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RESEARCH ARTICLE

Secondary forest buffers the effects of fragmentation on aerial insectivorous bat species following 30 years of passive forest restoration

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Passive forest restoration can buffer the effects of habitat loss on biodiversity. We acoustically surveyed aerial insectivorous bats in a whole-ecosystem fragmentation experiment in the Brazilian Amazon over a 2-year period, across 33 sites, comprising continuous old-growth forest, remnant fragments, and regenerating secondary forest matrix. We analyzed the activity of 10 species/sonotypes to investigate occupancy across habitat types and responses to fragment size and interior-edge-matrix (IEM) disturbance gradients. Employing a multiscale approach, we investigated guild (edge foragers, forest specialists, flexible forest foragers, and open space specialists) and species-level responses to vegetation structure and forest cover, edge, and patch density across six spatial scales (0.5–3 km). We found species-specific habitat occupancy patterns and nuanced responses to fragment size and the IEM disturbance gradient. For example, *Furipterus horrens* had lower activity in secondary forest sites and the interior and edge of the smallest fragments (1 and 10 ha) compared to continuous forest, and only two species (*Pteronotus* spp.) showed no habitat preference and no significant responses across the IEM and fragment size gradients. Only the *Molossus* sonotype responded negatively to vegetation structure. We uncovered no negative influence of forest cover or edge density at guild or species-level. Our results indicate that reforestation can buffer the negative effects of fragmentation and although these effects can still be detected in some species, generally aerial insectivorous bats appear to be in recovery after 30 years of passive forest restoration. Our findings reinforce the need to protect regenerating forests while conserving vast expanses of old-growth forest.

Key words: Amazon, bioacoustics, Chiroptera, forest restoration, fragmentation, multiscale analysis

Implications for Practice

- Passive forest restoration within human-modified landscapes can provide valuable habitat and considerable conservation value if afforded appropriate protection allowing the forest to regenerate for several decades (at least 30 years).
- From a land management perspective, it is important to preserve sufficiently large-sized fragments (>at least 10 ha) to buffer the pervasive effects of fragmentation and assist with the recovery of ecosystem functioning.
- For aerial insectivorous bats, activity is unrelated to landscape-level forest cover while a degree of forest disturbance (additional edges) can provide enhanced foraging opportunities for the most common species although this may not hold true for the rarest and most elusive species.

Introduction

Representing 45% of all forest cover on Earth (FAO & UNEP 2020) tropical forests are some of the most diverse ecosystems (ForestPlots.net et al. 2021), yet they are under constant threat due to a wide array of anthropogenic pressures (Malhi et al. 2014). Land use change continues to drive global deforestation, with agricultural expansion persisting as the major reason for forest clearance, accounting for at least half of all forest loss—circa 10 million ha/year (FAO & UNEP 2020; Laso Bayas et al. 2022). Human-modified landscapes are

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increasingly fragmented (Taubert et al. 2018) and the twin devils of habitat loss and fragmentation are eroding biodiversity by contracting species' ranges, causing widespread changes in species abundance and affecting species interactions, which is notably prominent in the species-rich tropical regions (Ceballos et al. 2017).

The Amazon is a deforestation hotspot and while scientific efforts continue to advocate for the significant and permanent reduction of forest clearance, regenerating secondary forests have been identified as the most effective method of passive restoration of the Amazon (Crouzeilles et al. 2017). The majority of Amazonian land use change resulted from the conversion of native forest into pasture for cattle and agricultural expansion (Silveira et al. 2022). However crop fields and pastures are often abandoned, allowing reforestation via successional processes (Chazdon 2014). Reforestation of abandoned lands has the capacity to support displaced forest biodiversity, contribute to carbon sequestration (Heinrich et al. 2023) and provide climate change mitigation (Locatelli et al. 2015). Secondary forests are a significant feature in the Amazon, covering greater than 234,000 km^2 by 2017 (Smith et al. 2021). These landscapes often contain remnant fragments, embedded in a matrix ranging from high-contrast agricultural to low-contrast regrowth forest (Neeff et al. 2006; Numata & Cochrane 2012). Where regenerating forests mature, the negative effects of fragmentation can be buffered, providing valuable habitats which can support a wide variety of taxa (Edwards et al. 2017; Derhé et al. 2018; De Aquino et al. 2022).

Aerial insectivorous bats provide essential ecosystem services and are useful bioindicators of ecosystem health (Jones et al. 2009; Kunz et al. 2011). In Brazil, they account for nearly half (48%) of the greater than 181 described bat species (Garbino et al. 2022). They are best sampled with acoustic methods, as their highly developed echolocation means that, unlike their phyllostomid counterparts, they are rarely captured in mist nets (Appel et al. 2021*a*; Carvalho et al. 2023). The sensitivity of aerial insectivorous bats to forest fragmentation is largely mediated by their wing morphology and echolocation (Bader et al. 2015; Colombo et al. 2023) which can determine foraging success within a habitat based on the level of clutter (Schnitzler & Kalko 2001). Forest specialists are often more vulnerable to fragmentation (Núñez et al. 2019; López-Bosch et al. 2022) as they are adapted to navigate and forage in highly cluttered space, whereas aerial-hawking species use uncluttered open space above the canopy and can fly longer distances to access suitable foraging habitat, making them more resilient to fragmentation (Bader et al. 2015).

Vulnerability of neotropical bats to fragmentation has been widely investigated at the Biological Dynamics of Forest Fragments Project (BDFFP) in the Brazilian Amazon, the world's largest and longest-running experimental study of habitat fragmentation and forest regeneration. While a significant proportion of this research has focused on the responses of phyllostomid bats (e.g. Farneda et al. 2018, 2022; Rocha et al. 2018), recent research has also targeted the ensemble of aerial insectivorous bats (e.g. Appel et al. 2021*b*; López-Baucells et al. 2022; Yoh et al. 2022), which comprises a considerable fraction of the BDFFP bat fauna.

Multi-dimensional (taxonomic, functional, and phylogenetic) diversity responses of the aerial insectivorous bat ensemble to vegetation and landscape structure indicated subtle scale-sensitive associations for functional diversity only (López-Baucells et al. 2022). The regenerating 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 with increasing fragment size. In contrast, forest edges generally harbored higher taxonomic, functional, and phylogenetic diversity compared to continuous forest interiors. Recent research investigating species-specific responses of aerial insectivores to edge effects across the interface of continuous and secondary forest suggested that the regenerating secondary forest might have recovered enough that edge effects are no longer evident for most common species (Yoh et al. 2022). In contrast, Appel et al. (2021*b*) found lower activity in the regenerating secondary forest suggesting that even after 30 years it remains less attractive as a foraging habitat.

Here, we build on our previous multi-dimensional diversity analysis (López-Baucells et al. 2022) and investigated (1) how species-specific occupancy and activity differ across the four main habitats (continuous forest [CF], forest fragment interiors [I], fragment edges [E], and secondary forest matrix sites [M]), considering both the disturbance interior-edge-matrix [IEM]) and fragment-size gradients; and (2) whether local vegetation structure and landscape metrics influence activity across multiple spatial scales. These comparisons were conducted for a selection of common species/sonotypes and four functional guilds (edge foragers [EF], forest specialists [FS], flexible forest foragers [FF] and open space specialists [OS] sensu Yoh et al. 2022).

We hypothesized that the 30 years of secondary forest regeneration would buffer the negative effects of fragmentation on the focal species. Specifically, we predicted that; (1) occupancy and activity would be species-specific, with similar responses within guilds, (2) FS would have higher occupancy in CF due to functional trait exclusion, (3) there would be a positive response for EF exploiting feeding opportunities generated around the fragment edges and secondary forest matrix sites, and (4) FF would show no response or preference for any habitat.

Methods

Study Area

The study was conducted at the BDFFP, an experimental fragmentation project located approximately 80 km north of Manaus, Central Amazon, Brazil (Fig. S1). The topography of the study area (approximately 1000 km^2) is relatively flat, with streamlets cutting through 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 when ranchers cleared continuous old-growth *terra firme* rainforest to accommodate cattle pastures and preserved forest patches of varying sizes (1, 10, and 100 ha) isolated from the CF by distances of 80–650 m (Bierregaard Jr et al. 1992). Within 10 years the cattle ranches were abandoned and secondary forest established in the matrix around the fragments (Laurance et al. 2018). Approximately every 10 years, to preserve isolation, a 100 m-wide strip of secondary forest surrounding the fragments is cleared (Rocha et al. 2020). Canopy height of fragment forest averages 30 and 37 m, with emergent trees exceeding 55 m. The most recent re-isolation of the fragments prior to data collection for this study occurred between 1999 and 2001 (Laurance et al. 2011). There was relatively little structural contrast between CF, fragments, and the advanced-stage (approximately 30 years old) secondary forest at the time of this study.

Acoustic Recordings

Acoustic surveys were conducted between November 2011 and September 2013 across a total of 33 sampling sites: (a) nine control sites in three CF areas (located in Cabo Frio, Florestal, and Km41 camps), (b) eight fragment sites (3 × 1, 3 × 10, and 2 × 100 ha, located in Colosso, Porto Alegre, and Dimona camps) with sampling conducted in the interiors and at the edges of all eight fragments (interior-edge distances 245 ± 208 m [mean ± SD]), and (c) eight secondary forest sites 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., Maynard, MA, U.S.A.). Recorders were positioned at 1.5 m height and programmed to record for 12 hours (from 18:00 to 6:00 hours). Recordings were captured in real time at full-spectrum resolution (16-bit), sampling rate of 384 kHz with a high pass filter set at fs/32 (12 kHz) and adaptive trigger level relative to noise floor of 18 signal-to-noise ratio. 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. Sampling of the interior, edge, and matrix sites of the same forest fragment was temporally spaced as far apart as logistically feasible.

Bioacoustic Analysis

Recordings were manually analyzed using Kaleidoscope Pro v4.0.4 software (Wildlife Acoustics Inc.) following the acoustic key in López-Baucells et al. (2016). Calls were identified to species level whenever possible or sonotypes (groups of taxa with similar calls). It is not possible to count individuals using bioacoustic data, thus activity was used as a proxy for abundance (Rowse et al. 2016) based on bat passes. A bat pass was defined as any call sequence containing at least two distinguishable echolocation pulses during a maximum duration of 5 seconds (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/sonotypes, however we only included species that were detected in at least 10% (102 nights) of total nights and in all three sampling years to minimize potential detection bias as per Appel et al. (2021*b*). This resulted in the selection of 272,201 calls from nine species and one sonotype; *Centronycteris maximiliani*, *Cormura brevirostris*, *Saccopteryx bilineata*, *S. leptura*, *Furipterus horrens*, *Molossus* sonotype (including *currentium/rufus* calls), *Pteronotus alitonus*, *P. rubiginosus*, *Eptesicus brasiliensis*, and *Myotis riparius* (Table S1). Following Yoh et al. (2022), we assigned species/sonotypes to guilds based on ecological requirements and foraging strategies: EF—*C. brevirostris*, *C. maximiliani*, *S. bilineata*, *S. leptura*; FS—*E. brasiliensis*, *F. horrens*, *M. riparius*; FF—both *Pteronotus* species; OS—*Molossus* sonotype (included in the guild analysis for comparison only as represented by a single sonotype).

Local Vegetation Structure and Landscape Predictor Variables

For each of the 33 sampling sites, within three plots of 100 m^2 (5 × 20 m) around the detector locations (during the same period as the acoustic sampling) we quantified seven vegetation variables (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) (López-Baucells et al. 2022). The first axis explained 38.3% of total variance (Table S2; Fig. S2), and was positively correlated with average DBH of trees greater than 10 cm, canopy height and percentage canopy cover, and scores were retained as a predictor variable summarizing vegetation structure (PCA1).

Methods for calculating landscape structure metrics followed López-Baucells et al. (2022). In brief, we used 2011 LandSat Thematic Mapper satellite images categorized into two land cover classes; CF and secondary forest. To avoid collinearity (a common problem with landscape predictor variables) and to allow for comparison with previous studies (López-Baucells et al. 2022), we selected the same three landscape metrics which were considered acceptable based on variance inflation factor calculations (Rocha et al. 2017). R package "landscapemetrics" (Hesselbarth et al. 2019) was used to calculate composition (CF cover) and configuration (patch density and edge density) metrics within circular buffers with radii of 0.5, 1, 1.5, 2, 2.5, and 3 km around 33 sampling sites. Little is known about the home range of the focal species in this study, we therefore took into consideration the scale of effect documented by Jackson and Fahrig (2015) and the utilization of 3 km landscape buffers in other tropical bat studies (e.g. Farneda et al. 2020; Martínez-Ferreira et al. 2020). Spatial scales greater than 3 km were not investigated to minimize spatial overlap between sites (Meyer & Kalko 2008) although it is acknowledged that landscape buffers which overlap may not necessarily violate statistical independence (Zuckerberg et al. 2020). To control for statistical correlation (Trzcinski et al. 1999), we fitted a linear model between the composition variable (CF cover) and configuration variables (edge and patch density) at each spatial scale and extracted the residuals creating new configuration variables (Bélisle et al. 2001; Klingbeil & Willig 2010).

Statistical Analysis

To visualize species-specific frequency of occurrence, activity per habitat type, expressed as percentage, was plotted (Fig. 1). We modeled each of the species' bat activity with (1) the fragment size/IEM variables and (2) the vegetation structure and landscape variables using Monte Carlo Markov Chain generalized linear mixed models via the R package MCMCglmm (Hadfield 2010), specifying a Poisson error distribution, and priors were set to be weakly informative in order to deal with overdispersion (inverse gamma parameters: $\nu = 0.002$ and $V = 1$; Kryvokhyzha et 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: CF 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; López-Baucells et al. 2022) and incorporated research camp location as a random effect. To model vegetation structure and landscape variables, we fit a set of models, each set contained 10 full models for each species with four fixed-effect variables (PCA1 and the new residual variables; CF 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. We also modeled vegetation and landscape variables (as previously detailed) for each guild (FS, ES, and FF). We ran 50,000 iterations, using a thinning-interval of 10 after "burn-in" of 5000. We evaluated convergence through (1) trace plot visual checks (2) lag k autocorrelation statistic, and (3) Gelman–Rubin diagnostic statistic (Gelman & Rubin 1992). All models achieved good convergence (potential scale reduction factor <1.1). 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 $^{*}p_{\mathrm{MCMC}}$ less than 0.05, $^{**}p_{\mathrm{MCMC}}$ less than 0.01, $^{***}p_{\mathrm{MCMC}}$ less than 0.001 (Sweeny et al. 2021).

Results

Across 33 sites, 272,201 bat passes from 10 species/sonotypes and 5 families encompassing four guilds were analyzed. All species/sonotypes were recorded across all four habitats, however patterns of occupancy were highly species-specific (Fig. 1). *Eptesicus brasiliensis* and *Furipterus horrens* had occurrence frequencies greater than 50% in CF. There were only three species with greater than 20% occurrence recorded in the secondary forest (*Pteronotus alitonus*, *P. rubiginosus*, and *Molossus* sonotype). *Cormura brevirostris* had over 75% of its frequency of occurrence in fragment interiors.

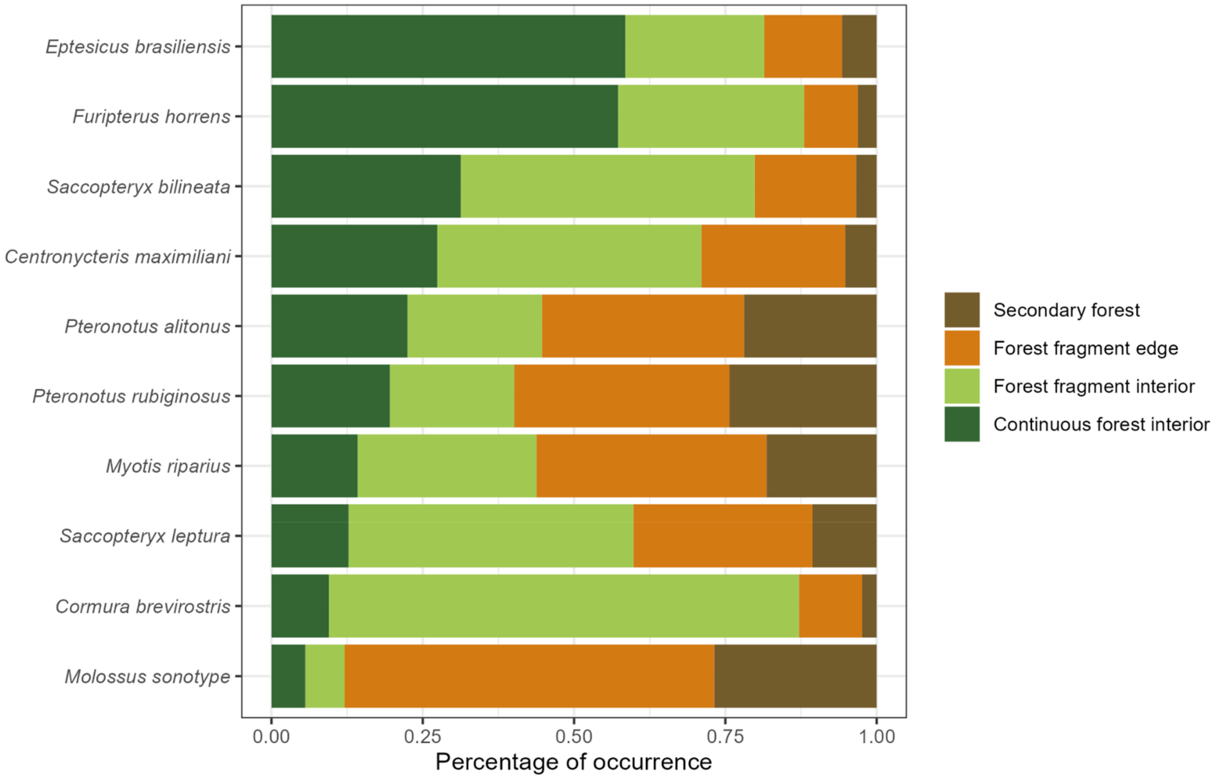

Figure 1. Species sorted by their frequency of occurrence in CF interiors, forest fragment interiors, forest fragment edges, and secondary forest. Percentage of occurrence was calculated using bat activity in each site per habitat type. Differences in sampling effort between habitat categories were accounted for in the percentage calculations.

Bat Activity Responses to IEM and Fragment Size Gradients

Across the IEM and fragment size gradients, we observed species-specific differences in activity (Table S3; Fig. 2), with most significant responses seen in the secondary matrix, particularly around the 1 and 10 ha fragments. Significant negative responses were observed in relation to the 100 ha matrix (*Centronycteris maximiliani*, *Saccopteryx bilineata*, *F. horrens*), the 10 ha matrix (*C. maximiliani*, *F. horrens*, *E. brasiliensis*) and the 1 ha matrix (*C. maximiliani*, *S. bilineata*, *S. leptura*, *F. horrens*, *E. brasiliensis*) as species reduced activity in these habitats. Five species showed no significant negative responses to either the IEM or fragment size gradients (*C. brevirostris*, *P. alitonus*, *P. rubiginosus*, *Myotis riparius*, *Molossus* sonotype) and two of these species (*M. riparius* and *Molossus* sonotype) evinced a positive response to the matrix habitat even around the smallest 1 ha fragment.

In particular, *C. maximiliani* showed a clear pattern with significantly reduced activity in all secondary forest sites and reduced activity at the edges of the 1 ha fragments. The activity of *S. bilineata* was significantly lower in the matrix around the smallest fragments and in matrix and edge sites of the 100 ha fragments. *S. leptura* activity was significantly higher in the

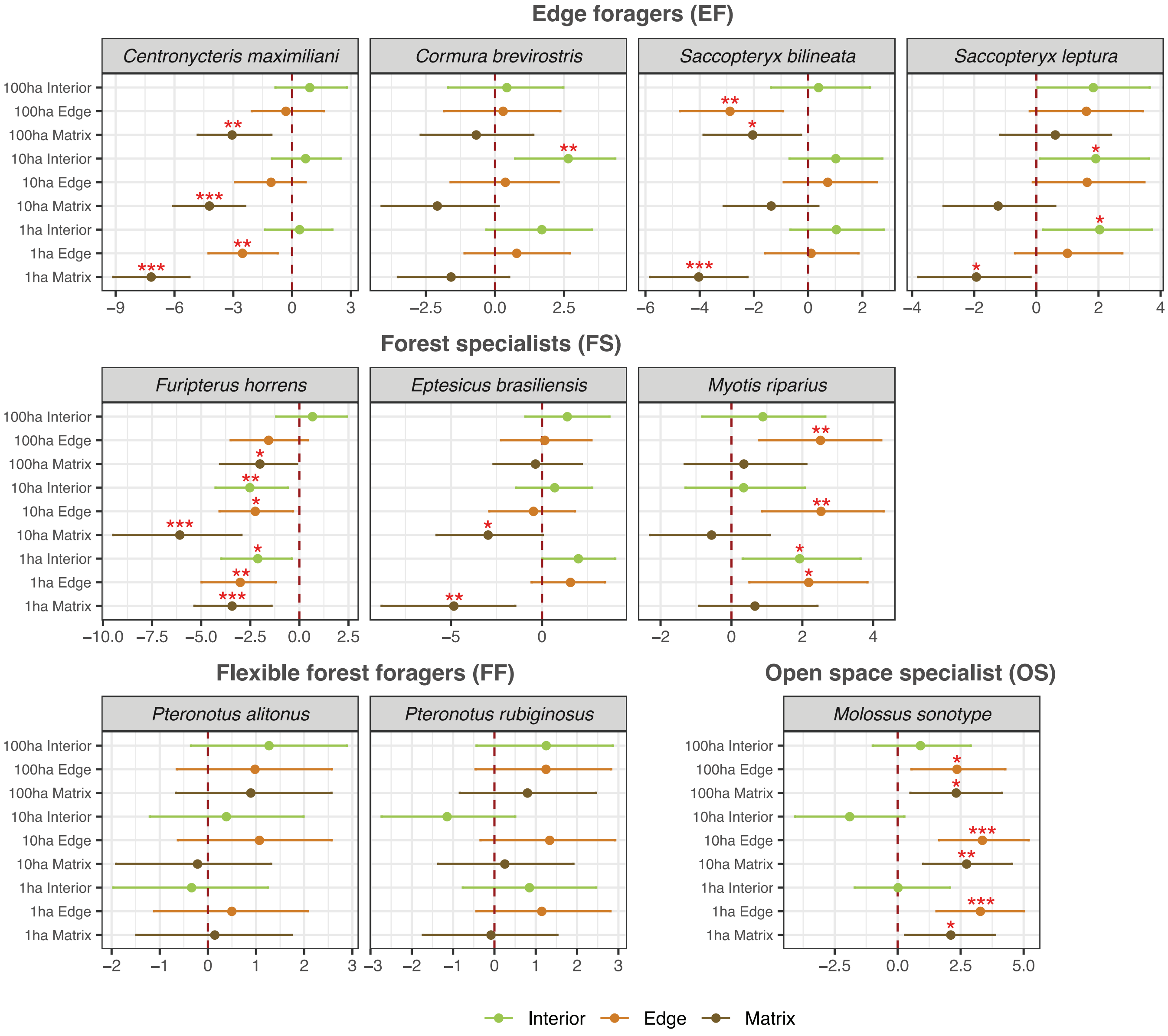

Figure 2. Comparison of total bat activity for species/guilds across the IEM and size gradients at the Biological Dynamics of Forest Fragments Project (forest fragment interiors, forest fragment edges, and adjoining secondary forest matrix). The predicted differences between each habitat and continuous old-growth forest interior, modeled using MCMCGLMM are plotted with their corresponding 95% CI. Those which do not touch or overlap the vertical dashed line (0) are considered significant (*$p_{\mathrm{MCMC}} < 0.05$, **$p_{\mathrm{MCMC}} < 0.01$, ***$p_{\mathrm{MCMC}} < 0.001$).

interiors of the 1 and 10 ha fragments whereas it was reduced in the matrix adjacent to the 1 ha fragments. *F. horrens* had significantly lower activity in all matrix sites and the interior and edge sites of the smallest fragments (1 and 10 ha). *M. riparius* activity responded positively to forest edges, irrespective of fragment size. Neither of the *Pteronotus* species showed any significant responses to the habitat gradient or fragment size. *Molossus* sonotype activity was significantly elevated across all matrix and edge sites for all fragment sizes.

Influence of Vegetation Structure and Landscape Predictors

Modeling showed species-specific variation in response to vegetation structure and landscape predictors (Table S4), 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). Species which showed no significant association with any of the vegetation structure or landscape variables, at any of the scales investigated, included *P. alitonus*, *P. rubiginosus*, and *M. riparius* (Fig. S3).

Vegetation structure was an important predictor of bat activity. *C. maximiliani*, *S. bilineata*, and *S. leptura*, exhibited a significant positive relationship at every scale. *F. horrens* and *C. brevirostris* evinced a consistent positive relationship at the larger scales (2.5–3 km). *E. 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.

Regarding landscape variables, forest cover and patch density were irrelevant predictors, with very little influence on bat activity and no significant associations at any scale. The configurational metric, edge density, exhibited a positive association with *C. maximiliani* activity at the 1 and 1.5 km scale.

The guild-level modeling results (Table S5; Fig. S4) further highlighted the influence of vegetation structure as FS revealed a positive relationship at scales 2.5 and 3 km. It was also a significant determinant of activity for EF at all scales, and highly so at the 0.5, 1, and 2.5 km scale. The configurational metrics, edge, and patch density, also influenced the EF with a negative relationship with patch density at 0.5 km and positive relationship with edge density at 1 km.

Discussion

Habitat Occupancy and Activity Responses to IEM and Fragment Size Gradients

Emballonurids 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). The four emballonurids in this study are categorized as EF although their frequency of occurrence suggests a broader habitat preference within the landscape. Our results concur and highlight the niche differentiation outlined by Denzinger et al. (2018) with *Saccopteryx bilineata*, known to forage above shrub layer, in small forest gaps and in the canopy whereas *S. leptura* can often be found foraging in subcanopy and canopy. Our results also show that *Cormura brevirostris* had the highest frequency of occurrence recorded in the forest fragment interiors compared to all other species and is the only edge-foraging species which showed no significant negative activity response across the IEM and fragment size gradients. A study comparing the echolocation calls of *S. bilineata* and *C. brevirostris* 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. This suggests that *C. brevirostris* has more call frequency composition control and acoustic dexterity allowing uninhibited foraging across the BDFFP landscape.

Building on conclusions drawn by Yoh et al. (2022), our results show that *Furipterus horrens* appears to be more sensitive to the restored secondary forest as activity was negatively affected across the whole IEM gradient and all bar the largest fragment interiors. Compared to other neotropical bats, *F. horrens* emits extremely high frequency, low intensity pulses which allows it to forage in dense rainforest vegetation (Falcão et al. 2015). However, this may result in *F. horrens* relying on old-growth forest due to trait-mediated exclusion from secondary forest. *Eptesicus brasiliensis* exhibited a similar frequency of occupancy to *F. horrens* but appears to be able to take advantage of a wider variety of habitats. Echolocation calls of *E. brasiliensis* are similar to its North American congener *Eptesicus furinalis* (Arias-Aguilar et al. 2018). Studies highlight examples of *E. furinalis* navigating through acoustically challenging environments and complicated scenes (Simmons et al. 2018, 2020). This acoustic dexterity trait is likely to be shared with *E. brasiliensis*, allowing it to utilize habitat created by fragmentation. For *Myotis riparius*, activity was consistently and significantly increased across all edge habitats, independent of fragment size. *M. riparius* shows significant plasticity in habitat usage (Novaes et al. 2017) and is often recorded at ground level, rather than subcanopy or canopy level (Marques et al. 2016). Due to *M. riparius'* small body size (Norberg & Rayner 1987) and echolocation call structure (Schnitzler & Kalko 2001) it appears to be taking advantage of a foraging niche in the lowest forest strata which in the case of this study is also extending to edge habitat.

Our results for *Pteronotus alitonus* and *P. rubiginosus* showed similar activity across all four habitat types. This absence of habitat preference was also noted in the IEM and fragment size gradient comparison where no significant effects were found. These results are in line with another study conducted at the BDFFP during the same time. Appel et al. (2021*b*) found elevated activity levels in secondary forest compared to continuous forest, however *P. alitonus* and *P. rubiginosus* exhibited foraging plasticity with increased activity in continuous forest on bright moonlit nights, possibly to reduce threats from avian predators. This flexibility was only evident in *Pteronotus* species which produce high duty cycle

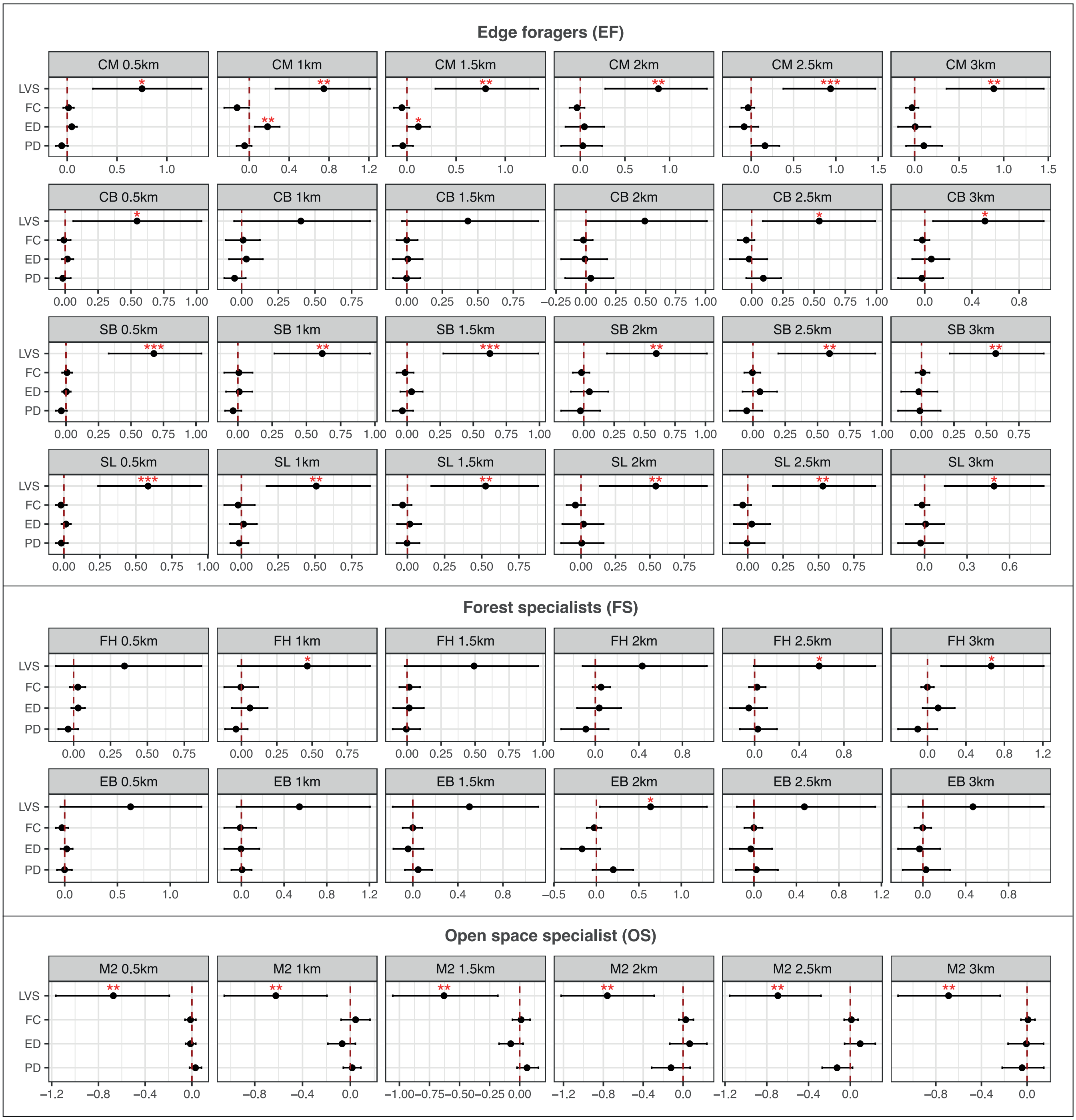

Figure 3. Species exhibiting significant scale-sensitive associations with metrics; EF × 4; *Centronycteris maximiliani* (CM), *Cormura brevirostris* (CB), *Saccopteryx bilineata* (SB), *S. leptura* (SL), FS x 2; *Furipterus horrens* (FH), *Eptesicus brasiliensis* (EB), and OS × 1; *Molossus* sonotype (M2). Bat activity modeled as a function of vegetation structure and landscape variables; vegetation structure (LVS), forest cover (FC), edge density (ED), and patch density (PD). Shown are posterior mean estimates 95% CI. Credible intervals which do not touch or overlap the zero line are considered significant (*$p_{\text{MCMC}} < 0.05$, **$p_{\text{MCMC}} < 0.01$, ***$p_{\text{MCMC}} < 0.001$).

constant-frequency echolocation calls, allowing them to accurately detect small mobile prey items in dense vegetation (Estrada-Villegas et al. 2012; de Oliveira et al. 2015; López-Baucells et al. 2018). They are well adapted to forage in regenerating forests where understory vegetation may be heavily cluttered. A later study conducted at the BDFFP, sampled aerial bat activity following fragment re-isolation in 2013 and found that *Pteronotus* spp. were more abundant in forest interiors than in the newly cleared areas or at fragment edges (Núñez et al. 2019). This flexibility across habitat types and response to biotic and abiotic variables illustrates how well adapted these mormoopid species are, occupying a relatively free acoustic niche (Siemers & Schnitzler 2004).

Molossids are associated with fast and economic flight (Castillo-Figueroa 2020). Their mobility is constrained within forest strata consisting of forest gaps and obstacles to navigate and so they are often precluded from foraging in these habitats due to the high energetic cost (Voigt & Holderied 2012). Our results found the *Molossus* sonotype most associated with fragment edges and secondary forest showing significantly elevated activity in these habitats. Bats of the Molossidae family generally show good tolerance to fragmentation (Estrada-Villegas et al. 2010) and are not overly sensitive to anthropogenic disturbance (Kemp et al. 2019; Meramo et al. 2022). We did not expect to see such bias in occupancy toward regenerating habitat. 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). The lower canopy height of the recovering secondary forest and the forest edges may allow molossids to fly lower and for their calls to be within recording range of detectors more often in disturbed forests compared to CF. We highlight that our results could be due to increased detectability from changes in flight behavior across habitat types.

Influence of Vegetation Structure and Landscape Predictors

Forest cover had no significant influence on the activity for any of the species or guilds. Inconsistent results have been reported for the effect of forest cover on aerial insectivorous bat activity (Azofeifa et al. 2019; Rodríguez-San Pedro et al. 2019; Colombo et al. 2023). We also found no negative responses associated with the configurational metrics (edge density and patch density). Aerial insectivorous bats, particularly those adapted to foraging around patch edges, often benefit from increased hunting opportunities and have shown resilience, per se, to fragmentation (Ethier & Fahrig 2011; Rodríguez-San Pedro & Simonetti 2015). Our results also concur with a study on edge effects at the BDFFP which provided evidence that the regenerated secondary forest can support comparable levels of aerial insectivorous bat activity relative to continuous old-growth forest as a result of edge sealing (Yoh et al. 2022). The *Molossus* sonotype consistently showed a significant negative response to vegetation structure across all scales. These open space foragers will find it acoustically and physically challenging to navigate through forested habitat (Voigt & Holderied 2012) and often 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; Kemp et al. 2019). Again, we acknowledge that detectability of the Molossus sonotype may have affected our results.

The Importance of Forest Restoration for Amazonian Aerial Insectivorous Bats

Cattle ranching is the main driver of deforestation in the Amazon (Skidmore et al. 2021), yet farms, akin to the situation at the BDFFP, often become unproductive soon after establishment, resulting in large expanses of abandoned pastureland (Kaimowitz & Angelsen 2008). Restoring forests and recovering degraded pasturelands are key strategies by the Brazilian government to fulfill its ambition to restore 12 million ha of forest by 2030 (Feltran-Barbieri & Féres 2021). Recent studies have estimated that approximately 40% of deforested areas in the Brazilian Amazon show high potential for passive restoration (Vieira et al. 2017) and natural regeneration is also considered the most cost-effective approach to forest restoration (Crouzeilles et al. 2019). The responses of the focal bat species/sonotypes reported here suggest that passive forest restoration can buffer the effects of fragmentation at landscape scale and provide sufficiently suitable habitat to maintain an ensemble of common aerial insectivorous bat species at the BDFFP if enough recovery time is afforded (i.e. at least 30 years). We found evidence of species-specific responses, including higher occupancy patterns for FS in the CF, highlighting there may still be functional trait exclusion based on the recovering habitat structure. We show that many aerial insectivorous bats, those adapted to forage around edge habitat, in open space or with flexible foraging requirements, can successfully exploit habitat features within the regenerating forest landscape. Our results also show limited negative effects of fragmentation across this restored forest at landscape scale. However, while the restored forest may present viable habitat for many of the common species this might not be the case for all species. Our sampling method made it difficult to detect the uncommon species which might be more sensitive to the effects of fragmentation and could require a longer period of time and/or more active restoration approaches to facilitate full recovery. In summary, especially in landscapes with high levels of forest cover such as the BDFFP, passive restoration of degraded pastures, when coupled with the long-term protection of the resulting secondary forest, is an important strategy to maximizing aerial insectivorous bat species richness in human-modified Amazonian landscapes.

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LITERATURE CITED

Appel G, Capaverde UD, De Oliveira LQ, do Amaral Pereira LG, da Cunha Tavares V, López-Baucells A, Magnusson WE, Baccaro FB, Bobrowiec PED (2021*a*) Use of complementary methods to sample bats in the Amazon. Acta Chiropterologica 23:499–511. https://doi.org/10.3161/15081109ACC2021.23.2.017

Appel G, López-Baucells A, Rocha R, Meyer CF, Bobrowiec PED (2021*b*) Habitat disturbance trumps moonlight effects on the activity of tropical insectivorous bats. Animal Conservation 24:1046–1058. https://doi.org/10.1111/acv.12706

Arias-Aguilar A, Hintze F, Aguiar L, Rufray V, Bernard E, Pereira MJR (2018) Who's calling? Acoustic identification of Brazilian bats. Mammal Research 63:231–253. https://doi.org/10.1007/s13364-018-0367-z

Azofeifa Y, Estrada-Villegas S, Mavarez J, Nassar JM (2019) Activity of aerial insectivorous bats in two rice fields in the northwestern llanos of Venezuela. Acta Chiropterologica 21:149–163. https://doi.org/10.3161/15081109ACC2019.21.1.012

Bader E, Jung K, Kalko EK, Page RA, Rodriguez R, Sattler T (2015) Mobility explains the response of aerial insectivorous bats to anthropogenic habitat change in the neotropics. Biological Conservation 186:97–106. https://doi.org/10.1016/j.biocon.2015.02.028

Bélisle M, Desrochers A, Fortin MJ (2001) Influence of forest cover on the movements of forest birds: a homing experiment. Ecology 82:1893–1904. https://doi.org/10.1890/0012-9658(2001)082[1893:IOFCOT]2.0.CO;2

Bierregaard RO Jr, Lovejoy TE, Kapos V, dos Santos AA, Hutchings RW (1992) The biological dynamics of tropical rainforest fragments. Bioscience 1: 859–866. https://doi.org/10.2307/1312085

Carvalho WD, Miguel JD, da Silva XB, Lopez-Baucells A, de Castro IJ, Hilario RR, de Toledo JJ, Rocha R, Palmeirim JM (2023) Complementarity between mist-netting and low-cost acoustic recorders to sample bats in Amazonian rainforests and savannahs. Community Ecology 24:47–60. https://doi.org/10.1007/s42974-022-00131-5

Castillo-Figueroa D (2020) Ecological morphology of neotropical bat wing structures. Zoological Studies 59:e60. https://doi.org/10.6620/ZS.2020.59-60

Ceballos G, Ehrlich PR, Dirzo R (2017) Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. Proceedings of the National Academy of Sciences 114:E6089–E6096. https://doi.org/10.1073/pnas.1704949114

Chazdon RL (2014) Second growth: the promise of tropical Forest regeneration in an age of deforestation. University of Chicago Press, Chicago, Illinois. https://doi.org/10.7208/chicago/9780226118109.001.0001

Colombo GT, Di Ponzio R, Benchimol M, Peres CA, Bobrowiec PED (2023) Functional diversity and trait filtering of insectivorous bats on forest islands created by an Amazonian mega dam. Functional Ecology 37:99–111. https://doi.org/10.1111/1365-2435.14118

Crouzeilles R, Barros FS, Molin PG, Ferreira MS, Junqueira AB, Chazdon RL, Lindenmayer DB, Tymus JR, Strassburg BB, Brancalion PH (2019) A new approach to map landscape variation in forest restoration success in tropical and temperate forest biomes. Journal of Applied Ecology 56: 2675–2686. https://doi.org/10.1111/1365-2664.13501

Crouzeilles R, Ferreira MS, Chazdon RL, Lindenmayer DB, Sansevero JB, Monteiro L, Iribarrem A, Latawiec AE, Strassburg BB (2017) Ecological restoration success is higher for natural regeneration than for active restoration in tropical forests. Science Advances 3:e1701345. https://doi.org/10.1126/sciadv.1701345

De Aquino KK, Baccaro FB, Appel G, Henriques AL, Dineli Bobrowiec PE, Borges SH (2022) Forest fragments, primary and secondary forests harbour similar arthropod assemblages after 40 years of landscape regeneration in the Central Amazon. Agricultural and Forest Entomology 24:178–188. https://doi.org/10.1111/afe.12481

de Oliveira LQ, Marciente R, Magnusson WE, Bobrowiec PE (2015) Activity of the insectivorous bat *Pteronotus parnellii* relative to insect resources and vegetation structure. Journal of Mammalogy 96:1036–1044. https://doi.org/10.1093/jmammal/gyv108

Denzinger A, Tschapka M, Schnitzler HU (2018) The role of echolocation strategies for niche differentiation in bats. Canadian Journal of Zoology 96: 171–181. https://doi.org/10.1139/cjz-2017-0161

Derhé MA, Murphy HT, Preece ND, Lawes MJ, Menéndez R (2018) Recovery of mammal diversity in tropical forests: a functional approach to measuring restoration. Restoration Ecology 26:778–786. https://doi.org/10.1111/rec.12582

Edwards DP, Massam MR, Haugaasen T, Gilroy JJ (2017) Tropical secondary forest regeneration conserves high levels of avian phylogenetic diversity. Biological Conservation 209:432–439. https://doi.org/10.1016/j.biocon.2017.03.006

Estrada-Villegas S, McGill BJ, Kalko EK (2012) Climate, habitat, and species interactions at different scales determine the structure of a neotropical bat community. Ecology 93:1183–1193. https://doi.org/10.1890/11-0275.1

Estrada-Villegas S, Meyer CF, Kalko EK (2010) Effects of tropical forest fragmentation on aerial insectivorous bats in a land-bridge Island system. Biological Conservation 143:597–608. https://doi.org/10.1016/j.biocon.2009.11.009

Ethier K, Fahrig L (2011) Positive effects of forest fragmentation, independent of forest amount, on bat abundance in eastern Ontario, Canada. Landscape Ecology 26:865–876. https://doi.org/10.1007/s10980-011-9614-2

Falcão F, Ugarte-Núñez JA, Faria D, Caselli CB (2015) Unravelling the calls of discrete hunters: acoustic structure of echolocation calls of furipterid bats (Chiroptera, Furipteridae). Bioacoustics 24:175–183. https://doi.org/10.1080/09524622.2015.1017840

FAO (Food and Agriculture Organization of the United Nations) UNEP (UN Environment Programme) (2020) The state of the world's forests 2020. Forests, biodiversity and people. FAO and UNEP, Rome, Italy. https://doi.org/10.4060/ca8642en

Farneda FZ, Grelle CE, Rocha R, Ferreira DF, López-Baucells A, Meyer CF (2020) Predicting biodiversity loss in Island and countryside ecosystems through the lens of taxonomic and functional biogeography. Ecography 43:97–106. https://doi.org/10.1111/ecog.04507

Farneda FZ, Rocha R, Aninta SG, López-Baucells A, Sampaio EM, Palmeirim JM, Meyer CF (2022) Bat phylogenetic responses to regenerating Amazonian forests. Journal of Applied Ecology 59:1986–1996. https://doi.org/10.1111/1365-2664.14041

Farneda FZ, Rocha R, López-Baucells A, Sampaio EM, Palmeirim JM, Bobrowiec PE, Meyer CF (2018) Functional recovery of Amazonian bat assemblages following secondary forest succession. Biological Conservation 218:192–199. https://doi.org/10.1016/j.biocon.2017.12.036

Feltran-Barbieri R, Féres JG (2021) Degraded pastures in Brazil: improving livestock production and forest restoration. Royal Society Open Science 8: 201854. https://doi.org/10.1098/rsos.201854

Ferreira DF, Rocha R, López-Baucells A, Farneda FZ, Carreiras JM, Palmeirim JM, Meyer CF (2017) Season-modulated responses of neotropical bats to forest fragmentation. Ecology and Evolution 7:4059–4071. https://doi.org/10.1002/ece3.3005

ForestPlots net, Blundo C, Carilla J, Grau R, Malizia A, Malizia L, et al. (2021) Taking the pulse of Earth's tropical forests using networks of highly distributed plots. Biological Conservation 260:108849. https://doi.org/10.1016/j.biocon.2020.108849

Garbino GST, Gregorin R, Lima IP, Loureiro L, Moras L, Moratelli R, et al. (2022) Updated checklist of Brazilian bats: version 2020. Brazilian Bat List Committee—CLMB Brazilian Society for the Study of Chiropterans (Sbeq). https://www.sbeq.net/lista-de-especies (accessed 13 Sep 2022)

Gelman A, Rubin DB (1992) Inference from iterative simulation using multiple sequences. Statistical Science 7:457–472. https://doi.org/10.1214/ss/1177011136

Hadfield JD (2010) MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. Journal of Statistical Software 33: 1–22. https://doi.org/10.18637/jss.v033.i02

Hadfield JD (2018) MCMCglmm course notes UK. https://mran.microsoft.com/snapshot/2018-08-24/web/packages/MCMCglmm/vignettes/CourseNotes.pdf (accessed 14 Jul 2021)

Heinrich VH, Vancutsem C, Dalagnol R, Rosan TM, Fawcett D, Silva-Junior CH, et al. (2023) The carbon sink of secondary and degraded humid tropical forests. Nature 615:436–442. https://doi.org/10.1038/s41586-022-05679-w

Hesselbarth MH, Sciaini M, With KA, Wiegand K, Nowosad J (2019) Landscapemetrics: an open-source R tool to calculate landscape metrics. Ecography 42:1648–1657. https://doi.org/10.1111/ecog.04617

Jackson HB, Fahrig L (2015) Are ecologists conducting research at the optimal scale? Global Ecology and Biogeography 24:52–63. https://doi.org/10.1111/geb.12233

Jakobsen L, Kalko EK, Surlykke A (2012) Echolocation beam shape in emballonurid bats, *Saccopteryx bilineata* and *Cormura brevirostris*. Behavioral Ecology and Sociobiology 66:1493–1502. https://doi.org/10.1007/s00265-012-1404-6

Jones G, Jacobs DS, Kunz TH, Willig MR, Racey PA (2009) Carpe noctem: the importance of bats as bioindicators. Endangered Species Research 8:93–115. https://doi.org/10.3354/esr00182

Jung K, Kalko EA, Von Helversen O (2007) Echolocation calls in central American emballonurid bats: signal design and call frequency alternation. Journal of Zoology 272:125–137. https://doi.org/10.1111/j.1469-7998.2006.00250.x

Kaimowitz D, Angelsen A (2008) Will livestock intensification help save Latin America's tropical forests? Journal of Sustainable Forestry 27:6–24. https://doi.org/10.1080/10549810802225168

Kemp J, López-Baucells A, Rocha R, Wangensteen OS, Andriatafika Z, Nair A, Cabeza M (2019) Bats as potential suppressors of multiple agricultural pests: a case study from Madagascar. Agriculture, Ecosystems & Environment 269:88–96. https://doi.org/10.1016/j.agee.2018.09.027

Klingbeil BT, Willig MR (2010) Seasonal differences in population-, ensemble-and community-level responses of bats to landscape structure in Amazonia. Oikos 119:1654–1664. https://doi.org/10.1111/j.1600-0706.2010.18328.x

Kryvokhyzha D, Holm K, Chen J, Cornille A, Glémin S, Wright SI, Lascoux M (2016) The influence of population structure on gene expression and flowering time variation in the ubiquitous weed *Capsella bursa-pastoris* (Brassicaceae). Molecular Ecology 25:1106–1121. https://doi.org/10.1111/mec.13537

Kunz TH, Braun de Torrez E, Bauer D, Lobova T, Fleming TH (2011) Ecosystem services provided by bats. Annals of the New York Academy of Sciences 1223:1–38. https://doi.org/10.1111/j.1749-6632.2011.06004.x

Laso Bayas JC, See L, Georgieva I, Schepaschenko D, Danylo O, Dürauer M, Fritz S (2022) Drivers of tropical forest loss between 2008 and 2019. Scientific Data 9:1–8. https://doi.org/10.1038/s41597-022-01227-3

Laurance WF, Camargo JL, Fearnside PM, Lovejoy TE, Williamson GB, Mesquita RC, Laurance SG (2018) An Amazonian rainforest and its fragments as a laboratory of global change. Biological Reviews 93:223–247. https://doi.org/10.1111/brv.12343

Laurance WF, Camargo JL, Luizão RC, Laurance SG, Pimm SL, Bruna EM, Lovejoy TE (2011) The fate of Amazonian forest fragments: a 32-year investigation. Biological Conservation 144:56–67. https://doi.org/10.1016/j.biocon.2010.09.021

Locatelli B, Catterall CP, Imbach P, Kumar C, Lasco R, Marín-Spiotta E, Mercer B, Powers JS, Schwartz N, Uriarte M (2015) Tropical reforestation and climate change: beyond carbon. Restoration Ecology 23:337–343. https://doi.org/10.1111/rec.12209

López-Baucells A, Rocha R, Bobrowiec PED, Bernard E, Palmeirim JM, Meyer CFJ (2016) Field guide to Amazonian bats. INPA, Manaus, Brazil

López-Baucells A, Rowley S, Rocha R, Bobrowiec PE, Palmeirim JM, Farneda FZ, Meyer CF (2022) Interplay between local and landscape-scale effects on the taxonomic, functional and phylogenetic diversity of aerial insectivorous neotropical bats. Landscape Ecology 37:2861–2875. https://doi.org/10.1007/s10980-022-01493-x

López-Baucells A, Torrent L, Rocha R, Pavan AC, Bobrowiec PED, Meyer CF (2018) Geographical variation in the high-duty cycle echolocation of the cryptic common mustached bat *Pteronotus cf. rubiginosus* (Mormoopidae). Bioacoustics 27:341–357. https://doi.org/10.1080/09524622.2017.1357145

López-Baucells A, Yoh N, Rocha R, Bobrowiec PE, Palmeirim JM, Meyer CF (2021) Optimizing bat bioacoustic surveys in human-modified neotropical landscapes. Ecological Applications 31:e02366. https://doi.org/10.1002/eap.2366

López-Bosch D, Rocha R, López-Baucells A, Wang Y, Si X, Ding P, Gibson L, Palmeirim AF (2022) Passive acoustic monitoring reveals the role of habitat affinity in sensitivity of sub-tropical east Asian bats to fragmentation. Remote Sensing in Ecology and Conservation 8:208–221. https://doi.org/10.1002/rse2.237

Malhi Y, Gardner TA, Goldsmith GR, Silman MR, Zelazowski P (2014) Tropical forests in the Anthropocene. Annual Review of Environment and Resources 39:125–159. https://doi.org/10.1146/annurev-environ-030713-155141

Marques JT, Ramos Pereira MJ, Palmeirim JM (2016) Patterns in the use of rainforest vertical space by neotropical aerial insectivorous bats: all the action is up in the canopy. Ecography 39:476–486. https://doi.org/10.1111/ecog.01453

Martínez-Ferreira SR, Alvarez-Añorve MY, Bravo-Monzón AE, Montiel-González C, Flores-Puerto JI, Morales-Díaz SP, Chiappa-Carrara X, Oyama K, Avila-Cabadilla LD (2020) Taxonomic and functional diversity and composition of bats in a regenerating neotropical dry forest. Diversity 12:332. https://doi.org/10.3390/d12090332

Meramo K, Ovaskainen O, Bernard E, Silva CR, Laine VN, Lilley TM (2022) Contrasting effects of chronic anthropogenic disturbance on activity and species richness of insectivorous bats in neotropical dry forest. Frontiers in Ecology and Evolution 10:822415. https://doi.org/10.3389/fevo.2022.822415

Meyer CF, Kalko EK (2008) Assemblage-level responses of phyllostomid bats to tropical forest fragmentation: land-bridge islands as a model system. Journal of Biogeography 35:1711–1726. https://doi.org/10.1111/j.1365-2699.2008.01916.x

Neeff T, Lucas RM, Santos JRD, Brondizio ES, Freitas CC (2006) Area and age of secondary forests in Brazilian Amazonia 1978–2002: an empirical estimate. Ecosystems 9:609–623. https://doi.org/10.1007/s10021-006-0001-9

Norberg UM, Rayner JM (1987) Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. Philosophical transactions of the Royal Society of London B: Biological Sciences 316:335–427. https://doi.org/10.1098/rstb.1987.0030

Novaes RLM, Souza RDF, Moratelli R (2017) *Myotis riparius* (Chiroptera: Vespertilionidae). Mammalian Species 49:51–56. https://doi.org/10.1093/mspecies/sex011

Numata I, Cochrane MA (2012) Forest fragmentation and its potential implications in the Brazilian Amazon between 2001 and 2010. Open Journal of Forestry 2:265–271. https://doi.org/10.4236/ojf.2012.24033

Núñez SF, López-Baucells A, Rocha R, Farneda FZ, Bobrowiec PE, Palmeirim JM, Meyer CF (2019) Echolocation and stratum preference: key trait correlates of vulnerability of insectivorous bats to tropical forest fragmentation. Frontiers in Ecology and Evolution 7:373. https://doi.org/10.3389/fevo.2019.00373

Rocha R, López-Baucells A, Farneda FZ, Ferreira DF, Silva I, Acácio M, Meyer CF (2020) Second-growth and small forest clearings have little effect on the temporal activity patterns of Amazonian phyllostomid bats. Current Zoology 66:145–153. https://doi.org/10.1093/cz/zoz042

Rocha R, López-Baucells A, Farneda FZ, Groenenberg M, Bobrowiec PE, Cabeza M, Palmeirim JM, Meyer CF (2017) Consequences of a large-scale fragmentation experiment for neotropical bats: disentangling the relative importance of local and landscape-scale effects. Landscape Ecology 32:31–45. https://doi.org/10.1007/s10980-016-0425-3

Rocha R, Ovaskainen O, López-Baucells A, Farneda FZ, Sampaio EM, Bobrowiec PE, Meyer CF (2018) Secondary forest regeneration benefits old-growth specialist bats in a fragmented tropical landscape. Scientific Reports 8:1–9. https://doi.org/10.1038/s41598-018-21999-2

Rodríguez-San Pedro A, Rodríguez-Herbach C, Allendes JL, Chaperon PN, Beltrán CA, Grez AA (2019) Responses of aerial insectivorous bats to landscape composition and heterogeneity in organic vineyards. Agriculture, Ecosystems & Environment 277:74–82. https://doi.org/10.1016/j.agee.2019.03.009

Rodríguez-San Pedro A, Simonetti JA (2015) The relative influence of forest loss and fragmentation on insectivorous bats: does the type of matrix matter? Landscape Ecology 30:1561–1572. https://doi.org/10.1007/s10980-015-0213-5

Rowse EG, Harris S, Jones G (2016) The switch from low-pressure sodium to light emitting diodes does not affect bat activity at street lights. PLoS One 11:e0150884. https://doi.org/10.1371/journal.pone.0150884

Schnitzler HU, Kalko EK (2001) Echolocation by insect-eating bats: we define four distinct functional groups of bats and find differences in signal structure that correlate with the typical echolocation tasks faced by each group. Bioscience 51:557–569. https://doi.org/10.1641/0006-3568(2001)051[0557:EBIEB]2.0.CO;2

Siemers BM, Schnitzler HU (2004) Echolocation signals reflect niche differentiation in five sympatric congeneric bat species. Nature 429:657–661. https://doi.org/10.1038/nature02547

Silveira JGD, Oliveira Neto SND, Canto ACBD, Leite FFGD, Cordeiro FR, Assad LT, et al. (2022) Land use, land cover change and sustainable intensification of agriculture and livestock in the Amazon and the Atlantic Forest in Brazil. Sustainability 14:2563. https://doi.org/10.3390/su14052563

Simmons JA, Brown PE, Vargas-Irwin CE, Simmons AM (2020) Big brown bats are challenged by acoustically-guided flights through a circular tunnel of hoops. Scientific Reports 10:1–10. https://doi.org/10.1038/s41598-020-57632-4

Simmons AM, Ertman A, Hom KN, Simmons JA (2018) Big brown bats (*Eptesicus fuscus*) successfully navigate through clutter after exposure to intense band-limited sound. Scientific Reports 8:13555. https://doi.org/10.1038/s41598-018-31872-x

Skidmore ME, Moffette F, Rausch L, Christie M, Munger J, Gibbs HK (2021) Cattle ranchers and deforestation in the Brazilian Amazon: production, location, and policies. Global Environmental Change 68:102280. https://doi.org/10.1016/j.gloenvcha.2021.102280

Smith CC, Healey JR, Berenguer E, Young PJ, Taylor B, Elias F, Barlow J (2021) Old-growth forest loss and secondary forest recovery across Amazonian countries. Environmental Research Letters 16:085009. https://doi.org/10.1088/1748-9326/ac1701

Surlykke A, Kalko EK (2008) Echolocating bats cry out loud to detect their prey. PLoS One 3:e2036. https://doi.org/10.1371/journal.pone.0002036

Sweeny AR, Albery GF, Venkatesan S, Fenton A, Pedersen AB (2021) Spatiotemporal variation in drivers of parasitism in a wild wood mouse population. Functional Ecology 35:1277–1287. https://doi.org/10.1111/1365-2435.13786

Taubert F, Fischer R, Groeneveld J, Lehmann S, Müller MS, Rödig E, Huth A (2018) Global patterns of tropical forest fragmentation. Nature 554:519–522. https://doi.org/10.1038/nature25508

Trzcinski MK, Fahrig L, Merriam G (1999) Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. Ecological Applications 9:586–593. https://doi.org/10.1890/1051-0761(1999)009[0586:IEOFCA]2.0.CO;2

Vieira I, Ferreira J, Salomão R, Brienza Júnior S, Matsumoto M, Braga J (2017) Potencial de regeneração natural da vegetação na Amazônia. MMA, Brasília, DF, Brazil

Voigt CC, Holderied MW (2012) High manoeuvring costs force narrow-winged molossid bats to forage in open space. Journal of Comparative Physiology B 182:415–424. https://doi.org/10.1007/s00360-011-0627-6

Yoh N, Clarke JA, López-Baucells A, Mas M, Bobrowiec PED, Rocha R, Meyer CFJ (2022) Edge effects and vertical stratification of aerial insectivorous bats across the interface of primary-secondary Amazonian rainforest. PLoS One 17:e0274637. https://doi.org/10.1371/journal.pone.0274637

Zuckerberg B, Cohen JM, Nunes LA, Bernath-Plaisted J, Clare JD, Gilbert NA, et al. (2020) A review of overlapping landscapes: pseudoreplication or a red herring in landscape ecology? Current Landscape Ecology Reports 5:140–148. https://doi.org/10.1007/s40823-020-00059-4

Supporting Information

The following information may be found in the online version of this article:

Figure S1. Map of the study area at the BDFFP, Central Amazon, Brazil.

Figure S2. Ordination biplot of the principal components analysis (PCA).

Figure S3. Three species exhibiting nonsignificant scale-sensitive associations with local vegetation structure and landscape predictor variables.

Figure S4. Guild bat activity modeled with local vegetation structure and landscape predictor variables.

Table S1. Total number of bat passes for the 10 bat species/sonotypes selected for study.

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

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

Table S4. Model output comparing bat species/sonotypes with local vegetation structure and landscape predictor variables.

Table S5. Model output comparing bat guilds with local vegetation structure and landscape predictor variables.

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