Consequences of a large-scale fragmentation experiment for Neotropical bats: disentangling the relative importance of local and landscape-scale effects

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Abstract

Context Habitat loss, fragmentation and degradation are widespread drivers of biodiversity decline. Understanding how habitat quality interacts with landscape context, and how they jointly affect species in human-modified landscapes, is of great importance for informing conservation and management.

Objectives We used a whole-ecosystem manipulation experiment in the Brazilian Amazon to investigate the relative roles of local and landscape attributes in affecting bat assemblages at an interior-edge-matrix disturbance gradient.

Methods We surveyed bats in 39 sites, comprising continuous forest, fragments, forest edges and intervening secondary regrowth. For each site, we assessed vegetation structure (local-scale variable) and, for five focal scales, quantified habitat amount and four landscape configuration metrics.

Results Smaller fragments, edges and regrowth sites had fewer species and higher levels of dominance than continuous forest. Regardless of the landscape scale analysed, species richness and evenness were mostly related to the amount of forest cover. Vegetation structure and configurational metrics were important predictors of abundance, whereby the magnitude and direction of response to configurational metrics were scale-dependent. Responses were ensemble-specific with local-scale vegetation structure being more important for frugivorous than for gleaning animalivorous bats.

Conclusions Our study indicates that scale-sensitive measures of landscape structure are needed for a more comprehensive understanding of the effects of fragmentation on tropical biota. Although forest fragments and regrowth habitats can be of conservation significance for tropical bats our results further emphasize that primary forest is of irreplaceable value, underlining that their conservation can only be achieved by the preservation of large expanses of pristine habitat.

Keywords Amazon; edge effects; FRAGSTATS; landscape context; matrix; secondary forest; spatial scale; vegetation structure.

Introduction

Anthropogenic forest loss and fragmentation are key drivers of the ongoing defaunation crisis (Dirzo et al 2014). This erosion of biological diversity has repeatedly been associated with human population growth and rising per-capita consumption (Laurance et al 2014) whose future increases are expected to be greatest in the tropics where much of the planet's biodiversity resides (Bradshaw et al 2008; Gibson et al 2011).

In human-modified landscapes, habitat loss and fragmentation typically co-occur with habitat degradation (Fischer and Lindenmayer 2007). Deterioration in habitat quality is most noteworthy near primary forest edges and in regenerating forests, where biotic and abiotic gradients and alternative successional pathways lead to marked differences in vegetation structure (Williamson et al 2014; Faria et al 2009). Forest edges and regenerating forests are ubiquitous features of tropical landscapes (Chazdon 2014). For instance, ~32000 km of new forest edges are created annually in the Brazilian Amazon by deforestation alone (Broadbent et al 2008) and, in 2000, ~140 x 10^3 km^2 of the region's land area was composed of regenerating forests (Carreiras et al 2006). Regenerating secondary forests profoundly influence the spatio-temporal distribution of many species (e.g. Barlow et al 2007; Banks-Leite et al 2010). However, studies focussing on the full disturbance gradient of continuous forest (CF) and fragment interiors (I), forest edges (E) and matrix (M) habitats (hereafter IEM gradients) in fragmented landscapes are scarce, and habitat quality metrics are rarely incorporated into landscape-scale fragmentation studies (Galitsky and Lawler 2015). This translates into a poor understanding of how habitat quality interacts with landscape context and how they jointly affect species persistence and abundance in human-modified landscapes.

Bats comprise a large fraction of tropical mammalian fauna and play key ecological roles in pollination, seed dispersal and insect suppression (Kunz et al 2011). They are acutely sensitive to human-induced landscape changes (García-Morales et al 2013; Meyer et al 2016) and their local abundance and diversity qualifies them as a well-suited indicator group to examine the effects of fragmentation on tropical biota (Jones et al 2009).

MacArthur and Wilson's (1967) island biogeographic theory profoundly influenced early research on fragmented ecosystems. Studies on tropical bats were no exception to this, with earlier work focusing mainly on the effects of patch area and isolation metrics (Cosson et al 1999; Schulze et al 2000). As the conceptual basis of fragmentation studies matured, landscape characteristics such as habitat amount and configuration came to be recognized as important determinants of bat species persistence in modified forest landscapes and the few studies that have explored tropical bat associations with landscape structure at multiple spatial scales have found assemblages to respond in a scale-sensitive manner (reviewed in Meyer et al 2016). This scale sensitivity in bat responses towards landscape structure likely reflects interspecific differences in species ecological traits such as diet, body size and home range which are linked to the scale at which individual species perceive and interact with their environment (Pinto and Keitt 2008; Meyer et al 2016). Scale dependency is also indicative of the influence of smaller scale drivers upon ecological processes that operate at larger spatial scales (McGill 2010). By imposing limitations on mobility and food detection, microhabitat characteristics such as vegetation structure strongly influence the type and number of bat species co-occurring on a local scale (Marciente et al 2015). However, vegetation structure is rarely included in multi-scale fragmentation studies although it has been suggested to constitute a better predictor of the activity of forest-dwelling bats than landscape-level features (Erickson and West 2003; Charbonnier et al 2016) and is likely to modulate ecological responses to fragmentation at the landscape level.

The Biological Dynamics of Forest Fragments Project (BDFFP) in the Brazilian Amazon is the world's largest and longest-running experimental study of forest fragmentation (Laurance et al 2011). Vertebrate assemblages at the BDFFP have been found to be sensitive to fragment size (Ferraz et al 2007; Boyle and Smith 2010), edge effects (Lenz et al 2014; Powell et al 2015), matrix composition (Antongiovanni and Metzger 2005; Bobrowiec and Gribel 2010), local vegetation structure (Stratford and Stouffer 2013; Mokross et al 2014) and landscape-scale characteristics (Stouffer et al 2006; Boyle and Smith 2010). However, no study has jointly investigated how vegetation structure and landscape composition and configuration affect the occurrence and abundance patterns of its vertebrate assemblages. Here we address this gap by examining how BDFFP bat assemblages respond to an IEM disturbance gradient in a landscape where fragments are embedded in a "soft" matrix composed of advanced secondary vegetation. Specifically, we address the following questions:

(1) How do bat species richness, evenness, abundance and assemblage composition change along IEM (interior, edge and matrix) and size (CF, 100, 10 and 1 ha fragments) gradients? Relative to CF interiors we expected forest fragments to exhibit reduced species richness and evenness and we hypothesized that differences in response metrics (species richness, evenness, abundance and assemblage composition) between IEM habitats would decrease with fragment size. Additionally, we predicted frugivores to be more edge- and matrix-tolerant than gleaning animalivorous bats.

(2) What is the relative importance of local vegetation structure versus landscape-scale primary forest cover and configuration as determinants of bat species richness, evenness and abundance? And how does it vary across multiple spatial scales? We anticipated different response metrics to relate differently to vegetation structure and landscape characteristics and predicted that responses would be scale-dependent with all three assemblage attributes (species richness, evenness and abundance) responding predominantly to forest cover. We also expected gleaning animalivores to present stronger negative effects towards configuration metrics than frugivorous bats.

Material and methods

Study area and site selection

Fieldwork was conducted at the BDFFP, located ~80 km north of Manaus (2°30'S, 60°W), Brazil (see Fig. S1 in the online supplementary material). The area is classified as tropical moist forest, and is characterized by a mosaic of *terra firme* rainforest, secondary regrowth, and primary forest fragments. Annual rainfall varies from 1900-3500 mm, with a dry season between June and October (Laurance et al 2011). The forest fragments were isolated from continuous forest by distances of 80-650 m in the early 1980s, and are categorized into size classes of 1, 10 and 100 ha. Each fragment was re-isolated on 3-4 occasions prior to this study, most recently between 1999 and 2001 (Laurance et al 2011). The matrix is composed of tall secondary forest dominated mainly by *Vismia* spp. and *Cecropia* spp. (Mesquita et al 2001).

Bats were sampled in eight forest fragments - three of 1 ha, three of 10 ha and two of 100 ha (Colosso, Porto Alegre and Dimona camps) - and nine control sites in three areas of

CF (Cabo Frio, Florestal and Km 41 camps) (Fig. S1). Sampling was conducted in the interiors and at the edges of all eight fragments, as well as at eight sites located in the nearby secondary regrowth, 100 m away from the edge of each fragment. A similar sampling scheme was employed for CF, with nine sampling sites in the interior, three at the edge, and three matrix sites located 100 m away from the forest edge. Therefore, a total of 39 sites were sampled. Distances between interior and edge sites of CF and fragments were respectively 1118 ± 488 and 245 ± 208 m (mean ± SD).

Bat surveys

Each sampling site was visited eight times over a 2-year period, between August 2011 and June 2013. Bats were captured using 14 ground-level mist nets (12 x 2.5 m, 16 mm mesh, ECOTONE, Poland) in CF and fragment interiors, and seven ground-level mist nets at the edge and matrix sites. Mist nets were deployed along existing trails which are known to be used by Neotropical bats as commuting flyways (Palmeirim and Etheridge 1985). At edge sites, these trails ran parallel to the border between primary forest and secondary regrowth. In our study area mist netting efficiency was found to be highest in the first few hours after sunset (Bernard 2002). Sampling therefore started at dusk and was performed for six hours during which nets were visited at intervals of ~20 minutes. Mist netting at the same location for consecutive days can lead to diminishing capture efficiency over time (Marques et al. 2013). Such net-shyness related bias was avoided by spacing visits to the same site three to four weeks apart. Species were identified following Gardner (2007) and Lim and Engstrom (2001), and taxonomy follows Gardner (2007). Most adult bats were marked with individually numbered ball-chain necklaces (frugivores and *Pteronotus parnellii*) or subcutaneous transponders (gleaning animalivores). We restricted analyses to phyllostomids and *P.*

parnellii, since all other species in Neotropical bat assemblages are known to be inadequately sampled with mist-nets (Kalko 1998).

Influence of fragment-size and interior-edge-matrix gradient

Species richness, evenness and abundance

Differences in species richness, evenness, and abundance between size- (CF, 100, 10 and 1 ha fragments) and IEM-gradients were assessed using generalized linear mixed-effects models (GLMMs), fitted in the R package "*lme4*" (Bates 2010). A categorical variable combining information of both the size- and IEM-gradient was specified as a fixed effect, and a random term nesting "site" within "location" (the latter referring to the six research camps; Fig. S1) was incorporated. This approach accounts for potential autocorrelation between sites within the same location (Bolker et al 2009). For each size category and IEM, species richness and evenness, the latter quantified as Hurlbert's probability of interspecific encounter (PIE), were computed using rarefaction. Rarefaction was performed using EcoSim software v.7 (Gotelli and Entsminger 2004) based on 1000 random rearrangements and independent sampling of individuals, rarefying to the abundance level of the site with the lowest number of captures. Total number of captures per site was used to compare differences in abundance using a Poisson GLMM, with the site's total number of mist-net hours (1 mist-net hour [mnh] equals one 12-m net open for 1 h) specified as an offset. High inter-fragment variation in capture rates precluded robust inference about how fragment size affects capture rates.

Differences in abundance between size- and IEM-gradients were therefore analysed by both considering the distinct fragment size categories (100, 10 and 1 ha fragments) independently and by lumping the capture data from all fragments. Significant effects were further evaluated via multiple comparison tests with Tukey contrasts (adjusted *P*-values reported) using the R package "*multcomp*" (Hothorn et al 2013).

Assemblage composition

Differences in assemblage composition were characterized by means of a non-metric multidimensional scaling (NMDS) ordination based on a Bray-Curtis dissimilarity matrix, using the number of captures standardized by the site's effort (bats per mnh) and scaled to a mean of 0 and standard deviation of 1. Compositional differences between size- and IEM-gradient habitat types were evaluated with a permutational multivariate analysis of variance (PERMANOVA). Both analyses were conducted using the *"vegan"* package in R (Oksanen et al 2013).

Ensemble-specific responses

According to available literature (Bernard 2001, 2002; Giannini and Kalko, 2004; Pereira et al 2010) species were grouped into frugivores (subdivided into shrub and canopy frugivores), gleaning animalivores, aerial insectivores and nectarivores (Table S1). The same approach used to compare total abundance was used to explore ensemble-specific differences in abundance across the size- and IEM-gradients.

Influence of local and landscape-scale variables

Vegetation structure

Vegetation structure was characterized within three 100 m^2 (5 x 20 m) plots established 5 m from each side of the mist net transects. In each plot, nine variables were quantified: (i) number of trees (diameter at breast height [DBH] ≥ 10 cm), (ii) number of woody stems (DBH < 10 cm), (iii) average DBH of trees ≥ 10 cm, (iv) percent canopy cover (estimated as the average of four spherical densiometer readings), (v) number of palms, (vi) number of *Vismia* spp. and *Cecropia* spp. (the fruits of both genera are consumed by several frugivorous bat species, e.g. Bernard 2002; Giannini and Kalko 2004), (vii) liana density (visually classified every 5 m in five categories varying from no lianas to very high liana density), (viii) tree height (based on visual estimates of 25 trees ≥ 10 cm DBH) and (ix) vertical foliage density (calculated as the sum of the values obtained by visual estimation at seven height intervals [0-1 m, 1-2 m, 2-4 m, 4-8 m, 8-16 m, 16-24 m, 24-32 m] using 6 categorical classes [0 = no foliage, 1 = very sparse 0-20%, 2 = sparse 20-40%, 3 = medium 40-60%, 4 = dense 60-80%, 5 = very dense 80-100%]).Values for each sampling site were calculated as the average across replicated plots (Table S2).

Vegetation variables were log(x + 1) transformed, standardized to a mean of zero and a standard deviation of one, and submitted to a Principal Components Analysis (PCA). The scores of the first axis (PCA1) were then used as predictor variable summarizing vegetation structure (Fig. S2 and Table S3) in modelling bat responses to local habitat and landscape structure.

Landscape structure

To quantify compositional and configurational aspects of landscape structure we used a detailed forest vs non-forest map of the BDFFP landscape based on 2004 LandSat Thematic Mapper (TM) satellite images (30 m spatial resolution). Land cover classification was obtained through supervised classification (bands 7, 5, 4, 3, 2 and 1), with thorough field checking performed to validate map accuracy. Primary forest (hereafter simply “forest”) was clearly distinguished from second growth. Landscape metrics were chosen based on their reported influence on Neotropical bats (Gorresen and Willig 2004; Meyer and Kalko 2008; Klingbeil and Willig 2009; Avila-Cabadilla et al 2012) and were calculated using Fragstats v.4.1 (McGarigal et al 2012) for buffers with radii of 250, 500, 750, 1000 and 1500 m around each of the 39 sampling points. Buffer scales were selected so as to encompass the home ranges of different-sized bat species while at the same time minimizing spatial overlap between neighboring sites (Meyer et al 2008). Five metrics were selected to represent: (a) habitat amount (forest cover) and (b) habitat configuration (mean patch area, patch density, edge density and mean shape index).

Relative importance of local and landscape-scale predictors of bat responses

The relative importance of local (vegetation structure) vs landscape-scale characteristics in determining species richness, evenness and abundance were investigated at the five different focal scales using GLMMs. For this, we used rarefied species richness, evenness and total number of captures at each site as response variables. Additionally, GLMMs using total number of captures per site of frugivores and gleaning animalivores, respectively, were used to explore ensemble-specific relationships. Low number of captures precluded separate analyses for the other ensembles. Severe collinearity between predictor variables can undermine statistical inference in GLMMs (Dormann et al 2013). We therefore quantified collinearity by calculating each predictor’s variance inflation factor (VIF) within a set of predictors that always included vegetation structure and habitat amount (forest cover). As VIFs > 10 are known to indicate ‘‘severe’’ collinearity (Neter et al 1990) we reduced our set of predictor variables (by excluding mean patch area and mean shape index) so that those included in the final set presented a VIF < 6 in all analysed buffers.

Analyses were restricted to a subset of a priori selected models comprising plausible combinations of local (vegetation structure) and landscape predictors (forest cover, edge density and patch density). For each response variable and landscape-scale separate sets of models were defined, which considered (i) each metric independently, (ii) vegetation structure and each landscape metric independently, (iii) vegetation structure and habitat configuration metrics, (iv) forest cover and each habitat configuration metric independently and (v) configuration metrics only. Each model included a random term accounting for the nested sampling design (site within location). Model goodness-of-fit was assessed as the marginal R^2_m and conditional R^2_c (Nakagawa and Schielzeth 2013). Following Burnham and Anderson (2002), the most parsimonious models were selected using Akaike's Information Criterion corrected for small samples sizes (AIC_c). Model-averaging was used to obtain parameter estimates for the models with an AIC_c difference from the best model (Δ_i) < 2 (Burnham and Anderson 2002). Residual spatial autocorrelation in the best-fit GLMMs was inspected by means of Moran's *I* test. For these best-fit models, the variation independently explained by each explanatory variable was then determined by hierarchical partitioning analysis using the "*hier.part*" package (Walsh and Mac Nally 2013), modified to accommodate a model offset [log(effort)] for abundance data (Jeppsson et al 2010). Following Benchimol and Peres (2015), hierarchical partitioning was conducted only considering fixed effects. Unless otherwise stated, all analyses were conducted in R v3.0.2 (R Development Core Team 2013).

Results

During 18650 mnh we captured 4210 bats belonging to six families and 55 species (Table S1). Phyllostomids and mormoopids (*P. parnellii*) were the dominant groups, accounting respectively for 90.9% (3827) and 6.5% (272) of total captures.

Responses to size- and interior-edge-matrix gradients

Species richness, evenness and abundance

Species richness was significantly higher in CF interiors than in any fragment size class, with the exception of the 100 ha fragment interiors (Fig. 1). Similarly, edge and matrix sites adjoining CF were more species-rich than those adjacent to fragments and, for both interior and matrix habitats, species richness tended to increase with fragment size. Conversely, this pattern did not hold for edge habitats as the edges of the 1 ha fragments were surprisingly diverse, attaining comparable richness to those of CF (Table S4).

#Figure 1 approximately here#

Evenness showed a similar pattern to species richness (Fig. 1), with all habitats other than the 100 ha fragment interiors and CF edges being significantly less even than CF interiors (Table S4). Evenness was higher for edge and matrix habitats adjoining CF and 100 ha fragments, and again, the edges of 1 ha fragments had significantly higher evenness than those of the other size classes.

For both CF and fragments, total species abundance increased progressively from interior to edge and matrix habitats, with capture rates in the edge and matrix habitats being significantly higher than in CF interiors. However, when the most common species (*Carollia perspicillata*) was excluded, the effect only remained significant for the comparison with CF edges (Fig. 2 and Table S5; see Fig. S3 for results by fragment size).

#Figure 2 approximately here#

Assemblage composition

The NMDS ordination had a stress value of 0.095, conveying a good representation of the data along two dimensions. Bat assemblage composition differed significantly across the size- and IEM-gradients (Fig. 3; F_{11} = 2.316, R^2 = 0.486, P = 0.001). The interiors of each fragment size category formed a distinct cluster and the 100 ha fragment interiors grouped closely to the cluster formed by CF interiors, indicating high assemblage similarity. Edge and matrix sites clustered independently from CF and 100 ha fragment interiors and presented a large spread along the first ordination axis.

#Figure 3 approximately here#

Ensemble-specific responses

Shrub frugivores was the ensemble with the most captures (69%), followed by gleaning animalivores with 12.5%. Shrub and canopy frugivores showed similar patterns of relative abundance, with higher capture rates in edge and matrix habitats compared to habitat interiors (Fig. 4; see Table S6 for results by fragment size). Capture rates for all frugivores and shrub frugivores were significantly lower at CF interiors than in any other habitat category. For canopy frugivores there was no significant difference between CF interiors and CF edges and fragment interiors. Conversely, compared with the same IEM habitat type, gleaning animalivores in fragments had significantly lower capture rates than in CF. The capture rate of aerial insectivores (*P. parnellii*) was lower in fragment interior, edge and matrix habitats than in CF interiors, and the abundance of nectarivores peaked in fragment interiors and CF edges. However, none of these differences were significant (Table S7).

#Figure 4 approximately here#

Influence of local and landscape-scale variables

Assemblage and ensemble associations with local and landscape metrics were scale-sensitive and varied according to the response variable analysed (Fig. 5 and 6). However, for most response metrics and spatial scales, relatively high model selection uncertainty made it difficult to unequivocally pinpoint either local vegetation structure or landscape-scale attributes as best predictors (Table S8 and Table S9). GLMM residuals were not significantly spatially autocorrelated for evenness or any of the abundance models (Moran's I from -0.23 to 0.02, $P > 0.05$). However, for species richness and at the smallest spatial scale (250 m), one of the models included in the most parsimonious set ($\Delta AIC_c < 2$) presented spatially structured residuals (Moran's $I = -0.23$, $P < 0.05$) (Table S10). Consequently, for this scale and response variable the results should be interpreted with caution as autocorrelation may prompt to an elevated Type I error.

#Figure 5 approximately here#

Vegetation structure, as represented by PCA1, was a particularly relevant predictor of total abundance and abundance of frugivores. Other than for the smallest (250, 500 and 750 m) spatial scales, with species richness and the abundance of gleaning animalivores as response variables and for the smallest spatial scale for evenness, vegetation structure was always included in the most parsimonious models. The PCA1 explained 42.02% of the total variance and represented a gradient from simpler vegetation structural complexity, typical of secondary forest (higher density of pioneer trees [*Vismia* spp. and *Cecropia* spp.] and woody stems [DBH <10 cm]; negative values), to higher structural complexity, typical of primary forest sites (more closed canopy cover and higher density of trees [DBH >10]; positive values) (Fig. S2 and Table S2). Its relationship was positive with respect to all response metrics analysed, indicating that more complex sites in terms of vegetation structure presented higher species richness, evenness and abundance. Forest cover emerged as the most important predictor of species richness and evenness, being positively associated with both and with the abundance of gleaning animalivores. Its influence on total and frugivore abundance was negative across all scales. The effect of edge density was particularly sensitive to scale, being positively correlated with total abundance and abundance of frugivores and gleaning animalivores at the smallest scales (≤ 500 m) and negatively at larger spatial scales. Lastly, patch density showed greater consistency as predictor across scales, being negatively associated with species richness, total abundance and, except at one spatial scale, with the abundance of frugivores and gleaning animalivores.

#Figure 6 approximately here#

Discussion

Our analyses revealed that patterns of bat species richness, evenness and abundance varied across the BDFFP landscape, and were affected by local- and landscape-level habitat attributes in a scale-dependent and ensemble-specific manner. This despite the low structural contrast between CF, forest fragments and surrounding secondary regrowth.

Responses to size- and interior-edge-matrix gradients

Compared with CF, smaller (≤ 10 ha) fragments harboured fewer species and their assemblages were characterized by higher levels of dominance, results consistent with previous studies addressing the impacts of fragmentation on tropical bats (Cosson et al 1999; Meyer and Kalko 2008; Struebig et al 2008; Estrada-Villegas et al 2010) and other taxa at the BDFFP (Laurance et al 2006b; Ferraz et al 2007; Boyle and Smith 2010) as well as elsewhere in the tropics (Benchimol and Venticinque 2014; Bregman et al 2014). These differences, though remarkable given the low fragment-matrix contrast at the time of our study and the relatively short distance between forest fragments and nearby CF, seem to result from the strong effect of trait-mediated environmental filters that selectively benefit bat species with reduced body mass and a phytophagous diet (Farneda et al 2015). This is likely attributable to the elevated abundance of pioneer plants in early successional habitats, which benefit many small-bodied nectarivorous and frugivorous phyllostomids (e.g., *Glossophaga* spp., *Carollia* spp., *Sturnira* spp.), but fail to provide enough food resources to fulfil the energetic requirements of larger species and those of higher trophic levels.

For both CF and forest fragments, edge habitats had fewer species and higher levels of dominance. These differences were more noticeable in larger fragments (100 ha) and CF, suggesting an area effect on the magnitude of contrast between interior and edge assemblages. Edge effects have long been identified as having major impacts on species distributions and dynamics (Ewers and Didham 2006). In the BDFFP fragments, edge effects are predominant drivers of ecological change (Laurance et al 2011), affecting vegetation structure (Didham and Lawton 1999) and acting synergistically with area effects (Laurance et al 2006a).

Neotropical bats are known to respond to habitat edges (Gorresen and Willig 2004; Meyer and Kalko 2008; Klingbeil and Willig 2009; Klingbeil and Willig 2010; Bolívar-Cimé et al 2013) and the few studies that have compared phyllostomid assemblages at the interiors and edges of fragments have reported declines in species richness (Faria 2006; Meyer and Kalko 2008). This pattern might result from the avoidance of these habitats by gleaning animalivorous bats, an ensemble identified as edge-sensitive in both high- (Meyer et al 2008) and low-contrast systems (Faria 2006). The underlying drivers of the higher edge-sensitivity exhibited by this ensemble remain to be tested but they might relate to changes in the densities of preferred arthropod prey or to restrictions to flight maneuverability imposed by denser understory vegetation near edges.

Although the most conspicuous edge effects at the BDFFP have been detected within 100 m of forest edges (Laurance et al 2002), results from French Guiana indicate that edge-mediated changes in bat assemblage structure may be noticeable as far as 3 km from the forest edge (Delaval and Charles-Dominique 2006). This suggests that even our CF interior sites (located on average more than 1 km away from the forest edge) are likely to suffer from the effects of edge penetration and consequently their bat assemblages may reflect the influence of the modified secondary forest matrix.

Bat assemblages in secondary regrowth adjoining CF and 100 ha fragments were also richer and more even than assemblages adjacent to smaller fragments, suggesting a spillover of species from the more diverse CF and 100 ha fragment interiors into the matrix. Low-contrast matrix habitats are known to harbour diverse bat assemblages, both at the BDFFP (Bobrowiec and Gribel 2010) and elsewhere in the Neotropics (Avila-Cabadilla et al 2009; Avila-Cabadilla et al 2014; Mendenhall et al 2014). Our results indicate not only that matrix habitats influence fragment ecology at the BDFFP (Gascon et al 1999; Laurance et al 2011) but that the influence is bidirectional and that, similarly to birds (Powell et al 2013), bat species dependent on old-growth stands may exploit the nearby secondary regrowth for feeding or as flyways between food patches.

Human-induced habitat changes, including fragmentation, act as non-random filters selecting those species with the best combination of traits to survive in modified ecosystems (Smart et al 2006). In the humid Neotropics, capture rates of frugivores generally increase in fragmented or disturbed areas, whereas gleaning animalivores tend to decline, if not disappear, in modified habitats (Meyer et al 2016). Our results are consistent with this pattern. The *Vismia*- and *Cecropia*-dominated secondary vegetation that surrounds the fragments in our study landscape provides additional food resources that augments the abundance of frugivores such as *C. perspicillata* (Bobrowiec and Gribel 2010). However, regrowth habitats and forest fragments are structurally less complex than CF, and constitute less suitable habitat conditions for most gleaning animalivores due to insufficient roosting and prey resources (Gorresen and Willig 2004; Meyer and Kalko 2008). Nectarivorous bats have been documented to remain stable or increase in forest remnants and edge habitats, owing to elevated densities of food resources following forest clearance and subsequent succession (García-Morales et al 2013; Meyer et al 2016; Chambers et al 2016, in press). At the BDFFP, both nectarivorous birds (Stouffer et al 2006) and bats follow this pattern, adding to the evidence that nectar-feeders, together with frugivores, are the most resilient ensembles to habitat modification.

Influence of local and landscape-scale variables

Our data suggest that both local and landscape metrics are important in explaining the effects of fragmentation on tropical bat assemblages. At the local-scale, we observed that sites that are more similar to CF in terms of vegetation structure are able to support assemblages that are richer, more even and comprised of greater abundances of both frugivorous and gleaning animalivorous bats. These results agree with several other studies on aerial and terrestrial forest-dependent tropical vertebrates in modified landscapes (e.g. Benchimol and Venticinque 2014; Rocha et al 2015). However, they contrast with the findings from a study of bat assemblages in a land-bridge island system in Panama (Meyer and Kalko 2008), which provided little evidence for an effect of vegetation structure on bat species richness and assemblage composition. This may reflect the wider environmental gradient of our study (which encompassed CF and fragment interiors, edges and matrix habitats) in relation to the one analysed in Panama (limited to CF and fragment interiors and CF edges). Vegetation structure may therefore be a stronger determinant of assemblage diversity and composition in systems with high vegetation heterogeneity such as the ones comprising present-day agricultural and countryside ecosystems.

Across taxa, habitat loss has consistently been found to have a strong negative impact on species persistence whereas the effects of habitat fragmentation per se appear to be weaker and more variable, both in terms of magnitude and direction (Fahrig 2013). This general pattern has also been repeatedly observed in tropical bat assemblages (Gorresen and Willig 2004; Meyer and Kalko 2008; Struebig et al 2008; Klingbeil and Willig 2009; Arroyo-Rodríguez et al 2016, in press; but see Cisneros et al 2015) and held true for our study. Regardless of landscape-scale, forest cover was the best predictor of species richness, having a strong positive effect, whereas the influence of configurational metrics varied in magnitude, but was consistently negative. These results mirror previous findings regarding the influence of landscape-scale forest cover in fragmented systems with an aquatic matrix (Meyer and Kalko 2008; Henry et al 2010), however, contrast with results from unflooded rainforest in Paraguay, Peru, Costa Rica and Mexico, where species richness was highest in partly deforested landscapes (Gorresen and Willig 2004; Klingbeil and Willig 2009; Cisneros et al 2015; Arroyo-Rodríguez et al 2016, in press). These opposing results may reflect an interaction between regional species pools and landscape-specific environmental filters, especially the ones associated with the nature of the matrix habitats in which fragments are embedded. The matrix at the BDFFP is relatively homogeneous, being composed almost entirely of secondary forests (Laurance et al 2011). The higher compositional diversity of the humanized matrix habitats studied by Gorresen and Willig (2004), Klingbeil and Willig (2009), Cisneros et al (2015) and Arroyo-Rodríguez et al (2016, in press) is probably associated with a greater variety of resources, which may consequently augment species diversity in moderately fragmented landscapes. These results highlight that the influence of matrix habitats on bat assemblages in forest fragments is highly context-specific (Meyer et al 2016), and are in line with previous findings that some agricultural habitats such as shade plantations can support a higher number of bat species than secondary forests (Faria 2006).

Edge density was positively correlated with total abundance and the abundances of both frugivores and gleaning animalivores at the smallest spatial scales, whereas the direction of the effect was negative at larger scales. This pattern matches recent findings from temperate areas, suggesting that at smaller scales edges may translate into increased foraging opportunities and promote connectivity between roosting and foraging areas, whereas at larger scales higher edge density implies increased habitat fragmentation and therefore negative effects on bat assemblages (Kalda et al 2015). Our modelling results regarding the response of gleaning animalivores to forest cover are also congruent with previous evidence that this ensemble is more sensitive to habitat modification than frugivores (Meyer et al 2016). However, contrary to our expectation, the associations of gleaning animalivores to configurational metrics were very similar to the ones observed for frugivorous bats. This indicates that the secondary regrowth habitats surrounding the BDFFP fragments may be buffering the impacts of forest fragmentation on these matrix-sensitive bats and suggests that fragment connectivity is of the utmost importance for the persistence of forest-associated species in modified landscapes.

Conclusions

The observed effects of fragment area on bat assemblages in the adjacent matrix highlights the importance of larger (> 10 ha) forest patches in the conservation of bat diversity, and in the regeneration and ecological recovery of anthropogenically disturbed forest habitats. Our results also emphasize that, although forest fragments and secondary forest habitats can be of conservation significance for tropical bats, old-growth forest is of irreplaceable value, adding to an increasing body of evidence that tropical biodiversity is overwhelmingly dependent on the maintenance of vast tracts of primary habitat (Barlow et al 2007; Gibson et al 2011).

Fragmentation effects operate at multiple spatial scales and consequently the relative influence of local- and landscape-scale attributes on tropical biota can only be better understood through a multi-scale analysis as presented here. Considering multiple spatial scales can bridge apparently contradictory results of landscape features influencing assemblages differently at distinct spatial scales and therefore greatly benefit the successful delineation of landscape-level management actions aimed at abating the wave of habitat loss and fragmentation currently eroding the biodiversity of our planet's tropical regions.

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Figure Captions

Fig. 1 Comparison of rarefied species richness and evenness (mean ± SE) across the interior-edge-matrix as well as fragment-size gradient. Asterisks denote significant differences relative to continuous forest interiors (*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$). See Table S4 for full results of multiple pairwise comparisons.

Fig. 2 Mean (± SE) capture rate (bats/mnh) for interior, edge and matrix sites of continuous forest and forest fragments. Asterisks denote significant differences relative to continuous forest interiors (*** $P < 0.001$). See Table S5 for full results of multiple pairwise comparisons.

Fig. 3 Arrangement of the 39 sampling sites along the axes of a nonmetric multidimensional scaling (NMDS) ordination based on Bray-Curtis dissimilarity.

Fig. 4 Mean (± SE) capture rate (bats/mnh) for total frugivores, shrub frugivores, canopy frugivores, gleaning animalivores, aerial insectivores (*Pteronotus parnellii*) and nectarivores for the interior, edge and matrix habitats of continuous forest and forest fragments. Asterisks denote significant differences relative to continuous forest interiors (*** $P < 0.001$; * $P < 0.05$). See Table S7 for full results of multiple pairwise comparisons.

Fig. 5 Summary results of model averaging of the most parsimonious generalized linear mixed models (Akaike differences < 2 from the best model) investigating the relationship between local and landscape-scale attributes and various response metrics (species richness, evenness and total abundance) at five focal scales across the BDFFP, Central Amazon, Brazil. Symbol size is proportional to the variation explained by the respective predictor variable based on hierarchical partitioning and colour denotes the direction of the relationship: black = positive, white = negative. See Tables S8 and S9 for additional modelling result.

Fig. 6 Summary results of model averaging of the most parsimonious generalized linear mixed models (Akaike differences < 2 from the best model) investigating the relationship between local and landscape-scale attributes and the abundance of frugivores and gleaning animalivores at five focal scales across the BDFFP, Central Amazon, Brazil. Symbol size is proportional to the variation explained by the respective predictor variable based on hierarchical partitioning and colour denotes the direction of the relationship: black = positive, white = negative. See Tables S8 and S9 for additional modelling result.

Figures

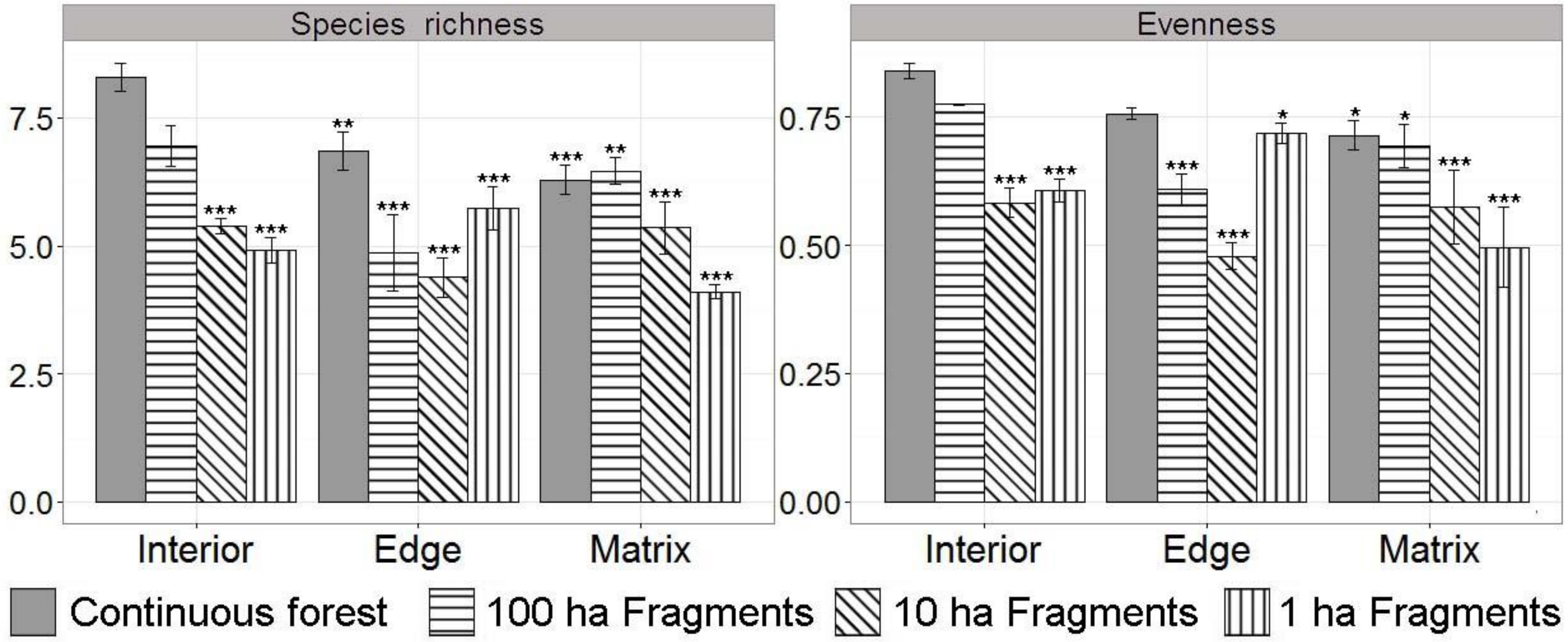

Fig. 1

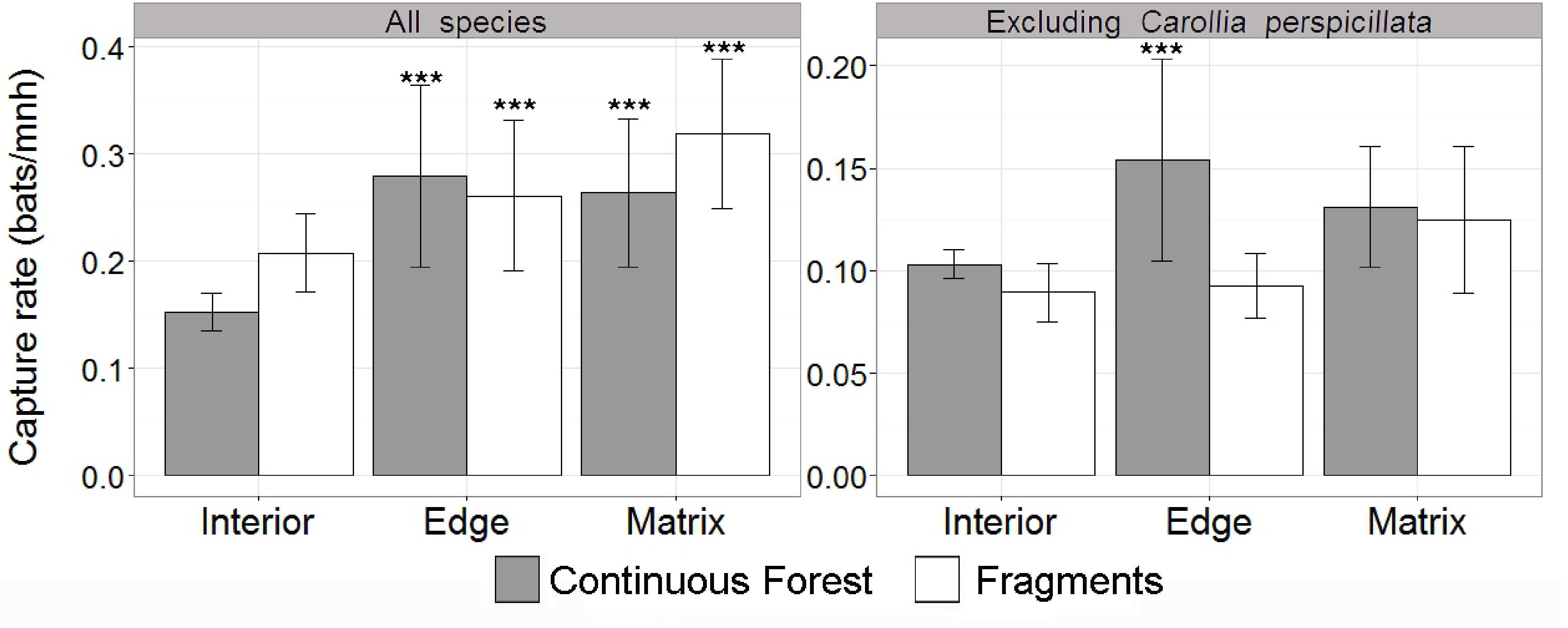
All species
Excluding Carollia perspicillata
Capture rate (bats/mnh)
0.4
0.3
0.2
0.1
0.0
0.20
0.15
0.10
0.05
0.00
***
***
***
***
***
Interior
Edge
Matrix
Interior
Edge
Matrix
Continuous Forest
Fragments

Fig. 2

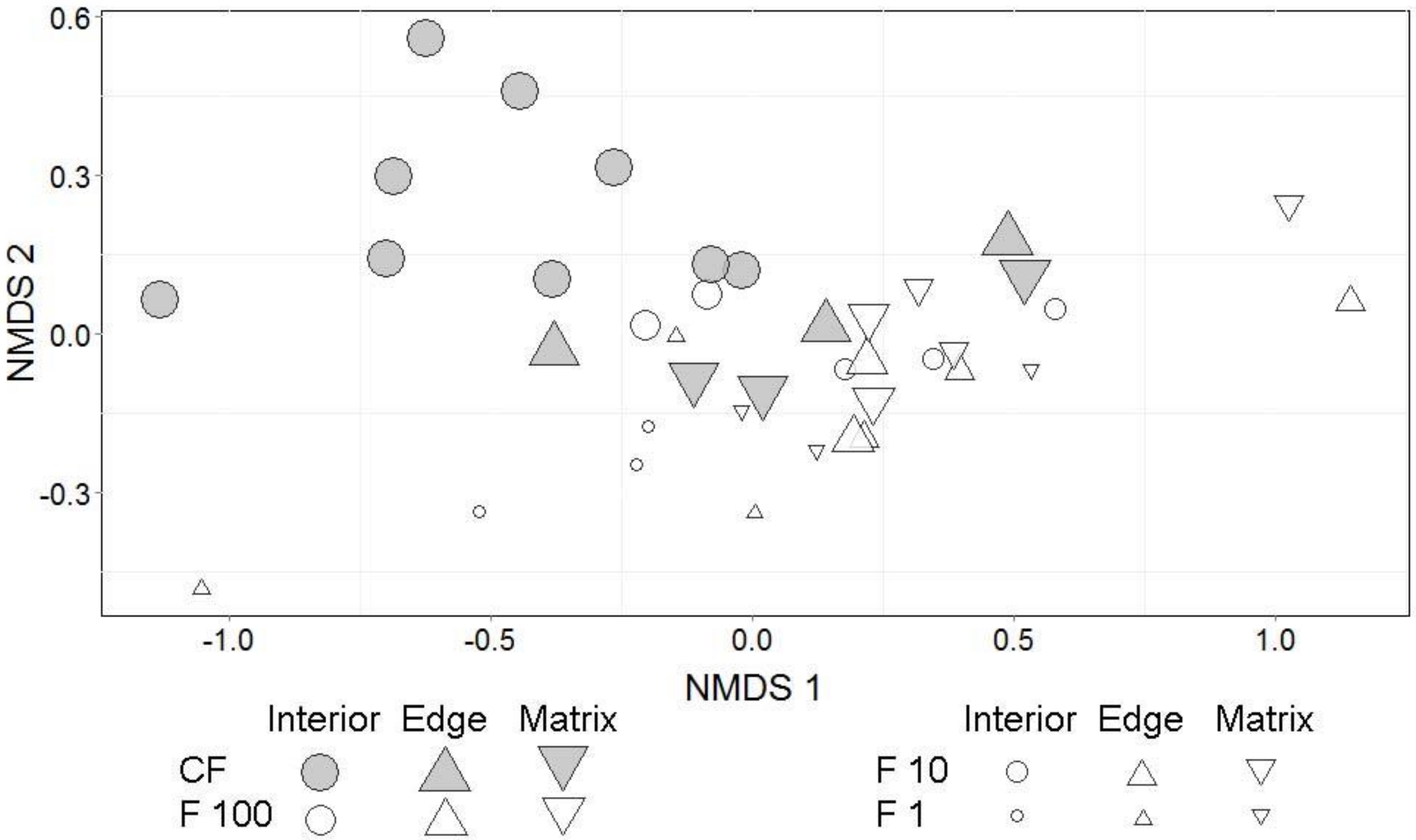
0.6
0.3
0.0
-0.3
NMDS 2
-1.0
-0.5
0.0
0.5
1.0
NMDS 1
Interior
Edge
Matrix
CF
F 100
Interior
Edge
Matrix
F 10
F 1

Fig. 3

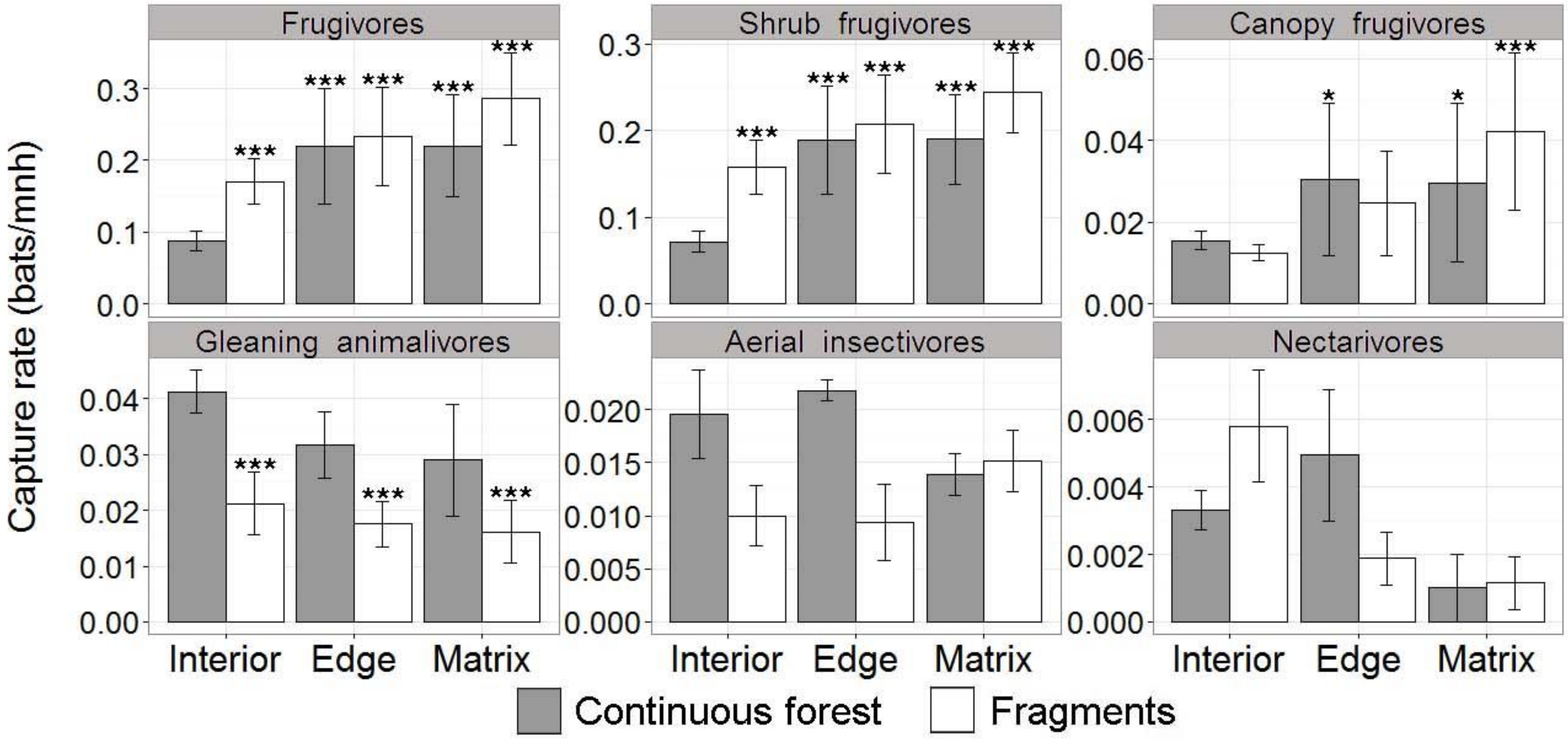
Frugivores
Shrub frugivores
Canopy frugivores
Gleaning animalivores
Aerial insectivores
Nectarivores
Capture rate (bats/mnh)
0.0
0.1
0.2
0.3
0.00
0.02
0.04
0.06
0.01
0.03
0.000
0.005
0.010
0.015
0.020
0.002
0.004
0.006
***
*
Interior
Edge
Matrix
Continuous forest
Fragments

Fig. 4

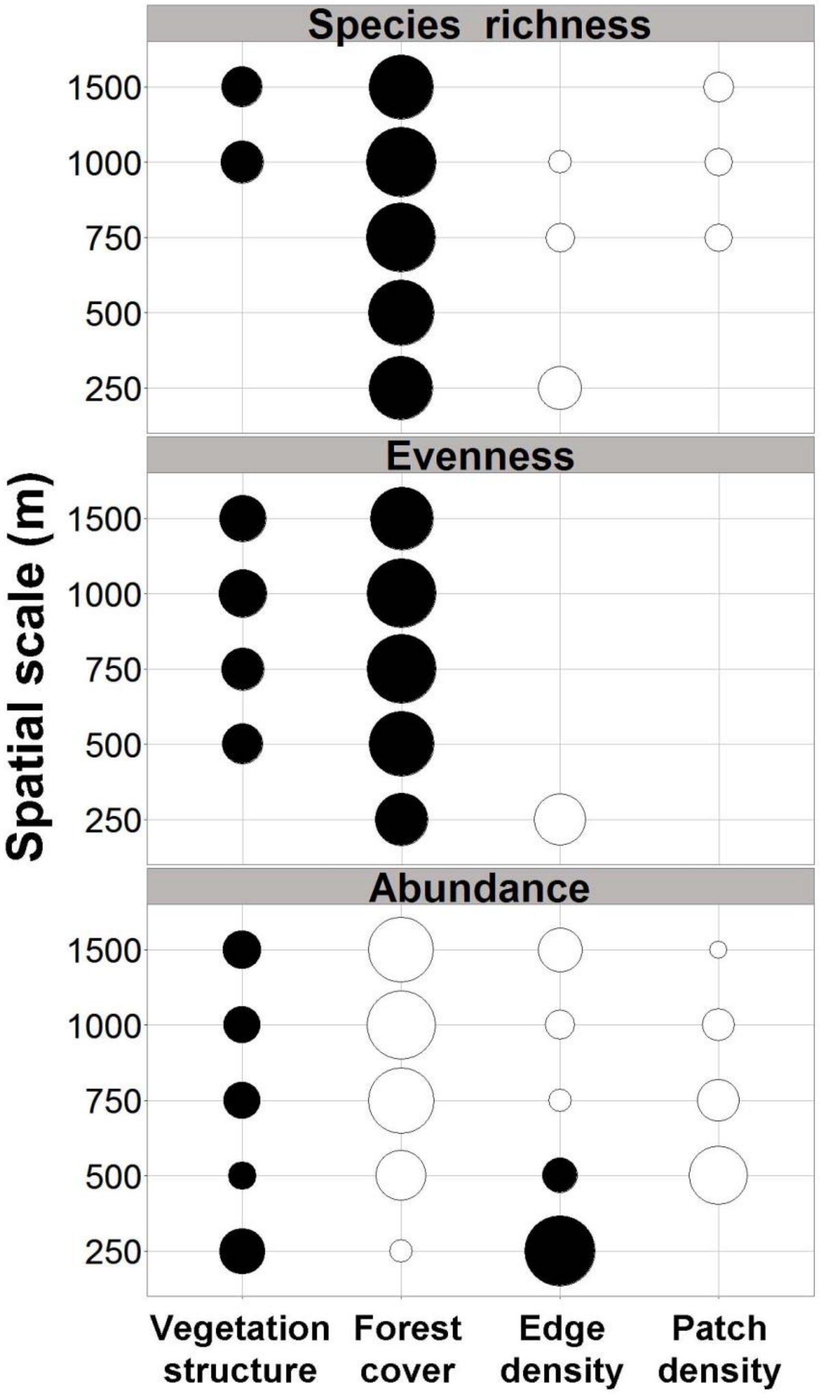
Species richness
Evenness
Abundance
Spatial scale (m)
1500
1000
750
500
250
Vegetation structure
Forest cover
Edge density
Patch density

Fig. 5

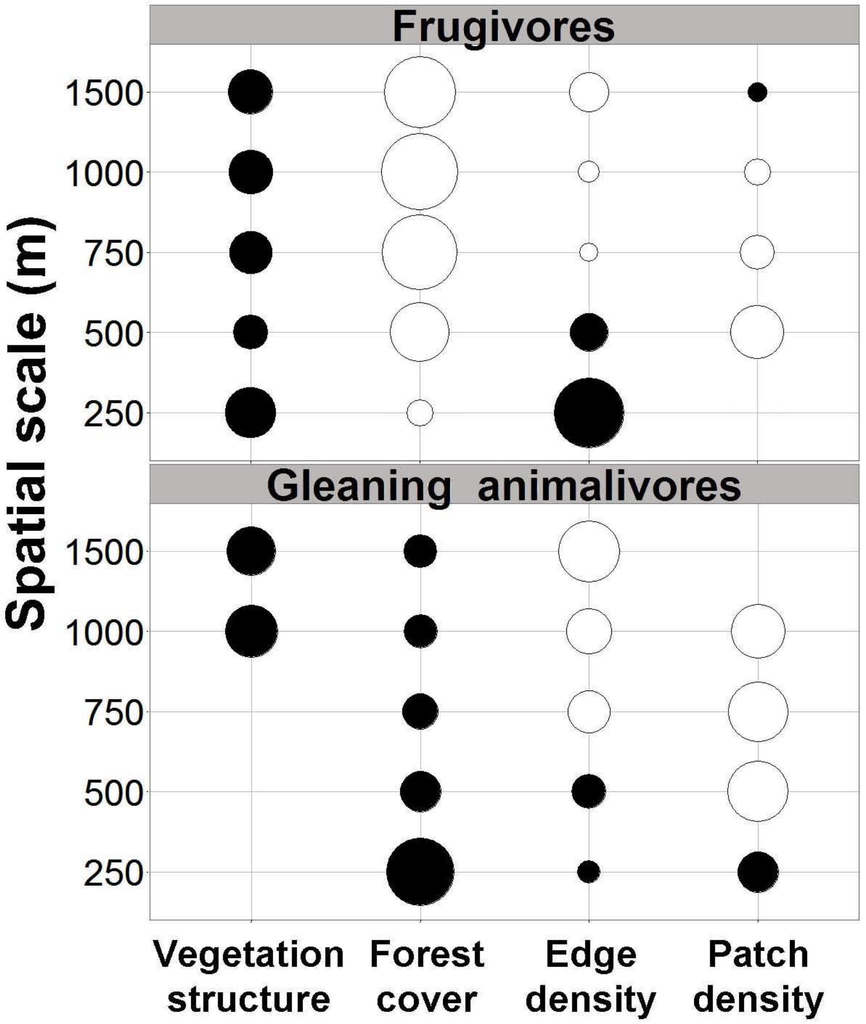
Frugivores
Gleaning animalivores
Spatial scale (m)
1500
1000
750
500
250
1500
1000
750
500
250
Vegetation structure
Forest cover
Edge density
Patch density

Fig. 6

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