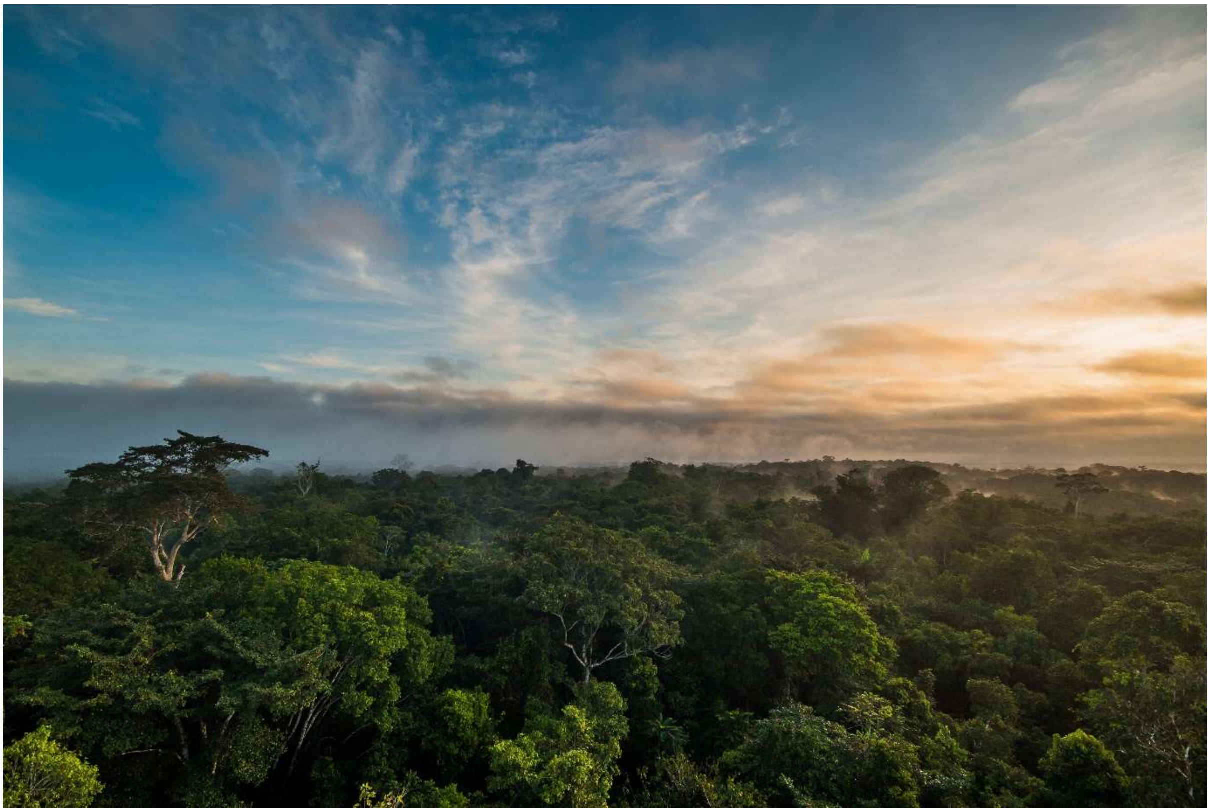
Local and landscape scale effects of fragmentation on aerial insectivorous bats in the Amazon



MSc by Research Thesis

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Statement of originality

I declare that, with the exception of any statements to the contrary, the contents of this report/dissertation are my own work, that the data presented herein has been obtained by experimentation and that no part of the report has been copied from previous reports/dissertations, books, manuscripts, research papers or the internet.

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Abstract

Deforestation is the main driver of the biodiversity crisis. Resulting landscapes are left fragmented with isolated remnant forest patches embedded in a human-modified matrix which has the propensity to regenerate into successional forest. The Biological Dynamics of Forest Fragments Project (BDFFP) in the Brazilian Amazon is the world's largest fragmentation experiment which, for over 40 years, has been investigating the effects of deforestation, fragmentation and recovery on tropical biota. Amazonian aerial insectivorous bats provide vital forest ecosystem services, yet as a group they are understudied compared to their phyllostomid counterparts. This study aims to address this research gap by investigating assemblage- (via multidimensional diversity), guild- and species-level responses of aerial insectivorous bats to fragment size and interior-edge-matrix disturbance gradients and conduct a multiscale analysis of the relative influence of local versus landscape characteristics. All three facets of assemblage-level diversity exhibited degradation in the secondary forest matrix around the smallest fragments compared to continuous forest. This negative effect became less pronounced as fragment size increased and in contrast, forest edges generally contained higher diversity. We only found subtle associations for assemblage functional diversity at landscape scale. Habitat occupancy patterns were species-specific, as were responses to fragment sizes and disturbance gradients. In particular, *Furipterus horrens* exhibited reduced activity across the whole interior-edge-matrix gradient of the smallest fragments. We found little evidence that the local or landscape variables were negatively influencing the aerial bats at guild- or species-level. Based on our findings we suggest the aerial insectivorous bat assemblage at the BDFFP could be approaching a point of recovery after 30 years of regeneration. The advanced secondary forest is buffering the pervasive effects of fragmentation and we therefore highlight the conservation value that second-growth forests can deliver within human modified landscapes and emphasise the need for them to be protected alongside primary forest areas.

Key words: Bioacoustics, Chiroptera, Fragmentation, Multiscale analysis, Neotropics

Chapter 1

General Introduction

Tropical forests

Globally, there are five main threats driving the biodiversity crisis, all of which are a direct consequence of anthropogenic activities: destruction of natural habitats, over-exploitation of Earth's natural resources, invasive species, pollution and climate change (Bellard et al., 2022). With an increasing human population, the demand for land for food production is omnipresent (Tilman et al., 2011) and tropical forests are on the front line (Roberts et al., 2021) as the agricultural frontier expands into forest habitat which is host to at least two-thirds of all terrestrial biodiversity (Gardner et al., 2009). It is estimated that around 80% of agricultural land gains in the tropics came from clearing intact and previously disturbed forests (Gibbs et al., 2010) with an estimated total of 100 million hectares deforested in the 12 years to 2012 (Hansen et al., 2013).

At a global level, tropical deforestation and degradation release carbon into the atmosphere which is estimated to account for 8% – 26% of global emissions (Sasaki et al., 2016). The process of land conversion from forest to agriculture also reduces carbon sequestration which is leading to a decline in the tropical carbon sink (Pan et al., 2011) and it is suggested that tropical forests may shift from a neutral contribution to becoming a carbon source as the effects of climate change progress (Mitchard, 2018). At local level, habitat destruction resulting from deforestation is far-reaching, causing desiccation of the ground, enhanced risk of fires and lowered productivity of surrounding forest areas (Foley et al., 2007). It divides remaining habitat, isolating forest remnants which are left embedded in a matrix of land which has been modified for human use (Haddad et al., 2015).

The deforestation offensive on the Amazon started in the early 1970s where the southern and eastern edges saw the most dramatic loss of forest cover (Fearnside, 2005). The Brazilian National Institute for Space Research (INPE) started monitoring deforestation and forest degradation in the early 1980s and performs annual mapping via PRODES (Deforestation Monitoring Project in the Legal Amazon by Satellite; Dos Santos et al., 2021). As a result of government initiatives to control deforestation and reduce greenhouse gas emissions, Brazil achieved a significant and steady reduction from a peak in 2004, when ~28,000 km^2 of forests were cleared, to less than 7,000 km^2 deforested in 2011 (Davidson et al., 2012). A deforestation target was established which would have seen a maximum forest loss in 2020 of 3,925 km^2 (Silva Junior et al., 2021) and Brazil leading the way on climate change. Instead, deforestation rates began to rise in 2012 and have sharply accelerated since Jari Bolsonaro was elected president in 2019, evidenced by a 34% increase on the previous year of 10,100 km^2 of forest cleared between August 2018 and July 2019 (Escobar, 2020).

Fragmentation

Fragmentation is a landscape-scale process whereby continuous habitats are separated or divided (Fahrig, 2003). This can occur naturally, for example, a river/waterfall coursing through a forested landscape, mountainous outcrops amongst alpine grasslands or naturally occurring volcanic islands surrounded by water. Under natural circumstances species in these separated habitats can become isolated and over time speciation can occur. The Galapagos finches would be a prominent example of this (Farrington et al., 2014). It is also this isolation which increases the extinction risk of isolated populations where gene flow is restricted (Miyanzono & Taylor, 2013).

Fragmentation caused by anthropogenic activity typically includes significant habitat loss, whereby the core habitat is reduced in size and shape, there is increased edge habitat at the margins of the artificially created fragments and the permeability of the matrix surrounding the fragments will influence the ability of species to move through it (Ewers & Didham, 2006). This connectivity between remaining core habitat and the species persisting following human-induced fragmentation was first described under the lens of Island Biogeographic Theory (IBT), which sought to predict species loss on islands surrounded by a 'hostile' matrix of water (MacArthur & Wilson, 1967). However, further exploration of species diversity responses to fragmentation uncovered limitations of IBT and alternative frameworks such as Countryside Biogeography were developed which better explained species' responses in terrestrial fragmented landscapes (Daily, 1997, Mendenhall et al., 2013). This framework helps to understand the conservation potential of human-dominated landscapes, acknowledging that composition and configuration of the core habitat, the quality of the intervening matrix habitat, and its permeability will strongly influence species responses to habitat fragmentation (Daily, 2003; Mendenhall et al., 2014).

The physical and biotic changes that occur at and within the edge habitat, termed 'edge effects', have a dramatic impact at species population level, the effects also radiate out and are detrimental to the wider community and ecosystem as a whole (Laurance et al., 2007). The penetration distance of most edge effects is between 100 and 300m from the habitat edge, however effect distances can extend considerably beyond these distances into forest interiors and these effects can be strongly influenced by the surrounding matrix habitat (Laurance et al., 2002). Matrix habitats can act as selective filters, either facilitating or impeding movement between forest fragments (Gascon et al., 1999), with agricultural land representative of a high-contrast matrix and regenerated second-growth forest indicative of a low-contrast matrix (Watson, 2002). A significant proportion of tropical fragmented landscapes have been recolonised by successional forests following deforestation and subsequent abandonment which is commonly associated with agricultural land-use change (Chazdon, 2014). These second-growth forests are a significant feature in the Amazon, covering an estimated ~235,000 km^2 by 2017 (Smith et al., 2021), and have a mean age of approximately 5 years (Neeff et al., 2006). They are capable of buffering the pervasive effects of fragmentation, and as they mature, can support diverse assemblages as species from remaining forest fragments reinhabit (Barlow et al., 2007, Chazdon et al., 2009).

Biological Dynamics of Forest Fragments Project

The Biological Dynamics of Forest Fragments Project (BDFFP) was created in 1979 by Thomas Lovejoy and is the world's largest and longest running experimental study focused on the effects of fragmentation, landscape dynamics, forest regeneration and how regional and global changes affect plant and animal communities (Laurance et al., 2002). The study landscape spans ~1000 km^2 and is located 80km north of Manaus, Brazil. The topography is relatively flat (80-160 m), with many small streams cutting through the nutrient-poor soil (Laurance et al., 2011). Annual rainfall varies from 1900 to 3500 mm with a dry season between July and November (Ferreira et al., 2017) and the temperatures range from 19 ºC to 39 ºC, with an average of 26 ºC (de Oliveira & Mori, 1999).

The study area consists of three large cattle ranches (~5000 ha each), which were cleared of continuous old-growth terra firme rainforest to accommodate cattle pastures. Researchers, in cooperation with the ranchers, preserved old-growth forest fragments of varying sizes (1, 10 and 100 ha) which were isolated from continuous forest by distances of 80–650 m (Bierregaard et al., 1992). In the late 80's the ranches were abandoned due to low productivity and a change in government land incentives. Successional forests began to establish in the matrix around the fragments and to maintain isolation of the fragments a strip of vegetation (100m wide) is cleared and burned periodically (Laurance et al., 2018). The established second-growth forest has been regenerating for at least 30 years. Canopy height is circa >20 m tall and (Laurance et al., 2018) and some areas have developed into species-rich, well-structured forests (Longworth et al., 2014).

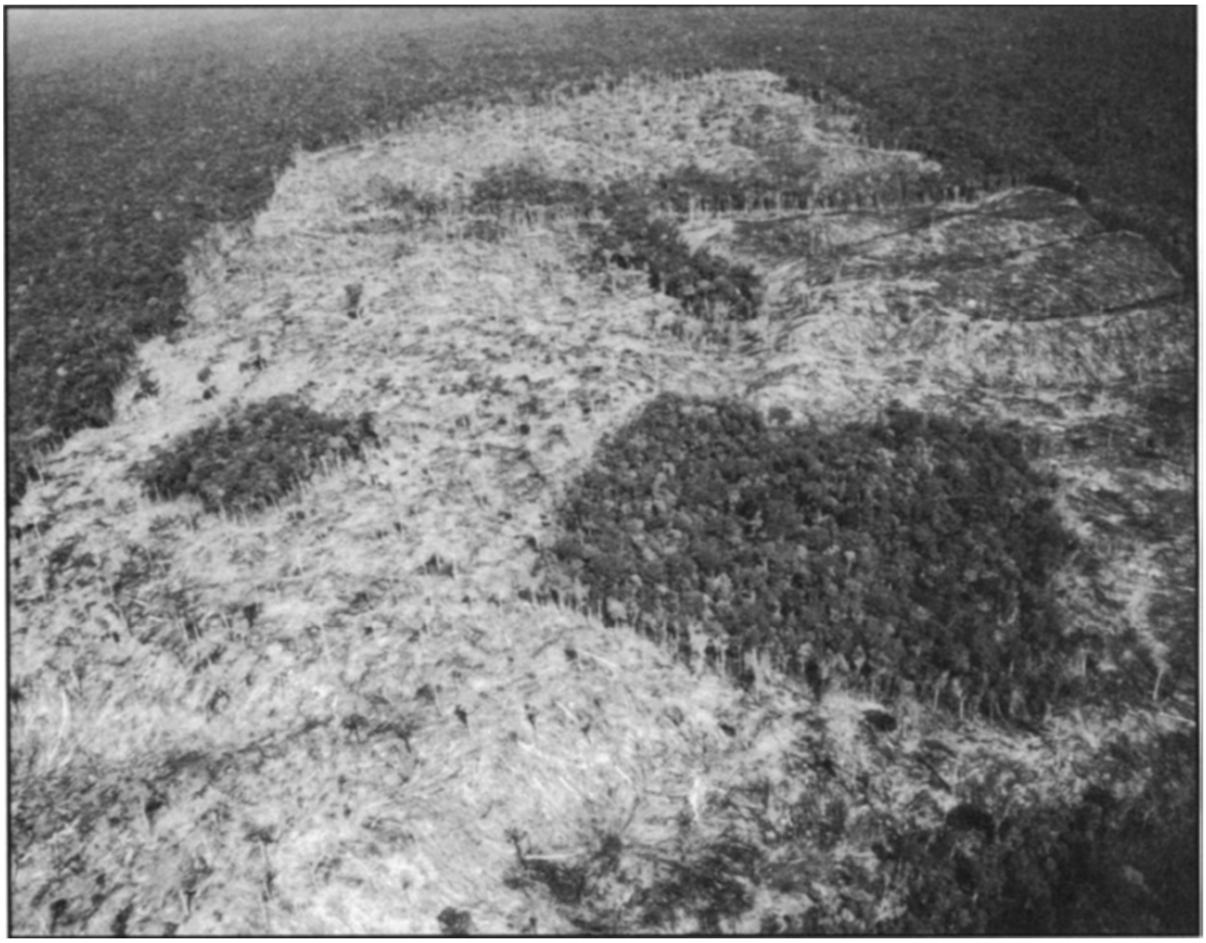

Fig. 1.1 Aerial photograph of a 10 ha and a 1 ha fragment following isolation (Photo sourced from Bierregaard et al., 1992)

Neotropical bats

Bats are the most widely distributed terrestrial mammals on earth (Frick et al., 2020) and there are currently 1456 recognised species within the order Chiroptera (Simmons & Cirranello, 2022). More than 180 species are known to occur in Brazil (Garbino et al., 2022), with diversity hotspots in the Amazon basin where up to 100 species can be found living sympatrically (Rex et al., 2008). Ninety-three species belong to the family Phyllostomidae and the remaining 88 species belong to 8 families which make up the aerial insectivorous bat ensemble (Emballonuridae, Furipteridae, Molossidae, Mormoopidae, Thyropteridae, Vespertilionidae, Noctilionidae and Natalidae) (Garbino et al., 2022).

Phyllostomids are best sampled with mist nets, a technique which has been used for over 100 years (MacSwiney et al., 2008). Aerial insectivorous bats forage and navigate exclusively via echolocation (Denzinger & Schnitzler, 2013). They are highly capable of detecting and avoiding mist nets, making them notoriously difficult to sample with this method (Marques et al., 2016). The aerial insectivorous bat ensemble is most efficiently sampled using ultrasound detectors to record echolocation calls (MacSwiney et al., 2008). The legacy of traditional mist netting techniques has led to a greater accumulation of knowledge for phyllostomids, with most aerial insectivorous species being omitted from community analyses (Cunto & Bernard, 2012). As a taxon, they possess positive qualities which make them ideal bioindicators including gradual responses to anthropogenic stress, rapid population decline, high species richness and global occurrence, but they are also difficult to detect, surveying technology can be costly, and a high degree of expertise is required to identify species (Russo et al., 2021).

Bat responses to fragmentation in the BDFFP

Unlike for other taxa, no baseline data was collected on the bat assemblage prior to forest clearing at the BDFFP. In the late 90's, the first project commenced shedding light on the BDFFP's bat fauna (Sampaio, 2000; Sampaio et al., 2003). Research focused on phyllostomids now includes: effects of forest fragmentation on taxonomic (Bernard & Fenton, 2002), functional (Farneda et al., 2018a; Farneda et al., 2018b; Farneda et al., 2020) and phylogenetic diversity (Aninta et al., 2019; Farneda et al., 2022), effects of second-growth forest (Bobrowiec & Gribel, 2010; Rocha et al., 2018), effect of small forest clearings (Rocha et al., 2017c; Rocha et al., 2020), trait-related responses (Farneda et al., 2015), gender-specific responses (Rocha et al., 2017a), seasonal responses (Ferreira et al., 2017), diet, activity and reproduction (Bernard, 2002), vertical stratification (Bernard, 2001; Silva et al., 2020), seed dispersal (Wieland et al., 2011) and the importance of local and landscape-scale effects (Rocha et al., 2017b).

Adrià López-Baucells was the first researcher to sample the BDFFP aerial insectivorous bat ensemble with bioacoustics (López-Baucells, 2019) and produce the first Field Guide to the Bats of the Amazon, featuring echolocation keys and descriptions (López-Baucells et al., 2016). Research on the aerial insectivorous bat fauna has investigated: optimising bioacoustics surveys (López-Baucells et al., 2021), combining acoustic automated classifiers with manual validation (López-Baucells et al., 2019), trait correlates of fragmentation vulnerability (Núñez et al., 2019), the importance of lakes in Amazonian rainforests (Torrent et al., 2018) responses to moonlight (Appel et al., 2021) and edge effects (Yoh et al., 2022). This thesis will further add to the expanding body of work on the aerial insectivorous bat fauna at the BDFFP.

The general objective of this thesis is to use a multiscale approach to investigate the assemblage-, guild- and species-level responses of aerial insectivorous bats to the interior-edge-matrix disturbance gradient, fragment size as well as local and landscape characteristics. Specifically, I will focus on two areas which each represent an independent research paper:

1. Interplay between local and landscape-scale effects on the taxonomic, functional and phylogenetic diversity of aerial insectivorous Neotropical bats (López-Baucells et al., 2022)
2. 30 years of regeneration: local- and landscape-scale effects on Neotropical aerial insectivorous bat species buffered by second-growth forest

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Chapter 2

Interplay between local and landscape-scale effects on the taxonomic, functional and phylogenetic diversity of aerial insectivorous Neotropical bats

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Abstract

Human-modified landscapes are globally ubiquitous. It is critical to understand how habitat loss and fragmentation impact biodiversity from both a local habitat context and landscape-scale perspective to inform land management and conservation strategies. We used an experimentally fragmented landscape in the Brazilian Amazon to investigate variation in aerial insectivorous bat diversity in response to local habitat and wider landscape characteristics, applying a multiscale approach. We conducted bat acoustic surveys at 33 sites, comprising old secondary forests and fragments of primary forest. Taxonomic, functional and phylogenetic diversity facets were calculated within a Hill numbers framework. We analysed responses to fragment size, interior-edge-matrix gradients, as well as local vegetation structure, continuous forest cover, edge density and patch density across five spatial scales (0.5 km - 3 km) surrounding detector locations. Compared with continuous forest, secondary forest matrix around the smallest fragments harboured lower diversity. The overall negative effect of the matrix became less pronounced with increasing fragment size. In contrast, forest edges generally contained higher taxonomic, functional and phylogenetic diversity. We found subtle scale-sensitive associations for FD, responding positively to forest cover (at the 1 km scale) and negatively to edge (1 km scale) and patch density (2.5 km scale). Despite a low-contrast matrix of tall secondary forest surrounding fragments after ~30 years of forest recovery, aerial insectivorous bat diversity is not comparable to continuous primary forest. Assemblage functional diversity responds to compositional and configurational landscape characteristics at scales deserving further evaluation at guild and species level.

Keywords: Amazon, Fragmentation, Landscape context, Diversity dimensions, Multiscale analysis

Introduction

Globally, over the past 300 years, there has been a net forest loss of ~7-11 million km^2, primarily due to logging and conversion to agricultural use (Foley et al., 2005). Loss of suitable habitat to sustain species populations leads to an overall increased risk of extinction (Ceballos et al., 2015; Powers & Jetz, 2015; Ceballos et al., 2017). Forest patches of varying sizes and shapes, embedded in various land cover types, are conspicuous features of present-day human-modified landscapes (Melo et al., 2013). The link between remaining native habitat and the species persisting in the aftermath of habitat fragmentation was first described through the lens of Island Biogeography Theory, which sought to predict species loss on islands surrounded by a ‘hostile’ matrix of water (MacArthur & Wilson, 1967). Yet, mounting evidence now supports that the structure and composition of the intervening matrix significantly affect species’ persistence in adjoining forest fragments, a dynamic that is better conceptualised under alternative theoretical frameworks, such as Countryside Biogeography (Daily, 1997; Mendenhall et al., 2013). Through this framework, community changes in modified landscapes are forecast based on the interaction between the species’ spatial requirements and their tolerance towards matrix habitats, thus offering a more realistic portrait of biodiversity persistence in landscapes with matrix habitats more salubrious than water (Mendenhall et al., 2014; Wolfe et al., 2015; Farneda et al., 2020).

In the Amazon, deforestation rates dropped from 30,000 km^2/year in the 1980s to 5,843 km^2/year in 2013 (Davidson et al., 2012; Nepstad et al., 2014). However, since 2013, alongside the main driver of deforestation in the Amazon, pasture expansion for cattle production (Skidmore et al., 2021), compounding threats such as oil palm plantations (Butler & Laurance, 2009), expanding soy agriculture (Rosa et al., 2017) and dam development (Lees et al., 2016) have contributed to a sharp increase. Much of this deforested land has been abandoned, and a recent study estimates a total of 262,791 km^2 of recovered secondary forests in Brazil between 1986 and 2018 (Silva Junior et al., 2020). Secondary forests make up a significant proportion of fragmented tropical landscapes (Chazdon et al., 2009; Chazdon, 2014). A growing body of literature supports that these regenerating forests can alleviate fragmentation impacts and support diverse assemblages and overall ecosystem functioning (Spake et al., 2015; Farneda et al., 2018; Rocha et al., 2018; Rozendaal et al., 2019).

The Neotropics are a major hotspot of chiropteran diversity and the Amazon basin, with over 160 species, is especially rich (López-Baucells et al., 2016). Throughout the region, bats play essential roles in countless ecological networks and provide valuable ecosystem services such as seed dispersal, pollination and arthropod population regulation (Aguiar et al., 2021; Ramírez-Fráncel et al., 2022). They are demonstrably sensitive to habitat loss, fragmentation, and habitat degradation (reviewed in Meyer et al., 2016) and have become a popular indicator group of environmental disturbance (Cunto & Bernard, 2012). Yet, while the consequences of anthropogenic forest fragmentation for phyllostomid bats have received substantial research attention (e.g., Klingbeil & Willig, 2009; Avila-Cabadilla et al., 2014; García-García et al., 2014; Arroyo-Rodríguez et al., 2016; Muylaert et al., 2016; Silva et al., 2020; Farneda et al., 2022), aerial insectivores - non-phyllostomid counterparts - have largely been neglected and their responses to habitat fragmentation remain understudied (but see e.g., Estrada-Villegas et al., 2010; Rodríguez-San Pedro & Simonetti 2015; Núñez et al., 2019).

Measures of diversity based solely on traditional species counts fail to encapsulate the complexities associated with the distinct functional roles of different species or the evolutionary history contained within a given assemblage (Cadotte et al., 2013). A multifaceted approach considering the complementary taxonomic, functional and phylogenetic dimensions of diversity can provide a more detailed and comprehensive understanding of the drivers of biodiversity change across human-modified landscapes (Swenson, 2011). However, studies simultaneously assessing how multiple dimensions of Neotropical bat diversity are affected by habitat gradients are still scarce (Cisneros et al., 2014; Frank et al., 2017; Carrasco-Rueda & Loiselle, 2020; Carvalho et al., 2021), particularly for aerial insectivores (but see e.g., Pereira et al., 2018).

Amongst the research questions commonly posed by fragmentation studies, the role of fragment size, edge effects, and compositional vs configurational aspects of the landscape has rarely been addressed for aerial insectivorous bats. Here, we set out to help fill this gap by investigating how local vegetation structure and landscape composition and configuration affect this ensemble along a disturbance gradient formed by continuous primary forest (CF) and primary forest fragment interiors (I), forest edges (E) and secondary forest matrix (M) habitats (hereinafter IEM gradients; *sensu* Rocha et al., 2017a). Specifically, we aimed to address two objectives:

1) Quantify between-habitat differences in the taxonomic, functional and phylogenetic diversity of aerial insectivorous bats along IEM and fragment-size gradients. We anticipated (i) that assemblages in CF are taxonomically, functionally and phylogenetically most diverse, with diversity being eroded through fragment interiors (<10 ha) and further still in the matrix, (ii) similar levels of diversity in CF and larger fragments (100 ha), with a reduction in the three biodiversity dimensions with decreasing fragment size (10 and 1 ha), (iii) a positive response of all three diversity facets at the fragment edges as more species are able to take advantage of foraging opportunities along the ecotone.
2) Assess the importance of the following variables as determinants of assemblage diversity, using a multiscale approach; local vegetation structure, landscape composition (forest cover), and landscape configuration (edge density and patch density). We predicted that (i) all taxonomic, functional and phylogenetic diversity would exhibit only subtle

responses to the local and landscape characteristics, (ii) local vegetation structure would generally have a weaker effect than landscape metrics and, when present, would manifest at the smallest scale (0.5 km), possibly turning neutral as the scale increases, (iii) forest cover would be the most important predictor of all three diversity facets at the landscape scale, similar to findings for the species richness and abundance of phyllostomids (Rocha et al., 2017a).

Materials and methods

Study area

Fieldwork was conducted at the Biological Dynamics of Forest Fragments Project (BDFFP), located ~80 km north of Manaus, Central Amazon, Brazil (see Fig. 1). Established in 1979, the BDFFP is the world's largest and longest running experimental study focused on habitat fragmentation, landscape dynamics, forest regeneration, and regional and global changes affecting plant and animal communities (Laurance et al., 2018). The topography of the ~1000 km^2 study area is relatively flat, with many small streams cutting through the nutrient-poor soil. Annual rainfall varies from 1900 to 3500 mm with a moderately strong dry season from June to October (Laurance et al., 2011). The area is characterised by a mosaic of primary forest fragments embedded in a second-growth forest matrix surrounded by large areas of continuous *terra firme* forest. The fragments were first isolated through logging and burning for cattle pasture in the early 1980s. Fragments of different sizes (1 ha, 10 ha and 100 ha) were isolated from CF by distances ranging from 80–650m. Following the abandonment of the cattle ranches, the second-growth forest matured around the fragments over ~30 years (Laurance et al., 2018), creating a landscape of low structural fragment-matrix contrast (Fig. 2.1). A 100 m-wide strip of regrowth vegetation has been cleared on at least five occasions since fragments' creation to maintain their integrity. The last re-isolation event prior to data collection for this study occurred between 1999–2001 (Rocha et al., 2020).

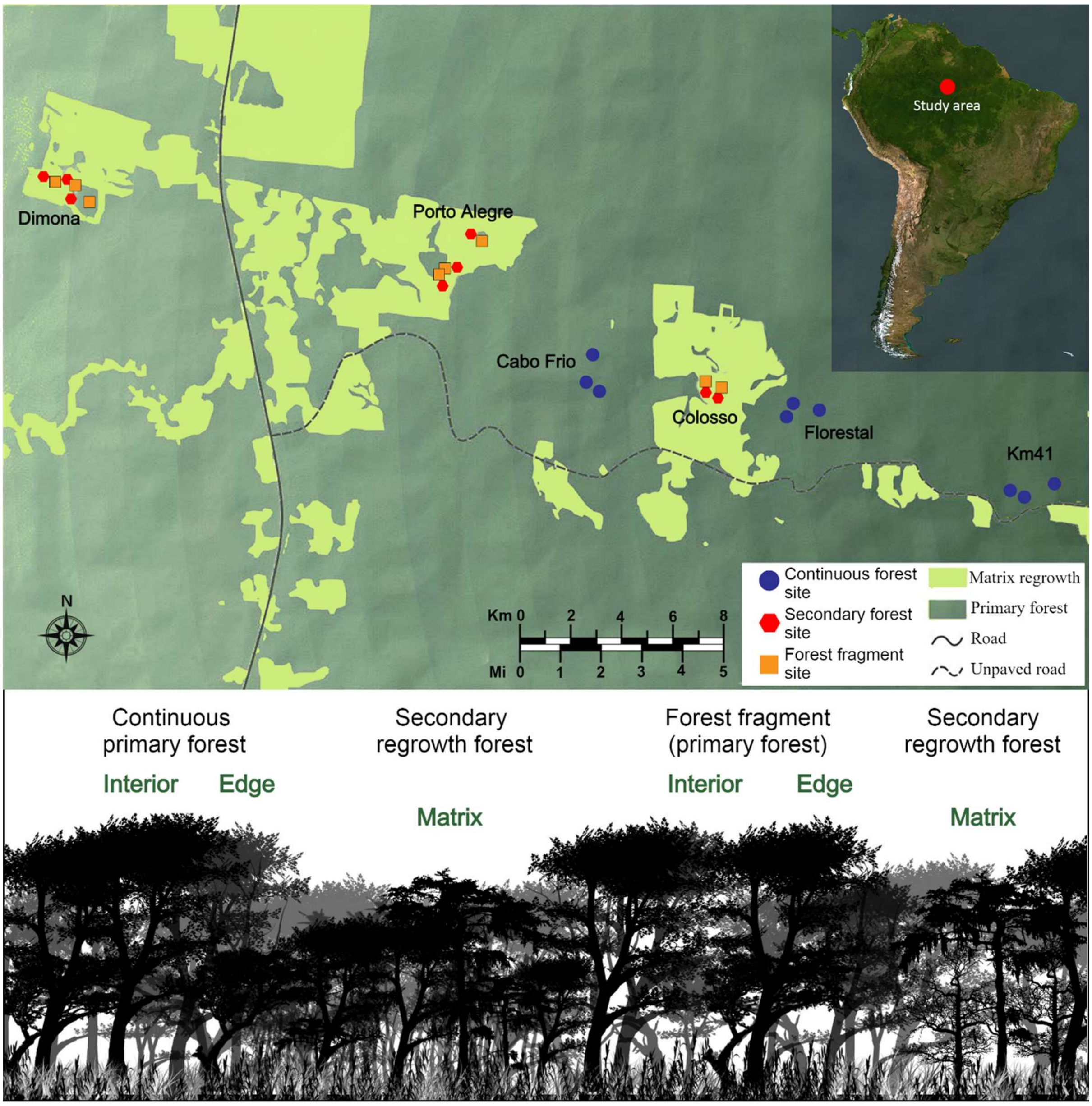

Fig. 2.1 Map of the study area at the BDFFP, Central Amazon, Brazil and schematic representation of the BDFFP landscape during data collection (2011-2013), illustrating the low structural contrast between the continuous forest, late-stage secondary regrowth forest matrix (approximately 30 years of regeneration) and forest fragments

Bat surveys

Acoustic data were collected between 2011-2013 in both the interior and at the edges of eight forest fragments (three of 1 ha, three of 10 ha, two of 100 ha), eight secondary forest sites (located 100 m into the matrix from the nearest fragment edge) and nine control sites in three continuous forest areas. Recordings were obtained with SM2Bat+ detectors with omnidirectional microphones SMX-US (Wildlife Acoustics Inc., Massachusetts, USA). At each site, the detector was positioned at ~1.5 m height and programmed to record from 18:00

to 06:00. Recordings were captured in real time with a full spectrum resolution of 16-bit, with a high pass filter set at fs/32 (12kHz) and a trigger level of 18SNR. Sites were sampled for one night each survey during the first year (2011) and five consecutive nights thereafter (2012-2013). Four surveys were conducted annually, two in the wet season and two in the dry season.

Sound analysis

Recordings were manually analysed with Kaleidoscope 4.0.4 software (Wildlife Acoustics Inc., Massachusetts, USA) following the acoustic key in López-Baucells et al., (2016) and a local reference call library (A. López-Baucells, *unpublished data).* Calls were identified to species level where possible or assigned to groups of taxa with similar calls (sonotypes). A total of 21 species/sonotypes were identified (Table S2.1). Since it is not possible to estimate abundance with acoustic data, we used activity as a proxy of abundance based on the number of bat passes (Rowse et al., 2016). The sample unit, a bat pass, was defined as any call sequence with a maximum duration of 5 s, which contained at least two distinguishable echolocation pulses (Torrent et al., 2018; López-Baucells et al., 2021). Bat activity was quantified by the total number of bat passes per night per species/sonotype.

Calculation of diversity response metrics

We calculated taxonomic (TD), functional (FD) and phylogenetic (PD) alpha diversity using a unified framework based on Hill numbers. Hill (1973) integrated species richness, the converted Shannon entropy and Gini-Simpson index measures into a family of diversity measures by order q or the effective number of species. The sensitivity of the measure to the relative frequency of species is determined by the parameter q and is expressed in units of species. Hill numbers offer advantages over standalone diversity measures, including satisfying the mathematical replication principle, allowing for direct comparison across orders q due to values being expressed as units of effective number of species. They can be partitioned into independent group components and by doing so can be generalised to taxonomic, functional, and phylogenetic diversities providing a unified framework for measuring biodiversity (Chao et al., 2014). Using the R package 'hillR' (Li, 2018), we calculated each diversity facet based on total bat activity per site and per night using the Hill numbers framework. Diversity values become more sensitive to common species as q increases. When $q = 0$, species/sonotype abundance is ignored (species richness); $q = 1$, all species/sonotypes are weighted by their abundance equally (Shannon diversity (the exponential of entropy)); $q = 2$, greater weight is placed on common than rare species/sonotypes (Simpson diversity (inverse of the Simpson index)). We calculated all three *q* values (0, 1 and 2), representing a full diversity profile illustrating the species abundance differentiation of the assemblage. For FD, we selected functional traits that have been shown to indicate potential vulnerability to habitat fragmentation in aerial insectivorous bats (Núñez et al., 2019). Trait information on echolocation call structure, frequency and alternation, body mass, aspect ratio and relative wing loading, as well as vertical stratification were considered, encompassing both continuous and categorical data (Table S2.2). To adhere with the Hill number framework, each 'species/sonotype' must be a distinct entity with its own (attribute) diversity data (Chiu & Chao, 2014). Complete trait data was not available for *Saccopteryx gymnura*, thus, calls of this species were removed from the analysis (1817 calls in total). Also, for molossid sonotypes, body mass, aspect ratio and relative wing loading were calculated using the mean of values for individual species within each sonotype. To quantify PD, phylogenetic information was extracted from a species-level supertree for bats (Shi & Rabosky, 2015) and pruned to include only the species of aerial insectivorous bats known to occur at the BDFFP (Fig. S2.1). Again, the 'hillR' methodology required a single entity species to be selected from the supertree, therefore to deal with sonotype data, we selected a single representative species, based on the likelihood of occurrence at the BDFFP, for the PD analysis; Molossidae II - *Molossus rufus*, Molossidae III - *Eumops auripendulus*, Molossops I - *Molossops neglectus* and Promops I - *Promops centralis* (Table S2.3). *Pteronotus alitonus* was not present in the supertree and so was replaced by its closest congener, *Pteronotus parnellii* (Pavan et al., 2018). It has been argued that this approach of substitution by close congeners does not cause serious changes in the distance matrices (Cisneros et al., 2014).

Local and landscape predictor variables

Local vegetation structure

Local vegetation structure was quantified within three plots of 100 m^2 (5×20 m) around the detector locations at each of the 33 sampling sites. In each plot, seven variables were assessed (details in Rocha et al., 2017a): i) number of trees (> 10 cm diameter at breast height [DBH]), (ii) number of woody stems (<10 cm DBH), (iii) average DBH of trees >10 cm, (iv) percentage canopy cover, (v) liana density (visually classified every 5 m in five categories varying from no lianas to very high liana density), (vi) canopy height (based on visual estimation) and (vii) vertical stratification in vegetation density. Vegetation variables were submitted to a Principal Component Analysis (PCA), and scores from the first axis (PCA1) were retained as predictor metric summarising local vegetation structure for use in subsequent modelling. PCA1 represented vegetation structure and explained 38.3% of the total variance (Fig. S2.2; Table S2.4). This first component was positively correlated with average DBH of trees >10 cm, canopy height and percentage canopy cover. Although these features describe more structurally complex habitats, the metric represented a gradient, including negative values, characteristic of secondary regrowth (matrix), with an increased number of woody stems and liana density.

Landscape structure

Landscape composition and configuration were quantified using 2011 LandSat Thematic Mapper ™ satellite images (30 m spatial resolution) with continuous forest and secondary forest land cover classes identified. Collinearity is a common problem with landscape predictor variables. Therefore, we selected the same three landscape metrics as Rocha et al., (2017a), which were acceptable based on variance inflation factor calculations (VIF). Metrics of landscape composition (primary forest cover) and configuration (patch density, edge density) were calculated using the R package ‘landscapemetrics’ (Hesselbarth et al., 2019). Circular buffers were defined with radii of 0.5, 1, 1.5, 2, 2.5, and 3 km around the 33 sampling sites. In selecting these buffer sizes, we took into consideration the observed scale of effect for bats (Jackson & Fahrig 2015) and their utilisation in other tropical aerial insectivorous bat studies (e.g., Rodríguez-San Pedro & Simonetti 2015; Ongole, 2018; Rodríguez-San Pedro et al., 2019; Falcao, 2021; López-Bosch et al., 2021). Although it is acknowledged that overlapping landscape buffers may not necessarily violate statistical independence (Zuckerberg et al., 2020), we chose not to investigate radii larger than 3 km to minimise spatial overlap between sites (Meyer & Kalko, 2008). At each spatial scale, we first fitted a linear model between the landscape composition variable (primary forest cover) and the landscape configuration variables (edge and patch density) (Trzcinski, 1999). The residuals of the simple linear regression were then extracted and new configuration variables were created for use in subsequent modelling (Bélisle, 2001; Klingbeil & Willig, 2010).

Modelling Taxonomic, Functional and Phylogenetic diversity

The diversity metrics (TD, FD, PD / $q = 0$, $q = 1$, $q = 2$) were modelled 1) with the fragment size/IEM variables (see below) and 2) the local- and landscape-scale variables, using Bayesian generalised linear mixed-effects models (GLMMs) as implemented in package MCMCglmm (Hadfield, 2010). A measure of significance of the difference between effects (p_{MCMC}) can be produced via the proportional overlap of the distribution estimates produced, accompanied by an estimate of the mean and 95% credible intervals without post-hoc tests (Sweeny et al., 2021). For fragment size/IEM variables we fit a set of nine models, three for each diversity facet (TD, FD, PD / $q = 0$, $q = 1$, $q = 2$), specifying a single categorical fixed effect with combined information on the fragment size and IEM gradient (10 categories: continuous forest interior, 100 ha interior, 100 ha edge, 100 ha matrix, 10 ha interior, 10 ha edge, 10 ha matrix, 1 ha interior, 1 ha edge, 1 ha matrix; Rocha et al., 2017a) and incorporated research camp location as a random effect. To model local- and landscape-scale variables, we fit a set of models using each by site alpha diversity metric (TD, FD, PD / $q = 0$, $q = 1$, $q = 2$) in turn, with four fixed effect local and landscape-scale variables (local vegetation structure, continuous forest cover, edge density, patch density) for each buffer size (0.5, 1, 1.5, 2, 2.5 and 3 km) and research camp location as a random effect. Each model set contained six full models and nine sets were run in total. All models were fitted with a Gaussian error distribution and a "non-informative" prior, which is weakly informative and is equivalent to an inverse-gamma prior with shape and scale equal to 0.001 (Gelman, 2006; Wilson et al., 2010).

Parameter sampling

Using the MCMCglmm package, each model chain was run for 50000 iterations. As the chain begins to run the early samples may show a strong dependence on the starting parametrisation. As such, we allowed 5000 iterations to pass before the samples were stored (burn-in period) and estimates were retained every 10 iterations (thinning interval) following burn-in. We then evaluated convergence through (a) visual check of parameter time series representations, i.e. trace plots, (b) calculation of the lag k autocorrelation statistic to check lag progress and independence of posterior distribution samples, and (c) calculation of the Gelman-Rubin diagnostic statistic (comparison of four chains). All point estimates of potential scale reduction factor were <1.1, indicating good convergence (Gelman & Rubin, 1992). All models achieved convergence. Posterior distributions for the predictor variables were obtained. As model output, we report posterior means, 95% credible intervals and Bayesian p-values (p_{MCMC}) indicating the significance of variables with a threshold of $^{*}\ p_{\mathrm{MCMC}} < 0.05$, $^{**}\ p_{\mathrm{MCMC}} < 0.01$, $^{***}\ p_{\mathrm{MCMC}} < 0.001$.

Results

Across the 33 sites, 281,425 bat passes were analysed belonging to 20 different species/sonotypes from five different families (Table S2.1). Given that there were a number of species/sonotypes with low call numbers we present here the results for Hill numbers of order $q = 2$, interpreted as the effective number of dominant or very abundant species in the assemblage. Results for *q* = 0 and *q* = 1 are included in Supplementary Material for comparison and completeness.

Fragment size and IEM gradients

The secondary forest matrix of the smallest fragments (1 ha) harboured significantly lower TD and PD compared to CF interiors (Fig. 2.2). The same was true for PD in the matrix of the 10 ha fragments, with a similar pattern of erosion exhibited for FD in the 1 ha and 10 ha fragments and TD in the 10 ha fragments, albeit not significantly so. The negative effect of the matrix gradually became less pronounced with increasing fragment size, with minimal differences evident between the 100 ha matrix sites compared with CF interiors. In contrast, the edges of the 1 ha and 10 ha fragments contained significantly higher TD, FD and PD compared with CF interiors (Fig. 2). This positive edge effect extended to even the largest fragments, with the 100 ha edge sites harbouring significantly greater PD than CF interiors (Table S2.5 for *q* = 2 (inverse Simpson) modelling results). Modelling results for *q* = 0 (Table S2.6) and *q* = 1 (Table S2.7) showed a larger number of significant effects. In particular FD was significantly reduced along with TD and PD in the matrix of the 1 ha fragments, contributing to the general pattern of significant erosion of all three diversity facets in the 1 ha fragments (Fig. S2.3).

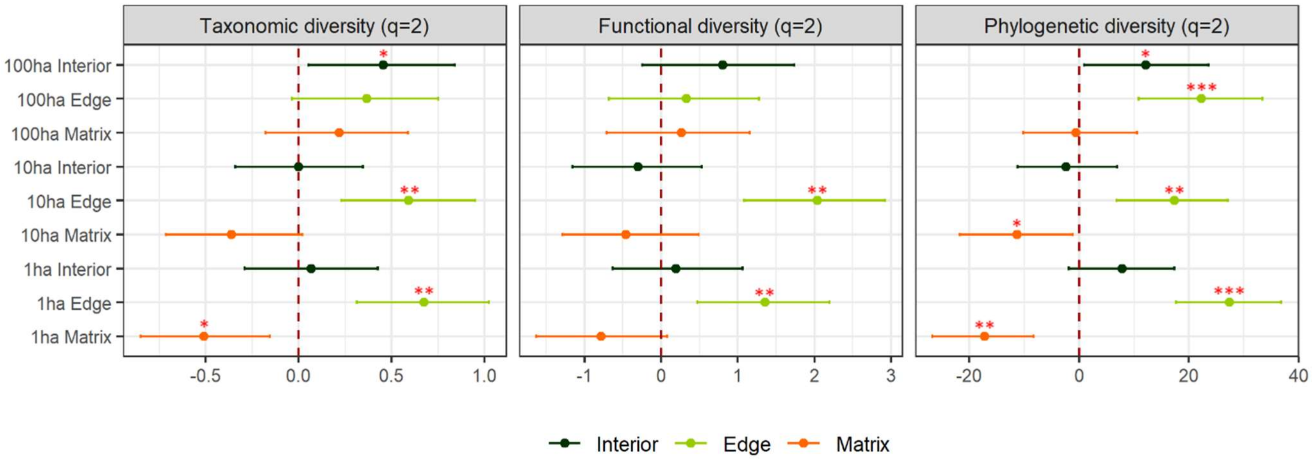

Fig. 2.2 Comparison of α-diversity metric q = 2 across the Interior-Edge-Matrix and size gradients at the Biological Dynamics of Forest Fragments Project (forest fragment interiors, forest fragment edges and adjoining secondary forest/matrix). The predicted differences between each habitat and continuous forest interior, modelled using $\text{MCMC}_{\text{GLMM}}$ are plotted with their corresponding 95% credible interval. Those which do not touch or overlap the vertical dashed line (0) are considered significant (* $p_{\text{MCMC}} < 0.05$, ** $p_{\text{MCMC}} < 0.01$, *** $p_{\text{MCMC}} < 0.001$). See Fig. S2.3 in Supplementary Material for q = 0 and q = 1

Influence of local and landscape-scale predictors

Overall, the assemblage response to local- and landscape-scale variables was subtle, with scale-sensitive associations for FD, whereas no significant relationships were found for TD or PD (Fig. 2.3). Vegetation structure does not appear to be a particularly relevant predictor of any diversity dimension. Vegetation structure had a negative relationship with FD across all diversity metrics (Table S2.6; Table S2.7; Table S2.8 for modelling output for q = 0; q = 1; q = 2), but this manifested as a significant result only for the 2.5 and 3 km scale for q = 1 (Fig. S2.5). FD responded significantly and positively to forest cover (compositional metric), and significantly and negatively to edge density (configurational metric) at the 1 km scale. These responses weakened with increasing buffer size. Finally, at the 2.5 km scale, patch density had a significant negative effect on FD (Fig. 3).

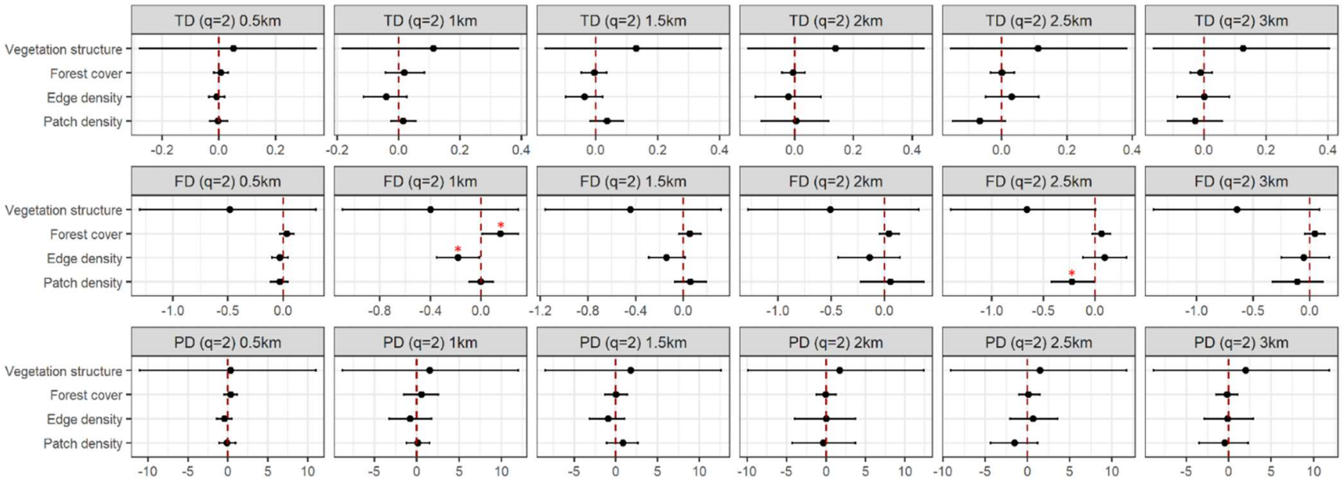

Fig. 2.3 Taxonomic, functional and phylogenetic diversity metrics $q = 2$ modelled as a function of local and landscape predictor variables (vegetation structure, forest cover, edge density and patch density) based on surveys of aerial insectivorous bats at the Biological Dynamics of Forest Fragments Project, Brazil. Shown are posterior mean estimates ± 95% credible intervals. Credible intervals which do not touch or overlap the zero line are considered significant ($^{*}\ p_{\mathrm{MCMC}} < 0.05$). See Fig. S2.4 for $q = 0$; Fig. S2.5 for $q = 1$

Discussion

Our study indicates that despite the advanced-stage secondary forest around the BDFFP fragments (~30 years), the diversity recovery of the aerial insectivorous bat assemblage in forest fragments and matrix habitats is still incomplete. Whilst our results indicated variation in FD, we found no clear evidence of the local- or landscape-scale variables analysed to accurately predict the diversity responses in our study area.

Responses to fragment size and IEM gradients

Despite the advanced stage of maturation of the secondary regrowth, its aerial insectivorous bat assemblage shows evidence of degradation compared to levels observed in CF interiors. These findings are consistent with similar phyllostomid bat studies at the BDFFP (Farneda et al., 2015; Rocha et al., 2017b; Farneda et al., 2018; Aninta et al., 2019). The loss of TD and FD in the secondary forest is likely to reduce ecosystem services provided by aerial insectivorous bats such as arthropod suppression (Kunz et al., 2011; Puig-Montserrat et al., 2015). Most importantly, our results support that specialist forest-dwelling bats might be strongly affected by deforestation even after ~30 years of forest recovery. The fact that PD is also lower in the secondary forest reflects depletion of evolutionary richness due to the loss of the overall genetic diversity of the assemblage (Struebig et al., 2011; Rivera-Ortíz et al., 2015; Edwards et al., 2021). The close relationship between the decrease in PD and the low structural complexity of secondary forests compared to CF suggests that habitat fragmentation reduces total evolutionary history by eliminating distantly related species in less complex habitats.

Forest fragment interiors were either not significantly different or slightly more diverse than CF, as was the case for the 100 ha fragments. This aligns with our prediction that diversity levels in CF and the larger fragments (100 ha) would be homogeneous, contrasting previous research on phyllostomids at the BDFFP, which found significantly lower diversity in the fragments than CF (Rocha et al., 2017a; Farneda et al., 2018; Aninta et al., 2019; Silva et al., 2020). As fragment size decreased, we found increasing erosion of all three facets of diversity in the intervening secondary matrix. Larger fragments (10 and 100 ha) and adjoining secondary forests tended to harbour higher TD, FD and PD than the smaller fragments (1 ha). The fact that TD, FD and PD in secondary forests next to the largest fragments (10 and 100 ha) were higher than in those adjoining smaller fragments (1 ha) suggests that, in this landscape, the largest fragments act as important reservoirs of aerial insectivorous bat diversity for the nearby regenerating areas.

In line with our prediction, all three diversity metrics peaked at the primary-secondary forest interface. Fragment edges were generally more diverse in TD, FD and PD than the CF and fragment interiors. Rodríguez-San Pedro et al., (2019) reported a similar positive response of aerial insectivorous bats to forest edges. The tall secondary forest at the BDFFP provides a low-contrast matrix that could facilitate connectivity, buffering the isolation effects of the smallest fragments and function as commuting corridors (Van Houtan et al., 2007; Jantzen & Fenton, 2013; Kalcounis-Rueppell et al., 2013). Coleoptera, Hymenoptera, Lepidoptera and

Araneae are among the more species-rich canopy invertebrates in tropical forests (Basset, 2001). Coleoptera and Hymenoptera are more abundant in secondary forest compared to the other habitats at the BDFFP (De Aquino et al., 2021). This increased abundance of prey items could also provide increased foraging opportunities simultaneously, for edge-, open- and interior- specialists in and around the edge habitat (Ingala et al., 2021).

Influence of local- and landscape-scale predictors

We anticipated subtle responses across the three diversity facets, but we only found statistically significant responses for FD. Uncovering significant responses at the community level is often difficult due to diversity metrics amalgamating species-specific responses that may cancel each other out (Klingbeil & Willig, 2009; López-Bosch et al., 2021).

Our results concur with some other studies on the effects of fragmentation on aerial insectivorous bats, in which community responses were muted. For instance, Estrada-Villegas et al., (2010) found that sonotype abundance levels were indistinguishable in a land-bridge island system which comprised interior and edge mainland sites and island sites (near and far/large and small) regardless of the sonotype group analysed and the level of island isolation or size. Falcão et al., (2021) compared activity levels and sonotype composition across two landscapes (forested vs deforested/pasture-dominated) in the Brazilian Atlantic Forest and found that aerial insectivorous bat community richness was not related to any landscape descriptors.

We predicted that vegetation structure would have an effect at the smallest spatial scale, possibly turning neutral at large scales. However, we found no such effect on any of the diversity facets at any scale. Our findings contradict that of Blakey et al., (2017) who utilised LiDAR technology to comprehensively scan and characterise vegetation structure and found evidence that understorey forest structure was related to overall taxonomic and functional bat diversity at the community level. In a study in Panama, density of obstacles or vegetation clutter, which restrict the flight manoeuvrability of aerial insectivorous bats, were the main factor explaining both species richness and total abundance (Estrada-Villegas et al., 2012). Aerial insectivorous bats are known to utilise vertical space in a number of ways; foraging below, at and above canopy level, with much less activity within the forest interior (Marques et al., 2015). Perhaps vegetation structure is a limiting factor, albeit the effect may not be of the same magnitude as for phyllostomids at the BDFFP, where vegetation structure was a relevant predictor of total abundance (Rocha et al., 2017a).

We only observed responses to landscape composition and configuration at the assemblage level from a FD perspective. We expected that the amount of forest cover would be an important predictor of all three diversity facets at the landscape scale, but it was only important at the 1 km scale. Some recent studies analysed the influence of landscape composition and forest cover on aerial insectivorous bat assemblages in agricultural systems (Azofeifa et al., 2019; Rodríguez-San Pedro et al., 2019; Put et al., 2019) illustrating the nuanced responses to forest cover embedded in "hard" matrix types (i.e., rice fields, vineyards, grazing lands). For instance, Azofeifa et al., (2019) found forest cover to have no effect on overall species richness or composition in a study comparing two rice field sites in Venezuela. However, forest cover had a differential effect on functional groups, with background-cluttered space species responding more sensitively to changes in forest cover than uncluttered/open space specialists. A study of vineyards in central Chile found that preservation of native vegetation cover positively affected bat diversity and species richness and that areas of landscape with more irregular and smaller patches and higher edge density facilitated a more diverse assemblage (Rodríguez-San Pedro et al., 2019).

We also found that FD responded to landscape configuration. At the 1 km scale, edge density had a negative effect, indicating that an increase in the total perimeter of edge habitat resulted in a functionally less diverse assemblage. A study quantifying edge effects across the interface of primary and secondary forest at the BDFFP suggested that the consequences of edge effects on some aerial insectivorous bat species could potentially extend for more than 2 km (Yoh et al., 2022). In contrast, at the 2.5 km scale, patch density had a positive effect, suggesting that the spatial configuration of patches at this landscape scale facilitates a more diverse assemblage. These two results for edge density and patch density agree with Chambers et al., (2016), who investigated scale dependence of habitat associations and scaling patterns of landscape metrics about bat occurrence in forests of southwestern Nicaragua and found that edge density and patch density may be as important as compositional metrics in predicting bat capture rates across multiple scales.

We have limited evidence to suggest a specific scale of effect for this community. It is reasonable to theorise that to gain access to both foraging and roost sites (landscape complementation), the species within the BDFFP community are responding, not at a single scale but across multiple scales, to both local and landscape features to secure the necessary resources (Ethier & Fahrig, 2011). We suggest that further species-specific analysis might show the complexity of responses from species within an assemblage (Rodríguez-San Pedro et al., 2019). We are currently exploring species and guild level responses, which might uncover interesting and possibly conflicting patterns that may be masking an effect in this study (Gomes et al., 2020). Appel et al., (2021) investigated the interaction between habitat and moonlight at the BDFFP and analysed aerial insectivores on a species-specific basis. They found that *Saccopteryx bilineata, Saccopteryx leptura, Centronycteris maximiliani, Cormura brevirostris, Eptesicus brasiliensis* and *Furipterus horrens* had lower activity in secondary forest and *Pteronotus alitonus* and *Furipterus horrens* showed lower activity in fragments compared to continuous forest. It is understandable to see how these contrasting species-specific preferences can make community-level interpretation challenging.

Conclusions

Our study shows that at the BDFFP aerial insectivorous bat diversity in secondary regrowth is still not comparable with that of undisturbed forest even after ~30 years of recovery. However, the low-contrast matrix at the BDFFP does, however, appear to create opportunities for aerial-hawking bats to take advantage of forest edge habitat created as a result of fragmentation. For aerial insectivorous bat diversity, specifically, this may help to buffer some of the negative isolation effects of the smaller remnants. It also reinforces the importance of including >10 ha forest patches in land management and conservation strategies to maximize bat diversity in human-modified landscapes. Whilst the effects of fragmentation manifest as different responses in aerial insectivores and phyllostomids, our findings reinforce the irreplaceable value of old-growth forest in tropical landscapes for both groups. We found significant variation in functional diversity which might be overlooked with a traditional taxonomic focus, and we observed responses to both local and landscape-scale variables at the 1 km and 2.5 km scale. We therefore recommend that future studies of tropical bats follow a multi-dimensional biodiversity approach integrated with a multiscale analysis when assessing responses to fragmentation in human-modified landscapes.

Author contributions

All authors contributed to the study conception and design. AL-B and RR collected data at the BDFFP. Data analysis was performed by AL-B and SR. The first draft of the manuscript was written by SR and all authors commented on previous versions of the manuscript and gave final approval for publication.

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Supplementary Material

Figure S2.1 Pruned phylogenetic tree depicting aerial insectivorous bat species/ sonotype

Figure S2.2 Ordination biplot of the PCA

Figure S2.3 Comparison of α-diversity metrics for TD, FD, PD; *q* = 0 (species richness) and *q* = 1 (Shannon diversity) between habitat types modelled using $\mathrm{MCMC_{GLMM}}$

Figure S2.4 TD, FD, PD metrics *q* = 0 modelled with local and landscape predictor variables

Figure S2.5 TD, FD ,PD metrics *q* = 1 modelled with local and landscape predictor variables

Table S2.1 BDFFP Bat echolocation call sonotypes and bat passes

Table S2.2 List of functional traits used to calculate functional diversity (FD)

Table S2.3 Species functional trait data used to calculate FD

Table S2.4 Vegetation principal components analysis variable loadings, eigenvalues and proportion of variance

Table S2.5 Model output comparing α-diversity metric *q* = 2 with habitat types

Table S2.6 Model output comparing α-diversity metric *q* = 0 with habitat types

Table S2.7 Model output comparing α-diversity metric *q* = 1 with habitat types

Table S2.8 Model output comparing α-diversity metric *q* = 0 with local and landscape predictor variables

Table S2.9 Model output comparing α-diversity metric *q* = 1 with local and landscape predictor variables

Table S2.10 Model output comparing α-diversity metric *q* = 2 with local and landscape predictor variables

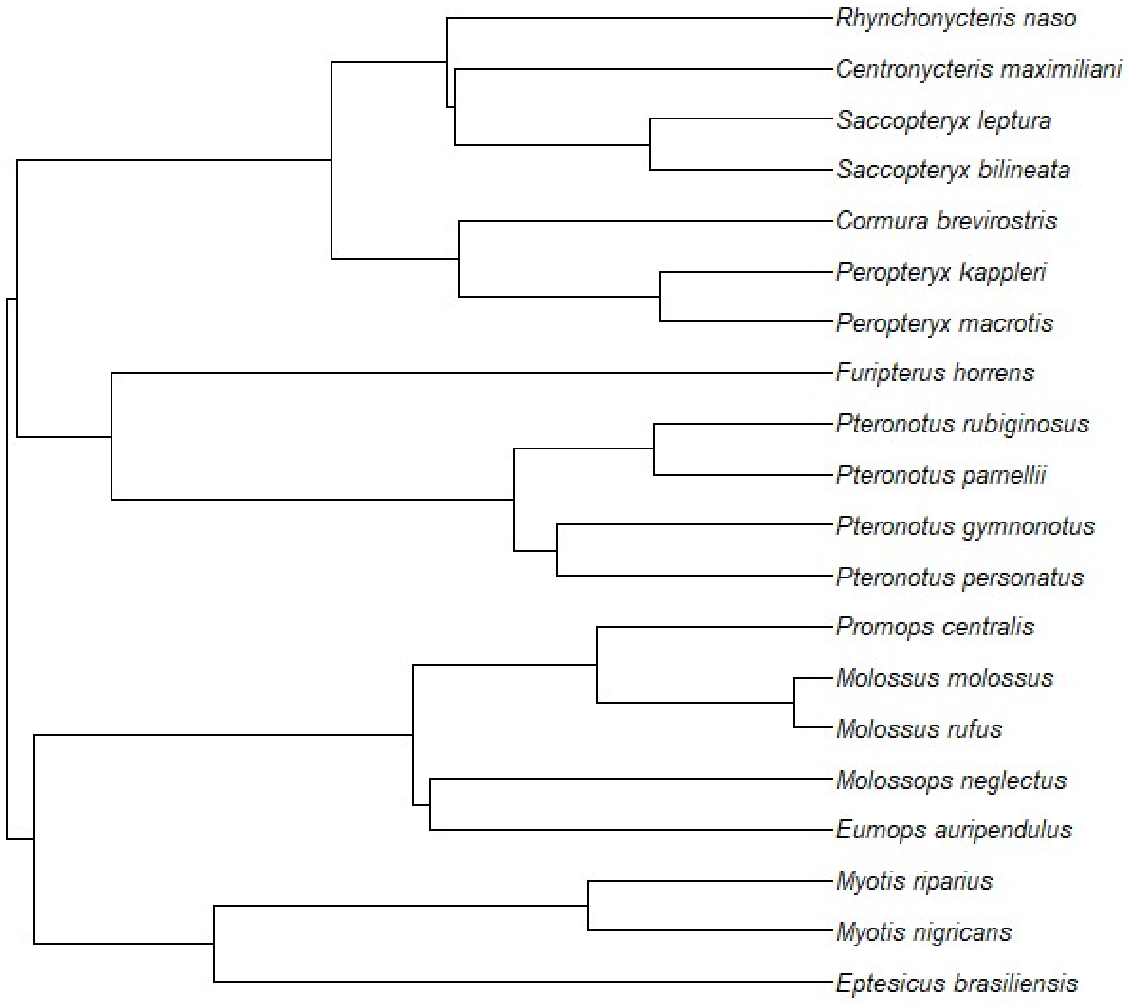

Fig. S2.1 Pruned phylogenetic tree depicting aerial insectivorous bat species /sonotype (Molossidae II; *Molossus rufus*, Molossidae III; *Eumops auripendulus*, Molossops I; *Molossops neglectus* and Promops I; *Promops centralis*) within the BDFFP landscape

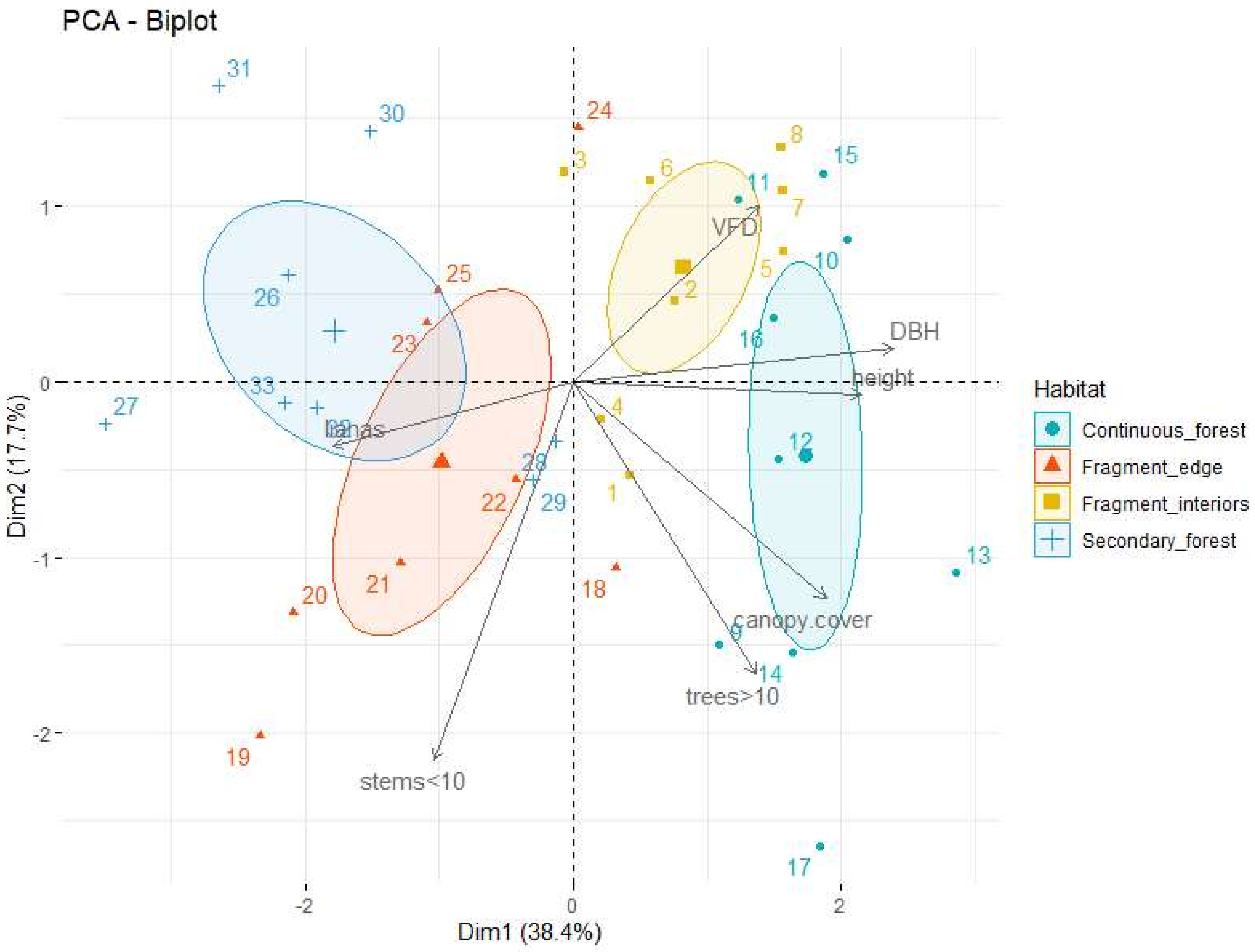

Fig. S2.2 Principal components analysis biplot examining the covariation between local vegetation structure variables across 33 sites and grouped by habitat type

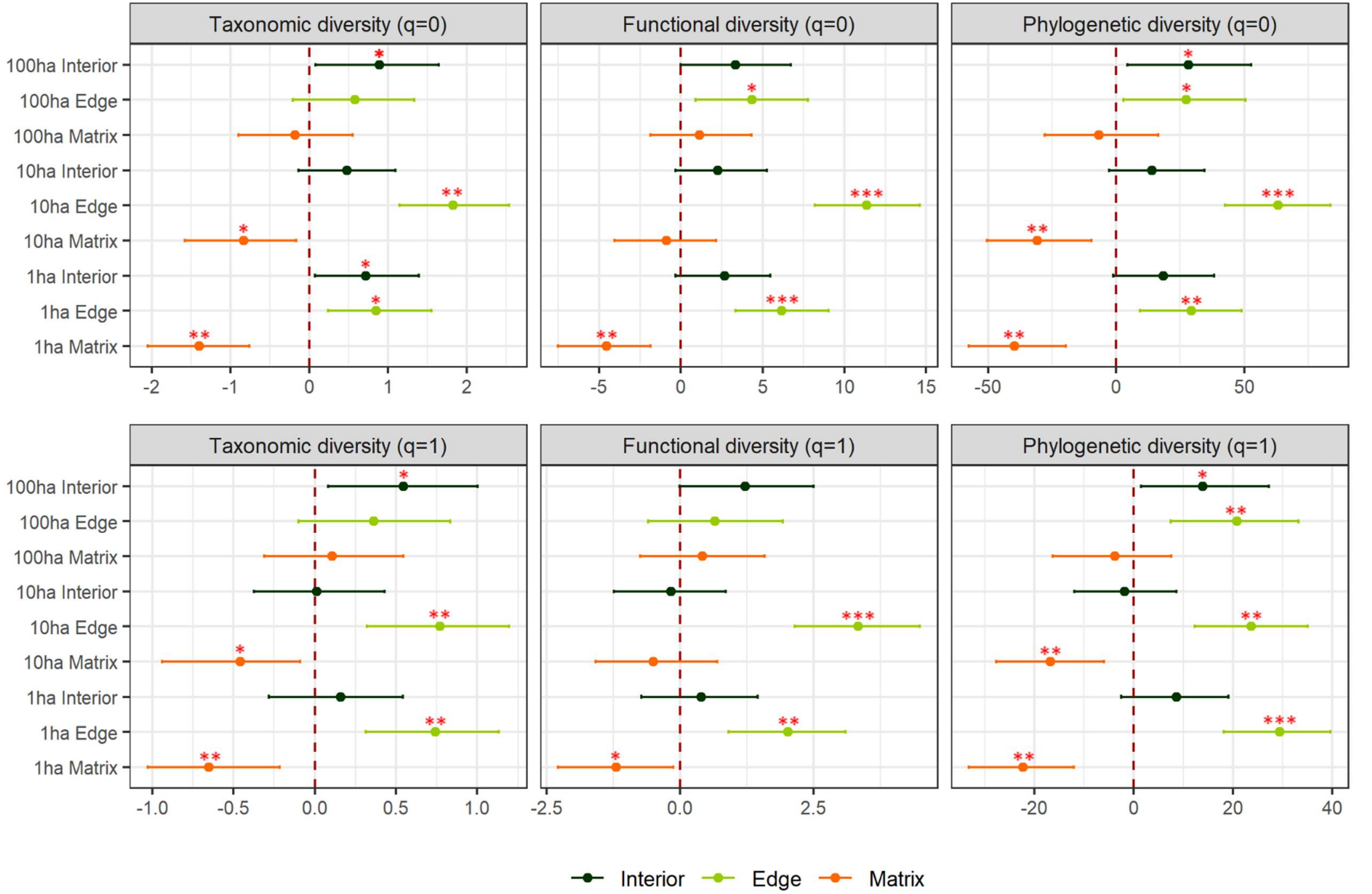

Fig. S2.3 Comparison of α-diversity metrics $q = 0$ and $q = 1$ across the interior-edge-matrix- and size gradients at the Biological Dynamics of Forest Fragments Project (forest fragment interiors, forest fragment edges and adjoining secondary forest/matrix). The predicted differences between each habitat and continuous forest interior, modelled using MCMC$_{\text{GLMM}}$ are plotted with their corresponding 95% credible interval. Those which do not touch or overlap the vertical dashed line (0) are considered significant (* $p_{\text{MCMC}} < 0.05$, ** $p_{\text{MCMC}} < 0.01$ *** $p_{\text{MCMC}} < 0.001$)

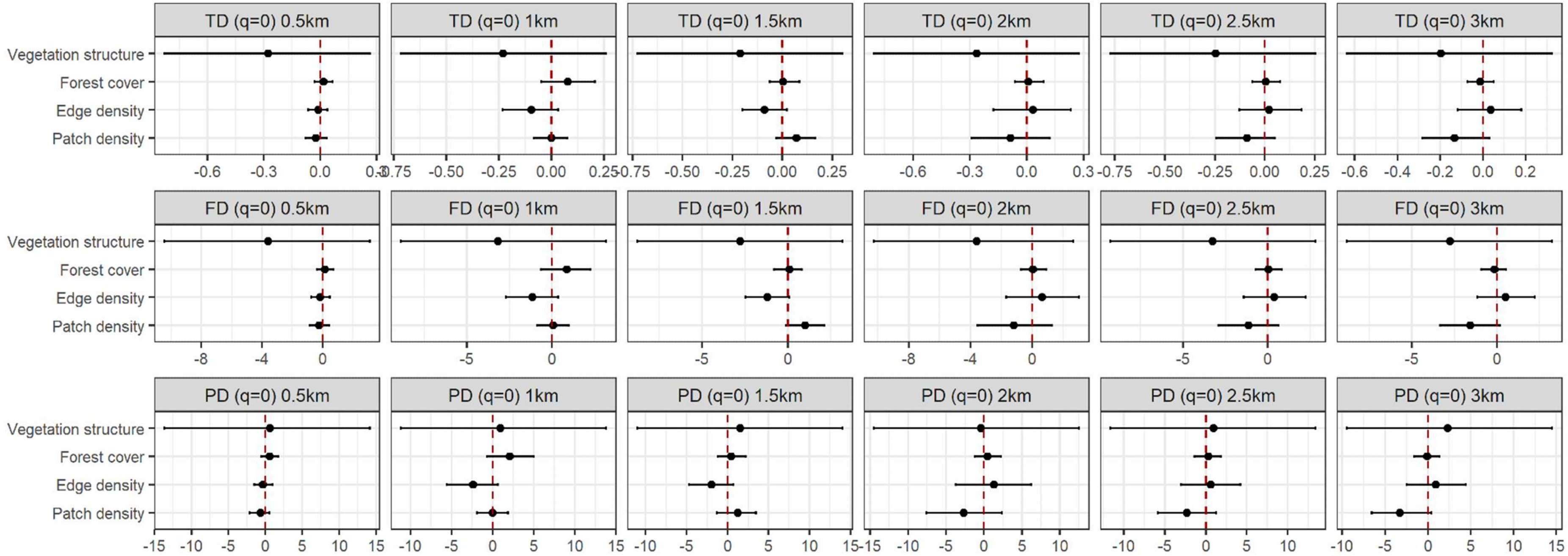

Fig. S2.4 Taxonomic, functional and phylogenetic diversity metrics $q = 0$ modelled as a function of local and landscape predictor variables (vegetation structure, forest cover, edge and patch density) based on surveys of aerial insectivorous bats at the Biological Dynamics of Forest Fragments Project, Brazil. Shown are posterior mean estimates ± 95% credible intervals. Credible intervals which do not touch or overlap the zero line are considered significant ($^{*}\ p_{\mathrm{MCMC}} < 0.05$)

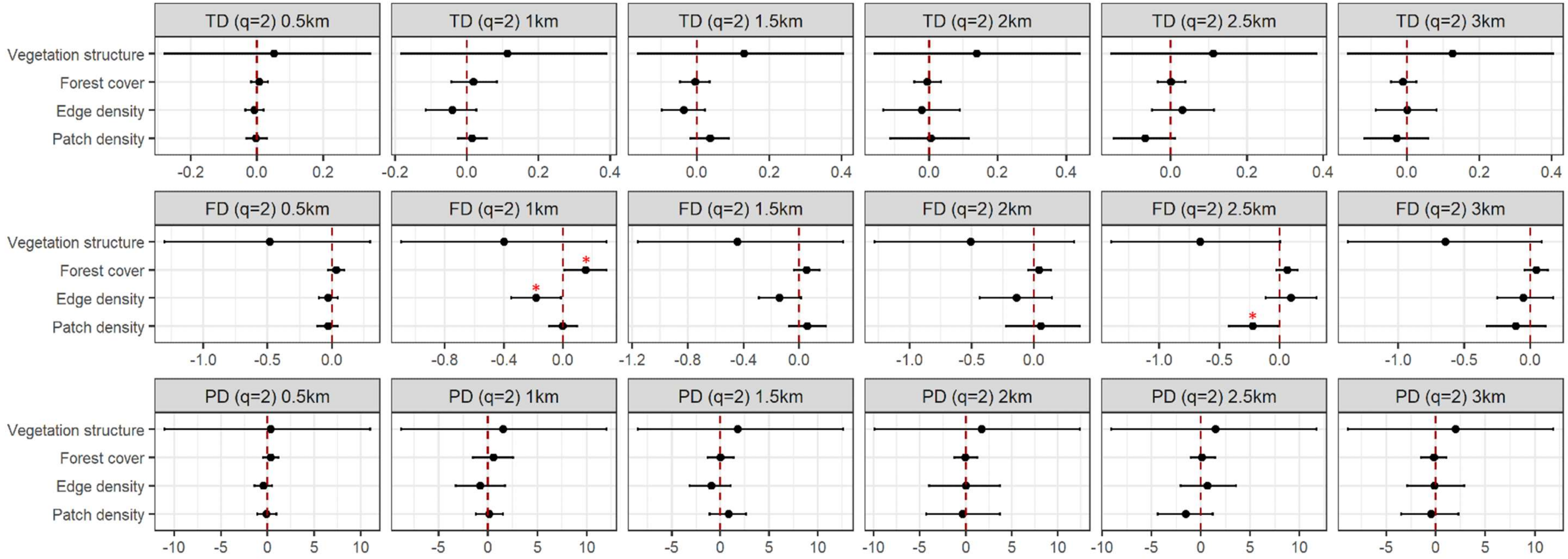

Fig. S2.5 Taxonomic, functional and phylogenetic diversity metrics $q = 1$ modelled as a function of local and landscape predictor variables (vegetation structure, forest cover, edge and patch density) based on surveys of aerial insectivorous bats at the Biological Dynamics of Forest Fragments Project, Brazil. Shown are posterior mean estimates ± 95% credible intervals. Credible intervals which do not touch or overlap the zero line are considered significant (* $p_{\text{MCMC}} < 0.05$)

Table S2.1 Total number of bat passes per species/sonotype detected at the Biological Dynamics of Forest Fragments Project, Central Amazon. Total bat passes recorded: 283,242. Total bat passes analysed: 281,425, following removal of *Saccopteryx gymnure (E1) sonotype*

Species / Sonotype	Species calls included:	Code	Total number bat passes
Emballonuridae			
Centronycteris maximiliani	*Centronycteris maximiliani*	CM	77247
Cormura brevirostris	*Cormura brevirostris*	CB	6079
Peropteryx kappleri	*Peropteryx kappleri*	PK	4262
Peropteryx macrotis	*Peropteryx macrotis*	PM	471
Rhynchonycteris naso	*Rhynchonycteris naso*	RN	3
Saccopteryx bilineata	*Saccopteryx bilineata*	SB	27675
Saccopteryx gymnura	*Saccopteryx gymnura*	E1	1817
Saccopteryx leptura	*Saccopteryx leptura*	SL	15862
Furipteridae			
Furipterus horrens	*Furipterus horrens*	FH	709
Molossidae			
Molossidae I	*Molossus molossus*	M1	42
Molossidae II	*Molossus sinaloae / currentium / rufus*	M2	1291
Molossidae III	*Cynomops planirostris / paranus, Cynomops greenhalli /abrasus, Eumops auripendulus / glaucinus / dabbenei / hansae / maurus, Nyctinomops laticaudatus, Tadarida brasiliensis*	M3	1444
Molossops I	*Molossops neglectus, Molossops temminckii*	MNE	4
Promops I	*Promops centralis, Promops nasutus*	P	555
Mormoopidae			
Pteronotus alitonus	*Pteronotus alitonus*	P6	50505
Pteronotus gymnonotus	*Pteronotus gymnonotus*	PG	1028
Pteronotus personatus	*Pteronotus personatus*	PP	164
Pteronotus rubiginosus	*Pteronotus rubiginosus*	P5	45603
Vespertilionidae			
Eptesicus brasiliensis	*Eptesicus brasiliensis*	EB	1206
Myotis nigricans	*Myotis nigricans*	MN	1251
Myotis riparius	*Myotis riparius*	MR	46024

Table S2.2 List of functional traits used to calculate functional diversity (FD)

Trait variable	Definition	Reference
Call frequency	Frequency with the highest intensity of each echolocation call (or the average of diagnostic call measurements)	López-Baucells et al., 2016
Call structure	Pulse shape, classified into three main categories: quasi constant frequency (QCF), constant frequency (CF), frequency modulated (FM)	López-Baucells et al., 2016
Call alternation	Categorization of call sequence: (1) single 'monotonous' pulse, (2) alternating frequency sequence containing two ‘low-high’ note pulse pairs or (3) a ‘low-medium-high’ triple pulse sequence	Jung et al., 2007; Ratcliffe et al., 2011; López-Baucells et al., 2016
Body mass	An average weight for each species based on BDFFP capture data (adults only)	Unpublished data collected at the BDFFP (Rocha et al., 2017b; Rocha et al., 2017)
Aspect ratio	Square of the wingspan divided by the wing area	Norberg & Rayner, 1987
Relative wing loading	Mass of the individual divided by the wing area (WL) divided by body mass raised to one third (RWL = WL/mass1/3)	Norberg & Rayner, 1987
Vertical stratification	Forest stratum where each species tends to forage; categorization based on three levels: understory, canopy and above the canopy	Mas et al., 2014

Table S2.3 Species functional trait data used to calculate FD. Sources listed in Table 1 (E1 excluded from analysis due to no available trait data)

Abbreviations: BM = Body Mass (Kg), AR = Aspect ratio, RWL = Relative Wing loading

Species / Sonotype	Species code	Call frequency	Call structure	Alternation	BM	AR	RWL	Vertical Stratification
Emballonuridae								
Centronycteris maximiliani	CM	40	QCF	1	0.0058	7.9575	11.9858432	2
Cormura brevirostris	CB	28	QCF	3	0.0089	8.73	21.77496447	2
Peropteryx kappleri	PK	31	QCF	1	0.0081	7.3268	15.49136026	2
Peropteryx macrotis	PM	38	QCF	1	0.0055	6.8	26.72867774	2
Rhynchonycteris naso	RN	97	QCF	1	0.0035	8.73	13.22988609	2
Saccopteryx bilineata	SB	43.5	QCF	2	0.0093	6.3546	13.6390583	2
Saccopteryx leptura	SL	51.5	QCF	2	0.0035	5.6774	19.2294856	2
Furipteridae								
Furipterus horrens	FH	176	FM	1	0.00365	5.4684	12.22694	2
Molossidae								
Molossidae I	M1	38.25	QCF	3	0.012	8.7	32.6465	3
Molossidae II	M2	33.5	QCF	3	0.0325	7.412433	41.08406	3
Molossidae III	M3	21	QCF	2	0.025763	8.804175	32.21455	3
Molossops I	MNE	50	QCF	2	0.0059	7.59	24.43008	3
Promops I	P	32.25	QCF	2	0.0375	11.0626	34.47177	3
Mormoopidae								
Pteronotus alitonus	P6	60	CF	1	0.02	6.68	11.15172	1
Pteronotus gymnonotus	PG	55	FM	1	0.013	7.26555	13.46973	1
Pteronotus personatus	PP	68.5	FM	1	0.0075	6.7	14.24725	1
Pteronotus rubiginosus	P5	55	CF	1	0.02	6.68	11.15172	1
Vespertilionidae								
Eptesicus brasiliensis	EB	32	FM	1	0.012	6.8648	18.24123	2
Myotis nigricans	MN	60	FM	1	0.0045	6.3	14.43033	2
Myotis riparius	MR	50	FM	1	0.0044	6.3	14.53884	2

Table S2.4 Variable loadings, eigenvalues and proportion of variance explained by the first two axes of a principal components analysis on the local vegetation structure variables#

Local vegetation variables	**Abbreviation**	**PC1**	**PC2**
Number of trees (DBH >10)	trees >10	0.48	-0.58
Number of woody stems (DBH <10 cm)	stems<10	-0.36	-0.75
Average DBH of trees ≥10 cm	DBH	0.84	0.07
Canopy cover (%)	canopy.cover	0.66	-0.43
Liana density	lianas	-0.63	-0.13
Canopy height (m)	height	0.75	0.03
Vertical foliage density	VFD	0.48	0.35
Eigenvalue		2.69	1.24
% explained		38.39	17.67
Cumulative Proportion		38.39	56.06

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Table S2.5 $MCMC_{GLMM}$ model output comparing α-diversity $q = 2$ across different habitat types (continuous forest interior, forest fragment interiors, forest fragment edges and adjoining secondary forest/matrix). We report mean posterior estimate, 95% credible intervals, the effective sample size and Bayesian p-values (p_{MCMC}) indicating the significance of variables with a threshold of * $p_{MCMC} < 0.05$, ** $p_{MCMC} < 0.01$ *** $p_{MCMC} < 0.001$

Inverse Simpson (q=2)	Size	Habitat	Estimate	Inferior	Superior	Effective sample	p_{MCMC}
Taxonomic	100ha	Interior	0.46	0.08	0.87	4500	0.03^{*}
Taxonomic	100ha	Edge	0.37	-0.06	0.75	4500	0.07
Taxonomic	100ha	Matrix	0.22	-0.15	0.60	4500	0.20
Taxonomic	10ha	Interior	0.00	-0.35	0.34	4164	0.98
Taxonomic	10ha	Edge	0.59	0.19	0.94	4500	0.01^{**}
Taxonomic	10ha	Matrix	-0.36	-0.73	-0.02	4500	0.05
Taxonomic	1ha	Interior	0.07	-0.29	0.42	4500	0.66
Taxonomic	1ha	Edge	0.68	0.34	1.04	4500	0.01^{**}
Taxonomic	1ha	Matrix	-0.51	-0.84	-0.16	4380	0.01^{*}
Functional	100ha	Interior	0.77	-0.15	1.84	4500	0.11
Functional	100ha	Edge	0.31	-0.71	1.29	4500	0.49
Functional	100ha	Matrix	0.25	-0.67	1.17	3946	0.55
Functional	10ha	Interior	-0.32	-1.16	0.51	4500	0.39
Functional	10ha	Edge	2.01	1.09	2.90	4295	0.00^{**}
Functional	10ha	Matrix	-0.47	-1.40	0.39	4500	0.27
Functional	1ha	Interior	0.17	-0.65	1.03	4500	0.67
Functional	1ha	Edge	1.34	0.48	2.21	4500	0.01^{**}
Functional	1ha	Matrix	-0.80	-1.68	0.04	4500	0.07
Phylogenetic	100ha	Interior	12.10	1.41	23.86	4547	0.04^{*}
Phylogenetic	100ha	Edge	22.34	10.84	33.61	4500	0.00^{***}
Phylogenetic	100ha	Matrix	-0.55	-11.32	9.05	4500	0.89
Phylogenetic	10ha	Interior	-2.31	-10.87	7.22	4500	0.58
Phylogenetic	10ha	Edge	17.44	7.04	27.02	4500	0.00^{**}
Phylogenetic	10ha	Matrix	-11.26	-21.39	-1.80	4500	0.03^{*}
Phylogenetic	1ha	Interior	7.83	-1.45	17.26	4500	0.09
Phylogenetic	1ha	Edge	27.31	18.20	37.17	4500	0.00^{***}
Phylogenetic	1ha	Matrix	-17.34	-26.55	-8.73	4476	0.00^{**}

Table S.26 $\text{MCMC}_{\text{GLMM}}$ model output comparing α-diversity metric $q = 0$ across different habitat types (continuous forest interior, forest fragment interiors, forest fragment edges and adjoining secondary forest/matrix). We report mean posterior estimate, 95% credible intervals, effective sample size and Bayesian p-values (p_{MCMC}) indicating the significance of variables with a threshold of $^{*}\, p_{\text{MCMC}} < 0.05$, $^{**}\, p_{\text{MCMC}} < 0.01$ $^{***}\, p_{\text{MCMC}} < 0.001$

Richness (q=0)	Size	Habitat	Estimate	Inferior	Superior	Effective sample	p_{MCMC}
Taxonomic	100ha	Interior	0.90	0.10	1.69	4500	0.02^{*}
Taxonomic	100ha	Edge	0.58	-0.21	1.38	4500	0.14
Taxonomic	100ha	Matrix	-0.18	-0.90	0.53	4233	0.60
Taxonomic	10ha	Interior	0.48	-0.15	1.16	4500	0.13
Taxonomic	10ha	Edge	1.81	1.10	2.52	4729	0.00^{**}
Taxonomic	10ha	Matrix	-0.83	-1.54	-0.13	4073	0.02^{*}
Taxonomic	1ha	Interior	0.72	0.02	1.38	4500	0.04^{*}
Taxonomic	1ha	Edge	0.85	0.19	1.52	4620	0.02^{*}
Taxonomic	1ha	Matrix	-1.40	-2.05	-0.75	4730	0.00^{**}
Functional	100ha	Interior	3.32	-0.17	6.83	4500	0.06
Functional	100ha	Edge	4.38	0.97	8.00	4500	0.01^{*}
Functional	100ha	Matrix	1.17	-2.15	4.12	4500	0.46
Functional	10ha	Interior	2.26	-0.57	4.92	4500	0.10
Functional	10ha	Edge	11.36	8.19	14.40	4500	0.00^{***}
Functional	10ha	Matrix	-0.83	-3.71	2.33	3965	0.58
Functional	1ha	Interior	2.66	-0.16	5.55	4500	0.06
Functional	1ha	Edge	6.14	3.46	9.11	4500	0.00^{***}
Functional	1ha	Matrix	-4.57	-7.42	-1.88	4500	0.00^{**}
Phylogenetic	100ha	Interior	28.10	3.52	52.05	4500	0.03^{*}
Phylogenetic	100ha	Edge	26.93	2.56	50.89	3986	0.03^{*}
Phylogenetic	100ha	Matrix	-6.67	-28.13	14.67	4500	0.53
Phylogenetic	10ha	Interior	13.54	-4.55	31.89	4500	0.14
Phylogenetic	10ha	Edge	63.02	43.25	85.52	3840	0.00^{***}
Phylogenetic	10ha	Matrix	-31.35	-52.04	-10.81	4218	0.01^{**}
Phylogenetic	1ha	Interior	18.21	-0.97	39.09	4500	0.07
Phylogenetic	1ha	Edge	29.26	9.23	47.70	4500	0.00^{**}
Phylogenetic	1ha	Matrix	-39.75	-58.41	-21.29	4500	0.00^{**}

Table S2.7 $\text{MCMC}_{\text{GLMM}}$ model output comparing α-diversity metric $q = 1$ across different habitat types (continuous forest interior, forest fragment interiors, forest fragment edges and adjoining secondary forest/matrix). We report mean posterior estimate, 95% credible intervals, the effective sample size and Bayesian p-values (p_{MCMC}) indicating the significance of variables with a threshold of $^{*}\ p_{\text{MCMC}} < 0.05$, $^{**}\ p_{\text{MCMC}} < 0.01$ $^{***}\ p_{\text{MCMC}} < 0.001$

Shannon entropy index (q=1)	Size	Habitat	Estimate	Inferior	Superior	Effective sample	p_{MCMC}
Taxonomic	100ha	Interior	0.54	0.06	0.99	4500	0.03^{*}
Taxonomic	100ha	Edge	0.36	-0.09	0.85	4500	0.12
Taxonomic	100ha	Matrix	0.10	-0.34	0.54	4500	0.66
Taxonomic	10ha	Interior	0.01	-0.42	0.40	4500	0.98
Taxonomic	10ha	Edge	0.77	0.30	1.21	4500	0.00^{**}
Taxonomic	10ha	Matrix	-0.46	-0.88	-0.04	4500	0.04^{*}
Taxonomic	1ha	Interior	0.16	-0.27	0.57	4500	0.44
Taxonomic	1ha	Edge	0.74	0.30	1.15	4500	0.00^{**}
Taxonomic	1ha	Matrix	-0.66	-1.09	-0.26	4500	0.01^{**}
Functional	100ha	Interior	1.23	-0.12	2.48	4500	0.06
Functional	100ha	Edge	0.67	-0.57	2.03	4290	0.30
Functional	100ha	Matrix	0.42	-0.75	1.66	4500	0.48
Functional	10ha	Interior	-0.16	-1.26	0.88	4500	0.74
Functional	10ha	Edge	3.33	2.18	4.54	4724	0.00^{***}
Functional	10ha	Matrix	-0.50	-1.63	0.68	4289	0.38
Functional	1ha	Interior	0.40	-0.73	1.46	4292	0.45
Functional	1ha	Edge	2.04	0.99	3.15	5231	0.00^{**}
Functional	1ha	Matrix	-1.18	-2.28	-0.11	4254	0.04^{*}
Phylogenetic	100ha	Interior	13.83	1.92	27.05	4500	0.03^{*}
Phylogenetic	100ha	Edge	20.64	7.17	33.18	4500	0.00^{**}
Phylogenetic	100ha	Matrix	-4.11	-15.14	7.58	4500	0.47
Phylogenetic	10ha	Interior	-1.93	-12.35	7.90	4278	0.69
Phylogenetic	10ha	Edge	23.57	11.41	35.00	4500	0.00^{**}
Phylogenetic	10ha	Matrix	-16.86	-28.30	-5.92	4247	0.01^{**}
Phylogenetic	1ha	Interior	8.43	-2.56	18.73	4500	0.11
Phylogenetic	1ha	Edge	29.35	18.61	39.90	4500	0.00^{***}
Phylogenetic	1ha	Matrix	-22.46	-32.52	-12.04	4500	0.00^{**}

Table S2.8 MCMC$_{\mathrm{GLMM}}$ Model output comparing α-diversity metric q = 0 modelled with local and landscape predictor variables (Vegetation structure, Forest cover, Edge density, Patch density) We report mean posterior estimate, 95% credible intervals, the effective sample size and Bayesian p-values (p_{MCMC}) indicating the significance of variables with a threshold of $^{*}\,p_{\mathrm{MCMC}} < 0.05$, $^{**}\,p_{\mathrm{MCMC}} < 0.01$ $^{***}\,p_{\mathrm{MCMC}} < 0.001$

Richness (q=0)	Buffer Size	Habitat	Estimate	Inferior	Superior	Effective sample	p_{MCMC}
Taxonomic	0.5km	Vegetation structure	-0.28	-0.84	0.26	4288	0.31
Taxonomic	0.5km	Forest Cover	0.02	-0.03	0.07	4500	0.45
Taxonomic	0.5km	Edge Density	-0.01	-0.06	0.04	4500	0.62
Taxonomic	0.5km	Patch Density	-0.02	-0.08	0.04	4500	0.43
Taxonomic	1km	Vegetation structure	-0.23	-0.74	0.25	3921	0.35
Taxonomic	1km	Forest Cover	0.08	-0.05	0.21	5401	0.20
Taxonomic	1km	Edge Density	-0.09	-0.23	0.03	4500	0.14
Taxonomic	1km	Patch Density	0.00	-0.08	0.08	4309	0.95
Taxonomic	1.5km	Vegetation structure	-0.22	-0.72	0.30	5151	0.39
Taxonomic	1.5km	Forest Cover	0.00	-0.07	0.08	4273	0.88
Taxonomic	1.5km	Edge Density	-0.09	-0.20	0.03	4201	0.12
Taxonomic	1.5km	Patch Density	0.07	-0.03	0.17	4500	0.15
Taxonomic	2km	Vegetation structure	-0.27	-0.81	0.30	4500	0.32
Taxonomic	2km	Forest Cover	0.01	-0.07	0.08	4500	0.88
Taxonomic	2km	Edge Density	0.03	-0.17	0.23	5017	0.74
Taxonomic	2km	Patch Density	-0.08	-0.30	0.11	4500	0.42
Taxonomic	2.5km	Vegetation structure	-0.25	-0.76	0.27	4234	0.33
Taxonomic	2.5km	Forest Cover	0.00	-0.06	0.08	4194	0.91
Taxonomic	2.5km	Edge Density	0.02	-0.14	0.17	4500	0.76
Taxonomic	2.5km	Patch Density	-0.09	-0.24	0.06	4500	0.22
Taxonomic	3km	Vegetation structure	-0.19	-0.66	0.31	4500	0.43
Taxonomic	3km	Forest Cover	-0.01	-0.07	0.05	4500	0.66
Taxonomic	3km	Edge Density	0.04	-0.11	0.18	3849	0.56
Taxonomic	3km	Patch Density	-0.14	-0.30	0.02	3984	0.09
Functional	0.5km	Vegetation structure	-3.70	-10.65	3.21	4500	0.29
Functional	0.5km	Forest Cover	0.17	-0.38	0.67	4359	0.50
Functional	0.5km	Edge Density	-0.16	-0.72	0.48	4063	0.59
Functional	0.5km	Patch Density	-0.21	-0.84	0.46	4500	0.52
Functional	1km	Vegetation structure	-3.16	-8.92	3.14	4500	0.30
Functional	1km	Forest Cover	0.86	-0.57	2.28	4930	0.20
Functional	1km	Edge Density	-1.14	-2.66	0.41	4500	0.13
Functional	1km	Patch Density	0.08	-0.87	0.98	4057	0.84
Functional	1.5km	Vegetation structure	-2.87	-8.74	3.40	4500	0.34
Functional	1.5km	Forest Cover	0.08	-0.75	0.84	4500	0.82
Functional	1.5km	Edge Density	-1.17	-2.48	0.10	4500	0.07
Functional	1.5km	Patch Density	0.97	-0.17	2.06	4500	0.09
Functional	2km	Vegetation structure	-3.54	-10.53	2.83	4500	0.28
Functional	2km	Forest Cover	0.06	-0.78	0.86	4500	0.90
Functional	2km	Edge Density	0.58	-1.86	3.00	4093	0.63

Functional	2km	Patch Density	-1.13	-3.63	1.23	4287	0.34
Functional	2.5km	Vegetation structure	-3.19	-9.05	2.98	4500	0.30
Functional	2.5km	Forest Cover	0.02	-0.71	0.82	4500	0.97
Functional	2.5km	Edge Density	0.39	-1.55	2.07	4500	0.66
Functional	2.5km	Patch Density	-1.14	-2.85	0.72	4306	0.21
Functional	3km	Vegetation structure	-2.74	-8.14	3.32	4212	0.34
Functional	3km	Forest Cover	-0.15	-0.83	0.58	4500	0.67
Functional	3km	Edge Density	0.51	-1.19	2.14	4500	0.52
Functional	3km	Patch Density	-1.55	-3.24	0.12	4500	0.07
Phylogenetic	0.5km	Vegetation structure	0.62	-13.24	14.18	4500	0.93
Phylogenetic	0.5km	Forest Cover	0.55	-0.49	1.78	4500	0.31
Phylogenetic	0.5km	Edge Density	-0.29	-1.46	1.04	4500	0.62
Phylogenetic	0.5km	Patch Density	-0.68	-2.04	0.67	4733	0.31
Phylogenetic	1km	Vegetation structure	0.96	-12.20	13.05	3974	0.88
Phylogenetic	1km	Forest Cover	2.10	-0.79	5.07	4500	0.13
Phylogenetic	1km	Edge Density	-2.37	-5.56	0.71	4500	0.13
Phylogenetic	1km	Patch Density	-0.05	-1.89	1.84	3935	0.97
Phylogenetic	1.5km	Vegetation structure	1.60	-11.48	13.63	3805	0.81
Phylogenetic	1.5km	Forest Cover	0.44	-1.42	2.10	4500	0.58
Phylogenetic	1.5km	Edge Density	-1.93	-4.50	0.78	4041	0.16
Phylogenetic	1.5km	Patch Density	1.20	-1.17	3.54	4197	0.31
Phylogenetic	2km	Vegetation structure	-0.19	-12.92	13.56	3910	0.97
Phylogenetic	2km	Forest Cover	0.45	-1.35	2.14	4500	0.59
Phylogenetic	2km	Edge Density	1.20	-3.66	6.29	3684	0.62
Phylogenetic	2km	Patch Density	-2.57	-7.28	2.83	3770	0.31
Phylogenetic	2.5km	Vegetation structure	0.93	-12.06	12.86	4699	0.87
Phylogenetic	2.5km	Forest Cover	0.30	-1.23	1.81	4311	0.69
Phylogenetic	2.5km	Edge Density	0.63	-2.84	4.54	4500	0.76
Phylogenetic	2.5km	Patch Density	-2.36	-5.73	1.37	4500	0.18
Phylogenetic	3km	Vegetation structure	2.31	-9.75	14.02	4500	0.69
Phylogenetic	3km	Forest Cover	-0.12	-1.54	1.33	4500	0.85
Phylogenetic	3km	Edge Density	0.90	-2.33	4.33	3896	0.58
Phylogenetic	3km	Patch Density	-3.25	-6.79	0.11	4500	0.06

Table S2.9 $\mathrm{MCMC_{GLMM}}$ Model output comparing α-diversity metric $q = 1$ modelled with local and landscape predictor variables (Vegetation structure, Forest cover, Edge density, Patch density) We report mean posterior estimate, 95% credible intervals, the effective sample size and Bayesian p-values (p_{MCMC}) indicating the significance of variables with a threshold of $^{*}\,p_{\mathrm{MCMC}} < 0.05$, $^{**}\,p_{\mathrm{MCMC}} < 0.01$ $^{***}\,p_{\mathrm{MCMC}} < 0.001$

Shannon entropy index (q=1)	Buffer Size	Habitat	Estimate	Inferior	Superior	Effective sample	p_{MCMC}
Taxonomic	0.5km	Vegetation structure	0.03	-0.31	0.36	4822	0.89
Taxonomic	0.5km	Forest Cover	0.01	-0.02	0.03	4500	0.51
Taxonomic	0.5km	Edge Density	0.00	-0.03	0.02	5591	0.74
Taxonomic	0.5km	Patch Density	-0.01	-0.04	0.02	4500	0.50
Taxonomic	1km	Vegetation structure	0.07	-0.23	0.37	4500	0.65
Taxonomic	1km	Forest Cover	0.03	-0.04	0.09	4500	0.38
Taxonomic	1km	Edge Density	-0.04	-0.12	0.03	4500	0.27
Taxonomic	1km	Patch Density	0.00	-0.04	0.05	4500	0.85
Taxonomic	1.5km	Vegetation structure	0.08	-0.24	0.38	4619	0.61
Taxonomic	1.5km	Forest Cover	0.00	-0.04	0.04	4500	0.83
Taxonomic	1.5km	Edge Density	-0.04	-0.11	0.02	4555	0.21
Taxonomic	1.5km	Patch Density	0.03	-0.02	0.09	4500	0.27
Taxonomic	2km	Vegetation structure	0.09	-0.23	0.43	4500	0.59
Taxonomic	2km	Forest Cover	0.00	-0.04	0.04	4500	0.99
Taxonomic	2km	Edge Density	-0.04	-0.16	0.08	5235	0.52
Taxonomic	2km	Patch Density	0.02	-0.10	0.14	4500	0.75
Taxonomic	2.5km	Vegetation structure	0.04	-0.26	0.33	4500	0.80
Taxonomic	2.5km	Forest Cover	0.01	-0.03	0.05	4500	0.70
Taxonomic	2.5km	Edge Density	0.03	-0.06	0.12	4500	0.47
Taxonomic	2.5km	Patch Density	-0.07	-0.16	0.02	4500	0.12
Taxonomic	3km	Vegetation structure	0.04	-0.27	0.34	4500	0.78
Taxonomic	3km	Forest Cover	0.00	-0.04	0.04	4500	0.95
Taxonomic	3km	Edge Density	-0.01	-0.10	0.08	4500	0.86
Taxonomic	3km	Patch Density	-0.03	-0.12	0.07	4500	0.51
Functional	0.5km	Vegetation structure	-1.04	-2.29	0.18	4500	0.09
Functional	0.5km	Forest Cover	0.05	-0.06	0.14	4500	0.33
Functional	0.5km	Edge Density	-0.04	-0.15	0.07	4773	0.51
Functional	0.5km	Patch Density	-0.04	-0.16	0.08	4500	0.45
Functional	1km	Vegetation structure	-0.95	-1.98	0.12	4500	0.07
Functional	1km	Forest Cover	0.23	0.02	0.45	3955	0.04^{*}
Functional	1km	Edge Density	-0.26	-0.51	-0.01	4500	0.04^{*}
Functional	1km	Patch Density	-0.01	-0.15	0.13	4796	0.90
Functional	1.5km	Vegetation structure	-1.07	-2.21	-0.04	4603	0.05
Functional	1.5km	Forest Cover	0.10	-0.04	0.23	4500	0.15
Functional	1.5km	Edge Density	-0.22	-0.44	0.02	4694	0.06
Functional	1.5km	Patch Density	0.09	-0.10	0.29	4694	0.37
Functional	2km	Vegetation structure	-1.15	-2.40	0.02	4500	0.07

Functional	2km	Forest Cover	0.06	-0.07	0.21	4500	0.35
Functional	2km	Edge Density	-0.23	-0.65	0.21	4500	0.29
Functional	2km	Patch Density	0.11	-0.34	0.57	4500	0.63
Functional	2.5km	Vegetation structure	-1.33	-2.40	-0.16	4639	0.03*
Functional	2.5km	Forest Cover	0.08	-0.06	0.22	4108	0.25
Functional	2.5km	Edge Density	0.11	-0.24	0.43	4500	0.49
Functional	2.5km	Patch Density	-0.27	-0.61	0.05	4780	0.10
Functional	3km	Vegetation structure	-1.33	-2.47	-0.26	4798	0.02*
Functional	3km	Forest Cover	0.07	-0.06	0.21	4500	0.32
Functional	3km	Edge Density	-0.05	-0.38	0.27	4500	0.74
Functional	3km	Patch Density	-0.16	-0.48	0.19	4500	0.32
Phylogenetic	0.5km	Vegetation structure	-0.40	-11.71	10.10	4500	0.95
Phylogenetic	0.5km	Forest Cover	0.35	-0.46	1.14	4500	0.37
Phylogenetic	0.5km	Edge Density	-0.31	-1.20	0.70	4500	0.50
Phylogenetic	0.5km	Patch Density	-0.21	-1.25	0.80	4500	0.67
Phylogenetic	1km	Vegetation structure	0.60	-8.91	10.73	4500	0.90
Phylogenetic	1km	Forest Cover	0.69	-1.37	2.65	4488	0.47
Phylogenetic	1km	Edge Density	-0.80	-3.29	1.60	4450	0.51
Phylogenetic	1km	Patch Density	-0.03	-1.38	1.36	4500	0.97
Phylogenetic	1.5km	Vegetation structure	0.56	-10.01	10.68	6017	0.91
Phylogenetic	1.5km	Forest Cover	0.21	-1.06	1.43	4500	0.73
Phylogenetic	1.5km	Edge Density	-1.03	-3.24	0.95	4500	0.33
Phylogenetic	1.5km	Patch Density	0.78	-1.13	2.56	4500	0.40
Phylogenetic	2km	Vegetation structure	0.55	-9.93	12.16	4500	0.92
Phylogenetic	2km	Forest Cover	0.10	-1.10	1.30	4500	0.88
Phylogenetic	2km	Edge Density	-0.71	-4.64	3.33	4500	0.72
Phylogenetic	2km	Patch Density	0.31	-3.83	4.30	4500	0.88
Phylogenetic	2.5km	Vegetation structure	-0.20	-10.70	10.03	4500	0.98
Phylogenetic	2.5km	Forest Cover	0.28	-0.92	1.49	4500	0.64
Phylogenetic	2.5km	Edge Density	0.57	-2.26	3.50	4500	0.68
Phylogenetic	2.5km	Patch Density	-1.46	-4.27	1.32	4500	0.32
Phylogenetic	3km	Vegetation structure	0.15	-9.92	10.72	4500	0.97
Phylogenetic	3km	Forest Cover	0.05	-1.24	1.24	4500	0.93
Phylogenetic	3km	Edge Density	-0.24	-3.02	2.67	4500	0.87
Phylogenetic	3km	Patch Density	-0.51	-3.36	2.37	4500	0.70

Table S2.10 MCMC$_{\text{GLMM}}$ Model output comparing α-diversity metric $q = 2$ modelled with local and landscape predictor variables (Vegetation structure, Forest cover, Edge density, Patch density) We report mean posterior estimate, 95% credible intervals, the effective sample size and Bayesian p-values (p_{MCMC}) indicating the significance of variables with a threshold of $^{*} p_{\text{MCMC}} < 0.05$, $^{**} p_{\text{MCMC}} < 0.01$ $^{***} p_{\text{MCMC}} < 0.001$

Inverse Simpson (q=2)	Buffer Size	Habitat	Estimate	Inferior	Superior	Effective sample	p_{MCMC}
Taxonomic	0.5km	Vegetation structure	0.06	-0.26	0.37	4500	0.71
Taxonomic	0.5km	Forest Cover	0.01	-0.02	0.03	4500	0.59
Taxonomic	0.5km	Edge Density	-0.01	-0.04	0.02	4500	0.57
Taxonomic	0.5km	Patch Density	0.00	-0.03	0.03	4308	0.87
Taxonomic	1km	Vegetation structure	0.11	-0.19	0.38	4500	0.42
Taxonomic	1km	Forest Cover	0.02	-0.04	0.09	4093	0.53
Taxonomic	1km	Edge Density	-0.04	-0.11	0.03	4229	0.27
Taxonomic	1km	Patch Density	0.02	-0.02	0.06	4500	0.45
Taxonomic	1.5km	Vegetation structure	0.13	-0.17	0.41	4500	0.36
Taxonomic	1.5km	Forest Cover	0.00	-0.04	0.04	4107	0.85
Taxonomic	1.5km	Edge Density	-0.04	-0.10	0.02	4114	0.21
Taxonomic	1.5km	Patch Density	0.04	-0.01	0.09	4295	0.15
Taxonomic	2km	Vegetation structure	0.14	-0.20	0.43	4500	0.34
Taxonomic	2km	Forest Cover	0.00	-0.04	0.03	3922	0.84
Taxonomic	2km	Edge Density	-0.02	-0.14	0.09	4500	0.72
Taxonomic	2km	Patch Density	0.01	-0.11	0.12	4500	0.95
Taxonomic	2.5km	Vegetation structure	0.11	-0.18	0.39	4500	0.43
Taxonomic	2.5km	Forest Cover	0.00	-0.04	0.04	4500	0.94
Taxonomic	2.5km	Edge Density	0.03	-0.05	0.12	4500	0.42
Taxonomic	2.5km	Patch Density	-0.07	-0.15	0.01	4500	0.08
Taxonomic	3km	Vegetation structure	0.13	-0.17	0.41	4500	0.37
Taxonomic	3km	Forest Cover	-0.01	-0.05	0.03	4500	0.55
Taxonomic	3km	Edge Density	0.00	-0.09	0.09	4500	0.94
Taxonomic	3km	Patch Density	-0.03	-0.12	0.06	4500	0.47
Functional	0.5km	Vegetation structure	-0.48	-1.24	0.39	4500	0.25
Functional	0.5km	Forest Cover	0.04	-0.03	0.10	4500	0.26
Functional	0.5km	Edge Density	-0.03	-0.10	0.04	4500	0.44
Functional	0.5km	Patch Density	-0.03	-0.11	0.04	4500	0.45
Functional	1km	Vegetation structure	-0.40	-1.12	0.28	4500	0.26
Functional	1km	Forest Cover	0.15	0.00	0.29	4500	0.04*
Functional	1km	Edge Density	-0.18	-0.35	-0.01	4500	0.04*
Functional	1km	Patch Density	0.00	-0.10	0.10	4500	0.99
Functional	1.5km	Vegetation structure	-0.45	-1.15	0.31	4500	0.23
Functional	1.5km	Forest Cover	0.06	-0.03	0.15	4500	0.21
Functional	1.5km	Edge Density	-0.14	-0.29	0.00	4500	0.06
Functional	1.5km	Patch Density	0.06	-0.08	0.19	4500	0.38
Functional	2km	Vegetation structure	-0.52	-1.36	0.28	4500	0.18
Functional	2km	Forest Cover	0.04	-0.05	0.14	4500	0.38
Functional	2km	Edge Density	-0.14	-0.41	0.16	4500	0.35
Functional	2km	Patch Density	0.05	-0.25	0.34	4500	0.72

Functional	2.5km	Vegetation structure	-0.65	-1.39	0.02	4671	0.07
Functional	2.5km	Forest Cover	0.06	-0.03	0.15	4697	0.16
Functional	2.5km	Edge Density	0.09	-0.12	0.31	4500	0.36
Functional	2.5km	Patch Density	-0.22	-0.43	-0.02	4500	0.03*
Functional	3km	Vegetation structure	-0.63	-1.37	0.07	4226	0.08
Functional	3km	Forest Cover	0.05	-0.04	0.14	4950	0.30
Functional	3km	Edge Density	-0.05	-0.27	0.15	4500	0.62
Functional	3km	Patch Density	-0.11	-0.34	0.10	4500	0.30
Phylogenetic	0.5km	Vegetation structure	0.35	-11.00	11.12	4149	0.95
Phylogenetic	0.5km	Forest Cover	0.35	-0.47	1.16	4262	0.38
Phylogenetic	0.5km	Edge Density	-0.40	-1.41	0.55	4500	0.40
Phylogenetic	0.5km	Patch Density	-0.10	-1.12	0.93	4500	0.84
Phylogenetic	1km	Vegetation structure	1.46	-8.75	11.73	4500	0.78
Phylogenetic	1km	Forest Cover	0.54	-1.66	2.48	4500	0.59
Phylogenetic	1km	Edge Density	-0.74	-3.10	1.79	4500	0.55
Phylogenetic	1km	Patch Density	0.09	-1.32	1.48	4709	0.90
Phylogenetic	1.5km	Vegetation structure	1.77	-8.20	12.06	4500	0.74
Phylogenetic	1.5km	Forest Cover	0.00	-1.24	1.29	3926	1.00
Phylogenetic	1.5km	Edge Density	-0.86	-2.98	1.15	4304	0.43
Phylogenetic	1.5km	Patch Density	0.81	-0.92	2.87	4181	0.39
Phylogenetic	2km	Vegetation structure	1.73	-8.96	13.50	4500	0.75
Phylogenetic	2km	Forest Cover	-0.02	-1.25	1.14	4500	0.97
Phylogenetic	2km	Edge Density	0.04	-3.70	4.32	3859	0.98
Phylogenetic	2km	Patch Density	-0.38	-4.46	3.52	4500	0.85
Phylogenetic	2.5km	Vegetation structure	1.43	-7.97	11.87	4500	0.77
Phylogenetic	2.5km	Forest Cover	0.15	-1.04	1.39	4500	0.80
Phylogenetic	2.5km	Edge Density	0.67	-2.11	3.65	4500	0.64
Phylogenetic	2.5km	Patch Density	-1.56	-4.42	1.21	4201	0.26
Phylogenetic	3km	Vegetation structure	1.99	-7.85	12.51	4500	0.68
Phylogenetic	3km	Forest Cover	-0.19	-1.40	1.10	4218	0.75
Phylogenetic	3km	Edge Density	-0.11	-2.96	2.75	4500	0.95
Phylogenetic	3km	Patch Density	-0.48	-3.36	2.43	4500	0.73

Chapter 3

30 years of regeneration: local- and landscape-scale effects on aerial insectivorous bat species buffered by second-growth forest

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Abstract

Regenerating secondary forests are a common feature of human modified landscapes. They have the capacity to support displaced forest biodiversity and contribute to carbon sequestration, helping to buffer the effects of landscape scale habitat loss and climate change resulting from deforestation. We used passive acoustic detectors to sample aerial insectivorous bats in an experimental habitat fragmentation and forest regeneration study site in the Brazilian Amazon. We surveyed bats over a two-year period across 33 sites comprising continuous old-growth forest, remnant fragments and regenerating secondary forest matrix. We analysed the activity of ten aerial insectivorous species/sonotypes to understand occupancy across habitat types and responses to fragment sizes and interior-edge-matrix (IEM) disturbance gradients. Applying a multiscale approach, we also investigated guild (forest specialists, flexible foragers, edge specialists and open space) and species-level responses to local vegetation structure and continuous forest cover, edge density and patch density across ten spatial scales (0.5km - 5km). We found species-specific habitat occupancy patterns and nuanced responses to fragment sizes and disturbance gradients, for example *Furipterus horrens* (forest specialist) had significantly lower activity in all second-growth forest sites and the interior and edge of the smallest fragments (1 ha and 10 ha), and only two species (*Pteronotus* spp.) showed no habitat preference and no significant responses across the IEM and fragment size gradients. We observed via our multiscale analysis that only the *Molossus* sonotype responded negatively to local vegetation structure and we uncovered no negative influence of continuous forest cover or edge density at guild or species-level, indicating the second-growth forest does appear to buffer the negative effects of fragmentation. This suggests the aerial insectivorous bat assemblage could be approaching a point of recovery after 30 years of regeneration. Our findings reinforce the requirement for protection of regenerating forests as important habitat within human modified landscapes as well as maintaining vast areas of pristine forest to help protect forest specialists that still rely on old-growth forest.

Keywords: Amazon, Chiroptera, Forest regeneration, Fragmentation, Multiscale analysis

Introduction

Tropical forests are some of the most diverse and productive ecosystems (ForestPlots.net et al., 2021), they represent 45% of all forest cover on earth (FAO & UNEP, 2020) and host between a half and two-thirds of terrestrial global biodiversity (Gardner et al., 2010). These forests are under sustained pressure and constant threat due to global anthropogenic activity (Malhi et al., 2014). Land use change continues to drive deforestation on a global scale, with agricultural expansion persisting as the major reason for forest clearance, accounting for at least half of all forest loss, estimated at around 10 million ha per year (FAO & UNEP, 2020; Laso Bayas et al., 2022). Global landscapes are fragmented, composed of an increasing number of fragments of varying sizes (Taubert et al., 2018). Habitat loss and fragmentation are catastrophically affecting biodiversity by contracting species' geographical ranges, causing considerable population declines and extinctions, which is notably prominent in the species-rich tropical regions (Ceballos et al., 2017).

The Amazon biome is a hotspot of deforestation with 813 944 km^2 of old-growth forest cleared by 2017 (Smith et al., 2021). Whilst scientific efforts continue to advocate for the significant and permanent reduction of primary forest clearance, regenerating secondary forests have been identified as the most effective method of 'passive' natural restoration of the Amazon (Crouzeilles et al., 2017). The majority of Amazonian land use change over the past 35 years resulted from the conversion of native forest for agricultural use (Silveira et al., 2022); including cattle ranching (Skidmore et al., 2021), expanding soybean production (Costa et al., 2017) and oil palm plantations (Butler & Laurance, 2009). However, the primary purpose for this land use change does not always persist and when left unused these pastures and crop fields give rise to the regeneration of a new forest system, termed second-growth forest (Chazdon, 2014).

By 2017 it was estimated that there were 234 795 km^2 of recovered secondary forests in the Amazon (Smith et al., 2021) which have the potential to capture vast amounts of atmospheric carbon (Chazdon et al., 2016) and provide much-needed habitat for forest-dependent species (Chazdon et al., 2009). Secondary forests develop through three successional phases over decades (Finegan et al., 1996) before reaching a point where they are capable of supporting levels of biodiversity and generating ecosystem services akin to those found in old-growth forest (Poorter et al., 2016; Lennox et al., 2018; Rozendaal et al., 2019; Poorter et al., 2021). They are now a significant feature within fragmented landscapes which often contain forest fragments, embedded within a matrix ranging from "hard", high-contrast agricultural/monoculture to "softer", low-contrast secondary regrowth forest at varying growth stages

(Neeff et al., 2006; Numata & Cochrane, 2012). Where regenerating forests are left to mature, the negative effects of fragmentation can be buffered, providing valuable habitats which can support a wide variety of taxa including; amphibians and reptiles (Hilje & Aide, 2012), arthropods (De Aquino et al., 2022), birds (Edwards et al., 2017) and mammals (Derhé et al., 2018).

Aerial insectivorous bats are vital for the health of natural and modified landscapes as they provide essential ecosystem services including insect regulation and dispersal of guano fertiliser (Ramírez-Fráncel et al., 2022). They have been highlighted as excellent bioindicators (Jones et al., 2009) because of their high insect consumption, wide foraging ranges and long life spans (Bayat et al., 2014), and due to this elevated trophic position they may accumulate organic contaminants quicker than those occupying lower trophic levels, i.e. herbivorous animals (Alleva et al., 2006). Their functional role in tropical ecosystems is crucial and in Brazil they account for just under half (48%) of the overall assemblage of 181 recognized species of bats (Garbino et al., 2022). Acoustic monitoring is the best method of sampling the aerial ensemble, as their highly developed echolocation means they are rarely captured in mist nets (MacSwiney et al., 2008). Despite advancements over the past 20 years in bioacoustics and lower-cost equipment making acoustic surveys increasingly popular (Lopez-Baucells et al., 2021) there is a much greater accumulation of knowledge for the family Phyllostomidae, of which the other half of the assemblage is made up (52%) and are best sampled with traditional mist netting techniques.

The sensitivity of aerial insectivorous bats to fragmentation is due to key trait adaptations relating to wing morphology and echolocation (Bader et al., 2015; Núñez et al., 2019) which determine specific foraging success within a habitat based on the clutter conditions (Schnitzler & Kalko, 2001). Forest specialist species are adapted to navigate highly cluttered space with short, broad wings and slow flight which provides increased manoeuvrability in dense forest (Estrada-Villegas et al., 2010). Their echolocation calls are adapted to provide detailed information which facilitates detection of prey items within this cluttered environment (Denzinger & Schnitzler, 2013). These forest specialists are potentially more vulnerable to the effects of fragmentation as they are less able to disperse if forest habitat degrades and their highly specialised echolocation is inappropriate for successful foraging in non-cluttered space (Núñez et al., 2019). Bats hunting in forest gaps and around forest edges capture insects in background cluttered space via aerial pursuits (Estrada-Villegas et al., 2010). These more mobile edge specialists can search for flying insects and simultaneously avoid collisions with background vegetation by using mixed echolocation call signals (Schnitzler & Kalko, 2001). Aerial species with long, narrow wings are adapted for faster flight in uncluttered open space above forest vegetation (Estrada-Villegas et al., 2010). Their echolocation calls provide information which allows them to capture prey whilst in flight where there are few obstacles (Schnitzler & Kalko, 2001). These open space species can fly over longer distances to access suitable foraging habitat and are generally less affected by habitat fragmentation due to their mobility (Bader et al., 2015). Echolocation behaviour is highly variable and some bats exhibit flexibility in foraging strategies (Schnitzler & Kalko, 2001) allowing them to exploit habitat generated after forest fragmentation i.e., edge, forest gaps and open space.

Neotropical bat vulnerability to fragmentation has been investigated at The Biological Dynamics of Forest Fragments Project (BDFFP) which is the world's largest and longest-running experimental study of habitat fragmentation and forest regeneration. Phyllostomid studies within the BDFFP have demonstrated, from a taxonomic perspective, that old-growth specialist bats benefited from forest regeneration in the matrix (Rocha et al., 2018), that functional diversity significantly increased as the regenerating forest matured (Farneda et al., 2018a; Farneda et al., 2018b) and that overall phylogenetic diversity increased in heterogeneity with advancing forest succession (Farneda et al., 2022). For the aerial insectivorous bat ensemble, biodiversity responses to local and landscape scale predictors were assessed at community level (Lopez-Baucells et al., 2022) which resulted in subtle scale-sensitive associations for functional diversity only and the secondary forest matrix around the smallest fragments was found to accommodate significantly lower diversity compared to the continuous forest. This biodiversity degradation became less pronounced as the fragment size increased and in contrast forest edges generally harboured higher taxonomic, functional and phylogenetic diversity. Aerial insectivorous species-specific research at the BDFFP has investigated edge effects across the interface of continuous and secondary forest (Yoh et al., 2022) and the interaction between habitat disturbance and moonlight intensity on bat activity (Appel et al., 2021). Yoh et al. (2022) revealed limited evidence of edge effects for common aerial insectivorous species suggesting that the secondary forest matrix has led to 'edge sealing' as a result of dense vegetation regenerating at and around the fragment edges (Harper et al., 2005), which over time has reduced the negative influence of the edge, providing habitat for primary forest (forest relatively undisturbed by human activities) specialists. Appel et al. (2021) found that aerial insectivorous bats responded more to habitat type than to moonlight with species reducing the level of activity in fragments (*Pteronotus alitonus, Furipterus horrens*) and secondary forest (*Saccopteryx bilineata, S. leptura, Centronycteris maximiliani, Cormura brevirostris, Eptesicus brasiliensis, Furipterus horrens*) compared to continuous forest. Evidence of response modulation was also found for the two Pteronotus spp. (*P. alitonus, P. rubiginosus*) which exhibited elevated activity levels in the secondary forest habitat and decreased activity in disturbed habitat on extremely bright nights to reduce the risk of predation. Yoh et al. (2022) suggests that the regenerating secondary forest at the BDFFP might have recovered enough that edge effects are no longer evident for most common species of aerial insectivorous whereas Appel et al. (2021) highlights that the lower activity in the secondary forest suggests that even after 30 years it is less attractive as foraging habitat for aerial bats.

The present study will further expand understanding about species-specific responses of this group and is the first to evaluate fragment size effects and landscape scale responses of aerial insectivorous bats to fragmentation and forest regeneration at the BDFFP. Specifically, we investigated occupancy patterns and differences in activity across the four main habitats (continuous old-growth forest interiors, old-growth forest fragment interiors (I), fragment edges (E) and secondary forest matrix sites (M)), also considering the disturbance gradient (hereinafter IEM gradient) and fragment sizes. Similar to our previous approach at the assemblage level (Lopez-Baucells et al., 2022), we investigated whether local and landscape scale metrics influenced activity across multiple spatial scales. These comparisons were conducted for a selection of common aerial insectivorous species/sonotypes (for which we had collected sufficient data over our sampling period) and three functional guilds (Forest specialists, Edge specialists and Flexible foragers) following Yoh et al. (2022) to expand our knowledge of how individual species and guilds respond to this fragmented landscape with mature secondary forest (approximately 30 years of regeneration). We hypothesized that habitat occupancy patterns and activity will be species-specific with similar responses from species within guilds. Forest specialists will have higher occupancy in continuous forest compared to IEM gradient, due to functional trait exclusion based on echolocation and morphological constraints. We expected a positive response for Edge specialists exploiting foraging opportunities generated in background cluttered and open spaces around the fragment edges and secondary forest matrix sites. We also predicted that Flexible foragers will show no response or preference for any specific habitat, indicating that these species can change their echolocation behaviour to exploit preferential hunting as required across the landscape. We did not expect to see significant influence from local or landscape scale metrics on bat activity, as we hypothesized that the 30 years of regeneration and secondary forest regrowth will buffer the negative effects of fragmentation and the aerial insectivorous species investigated will show resilient responses across multiple spatial scales.

Materials and methods

Study area

This study was conducted at the BDFFP, an experimental fragmentation project located ~80 km north of Manaus, Central Amazon, Brazil. Topography of the ~1000 km^2 study area is relatively flat, with many small streams cutting through the nutrient-poor soil (Laurance et al., 2011). Annual rainfall varies from 1900 to 3500 mm with a dry season between July and November (Ferreira et al., 2017). The BDFFP began in 1979 as researchers cooperated with ranchers who cleared continuous old-growth terra firme rainforest to accommodate cattle pastures, also allowing old-growth forest patches of varying sizes (1, 10 and 100 ha) to be preserved, but isolated from the continuous forest by distances of 80–650 m (Bierregaard et al., 1992). Within 5-10 years the cattle ranches were abandoned, and secondary forest began to establish in the matrix around the fragments (Laurance et al., 2018). Vismia-dominated regrowth occurred in pasture areas that were cleared and burned. This forest matured at a slower rate and is relatively species-poor (Williamson et al., 2014). In comparison, areas that were deforested without fire were initially dominated by Cecropia spp. but later developed into species-rich, well-structured forests (Longworth et al., 2014). We did not differentiate between Vismia or Cecropia dominated secondary regrowth forest types for this study. Approximately every 10 years, a 100 m-wide strip of secondary forest surrounding each of the old-growth forest fragments is cleared to help preserve isolation (Rocha et al., 2020). Canopy height averages between 30 and 37 m, while some emergent trees exceed 55 m. Prior to this study, the most recent re-isolation of the forest fragments had occurred between 1999 and 2001 (Laurance et al., 2011). There was relatively little structural contrast between the continuous old-growth forest, the experimental forest fragments and the advanced-stage (~ 30 year-old) secondary forest when data were collected.

Acoustic recordings

Acoustic surveys were conducted between November 2011 and September 2013 in nine control sites in three continuous old-growth forest areas (located in Cabo Frio, Florestal and Km41 camps), in both the interior and at the edges of eight old-growth forest fragments (3 x 1 ha, 3 x 10 ha, 2 x 100 ha, located in Colosso, Porto Alegre, and Dimona camps) and eight secondary forest matrix sites (Cabo Frio, Colosso, Dimona, Florestal and Porto Alegre camps) located 100 m into the matrix from the nearest fragment edge. Bats were acoustically sampled with Song Meter 2 (SM2Bat+) recorders fitted with omnidirectional ultrasonic SMX US microphones (Wildlife Acoustics Inc., Massachusetts, USA). Recorders were positioned at 1.5 m height and programmed to record for 12 hours (from 18:00 to 6:00 h). Recordings were captured in real time at full-spectrum resolution (16-bit), sampling rate of 384kHz with a high pass filter set at fs/32 (12kHz) and adaptive trigger level relative to noise floor of 18 SNR. Each site was surveyed for five consecutive nights, four times annually, with two surveys in the wet season and two in the dry season, amounting to a total of 1021 recording nights.

Bioacoustic analysis

Kaleidoscope Pro v4.0.4 software (Wildlife Acoustics Inc., Massachusetts, USA) was used to manually analyse all recordings following the acoustic key in López-Baucells et al., (2016) and a regional reference call library (A. López-Baucells, *unpublished data*). Calls were identified to species level or assigned to groups (sonotypes) of taxa with similar calls. The main constraint of acoustic data is that it is not possible to count individuals and therefore abundance cannot be derived. Here we use activity as a proxy for abundance (Rowse et al., 2016) based on the number of bat passes. A bat pass was defined as any call sequence which contained at least two distinguishable echolocation pulses during a maximum duration of 5 s (Appel et al., 2019; López-Baucells et al., 2021). Bat activity was quantified by the number of bat passes per night per species/sonotype. We identified 283,242 bat passes belonging to 17 aerial insectivorous bat species and sonotypes from four different families. To minimise potential detection bias we only included species in the analysis that were detected in at least 10% (102 nights) of total nights and in all three sampling years as per Appel et al. (2021). This resulted in the selection of nine species and one sonotype; *Centronycteris maximiliani*, *Cormura brevirostris*, *Saccopteryx bilineata*, *S. leptura, Furipterus horrens, Molossus* sonotype (including *sinaloae* / *currentium* / *rufus* calls), *Pteronotus alitonus, P. rubiginosus, Eptesicus brasiliensis* and *Myotis riparius* (Table S3.1). We also assigned the species/sonotypes to guilds based on their ecological requirements and foraging strategies following Yoh et al. (2022). Forest specialists (FS), which typically inhabit forest interiors included *E. brasiliensis, F. horrens*, and *M. riparius*. The two *Pteronotus* species were grouped as Flexible foragers (FF), as they are known to commonly exploit a variety of habitats. The Edge specialists (ES) included: *C. brevirostris, C. maximiliani, S. bilineata* and *S. leptura*, species which typically forage along forest edges or in forest gaps. The *Molossus* sonotype represents Open space (OS) bats and was included in the guild analysis for comparison only as it is represented by a single sonotype.

Local and landscape predictor variables

Local vegetation structure

For each of the 33 sampling sites, within three plots of 100 m2 (5×20 m) around the detector locations, we quantified seven local-scale vegetation variables (Rocha et al., 2017; López-Baucells et al., 2022): (1) number of trees (> 10 cm diameter at breast height [DBH]), (2) number of woody stems (<10 cm DBH), (3) average DBH of trees >10 cm, (4) percentage canopy cover, (5) liana density (visually classified every 5 m in five categories varying from no lianas to very high liana density), (6) canopy height (based on visual estimation) and (7) vertical stratification in vegetation density. To reduce the dimensionality of the data we performed a Principal Components Analysis (PCA). The first axis explained 38.3% of total variance and was positively correlated with average DBH of trees >10 cm, canopy height and percentage canopy cover, all features which describe more structurally complex habitats, albeit the metric represented a gradient, also including negative values characteristic of varying types of regenerating forests, with an increased number of woody stems and liana density. (Refer to Chapter 2 Supplementary Material; Fig. S2.1; Table S2.2). The scores of the first axis (PCA1) were used as a predictor variable summarising local vegetation structure.

Landscape structure

Measurements of landscape composition and configuration were obtained using 2011 LandSat Thematic Mapper™ satellite images (30 m spatial resolution). For the purpose of this study, the map was categorised into two land cover classes; continuous primary forest and secondary forest. To avoid collinearity (a common problem with landscape predictor variables) and to allow for comparison with previous studies (Rocha et al., 2017; López-Baucells et al., 2022), we selected the same three landscape metrics which were considered acceptable based on variance inflation factor calculations (VIF). The R package 'landscapemetrics' (Hesselbarth et al., 2019) was used to calculate landscape composition (continuous forest cover) and configuration (patch density, edge density) metrics. To assess scale dependency in responses of individual species to fragmentation, we quantified the aforementioned metrics within circular buffers with radii of 0.5, 1, 1.5, 2, 2.5, 3, 3.5, 4, 4.5 and 5 km around each of the 33 sampling sites. Unfortunately, since little is known about the home range of the focal species in this study, we took into consideration the scale of effect documented by Jackson & Fahrig, (2015) and the utilisation of 5 km landscape buffers in other tropical aerial insectivorous bat studies (e.g., Rodríguez-San Pedro & Simonetti, 2015; Rodríguez-San Pedro et al., 2019). Larger spatial scales were not considered to minimise spatial overlap between sites, although it is acknowledged that overlapping landscape buffers may not necessarily violate statistical independence (Zuckerberg et al., 2020). To control for statistical correlation (Trzcinski, 1999), we fitted a linear model between the landscape composition variable (continuous forest cover) and the landscape configuration variables (edge and patch density) at each spatial scale. From this simple linear regression, new configuration variables were created using the extracted residuals which were then used in subsequent modelling (Bélisle, 2001; Klingbeil & Willig, 2010).

Statistical analysis

To visualise specific-specific frequency of occurrence in continuous old-growth forest, forest fragment interiors, forest fragment edges and secondary forest matrix sites, activity per habitat type, expressed as percentage, was plotted (Fig. 3.1). In order to gain insight into the species-specific responses to habitat type and the local and landscape scale attributes, we modelled each of the species' bat activity with 1) the fragment size/IEM variables and 2) the local- and landscape-scale variables. For this, we performed Monte Carlo Markov Chain generalised linear mixed models using the R package MCMCglmm (Hadfield, 2010), specifying a Poisson error distribution. Upon investigation, each species´ response variable indicated overdispersion, which is not unusual for bat activity data (López-Baucells et al., 2021). Therefore, priors were set to be weakly informative in order to deal with overdispersion (inverse gamma parameters: ν=0.002 and V=1; Kryvokhyzhaet al., 2016; Hadfield, 2018).

For fragment size/IEM variables we fit a full model for each species, specifying a single categorical fixed effect with combined information on the fragment size and IEM gradient (10 categories: continuous forest interior, 100 ha interior, 100 ha edge, 100 ha matrix, 10 ha interior, 10 ha edge, 10 ha matrix, 1 ha interior, 1 ha edge, 1 ha matrix; Rocha et al., 2017; López-Baucells et al., 2022) and incorporated research camp location as a random effect. To model local- and landscape-scale variables, we fit a set of models for each species with four fixed-effect local and landscape scale variables (local vegetation structure (as represented by PCA1), continuous forest cover, edge density, patch density) for each buffer size (0.5, 1, 1.5, 2, 2.5, 3, 3.5, 4, 4.5 and 5 km) and research camp location as a random effect. Each model set contained 10 full models. We also modelled local- and landscape-scale variables (as previously detailed) for each guild (FS, ES and FF). We ran 50,000 iterations with a thinning-interval of 10 after 'burn-in' of 5,000. We evaluated convergence through (a) visual check of parameter time series representations, i.e., trace plots, (b) calculation of the lag k autocorrelation statistic to check lag progress and independence of posterior distribution samples, (c) calculation of the Gelman-Rubin diagnostic statistic (comparison of four chains). All point estimates of potential scale reduction factor were <1.1, indicating good convergence (Gelman & Rubin, 1992). All models achieved convergence. Posterior distributions for the predictor variables were obtained. A measure of significance of the difference between effects (p_{MCMC}) can be produced via the proportional overlap of the distribution estimates produced, accompanied by an estimate of the mean and 95% credible intervals without the use of post-hoc tests (Sweeny et al., 2021). As model output, we report posterior means, 95% credible intervals and Bayesian p-values (p_{MCMC}) indicating the significance of variables with a threshold of * $p_{\mathrm{MCMC}} < 0.05$, ** $p_{\mathrm{MCMC}} < 0.01$, *** $p_{\mathrm{MCMC}} < 0.001$.

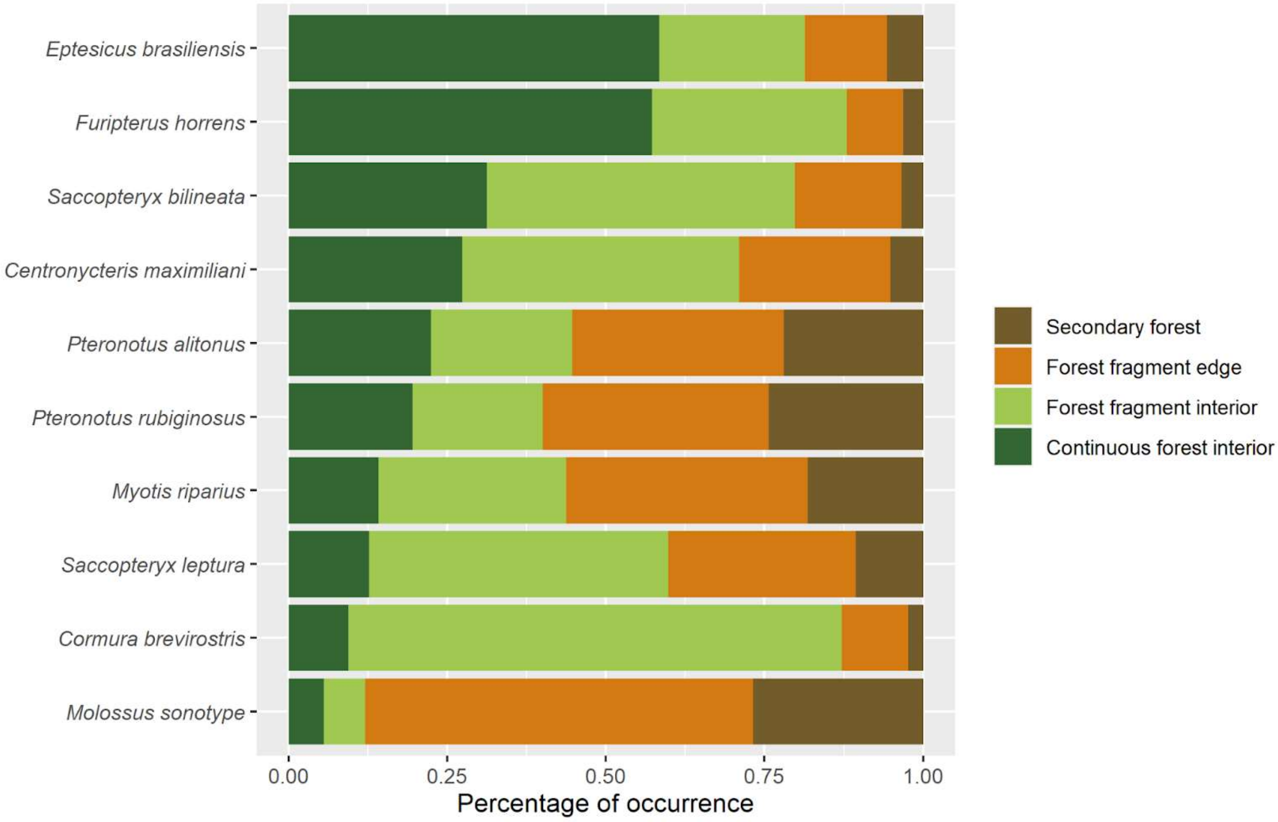

Fig. 3.1 Species sorted by their frequency of occurrence in continuous forest interiors, forest fragment interiors, forest fragment edges and secondary forest. Percentage of occurrence was calculated using bat activity in each site per habitat type. Differences in sampling effort between habitat categories were accounted for in the percentage calculations.

Results

Across 33 sites, 272,201 bat passes were analysed belonging to 10 different species/sonotypes from five different families (Emballonuridae, Furipteridae, Molossidae, Mormoopidae, Vespertilionidae) encompassing four guilds (edge foragers, forest specialists, open space foragers, flexible forest foragers). All species/sonotypes were recorded across all four habitat types, however patterns of occupancy were highly species-specific (Fig. 3.1). *Eptesicus brasiliensis* and *Furipterus horrens* had occurrence frequencies greater than 50% in continuous forest. There were only three species with over 20% occurrence recorded in the secondary forest (*Pteronotus alitonus, P. rubiginosus* and *Molossus* sonotype). *Cormura brevirostris* was recorded mainly in fragment interiors with over 75% frequency of occurrence in that habitat.

Bat activity responses to IEM and fragment size gradients

Habitat modelling revealed species-specific differences in bat activity across the IEM and fragment size gradients relative to continuous forest interiors (Fig. 3.2; Table S3.2). *Centronycteris maximiliani* shows a clear pattern with significantly reduced activity in all second-growth forest sites and reduced activity at the edges of the 1ha fragments. *Cormura brevirostris* activity was significantly higher in the 10 ha fragment interiors. The reduction in bat activity for *Saccopteryx bilineata* was highly significant in the matrix around the smallest fragments and significantly reduced in matrix and edge sites of the 100ha fragment sites. *Saccopteryx leptura* activity responded significantly and positively in the interior sites of the 10 ha and 1 ha sites and negatively in the matrix of the 1 ha fragments. *Furipterus horrens* had significantly lower activity in all matrix sites and the interior and edge sites of the smallest fragments (1 ha and 10 ha). *Molossus* sonotype activity was significantly elevated across all matrix and edge sites for all fragment sizes. Neither of the *Pteronotus* species showed any significant responses to the habitat gradient or fragment size. Activity of *Eptesicus brasiliensis* was curtailed in the 1ha and 10 ha secondary forest matrix sites. *Myotis riparius* activity responded positively to each of the edge habitat sites in addition to an increase in activity in the interior of the 1 ha fragments.

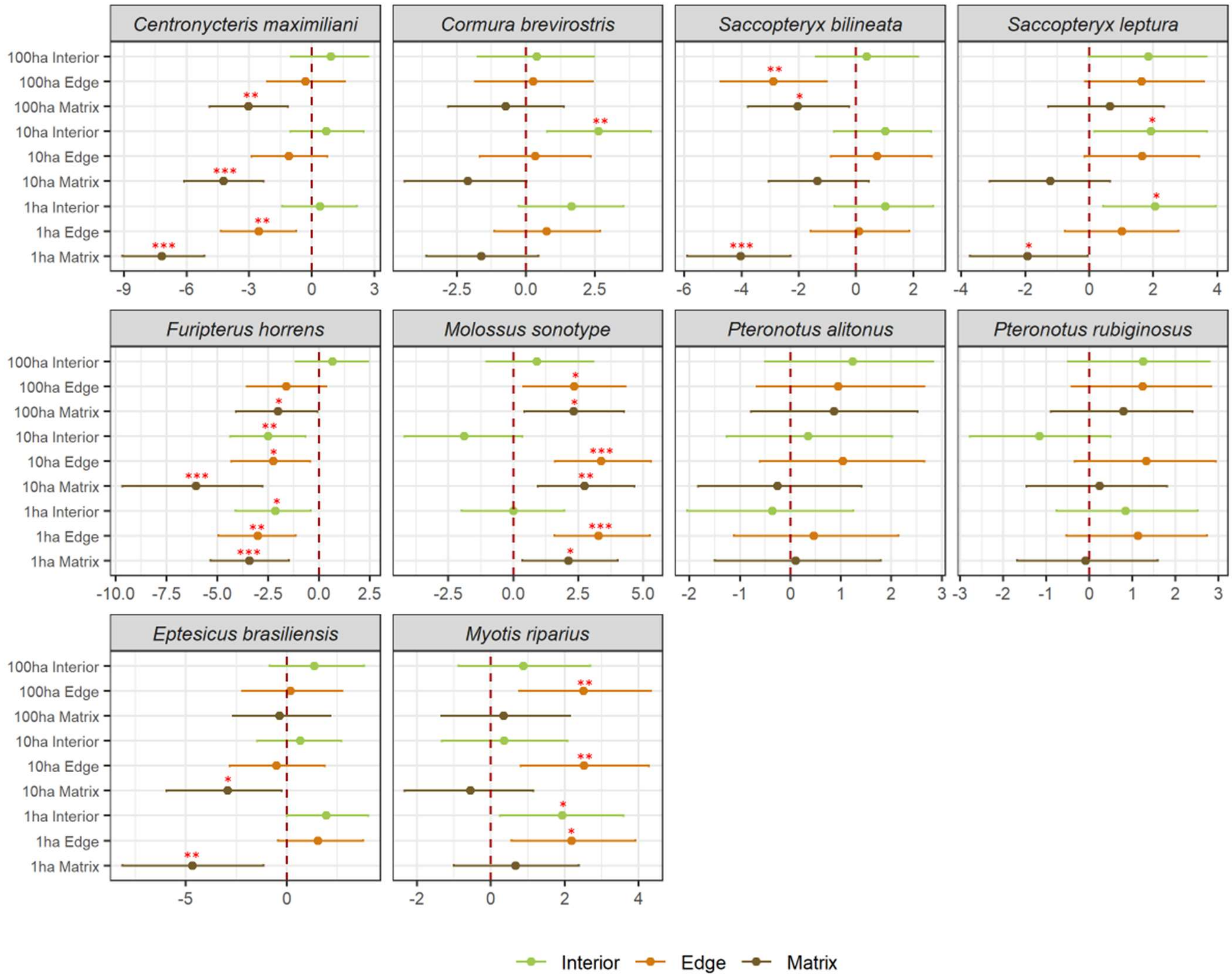

Fig. 3.2 Comparison of total bat activity for species across the Interior-Edge-Matrix and size gradients at the Biological Dynamics of Forest Fragments Project (forest fragment interiors, forest fragment edges and adjoining secondary forest matrix). The predicted differences between each habitat and continuous old growth forest interior, modelled using $\text{MCMC}_{\text{GLMM}}$ are plotted with their corresponding 95% credible interval. Those which do not touch or overlap the vertical dashed line (0) are considered significant (* $p_{\text{MCMC}} < 0.05$, ** $p_{\text{MCMC}} < 0.01$. *** $p_{\text{MCMC}} < 0.001$).

Influence of local- and landscape-scale predictors

Aerial insectivorous bat activity modelling showed species-specific variation in response to the local and landscape predictors (Table S3.3), with seven species (*C. maximiliani, C. brevirostris, S. bilineata, S. leptura, F. horrens, Molossus* sonotype and *E. brasiliensis*) exhibiting significant scale-sensitive associations with the metrics (Fig. 3.3). Species which showed no significant association with any of the local or landscape variables, at any of the scales investigated, included *P. alitonus, P. rubiginosus* and *M. riparius* (Fig. S3.1).

In this study, vegetation structure was an important predictor of bat activity, in particular *C. maximiliani*, *S. bilineata* and *S. leptura*, exhibited a significant positive relationship at every scale. *Furipterus horrens* and *C. brevirostris* evinced a consistent positive relationship at the larger scales (2.5 - 5 km scale). *Eptesicus brasiliensis* responded positively and exclusively at the 2 km scale to vegetation structure. In contrast, the *Molossus* sonotype exhibited a significant negative relationship at every scale. For the focal species in this study, forest cover was an irrelevant predictor, with very little influence on bat activity and no significant associations at any scale of our analysis. The configurational metrics (edge and patch density) exhibited nuanced associations which included significant responses by *F. horrens, S. bilineata* and *C. maximiliani*. *Furipterus horrens* responded positively to edge density at the 3.5 km and 4.5 km scale and negatively to patch density at the 4 km and 4.5 km scale. Patch density had a negative relationship with *S. bilineata* activity at the 3.5 km scale. Edge density exhibited a positive association with *C. maximiliani* activity at the small scale of 1 km and 1.5 km.

The guild-level modelling results further highlighted the influence of vegetation structure as an important predictor metric for aerial insectivorous bat guilds (Fig. S3.2; Table S3.4). For forest specialists, vegetation structure had a positive relationship at scales of 2.5 km through to 5 km (excluding 4.5 km) and was a significant influencer for edge foragers at all scales and highly so at 0.5 km, 1 km, 2.5 km and 4 km scale. The configurational metrics, edge and patch density, also influenced the edge foragers at the local scale, with a negative relationship with patch density at 0.5 km and positive relationship with edge density at 1 km. There were no relationships with any of the local or landscape variables evident for the flexible forest foragers.

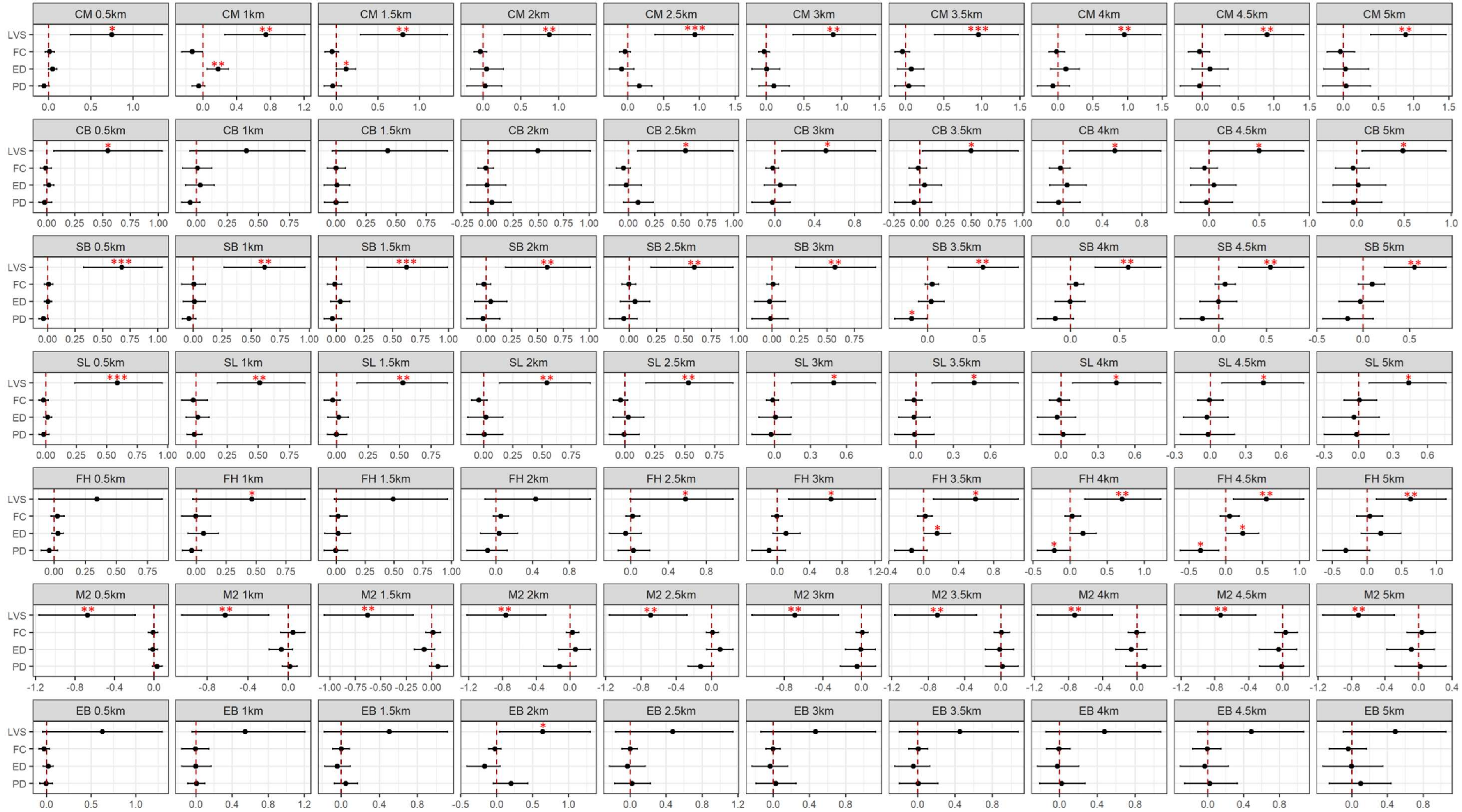

Fig. 3.3 Seven species exhibiting significant scale-sensitive associations with metrics; *C. maximiliani* (CM), *C. brevirostris* (CB), *S. bilineata* (SB), *S. leptura* (SL), *F. horrens* (FH), *Molossus* sonotype (M2) and *E. brasiliensis* (EB). Bat activity modelled as a function of local and landscape predictor variables; vegetation structure (LVS), forest cover (FC), edge density (ED) and patch density (PD). Shown are posterior mean estimates ± 95% credible intervals. Credible intervals which do not touch or overlap the zero line are considered significant (* $p_{\mathrm{MCMC}} < 0.05$, ** $p_{\mathrm{MCMC}} < 0.01$, *** $p_{\mathrm{MCMC}} < 0.001$).

Discussion

We present findings which advance understanding of how 10 aerial insectivorous bat species/sonotypes at the BDFFP respond to gradients of fragment size and habitat quality in this regenerating landscape, building on previous research which investigated assemblage-level responses from a multidimensional diversity perspective (López-Baucells et al., (2022). Second-growth forests can provide new habitat for forest-dwelling species and contribute to the recovery of ecosystems in fragmented primary forests (Derrorie et al., 2016). At the time of data collection, fragment-matrix contrast of the BDFFP landscape was considered to be low, with late-stage secondary forest which had been regenerating for approximately 30 years. Studies have estimated species recovery in second-growth forests including tree species richness which can be comparable to old-growth forest within 50 years (Martin et al., 2013) and under optimal conditions bird and ant species recovery can take up to 40 years (Dunn, 2004). More specifically, within the BDFFP, examples include; Quintero & Roslin (2005) who estimate a maximum of 17 years for the complete recovery of dung beetles, Powell et al., (2013) who concluded that 90% of bird assemblages showed full recovery after 30 years, and Rocha et al., (2018) who found a landscape-wide increase in the occupancy and abundance of primary forest specialist phyllostomid bat species. However, primates were still responding to habitat edges up to 30 years following matrix regeneration (Lenz et al., 2014) and whilst specialist phyllostomid species showed signs of recovery after 30 years, there were still considerable differences between the second-growth and continuous forest assemblages, especially in the smallest fragments (Rocha et al., 2018).

Habitat occurrence patterns and activity responses to the IEM and fragment size gradients

Our species-specific results reveal that the tall second-growth forest in which the BDFFP fragments are now embedded does appear to buffer some of the negative effects of fragmentation, but we also observed that there are some species which inevitably still rely on old-growth forest due to trait-mediated exclusion from second-growth forest habitat. The flexible foragers, e.g., *Pteronotus* spp., showed no preference for any type of habitat or fragment size. The *Molossus* sonotype (the only open space species) showed increased activity around the edge and matrix for all fragment sizes. Edge-foragers such as the emballonurid bats were more commonly recorded at the fragment edges and in fragment interiors, albeit most species showed a reduction in activity around the 1ha fragments. Forest specialists, in particular *F. horrens*, appear to be more sensitive to the second-growth forest and activity was negatively affected across the whole IEM gradient and all bar the largest fragment interiors.

Our results show that *P. alitonus* and *P. rubiginosus* were detected evenly across all four habitats. This absence of habitat preference is also noted in the IEM and fragment size gradients comparison where no significant effects were found. These *Pteronotus* species of the family Mormoopidae, produce high-duty cycle echolocation calls, different to the other species of aerial insectivorous bats. They emit constant frequency (CF) calls, which are pulses of long duration and allow them to accurately detect small mobile prey items in dense vegetation (Estrada-Villegas et al., 2012; López-Baucells et al., 2018). Núñez et al., (2019) sampled aerial insectivorous bats following the last fragment re-isolation event and found that these high duty-cycle species were more abundant in forest interiors than in the newly cleared areas or at fragment edges. Our results do not reflect this distinction. Appel et al., (2021) found that *Pteronotus* spp. had lower activity in secondary forest, preferring continuous forest on bright nights with increased moonlight intensity, possibly as a way to reduce threats from avian predators around fragment edges. This flexibility across habitat types and response to abiotic variables (moonlight) perhaps illustrates how well adapted these *Pteronotus* species are, occupying a relatively free acoustic niche (Siemers & Schnitzler, 2004).

The *Molossus* sonotype was most associated with fragment edges and second-growth forest and showed significantly elevated activity in these habitats. Bats of the family Molossidae have long, narrow wings which are associated with fast, economic flight (Castillo-Figueroa, 2020). Their mobility is constrained within forest strata consisting of forest gaps and obstacles to navigate and so are often precluded from foraging in these habitats due to the high energetic cost (Voigt & Holderied, 2012). Whilst molossids generally show good tolerance to fragmentation (Estrada-Villegas et at., 2010) and are not overly sensitive to anthropogenic disturbance (Meramo et al., 2022), we acknowledge this result could also be due to increased detectability from changes in flight behaviour. Molossids generally forage high above the forest canopy in open space (Surlykke & Kalko 2008) which can make detecting their calls difficult if they are a significant distance away from the detectors (Marques et al., 2016). Secondary forest with lower canopy height may allow molossids to fly lower and for their calls to be within recording range of detectors more often in disturbed forests compared to continuous forest.

Emballonurid bats produce shallow-modulated and multi-harmonic echolocation calls, which allow them to forage across a range of habitats including forest edge vegetation, forest gaps and above canopy and over open landscapes (Jung et al., 2007). Specifically, although the four species in this study are categorised as edge foragers, their frequency of occurrence suggests a broader habitat preference within the BDFFP landscape. *Saccopteryx bilineata*, known to forage above shrub layer, in small forest gaps and in the canopy (Denzinger et al., 2018), was recorded more often in the fragment interiors and the continuous forest interior than at fragment edges or in second-growth. *Saccopteryx leptura* occupancy was greater in the forest fragment interiors and edges, preferring to forage in subcanopy and canopy (Denzinger et al., 2018), with significantly increased activity in the smaller fragment interiors. Both species had significantly reduced activity in the matrix around the 1 ha fragments and *S. bilineata* activity was significantly reduced at the edge and in the matrix of those smallest fragments when compared to continuous forest. A study comparing the echolocation calls of *S. bilineata* and *C. brevirostris*, to understand how they might differ in the perception of their surroundings, found that *C. brevirostris* was better able to adapt its calls in the flight chamber whereas *S. bilineata* rarely changed its call structure (Jakobsen et al., 2012). This study suggested two plausible possibilities; that *C. brevirostris* has more call frequency composition control and acoustic dexterity, compared to *S. bilineata*, or conversely that *S. bilineata* is more clutter-tolerant and does not need to make changes to its echolocation to navigate such habitats. Our results also show that *C. brevirostris* had the highest frequency of occurrence (over 75%) recorded in the forest fragment interiors compared to all other species and is the only edge foraging species which showed no significant negative effect on its activity across the IEM and fragment size gradients. Our results would support the suggestion that *C. brevirostris* had more call frequency composition control and acoustic dexterity allowing it to forage uninhibited across the BDFFP landscape. *Centronycteris maximiliani* had significantly lower activity in the matrix of all three fragment sizes, indicating that the regrowth habitat at the time of this study was not preferable foraging ground for this species.

Furipterus horrens was most commonly detected in the continuous old-growth forest, followed by the fragment interiors. This forest specialist exhibited particular sensitivity to habitat disturbance, a conclusion also drawn by Yoh et al. (2022), with significantly reduced activity compared to continuous forest interiors across the IEM gradient for all fragments apart from the largest 100 ha interior and edge. Compared to other Neotropical bats, *F. horrens* emit extremely high frequency, low intensity pulses which allows it to forage in dense rainforest vegetation (Falcão et al., 2015). *Eptesicus brasiliensis* exhibited a similar frequency of occupancy to *F. horrens* but this forest specialist appears to be able to take advantage of a wider variety of habitats compared to *F. horrens*. Its activity was significantly reduced in the matrix of the smallest fragments (1 ha and 10 ha). Echolocation calls of *Eptesicus brasiliensis* are similar to its North American congener *Eptesicus furinalis*. Studies highlight examples of *E. furinalis* navigating through acoustically-challenging environments and complicated scenes (Simmons et al., 2018; Simmons et al., 2020). This acoustic dexterity trait is likely to be shared with *E. brasiliensis*, allowing it to utilise habitat created by fragmentation. In contrast with the other two forest specialists, *M. riparius* was detected more often at fragment edges and in second-growth forest. Its activity was consistently and significantly increased across all edge habitats, independent of fragment size. Aerial insectivorous bats, in particular edge specialists, are often detected foraging at subcanopy and canopy level, however Marques et al., (2016) found that *M. riparius* was an exception and was more frequently recorded at ground level. *Myotis riparius* is ideally suited to take advantage of this foraging niche in the lowest forest strata due to its small body size (Norberg & Rayner, 1987) and echolocation call structure (Schnitzler & Kalko, 2001).

Influence of local- and landscape-scale predictors on species-specific activity

The buffering effects provided by the advanced-stage secondary forest are also evident from the modelling of the effects of local and landscape scale predictors on species' activity levels. Our results show limited negative effects of fragmentation at the landscape scale and only the *Molossus* sonotype responded negatively to local vegetation structure, indicating that the aerial bat assemblage is approaching a point of recovery whereby the pervasive fragmentation effects are no longer pronounced and ubiquitous, consistent with research on phyllostomid (Rocha et al., 2018), dung beetle (Quintero & Roslin, 2005) and bird (Powell et al., 2013) recovery at the BDPPF.

We assessed overall landscape composition in terms of forest cover and found no significant relationships with activity for any of the species or guilds. Even across agricultural landscapes, which may feature "harder" matrix habitats (i.e., monocultures or open areas) surrounding forest patches, inconsistent results have been reported for the effect of forest cover on aerial insectivorous bat activity (Azofeifa et al., 2019; Put et al., 2019; Rodríguez-San Pedro et al., 2019). We also found no negative responses associated with the configurational metric edge density. The creation of edges due to deforestation has been proven to have a pervasive effect on vertebrate species (Pfeifer et al., 2017) and forest ecosystem functioning (Harper et al., 2005). However, aerial insectivorous bats, particularly those which are adapted to foraging around vegetation edges, have in many cases benefited from increased hunting opportunities and have shown resilience, per se, to fragmentation (Ethier & Fahrig, 2011; Rodríguez-San Pedro & Simonetti, 2015). Our results concur with a study on edge effects at the BDFFP which provided evidence that the regenerated second-growth forest could support comparable levels of aerial insectivorous bat activity compared to continuous primary forest as a result of edge sealing (Yoh et al., 2022). We uncovered two species which exhibited a positive response to edge density at contrasting scales in this landscape; *C. maximiliani* at the smaller scales of 1 km and 1.5 km and *F. horrens* at the 3.5 km and 4.5 km scale. *Furipterus horrens* is one of the smallest neotropical bats and has been documented to live in tree hollows, buildings, but is more frequently found in caves (Portella et al., 2017). Little is known about this elusive species due to challenges with acoustic detectability and mist netting capture techniques (Falcão et al., 2015) but as a forest specialist, with short broad wings and extremely high frequency echolocation calls (Schnitzler & Kalko, 2001), it is well adapted to forage within cluttered forest environments. The positive response to edge density at larger scales could indicate that edge sealing is having an impact at the landscape scale for this species. The *Molossus* sonotype consistently showed a significant negative response to local vegetation structure across all scales. As previously detailed, these open space foragers will find it acoustically and physically challenging to navigate through forested habitat (Voigt & Holderied ,2012) and they have been found to have reduced activity in mature forest where, on account of their increased mobility and fast flight speed, they can commute longer distances and access anthropogenically altered habitats to take advantage of increased roost and food availability created by human settlements (Bader et al., 2015). Again, we acknowledge that detection of the *Molossus* sonotype may affect our results. This is also a consideration across the whole of our study as detection of species will vary depending on sampling method, habitat, weather conditions (Gorresen et al., 2008) and variation in echolocation call intensity (López-Baucells et al., 2016). Our standardisation of recording equipment and nightly sampling method provided a consistent number of encounter histories over the course of the sampling period which should average out the detection variability in our study but we also acknowledge that by virtue of our statistical analysis (only including species which were detected in at least 10% (102 nights) of total nights and in all three sampling years) we have effectively removed the rarest species and those which might be more sensitive to the effects of fragmentation across this experimental landscape.

Conclusions

The BDFFP fragments are now surrounded by a low-contrast matrix of tall secondary forest which has been regenerating for at least 30 years. We found no evidence of trait-mediated filtering as all species were recorded, albeit to different extents, in the continuous forest, fragments and secondary forest habitats. Activity patterns compared with continuous forest were species-specific with results suggesting that this patchwork landscape is favourable for most but not all species. *Furipterus horrens* was the only species which exhibited significantly reduced activity across the whole IEM disturbance gradient and smallest fragments, indicating that even after 30 years, the activity of this forest specialist is still moderated by the effects of fragmentation. Half of the species had significantly reduced activity in the matrix habitat around the 1 ha fragment, highlighting that from a land management perspective, it is important that sufficiently large-sized fragments should be preserved (at least 10 ha) to help reduce the detrimental edge effects that can engulf smaller fragments. The multiscale analysis indicated no negative influence of the composition (amount of forest cover) of the landscape at any of the spatial scales (0.5 km - 5 km) and limited effects were evident for the configuration variables (edge and patch density). In fact, most of the statistically significant responses were positive indicating that these aerial-hawking species benefited from a degree of disturbance which has generated increased edges for foraging. Our results suggest the common species of the aerial insectivorous bat assemblage in the BDFFP could be approaching a point of recovery after 30 years of regeneration. However, this conclusion is delivered with caution, acknowledging that the BDFFP is a unique experiment and represents a best-case scenario in the real world as the fragments are regular in shape, are in relatively close proximity to continuous forest and are not exposed to additional threats from human disturbance including; logging, hunting and fires (Laurance et al., 2011). Advanced secondary forest, particularly that which has been regenerating for a number of decades, is of considerable conservation value within human modified landscapes and should be afforded protection alongside primary forest areas.

Author contributions

All authors contributed to the study conception and design. AL-B and RR collected data at the BDFFP. Data analysis was performed by SR with input from AL-B. The manuscript was written by SR and CFJM provided comments.

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Supplementary Material

Fig. S3.1 Three species exhibiting non-significant scale-sensitive associations with local and landscape predictor variables

Fig. S3.2 Guild bat activity modelled with local and landscape predictor variables

Table S3.1 Total number of bat passes for the ten bat species/sonotypes selected for study

Table S3.2 Model output comparing bat species/sonotypes activity with habitat types

Table S3.3 Model output comparing bat species/sonotypes with local and landscape predictor variables

Table S3.4 Model output comparing bat guilds with local and landscape predictor variables

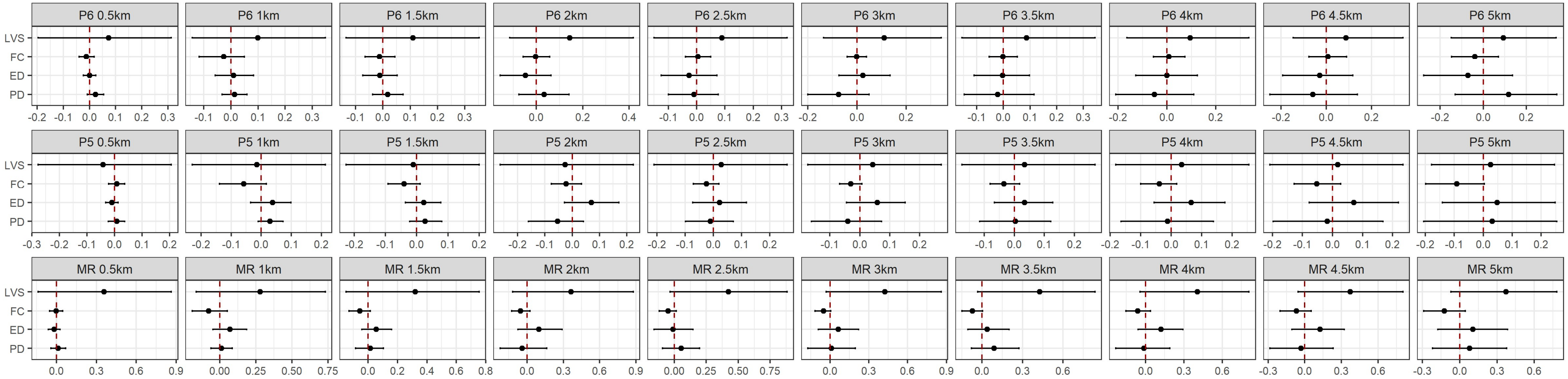

Fig. S3.1 Three species exhibiting non-significant scale-sensitive associations with metrics; *P. alitonus* (P6)*, P. rubiginosus* (P5) and *M. riparius* (MR). Bat activity modelled as a function of local and landscape predictor variables; vegetation structure (LVS), forest cover (FC), edge density (ED) and patch density (PD). Shown are posterior mean estimates ± 95% credible intervals.

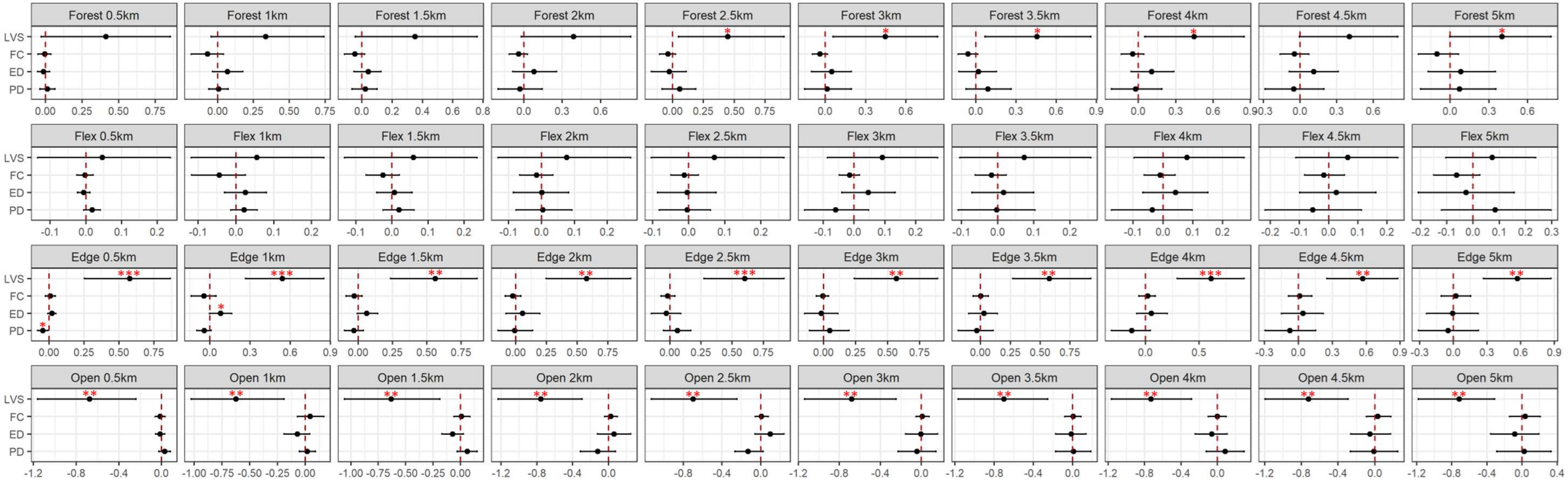

Fig. S3.2 Guild (Forest specialists, Flexible forest foragers, Edge foragers, Open Space) bat activity modelled as a function of local and landscape predictor variables (vegetation structure, forest cover, edge density and patch density). Shown are posterior mean estimates ± 95% credible intervals. Credible intervals which do not touch or overlap the zero line are considered significant (* $p_{\mathrm{MCMC}} < 0.05$).

Table S3.1 Total number of bat passes for the ten bat species/sonotypes selected for study at the Biological Dynamics of Forest Fragments Project, Central Amazon. Total calls analysed 272,201 Guild: EF =Edge foragers, FS = Forest specialists, OS = Open Space, FF = Flexible forest foragers.

Species / Sonotype	Species calls included:	Code	Guild	Total number bat passes
Emballonuridae				
Centronycteris maximiliani	*Centronycteris maximiliani*	CM	EF	77247
Cormura brevirostris	*Cormura brevirostris*	CB	EF	6079
Saccopteryx bilineata	*Saccopteryx bilineata*	SB	EF	27675
Saccopteryx leptura	*Saccopteryx leptura*	SL	EF	15862
Furipteridae				
Furipterus horrens	*Furipterus horrens*	FH	FS	709
Molossidae				
Molossidae II	*Molossus sinaloae / currentium / rufus*	M2	OS	1291
Mormoopidae				
Pteronotus alitonus	*Pteronotus alitonus (parnelli)*	P6	FF	50505
Pteronotus rubiginosus	*Pteronotus rubiginosus*	P5	FF	45603
Vespertilionidae				
Eptesicus brasiliensis	*Eptesicus brasiliensis*	EB	FS	1206
Myotis riparius	*Myotis riparius*	MR	FS	46024

Table S3.2 MCMC$_{\text{GLMM}}$ model output comparing total bat activity for species across the Interior-Edge-Matrix (forest fragment interiors, forest fragment edges and adjoining secondary forest/matrix). We report mean posterior estimate, 95% credible intervals, the effective sample size and Bayesian p-values (p_{MCMC}) indicating the significance of variables with a threshold of $^{*}\,p_{\text{MCMC}} < 0.05$, $^{**}\,p_{\text{MCMC}} < 0.01$, $^{***}\,p_{\text{MCMC}} < 0.001$

Species	Size	Habitat	Estimate	Inferior	Superior	eff.sample	p_{MCMC}
CM	100ha	Interior	0.90	-0.89	2.74	4500	0.33
CM	100ha	Edge	-0.31	-2.12	1.56	4500	0.75
CM	100ha	Matrix	-3.06	-4.96	-1.26	4500	0.00**
CM	10ha	Interior	0.70	-1.07	2.40	4500	0.43
CM	10ha	Edge	-1.07	-2.85	0.76	4500	0.25
CM	10ha	Matrix	-4.21	-6.08	-2.46	4264	0.00***
CM	1ha	Interior	0.38	-1.41	2.06	4500	0.67
CM	1ha	Edge	-2.53	-4.31	-0.77	4500	0.01**
CM	1ha	Matrix	-7.18	-9.16	-5.21	3587	0.00***
CB	100ha	Interior	0.39	-1.81	2.41	4500	0.71
CB	100ha	Edge	0.26	-1.91	2.40	4094	0.81
CB	100ha	Matrix	-0.72	-2.88	1.35	4186	0.50
CB	10ha	Interior	2.63	0.76	4.56	4500	0.01**
CB	10ha	Edge	0.36	-1.67	2.36	4500	0.74
CB	10ha	Matrix	-2.08	-4.38	0.00	3787	0.06
CB	1ha	Interior	1.64	-0.27	3.62	4500	0.10
CB	1ha	Edge	0.75	-1.13	2.69	4500	0.45
CB	1ha	Matrix	-1.61	-3.77	0.37	4038	0.12
SB	100ha	Interior	0.39	-1.39	2.16	4500	0.67
SB	100ha	Edge	-2.88	-4.72	-1.05	4107	0.00**
SB	100ha	Matrix	-2.01	-3.75	-0.18	4500	0.03*
SB	10ha	Interior	1.04	-0.63	2.76	4500	0.24
SB	10ha	Edge	0.73	-1.02	2.50	4265	0.42
SB	10ha	Matrix	-1.34	-2.97	0.53	3576	0.14
SB	1ha	Interior	1.05	-0.63	2.79	3502	0.24
SB	1ha	Edge	0.13	-1.64	1.85	4500	0.88
SB	1ha	Matrix	-4.02	-5.76	-2.11	3979	0.00***
SL	100ha	Interior	1.80	-0.10	3.56	4228	0.06
SL	100ha	Edge	1.59	-0.31	3.35	4204	0.09
SL	100ha	Matrix	0.61	-1.16	2.52	4071	0.52
SL	10ha	Interior	1.90	0.17	3.63	4161	0.03*
SL	10ha	Edge	1.61	-0.16	3.37	4281	0.08
SL	10ha	Matrix	-1.27	-3.10	0.55	4131	0.17
SL	1ha	Interior	2.02	0.24	3.78	4500	0.02*
SL	1ha	Edge	0.98	-0.73	2.79	4257	0.28
SL	1ha	Matrix	-1.97	-3.87	-0.17	4024	0.04*
FH	100ha	Interior	0.66	-1.09	2.56	4118	0.47
FH	100ha	Edge	-1.58	-3.62	0.30	3513	0.10
FH	100ha	Matrix	-1.97	-4.01	-0.11	2846	0.04*
FH	10ha	Interior	-2.50	-4.30	-0.61	3012	0.01**
FH	10ha	Edge	-2.25	-4.11	-0.30	3095	0.02*
FH	10ha	Matrix	-5.89	-9.14	-2.92	316	0.00***
FH	1ha	Interior	-2.12	-4.00	-0.28	3376	0.02*
FH	1ha	Edge	-3.01	-4.84	-1.05	2640	0.00**
FH	1ha	Matrix	-3.43	-5.45	-1.55	1929	0.00***

M2	100ha	Interior	0.91	-1.01	3.02	3821	0.37
M2	100ha	Edge	2.33	0.48	4.26	3531	0.02*
M2	100ha	Matrix	2.30	0.53	4.27	4500	0.02*
M2	10ha	Interior	-1.85	-3.92	0.58	1223	0.10
M2	10ha	Edge	3.34	1.45	5.18	4156	0.00***
M2	10ha	Matrix	2.72	0.87	4.55	4228	0.00**
M2	1ha	Interior	0.00	-1.94	2.05	3322	0.99
M2	1ha	Edge	3.26	1.42	5.06	4145	0.00***
M2	1ha	Matrix	2.10	0.24	3.90	4188	0.03*
P6	100ha	Interior	1.25	-0.48	2.84	4500	0.15
P6	100ha	Edge	0.96	-0.73	2.56	4500	0.27
P6	100ha	Matrix	0.87	-0.76	2.51	4500	0.32
P6	10ha	Interior	0.36	-1.23	2.03	4500	0.67
P6	10ha	Edge	1.05	-0.58	2.72	4500	0.22
P6	10ha	Matrix	-0.24	-1.81	1.42	4500	0.77
P6	1ha	Interior	-0.36	-1.99	1.28	4500	0.68
P6	1ha	Edge	0.47	-1.13	2.13	4500	0.57
P6	1ha	Matrix	0.12	-1.46	1.81	4500	0.89
P5	100ha	Interior	1.25	-0.39	2.84	4500	0.13
P5	100ha	Edge	1.24	-0.39	2.84	4500	0.14
P5	100ha	Matrix	0.80	-0.93	2.31	4500	0.33
P5	10ha	Interior	-1.16	-2.86	0.33	4500	0.16
P5	10ha	Edge	1.32	-0.29	2.91	4500	0.12
P5	10ha	Matrix	0.24	-1.39	1.81	4500	0.77
P5	1ha	Interior	0.84	-0.71	2.51	4500	0.31
P5	1ha	Edge	1.13	-0.54	2.66	4500	0.17
P5	1ha	Matrix	-0.09	-1.70	1.51	4500	0.91
EB	100ha	Interior	1.33	-0.98	3.51	4049	0.26
EB	100ha	Edge	0.16	-2.27	2.56	3619	0.90
EB	100ha	Matrix	-0.36	-2.78	1.92	3279	0.78
EB	10ha	Interior	0.70	-1.41	2.72	3466	0.52
EB	10ha	Edge	-0.49	-2.79	1.72	2962	0.68
EB	10ha	Matrix	-2.97	-5.98	-0.25	1362	0.03*
EB	1ha	Interior	1.96	0.01	4.10	4090	0.06
EB	1ha	Edge	1.54	-0.42	3.64	3987	0.13
EB	1ha	Matrix	-4.74	-8.55	-1.58	508	0.00**
MR	100ha	Interior	0.92	-0.86	2.63	4500	0.31
MR	100ha	Edge	2.55	0.83	4.33	4500	0.00**
MR	100ha	Matrix	0.39	-1.35	2.17	4500	0.66
MR	10ha	Interior	0.39	-1.33	2.04	4500	0.65
MR	10ha	Edge	2.56	0.86	4.31	4500	0.00**
MR	10ha	Matrix	-0.54	-2.26	1.19	4500	0.54
MR	1ha	Interior	1.96	0.38	3.79	4709	0.02*
MR	1ha	Edge	2.22	0.51	3.91	4500	0.01*
MR	1ha	Matrix	0.70	-0.93	2.53	4500	0.41

Table S3.3 $\text{MCMC}_{\text{GLMM}}$ Model output comparing total bat activity for species modelled with local and landscape predictor variables (Vegetation structure, Forest cover, Edge density, Patch density) We report mean posterior estimate, 95% credible intervals, the effective sample size and Bayesian p-values (p_{MCMC}) indicating the significance of variables with a threshold of $^{*}\,p_{\text{MCMC}} < 0.05$, $^{**}\,p_{\text{MCMC}} < 0.01$, $^{***}\,p_{\text{MCMC}} < 0.001$

Species	Buffer Size	Variable	Estimate	Inferior	Superior	eff.sample	p_{MCMC}
CM	0.5km	Forest Cover	0.01	-0.04	0.07	4500	0.665
CM	0.5km	Edge Density	0.05	-0.01	0.09	4306	0.066
CM	0.5km	Patch Density	-0.05	-0.12	0.01	4500	0.088
CM	0.5km	Vegetation structure	0.75	0.18	1.30	3633	0.012*
CM	1km	Forest Cover	-0.13	-0.27	-0.01	4176	0.054
CM	1km	Edge Density	0.18	0.05	0.31	4332	0.008**
CM	1km	Patch Density	-0.05	-0.12	0.03	4500	0.228
CM	1km	Vegetation structure	0.76	0.26	1.21	4500	0.006**
CM	1.5km	Forest Cover	-0.05	-0.13	0.03	4500	0.220
CM	1.5km	Edge Density	0.12	0.01	0.23	4500	0.045*
CM	1.5km	Patch Density	-0.04	-0.15	0.06	4279	0.404
CM	1.5km	Vegetation structure	0.80	0.29	1.32	4500	0.005**
CM	2km	Forest Cover	-0.04	-0.12	0.05	4500	0.392
CM	2km	Edge Density	0.05	-0.17	0.26	4500	0.664
CM	2km	Patch Density	0.03	-0.20	0.25	4269	0.830
CM	2km	Vegetation structure	0.88	0.25	1.45	4500	0.007**
CM	2.5km	Forest Cover	-0.04	-0.11	0.04	4841	0.335
CM	2.5km	Edge Density	-0.08	-0.25	0.09	4500	0.333
CM	2.5km	Patch Density	0.16	-0.01	0.32	4020	0.068
CM	2.5km	Vegetation structure	0.93	0.39	1.45	4436	0.000***
CM	3km	Forest Cover	-0.03	-0.10	0.04	4500	0.409
CM	3km	Edge Density	0.01	-0.17	0.19	4269	0.940
CM	3km	Patch Density	0.10	-0.10	0.31	4500	0.303
CM	3km	Vegetation structure	0.89	0.34	1.40	4500	0.001**
CM	3.5km	Forest Cover	-0.04	-0.13	0.05	4256	0.389
CM	3.5km	Edge Density	0.07	-0.10	0.24	4461	0.407
CM	3.5km	Patch Density	0.04	-0.15	0.23	4500	0.670
CM	3.5km	Vegetation structure	0.94	0.40	1.48	4500	0.000***
CM	4km	Forest Cover	-0.02	-0.14	0.09	4500	0.694
CM	4km	Edge Density	0.11	-0.10	0.31	4500	0.294
CM	4km	Patch Density	-0.07	-0.31	0.16	4500	0.552
CM	4km	Vegetation structure	0.94	0.41	1.49	4500	0.002**
CM	4.5km	Forest Cover	-0.04	-0.17	0.13	4500	0.638
CM	4.5km	Edge Density	0.11	-0.15	0.36	4500	0.386
CM	4.5km	Patch Density	-0.04	-0.33	0.24	4696	0.751
CM	4.5km	Vegetation structure	0.91	0.40	1.44	4295	0.002**
CM	5km	Forest Cover	-0.04	-0.24	0.17	4500	0.662
CM	5km	Edge Density	0.03	-0.31	0.34	4500	0.854
CM	5km	Patch Density	0.04	-0.29	0.39	4895	0.809
CM	5km	Vegetation structure	0.90	0.37	1.43	4500	0.002**
CB	0.5km	Forest Cover	-0.01	-0.06	0.03	5221	0.638
CB	0.5km	Edge Density	0.02	-0.03	0.06	4500	0.420
CB	0.5km	Patch Density	-0.02	-0.08	0.04	4500	0.480
CB	0.5km	Vegetation structure	0.55	0.08	1.02	4500	0.028*

CB	1km	Forest Cover	0.01	-0.11	0.14	4500	0.872
CB	1km	Edge Density	0.03	-0.09	0.15	4500	0.579
CB	1km	Patch Density	-0.05	-0.12	0.02	4500	0.196
CB	1km	Vegetation structure	0.41	-0.05	0.86	4500	0.087
CB	1.5km	Forest Cover	0.00	-0.08	0.07	4500	0.964
CB	1.5km	Edge Density	0.01	-0.09	0.12	4500	0.912
CB	1.5km	Patch Density	0.00	-0.10	0.10	4500	0.996
CB	1.5km	Vegetation structure	0.42	-0.03	0.91	4813	0.080
CB	2km	Forest Cover	-0.02	-0.10	0.06	4500	0.596
CB	2km	Edge Density	-0.01	-0.20	0.19	4803	0.932
CB	2km	Patch Density	0.04	-0.16	0.23	4473	0.679
CB	2km	Vegetation structure	0.49	-0.02	1.01	4500	0.063
CB	2.5km	Forest Cover	-0.04	-0.11	0.02	4500	0.196
CB	2.5km	Edge Density	-0.02	-0.17	0.13	4109	0.755
CB	2.5km	Patch Density	0.10	-0.04	0.24	4500	0.166
CB	2.5km	Vegetation structure	0.54	0.07	0.96	4500	0.019*
CB	3km	Forest Cover	-0.02	-0.09	0.04	4500	0.522
CB	3km	Edge Density	0.06	-0.10	0.23	4228	0.482
CB	3km	Patch Density	-0.03	-0.23	0.16	4500	0.786
CB	3km	Vegetation structure	0.50	0.05	0.96	4500	0.032*
CB	3.5km	Forest Cover	-0.01	-0.10	0.07	4500	0.775
CB	3.5km	Edge Density	0.05	-0.12	0.20	4500	0.550
CB	3.5km	Patch Density	-0.06	-0.24	0.12	4505	0.506
CB	3.5km	Vegetation structure	0.49	0.01	0.94	4500	0.040*
CB	4km	Forest Cover	-0.03	-0.13	0.07	4500	0.573
CB	4km	Edge Density	0.04	-0.15	0.21	4696	0.642
CB	4km	Patch Density	-0.05	-0.26	0.16	4500	0.655
CB	4km	Vegetation structure	0.53	0.09	0.99	5399	0.025*
CB	4.5km	Forest Cover	-0.05	-0.18	0.08	4500	0.491
CB	4.5km	Edge Density	0.05	-0.16	0.29	4628	0.664
CB	4.5km	Patch Density	-0.02	-0.27	0.25	4500	0.880
CB	4.5km	Vegetation structure	0.51	0.03	0.94	4500	0.028*
CB	5km	Forest Cover	-0.04	-0.22	0.13	4500	0.673
CB	5km	Edge Density	0.02	-0.27	0.30	3937	0.922
CB	5km	Patch Density	-0.04	-0.37	0.27	4500	0.810
CB	5km	Vegetation structure	0.48	0.04	0.92	4500	0.038*
SB	0.5km	Forest Cover	0.01	-0.03	0.05	3794	0.656
SB	0.5km	Edge Density	0.00	-0.03	0.04	4500	0.845
SB	0.5km	Patch Density	-0.04	-0.08	0.00	4500	0.095
SB	0.5km	Vegetation structure	0.68	0.34	1.05	4500	0.000***
SB	1km	Forest Cover	0.01	-0.10	0.10	4500	0.920
SB	1km	Edge Density	0.01	-0.09	0.10	4120	0.827
SB	1km	Patch Density	-0.03	-0.10	0.03	4500	0.281
SB	1km	Vegetation structure	0.62	0.27	0.99	4500	0.002**
SB	1.5km	Forest Cover	-0.02	-0.08	0.05	4500	0.641
SB	1.5km	Edge Density	0.03	-0.05	0.12	4500	0.442
SB	1.5km	Patch Density	-0.03	-0.11	0.04	4500	0.371
SB	1.5km	Vegetation structure	0.63	0.27	0.97	4500	0.001***
SB	2km	Forest Cover	-0.02	-0.09	0.05	4500	0.603
SB	2km	Edge Density	0.05	-0.11	0.21	4500	0.543
SB	2km	Patch Density	-0.03	-0.19	0.14	4500	0.728
SB	2km	Vegetation structure	0.60	0.17	1.00	4624	0.006**
SB	2.5km	Forest Cover	0.00	-0.06	0.05	4716	0.876

SB	2.5km	Edge Density	0.05	-0.08	0.18	4500	0.432
SB	2.5km	Patch Density	-0.05	-0.18	0.07	4500	0.453
SB	2.5km	Vegetation structure	0.60	0.23	0.98	4500	0.003**
SB	3km	Forest Cover	0.01	-0.05	0.06	4390	0.726
SB	3km	Edge Density	-0.02	-0.16	0.13	4500	0.794
SB	3km	Patch Density	-0.02	-0.18	0.15	4500	0.852
SB	3km	Vegetation structure	0.58	0.20	0.94	4274	0.003**
SB	3.5km	Forest Cover	0.04	-0.02	0.11	4500	0.179
SB	3.5km	Edge Density	0.04	-0.09	0.16	4500	0.552
SB	3.5km	Patch Density	-0.16	-0.31	0.00	4500	0.048*
SB	3.5km	Vegetation structure	0.53	0.20	0.88	4467	0.004**
SB	4km	Forest Cover	0.05	-0.03	0.13	4833	0.189
SB	4km	Edge Density	0.00	-0.15	0.15	4500	0.999
SB	4km	Patch Density	-0.15	-0.34	0.04	4500	0.105
SB	4km	Vegetation structure	0.59	0.23	0.92	4500	0.003**
SB	4.5km	Forest Cover	0.07	-0.04	0.17	4697	0.184
SB	4.5km	Edge Density	0.00	-0.20	0.18	3920	0.981
SB	4.5km	Patch Density	-0.17	-0.39	0.07	4500	0.149
SB	4.5km	Vegetation structure	0.54	0.20	0.89	4500	0.005**
SB	5km	Forest Cover	0.10	-0.04	0.23	4500	0.168
SB	5km	Edge Density	-0.03	-0.25	0.23	4500	0.808
SB	5km	Patch Density	-0.17	-0.43	0.12	4364	0.242
SB	5km	Vegetation structure	0.55	0.22	0.88	4500	0.002**
SL	0.5km	Forest Cover	-0.02	-0.06	0.02	4500	0.332
SL	0.5km	Edge Density	0.01	-0.02	0.05	4500	0.361
SL	0.5km	Patch Density	-0.02	-0.06	0.03	4500	0.427
SL	0.5km	Vegetation structure	0.57	0.21	0.94	4500	0.001***
SL	1km	Forest Cover	-0.02	-0.12	0.08	4500	0.681
SL	1km	Edge Density	0.01	-0.08	0.11	4713	0.765
SL	1km	Patch Density	-0.02	-0.08	0.05	4500	0.610
SL	1km	Vegetation structure	0.51	0.18	0.86	4500	0.004**
SL	1.5km	Forest Cover	-0.03	-0.10	0.03	4500	0.303
SL	1.5km	Edge Density	0.02	-0.06	0.10	4528	0.685
SL	1.5km	Patch Density	0.00	-0.08	0.07	4500	0.948
SL	1.5km	Vegetation structure	0.53	0.18	0.88	4445	0.005**
SL	2km	Forest Cover	-0.04	-0.11	0.02	4500	0.236
SL	2km	Edge Density	0.02	-0.14	0.16	4500	0.819
SL	2km	Patch Density	0.01	-0.15	0.16	4500	0.917
SL	2km	Vegetation structure	0.55	0.17	0.92	4245	0.007**
SL	2.5km	Forest Cover	-0.04	-0.09	0.03	4500	0.242
SL	2.5km	Edge Density	0.03	-0.10	0.17	4500	0.649
SL	2.5km	Patch Density	-0.01	-0.14	0.11	4500	0.893
SL	2.5km	Vegetation structure	0.53	0.16	0.89	4500	0.006**
SL	3km	Forest Cover	-0.02	-0.07	0.04	4500	0.517
SL	3km	Edge Density	0.01	-0.13	0.14	4500	0.931
SL	3km	Patch Density	-0.03	-0.18	0.15	4500	0.743
SL	3km	Vegetation structure	0.48	0.14	0.87	4500	0.013*
SL	3.5km	Forest Cover	-0.02	-0.08	0.05	5025	0.639
SL	3.5km	Edge Density	-0.02	-0.15	0.11	4897	0.795
SL	3.5km	Patch Density	-0.01	-0.16	0.15	4886	0.899
SL	3.5km	Vegetation structure	0.47	0.12	0.85	4500	0.014*
SL	4km	Forest Cover	-0.02	-0.10	0.07	4500	0.666
SL	4km	Edge Density	-0.03	-0.19	0.13	4741	0.675

SL	4km	Patch Density	0.01	-0.17	0.20	4500	0.880
SL	4km	Vegetation structure	0.46	0.09	0.81	4500	0.015*
SL	4.5km	Forest Cover	-0.01	-0.12	0.10	4500	0.907
SL	4.5km	Edge Density	-0.03	-0.22	0.16	4500	0.765
SL	4.5km	Patch Density	-0.02	-0.26	0.21	4500	0.891
SL	4.5km	Vegetation structure	0.45	0.08	0.77	4500	0.011*
SL	5km	Forest Cover	0.01	-0.14	0.14	4500	0.888
SL	5km	Edge Density	-0.04	-0.28	0.20	4300	0.725
SL	5km	Patch Density	-0.02	-0.30	0.25	4456	0.864
SL	5km	Vegetation structure	0.44	0.12	0.79	4789	0.017*
FH	0.5km	Forest Cover	0.03	-0.02	0.08	3189	0.264
FH	0.5km	Edge Density	0.03	-0.02	0.08	3001	0.171
FH	0.5km	Patch Density	-0.04	-0.10	0.03	2440	0.255
FH	0.5km	Vegetation structure	0.35	-0.14	0.84	3766	0.143
FH	1km	Forest Cover	0.00	-0.12	0.12	4132	0.941
FH	1km	Edge Density	0.06	-0.06	0.18	3667	0.336
FH	1km	Patch Density	-0.04	-0.13	0.04	3239	0.369
FH	1km	Vegetation structure	0.46	0.00	0.92	3727	0.041*
FH	1.5km	Forest Cover	0.02	-0.06	0.09	3886	0.671
FH	1.5km	Edge Density	0.01	-0.11	0.12	3110	0.762
FH	1.5km	Patch Density	-0.01	-0.11	0.09	4160	0.888
FH	1.5km	Vegetation structure	0.48	0.02	1.03	3986	0.049*
FH	2km	Forest Cover	0.05	-0.03	0.13	3944	0.207
FH	2km	Edge Density	0.04	-0.16	0.24	4500	0.722
FH	2km	Patch Density	-0.09	-0.31	0.12	3860	0.417
FH	2km	Vegetation structure	0.44	-0.13	1.00	3700	0.115
FH	2.5km	Forest Cover	0.02	-0.05	0.09	4063	0.594
FH	2.5km	Edge Density	-0.05	-0.21	0.12	4500	0.541
FH	2.5km	Patch Density	0.03	-0.15	0.19	4170	0.699
FH	2.5km	Vegetation structure	0.57	0.07	1.14	3494	0.031*
FH	3km	Forest Cover	0.00	-0.07	0.07	4500	0.962
FH	3km	Edge Density	0.11	-0.06	0.27	4255	0.183
FH	3km	Patch Density	-0.10	-0.32	0.09	3488	0.323
FH	3km	Vegetation structure	0.66	0.15	1.22	3121	0.013*
FH	3.5km	Forest Cover	0.02	-0.06	0.10	4590	0.716
FH	3.5km	Edge Density	0.15	0.00	0.30	4500	0.047*
FH	3.5km	Patch Density	-0.14	-0.32	0.04	4292	0.123
FH	3.5km	Vegetation structure	0.60	0.09	1.10	3371	0.013*
FH	4km	Forest Cover	0.03	-0.07	0.14	4145	0.535
FH	4km	Edge Density	0.17	-0.02	0.35	4500	0.068
FH	4km	Patch Density	-0.22	-0.44	0.00	3550	0.050*
FH	4km	Vegetation structure	0.69	0.20	1.23	3162	0.007**
FH	4.5km	Forest Cover	0.06	-0.07	0.19	4279	0.405
FH	4.5km	Edge Density	0.23	0.01	0.44	4500	0.037*
FH	4.5km	Patch Density	-0.35	-0.61	-0.09	4049	0.009**
FH	4.5km	Vegetation structure	0.56	0.09	1.05	3508	0.015*
FH	5km	Forest Cover	0.04	-0.14	0.23	3304	0.659
FH	5km	Edge Density	0.20	-0.08	0.50	4500	0.182
FH	5km	Patch Density	-0.30	-0.65	0.03	3261	0.078
FH	5km	Vegetation structure	0.63	0.10	1.12	3739	0.009**
M2	0.5km	Forest Cover	-0.01	-0.06	0.04	4500	0.624
M2	0.5km	Edge Density	-0.01	-0.06	0.03	3983	0.556
M2	0.5km	Patch Density	0.03	-0.02	0.09	4500	0.245

M2	0.5km	Vegetation structure	-0.68	-1.14	-0.19	4120	0.008**
M2	1km	Forest Cover	0.04	-0.08	0.16	4043	0.472
M2	1km	Edge Density	-0.07	-0.19	0.05	4045	0.236
M2	1km	Patch Density	0.02	-0.06	0.09	4301	0.660
M2	1km	Vegetation structure	-0.62	-1.08	-0.19	3770	0.006**
M2	1.5km	Forest Cover	0.01	-0.06	0.08	4500	0.797
M2	1.5km	Edge Density	-0.07	-0.16	0.03	4500	0.129
M2	1.5km	Patch Density	0.06	-0.03	0.15	4500	0.172
M2	1.5km	Vegetation structure	-0.64	-1.08	-0.21	4183	0.003**
M2	2km	Forest Cover	0.02	-0.05	0.10	4500	0.499
M2	2km	Edge Density	0.07	-0.12	0.24	3862	0.445
M2	2km	Patch Density	-0.12	-0.31	0.07	3837	0.199
M2	2km	Vegetation structure	-0.76	-1.21	-0.26	3364	0.001**
M2	2.5km	Forest Cover	0.01	-0.06	0.08	4500	0.805
M2	2.5km	Edge Density	0.10	-0.06	0.24	4500	0.197
M2	2.5km	Patch Density	-0.13	-0.27	0.02	4500	0.086
M2	2.5km	Vegetation structure	-0.69	-1.15	-0.26	4311	0.003**
M2	3km	Forest Cover	0.01	-0.06	0.07	4226	0.808
M2	3km	Edge Density	0.00	-0.16	0.15	4261	0.967
M2	3km	Patch Density	-0.04	-0.23	0.14	4012	0.639
M2	3km	Vegetation structure	-0.68	-1.11	-0.23	3684	0.006**
M2	3.5km	Forest Cover	0.00	-0.08	0.09	4500	0.940
M2	3.5km	Edge Density	-0.02	-0.17	0.13	4238	0.827
M2	3.5km	Patch Density	0.01	-0.16	0.19	4500	0.883
M2	3.5km	Vegetation structure	-0.70	-1.16	-0.26	4138	0.003**
M2	4km	Forest Cover	0.00	-0.10	0.10	4162	0.952
M2	4km	Edge Density	-0.06	-0.24	0.12	4129	0.472
M2	4km	Patch Density	0.08	-0.11	0.30	4301	0.428
M2	4km	Vegetation structure	-0.73	-1.16	-0.27	3883	0.002**
M2	4.5km	Forest Cover	0.03	-0.09	0.17	4500	0.652
M2	4.5km	Edge Density	-0.05	-0.26	0.18	4500	0.671
M2	4.5km	Patch Density	-0.01	-0.26	0.26	4145	0.947
M2	4.5km	Vegetation structure	-0.72	-1.17	-0.28	4076	0.001**
M2	5km	Forest Cover	0.04	-0.13	0.21	4370	0.664
M2	5km	Edge Density	-0.09	-0.35	0.19	4727	0.537
M2	5km	Patch Density	0.02	-0.31	0.33	4067	0.874
M2	5km	Vegetation structure	-0.71	-1.14	-0.29	3840	0.001**
P6	0.5km	Forest Cover	-0.01	-0.04	0.02	4500	0.443
P6	0.5km	Edge Density	0.00	-0.02	0.02	4500	0.959
P6	0.5km	Patch Density	0.02	-0.01	0.06	4500	0.144
P6	0.5km	Vegetation structure	0.07	-0.18	0.31	4293	0.579
P6	1km	Forest Cover	-0.03	-0.11	0.06	4466	0.558
P6	1km	Edge Density	0.01	-0.06	0.08	4500	0.807
P6	1km	Patch Density	0.01	-0.03	0.06	4500	0.540
P6	1km	Vegetation structure	0.10	-0.14	0.35	3989	0.402
P6	1.5km	Forest Cover	-0.01	-0.07	0.04	4500	0.668
P6	1.5km	Edge Density	-0.01	-0.07	0.05	4500	0.728
P6	1.5km	Patch Density	0.02	-0.04	0.07	4500	0.545
P6	1.5km	Vegetation structure	0.11	-0.13	0.36	4171	0.361
P6	2km	Forest Cover	0.00	-0.06	0.05	4500	0.895
P6	2km	Edge Density	-0.05	-0.14	0.07	4500	0.376
P6	2km	Patch Density	0.03	-0.08	0.13	4717	0.531
P6	2km	Vegetation structure	0.14	-0.13	0.41	4500	0.275

P6	2.5km	Forest Cover	0.00	-0.04	0.06	4500	0.833
P6	2.5km	Edge Density	-0.03	-0.12	0.07	4302	0.580
P6	2.5km	Patch Density	-0.01	-0.10	0.08	4277	0.857
P6	2.5km	Vegetation structure	0.09	-0.16	0.33	4500	0.492
P6	3km	Forest Cover	0.00	-0.04	0.04	4500	0.936
P6	3km	Edge Density	0.02	-0.08	0.13	4500	0.642
P6	3km	Patch Density	-0.07	-0.19	0.05	4500	0.233
P6	3km	Vegetation structure	0.11	-0.12	0.34	4114	0.331
P6	3.5km	Forest Cover	0.00	-0.05	0.05	4500	0.929
P6	3.5km	Edge Density	0.00	-0.11	0.10	4569	0.922
P6	3.5km	Patch Density	-0.02	-0.15	0.11	4500	0.780
P6	3.5km	Vegetation structure	0.08	-0.17	0.33	4500	0.500
P6	4km	Forest Cover	0.01	-0.05	0.07	4702	0.796
P6	4km	Edge Density	0.00	-0.13	0.13	4132	0.943
P6	4km	Patch Density	-0.05	-0.21	0.11	4500	0.492
P6	4km	Vegetation structure	0.10	-0.14	0.34	4764	0.410
P6	4.5km	Forest Cover	0.01	-0.07	0.09	4500	0.841
P6	4.5km	Edge Density	-0.03	-0.17	0.13	4500	0.683
P6	4.5km	Patch Density	-0.06	-0.25	0.13	4500	0.530
P6	4.5km	Vegetation structure	0.08	-0.14	0.33	4308	0.464
P6	5km	Forest Cover	-0.04	-0.15	0.07	3741	0.451
P6	5km	Edge Density	-0.07	-0.28	0.13	4500	0.517
P6	5km	Patch Density	0.12	-0.11	0.36	4500	0.336
P6	5km	Vegetation structure	0.09	-0.15	0.33	4438	0.423
P5	0.5km	Forest Cover	0.01	-0.02	0.04	4500	0.569
P5	0.5km	Edge Density	-0.01	-0.03	0.01	4500	0.368
P5	0.5km	Patch Density	0.01	-0.02	0.04	4500	0.559
P5	0.5km	Vegetation structure	-0.04	-0.26	0.21	4500	0.731
P5	1km	Forest Cover	-0.06	-0.14	0.02	4500	0.142
P5	1km	Edge Density	0.04	-0.03	0.10	4500	0.237
P5	1km	Patch Density	0.03	-0.01	0.07	4712	0.160
P5	1km	Vegetation structure	-0.01	-0.24	0.20	3768	0.930
P5	1.5km	Forest Cover	-0.04	-0.09	0.02	4500	0.142
P5	1.5km	Edge Density	0.02	-0.03	0.08	4705	0.421
P5	1.5km	Patch Density	0.03	-0.02	0.08	4500	0.296
P5	1.5km	Vegetation structure	-0.01	-0.24	0.20	4500	0.916
P5	2km	Forest Cover	-0.02	-0.08	0.03	4500	0.447
P5	2km	Edge Density	0.07	-0.03	0.17	4500	0.177
P5	2km	Patch Density	-0.05	-0.16	0.05	4500	0.285
P5	2km	Vegetation structure	-0.03	-0.27	0.23	4180	0.811
P5	2.5km	Forest Cover	-0.03	-0.07	0.02	4500	0.272
P5	2.5km	Edge Density	0.02	-0.08	0.11	5042	0.659
P5	2.5km	Patch Density	-0.01	-0.10	0.07	4500	0.804
P5	2.5km	Vegetation structure	0.03	-0.21	0.26	4500	0.826
P5	3km	Forest Cover	-0.03	-0.07	0.01	4500	0.120
P5	3km	Edge Density	0.06	-0.04	0.16	4500	0.226
P5	3km	Patch Density	-0.04	-0.16	0.08	4500	0.480
P5	3km	Vegetation structure	0.04	-0.18	0.27	4500	0.687
P5	3.5km	Forest Cover	-0.04	-0.08	0.01	4500	0.151
P5	3.5km	Edge Density	0.03	-0.06	0.13	4290	0.510
P5	3.5km	Patch Density	0.00	-0.11	0.13	4870	0.941
P5	3.5km	Vegetation structure	0.03	-0.19	0.25	4500	0.777
P5	4km	Forest Cover	-0.04	-0.10	0.02	4781	0.213

P5	4km	Edge Density	0.07	-0.05	0.18	4500	0.274
P5	4km	Patch Density	-0.01	-0.16	0.13	4500	0.844
P5	4km	Vegetation structure	0.03	-0.18	0.26	4500	0.776
P5	4.5km	Forest Cover	-0.05	-0.13	0.03	4500	0.174
P5	4.5km	Edge Density	0.07	-0.08	0.21	4500	0.346
P5	4.5km	Patch Density	-0.02	-0.20	0.16	4500	0.867
P5	4.5km	Vegetation structure	0.02	-0.20	0.22	4500	0.876
P5	5km	Forest Cover	-0.09	-0.19	0.02	4500	0.081
P5	5km	Edge Density	0.05	-0.15	0.25	4265	0.607
P5	5km	Patch Density	0.03	-0.21	0.26	4500	0.802
P5	5km	Vegetation structure	0.02	-0.20	0.24	4500	0.831
EB	0.5km	Forest Cover	-0.03	-0.08	0.03	3918	0.379
EB	0.5km	Edge Density	0.02	-0.04	0.08	4311	0.497
EB	0.5km	Patch Density	0.00	-0.08	0.07	4005	0.951
EB	0.5km	Vegetation structure	0.63	0.00	1.33	4051	0.060
EB	1km	Forest Cover	-0.01	-0.15	0.14	4500	0.866
EB	1km	Edge Density	0.00	-0.15	0.16	4258	0.975
EB	1km	Patch Density	0.01	-0.09	0.10	4500	0.880
EB	1km	Vegetation structure	0.55	-0.07	1.19	3620	0.083
EB	1.5km	Forest Cover	0.00	-0.09	0.09	4254	0.977
EB	1.5km	Edge Density	-0.04	-0.17	0.10	4500	0.573
EB	1.5km	Patch Density	0.04	-0.08	0.16	4500	0.464
EB	1.5km	Vegetation structure	0.50	-0.14	1.14	4071	0.111
EB	2km	Forest Cover	-0.03	-0.11	0.06	4500	0.544
EB	2km	Edge Density	-0.17	-0.39	0.08	4500	0.154
EB	2km	Patch Density	0.20	-0.05	0.43	4310	0.108
EB	2km	Vegetation structure	0.64	0.00	1.24	3578	0.039*
EB	2.5km	Forest Cover	0.00	-0.09	0.09	4500	0.990
EB	2.5km	Edge Density	-0.03	-0.22	0.17	4500	0.763
EB	2.5km	Patch Density	0.02	-0.16	0.21	4500	0.798
EB	2.5km	Vegetation structure	0.48	-0.17	1.10	4039	0.128
EB	3km	Forest Cover	0.00	-0.08	0.08	3873	0.993
EB	3km	Edge Density	-0.03	-0.23	0.17	3499	0.759
EB	3km	Patch Density	0.03	-0.21	0.25	4500	0.800
EB	3km	Vegetation structure	0.47	-0.13	1.08	3332	0.112
EB	3.5km	Forest Cover	0.01	-0.10	0.11	4198	0.880
EB	3.5km	Edge Density	-0.05	-0.23	0.14	4500	0.620
EB	3.5km	Patch Density	0.00	-0.21	0.23	4500	0.974
EB	3.5km	Vegetation structure	0.45	-0.15	1.06	4500	0.137
EB	4km	Forest Cover	0.00	-0.13	0.13	5677	0.948
EB	4km	Edge Density	-0.03	-0.25	0.20	4500	0.816
EB	4km	Patch Density	0.02	-0.22	0.27	4302	0.849
EB	4km	Vegetation structure	0.47	-0.17	1.06	4544	0.120
EB	4.5km	Forest Cover	-0.01	-0.16	0.17	4500	0.945
EB	4.5km	Edge Density	-0.03	-0.32	0.23	4139	0.800
EB	4.5km	Patch Density	0.03	-0.28	0.32	4268	0.866
EB	4.5km	Vegetation structure	0.49	-0.08	1.12	3965	0.109
EB	5km	Forest Cover	-0.05	-0.26	0.15	4150	0.652
EB	5km	Edge Density	0.00	-0.32	0.33	4500	0.963
EB	5km	Patch Density	0.10	-0.23	0.45	4500	0.561
EB	5km	Vegetation structure	0.49	-0.06	1.07	4202	0.084
MR	0.5km	Forest Cover	0.00	-0.05	0.04	4500	0.952
MR	0.5km	Edge Density	-0.02	-0.06	0.03	4500	0.416

MR	0.5km	Patch Density	0.01	-0.05	0.07	4500	0.683
MR	0.5km	Vegetation structure	0.36	-0.16	0.82	4500	0.148
MR	1km	Forest Cover	-0.08	-0.20	0.04	4500	0.205
MR	1km	Edge Density	0.07	-0.05	0.18	4500	0.230
MR	1km	Patch Density	0.01	-0.07	0.09	4421	0.723
MR	1km	Vegetation structure	0.28	-0.16	0.73	4500	0.216
MR	1.5km	Forest Cover	-0.06	-0.12	0.02	4188	0.117
MR	1.5km	Edge Density	0.06	-0.03	0.17	4500	0.250
MR	1.5km	Patch Density	0.01	-0.08	0.11	4500	0.751
MR	1.5km	Vegetation structure	0.32	-0.11	0.76	4500	0.145
MR	2km	Forest Cover	-0.05	-0.13	0.02	4500	0.165
MR	2km	Edge Density	0.10	-0.08	0.29	4500	0.288
MR	2km	Patch Density	-0.04	-0.24	0.16	4500	0.677
MR	2km	Vegetation structure	0.36	-0.15	0.83	4500	0.146
MR	2.5km	Forest Cover	-0.05	-0.12	0.02	4500	0.170
MR	2.5km	Edge Density	-0.01	-0.18	0.14	4500	0.930
MR	2.5km	Patch Density	0.05	-0.10	0.20	4370	0.470
MR	2.5km	Vegetation structure	0.43	-0.07	0.88	4500	0.072
MR	3km	Forest Cover	-0.05	-0.11	0.01	4500	0.100
MR	3km	Edge Density	0.07	-0.09	0.22	4500	0.390
MR	3km	Patch Density	0.01	-0.17	0.20	4500	0.934
MR	3km	Vegetation structure	0.42	-0.04	0.84	4500	0.064
MR	3.5km	Forest Cover	-0.07	-0.16	0.00	4161	0.074
MR	3.5km	Edge Density	0.04	-0.11	0.19	4712	0.642
MR	3.5km	Patch Density	0.09	-0.09	0.26	4297	0.318
MR	3.5km	Vegetation structure	0.43	-0.03	0.87	4205	0.065
MR	4km	Forest Cover	-0.06	-0.16	0.03	4500	0.211
MR	4km	Edge Density	0.12	-0.05	0.31	4500	0.188
MR	4km	Patch Density	-0.01	-0.21	0.21	4500	0.893
MR	4km	Vegetation structure	0.41	-0.02	0.86	4500	0.072
MR	4.5km	Forest Cover	-0.07	-0.19	0.06	4500	0.292
MR	4.5km	Edge Density	0.13	-0.10	0.34	4472	0.253
MR	4.5km	Patch Density	-0.03	-0.29	0.22	4423	0.799
MR	4.5km	Vegetation structure	0.37	-0.06	0.81	3989	0.099
MR	5km	Forest Cover	-0.12	-0.28	0.05	4500	0.153
MR	5km	Edge Density	0.10	-0.15	0.38	4500	0.450
MR	5km	Patch Density	0.08	-0.21	0.38	4500	0.612
MR	5km	Vegetation structure	0.37	-0.07	0.78	4809	0.093

Table S3.4 $\text{MCMC}_{\text{GLMM}}$ Model output comparing total bat activity for guild modelled with local and landscape predictor variables (Vegetation structure, Forest cover, Edge density, Patch density) We report mean posterior estimate, 95% credible intervals, the effective sample size and Bayesian p-values (p_{MCMC}) indicating the significance of variables with a threshold of $^{*}\, p_{\text{MCMC}} < 0.05$, $^{**}\, p_{\text{MCMC}} < 0.01$, $^{***}\, p_{\text{MCMC}} < 0.001$

Guild	Buffer Size	Variable	Estimate	Inferior	Superior	eff.sample	p_{MCMC}
Forest	0.5km	Forest Cover	0.00	-0.05	0.04	4500	0.85
Forest	0.5km	Edge Density	-0.01	-0.05	0.03	4500	0.50
Forest	0.5km	Patch Density	0.01	-0.04	0.06	4500	0.65
Forest	0.5km	Vegetation	0.41	-0.03	0.85	4500	0.06
Forest	1km	Forest Cover	-0.07	-0.18	0.04	4500	0.22
Forest	1km	Edge Density	0.07	-0.04	0.18	4714	0.20
Forest	1km	Patch Density	0.01	-0.06	0.07	4500	0.80
Forest	1km	Vegetation	0.34	-0.04	0.74	4605	0.09
Forest	1.5km	Forest Cover	-0.05	-0.12	0.02	4500	0.18
Forest	1.5km	Edge Density	0.04	-0.05	0.13	4301	0.34
Forest	1.5km	Patch Density	0.02	-0.06	0.10	4179	0.59
Forest	1.5km	Vegetation	0.35	-0.04	0.76	4500	0.09
Forest	2km	Forest Cover	-0.04	-0.11	0.03	5581	0.26
Forest	2km	Edge Density	0.08	-0.09	0.25	4500	0.34
Forest	2km	Patch Density	-0.03	-0.20	0.14	4283	0.72
Forest	2km	Vegetation	0.39	-0.02	0.83	4720	0.07
Forest	2.5km	Forest Cover	-0.04	-0.11	0.02	3958	0.28
Forest	2.5km	Edge Density	-0.03	-0.17	0.11	4305	0.71
Forest	2.5km	Patch Density	0.06	-0.08	0.19	4000	0.39
Forest	2.5km	Vegetation	0.45	0.05	0.90	4500	0.04*
Forest	3km	Forest Cover	-0.04	-0.10	0.02	4500	0.16
Forest	3km	Edge Density	0.05	-0.10	0.19	4500	0.53
Forest	3km	Patch Density	0.01	-0.15	0.19	4500	0.89
Forest	3km	Vegetation	0.45	0.06	0.83	4500	0.03*
Forest	3.5km	Forest Cover	-0.06	-0.13	0.01	4500	0.12
Forest	3.5km	Edge Density	0.02	-0.13	0.15	4717	0.81
Forest	3.5km	Patch Density	0.09	-0.07	0.26	4500	0.30
Forest	3.5km	Vegetation	0.46	0.07	0.86	4227	0.03*
Forest	4km	Forest Cover	-0.05	-0.14	0.04	4500	0.32
Forest	4km	Edge Density	0.11	-0.06	0.29	4874	0.22
Forest	4km	Patch Density	-0.02	-0.22	0.19	4500	0.82
Forest	4km	Vegetation	0.45	0.05	0.85	3922	0.03*
Forest	4.5km	Forest Cover	-0.05	-0.16	0.07	3813	0.44
Forest	4.5km	Edge Density	0.11	-0.09	0.31	4500	0.30
Forest	4.5km	Patch Density	-0.05	-0.29	0.19	4500	0.67
Forest	4.5km	Vegetation	0.40	-0.01	0.80	4500	0.05
Forest	5km	Forest Cover	-0.10	-0.25	0.07	4500	0.21
Forest	5km	Edge Density	0.08	-0.17	0.35	4500	0.52
Forest	5km	Patch Density	0.07	-0.23	0.35	4500	0.62
Forest	5km	Vegetation	0.40	0.00	0.78	4500	0.05*
Flex	0.5km	Forest Cover	0.00	-0.03	0.02	4675	0.87
Flex	0.5km	Edge Density	-0.01	-0.02	0.01	4500	0.52
Flex	0.5km	Patch Density	0.02	-0.01	0.04	4500	0.15
Flex	0.5km	Vegetation	0.05	-0.13	0.24	4378	0.60
Flex	1km	Forest Cover	-0.04	-0.12	0.03	3713	0.23

Flex	1km	Edge Density	0.02	-0.03	0.08	4049	0.38
Flex	1km	Patch Density	0.02	-0.01	0.06	4766	0.22
Flex	1km	Vegetation	0.06	-0.12	0.23	4500	0.53
Flex	1.5km	Forest Cover	-0.02	-0.07	0.02	4500	0.30
Flex	1.5km	Edge Density	0.01	-0.04	0.06	4500	0.79
Flex	1.5km	Patch Density	0.02	-0.02	0.06	4500	0.36
Flex	1.5km	Vegetation	0.06	-0.13	0.24	4040	0.51
Flex	2km	Forest Cover	-0.01	-0.07	0.04	4500	0.57
Flex	2km	Edge Density	0.00	-0.09	0.08	4500	0.98
Flex	2km	Patch Density	0.00	-0.08	0.09	4500	0.92
Flex	2km	Vegetation	0.08	-0.13	0.27	4500	0.43
Flex	2.5km	Forest Cover	-0.01	-0.05	0.03	4500	0.54
Flex	2.5km	Edge Density	0.00	-0.09	0.08	4953	0.89
Flex	2.5km	Patch Density	0.00	-0.08	0.06	4538	0.92
Flex	2.5km	Vegetation	0.07	-0.10	0.26	4759	0.42
Flex	3km	Forest Cover	-0.01	-0.05	0.02	4455	0.39
Flex	3km	Edge Density	0.05	-0.04	0.13	4500	0.30
Flex	3km	Patch Density	-0.06	-0.16	0.05	4500	0.26
Flex	3km	Vegetation	0.09	-0.09	0.27	4833	0.30
Flex	3.5km	Forest Cover	-0.02	-0.06	0.02	5008	0.45
Flex	3.5km	Edge Density	0.02	-0.07	0.10	4500	0.72
Flex	3.5km	Patch Density	0.00	-0.11	0.10	4500	0.97
Flex	3.5km	Vegetation	0.07	-0.11	0.26	5029	0.43
Flex	4km	Forest Cover	-0.01	-0.06	0.04	4500	0.72
Flex	4km	Edge Density	0.04	-0.07	0.15	4737	0.44
Flex	4km	Patch Density	-0.04	-0.17	0.10	4500	0.59
Flex	4km	Vegetation	0.08	-0.10	0.27	4500	0.39
Flex	4.5km	Forest Cover	-0.02	-0.08	0.05	4500	0.63
Flex	4.5km	Edge Density	0.03	-0.10	0.16	4500	0.70
Flex	4.5km	Patch Density	-0.05	-0.22	0.11	4500	0.51
Flex	4.5km	Vegetation	0.07	-0.11	0.24	4666	0.45
Flex	5km	Forest Cover	-0.06	-0.15	0.03	4500	0.16
Flex	5km	Edge Density	-0.03	-0.21	0.16	4500	0.77
Flex	5km	Patch Density	0.08	-0.12	0.30	4500	0.42
Flex	5km	Vegetation	0.07	-0.10	0.24	4500	0.40
Edge	0.5km	Forest Cover	0.01	-0.03	0.04	4500	0.58
Edge	0.5km	Edge Density	0.02	-0.01	0.05	4500	0.13
Edge	0.5km	Patch Density	-0.04	-0.08	-0.01	4500	0.02*
Edge	0.5km	Vegetation	0.58	0.25	0.87	4500	0.00***
Edge	1km	Forest Cover	-0.04	-0.14	0.05	4500	0.36
Edge	1km	Edge Density	0.08	0.00	0.16	4500	0.05*
Edge	1km	Patch Density	-0.04	-0.10	0.01	5047	0.12
Edge	1km	Vegetation	0.54	0.26	0.85	4500	0.00***
Edge	1.5km	Forest Cover	-0.03	-0.09	0.03	4500	0.33
Edge	1.5km	Edge Density	0.06	-0.01	0.14	4500	0.10
Edge	1.5km	Patch Density	-0.03	-0.10	0.04	4500	0.38
Edge	1.5km	Vegetation	0.56	0.24	0.87	4500	0.00**
Edge	2km	Forest Cover	-0.03	-0.09	0.04	4560	0.41
Edge	2km	Edge Density	0.06	-0.08	0.20	4500	0.42
Edge	2km	Patch Density	-0.01	-0.15	0.14	4500	0.90
Edge	2km	Vegetation	0.58	0.25	0.94	4854	0.00**
Edge	2.5km	Forest Cover	-0.02	-0.07	0.04	4500	0.53
Edge	2.5km	Edge Density	-0.03	-0.15	0.09	4500	0.62

Edge	2.5km	Patch Density	0.06	-0.05	0.17	4500	0.28
Edge	2.5km	Vegetation	0.60	0.27	0.92	4500	0.00***
Edge	3km	Forest Cover	-0.01	-0.06	0.04	4500	0.81
Edge	3km	Edge Density	-0.02	-0.15	0.11	4500	0.76
Edge	3km	Patch Density	0.05	-0.11	0.20	4500	0.54
Edge	3km	Vegetation	0.57	0.24	0.89	4500	0.00**
Edge	3.5km	Forest Cover	0.00	-0.06	0.07	4500	0.96
Edge	3.5km	Edge Density	0.03	-0.10	0.14	4500	0.61
Edge	3.5km	Patch Density	-0.03	-0.19	0.11	4725	0.69
Edge	3.5km	Vegetation	0.58	0.27	0.92	4500	0.00**
Edge	4km	Forest Cover	0.02	-0.06	0.09	4500	0.58
Edge	4km	Edge Density	0.06	-0.08	0.20	4500	0.45
Edge	4km	Patch Density	-0.13	-0.31	0.05	4500	0.17
Edge	4km	Vegetation	0.61	0.29	0.92	4500	0.00***
Edge	4.5km	Forest Cover	0.01	-0.09	0.12	5396	0.79
Edge	4.5km	Edge Density	0.04	-0.15	0.22	4500	0.66
Edge	4.5km	Patch Density	-0.08	-0.30	0.15	4500	0.51
Edge	4.5km	Vegetation	0.57	0.25	0.88	4145	0.00***
Edge	5km	Forest Cover	0.02	-0.11	0.15	5008	0.73
Edge	5km	Edge Density	-0.01	-0.24	0.22	4500	0.96
Edge	5km	Patch Density	-0.05	-0.31	0.22	4777	0.73
Edge	5km	Vegetation	0.57	0.27	0.87	4500	0.00**
Open	0.5km	Forest Cover	-0.01	-0.06	0.03	4500	0.63
Open	0.5km	Edge Density	-0.01	-0.05	0.03	3856	0.58
Open	0.5km	Patch Density	0.03	-0.02	0.08	4500	0.26
Open	0.5km	Vegetation	-0.68	-1.16	-0.24	4182	0.01**
Open	1km	Forest Cover	0.04	-0.07	0.17	4500	0.46
Open	1km	Edge Density	-0.07	-0.19	0.04	4500	0.22
Open	1km	Patch Density	0.02	-0.05	0.09	4500	0.64
Open	1km	Vegetation	-0.62	-1.03	-0.19	4232	0.00**
Open	1.5km	Forest Cover	0.01	-0.06	0.09	4003	0.80
Open	1.5km	Edge Density	-0.07	-0.17	0.03	3133	0.15
Open	1.5km	Patch Density	0.06	-0.03	0.15	3601	0.17
Open	1.5km	Vegetation	-0.63	-1.06	-0.19	4075	0.00**
Open	2km	Forest Cover	0.03	-0.05	0.10	4027	0.49
Open	2km	Edge Density	0.06	-0.13	0.25	4165	0.50
Open	2km	Patch Density	-0.12	-0.32	0.07	3776	0.22
Open	2km	Vegetation	-0.75	-1.23	-0.30	3673	0.00**
Open	2.5km	Forest Cover	0.01	-0.06	0.08	4500	0.80
Open	2.5km	Edge Density	0.10	-0.06	0.24	4500	0.19
Open	2.5km	Patch Density	-0.13	-0.27	0.03	4164	0.08
Open	2.5km	Vegetation	-0.70	-1.13	-0.25	4131	0.00**
Open	3km	Forest Cover	0.01	-0.05	0.07	4500	0.82
Open	3km	Edge Density	-0.01	-0.16	0.16	4312	0.94
Open	3km	Patch Density	-0.04	-0.23	0.14	4500	0.63
Open	3km	Vegetation	-0.68	-1.14	-0.25	4500	0.00**
Open	3.5km	Forest Cover	0.01	-0.08	0.08	4500	0.89
Open	3.5km	Edge Density	-0.01	-0.17	0.13	4271	0.86
Open	3.5km	Patch Density	0.01	-0.17	0.19	4500	0.91
Open	3.5km	Vegetation	-0.70	-1.17	-0.25	4164	0.00**
Open	4km	Forest Cover	0.00	-0.10	0.10	4500	0.95
Open	4km	Edge Density	-0.06	-0.25	0.11	4500	0.50
Open	4km	Patch Density	0.08	-0.12	0.29	4500	0.42

Open	4km	Vegetation	-0.73	-1.16	-0.28	4373	0.00**
Open	4.5km	Forest Cover	0.03	-0.09	0.18	3827	0.63
Open	4.5km	Edge Density	-0.05	-0.26	0.17	4213	0.67
Open	4.5km	Patch Density	-0.01	-0.27	0.25	3625	0.95
Open	4.5km	Vegetation	-0.72	-1.20	-0.29	3621	0.00**
Open	5km	Forest Cover	0.03	-0.14	0.20	4147	0.70
Open	5km	Edge Density	-0.09	-0.36	0.19	3920	0.54
Open	5km	Patch Density	0.02	-0.29	0.33	4500	0.88
Open	5km	Vegetation	-0.72	-1.18	-0.31	4278	0.00**

Chapter 4

General conclusion

Whilst Earth's sixth mass extinction is covertly encroaching; humans, in the name of advancement and to satisfy an exponentially growing global population (Tilman et al., 2011), continue to perpetrate habitat destruction, over-exploitation and pollution of the land (Caballos et al., 2017, Bellard et al., 2022). Agricultural land use change is driving deforestation across the tropics (Laso Bayas, 2022), leaving increasingly fragmented habitats in its wake. It is essential that we understand how biodiversity responds to fragmentation and what land management actions can be taken to help avoid species extinctions in these human-modified landscapes. The general objective of this thesis was to investigate assemblage-, guild- and species-level responses of Amazonian aerial insectivorous bats to fragmentation using a multi-scale approach and further contribute to a growing body of research which includes the first acoustic key produced as part of a PhD project started in 2011 by Adrià López-Baucells (López-Baucells, 2019).

I specifically investigated responses to the disturbance gradient formed by fragment interiors (I), forest edges (E) and secondary forest matrix (M) habitats, also considering fragment size (1 ha, 10 ha, 100 ha). I used a multiscale approach to assess the influence of local vegetation structure, compositional and configurational landscape characteristics. The previous chapters address this first at assemblage-level (chapter 2), and then at guild- and species-level (chapter 3) to comprehensively evaluate aerial insectivorous bat responses to the experimentally fragmented landscape of the BDFFP.

The use of multi-dimensional diversity and multiscale analysis in bat studies in the Neotropics

In chapter 2, I focused on assemblage-level responses utilising a multi-dimensional diversity approach which focused on the taxonomic, functional and phylogenetic facets of diversity within a Hill numbers framework (Hill, 1973). This approach provides a complete understanding of assemblage diversity, appreciating the evolutionary history and the complexities associated with the distinct functional roles of different species, thus going beyond simple metrics of taxonomic diversity such as species counts. To date, one other tropical study, in the Cerrado biome in Central Brazil, has assessed multi-dimensional diversity for aerial-hawking insectivorous bats (Pereira et al., 2018). The multi-dimensional approach used in chapter 2 uncovered significant variation in functional diversity which might have been overlooked if a traditional taxonomic approach was implemented exclusively. It is recommended that future studies analysing tropical bat responses to fragmentation follow such an integrated biodiversity approach.

I also evaluated scale-sensitivity in bat responses, employing multiscale analysis which assessed assemblage-level responses within landscape buffers up to 3 km (chapter 2) and guild- and species-level responses within buffers up to 5 km (chapter 3). It is important to assess fragmentation at the landscape scale as this is the level at which the effects manifest i.e., not just differences attributed to local habitat types. Bats are highly mobile, with the capability to fly between fragments, but many species are unable to travel significant distances and so high mortality rates crossing the matrix or the inability to cross make them vulnerable to fragmentation (Peixoto et al., 2018). Research has shown that bat responses are complex and scale-dependent (reviewed in Meyer et al., 2016). As there are still very few landscape-scale studies of Neotropical aerial insectivorous bats (Estrada-Villegas et al., 2010), and very little knowledge about the home ranges of focal species, the scale of effect (Jackson & Fahrig, 2015) and previously published maximum buffer sizes (Rodríguez-San Pedro & Simonetti, 2015; Rodríguez-San Pedro et al., 2019) were considered when assessing scale-dependency. I extended the spatial scales analysis to 3 km for assemblage-level and 5 km for species-level which proved fruitful, uncovering that functional diversity at assemblage-level responded to patch density at the 2.5 km scale and at species-level, *Furipterus horrens* responded to landscape configuration at 3.5 km, 4 km and 4.5 km buffer sizes. These findings further contribute to previous studies (Chambers et al., 2016; Fuentes-Montemayer et al., 2017; Put et al., 2019; Falcão et al., 2021; Froidevaux et al., 2021) on the scale of effect and stand as an example for future multiscale research on aerial insectivorous bat responses to forest fragmentation.

Aerial insectivorous bat responses to fragment-size and interior-edge-matrix disturbance gradients

We found evidence of diversity degradation in the secondary forest matrix around the smallest fragments compared to continuous forest. Taxonomic diversity was significantly reduced in the 1 ha matrix as was phylogenetic diversity which was significantly reduced in the 1 ha and 10 ha matrix, with similar patterns of phylogenetic degradation reported for phyllostomid bats (Aninta et al., 2019). The limited fragment area is less able to sustain a full assemblage of species and we found evidence of reduced evolutionary richness, which can be associated with local extinctions, albeit none were found in this study. We also found slightly higher levels of diversity for all three facets within the 100 ha forest fragment interiors compared to continuous forest interiors, and all three diversity facets were higher in the regenerated secondary forests around the larger fragments, although not significantly so, a finding also replicated for phyllostomid bats (Rocha et al., 2017). This suggests that these large fragments may have acted as important reservoirs for aerial insectivorous bat diversity following fragmentation. We found that all three facets of diversity peaked at the primary-secondary forest interface and that fragment edges were generally more diverse compared to continuous forest. Aerial insectivores utilise edge habitat for navigation and commuting, but there could also be increased prey availability around the fragment edges. We did not monitor insect distribution or feeding buzzes in this study, however results from another study assessing the impact of edge effects indicated that prey distribution was not a significant predictor of bat activity (Yoh et al., 2022). The second-growth forest appears to facilitate connectivity, buffering the isolation effects of the smallest fragments and function as commuting corridors. Our species-specific results also reveal that the second-growth forest does appear to buffer some of the negative effects of fragmentation, but we also observed that there are some species which inevitably still rely on old-growth forest due to trait-mediated exclusion from second-growth forest habitat. *Furipterus horrens* was a good example of this, exhibiting reduced activity across the whole IEM gradient and all but the largest fragment interiors.

Influence of local habitat quality and landscape structure on aerial insectivorous bat responses

We assessed assemblage-level responses via the three diversity facets at 6 spatial scales, and guild- and species-level at 10 spatial scales. At assemblage-level, functional diversity was the only metric which was influenced by any of the landscape characteristics, and these occurred at the 1 km and 2.5 km scale. Our findings are similar to other studies, which found no influence of landscape predictors (Blakey et al., 2017; Falcão et al., 2021) or uncovered muted responses (Estrada-Villegas et al., 2010; Klingbeil & Willig, 2010). Some studies have observed varying responses at landscape scale; however, these results originate from investigations into aerial insectivorous bat responses in agricultural landscapes with high-contrast matrices (Azofeifa et al., 2019; Put et al., 2019; Rodríguez-San Pedro et al., 2019). We also found no influence of local vegetation structure at the assemblage-level, which was unexpected. The density of obstacles or vegetation clutter has been shown to influence species richness (Estrada-Villegas et al., 2012) and functional diversity at community level (Blakey et al., 2017). This is due to functional trait adaptations, in particular echolocation and wing morphology (Bader et al., 2015; Núñez et al., 2019), which either prevents or facilitates foraging in different types of local habitat based on the level of clutter (Schnitzler & Kalko, 2001). Whilst the responses to local vegetation were muted at assemblage-level, they were evident at guild- and species-level. This metric was a significant positive predictor of activity for the edge specialist and forest specialist guilds and for *Centronycteris maximiliani*, *Saccopteryx bilineata*, *Saccopteryx leptura* and *Furipterus horrens*. The *Molossus* sonotype responded negatively to local vegetation structure at every scale. Molossids are open space bats and have long, narrow wings for fast, economic flight (Castillo-Figueroa, 2020) and foraging in any amount of vegetation clutter will be energetically costly, which could account for the negative relationship whereby it is an example of a trait-mediated response. However, it could also be due to detection limitations which were discussed in more detail in chapter 3. Overall, at guild- and species-level, there were limited responses to landscape structure, with only significant responses to the landscape configuration variables (edge and patch density) for three species including; *Saccopteryx bilineata, Centronycteris maximiliani* and *Furipterus horrens.* Taking into consideration the assemblage-, guild- and species-level responses of aerial insectivores to fragmentation at local and landscape scale, our results indicate that this group is approaching a point of recovery whereby the pervasive fragmentation effects are no longer pronounced and ubiquitous at the BDFFP.

The BDFFP is an invaluable site which has facilitated significant contributions to literature, advancing our understanding of the effects of fragmentation on a whole ecosystem over four decades (Laurence et al., 2018). However, it is an experimental landscape and as such, is protected from additional human disturbance, i.e., logging, hunting, wildfires and by virtue of the way the study site evolved, isolation is minimal with the fragments in close proximity to vast expanses of continuous forest. This enables faster re-colonisation from a healthy core population compared to fragments which are isolated in a belt of agricultural land. Therefore, the conclusions drawn here are based on a best-case scenario. The second-growth forest at the BDFFP has been regenerating for at least 30 years. Stand development happens over many decades. The average age of second-growth forests across the Amazon is approximately 5 years (Neeff et al 2006) and most regenerating forests are cleared again within the first 5 years. If secondary forests are to deliver the promise of regeneration for tropical landscapes (Chazdon, 2014) then it will require protection from further deforestation and decades of time to mature. Globally, most remaining forest fragments are less than 10 ha in area (Haddad et al., 2015), which makes it difficult to support the level of biodiversity required to maintain ecosystem services. We reiterate that there is no such thing as an ‘unimportant’ forest fragment (Laurance et al., 2018) however, where deforestation must take place, every effort should be made to preserve fragments which are no less than 10 ha in area, and ideally larger than 100 ha to sustain viable populations.

Finally, to recover is to return to a ‘normal’ state of health or strength. Forest recovery often compares second regrowth forest to old-growth forest in terms of structure, function and composition before deforestation. The lasting scar from deforestation may never allow landscapes to fully recover during the Anthropocene. So perhaps conservation must work towards a ‘new normal’ which might be the next-best alternative to pristine forest - mature second regrowth forest - which, if protected, may still have the capacity to heal fragmented landscapes.

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Appendix 1

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RESEARCH ARTICLE

Interplay between local and landscape-scale effects on the taxonomic, functional and phylogenetic diversity of aerial insectivorous neotropical bats

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Abstract

Context Human-modified landscapes are globally ubiquitous. It is critical to understand how habitat loss and fragmentation impact biodiversity from both a local habitat context and landscape-scale perspective to inform land management and conservation strategies.

Objectives We used an experimentally fragmented landscape in the Brazilian Amazon to investigate variation in aerial insectivorous bat diversity in response to local habitat and wider landscape characteristics, applying a multiscale approach.

Methods We conducted bat acoustic surveys at 33 sites, comprising old secondary forests and fragments of primary forest. Taxonomic, functional and phylogenetic diversity facets were calculated within a Hill numbers framework. We analysed responses to fragment size, interior-edge-matrix gradients, as well as local vegetation structure, continuous forest cover, edge density and patch density across five spatial scales (0.5–3 km) surrounding detector locations.

Results Compared with continuous forest, secondary forest matrix around the smallest fragments harboured lower diversity. The overall negative effect of the matrix became less pronounced with increasing fragment size. In contrast, forest edges generally contained higher taxonomic, functional and phylogenetic

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diversity. We found subtle scale-sensitive associations for functional diversity, responding positively to forest cover (at the 1 km scale) and negatively to edge (1 km scale) and patch density (2.5 km scale).

Conclusions Despite a low-contrast matrix of tall secondary forest surrounding fragments after ~30 years of forest recovery, aerial insectivorous bat diversity is not comparable to continuous primary forest. Assemblage functional diversity responds to compositional and configurational landscape characteristics at scales deserving further evaluation at guild and species level.

Keywords Amazon · Fragmentation · Landscape context · Diversity dimensions · Multiscale analysis

Introduction

Globally, over the past 300 years, there has been a net forest loss of ~7–11 million km^2, primarily due to logging and conversion to agricultural use (Foley et al. 2005). Loss of suitable habitat to sustain species populations leads to an overall increased risk of extinction (Ceballos et al. 2015, 2017; Powers and Jetz 2015). Forest patches of varying sizes and shapes, embedded in various land cover types, are conspicuous features of present-day human-modified landscapes (Melo et al. 2013). The link between remaining native habitat and the species persisting in the aftermath of habitat fragmentation was first described through the lens of Island Biogeography Theory, which sought to predict species loss on islands surrounded by a 'hostile' matrix of water (MacArthur and Wilson 1967). Yet, mounting evidence now supports that the structure and composition of the intervening matrix significantly affect species' persistence in adjoining forest fragments, a dynamic that is better conceptualised under alternative theoretical frameworks, such as Countryside Biogeography (Daily 1997; Mendenhall et al. 2013). Through this framework, community changes in modified landscapes are forecast based on the interaction between the species' spatial requirements and their tolerance towards matrix habitats, thus offering a more realistic portrait of biodiversity persistence in landscapes with matrix habitats more salubrious than water (Mendenhall et al. 2014; Wolfe et al. 2015; Farneda et al. 2020).

In the Amazon, deforestation rates dropped from 30,000 km^2/year in the 1980s to 5843 km^2/year in 2013 (Davidson et al. 2012; Nepstad et al. 2014). However, since 2013, alongside the main driver of deforestation in the Amazon, pasture expansion for cattle production (Skidmore et al. 2021), compounding threats such as oil palm plantations (Butler and Laurance 2009), expanding soy agriculture (Rosa et al. 2017) and dam development (Lees et al. 2016) have contributed to a sharp increase. Much of this deforested land has been abandoned, and a recent study estimates a total of 262,791 km^2 of recovered secondary forests in Brazil between 1986 and 2018 (Silva Junior et al. 2020). Secondary forests make up a significant proportion of fragmented tropical landscapes (Chazdon et al. 2009; Chazdon 2014). A growing body of literature supports that these regenerating forests can alleviate fragmentation impacts and support diverse assemblages and overall ecosystem functioning (Spake et al. 2015; Farneda et al. 2018; Rocha et al. 2018; Rozendaal et al. 2019).

The Neotropics are a major hotspot of chiropteran diversity and the Amazon basin, with over 160 species, is especially rich (López-Baucells et al. 2018). Throughout the region, bats play essential roles in countless ecological networks and provide valuable ecosystem services such as seed dispersal, pollination and arthropod population regulation (Aguiar et al. 2021; Ramírez-Fráncel et al. 2022). They are demonstrably sensitive to habitat loss, fragmentation, and habitat degradation (reviewed in Meyer et al. 2016) and have become a popular indicator group of environmental disturbance (Cunto and Bernard 2012). Yet, while the consequences of anthropogenic forest fragmentation for phyllostomid bats have received substantial research attention (e.g., Klingbeil and Willig 2009; Avila-Cabadilla et al. 2014; García-García et al. 2014; Arroyo-Rodríguez et al. 2016; Muylaert et al. 2016; Farneda et al. 2021; Silva et al. 2020), aerial insectivores—non-phyllostomid counterparts—have largely been neglected and their responses to habitat fragmentation remain understudied (but see

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e.g., Estrada-Villegas et al. 2010; Rodríguez-San Pedro and Simonetti 2015; Núñez et al. 2019).

Measures of diversity based solely on traditional species counts fail to encapsulate the complexities associated with the distinct functional roles of different species or the evolutionary history contained within a given assemblage (Cadotte et al. 2013). A multifaceted approach considering the complementary taxonomic, functional and phylogenetic dimensions of diversity can provide a more detailed and comprehensive understanding of the drivers of biodiversity change across human-modified landscapes (Swenson 2011). However, studies simultaneously assessing how multiple dimensions of Neotropical bat diversity are affected by habitat gradients are still scarce (Cisneros et al. 2014; Frank et al. 2017; Carrasco-Rueda and Loiselle 2020; Carvalho et al. 2021), particularly for aerial insectivores (but see e.g., Pereira et al. 2018).

Amongst the research questions commonly posed by fragmentation studies, the role of fragment size, edge effects, and compositional vs. configurational aspects of the landscape has rarely been addressed for aerial insectivorous bats. Here, we set out to help fill this gap by investigating how local vegetation structure and landscape composition and configuration affect this ensemble along a disturbance gradient formed by continuous primary forest (CF) and primary forest fragment interiors (I), forest edges (E) and secondary forest matrix (M) habitats (hereinafter IEM gradients; *sensu* Rocha et al. 2017a). Specifically, we aimed to address two objectives:

(1) Quantify between-habitat differences in the taxonomic, functional and phylogenetic diversity of aerial insectivorous bats along IEM and fragment-size gradients. We anticipated (i) that assemblages in CF are taxonomically, functionally and phylogenetically most diverse, with diversity being eroded through fragment interiors (< 10 ha) and further still in the matrix, (ii) similar levels of diversity in CF and larger fragments (100 ha), with a reduction in the three biodiversity dimensions with decreasing fragment size (10 and 1 ha), (iii) a positive response of all three diversity facets at the fragment edges as more species are able to take advantage of foraging opportunities along the ecotone.

(2) Assess the importance of the following variables as determinants of assemblage diversity, using a multiscale approach; local vegetation structure, landscape composition (forest cover), and landscape configuration (edge density and patch density). We predicted that (i) taxonomic, functional and phylogenetic diversity would exhibit only subtle responses to the local and landscape characteristics, (ii) local vegetation structure would generally have a weaker effect than landscape metrics and, when present, would manifest at the smallest scale (0.5 km), possibly turning neutral as the scale increases, (iii) forest cover would be the most important predictor of all three diversity facets at the landscape scale, similar to findings for the species richness and abundance of phyllostomids (Rocha et al. 2017a).

Materials and methods

Study area

Fieldwork was conducted at the Biological Dynamics of Forest Fragments Project (BDFFP), located ~ 80 km north of Manaus, Central Amazon, Brazil (see Fig. 1). Established in 1979, the BDFFP is the world's largest and longest running experimental study focused on habitat fragmentation, landscape dynamics, forest regeneration, and regional and global changes affecting plant and animal communities (Laurance et al. 2018). The topography of the ~ 1000 km^2 study area is relatively flat, with many small streams cutting through the nutrient-poor soil. Annual rainfall varies from 1900 to 3500 mm with a moderately strong dry season from June to October (Laurance et al. 2011). The area is characterised by a mosaic of primary forest fragments embedded in a second-growth forest matrix surrounded by large areas of continuous *terra firme* forest. The fragments were first isolated through logging and burning for cattle pasture in the early 1980s. Fragments of different sizes (1 ha, 10 ha and 100 ha) were isolated from CF by distances ranging from 80 to 650 m. Following the abandonment of the cattle ranches, the second-growth forest matured around the fragments over ~ 30 years (Laurance et al. 2018), creating a landscape of low structural

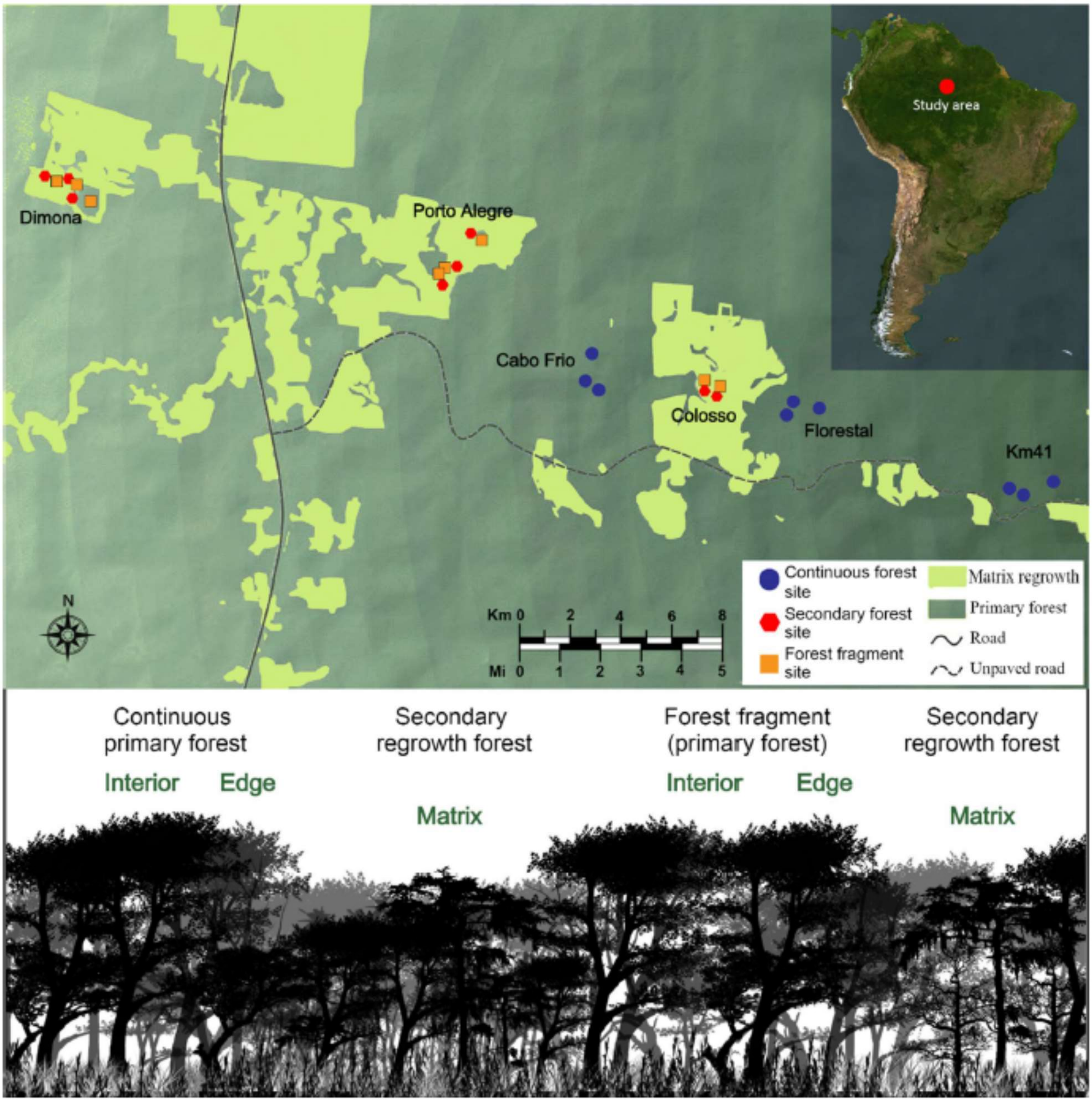

Fig. 1 Map of the study area at the BDFFP, Central Amazon, Brazil and schematic representation of the BDFFP landscape during data collection (2011–2013), illustrating the low structural contrast between the continuous forest, late-stage secondary regrowth forest matrix (approximately 30 years of regeneration) and forest fragments

fragment-matrix contrast (Fig. 1). A 100 m-wide strip of regrowth vegetation has been cleared on at least five occasions since fragments' creation to maintain their integrity. The last re-isolation event prior to data collection for this study occurred between 1999 and 2001 (Rocha et al. 2020).

Bat surveys

Acoustic data were collected between 2011 and 2013 in both the interior and at the edges of eight forest fragments (three of 1 ha, three of 10 ha, two of 100 ha), eight secondary forest sites (located 100 m into the matrix from the nearest fragment edge) and nine control sites in three continuous forest areas. Recordings were obtained with SM2Bat + detectors with omnidirectional microphones SMX-US (Wildlife Acoustics Inc., Massachusetts, USA). At each site, the detector was positioned at ~ 1.5 m height and programmed to record from 18:00 to 06:00. Recordings were captured in real time with a full spectrum resolution of 16-bit, with a high pass filter set at fs/32 (12 kHz) and a trigger level of 18SNR. Sites were sampled for one night each survey during the first year (2011) and five consecutive nights thereafter (2012–2013) (López-Baucells et al. 2021). Four surveys were conducted annually, two in the wet season and two in the dry season.

Sound analysis

Recordings were manually analysed with Kaleidoscope 4.0.4 software (Wildlife Acoustics Inc., Massachusetts, USA) following López-Baucells et al. (2019), using the acoustic key in López-Baucells et al. (2018) and a local reference call library (A. López-Baucells, *unpublished data).* Calls were identified to species level when possible or assigned to groups of taxa with similar calls (sonotypes). A total of 21 species/sonotypes were identified (Table S1 in Online Supplementary Material). Since it is not possible to estimate abundance with acoustic data, we used activity as a proxy of abundance based on the number of bat passes (Rowse et al. 2016). The sample unit, a bat pass, was defined as any call sequence with a maximum duration of 5 s, which contained at least two distinguishable echolocation pulses (Torrent et al. 2018; López-Baucells et al. 2021). Bat activity was quantified by the total number of bat passes per night per species/sonotype.

Calculation of diversity response metrics

We calculated taxonomic (TD), functional (FD) and phylogenetic (PD) alpha diversity using a unified framework based on Hill numbers. Hill (1973) integrated species richness, the converted Shannon entropy and Gini-Simpson index measures into a family of diversity measures by order q or the effective number of species. The sensitivity of the measure to the relative frequency of species is determined by the parameter q and is expressed in units of species. Hill numbers offer advantages over standalone diversity measures, including satisfying the mathematical replication principle, allowing for direct comparison across orders q due to values being expressed as units of effective number of species. They can be partitioned into independent group components and by doing so can be generalised to taxonomic, functional, and phylogenetic diversities providing a unified framework for measuring biodiversity (Chao et al. 2014). Using the R package 'hillR' (Li 2018), we calculated each diversity facet based on total bat activity per site and per night using the Hill numbers framework. Diversity values become more sensitive to common species as q increases. When $q=0$, species/sonotype abundance is ignored (species richness); $q=1$, all species/sonotypes are weighted by their abundance equally (Shannon diversity (the exponential of entropy)); $q=2$, greater weight is placed on common than rare species/sonotypes (Simpson diversity (inverse of the Simpson index)). We calculated all three q values (0, 1 and 2), representing a full diversity profile illustrating the species abundance differentiation of the assemblage. For FD, we selected functional traits that have been shown to indicate potential vulnerability to habitat fragmentation in aerial insectivorous bats (Núñez et al. 2019). Trait information on echolocation call structure, frequency and alternation, body mass, aspect ratio and relative wing loading, as well as vertical stratification were considered, encompassing both continuous and categorical data (Table S2 in Online Supplementary Material). To adhere with the Hill number framework, each 'species/sonotype' must be a distinct entity with its own (attribute) diversity data (Chiu and Chao 2014). Complete trait data was not available for *Saccopteryx gymnura*, thus, calls of this species were removed from the analysis (1817 calls in total). Also, for molossid sonotypes, body mass, aspect ratio and relative wing loading were calculated using the mean of values for individual species within each sonotype. To quantify PD, phylogenetic information was extracted from a species-level supertree for bats (Shi and Rabosky 2015) and pruned to include only the species of aerial insectivorous bats known to occur at the BDFFP (Fig. S1 in Online Supplementary Material). Again, the 'hillR' methodology required a single entity species to be selected from the supertree, therefore to deal with sonotype data, we selected a single representative species, based on the likelihood of occurrence at the BDFFP, for the PD analysis; Molossidae II—*Molossus rufus*, Molossidae III—*Eumops auripendulus*, Molossops I—*Molossops neglectus* and Promops I—*Promops centralis* (See Table S3 in the Online Supplementary Material). *Pteronotus alitonus* was not present in the supertree and so was replaced by its closest congener, *Pteronotus parnellii* (Pavan et al. 2018). It has been argued that this approach of substitution by close congeners does not cause serious changes in the distance matrices (Cisneros et al. 2014).

Local and landscape predictor variables

Local vegetation structure

Local vegetation structure was quantified within three plots of 100 m^2 (5×20 m) around the detector locations at each of the 33 sampling sites. In each plot, seven variables were assessed (details in Rocha et al. 2017a): (i) number of trees (> 10 cm diameter at breast height [DBH]), (ii) number of woody stems (< 10 cm DBH), (iii) average DBH of trees > 10 cm, (iv) percentage canopy cover, (v) liana density (visually classified every 5 m in five categories varying from no lianas to very high liana density), (vi) canopy height (based on visual estimation) and (vii) vertical stratification in vegetation density. Vegetation variables were submitted to a Principal Component Analysis (PCA), and scores from the first axis (PCA1) were retained as predictor metric summarising local vegetation structure for use in subsequent modelling. PCA1 represented vegetation structure and explained 38.3% of the total variance (Fig. S2; Table S4 in Online Supplementary Material). This first component was positively correlated with average DBH of trees > 10 cm, canopy height and percentage canopy cover. Although these features describe more structurally complex habitats, the metric represented a gradient, including negative values, characteristic of secondary regrowth (matrix), with an increased number of woody stems and liana density.

Landscape structure

Landscape composition and configuration were quantified using 2011 LandSat Thematic Mapper™ satellite images (30 m spatial resolution) with continuous forest and secondary forest land cover classes identified. Collinearity is a common problem with landscape predictor variables. Therefore, we selected the same three landscape metrics as Rocha et al. (2017a), which were acceptable based on variance inflation factor calculations (VIF). Metrics of landscape composition (primary forest cover) and configuration (patch density, edge density) were calculated using the R package ‘landscapemetrics’ (Hesselbarth et al. 2019). Circular buffers were defined with radii of 0.5, 1, 1.5, 2, 2.5, and 3 km around the 33 sampling sites. In selecting these buffer sizes, we took into consideration the observed scale of effect for bats (Jackson and Fahrig 2015) and their utilisation in other tropical aerial insectivorous bat studies (e.g., Rodríguez-San Pedro and Simonetti 2015; Ongole et al. 2018; Rodríguez-San Pedro et al. 2019; Falcao 2021; López-Bosch et al. 2021). Although it is acknowledged that overlapping landscape buffers may not necessarily violate statistical independence (Zuckerberg et al. 2020), we chose not to investigate radii larger than 3 km to minimise spatial overlap between sites (Meyer and Kalko 2008). At each spatial scale, we first fitted a linear model between the landscape composition variable (primary forest cover) and the landscape configuration variables (edge and patch density) (Trzcinski et al. 1999). The residuals of the simple linear regression were then extracted and new configuration variables were created for use in subsequent modelling (Bélisle et al. 2001; Klingbeil and Willig 2010).

Modelling taxonomic, functional and phylogenetic diversity

The diversity metrics (TD, FD, PD/$q=0$, $q=1$, $q=2$) were modelled (1) with the fragment size/IEM variables (see below) and (2) the local- and landscape-scale variables, using Bayesian generalised linear mixed-effects models (GLMMs) as implemented in package MCMCglmm (Hadfield 2010). A measure of significance of the difference between effects (p_{MCMC}) can be produced via the proportional overlap of the distribution estimates produced, accompanied by an estimate of the mean and 95% credible intervals without post-hoc tests (Sweeny et al. 2021). For fragment size/IEM variables we fit a set of nine models, three for each diversity facet (TD, FD, PD/$q=0$, $q=1$, $q=2$), specifying a single categorical fixed effect with combined information on the fragment size and

IEM gradient (10 categories: continuous forest interior, 100 ha interior, 100 ha edge, 100 ha matrix, 10 ha interior, 10 ha edge, 10 ha matrix, 1 ha interior, 1 ha edge, 1 ha matrix; Rocha et al. 2017a) and incorporated research camp location as a random effect. To model local- and landscape-scale variables, we fit a set of models using each by site alpha diversity metric (TD, FD, PD/$q=0$, $q=1$, $q=2$) in turn, with four fixed effect local and landscape-scale variables (local vegetation structure, continuous forest cover, edge density, patch density) for each buffer size (0.5, 1, 1.5, 2, 2.5 and 3 km) and research camp location as a random effect. Each model set contained six full models and nine sets were run in total. All models were fitted with a Gaussian error distribution and a "non-informative" prior, which is weakly informative and is equivalent to an inverse-gamma prior with shape and scale equal to 0.001 (Gelman 2006; Wilson et al. 2010).

Parameter sampling

Using the MCMCglmm package, each model chain was run for 50,000 iterations. As the chain begins to run the early samples may show a strong dependence on the starting parametrisation. As such, we allowed 5000 iterations to pass before the samples were stored (burn-in period) and estimates were retained every 10 iterations (thinning interval) following burn-in. We then evaluated convergence through (a) visual check of parameter time series representations, i.e. trace plots, (b) calculation of the lag k autocorrelation statistic to check lag progress and independence of posterior distribution samples, and (c) calculation of the Gelman-Rubin diagnostic statistic (comparison of four chains). All point estimates of potential scale reduction factor were < 1.1, indicating good convergence (Gelman and Rubin 1992). All models achieved convergence. Posterior distributions for the predictor variables were obtained. As model output, we report posterior means, 95% credible intervals and Bayesian *p*-values (p_{MCMC}) indicating the significance of variables with a threshold of $^{*}p_{\mathrm{MCMC}} < 0.05$, $^{**}p_{\mathrm{MCMC}} < 0.01$ $^{***}p_{\mathrm{MCMC}} < 0.001$.

Results

Across the 33 sites, 281,425 bat passes were analysed belonging to 20 different species/sonotypes from five different families (Table S1 in Online Supplementary Material). Given that there were a number of species/sonotypes with low call numbers we present here the results for Hill numbers of order $q=2$, interpreted as the effective number of dominant or very abundant species in the assemblage. Results for $q=0$ and $q=1$ are included in Online Supplementary Material for comparison and completeness.

Fragment size and IEM gradients

The secondary forest matrix around the smallest fragments (1 ha) harboured significantly lower TD and PD compared to CF interiors (Fig. 2). The same was true for PD in the matrix of the 10 ha fragments, with a similar pattern of erosion exhibited for FD in the 1 ha and 10 ha fragments and TD in the 10 ha fragments, albeit not significantly so. The negative effect of the matrix gradually became less pronounced with increasing fragment size, with minimal differences evident between the 100 ha matrix sites compared with CF interiors. In contrast, the edges of the 1 ha and 10 ha fragments contained significantly higher TD, FD and PD compared with CF interiors (Fig. 2). This positive edge effect extended to even the largest fragments, with the 100 ha edge sites harbouring significantly greater PD than CF interiors (see Table S5 in Online Supplementary Material for $q=2$ (inverse Simpson) modelling results). Modelling results for $q=0$ (Table S6 in Online Supplementary Material) and $q=1$ (Table S7 in Online Supplementary Material) showed a larger number of significant effects. In particular FD was significantly reduced along with TD and PD in the matrix of the 1 ha fragments, contributing to the general pattern of significant erosion of all three diversity facets in the 1 ha fragments (Fig. S3 in Online Supplementary Material).

Influence of local and landscape-scale predictors

Overall, the assemblage response to local- and landscape-scale variables was subtle, with scale-sensitive associations for FD, whereas no significant relationships were found for TD or PD (Fig. 3). Vegetation structure does not appear to

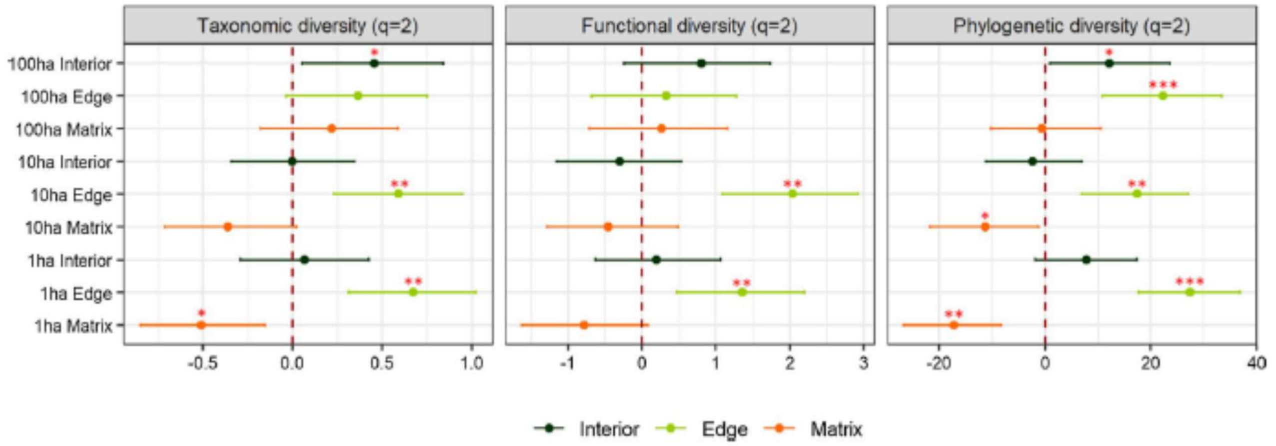

Fig. 2 Comparison of α-diversity metric $q=2$ across the Interior-Edge-Matrix and size gradients at the Biological Dynamics of Forest Fragments Project (forest fragment interiors, forest fragment edges and adjoining secondary forest/matrix). The predicted differences between each habitat and continuous forest interior, modelled using $\mathrm{MCMC}_{\mathrm{GLMM}}$ are plotted with their corresponding 95% credible interval. Those which do not touch or overlap the vertical dashed line (0) are considered significant ($^{*}p_{\mathrm{MCMC}} < 0.05$, $^{**}p_{\mathrm{MCMC}} < 0.01$ $^{***}p_{\mathrm{MCMC}} < 0.001$). See Fig. S3 in Online Supplementary Material for $q=0$ and $q=1$

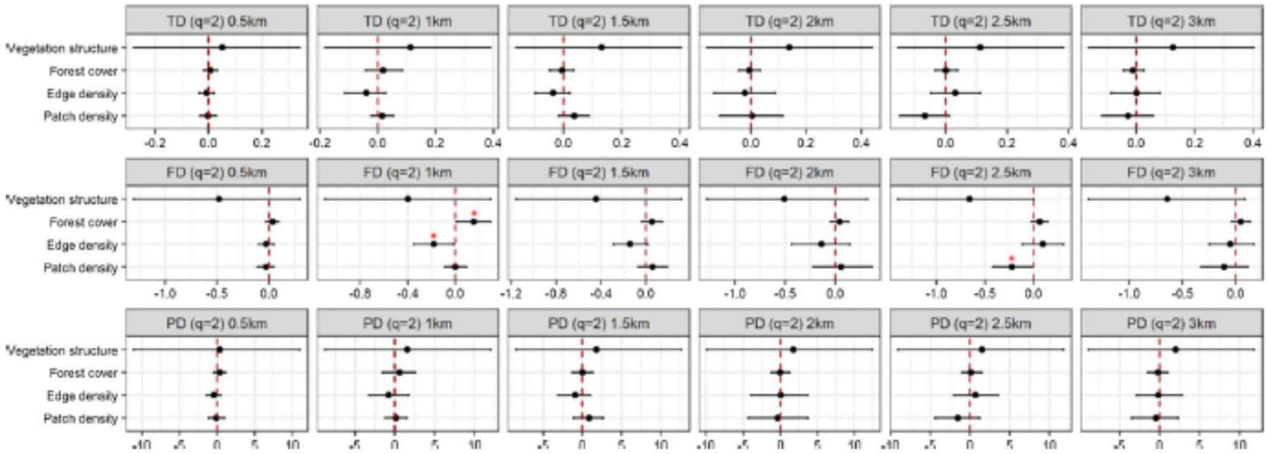

Fig. 3 Taxonomic, functional and phylogenetic diversity metrics $q=2$ modelled as a function of local and landscape predictor variables (vegetation structure, forest cover, edge density and patch density) based on surveys of aerial insectivorous bats at the Biological Dynamics of Forest Fragments Project, Brazil. Shown are posterior mean estimates ± 95% credible intervals. Credible intervals which do not touch or overlap the zero line are considered significant (* $p_{\mathrm{MCMC}} < 0.05$). See Fig. S4 in Online Supplementary Material for $q=0$; Fig. S5 in Online Supplementary Material for $q=1$

be a particularly relevant predictor of any diversity dimension. Vegetation structure had a negative relationship with FD across all diversity metrics (see Table S6; Table S7; Table S8 in Online Supplementary Material for modelling output for $q=0$; $q=1$; $q=2$), but this manifested as a significant result only for the 2.5 and 3 km scale for $q=1$ (Fig. S5 in Online Supplementary Material). FD responded significantly and positively to forest cover (compositional metric), and significantly and negatively to edge density (configurational metric) at the 1 km scale. These responses weakened with increasing buffer size. Finally, at the 2.5 km scale, patch density had a significant negative effect on FD (Fig. 3).

Discussion

Our study indicates that despite the advanced-stage secondary forest around the BDFFP fragments (~ 30 years), the diversity recovery of the aerial insectivorous bat assemblage in forest fragments and matrix habitats is still incomplete. Whilst our results indicated variation in FD, we found no clear evidence of the local- or landscape-scale variables analysed to accurately predict the diversity responses in our study area.

Responses to fragment size and IEM gradients

Despite the advanced stage of maturation of the secondary regrowth, its aerial insectivorous bat assemblage shows evidence of degradation compared to levels observed in CF interiors. These findings are consistent with similar phyllostomid bat studies at the BDFFP (Farneda et al. 2015, 2018; Rocha et al. 2017b; Aninta et al. 2019). The loss of TD and FD in the secondary forest is likely to reduce ecosystem services provided by aerial insectivorous bats such as arthropod suppression (Kunz et al. 2011; Puig-Montserrat et al. 2015). Most importantly, our results support that specialist forest-dwelling bats might be strongly affected by deforestation even after ~ 30 years of forest recovery. The fact that PD is also lower in the secondary forest reflects depletion of evolutionary richness due to the loss of the overall genetic diversity of the assemblage (Struebig et al. 2011; Rivera-Ortíz et al. 2015; Edwards et al. 2021). The close relationship between the decrease in PD and the low structural complexity of secondary forests compared to CF suggests that habitat fragmentation reduces total evolutionary history by eliminating distantly related species in less complex habitats.

Forest fragment interiors were either not significantly different or slightly more diverse than CF, as was the case for the 100 ha fragments. This aligns with our prediction that diversity levels in CF and the larger fragments (100 ha) would be homogeneous, contrasting previous research on phyllostomids at the BDFFP, which found significantly lower diversity in the fragments than CF (Rocha et al. 2017a; Farneda et al. 2018; Aninta et al. 2019; Silva et al. 2020). As fragment size decreased, we found increasing erosion of all three facets of diversity in the intervening secondary matrix. Larger fragments (10 and 100 ha) and adjoining secondary forests tended to harbour higher TD, FD and PD than the smaller fragments (1 ha). The fact that TD, FD and PD in secondary forests next to the largest fragments (10 and 100 ha) were higher than in those adjoining smaller fragments (1 ha) suggests that, in this landscape, the largest fragments act as important reservoirs of aerial insectivorous bat diversity for the nearby regenerating areas.

In line with our prediction, all three diversity metrics peaked at the primary-secondary forest interface. Fragment edges were generally more diverse in TD, FD and PD than the CF and fragment interiors. Rodríguez-San Pedro et al. (2019) reported a similar positive response of aerial insectivorous bats to forest edges. The tall secondary forest at the BDFFP provides a low-contrast matrix that could facilitate connectivity, buffering the isolation effects of the smallest fragments and function as commuting corridors (Van Houtan et al. 2007; Jantzen and Fenton 2013; Kalcounis-Rueppell et al. 2013). Coleoptera, Hymenoptera, Lepidoptera and Araneae are among the most species-rich canopy invertebrates in tropical forests (Basset 2001). Coleoptera and Hymenoptera are more abundant in secondary forest compared to the other habitats at the BDFFP (De Aquino et al. 2021). This increased abundance of prey items could also provide increased foraging opportunities simultaneously, for edge-, open- and interior- specialists in and around the edge habitat (Ingala et al. 2021).

Influence of local- and landscape-scale predictors

We anticipated subtle responses across the three diversity facets, but we only found statistically significant responses for FD. Uncovering significant responses at the community level is often difficult due to diversity metrics amalgamating species-specific responses that may cancel each other out (Klingbeil and Willig 2009; López-Bosch et al. 2021).

Our results concur with some other studies on the effects of fragmentation on aerial insectivorous bats, in which community responses were muted. For instance, Estrada-Villegas et al. (2010) found that sonotype abundance levels were indistinguishable in a land-bridge island system which comprised interior and edge mainland sites and island sites (near and far/large and small) regardless of the sonotype group analysed and the level of island isolation or size. Falcão et al. (2021) compared activity levels and sonotype composition across two landscapes (forested vs. deforested/pasture-dominated) in the Brazilian Atlantic Forest and found that aerial insectivorous bat community richness was not related to any landscape descriptors.

We predicted that vegetation structure would have an effect at the smallest spatial scale, possibly turning neutral at large scales. However, we found no such effect on any of the diversity facets at any scale. Our findings contradict that of Blakey et al. (2017) who utilised LiDAR technology to comprehensively scan and characterise vegetation structure and found evidence that understorey forest structure was related to overall taxonomic and functional bat diversity at the community level. In a study in Panama, density of obstacles or vegetation clutter, which restrict the flight manoeuvrability of aerial insectivorous bats, were the main factor explaining both species richness and total abundance (Estrada-Villegas et al. 2012). Aerial insectivorous bats are known to utilise vertical space in a number of ways; foraging below, at and above canopy level, with much less activity within the forest interior (Marques et al. 2015). Perhaps vegetation structure is a limiting factor, albeit the effect may not be of the same magnitude as for phyllostomids at the BDFFP, where vegetation structure was a relevant predictor of total abundance (Rocha et al. 2017a).

We only observed responses to landscape composition and configuration at the assemblage level from a FD perspective. We expected that the amount of forest cover would be an important predictor of all three diversity facets at the landscape scale, but it was only important at the 1 km scale. Some recent studies analysed the influence of landscape composition and forest cover on aerial insectivorous bat assemblages in agricultural systems (Azofeifa et al. 2019; Rodríguez-San Pedro et al. 2019; Put et al. 2019), illustrating the nuanced responses to forest cover embedded in “hard” matrix types (i.e., rice fields, vineyards, grazing lands). For instance, Azofeifa et al. (2019) found forest cover to have no effect on overall species richness or composition in a study comparing two rice field sites in Venezuela. However, forest cover had a differential effect on functional groups, with background-cluttered space species responding more sensitively to changes in forest cover than uncluttered/open space specialists. A study of vineyards in central Chile found that preservation of native vegetation cover positively affected bat diversity and species richness and that areas of landscape with more irregular and smaller patches and higher edge density facilitated a more diverse assemblage (Rodríguez-San Pedro et al. 2019).

We also found that FD responded to landscape configuration. At the 1 km scale, edge density had a negative effect, indicating that an increase in the total perimeter of edge habitat resulted in a functionally less diverse assemblage. A study quantifying edge effects across the interface of primary and secondary forest at the BDFFP suggested that the consequences of edge effects on some aerial insectivorous bat species could potentially extend for more than 2 km (Yoh et al. 2022). In contrast, at the 2.5 km scale, patch density had a positive effect, suggesting that the spatial configuration of patches at this landscape scale facilitates a more diverse assemblage. These two results for edge density and patch density agree with Chambers et al. (2016), who investigated scale dependence of habitat associations and scaling patterns of landscape metrics about bat occurrence in forests of southwestern Nicaragua and found that edge density and patch density may be as important as compositional metrics in predicting bat capture rates across multiple scales.

We have limited evidence to suggest a specific scale of effect for this community. It is reasonable to theorise that to gain access to both foraging and roost sites (landscape complementation), the species within the BDFFP community are responding, not at a single scale but across multiple scales, to both local and landscape features to secure the necessary resources (Ethier and Fahrig 2011). We suggest that further species-specific analysis might show the complexity of responses from species within an assemblage (Rodríguez-San Pedro et al. 2019). We are currently exploring species and guild level responses, which might uncover interesting and possibly conflicting patterns that may be masking an effect in this study (Gomes et al. 2020). Appel et al. (2021) investigated the interaction between habitat and moonlight at the BDFFP and analysed aerial insectivores on a species-specific basis. They found that *Saccopteryx bilineata, Saccopteryx leptura, Centronycteris maximiliani, Cormura brevirostris, Eptesicus brasiliensis* and *Furipterus horrens* had lower activity in secondary forest and *Pteronotus alitonus* and *Furipterus horrens* showed lower activity in fragments compared to continuous forest. It is understandable to see how these contrasting species-specific preferences can make community-level interpretation challenging.

Conclusions

Our study shows that at the BDFFP aerial insectivorous bat diversity in secondary regrowth is still not comparable with that of undisturbed forest even after ~ 30 years of recovery. The low-contrast matrix at the BDFFP does, however, appear to create opportunities for aerial-hawking bats to take advantage of forest edge habitat created as a result of fragmentation. For aerial insectivorous bat diversity, specifically, this may help to buffer some of the negative isolation effects of the smaller remnants. It also reinforces the importance of including > 10 ha forest patches in land management and conservation strategies to maximize bat diversity in human-modified landscapes. Whilst the effects of fragmentation manifest as different responses in aerial insectivores and phyllostomids, our findings reinforce the irreplaceable value of old-growth forest in tropical landscapes for both groups. We found significant variation in functional diversity which might be overlooked with a traditional taxonomic focus, and we observed responses to both local and landscape-scale variables at the 1 and 2.5 km scale. We therefore recommend that future studies of tropical bats follow a multidimensional biodiversity approach integrated with a multiscale analysis when assessing responses to fragmentation in human-modified landscapes.

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Author contributions All authors contributed to the study conception and design. AL-B and RR collected data at the BDFFP. Data analysis was performed by AL-B and SR. The first draft of the manuscript was written by SR and all authors commented on previous versions of the manuscript and gave final approval for publication.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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