RESEARCH ARTICLE

Edge effects and vertical stratification of aerial insectivorous bats across the interface of primary-secondary Amazonian rainforest

Natalie Yoh, James A. Clarke, Adrià López-Baucells, Maria Mas, Paulo E. D. Bobrowiec, Ricardo Rocha, Christoph F. J. Meyer

1 School of Science, Engineering and Environment, University of Salford, Salford, United Kingdom, 2 Durrell Institute of Conservation and Ecology, University of Kent, Canterbury, United Kingdom, 3 Statistical Ecology at Kent, National Centre for Statistical Ecology, School of Mathematics Statistics and Actuarial Science, University of Kent, Canterbury, United Kingdom, 4 Natural Sciences Museum of Granollers, Granollers, Spain, 5 Biological Dynamics of Forest Fragments Project, National Institute for Amazonian Research and Smithsonian Tropical Research Institute, Manaus, Brazil, 6 CIBIO, Centro de Investigación em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Campus de Vairão, Universidade do Porto, Vairão, Portugal, 7 CIBIO, Centro de Investigación em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Instituto Superior de Agronomia, Universidade de Lisboa, Lisboa, Portugal, 8 Department of Biology, University of Oxford, Oxford, United Kingdom

Current address: The Nelson Institute for Environmental Studies, University of Wisconsin-Madison, Madison, Wisconsin, United States of America

C.F.J.Meyer@salford.ac.uk

Abstract

Edge effects, abiotic and biotic changes associated with habitat boundaries, are key drivers of community change in fragmented landscapes. Their influence is heavily modulated by matrix composition. With over half of the world’s tropical forests predicted to become forest edge by the end of the century, it is paramount that conservationists gain a better understanding of how tropical biota is impacted by edge gradients. Bats comprise a large fraction of tropical mammalian fauna and are demonstrably sensitive to habitat modification. Yet, knowledge about how bat assemblages are affected by edge effects remains scarce. Capitalizing on a whole-ecosystem manipulation in the Central Amazon, the aims of this study were to i) assess the consequences of edge effects for twelve aerial insectivorous bat species across the interface of primary and secondary forest, and ii) investigate if the activity levels of these species differed between the understory and canopy and if they were modulated by distance from the edge. Acoustic surveys were conducted along four 2-km transects, each traversing equal parts of primary and ca. 30-year-old secondary forest. Five models were used to assess the changes in the relative activity of forest specialists (three species), flexible forest foragers (three species), and edge foragers (six species). Modelling results revealed limited evidence of edge effects, except for forest specialists in the understory. No significant differences in activity were found between the secondary or primary forest but almost all species exhibited pronounced vertical stratification. Previously defined bat guilds appear to hold here as our study highlights that forest bats are more edge-sensitive than edge foraging bats. The absence of pronounced edge effects and the comparable activity levels between primary and old secondary forests indicates that old secondary forest...
can help ameliorate the consequences of fragmentation on tropical aerial insectivorous bats.

Introduction

Deforestation and fragmentation of tropical forests continue to be major contributors to global biodiversity loss [1]. The Brazilian Amazon currently hosts over 10,000 plant species and is a global hotspot for terrestrial vertebrate diversity [2,3]. Declines in Amazonian deforestation over the last two decades provided some with optimism for Brazil’s commitment to conservation. However, in 2020 the Brazilian Amazon experienced the highest deforestation rates for the last decade [4]. This was largely driven by the dismantling of environmental regulations and enforcement capacity, compounded by political and economic uncertainty left by the wake of the COVID-19 tragedy in Brazil [4–7]. Such deforestation has massive implications for global biodiversity, as well as global carbon emissions [5,8,9].

Deforestation creates a patchwork of isolated forest fragments across modified landscapes. The interface between these artificially created fragments and the matrix (e.g., pasture or agricultural land) is subjected to edge effects [10]. Edge effects, the changes in abiotic conditions and biotic interactions at the boundary between two contrasting habitats, are strong determinants of ecological processes in humanized landscapes [1,11]. As edge conditions exceed the variability typically associated with habitat interiors, environmental deterioration often decreases the habitat suitability for the assemblages it previously supported [8,11–15]. Approximately 70% of remaining global forests are within 1 km of the edge [1] and 85% of 1,673 vertebrate populations are already affected by edge effects [11], with edge area globally increasing from 27% to 37% over the last decade [16]. By 2100, half of tropical forest is predicted to become forest edge [16]. In the Brazilian Amazon, at least 35,000–50,000 km of new edge is created annually [17].

Despite being one of the most well-studied ecological phenomena of the last century [18], edge effects are still not well understood due to their diversity and complexity. Two components of edge influence, edge extent and edge magnitude, can be distinguished. The extent of edge effects is defined as the distance over which changes in natural conditions that are associated with habitat boundaries penetrate habitat interiors, whereas magnitude is the relative strength of an edge effect [19]. Both metrics are highly taxon- and context-specific, and the range of extent/magnitude can be debated. Most edge effects have been documented to occur between 100–300 m from the edge (e.g., changes to canopy height and understory bird densities; [15,19,20]). However, other studies estimate they may extend 1–10 km into forest interiors (e.g., shifts in carnivore abundance; [21–25]). Matrix composition is known to significantly affect both the extent and magnitude of edge effects, with low-contrast matrices (e.g., secondary forest in advanced regeneration) increasing connectivity between remnant forest patches and reducing the gradient of microclimatic change [12,26–28]. Therefore, forest regeneration can lead to ‘edge sealing’ or ‘edge softening’ [26], as the disturbed, secondary forest can provide habitat for primary forest (forest relatively undisturbed by human activities) specialists. Many tropical studies fail to consider source-sink dynamics between populations in primary forest and the matrix [29]. This is the process whereby species can persist in the secondary forest (a “sink” habitat) so long as there is continual immigration from primary forest (a “source” habitat). Without such proximity to the source habitat, populations in the sink habitat would begin to decline [29]. As such, studies comparing species responses across a habitat
boundary should consider the habitats on either side as interactive and not as independent units.

There have been over 405 reforestation projects across the Brazilian Amazon since 1950, and vast areas of abandoned pastureland are now under natural forest regeneration [9]. Between 1986 and 2018, over 260,000 km$^2$ of secondary forest has regenerated in the Brazilian Amazon which equates to almost 60% of the area of old-growth forest which was lost between 1988 and 2019 [4, 30]. Secondary forests are increasingly recognized for improving species’ persistence in tropical human-modified landscapes [31]. As secondary forests mature, they reduce the gradient of structural differences between the matrix and the primary forest [28, 31, 32]. This helps to mitigate the impact of edge effects in primary forest and increase habitat suitability across the landscape [32, 33]. Whilst secondary forests are no substitute for old-growth forests, they typically support around 57% of the diversity of primary forests [31], even after only 14–19 years of regeneration [34]. For indicator species, such as dung beetles and birds, there is evidence to suggest secondary forests can support the equivalent diversity of primary forests within 15 to 30 years, respectively [35]. As secondary regrowth continues to mature, it has been shown to support more forest specialist species, including bats [32, 35–38].

The Amazon supports over 200 bat species that perform important ecological roles in tropical forests, such as pollination, seed dispersal and insect suppression [39, 40]. Few studies to date have investigated how tropical bats respond to edge effects and existing studies have focused predominantly on phyllostomids, the ecologically most diverse Neotropical bat family, as these species can be reliably sampled using mist nets [e.g., 12, 22, 41]. These studies suggest bats may be affected by edge effects up to 3 km from the habitat boundary [22], with most studies indicating species richness declines at the forest edge, whereas the abundance of several dominant generalist species increases [13, 42]. Aerial insectivores, which represent a large fraction of Amazonian bat diversity [43], have so far been overlooked. There have also been limited studies investigating how fragmentation and edge effects may affect bats differently between forest strata [but see 43–45]. It is widely accepted that there are differences in both bat diversity and abundances between the canopy and understory in the Amazon [46, 47]. However, due to sampling logistics, it is often difficult to incorporate canopy sampling into mist-netting surveys. Alternatively, acoustic monitoring enables us to include aerial insectivores in such studies and provides an effective method for cross-strata comparisons, thereby providing a more comprehensive understanding of how the wider bat community may be impacted by edge effects.

Working within an experimentally fragmented landscape with low fragment-matrix contrast, the overarching goal of this study was to assess edge influence, both in terms of extent and magnitude, on Amazonian aerial insectivorous bats. Specifically, we evaluated how bat activity varied along a habitat gradient of increasing distance from the habitat boundary in both secondary and primary forest. We assessed how this response in activity varied along this gradient between the understory and canopy. These comparisons were conducted for common species/sonotypes and three functional guilds. We hypothesized that forest specialist activity would exhibit a negative edge effect response in both habitats, whereas we expected to see a positive or null response for flexible forest foragers and edge foragers. Furthermore, we anticipated that responses to edge effects differ between the understory and canopy, with a greater extent and magnitude being observed in the canopy.

Materials and methods

This research was conducted under ICMBio (Instituto Chico Mendes de Conservação da Biodiversidade) permit (26877–3).
Study sites

Our study was conducted in the Central Brazilian Amazon, 80 km north of Manaus, at the Biological Dynamics of Forest Fragments Project (BDFFP; 20°26′S, 59°04′40″W; Fig 1). The BDFFP is the world’s most comprehensive, long-term experimental study into the effects of habitat fragmentation across a broad range of taxa [12]. The primary forest is classified as terra firme forest, with an average tree diversity of 280 species per hectare [48]. In the early 1980s, a series of primary forest fragments (1, 10, and 100 ha) were experimentally isolated within cattle ranches, separated 80–650 m from continuous forest. However, forest regeneration quickly occurred after the ranches were abandoned 5–10 years later due to economic unviability [49,50]. Regrowth forest was dominated by *Vismia* spp., in areas that were cleared and burned, or *Cecropia* spp., in areas that were cleared without fire [51]. The understory is dominated by palms [50] and is characterized by an average canopy height of 23 m [50]. The secondary forest at the time of the study was classified as ‘old secondary forest’ using the age classes proposed by Powell et al. [38] (27–31 years old with a mean canopy height ≥ 19 m). A small strip has been periodically cleared to ensure fragment isolation, most recently between late 2013 and early 2014 [52]. Average annual rainfall ranges between 2.3–2.5 m, with large interannual variation (1.9–3.5 m). The wet season occurs between November and June (monthly rainfall > 250 mm) and the dry season occurs between July and October (monthly rainfall < 100 mm). The average temperature is between 26–30°C and the study area is characterized by low-lying topography (80–160 m elevation [32,53]).

Acoustic sampling

Two static detectors (SM2Bat+, Wildlife Acoustics) with omnidirectional microphones (SMX-US Ultrasonic Microphone) were placed in the understory and canopy of 164 sample points. These sample points were spaced 50 m apart along four 2-km transects. Transects were located across two spatially independent sites to reduce site bias (Fig 1). Each transect extended through 1 km of secondary forest and then continued 1 km into the neighboring primary forest. Surveys were conducted in the dry season of 2013 and the wet season of 2014 to minimize seasonal bias, equating to eight transect visits in total. As bats are known to favour established flyways for commuting [54], each transect was established specifically for this study.

As Amazonian bats are known to exhibit vertical stratification [45,55], we recorded bats separately using two detectors simultaneously, with one detector in the understory and one in the canopy. For this study, the understory was defined as extending from the ground to a height of approximately 10 m and the canopy was defined as approximately 30 m from ground level. To ensure the understory and canopy samples could be considered independent, plastic dividers were attached to the detectors to create discrete directional microphones (Fig 1C; [56]). Additionally, sample points were manually rotated so that actively recording detectors were always 250 m apart. Each active detector was programmed to record for 12 hours (18:00–06:00) for three consecutive nights, amounting to 11,808 recording hours. Detectors recorded at 384 kHz sampling rate in full spectrum with 16-bit resolution. The high pass filter was set at 12 kHz (fs/32), with a trigger level of 18SNR. Recordings were split into five-second fragments with at least two distinguishable pulses to define a bat pass which was used as the surrogate measure of bat activity [57].

Call classification to species/sonotype

We used a combination of manual and automatic methods to classify calls to species or sonotype (a group of species with similar calls). We tested which species could be reliably classified using automated methods by first manually processing a subset of calls (all calls recorded in
the understory) and then comparing the results against those generated using the classifier for Amazonian bats developed by López-Baucells et al. [58]. To improve the performance of the classifier, we included additional reference calls into the classifier training dataset (S1 Table) following the methodology of López-Baucells et al. [58]. We compared the difference between manual identification (45,554 bat passes) and automatic identification (41,702 bat passes) of the understory data using non-paired Wilcoxon Signed-Rank tests to confirm the reliability of the automatic classifications. Overall, the automatic classifier generated comparable results to calls identified manually (W = 123,260, p = 0.87). However, to increase consistency and robustness for the edge-effect analysis, we only included the calls for those 12 species where there was no difference between manual identification and automatic identification. See supporting information for full classifier performance results.

Statistical analysis

The 12 species we selected were assigned to guild depending on their ecological requirements and family [59,60]. Species/sonotypes that were considered forest specialists included *Eptesicus brasiliensis*, *Furipterus horrens*, and *Myotis riparius*. *Pteronotus* spp. also typically inhabit forest areas. However, in our study, we have defined them as ‘flexible forest’ species as they are known to commonly exploit other habitats, such as forest edges, as well as hunt in highly cluttered spaces [61,62]. The final guild consisted of six ‘edge’ species/sonotypes which typically forage along forest edges or in forest gaps. This included *Cormura brevirostris*, *Centronycteris maximiliani/centralis*, *Peropteryx kappleri*, *P. macrotis*, *Saccopteryx bilineata*, and *S. leptura*. By grouping species, we were able to assess guild-level responses to edge effects. Continuous response functions, as described in Ewers and Didham [19], were used to identify edge effects across the primary and secondary forest interface (Fig 2).
Fig 2. Visual representation of the five models proposed by Ewers & Didham [19] to delineate species’ theoretical responses to edge effects. (a) For the null, linear, and power models it is not possible to calculate extent or magnitude as there is either no response present or the response exceeds the sampling area; (b) in the sigmoid model, species exhibit a negative response to edge effects and asymptotes are reached in each habitat; and (c) in the unimodal model, species demonstrate a preference for edge habitat. Note, we have illustrated here a hypothetical preference for secondary forest using the linear and...
The five models can be used to describe mean bat activity per guild, $\eta$, at a certain distance (D) from the edge, and these models are as follows:

1. **Null model**

   $$\eta_D = \bar{\eta} + \epsilon$$  \hspace{1cm} (1)

   With $\epsilon$ denoting the error term and $\bar{\eta}$ mean bat activity across all distances from the edge. This model describes a scenario in which no discernible edge effect can be detected using the data (i.e., generalist activity).

2. **Linear model**

   $$\eta_D = \beta_0 + \beta_1 D + \epsilon$$  \hspace{1cm} (2)

   This model describes a simple linear gradient in mean bat activity for a particular guild across the edge. $\beta_0$ and $\beta_1$ denote constants and D the distance from the habitat edge.

3. **Power model**

   $$\eta_D = \beta_0 e^{\beta_1 D} + \epsilon$$  \hspace{1cm} (3)

   This model describes a scenario in which there is an asymptote on one side of the edge.

4. **Sigmoid model**

   $$\eta_D = \beta_0 \frac{\beta_1 - \beta_0}{1 + e^{(\beta_2 - \beta_3)D}} + \epsilon$$  \hspace{1cm} (4)

   This model describes a scenario in which there is an asymptote on each side of the edge, with $\beta_2$ and $\beta_3$ as constants. This represents groups in which there is a discrete change in activity from one habitat to the next.

5. **Unimodal model**

   $$\eta_D = \beta_0 \frac{\beta_1 - \beta_0}{1 + e^{(\beta_2 - \beta_3)D}} + \epsilon$$  \hspace{1cm} (5)

   This model describes a situation similar to the sigmoid model, but with a clear peak in the response at the edge (i.e., groups with a preference for habitat edges). This is described through the inclusion of the constant $\beta_4$.

The canopy and understory data for each guild were analysed separately as we expected that the model of best fit would depend on forest stratum. Average activity was log-transformed to ensure normality assumptions were met. Non-linear models were fit using the “nlsLM” function from the R package “minpack.lm” [63]. Once each model was fitted, we compared them using the second-order Akaike Information Criterion (AICc) to determine the model of best fit whilst correcting for small sample sizes [64]. An advantage of using these models is the ability to calculate the magnitude and extent of the edge effects for Eqs 4 and 5, if they were the best-fit models. Full model parameters are available in S2 Table.
We then applied generalized linear mixed effect models (GLMMs) with negative binomial distributions to determine if bat activity varied with distance from the edge or between strata. Only non-correlated variables were included in the models to avoid collinearity ($r < 0.5$). Activity data was not log-transformed in the GLMMs [65]. The final fixed covariates were Strata (“understory” vs. “canopy,” categorical with two levels), ForestType (categorical with three levels) and Distance (continuous). We included Transsect as a random intercept, to incorporate the dependency among observations of the same transects, as well as Season, to account for any seasonal variation in activity. All covariates were centred and standardized before analysis [66]. We fit the models using the package “glmmADMB” [67] (S3 Table). The top three models were determined based on their AICc values. We then undertook likelihood ratio tests to determine which covariates from these models were statistically significant (S4 Table). The best-fit model included all covariates identified as statistically significant from the likelihood ratio tests. This analysis was repeated for each guild and species/sonotype.

Results
In total 252,912 bat passes were automatically identified to 12 aerial insectivorous species or sonotypes. This included species from four families: two Vespertilionidae species/sonotypes, six Emballonuridae species/sonotypes, three Mormoopidae species and one species of Furipteridae (Table 1). Three species/sonotypes were not included in the edge effect analysis. This includes Emballonuridae spp. (n = 8,205) and Pteronotus personatus (n = 459), which had insufficient bat passes manually identified in the understory to test for agreement between the manual and automatic identification methods, and Molossidae spp. (n = 9,236) as we found the automatic classification for this sonotype was significantly different from manual identification, suggesting incorrect classifications (S1 Table). Finally, three bat passes were manually identified as Thyroptera tricolor in the understory but this species is not specified in the automatic classifier and therefore was excluded.

The null model provided the model of best fit for forest specialists in the canopy which indicates that there was no edge effect on mean activity in this stratum (Table 2). The linear and power models provided the best fit for forest specialists in the understory. There was little variation between the linear and power model fit (Fig 3). Despite considerable variation in the data, both models showed that activity increased from the interior in primary forest towards the edge and into the secondary forest, whereby activity peaked in secondary forest farthest from the forest edge, therefore indicating a preference for secondary forest (Fig 3).

For both flexible forest foragers and edge foragers, we found the null model provided the best fit for both the canopy and understory. This indicates there is no evidence that edge effects were affecting either of these guilds (Table 2). In contrast to our hypothesis, the unimodal models provided the poorest fit for edge foragers. No calculations were possible for edge extent or magnitude as no guild demonstrated a relevant edge effect response (e.g., sigmoid or unimodal), and it is not recommended to infer magnitude or extent from the power model [19].

Distance from the edge did not explain edge forager activity or forest specialist activity based on GLMMs (Table 3, S3 and S4 Tables). However, compared to the habitat boundary, flexible forest forager activity was significantly higher with increasing distance from the edge (Table 3). There was no difference in response between primary and secondary forest and the forest edge for any guild (Table 3). We also observed no significant differences in bat activity between the primary and secondary forest or edge for any species/sonotype (Table 3). Only one species demonstrated a significant response to distance from the edge, Peropteryx macrotis, which had greater activity closer to the edge.
We found that stratum was an important predictor for the activity of each guild (Table 3, S3 and S4 Tables). Activity was highest in the canopy for edge foragers and forest specialists, but highest in the understory for flexible forest foragers. We observed that ten of the twelve species were significantly more active in the canopy than the understory (Table 3; Fig 4). Only one species, *Pteronotus cf. rubiginosus*, showed a significant preference for the understory.

**Table 1. Total number of bat passes per species/sonotype in both the understory and canopy of secondary forest, forest edge, and primary forest.**

|                     | Understory | Canopy | Total |
|---------------------|------------|--------|-------|
|                     | Secondary  | Edge   | Primary | Secondary | Edge   | Primary |       |
| Forest specialists  |            |        |        |            |        |        |       |
| *Eptesicus brasiliensis* | 99        | 2      | 29     | 589       | 21     | 945     | 1,685 |
| *Furipterus horrens* | 25        | 0      | 10     | 27        | 1      | 13      | 76    |
| *Myotis riparius*   | 489       | 16     | 148    | 2,629     | 105    | 1,390   | 4,777 |
| Flexible forest foragers |        |        |        |            |        |        |       |
| *Pteronotus gymnonotus* | 164      | 5      | 72     | 336       | 17     | 143     | 737   |
| *Pteronotus alitonus*   | 5,573     | 278    | 4,444  | 5,579     | 159    | 4,020   | 20,053|
| *Pteronotus cf. rubiginosus* | 5,773 | 136    | 2,660  | 1,699     | 37     | 959     | 11,264|
| Edge foragers        |            |        |        |            |        |        |       |
| *Cormura brevirostris* | 188       | 4      | 259    | 1,781     | 50     | 3,317   | 5,599 |
| *Centronycteris maximiliani/centrals* | 10,838 | 7      | 4,370  | 51,742    | 4,352  | 50,651  | 121,960|
| *Peropteryx kappleri*      | 82        | 1      | 22     | 3,196     | 151    | 3,717   | 7,169 |
| *Peropteryx macrotis*     | 337       | 3      | 195    | 6,923     | 1,174  | 5,238   | 13,870|
| *Saccopteryx bilineata*   | 604       | 4      | 2,416  | 6,089     | 836    | 30,319  | 40,268|
| *Saccopteryx leptura*     | 271       | 0      | 651    | 7,231     | 957    | 16,344  | 25,454|
| Excluded from analysis  |            |        |        |            |        |        |       |
| *Emballonuridae spp.*    | 177       | 10     | 182    | 2,629     | 982    | 4,225   | 8,205 |
| *Molossidae spp.*        | 438       | 44     | 733    | 5,195     | 159    | 2,667   | 9,236 |
| *Pteronotus personatus*  | 46        | 0      | 17     | 222       | 5      | 169     | 459   |
| *Rhynchonycteris naso*   | 0         | 0      | 0      | 8         | 0      | 2       | 10    |
| Total                  | 25,104    | 510    | 16,208 | 95,875    | 9,006  | 124,119 | 270,822|

These values represent bat passes as determined by the automatic classifier. Data for *Thyroptera tricolor* not given as this species was only identified manually and is not included in the classifier.

We found that stratum was an important predictor for the activity of each guild (Table 3, S3 and S4 Tables). Activity was highest in the canopy for edge foragers and forest specialists, but highest in the understory for flexible forest foragers. We observed that ten of the twelve species were significantly more active in the canopy than the understory (Table 3; Fig 4). Only one species, *Pteronotus cf. rubiginosus*, showed a significant preference for the understory.

**Discussion**

An expanding body of literature supports the conservation benefits to bats, and multiple other taxonomic groups, associated with the regeneration of secondary forests in fragmented tropical landscapes [32,36,37,68]. By providing evidence of edge sealing, our study supports this by showing that old secondary forest adjacent to primary forest can support comparable activity to primary forest for 12 aerial insectivorous bat species/sonotypes. However, we still found evidence of the impact of edge effects for both forest specialists and flexible forest foragers at the guild level, although results between different statistical approaches were conflicting.
Table 2. Comparison of model fit using Ewers and Didham’s (2006) edge effect models.

| Guild                     | Habitat | Model  | AICc  |
|---------------------------|---------|--------|-------|
| Forest specialists        | Canopy  | Null   | 116.357 |
|                           |         | Linear | 118.245 |
|                           |         | Power  | 118.258 |
|                           |         | Sigmoid| 121.775 |
|                           |         | Unimodal| 125.423 |
|                           | Understory| Null | 91.427 |
|                           |         | Linear | 89.507 |
|                           |         | Power  | 89.722 |
|                           |         | Sigmoid| 90.100 |
|                           |         | Unimodal| 98.100 |
| Flexible forest foragers  | Canopy  | Null   | 114.132 |
|                           |         | Linear | 116.003 |
|                           |         | Power  | 115.974 |
|                           |         | Sigmoid| 116.072 |
|                           |         | Unimodal| 119.413 |
|                           | Understory| Null | 127.412 |
|                           |         | Linear | 129.054 |
|                           |         | Power  | 129.066 |
|                           |         | Sigmoid| 131.469 |
|                           |         | Unimodal| 137.224 |
| Edge foragers             | Canopy  | Null   | 148.845 |
|                           |         | Linear | 149.609 |
|                           |         | Power  | 149.654 |
|                           |         | Sigmoid| 155.166 |
|                           |         | Unimodal| 157.421 |
|                           | Understory| Null | 162.503 |
|                           |         | Linear | 164.652 |
|                           |         | Power  | 164.655 |
|                           |         | Sigmoid| 169.718 |
|                           |         | Unimodal| 171.593 |

Results are provided for each of the three guilds in both the understory and canopy. **Bold** — model(s) of best fit.

https://doi.org/10.1371/journal.pone.0274637.t002

**Guild and species-specific responses**

We did not find evidence of edge effects for both flexible forest foragers and edge foragers, as well as forest specialists in the canopy, using Ewers and Didham’s [19] models. As suggested by Powell et al. [38], the old secondary forest at the BDFFP might have reached the point of recovery where edge effects can no longer be detected for most species/sonotypes. This would
be consistent with findings for other taxonomic groups (e.g., dung beetles; [33,36]), suggesting that old secondary forest provides valuable habitat for common aerial insectivores. In contrast, forest specialist activity demonstrated a response to edge effects using Ewers and Didhams’ [19] models, suggesting the secondary forest was not yet sufficiently mature to prevent edge effects penetrating the primary forest. However, different statistical approaches demonstrated conflicting results. Using the GLMM approach, we did find evidence that flexible forest forager activity increased with increasing distance from the edge, whereas no response was detected for forest specialists. Therefore, it is possible these models do not capture the full breadth of response. As such, we advise multiple approaches are used when assessing edge effects.

Whilst old secondary forests at the BDFFP may support several common aerial insectivorous bat species, López-Baucells [61] demonstrated that a complete assemblage-level recovery was not observed after 15 years of forest regrowth. However, recovery rates can vary between bat species and guilds. Even after ~30 years, phyllostomid assemblages in secondary forest may not fully resemble the assemblages within primary forest [32,68]. Trophic level, dispersal ability, and habitat specialization all affect a species’ sensitivity to edge effects [69,70]. Species which are highly dependent on primary forest interiors are more likely to be edge sensitive, to
Table 3. Summary of the best-fit generalized linear mixed effect models for each bat guild and species/sonoty.

| Species/sonoty                  | Estimate | SE      | z      | p-value  |
|---------------------------------|----------|---------|--------|----------|
| **Forest specialists**          |          |         |        |          |
| Intercept                       | 3.595    | 0.446   | 8.05   | $8.1 	imes 10^{-16}$ *** |
| Understory                      | -1.609   | 0.144   | -11.17 | $< 2 	imes 10^{-16}$ *** |
| Primary forest                  | 0.530    | 0.426   | 1.24   | 0.210    |
| Secondary forest                | -0.036   | 0.427   | -0.08  | 0.930    |
| **Flexible forest foragers**    |          |         |        |          |
| Intercept                       | 4.287    | 0.464   | 9.24   | $< 2 	imes 10^{-16}$ *** |
| Understory                      | 0.449    | 0.140   | 3.26   | 0.001 ** |
| Primary forest                  | 0.170    | 0.416   | 0.41   | 0.683    |
| Secondary forest                | -0.193   | 0.426   | -0.45  | 0.650    |
| Distance                        | $1.23 	imes 10^{-03}$ | $2.66 	imes 10^{-04}$ | 1.97 | 0.048 * |
| **Edge foragers**               |          |         |        |          |
| Intercept                       | 6.504    | 0.607   | 10.72  | $< 2 	imes 10^{-16}$ *** |
| Understory                      | -2.177   | 0.181   | -12.06 | $< 2 	imes 10^{-16}$ *** |
| Primary forest                  | 0.552    | 0.525   | 1.05   | 0.294    |
| Secondary forest                | 0.896    | 0.538   | 1.66   | 0.096    |
| **Eptesicus brasiilenis**       |          |         |        |          |
| Intercept                       | 2.797    | 0.102   | 27.43  | $< 2 	imes 10^{-16}$ *** |
| Understory                      | -1.350   | 0.202   | -6.67  | $2.6 	imes 10^{-11}$ *** |
| **Furipeterus horrens**         |          |         |        |          |
| Intercept                       | 1.183    | 0.208   | 5.69   | $2 	imes 10^{-08}$ |
| **Myotis riparius**             |          |         |        |          |
| Intercept                       | 3.393    | 0.473   | 7.18   | $1 	imes 10^{-13}$ *** |
| Understory                      | -1.397   | 0.162   | -8.64  | $< 2 	imes 10^{-16}$ *** |
| Primary forest                  | 0.469    | 0.454   | 1.03   | 0.300    |
| Secondary forest                | -0.182   | 0.457   | -0.40  | 0.690    |
| **Pteronotus gymmonotus**       |          |         |        |          |
| Intercept                       | 1.670    | 0.327   | 5.11   | $3 	imes 10^{-07}$ *** |
| Understory                      | -0.321   | 0.127   | -2.53  | 0.011 *  |
| Primary forest                  | 0.390    | 0.331   | 1.18   | 0.239    |
| Secondary forest                | -0.034   | 0.336   | -0.10  | 0.919    |
| **Pteronotus alitonus**         |          |         |        |          |
| Intercept                       | 4.340    | 0.303   | 14.30  | $< 2 	imes 10^{-16}$ *** |
| **Pteronotus cf. rubiginosus**   |          |         |        |          |
| Intercept                       | 3.456    | 0.327   | 10.56  | $< 2 	imes 10^{-16}$ *** |
| Understory                      | 0.821    | 0.182   | 4.51   | $6.5 	imes 10^{-06}$ *** |
| **Cormura brevirostris**        |          |         |        |          |
| Intercept                       | 3.641    | 0.294   | 12.37  | $< 2 	imes 10^{-16}$ *** |
| Understory                      | -1.548   | 0.164   | -9.41  | $< 2 	imes 10^{-16}$ *** |
| **Centronycteris maximiliani/ centrals** |          |         |        |          |
| Intercept                       | 6.558    | 0.408   | 16.08  | $< 2 	imes 10^{-16}$ *** |
| Understory                      | -1.743   | 0.214   | -8.15  | $3.7 	imes 10^{-16}$ *** |
| **Peropteryx kappleri**         |          |         |        |          |
| Intercept                       | 4.112    | 0.150   | 27.40  | $< 2 	imes 10^{-16}$ *** |
| Understory                      | -2.632   | 0.257   | -10.20 | $< 2 	imes 10^{-16}$ *** |
| **Peropteryx macrotis**         |          |         |        |          |
| Intercept                       | 4.967    | 0.334   | 14.85  | $< 2 	imes 10^{-16}$ *** |

(Continued)
be affected over a larger extent, as well as at greater magnitudes \[8,24\]. Forest specialist bats typically have low wing loading which gives them the maneuverability to navigate dense forest clutter \[71\]. Other traits related to their echolocation call design, also facilitate navigating and locating prey in clutter and are poorly suited for more open spaces \[71,72\]. Compounded, these traits limit their dispersal ability. Fast-flying, more mobile species are less affected by fragmentation as they are more capable of exploiting landscape mosaics \[13,61,73\]. Whilst we did not observe a significant difference in activity between secondary and primary forest based on the GLMMs, there was evidence forest specialists were to some degree influenced by edge effects in the understory using Ewers and Didhams’ \[19\] models. However, contrary to our expectations, they exhibited higher activity in the secondary forest. This response may be driven by increased prey availability \[74\], however we were not able to test this. Increased food availability can lead to an increased abundance of generalist phyllostomids up to 3 km from the forest edge \[22\]. As the linear model provided the model of best fit for forest specialists in the understory, our results indicate these species may also be impacted by edge effects beyond 2 km.

It is important to note that only four transects in two locations were sampled in this study. Therefore, there may be location-specific factors which have influenced the patterns we observed and the results may not necessarily generalize across the Amazon. Old-growth, continuous forest acts as a source for many species across the BDFFP landscape. Elsewhere in the Amazon, many remaining forest fragments are isolated within a matrix of pasture. As the wider, landscape-scale effects of fragmentation are known to strongly influence edge effects and disrupt source-sink dynamics \[11,75\], it is likely the magnitude of edge effects in these fragments will be exacerbated. Similarly, whether secondary forest neighbours primary forest is an important determinant of bat abundance and diversity \[28\]. Many resources may not be available in secondary forest until it matures, e.g., mature/dead trees for roosting. However, more mobile species such as flexible forest foragers and edge foragers may move between habitats to exploit the resources available in each \[29\]. This could explain why we observe high activity in the secondary forest and would contradict previous findings that suggest that the intermediate disturbance hypothesis does not apply to neotropical bats \[28\]. Finally, we stress that our study should only be used to draw conclusions about the responses of common species and not to infer how more specialist species are impacted. Nevertheless, our results align

| Table 3. (Continued) |
|----------------------|
|                      |
| **Estimate** | **SE** | **z** | **p-value** |
| Understory  | -2.107 | 0.194 | -10.88 | <2e-16 |
| **Distance** | -0.001 | 3.25e-05 | -4.19 | 2.8e-05 |

**Saccopteryx bilineata**

|                      |
|----------------------|
| **Intercept** | 5.154 | 0.618 | 8.34 | <2e-16 |
| Understory  | -1.858 | 0.204 | -9.11 | <2e-16 |
| Primary forest | -0.452 | 0.586 | 0.77 | 0.440 |
| Secondary forest | 0.928 | 0.598 | 1.55 | 0.120 |

**Saccopteryx leptura**

|                      |
|----------------------|
| **Intercept** | 5.884 | 0.647 | 9.10 | <2e-16 |
| Understory  | -2.577 | 0.177 | -14.59 | <2e-16 |
| Primary forest | -1.034 | 0.648 | -1.59 | 0.110 |
| Secondary forest | -0.294 | 0.648 | -0.45 | 0.650 |

See S3 and S4 Tables for complete models.

https://doi.org/10.1371/journal.pone.0274637.t003
with previous studies highlighting that forest species are more edge-sensitive than generalist species [8,24]. As such, primary forest is of irreplaceable value, not only for edge-sensitive phyllostomid bats but also for aerial insectivorous bats [61,76].

**Vertical stratification**

Our results support previous findings that tropical bat activity differs between strata, with most species showing a strong preference for the canopy [47,55,77,78]. However, we found different stratum preferences than those previously reported. *Myotis riparius* has previously been shown to prefer the understory in Costa Rica [77] and in French Guiana, where *C. maximiliani* also demonstrated a preference for the same stratum [78]. Both were significantly more active in the canopy in our study. *Centronycteris maximiliani* is known to vary its activity in the understory and canopy across the night, with peak canopy activity in the middle of the night [78]. However, this does not account for the differences demonstrated in our study as recordings were collected across the whole night. Both species are relatively small, slow fliers with
short call durations (< 6ms) [46,79] which suggests they are well suited to foraging in understory vegetation. Similarly, there has previously been a lack of vertical stratification reported for Saccopteryx bilineata and S. leptura [46,78]. Forest structure is not the only consideration affecting a species’ spatial distribution. Fluctuations in prey availability and moon illumination influence how bats utilize different strata [77,78,80]. Gomes et al. [78] demonstrated how species modulate their stratification preferences across the night to forage opportunistically. However, the scale of the differences we observed in our study (e.g., a seven-fold increase in C. maximiliani activity between the understory and canopy) suggests a strong affiliation with the canopy. Unlike understory specialists, species that forage in the canopy are considered less vulnerable to the effects of fragmentation, including edge effects [69]. Almost all of the species assessed in this study showed a preference for the canopy. Therefore, our study should not be used to infer how interior, understory specialists will be affected by edge effects.

Whilst we did not detect many direct changes in bat activity in response to edges, the deviation we observed from typical stratum use may reflect the potential for more subtle effects on bat populations. Habitat disturbance, including edge effects, can affect a species’ behaviour, physiology, and other fitness parameters [8,11,81,82]. At least two Amazonian phyllostomids change their habitat preferences to utilize more strata in forest fragments than in continuous forest when locating prey [45]. If edge effects are increasing understory clutter or altering prey distributions, this may have knock-on effects on where bats can forage. This may partially explain why we observe lower understory activity than expected for forest specialists. However, more research is needed to test this hypothesis. Habitat deterioration can also reduce the richness of prey in insectivorous bat diets in disturbed habitats and the long-term impacts of this are not yet fully understood [81,82]. Similarly, Estrada-Villegas et al. [73] showed fragmentation increased the activity of aerial insectivorous forest bats and altered their assemblage composition. This is also reflected in the responses of other taxonomic groups, including birds, plants, and invertebrates [1]. Therefore, we cannot rule out the presence of edge effects by measuring activity alone. Nevertheless, our study does demonstrate that if edge effects are present, common bat species have been able to adapt their behaviour to cope with them at their current magnitude. More specialist species are less adaptable and therefore are more vulnerable to potential edge effects.

Considerations for study design

One limitation of the statistical approach employed here is that the models by Ewers and Didham [19] assume a unidirectional response to edge effects in each habitat [19,24]. This does not necessarily account for the interaction between habitats at the border. As previously discussed, individuals may leave the primary forest to exploit resources in the secondary forest within a certain distance from the edge [29,33,83]. This may create an inflated decrease of activity in the immediate area adjacent to the edge in the primary forest (Fig 5). Habitat complementation, the use of different habitats across a landscape, is the key process thought to underpin the distribution of mobile species in heterogeneous landscapes, including bats [83]. Further studies should consider incorporating a model (e.g., a spline regression model) which could test for bidirectional responses to edge effects, e.g., where activity increases in the first 200 m from the edge but then decreases for 400 m before stabilizing to natural activity levels (Fig 5; hypothetical values). Whilst it would not be possible to calculate magnitude and extent from this type of model, it would help to test for source-sink dynamics (see [29]).

For management purposes, future research could also examine the impact that different land clearing approaches have on later regeneration. This study was predominantly restricted to Vismia-dominated regrowth, therefore further studies could also investigate whether
comparable patterns are observed with a matrix dominated by *Cecropia* regrowth. This would enable land-owners to clear the forest in a manner (with or without the use of fire) that would minimize its effects on bat assemblages (see [69]). Additionally, we recommend future studies extend the transect length and repeat across more replicates. This will help identify the extent of edge effects for forest specialists, as well as eliminate the risk that extent is not being detected for other guilds due to sampling design. Increased replication may also facilitate species-specific analyses using Ewers and Didham’s [19] models which were not possible in this study due to small sample sizes.

Only one species classified as an edge forager demonstrated a preference for the forest edge in our study. This may be because our “edge” did not represent a hard edge between forest and non-forest. Therefore, our findings support Jantzen & Fenton [84] which suggests this type of labelling oversimplifies the relationship between species and edge effects and does not capture variation in species responses due to different types of edge. As matrix contrast plays a pivotal role in determining the impact of edge effects [12,26–28], future research would also benefit from comparing the responses we observed in a low-contrast matrix to those detected in high-contrast matrix landscapes, e.g., in soy plantations, without first classifying species into guilds.

**Conclusions**

Investigating how we can buffer the impacts of edge effects will be increasingly important to protect species in human-modified tropical landscapes. Our results demonstrate that maintaining secondary forest in an advanced regeneration state (> 30 years) adjacent to primary forest can help support common aerial insectivorous bats at the landscape level. However, it also highlights that edge effect responses can be guild- and species-specific and that their increased specialization means forest specialists are more susceptible to edge effects, even in a mosaic of primary and ca. 30-year-old secondary forests. Consequently, primary forest remains irreplaceable for supporting the whole bat assemblage. We advocate that future
studies also consider how vertical stratification and source-sink dynamics may affect species responses to edge effects. Whilst secondary forest in isolation may not be able to support the same bat diversity and abundance as primary forest, we argue it can reduce extinction pressure from edge effects at the landscape level and mitigate habitat degradation in the remaining primary forest. Therefore, the long-term protection of secondary forests would greatly benefit the conservation of neotropical bats in human-modified landscapes.

Supporting information

S1 Table. The training data for the classifier and the comparison between manual classification and automatic classification. The Wilcoxon test was used to compare the difference between the number of bat passes (≥ 2 pulses) automatically identified by the classifier to at least 60% confidence (Auto ID) compared to manual identification (Manual ID) in the understory. “–” represents insufficient files for statistical comparison. Training data represents the total number of individual pulses available to train the classifier, see López-Baucells et al. [58] for full methodology.

S2 Table. Model parameter estimates after fitting Ewers and Didham’s [19] edge effect models. Each model below represents the best-fit model(s) per guild and stratum as determined using the second-order Akaike Information Criterion (AICc). These include the raw estimates on the logarithmic scale as well as the back-transformed estimates (true bat passes). Mean number of bat passes in stratum (η or β0). Change in bat passes with distance from the edge (β1). Confidence intervals (CI) for the transformed scale were calculated using the delta method.

S3 Table. Generalized linear mixed-effect model equations. Generalized linear mixed-effect model (GLMMs) equations used to model bat activity (n) as a function of the distance from the forest edge (Distance), forest type (ForestType) and stratum (Strata) for each of the three bat guilds and per species. The models are ordered based on their AICc. Bold—top three models per guild.

S4 Table. Results of likelihood ratio tests comparing the top generalized linear mixed-effect models for each guild and species/sonotype (see S3 Table).

Acknowledgments

We are grateful to the many students, volunteers and field assistants that helped us during fieldwork and José L.C. Camargo, Rosely Hipólito and Ary Jorge Ferreira for logistic support. We would also like to thank Dylan Gomes, Amanda Adams, and an anonymous reviewer for their constructive feedback and contributions in improving our manuscript.

Author Contributions

Conceptualization: Adrià López-Baucells, Paulo E. D. Bobrowiec, Ricardo Rocha, Christoph F. J. Meyer.

Data curation: Adrià López-Baucells, Maria Mas.

Formal analysis: Natalie Yoh, James A. Clarke, Adrià López-Baucells, Maria Mas.
Methodology: Natalie Yoh, Adrià López-Baucells, Maria Mas.

Supervision: Christoph F. J. Meyer.

Visualization: Natalie Yoh.

Writing – original draft: Natalie Yoh.

Writing – review & editing: Natalie Yoh, James A. Clarke, Adrià López-Baucells, Maria Mas, Paulo E. D. Bobrowiec, Ricardo Rocha, Christoph F. J. Meyer.

References

1. Haddad NM, Brudvig LA, Clobert J, Davies KF, Gonzalez A, Holt RD, et al. Habitat fragmentation and its lasting impact on Earth’s ecosystems. Science Advances. 2015; 1(2):e1500052. https://doi.org/10.1126/sciadv.1500052 PMID: 26601154

2. Hubbell SP, He F, Condit R, Borda-de-Água L, Kellner J, Steege HT. How many tree species are there in the Amazon and how many of them will go extinct? PNAS. 2008; 105(1):11498–504.

3. Jenkins CN, Pimm SL, Joppa LN. Global patterns of terrestrial vertebrate diversity and conservation. PNAS. 2013; 110(28):e2602–10. https://doi.org/10.1073/pnas.1302251110 PMID: 23803854

4. Silva Junior CHL, Pessôa ACM, Carvalho NS, Reis JBC, Anderson LO, Aragão LEOC. The Brazilian Amazon deforestation rate in 2020 is the greatest of the decade. Nature Ecology & Evolution. 2021; 5(2):144–5.

5. Barni PE, Fearnside PM. Graça PML de A. Simulating Deforestation and Carbon Loss in Amazonia: Impacts in Brazil’s Roraima State from Reconstructing Highway BR-319 (Manaus-Porto Velho). Environmental Management. 2015; 55(2):259–78. https://doi.org/10.1007/s00267-014-0408-6 PMID: 25472831

6. Malta M, Vettore MV, da Silva CMFP, Silva AB, StratTHE 2021; 31(5):1221–9.

7. Pfeiffer M, Lefebvre V, Peres C, Banks-Leite C, Wearn O, Marsh C, et al. Creation of forest edges has a global impact on forest vertebrates. Nature. 2017; 551(7679):187–91. https://doi.org/10.1038/nature24457 PMID: 29088701

8. da Cruz DC, Benayas JMR, Ferreira GC, Santos SR, Schwartz G. An overview of forest loss and restoration in the Brazilian Amazon. New Forests. 2021; 52(1):1–16.

9. Laurance WF, Camargo JLC, Fearnside PM, Lovejoy TE, Williamson GB, Mesquita RCG, et al. An Amazonian rainforest and its fragments as a laboratory of global change: Amazonian fragments and global change. Biol Rev. 2018; 93(1):23–47.

10. Laurance WF, Nascimento HEM, Laurance SG, Andrade A, Ewers RM, Harms KE, et al. Habitat Fragmentation, Variable Edge Effects, and the Landscape-Divergence Hypothesis. PLOS One. 2007; 2(10):e1017. https://doi.org/10.1371/journal.pone.0001017 PMID: 17925865

11. Laurance WF, Lovejoy TE, Vasconcelos HL, Bruna EM, Didham RK, Stouffer PC, et al. Ecosystem Decay of Amazonian Forest Fragments: a 22-Year Investigation. Conservation Biology. 2002; 16(3):605–18.

12. Rocha R, López-Baucells A, Famedal FZ, Groeneveld M, Bobrowiec PED, Cabeza M, et al. Consequences of a large-scale fragmentation experiment for Neotropical bats: disentangling the relative importance of local and landscape-scale effects. Landscape Ecology. 2017; 32(1):31–45.

13. Harrison MLK, Banks-Leite C. Edge effects on trophic cascades in tropical rainforests. Conservation Biology. 2019; 34(4):777–87.

14. Oliveira MA, Grillo AS, Tabarelli M. Forest edge in the Brazilian Atlantic forest: drastic changes in tree species assemblages. Oryx. 2004; 38(4):389–94.

15. Fischer R, Taubert F, Müller MS, Groeneveld J, Lehmann S, Wiegand T, et al. Accelerated forest fragmentation leads to critical increase in tropical forest edge area. Science Advances. 2021; 7(37):eabg7012. https://doi.org/10.1126/sciadv.abg7012 PMID: 34516875

16. Broadbent EN, Asner GP, Keller M, Knapp DE, Oliveira PJC, Silva JN. Forest fragmentation and edge effects from deforestation and selective logging in the Brazilian Amazon. Biological Conservation. 2008; 141(7):1745–57.
18. Ries L, Murphy SM, Wimp GM, Fletcher RJ. Closing Persistent Gaps in Knowledge About Edge Ecology. Current Landscape Ecology Reports. 2017; 2(1):30–41.
19. Ewers RM, Didham RK. Continuous response functions for quantifying the strength of edge effects. Journal of Applied Ecology. 2006; 43(3):527–36.
20. Nascimento HEM, Laurance WF. Biomass Dynamics in Amazonian Forest Fragments. Ecological Applications. 2004; 14(4):127–38.
21. Curran LM, Caniago I, Paoli GD, Astianti D, Kusneti M, Leighton M, et al. Impact of El Nino and logging on canopy tree recruitment in Borneo. Science. 1999; 286(5447):2184–8. https://doi.org/10.1126/science.286.5447.2184 PMID: 10591655
22. Delaval M, Charles-Dominique P. Edge effects on Frugivorous and Nectarivorous Bat Communities in a Neotropical Primary Forest in French Guiana. Revue d’écologie (Terre Vie). 2006; 61(4):342–52.
23. Laurance WF. Do edge effects occur over large spatial scales? Trends in Ecology & Evolution. 2000; 15(4):134–5. https://doi.org/10.1016/S0169-5347(00)01838-3 PMID: 10717681
24. Ewers RM, Didham RK. Confounding factors in the detection of species responses to habitat fragmentation. Biological Reviews. 2006; 81(1):117–42. https://doi.org/10.1017/S1464793105006949 PMID: 16318651
25. Zurita G, Pe’er G, Bellocq M, Hansbauer MM. Edge effects and their influence on habitat suitability calculations: a continuous approach applied to birds of the Atlantic forest: Edge effects and habitat suitability. Journal of Applied Ecology. 2012; 49(2):503–12.
26. Harper KA, Macdonald SE, Burton PJ, Chen J, Brosolofske KD, Saunders SC, et al. Edge Influence on Forest Structure and Composition in Fragmented Landscapes. Conservation Biology. 2005; 19(3):768–82.
27. Brändel SD, Hiller T, Halczok TK, Kerth G, Page RA, Tschapka M. Consequences of fragmentation for Neotropical bats: The importance of the matrix. Biological Conservation. 2020; 252:108792.
28. Vlieut I, Levy-Tacher SI, Galindo-González J, de Boer WF, Ramírez-Marial N. Tropical rain-forest matrix quality affects bat assemblage structure in secondary forest patches. Journal of Mammalogy. 2012; 93(6):1469–79.
29. Gilroy JJ, Edwards DP. Source-Sink Dynamics: a Neglected Problem for Landscape-Scale Biodiversity Conservation in the Tropics. Current Landscape Ecology Reports. 2017; 2(1):51–60.
30. PRODES—Coordenação-Geral de Observação da Terra. Available from: http://www.obt.inpe.br/OBT/assuntos/programas/amazonia/prodes.
31. Chazdon RL, Peres CA, Dent D, Sheil D, Lugo AE, Lamb D, et al. The Potential for Species Conservation in Tropical Secondary Forests. Conservation Biology. 2009; 23(6):1406–17. https://doi.org/10.1111/j.1523-1739.2009.01338.x PMID: 20078641
32. Rocha R, Ovaskainen O, López-Baucells A, Farneda FZ, Sampaio EM, Bobrowiec PED, et al. Secondary forest regeneration benefits old-growth specialist bats in a fragmented tropical landscape. Scientific Reports. 2018; 8(1):3819. https://doi.org/10.1038/s41598-018-21999-2 PMID: 29491428
33. Baun KA, Haynes KJ, Dillenmuth FP, Cronin JT. The Matrix Enhances the Effectiveness of Corridors and Stepping Stones. Ecology. 2004; 85(10):2671–6.
34. Barlow J, Gardner TA, Louzada J, Peres CA. Measuring the Conservation Value of Tropical Primary Forests: The Effect of Occasional Species on Estimates of Biodiversity Uniqueness. PLOS ONE. 2010; 5(3):e9609. https://doi.org/10.1371/journal.pone.0009609 PMID: 20231897
35. Edwards FA, Massam MR, Cosset CCP, Cannon PG, Haugaasen T, Gilroy JJ, et al. Sparing land for secondary forest regeneration protects more tropical biodiversity than land sharing in cattle farming landscapes. Current Biology. 2021; 31(6):1284–1293.e4. https://doi.org/10.1016/j.cub.2020.12.030 PMID: 33482111
36. Stouffer PC, Strong C, Naka LN. Twenty years of understory bird extinctions from Amazonian rain forest fragments: consistent trends and landscape-mediated dynamics. Diversity and Distributions. 2009; 15(1):86–97.
37. Quintero I, Roslin T. Rapid Recovery of Dung Beetle Communities Following Habitat Fragmentation in Central Amazonia. Ecology. 2005; 86(12):3303–11.
38. Powell LL, Zurita G, Wolfe JD, Johnson EI, Stouffer PC. Changes in Habitat Use at Rain Forest Edges Through Succession: a Case Study of Understory Birds in the Brazilian Amazon. Biotropica. 2015; 47(6):723–32.
39. López-Baucells A, Rocha R, Bobrowiec P, Bernard E, Palmeirim J, Meyer C. Field Guide to Amazonian Bats. 1st ed. 2016.
40. Kunz TH, Braun de Torrez E, Bauer D, Lobova T, Fleming TH. Ecosystem services provided by bats. Annals of the New York Academy of Sciences. 2011; 1223(1):1–38. https://doi.org/10.1111/j.1749-6632.2011.06004.x PMID: 21449963

41. Meyer CFJ, Stru ebig MJ, Willig MR. Responses of tropical bats to habitat fragmentation, logging, and deforestation. In: Bats in the Anthropocene: Conservation of bats in a changing world. Springer; 2016. p. 63–103. Available from: https://link.springer.com/chapter/10.1007/978-3-319-25220-9_4.

42. Meyer CFJ, Kalko EKV. Assemblage-level responses of phyllostomid bats to tropical forest fragmentation: land-bridge islands as a model system. Journal of Biogeography. 2008; 35(9):1711–26.

43. López-Baucells A, Yoh N, Rocha R, Bobrowiec PED, Palmeirim JM, Meyer CFJ. Optimizing bat bioacoustic surveys in human-modified Neotropical landscapes. Ecological Applications. 2021; 31(6): e02366. https://doi.org/10.1002/eap.2366 PMID: 33938592

44. Rojas D, Vale A, Ferrero V, Navarro L. When did plants become important to leaf-nosed bats? Diversification of feeding habits in the family Phyllostomidae. Molecular Ecology. 2011; 20(10), 2217–2228. https://doi.org/10.1111/j.1365-294X.2011.05082.x PMID: 21481051

45. Silva I, Rocha R, López-Baucells A, Farneda FZ, Meyer CFJ. Effects of Forest Fragmentation on the Vertical Stratification of Neotropical Bats. Diversity. 2020; 12(2):67.

46. Bernard E. Vertical stratification of bat communities in primary forests of Central Amazon, Brazil. Journal of Tropical Ecology. 2001; 17(1):115–26.

47. Silva RC, Silveira M, Verde RS. Vertical stratification of phyllostomid bats assemblage (Chiroptera, Phyllostomidae) in a forest fragment in Brazilian Southwestern Amazon. Neotropical Biology and Conservation. 2020; 15(2):107–20.

48. de Oliveira AA, Mori SA. A central Amazonian terra firme forest. I. High tree species richness on poor soils. Biodiversity and Conservation. 1999; 8(9):1219–44.

49. Bierregaard RO, Lovejoy TE, Kapos V, Augusto dos Santos A, Hutchings RW. The Biological Dynamics of Tropical Rainforest Fragments. 1992; 42(11):859–66.

50. Gascon C, Lovejoy TE, Bierregaard RO Jr., Malcolm JR, Stouffer PC, Vasconcelos HL, et al. Matrix habitat and species richness in tropical forest remnants. Biological Conservation. 1999; 91(2–3)223–9.

51. Mesquita RCG, Ickes K, Granade G, Williamson GB. Alternative successional pathways in the Amazon Basin. Journal of Ecology. 2001; 89(4):528–37.

52. Rocha R, López-Baucells A, Farneda FZ, Ferreira DF, Silva I, Acácio M, et al. Second-growth and small forest clearings have little effect on the temporal activity patterns of Amazonian phyllostomid bats. Current Zoology. 2019; 66(2):145–153. https://doi.org/10.1093/cz/zoz042 PMID: 32440274

53. Ferreira DF, Rocha R, López-Baucells A, Farneda FZ, Carreiras JMB, Palmeirim JM, et al. Season-modulated responses of Neotropical bats to forest fragmentation. Ecology and Evolution. 2017; 7(11). https://doi.org/10.1002/ece3.3005 PMID: 28616200

54. Palmeirim J, Etheridge K. The influence of man-made trails on foraging by tropical frugivorous bats. Biotropica. 1985; 17:82–3.

55. Pereira MJR, Marques JT, Palmeirim JM. Vertical stratification of bat assemblages in flooded and unflooded Amazonian forests. Current Zoology. 2010; 56(4):469–78.

56. Celis-Murillo A, Deppe JL, Allen MF. Using soundscape recordings to estimate bird species abundance, richness, and composition. Journal of Field Ornithology. 2009; 80(1):64–78.

57. Torrent L, López-Baucells A, Rocha R, Bobrowiec PED, Meyer CFJ. The importance of lakes for bat conservation in Amazonian rainforests: an assessment using autonomous recorders. Remote Sensing in Ecology and Conservation. 2018; 4:339–51.

58. López-Baucells A, Torrent L, Rocha R, Bobrowiec PED, Palmeirim JM, Meyer CFJ. Stronger together: Combining automated classifiers with manual post-validation optimizes the workload vs reliability trade-off of species identification in bat acoustic surveys. Ecological Informatics. 2019; 49:45–53.

59. Schnitzler HU, Kalko EKV. 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. 2001; 51(7):557–69.

60. Schnitzler HU, Kalko EKV. How echolocating bats search and find food. In: Kunz TH, Racey PA, editors. Bat Biology and Conservation. Washington, DC: Smithsonian Institution Press; 1998. p. 183–96.

61. López-Baucells A. Assessment of the effects of forest fragmentation on aerial insectivorous bats in the Amazonian rainforest. PhD Thesis, University of Lisbon. 2019. Available from: https://repositorio.ul.pt/handle/10451/42288.

62. de Oliveira LQ, Marciento R, Magnusson WE, Bobrowiec PED. Activity of the insectivorous bat Pteronotus parnellii relative to insect resources and vegetation structure. Journal of Mammalogy. 2015; 96(5):1036–44.
63. Elzhov TV, Mullen KM, Spiess AN, Bolker B. minpack.lm: R Interface to the Levenberg-Marquardt Nonlinear Least-Squares Algorithm Found in MINPACK, Plus Support for Bounds. 2019. Available from: https://rdrd.io/cran/minpack.lm/.
64. Burnham KP, Anderson DR. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. 2nd ed. New York: Springer-Verlag; 2002. Available from: https://www.springer.com/gp/book/9780387953649.
65. Ives AR. For testing the significance of regression coefficients, go ahead and log-transform count data. Methods in Ecology and Evolution. 2015; 6(7):828–35.
66. Gelman A. Scaling regression inputs by dividing by two standard deviations. Statistics in Medicine. 2008; 27(15):2865–73. https://doi.org/10.1002/sim.3107 PMID: 17960576
67. Skaug H, Fournier D, Nielsen A, Magnusson A, Bolker B. glmmADMB: generalized linear mixed models using AD Model Builder. Vol. 5, R package version 0.6. 2010. r143 p.
68. Farneda FZ, Rocha R, López-Baucells A, Sampaio EM, Palmeirim JM, et al. Bat phylogenetic responses to regenerating Amazonian forests. Journal of Applied Ecology. 2022; 59(8):1986–96.
69. Núñez SF, López-Baucells A, Rocha R, Farneda FZ, Bobrowiec PED, Palmeirim JM, et al. Echolocation and Stratum Preference: Key Trait Correlates of Vulnerability of Insectivorous Bats to Tropical Forest Fragmentation. Frontiers in Ecology and Evolution. 2019; 7:373.
70. Farneda FZ, Rocha R, López-Baucells A, Groenenberg M, Silva I, Palmeirim JM, et al. Trait-related responses to habitat fragmentation in Amazonian bats. Journal of Applied Ecology. 2015; 52(5):1381–91.
71. Norberg UM, Rayner JMV, Lighthill MJ. 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. 1987; 316(1179):335–427.
72. Denzinger A, Schnitzler HU. Bat guilds, a concept to classify the highly diverse foraging and echolocation behaviors of microchiropteran bats. Frontiers in Physiology. 2013; 4:164. https://doi.org/10.3389/fphys.2013.00164 PMID: 23840190
73. Estrada-Villegas S, Meyer CFJ, Kalko EKV. Effects of tropical forest fragmentation on aerial insectivorous bats in a land-bridge island system. Biological Conservation. 2010; 143(3):597–608.
74. Hawes J, Motta C da S, Overal WL, Barlow J, Gardner TA, Peres CA. Diversity and composition of Amazonian moths in primary, secondary and plantation forests. Journal of Tropical Ecology. 2009; 25 (3):281–300.
75. Lloyd P, Martin TE, Redmond RL, Langner U, Hart MM. Linking demographic effects of habitat fragmentation across landscapes to continental source-sink dynamics. Ecological Applications. 2005; 15 (5):1504–14.
76. Gibson L, Lee TM, Koh LP, Brook BW, Gardner TA, Barlow J, et al. Primary forests are irreplaceable for sustaining tropical biodiversity. Nature. 2011; 478(7369):378–81. https://doi.org/10.1038/nature10425 PMID: 21918513
77. Marques JT, Pereira MJR, Palmeirim JM. Patterns in the use of rainforest vertical space by Neotropical aerial insectivorous bats: all the action is up in the canopy. Ecography. 2015; 38(5):476–86.
78. Gomes DGE, Appel G, Barber JR. Time of night and moonlight structure vertical space use by insectivorous bats in a Neotropical rainforest: an acoustic monitoring study. PeerJ. 2020; 8:e10591. https://doi.org/10.7717/peerj.10591 PMID: 33384906
79. Bernard E, Hintze F, Barbier E. Emballonuridae Gervais, 1855 (Chiroptera) of Reserva Biológica de Saltinho (Atlantic Forest), in Brazil, revealed by echolocation. Check List. 2016; 12(4):1–9.
80. Appel G, López-Baucells A, Magnusson WE, Bobrowiec PED. Aerial insectivorous bat activity in relation to moonlight intensity. Mammalian Biology. 2017; 85:37–46.
81. Hemprich-Bennett DR, Kemp VA, Blackman J, Struebig MJ, Lewis OT, Rossiter SJ, et al. Altered structure of bat-prey interaction networks in logged tropical forests revealed by metabarcoding. Molecular Ecology. 2021; 30(22):5844–57. https://doi.org/10.1111/mec.16153 PMID: 34437745
82. Alpizar P, Risely A, Tschapka M, Sommer S. Agricultural Fast Food: Bats Feeding in Banana Monocultures Are Heavier but Have Less Diverse Gut Microbiota. Frontiers in Ecology and Evolution. 2021; 9:608.
83. Dunning JB, Danielson BJ,Pulliam HR. Ecological Processes That Affect Populations in Complex Landscapes. Oikos. 1992; 65(1):169–75.
84. Jantzen MK, Fenton MB. The depth of edge influence among insectivorous bats at forest–field interfaces. Can J Zool. 2013; 91(5):287–92.