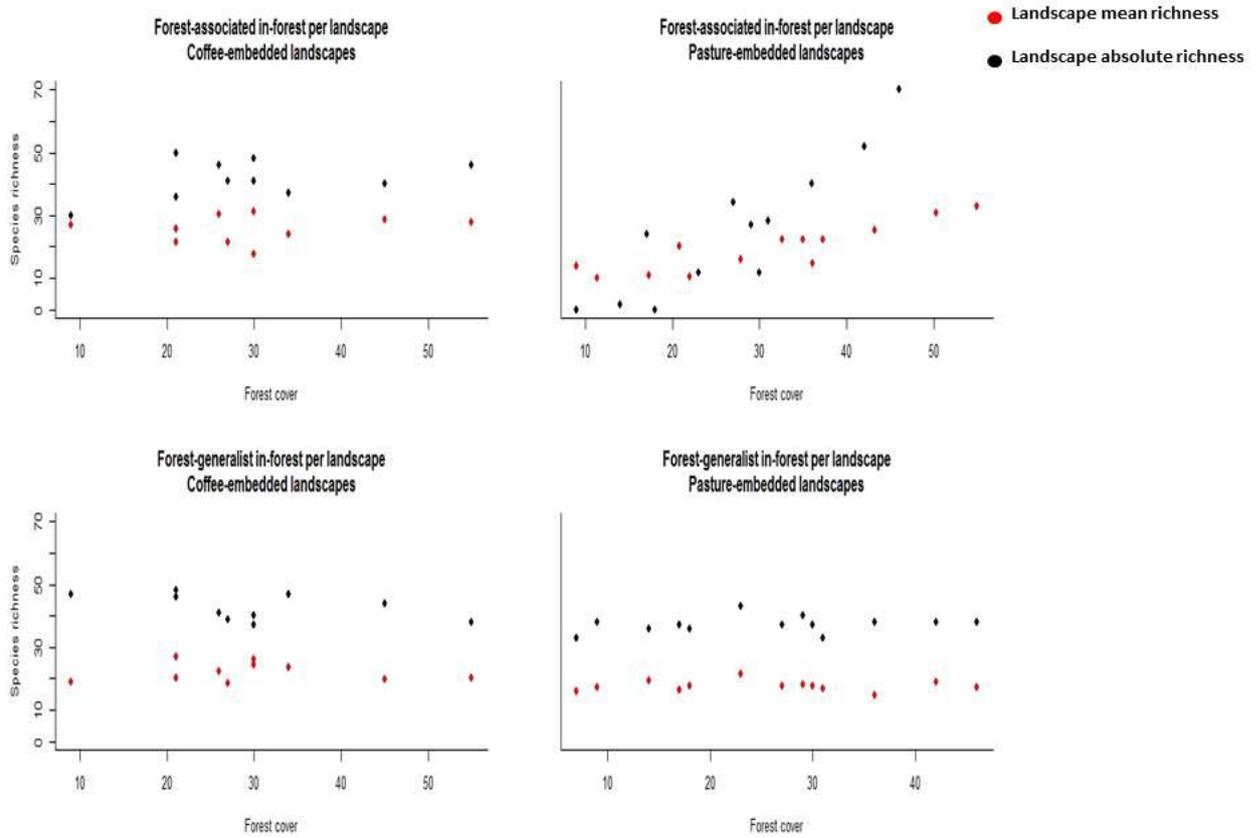


Figure S4: Landscape mean and absolute species richness in-forest for forest-associated and forest-generalist species at coffee-embedded and pasture-embedded landscapes across a forest cover gradient.

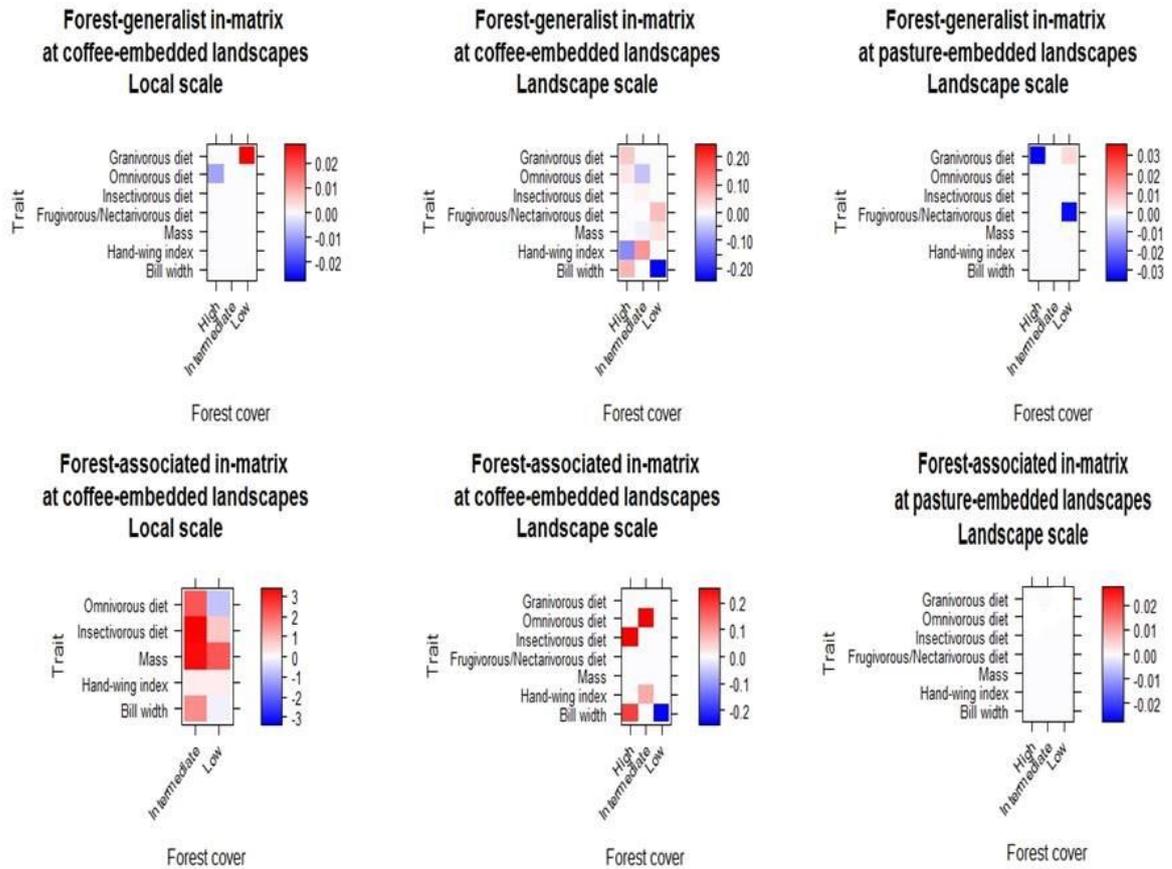


Figure S5: Fourth corner analysis for forest-generalist and forest-associated species in-matrix at local and landscape scale for diet (granivorous, omnivorous, insectivorous and frugivorous/nectarivorous), mass, hand-wing index and bill width, according to forest cover amount (high, intermediate and low) at coffee-embedded and pasture-embedded landscapes. Positive coefficients (i.e. red) and negative coefficients (i.e. blue) describe the increase and decrease of ecological traits, respectively.

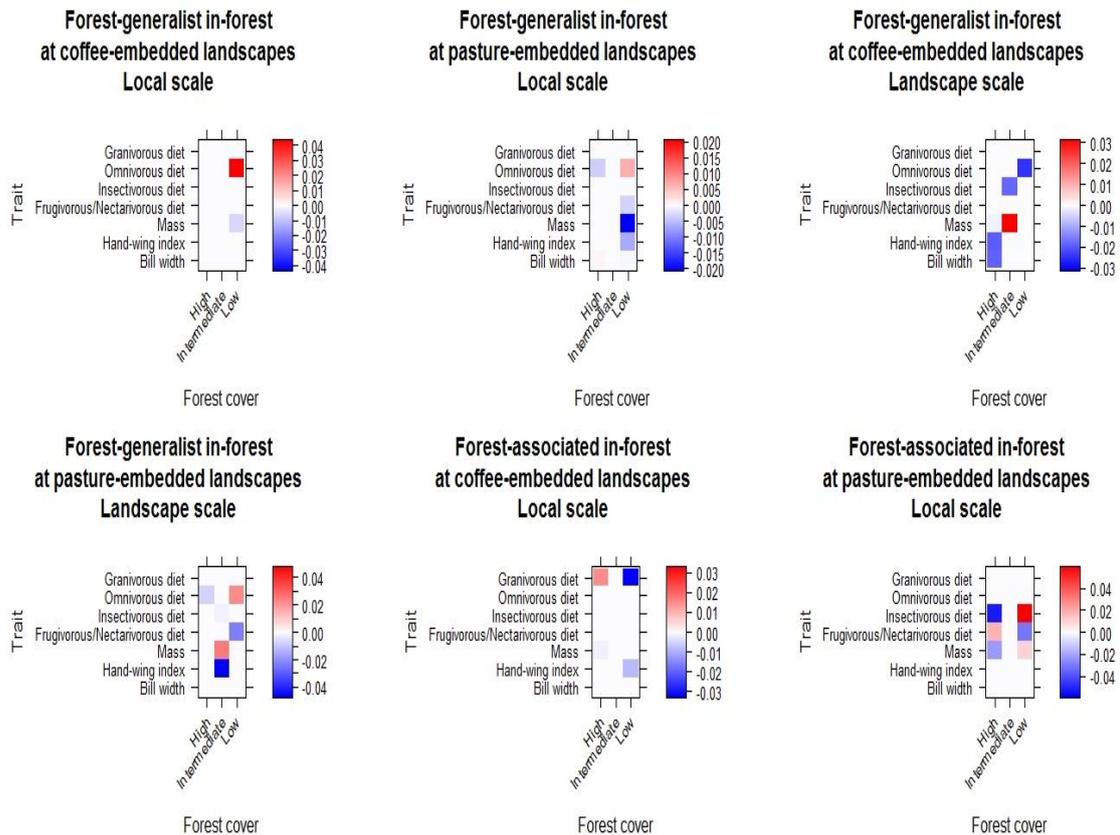


Figure S6: Fourth corner analysis for forest-generalist and forest-associated species in-forest at local and landscape scale for diet (granivorous, omnivorous, insectivorous and frugivorous/nectarivorous), mass, hand-wing index and bill width, according to forest cover amount (high, intermediate and low) at coffee-embedded and pasture-embedded landscapes. Positive coefficients (i.e. red) and negative coefficients (i.e. blue) describe the increase and decrease of ecological traits, respectively.