

## **A17753S1 PROJECT DISSERTATION**

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<b>Title</b>	Examining the trait-based response of aerial-insectivorous bats to land-use change for cattle farming in the Brazilian Amazon
<b>Word Count</b>	6977

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## Abstract

Bats provide essential ecosystem services and act as indicators of biodiversity and ecosystem health. However, they are increasingly threatened by the conversion of natural habitats to agriculture, particularly in the Neotropics. In this study, I used bioacoustic and trait data to investigate the relationship between bat functional traits and sensitivity to land-use change in aerial insectivorous bats (AIBs) across forest and cattle-farmed sites in Mato Grosso, Brazil. RLQ and fourth-corner analyses found significant associations between sonotype traits, activity, and environmental variables, suggesting functional traits have a significant role in determining AIB sensitivity to land-use change. Wing morphology, call structure, and foraging strata emerged as key traits determining vulnerability to land-use change, whereby understory and canopy bats with low relative wing loading and aspect ratio, and calls associated with foraging in cluttered environments were associated with forest cover. In contrast, bats with high relative wing loading and aspect ratio that forage above the forest canopy were associated with pastoral, fragmented landscapes. These findings suggest AIBs are differentially affected by land-use change depending on their functional traits, with clutter-space foragers and the ecosystem services they provide most at risk. As well as maintaining forest cover, conservation efforts should reduce fragmentation to safeguard the functional diversity and ecosystem services of AIB communities in agricultural landscapes.

## Introduction

Demands of human requirements are increasingly coming at a substantial cost to the environment. With exponential increases in global population and per-capita food consumption, natural landscapes are being replaced by agriculture at an unforeseen rate to keep pace (Laurance et al., 2014). By 2021, the area of agriculture was greater than any other land type at 4.8 billion hectares (ha), constituting one-third of the world's land area (FAO, 2023). The Neotropics are on the forefront of agricultural expansion, with Brazil having experienced one of the highest rates of deforestation globally (Zarin et al., 2016). As of 2022, around 26% of the Amazon had been deforested or highly degraded (Quintanilla et al., 2022). Livestock farming, particularly of cattle, is one of the leading drivers of deforestation in the Amazon, accounting for ~60% of total forest loss (Lapola et al., 2023; Alexandre-Benavent et al., 2018).

Such widescale destruction in the Amazon rainforest is particularly devastating as it is one of the planet's most valuable natural resources. It acts as a vital carbon sink, regulates climate, and provides food and medicinal resources among many other ecosystem services (Strand et al., 2018; Heinrich et al., 2021). Perhaps most significantly, it is one of the planet's most important areas for biodiversity, containing almost 10% of the world's species (WWF, 2022).

In the tropics, human-modified landscapes are becoming increasingly fragmented, resulting in smaller and more isolated patches of primary habitat being embedded within a matrix of altered land (Haddad et al., 2015). Forest fragmentation is one of the key drivers of biodiversity loss, as it reduces suitable habitat area and increases isolation of remaining habitat patches (Gonçalves-Souza et al., 2025). Increased isolation limits species dispersal and their subsequent ability to colonise habitat fragments, and when combined with reduced habitat area, leads to a decline in available resources and ecological niches within the remaining patches (Moir et al., 2021).

Whilst the impacts of land-use change on taxonomic diversity have been relatively well-studied (e.g. Püttker et al., 2020), its effects on functional diversity have received less attention (Cardinale et al., 2012). Functional diversity refers to the variety of roles that different species perform within an ecosystem (García-Morales et al., 2016). It is measured using functional traits, defined as the 'phenotypic, observable, or operational characteristics that affect species performance' (Violle et al., 2014). Studying functional traits therefore provides insights into species' ecological roles (Suárez-Castro et al., 2020). It also helps to assess the overall health of an ecosystem: if certain traits are less likely to persist in an environment, the services they provide are also likely to decline (Moir et al., 2021; Mouillot et al., 2013). Ecosystem stability and service provisioning are therefore fundamentally reliant on functional diversity (Cardinale

et al., 2012; Suárez-Castro et al., 2020). Using only measures of taxonomic diversity is thus likely to underestimate the effects of habitat change on whole ecosystems (Mouillot et al., 2013; Nock et al., 2016). Another benefit to studying functional diversity is the insight it gives into which traits make species liable to persist or decline in modified landscapes (Wolf et al., 2021). A trait-based approach can therefore help to direct conservation efforts towards the species and ecosystem processes identified as most sensitive to habitat modification (Miatta et al., 2021; Wolf et al., 2021).

Bats are an incredibly important and diverse taxon, comprising one-fifth of all mammal species and demonstrating a wide range of morphologies, echolocation characteristics, foraging styles, diets, and habitats (Frank et al., 2017). They are key members of their ecosystems, performing vital services such as pollination, insect control, and seed dispersal (Kunz et al., 2011). To exemplify their importance, the estimated economic value of bats to North American agriculture is \$23 billion (Boyles et al., 2011). Due to their high diversity, importance for many ecological services, and sensitivity to land-use changes, they are also a useful indicator group to understand the effects of pressures on biodiversity (Farneda et al., 2024; Rowley et al., 2024; Jones et al., 2009). Unfortunately, agricultural expansion has severely impacted bat conservation: of the ~1400 bat species worldwide, 15% are threatened with extinction according to the IUCN (Frick et al., 2020). Also of concern, the proportion of bat species reported as Data Deficient on the IUCN Red List (18%) is significantly higher than that of other mammals (13%) or birds (1%) (Frick et al., 2020), highlighting the disparity of research between bats and other, more charismatic mammals.

There is a growing body of research examining the effects of land-use changes on bat communities, particularly in the Neotropics where bat diversity is greatest (Kinap et al., 2024; Otálora-Ardila et al., 2024; Colombo et al., 2023), but also from Asia (Wordley et al., 2017), Africa (Moir et al., 2021; Hending et al., 2023) and Australia (Hanspach et al., 2012; Threlfall et al., 2011). These studies have highlighted the importance of incorporating functional diversity when assessing biodiversity responses to habitat loss and fragmentation. However, the effects of land-use change in livestock-dominated landscapes remain uncertain, despite livestock production being a major driver of Neotropical deforestation, and the uncertainty surrounding how biodiversity interacts with such production systems (Alvarado et al., 2018). Furthermore, most Neotropical studies have focussed on just one family of bats, the Phyllostomidae. The Phyllostomidae are a highly diverse family of primarily frugivorous and gleaning insectivorous bats. They are relatively easy to capture and study using mist-netting techniques (Yoh et al., 2020), and thus have been the primary focus of bat research. Aerial insectivorous bats (AIBs) constitute almost half of all 160 described bat species in Brazil (Garbino et al., 2022), and play a fundamental role in controlling insect pests (Boyles et al.,

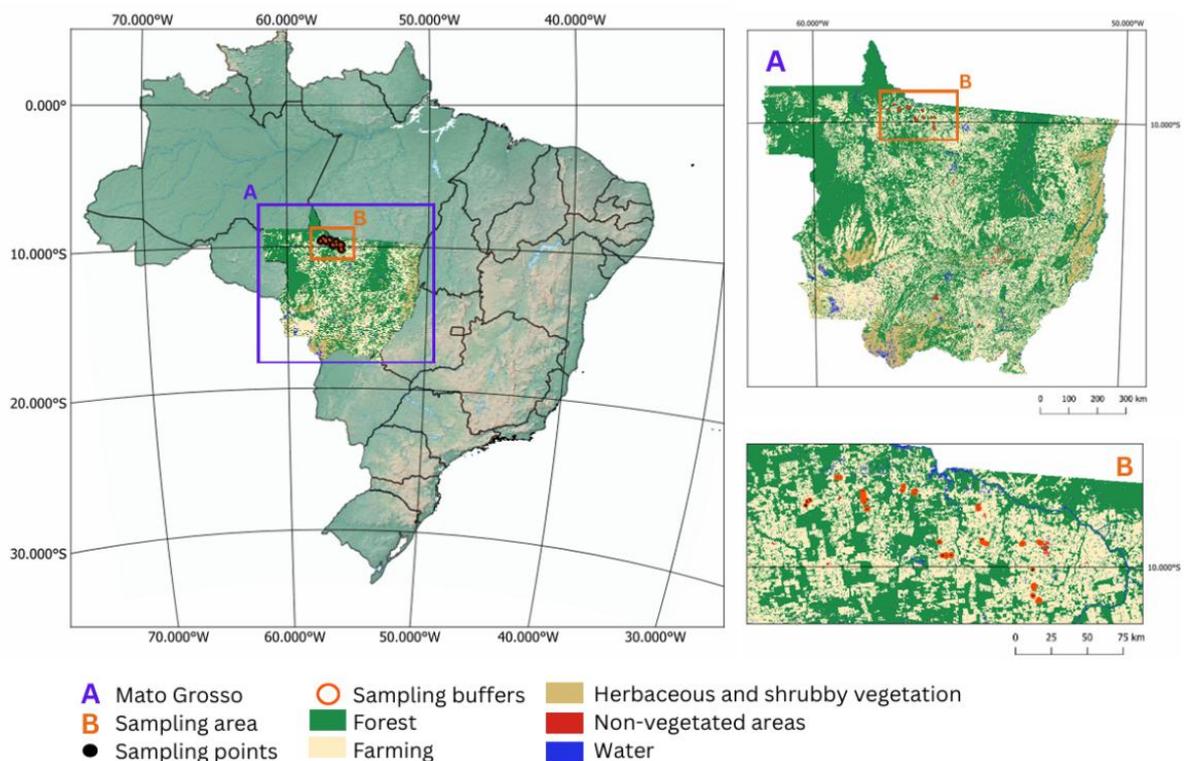
2013). However, they typically avoid mist-nets due to their advanced echolocation abilities, and are therefore under-represented in the literature (Carvalho et al., 2023). Fortunately, with the recent advance of autonomous bioacoustics detectors, studying AIBs has become significantly easier (López-Bosch et al., 2022). Bioacoustic methods use autonomous detectors to survey bats based on their echolocation calls. This is a non-invasive, cost-effective strategy which complements mist-netting by covering not only species that were previously more difficult to study, but environments too (e.g. the canopy, or across large spatial scales; López-Baucells et al., 2022).

Here, I use bioacoustic data to compare the taxonomic and functional alpha ( $\alpha$ ) diversity of AIBs in forest and pasture sites, and evaluate the relationship between AIB distribution, functional traits, and environmental variables in the study region of Mato Grosso, Brazil. Specifically, this study explores: (i) how  $\alpha$ -diversity differs between forest and pasture sites, (ii) which functional traits best predict sensitivity to land-use change in cattle-dominated landscapes, (iii) which environmental variables are likely to be the most important for maintaining functional traits, and (iv) which AIBs are most vulnerable to land-use change based on the traits identified in (ii). As the sampling region's native vegetation is Amazonian rainforest, I hypothesise that forest habitats will have higher taxonomic and functional  $\alpha$ -diversity than modified, pasture habitats (Kuschnig et al., 2021; Kinap et al., 2024). Previous studies have consistently highlighted the importance of traits related to mobility, i.e. the distance species are able to travel, in determining disturbance sensitivity in bats (Núñez et al., 2019; Colombo et al., 2023; Díaz-B et al., 2023). I therefore hypothesise that wing morphology, a key trait influencing mobility, will strongly influence sensitivity to land-use change: highly mobile species will be better adapted to the open, fragmented agricultural landscapes. Additionally, prior research has emphasised the role of native vegetation cover in conserving vulnerable species within altered landscapes (Otálora-Ardila et al., 2024; García-Morales et al., 2016). Accordingly, I hypothesise that environmental variables related to forest cover will be the most important to maintain functional diversity across the study area.

# Methods

## Study Area

Data collection was conducted from May to December 2023 in Mato Grosso, Brazil's third largest state (over 90 million ha), located in the country's midwest (7.23°–17.87° S, 50.57°–61.52° W) (Simoes et al., 2020). It has a mean annual temperature of 26°C and mean rainfall of 111 mm a month (ranging from 248 mm in February to 0 mm in July). Mato Grosso is the only Brazilian state to hold significant portions of three biomes: Amazon (480 000 km<sup>2</sup>), Cerrado (360 000 km<sup>2</sup>), and Pantanal (60 000 km<sup>2</sup>) (Spera et al., 2014). Data were collected in the north of Mato Grosso, in the Amazon biome (Figure 1).



**Figure 1:** Map of Brazil, showing A) the state of Mato Grosso, where sampling was conducted, and B) a close-up of the region in which the 20 farms were sampled. Land cover was imported from MapBiomass Brazil for the year 2023.

Mato Grosso is one of Brazil's most heavily farmed states, holding the largest cattle herd in the country (Spera et al., 2014). Rapid expansion of agricultural areas in the early 2000s, most significantly for soy and cattle farming, resulted in Mato Grosso becoming a deforestation hotspot (Zalles et al., 2019). As a result of such rapid land-use changes, the region is of high research interest (Kuschnig et al., 2021). The Brazilian Forest Code (Law 12651/2012) legally requires landowners to maintain 20-80% of their property under native vegetation (Chiavari et

al., 2023). Despite high levels of deforestation in Brazil, this law has helped to retain a considerable amount of forest within the landscape.

## Bat sampling

### Study design

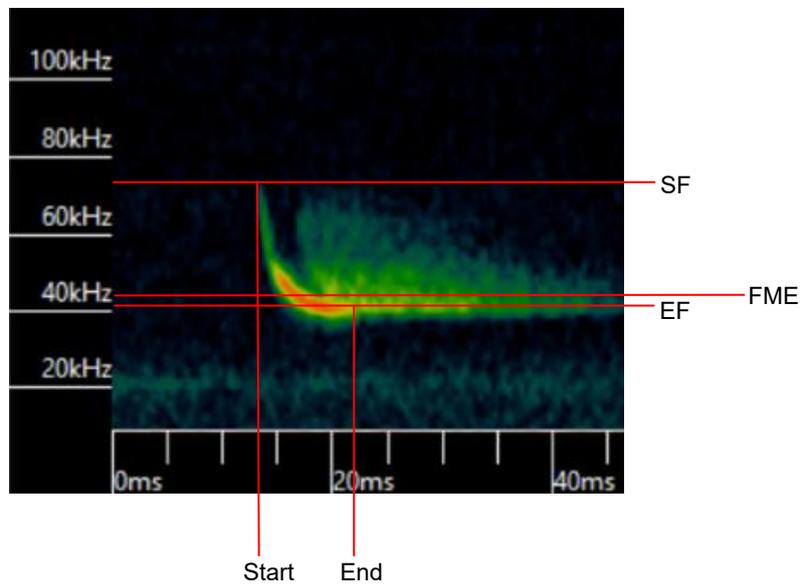
Acoustic data was collected across 20 cattle farms in Mato Grosso by researchers from the University of Sao Paulo and the University of Passo Fundo, Brazil (see Appendix Figure A1). At each farm, six sites were surveyed for one night: three in pasture, and three in forest. This resulted in a total of 120 sampling sites, although due to equipment malfunctioning, only 112 were included in the analysis (56 forest and 56 pasture). Song Meter bat mini detectors (Wildlife Acoustics, Inc, USA) were set to record during the night, defined as 30 minutes post and prior to sunset and sunrise (respectively), using a sample rate of 384 kHz. To reduce data volumes, the detectors were set to trigger detection of ultrasonic sounds at frequencies >15 kHz, suitable for AIBs which locate prey using ultrasonic echolocation.

### Bioacoustic analysis

I manually analysed acoustic data using Kaleidoscope Software v5.6.8 (Wildlife Acoustics, Inc, USA), following the bat ultrasound key in López-Baucells et al. (2016) to identify the bat calls in each sound file. Only the first four hours of the night (18:00-22:00) were analysed, as AIB activity has been found to decrease substantially after 22:00 (Estrada-Villegas et al., 2010; López-Baucells et al., 2021). Echolocation call characteristics such as frequency of maximum energy (FME) and end frequency (EF) were used for identifications (see Figure 2).

Sonotypes, which are groups of species with indistinguishable calls, were used when identification was not possible at the species level (López-Baucells et al., 2021). From henceforth, I use the term 'sonotypes' to refer to both single species and species groups (see Table 2 for the 'sonotypes' used in this study). In addition to the given sonotypes in López-Baucells et al. (2016), I grouped *Saccopteryx leptura* and *Saccopteryx bilineata* into a single 'Sac bil/lep' sonotype, as it wasn't possible to differentiate between the two species' calls. Following Colombo et al. (2023), I also separated *Pteronotus parnelli* into two sonotypes based on their FME, as a new species was discovered in the region (Pavan et al., 2018): *Pteronotus* 55 kHz (*P. rubiginosus*) and *Pteronotus* 60 kHz (*P. alitonus*). Due to inherent

limitations of acoustic data, individuals cannot be counted. Therefore, bat activity was measured using the unit of a 'bat pass', defined as any call sequence of 5-seconds containing a minimum of two distinguishable pulses of one sonotype (López-Baucells et al., 2021). Only passes with an intensity that exceeded 15 dB from background noise were identified.



**Figure 2:** An example echolocation call from the sonotype 'Eptesicus I' shown in Kaleidoscope. Time (ms) is shown on the x-axis, and frequency (kHz) on the y-axis. Measurements such as start frequency (SF), end frequency (EF) and frequency of maximum energy (FME) were extracted and used for sonotype identification. Adapted from López-Baucells et al. (2016).

## Functional traits of bats

For each of the sonotypes detected, I considered seven functional traits as potential predictors of vulnerability (Table 1). When species were grouped into sonotypes, average trait values across species were calculated for FME, weight, forearm length, relative wing loading, and aspect ratio.

**Table 1:** Summary of functional traits used in the analysis of aerial-insectivorous bat vulnerability to habitat loss and fragmentation in Mato Grosso, Brazil

Functional trait	Label	Source
Frequency of maximum energy	FME	Núñez et al., 2019; Colombo et al., 2023
Call structure	Call_CF Call_CF.FM Call_FM Call_QCF	López-Baucells et al., 2016; Arias-Aguilar et al., 2018
Body size: Forearm length	FA	López-Baucells et al., 2016
Body mass (weight)	Weight	Núñez et al., 2019; Colombo et al., 2023
Relative wing loading	rWL	Núñez et al., 2019; Extrapolation following Colombo et al., 2023
Aspect ratio	AR	Núñez et al., 2019; Extrapolation following Colombo et al., 2023
Vertical stratification	VertS	Núñez et al., 2019

### Echolocation: Frequency of maximum energy & Call structure

Frequency of maximum energy (the most intense frequency of the search-phase call) is an important determinant of bat habitat preference (Wordley et al., 2017; Núñez et al., 2019). Sonotypes in cluttered environments such as forests typically use high-frequency calls to reduce background echoes, compared to those in open environments which use lower frequency calls to increase detection ranges (Denzinger & Schnitzler, 2013).

Echolocation call structure is another important predictor of habitat preference. Sonotypes with constant-frequency (CF) calls are typically associated with open habitats, constant-frequency frequency-modulated (CF-FM) and frequency-modulated (FM) calls with cluttered habitats, and quasi-contrast frequency (qCF) calls with open or edge habitats (Altringham, 2011; Núñez et al., 2019).

## **Body size & Body mass**

Forearm length (FA) is used as a surrogate of body size, an important predictor in trait-based analyses due to its association with bat foraging behaviour and habitat preferences. It is measured as the average distance (mm) between an adult's elbow and wrist. Body mass is measured as the average adult body weight (g). Both body mass and size are intrinsically linked to bat mobility and agility (Díaz-B et al., 2023): larger bats are often better able to travel across fragmented landscapes, although they lack agility in cluttered habitats (Altringham, 2011). However, larger bats may be more vulnerable to disturbances due to slower life histories, smaller populations, and larger energy requirements (Meyer & Kalko, 2008).

## **Wing Morphology: Relative Wing Loading & Aspect Ratio**

Wing morphology directly correlates with flight speed, manoeuvrability, and agility in bats (Marinello & Bernard, 2014). These are important variables that influence foraging habitat (Norberg & Rayner, 1987). Wing loading (WL) represents the force exerted on the wings during flight. Studies typically use measures of relative wing loading (rWL) to ensure values are independent of size for similarly shaped bats (Marinello & Bernard, 2014). Aspect ratio (AR) represents the velocity that a bat must reach to sustain flight (Norberg & Rayner, 1987). Sonotypes with low rWL and AR typically have high manoeuvrability and low flight speed, which is advantageous in cluttered environments. In contrast, those with high rWL and AR are less manoeuvrable, but can fly faster allowing them to travel further in open spaces (Denzinger & Schnitzler, 2013; Marinello & Bernard, 2014).

Due to missing wing morphology data for *Noctilio albiventris*, *Saccopteryx canescens*, and *Peropteryx trinitatis*, I estimated rWL and AR using the equation of linear regressions of rWL and AR based on body mass values taken from Colombo et al. (2023) [ $rWL = 642.732 * \text{Weight} + 2.187$ , adjusted  $R^2 = 0.7558$ ;  $AR = 123.4593 * \text{Weight} + 6.0485$ , adjusted  $R^2 = 0.6503$ ] (Figure A3).

## **Vertical stratification**

The different strata of a tropical forest act as different habitats, holding varying levels of bat activity and richness, and with sonotypes being adapted to the stratum in which they forage most (Silva et al., 2020; Yoh et al., 2022). In AIBs, sonotypes are usually classified as under-canopy (VertS 1), canopy (VertS 2), or above-canopy (VertS 3) foragers (Núñez et al., 2019). Sonotypes adapted to forage above the canopy are typically fast flyers that can travel across landscapes to locate the patchy resources associated with this foraging niche. In contrast, understory sonotypes tend to have lower mobility across large distances, but higher

manoeuvrability, as they forage on locally restricted food resources in a cluttered environment (Meyer & Kalko, 2008).

## Environmental variables

I measured six aspects of landscape composition and configuration in the study region using QGIS software v3.40 and Google Earth Pro. These were (1) habitat type (forest or pasture), (2) forest cover (ha), (3) pasture cover (ha), (4) shortest distance to water (m), (5) patch density (patches/ha), and (6) edge density (m/ha). Habitat type was either classified as forest or pasture depending on the habitat cover at the point where each of the recorders were deployed. Forest and pasture cover were measured with land-use data from MapBiomass Brazil, using QGIS to extract pixels of respective habitat types around each sampling site. All agricultural land, which includes livestock and crop farming, was grouped under 'pasture' cover, as cattle pastures constituted an average of 95% of the agricultural land-use at each site. Patch and edge density are measures of how fragmented the landscape is. These two metrics were calculated by my collaborator (equations in Appendix). Shortest distance to water was calculated using Google Earth Pro as the shortest distance between each site and the nearest source of water. Landscape metrics were quantified within a circular buffer of 1500 m radius. Buffer distance was selected based on the spatial scale at which AIBs have been found to respond to land-use changes, whilst aiming to reduce overlap between sites (Chambers et al., 2016).

## Data analysis

All statistical analyses were conducted using RStudio v4.4.3. Although 28 sonotypes were identified across the study, only 19 were retained for analysis (Table 2). Phyllostomidae were excluded as they are difficult to detect and identify using bioacoustic methods. *Noctilio leptura* was removed as it is mainly piscivorous, and this study focuses on insectivorous species. There were no trait data for the *Diclidurus* species or Vespertilionidae I and II sonotypes, whilst *Molossops neglectus* and Thyropteridae were excluded as they were only recorded once.

To increase comparability between sites, bat activity was standardised using relative abundance: the number of bat passes of each sonotype was divided by the total number of passes at each site ('decostrand' function, standardisation method = total, MARGIN = 1, *vegan* package, Oksanen et al., 2020). Continuous variables in both the trait and environmental

tables were log-transformed ( $\log_{10} +1$ ) to normalise their distributions. To increase comparability between variables, all functional traits and environmental variables were centred and standardised to have a mean of zero and standard distribution of one ('scale' function; base R package, R Core Team 2019).

### **Taxonomic and functional $\alpha$ -diversity across land use type**

Using sonotype activity data from the sampling sites, functional trait data for these sonotypes gathered from previous studies, and the habitat type at each site, three aspects of alpha diversity were calculated for each site: taxonomic  $\alpha$ -diversity, measured with Simpson's taxonomic index (D); functional  $\alpha$ -diversity, measured with Rao's quadratic functional index (Q); and community-level functional uniqueness (U). Simpson's D assumes all species (in this study, sonotypes) are 'equally and maximally dissimilar' (Ricotta et al., 2016). It ranges from zero to one, with lower values indicating higher diversity. To align with the other diversity indices, the R package *adiv* calculates Simpson's Diversity Index as  $D = 1 - \sum n_i(n_i-1)/N(N-1)$ , so that higher values indicate higher diversity. Rao's Q (functional richness) is a similar index to Simpson's D, except it considers differences in traits between pairs of species (sonotypes), as well as relative abundance (Cisneros et al., 2015). Higher values of Q indicate that more functionally unique or rare species are present, suggesting a more diverse community (Ricotta et al., 2016). Community functional uniqueness (U) captures the level of functional uniqueness of species in a community, given the species present and their abundances. It is measured as the ratio between Simpson's U and Rao's Q ( $U = Q/D$ ), with higher values indicating a more functionally diverse community. Q, D, and U were calculated based on Gower's distance ('uniqueness' function, *adiv* package, Pavoine, 2020).

To understand the influence of habitat type (forest or pasture) on Q, D, and U, I ran beta regression models for each diversity index, suitable for response variables which range between 0 and 1 (as these diversity indices do). I used a logit link function to ensure response variables remained between 0 and 1, with habitat type as a fixed effect. To account for the hierarchical structure in which data were collected, where multiple sites are nested within farms, I added 'farm' as a random effect and ran mixed-effects beta regression models. I used Akaike's Information Criterion (AIC) to determine whether adding 'farm' as a random effect improved the fit of the model. Residual plots and tests of overdispersion were used to check for violations in model assumptions. All analyses were conducted in R v4.4.3 using packages *betareg* and *glmmTMB*.

## **RLQ and fourth-corner analysis**

To understand the relationship between sonotype activity, functional traits, and environmental variables, I used RLQ and fourth-corner analyses. These two complementary approaches, introduced by Dray et al. (2014), are widely used in ecological research to infer trait-environment relationships. RLQ provides ordination scores to summarise the relationship between three matrices: sonotype functional traits (Q); environmental variables at each sampling site (R); and sonotype activity levels per site (L). The L matrix was analysed using Correspondence Analysis (CA). R and Q matrices contain both continuous and categorical variables so were analysed using Hill-Smith Principal Component Analysis (PCA) which allows the inclusion of qualitative and quantitative variables. To link traits (Q) and environmental variables (R) to bat activity (L), the ordinations of Q and R were weighted using sonotype and site scores (respectively) derived from the CA.

To statistically test the trait-environment relationships, I combined RLQ and fourth-corner approaches following Dray et al. (2014). Three permutation models were used in this RLQ-fourth corner analysis. Model 2 tests the null hypothesis that sonotype distribution with fixed traits is not influenced by environmental conditions, i.e. there is no relationship between sonotype activity and environmental conditions. Model 4 tests the null hypothesis that sonotype distribution with fixed environmental conditions is not influenced by functional traits, i.e. there is no relationship between sonotype activity and traits. Model 6 tests the combination of the two models' outputs, against the null hypothesis that at least R or Q is not linked to L (with the alternative hypothesis that both environmental variables and traits influence sonotype distribution; Dray et al., 2014). Significance was based on 49,999 permutations, and the false discovery rate method was used to adjust p-values for multiple comparisons (FDR; Benjamini & Hochberg, 1995; Dray et al., 2014). All analyses were carried out using *ade4* package (Dray & Dufour, 2007).

## Results

A total of 64,918 bat passes were retained in the analysis, with 19 sonotypes identified across five families (Emballonuridae, Vespertilionidae, Mormoopidae, Noctilidae, and Molossidae) (Table 2). All sonotypes were recorded in both forest and pasture sites, apart from *Rhynchonycteris naso*, which was only recorded in pasture. The most frequently identified sonotypes overall were Sac bil/lep, Molossus II, and Molossidae D, present in 110, 109, and 107 of the 115 sites respectively. For forest sites, the most common sonotype was Sac bil/lep (present in 56 sites), and for pasture sites, Molossus II and Molossidae D equally (58 sites).

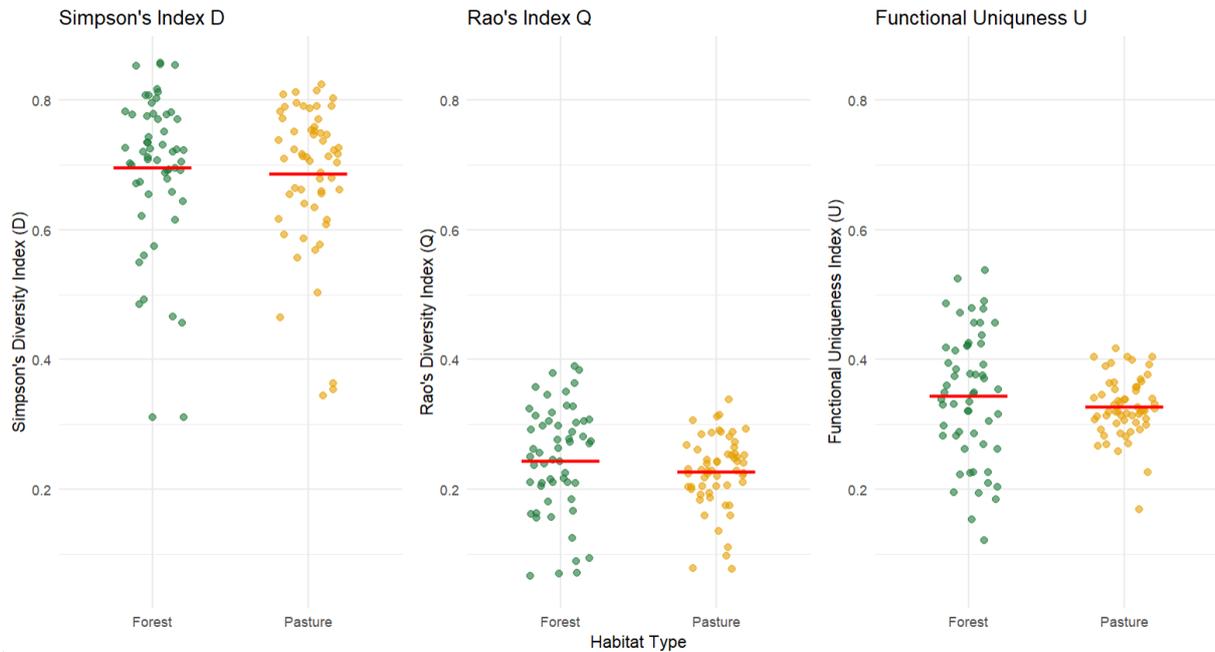
**Table 2:** The 19 sonotypes retained in the analysis, identified from bioacoustic data across the 20 sampled farms in Mato Grosso, Brazil. Sonotypes are coloured according to family: Purple = Emballonuridae, Green = Vespertilionidae, Blue = Mormoopidae, Yellow = Noctilionidae, Orange = Molossidae

Sonotype name	Species included Genus      Species	Guild	Total sites	Total n. passes
Sac bil/lep (S)	<i>Saccopteryx</i> <i>S. leptura</i> <i>S. bilineata</i>	Edge	110	5995 (9.04%)
Emballonuridae I (E1)	<i>Saccopteryx</i> <i>S. gymnura</i> <i>S. canescens</i>	Edge	12	49 (0.07%)
Emballonuridae II (E2)	<i>Centronycteris</i> <i>C. centralis</i> <i>C. maximiliani</i>	Edge	46	642 (0.97%)
Cor bre (CB)	<i>Cormura</i> <i>C. brevirostris</i>	Edge	68	546 (0.82%)
Per kap (PK)	<i>Peropteryx</i> <i>P. kappleri</i>	Edge	75	5408 (8.16%)
Per mac (PM)	<i>Peropteryx</i> <i>P. macrotis</i>	Edge	59	1513 (2.28%)
Per tri (PT)	<i>Peropteryx</i> <i>P. trinitatis</i>	Edge	44	2200 (3.32%)
Rhy nas (RN)	<i>Rhynchonycteris</i> <i>R. naso</i>	Open	9	29 (0.04%)
Eptesicus I (EP)	<i>Eptesicus</i> <i>E. brasiliensis</i> <i>E. chiriquinus</i> <i>E. furinalis</i>	Forest	94	5065 (7.64%)
Myo rip (MR)	<i>Myotis</i> <i>M. riparius</i>	Forest	43	1023 (1.54%)
Myo nig (MN)	<i>Myotis</i> <i>M. nigricans</i>	Forest	71	855 (1.29%)
Pter parn 55 (P5)	<i>Pteronotus</i> <i>P. rubiginosus</i>	Forest	43	601 (0.91%)
Pte gym (PG)	<i>Pteronotus</i> <i>P. gymnonotus</i>	Forest	30	114 (0.17%)
Pte per (PP)	<i>Pteronotus</i> <i>P. personatus</i>	Forest	25	130 (0.20%)
Noc alb (NA)	<i>Noctilio</i> <i>N. albiventris</i>	Water	20	124 (0.19%)

<b>Molossus I (M1)</b>	<i>Molossus</i>	Open	96	5278 (7.96%)
		<i>M. molossus</i>		
<b>Molossus II (M2)</b>	<i>Molossus</i>	Open	109	12025 (18.14%)
		<i>M. sinaloae</i>		
		<i>M. currentium</i>		
		<i>M. rufus</i>		
<b>Molossidae D (MD)</b>	<i>Neoplatymops</i>	Open	107	22818 (34.42%)
		<i>N. mattogrossensis</i>		
	<i>Nyctinomops</i>	<i>N. macrotis</i>		
		<i>Eumops</i>		
	<i>E. glaucinus</i>			
	<i>E. dabbenei</i>			
	<i>E. hansae</i>			
	<i>E. maurus</i>			
	<i>Nyctinomops</i>	<i>N. laticaudatus</i>		
	<i>Tadarida</i>	<i>T. brasiliensis</i>		
	<b>Promops sp. (P)</b>	<i>Promops</i>		
<i>P. nasutus</i>				
<i>P. centralis</i>				

## Taxonomic and functional $\alpha$ -diversity

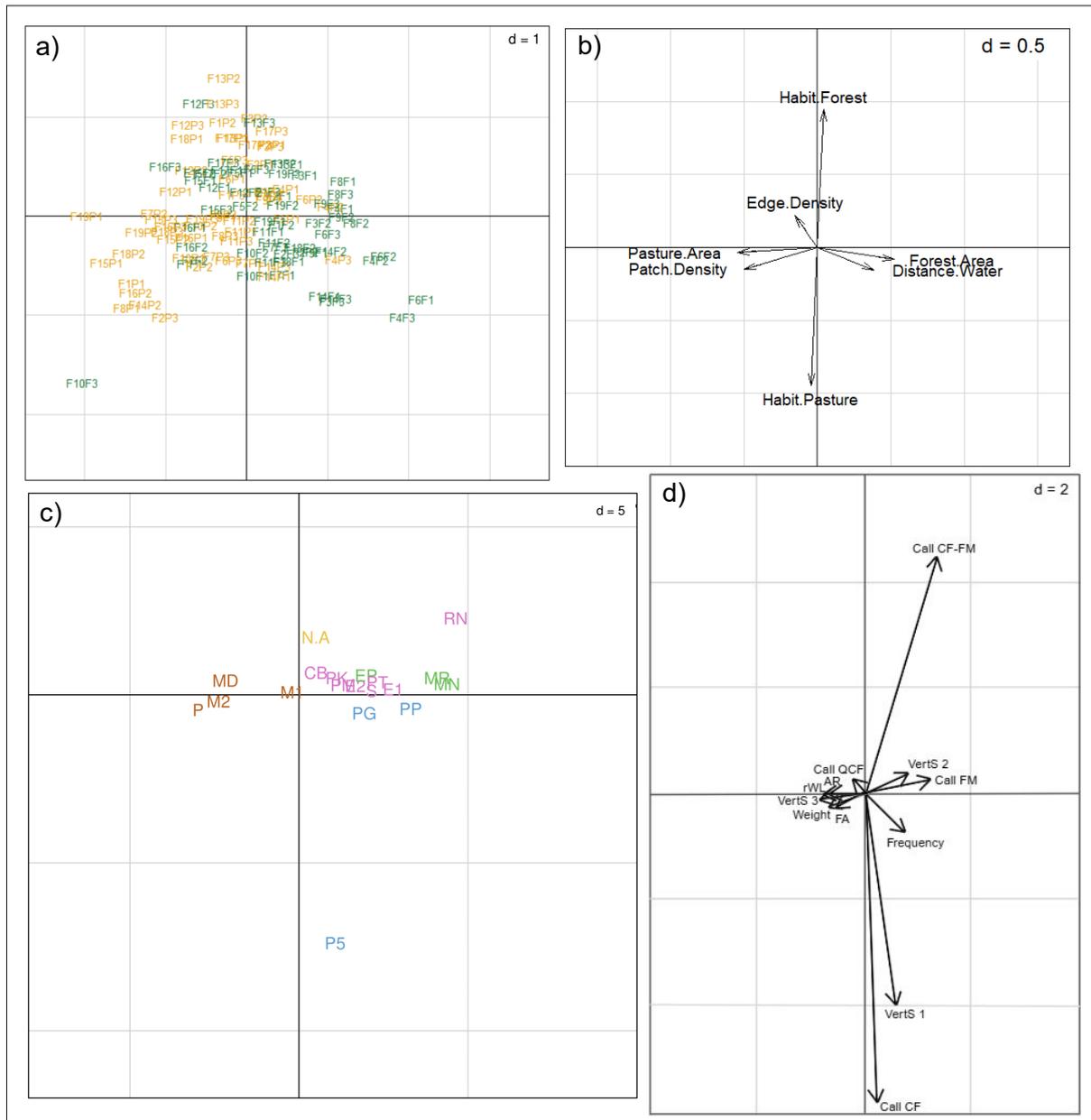
The mean values of taxonomic diversity (measured by Simpson's D), functional richness (Rao's Q) and functional uniqueness (Functional Uniqueness U) were all higher in forest than pasture (0.695 vs 0.685; 0.244 vs 0.227; 0.344 vs 0.327 respectively) (Figure 3). However, none of these differences were statistically significant in the beta regression models. The best fitting models were those that included 'farm' as a random effect, suggesting that some of the variation in diversity was attributable to differences between farms. Nonetheless, even when accounting for this variation, the effect of habitat type still appeared small and remained insignificant across all diversity indices (Raos Q = -0.054, SE = 0.074, p = 0.468; Simpson's D = -0.053, SE = 0.087, p = 0.54; Functional Uniqueness = -0.053, SE = 0.060, p = 0.376).



**Figure 3:** Comparisons of taxonomic  $\alpha$ -diversity (Simpson's index D), functional  $\alpha$ -diversity (Rao's index Q), and community-level functional uniqueness (U) between forest and pasture sites. Red lines represent the site's mean, green dots show forest sites, and orange dots show pasture sites.

## Trait-environment relationships

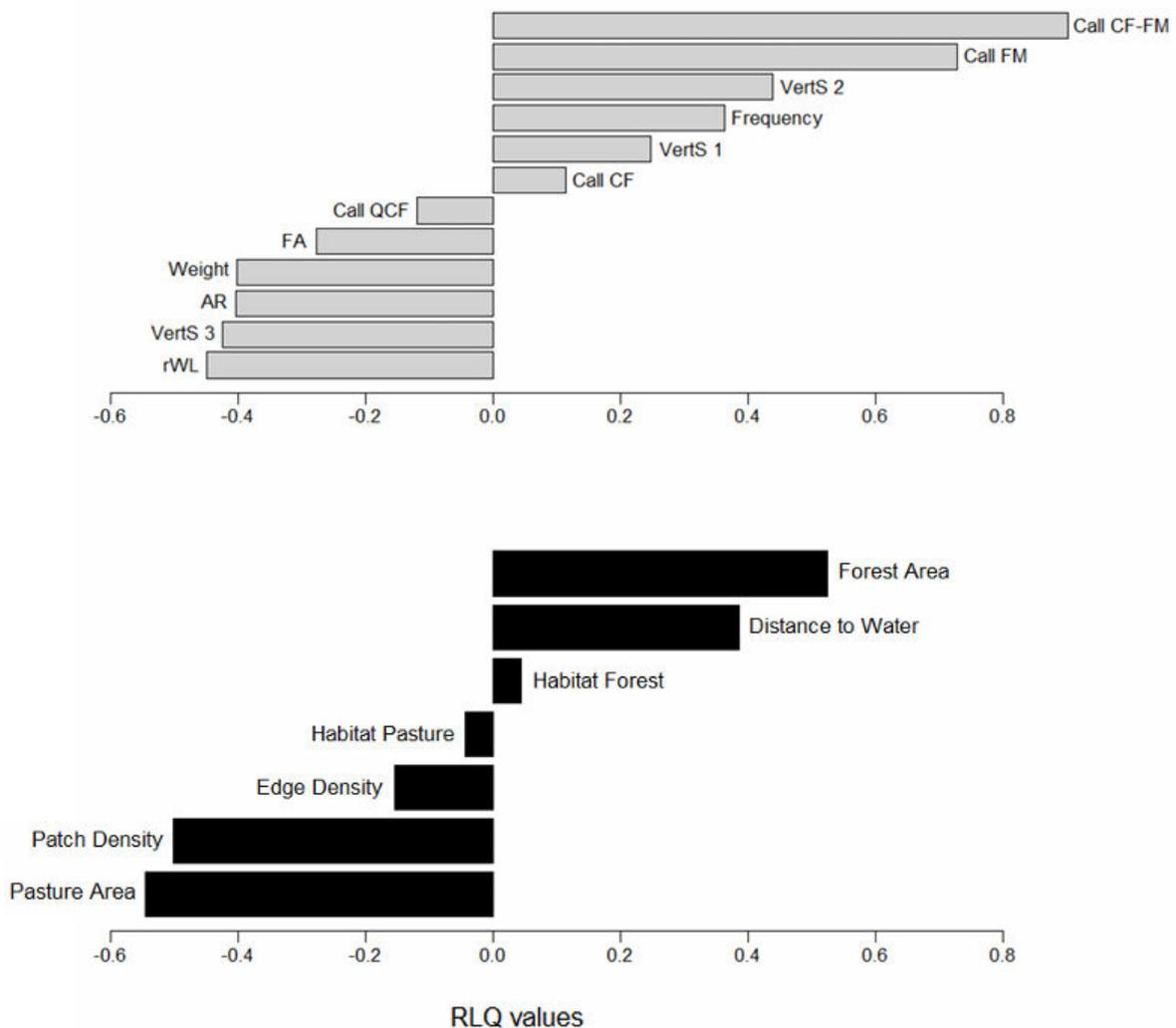
The first axis of the RLQ ordination, which considers tables R, L and Q, explained 97.39% of the total variance between traits and environmental variables. The combination of the first and second axis explained 99.55%. According to the graphical representation of the RLQ, there was a slight grouping of sites according to proportion of pasture or forest cover in the site's buffer along the first axis of RLQ ordination (Figure 4a & b). Pasture cover was also associated with patch density, and forest cover with distance to water. Sonotypes clustered according to family and certain traits, particularly call structure and foraging stratum (Figure 4c & d). Sonotypes with CF-FM (*P. gymnonotus*, *R. naso*) and FM (*M. riparius*, *M. nigricans*) calls which forage in and among the canopy (VertS 1 & 2) were associated with forest area. In contrast, above-canopy foragers (VertS 3) clustered in ordination space with pasture area (*P. centralis*, *Molossus* II).



**Figure 4:** The first two axes from the RLQ analysis showing the distribution in ordination space of (a) Sites: Yellow = Pasture, Green = Forest (b) Environmental variables (c) Sonotypes: Orange = Molossidae, Purple = Emballonuridae, Green = Vespertilionidae, Yellow = Noctilionidae, Blue = Mormoopidae (See Table 2 for sonotype abbreviations) and (d) Traits (see Table 1 for trait abbreviations).

The eigenvalues of the first axis of the RLQ analysis showed call structure as the most important trait variable, and habitat area as the most important environmental variable, explaining sonotype distribution (Figure 5). Sonotypes with high-frequency CF-FM and FM echolocation calls that forage beneath and amongst the canopy were associated with greater forest cover and distances to water. In contrast, sonotypes with high relative wing loading and

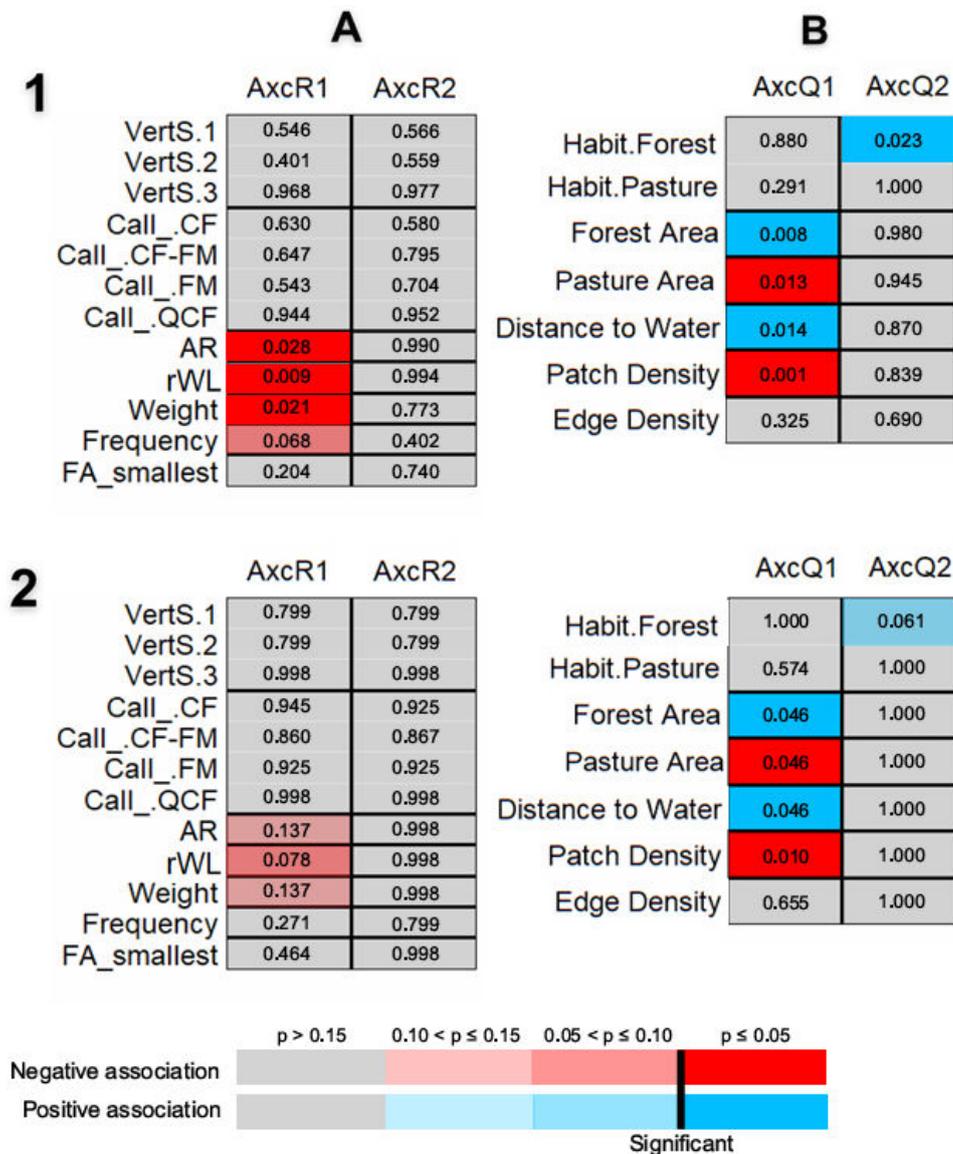
aspect ratio that forage above the canopy were associated with increased pasture area and patch density, corresponding to a more heavily fragmented landscape.



**Figure 5:** RLQ eigenvalues showing the relationship between AIB sonotype traits (grey bars) and environmental variables (black bars) along axis 1.

The fourth-corner analysis indicated that the distribution of AIBs was significantly associated with both environmental variables (model 2,  $p < 0.001$ ) and functional traits (model 4,  $p < 0.05$ ). Furthermore, model 6 which combines models 2 and 4 by measuring the link between sonotype activity, traits, and environmental variables was also significant ( $p < 0.05$ ). The combination of the RLQ and fourth-corner analysis revealed that the first RLQ axis for functional traits (AxcQ1) was significantly associated with larger areas of forest and distances to water, and with smaller areas of pasture and values of patch density ( $p < 0.05$ ) (Figure 6). Before controlling for multiple comparisons, there was a significant association between aspect ratio, relative wing loading, and weight with the first axis for environmental variables

(AxR1) (Figure 6.1). However, after controlling for multiple comparisons (FDR), all the trait relationships with the environmental axis lost their significance at the  $p < 0.05$  level (Figure 6.2).



**Figure 6:** Fourth-corner analysis showing the relationships between AIB functional traits and environmental variables in Mato Grosso, Brazil, 1) before controlling for multiple testing (FDR) and 2) after.

Tests were conducted between (A) the first two RLQ axes for environmental variables (AxR1/AxR2) and functional traits and (B) the first two RLQ axes for functional traits (AxQ1/AxQ2) and environmental variables. P-values are shown on a scale, with only the darkest shade of red and blue indicating significant results. Blue = positive association, Red = negative association. Variables are separated by black lines, and different levels of the same categorical variable are separated by grey lines. See Table 1 for trait abbreviations.

## Discussion

Limited studies to date have considered the trait-based vulnerability of bats to land-use change in the Neotropics, and fewer still of AIBs, despite their key roles in ecosystems and importance as bioindicators (but see Núñez et al., 2019; Colombo et al., 2023; Díaz-B et al., 2023). In this study, I investigated the differences in taxonomic and functional  $\alpha$ -diversity between forest and pasture sites, and the trait-environment relationships shaping species' distributions across the study region of Mato Grosso, Brazil. This is one of the first studies to consider such trait-environment relationships in AIBs across a livestock-dominated landscape. I found that whilst there were no significant differences in  $\alpha$ -diversity between forest and pasture sites, there were several significant trait-environment associations.

### **Taxonomic and functional $\alpha$ -diversity in forest and pasture**

Inconsistent with my hypothesis, I found no evidence that taxonomic diversity, functional diversity, and functional uniqueness differed in forest compared to pasture sites. Habitat fragmentation typically reduces  $\alpha$ -diversity (Gonçalves-Souza et al., 2025). As all sites were sampled within a heavily fragmented landscape, both 'forest' and 'pasture' sites likely have similarly reduced  $\alpha$ -diversity, regardless of the habitat type at the sampling site. Furthermore, many sites were close together, with 'forest' sites sometimes close to large patches of pasture and vice versa. Given that bats can forage across several kilometres per night (Aharon et al., 2017), the lack of significant differences may be a result of this spatial overlap between sites and habitats. Detection bias may also have contributed: forests are noisy environments with high sound attenuation, and detecting bat calls above background noise is challenging (Froidevaux et al., 2014). Diversity estimates may therefore have been influenced if sonotypes were under-detected in forest (Ferreira et al., 2022).

Whilst measures of taxonomic diversity in both habitats were relatively high, functional diversity was noticeably lower. This discrepancy highlights the importance of using suitable diversity metrics for every research question, lest important patterns of biodiversity loss are missed (Guillerme et al., 2025). These patterns suggest that habitat degradation had little effect on the region's taxonomic diversity, but may have reduced AIB functional diversity, with only certain traits able to persist in the modified landscape. However, baseline data from before habitat modification would be needed to make fair comparisons.

## Functional trait variables

Consistent with other studies on Neotropical bats, I identified several functional traits influencing sonotype distribution across the study region, most importantly wing shape, call characteristics, and vertical foraging niche (Núñez et al., 2019; Colombo et al., 2023; Farneda et al., 2015). Two measures of wing morphology, relative wing loading and aspect ratio, are highly important predictors of bat mobility and habitat preference (Norberg & Rayner, 1987; Marinello & Bernard, 2014). High values of relative wing loading and aspect ratio indicate narrow, aerodynamic wings suited for fast and energy-efficient flight across open spaces but with reduced manoeuvrability in cluttered environments (Altringham, 2011). In contrast, bats with low relative wing loading and aspect ratio (indicating short and wide wings) are highly manoeuvrable in cluttered environments like forests (Marinello & Bernard, 2014), but less able to travel long distances such as between habitat patches (Estrada-Villegas et al., 2010; Bader et al., 2015). As hypothesised, RLQ and fourth-corner analyses revealed wing morphology was strongly associated with land-use. Sonotypes with high relative wing loading and aspect ratio were associated with open, pastoral landscapes, whereas those with low relative wing loading and aspect ratio were associated with forest. This suggests bats with wings adapted for cluttered habitats are more vulnerable to agricultural expansion, as they are less able to traverse the open landscapes associated with agriculture. In contrast, sonotypes with wings adapted for flight in open spaces may be better suited to persist in these modified, more open, landscapes.

Bats with higher body mass were associated with more heavily farmed and fragmented landscapes according to the RLQ and fourth-corner analyses. Other studies on various bat guilds have found conflicting results regarding the relationship between body mass and vulnerability to land-use change. Looking at Phyllostomids in Brazil, Farneda et al (2015) found that larger bats are more vulnerable to land-use change, perhaps as they typically have smaller population sizes and sit at higher (less stable) tropic levels (Henle et al., 2004). Similar results were found in India when primarily considering AIBs (Wordley et al., 2017). In contrast, studies in Australia found that larger bats were associated with more modified landscapes (Threlfall et al., 2011; Hanspach et al., 2012), perhaps because they can fly further across fragmented landscapes (García-Morales et al., 2016). In the Neotropical landscape of my study, results are influenced by the Molossidae, a family of heavy bats associated with open habitats. This ambiguous relationship between body mass and vulnerability to land-use change suggests this trait may not be particularly well-suited to predict species' sensitivity to habitat modification (Wordley et al., 2017).

Echolocation call characteristics tend to reflect the type of habitat in which AIB sonotypes forage, and multiple studies have identified echolocation characteristics as valuable predictors of vulnerability to habitat change (Luo et al., 2019; Colombo et al., 2023). Frequency-modulated (FM) calls, which steeply sweep down the frequencies, are well-suited for cluttered habitats; they provide detailed information on the target prey and surrounding environment (Altringham 2011). On the other end of the spectrum, narrowband constant-frequency (CF) calls instead evolved to have high signal energy and low attenuation for long-range prey detection in open spaces (Luo et al., 2019). Constant-frequency frequency-modulated (CF-FM) calls are a special adaptation to foraging in cluttered spaces where many other individuals may be echolocating, and the echoes from prey are hidden within background echoes (Denzinger & Schnitzler, 2013; Altringham, 2011). They avoid signal jamming through the complementary functions of their CF and FM components (Ding et al., 2024). In this study, one of the strongest RLQ associations was between sonotypes with CF-FM and FM sonotypes and forest cover. This suggests sonotypes with calls adapted for cluttered, forested environments are more vulnerable to habitat loss and conversion to pastoral landscapes than those with open-space (CF) or flexible (qCF) calls.

Two other studies found results contrasting with mine, associating FM sonotypes with open spaces and CF sonotypes with forest (Núñez et al., 2019; Wordley et al., 2017). However, they classified some sonotypes' calls differently to my study, primarily by classifying Molossidae D calls as FM compared to qCF as in my study (based on Arias-Aguilar et al., 2018 & López-Baucells et al., 2016). It isn't always clear which category a call belongs to, as some show features of multiple categories (e.g. CF-FM, or FM-qCF), and distinctions between qCF and FM calls can be subtle. Classifying Molossidae D is particularly challenging, as it contains nine different species with varying calls. Even within a species, call-shape can vary during prey capture or social calls (see Figure S2). The large majority of calls I classified as Molossidae D appeared qCF to me, and this was consistent with the classification guide by Lopez-Baucells et al (2016) that I used to inform my identifications. Given the lack of consistency in call-shape classification across studies, findings related to call shape may be less robust than of other trait variables, both in my work and similar studies. Another limitation is that only one sonotype was classified as CF in my study (*P. parnelli*), whereas four sonotypes were classified as CF-FM, three as FM, and eleven as qCF. The associations between CF sonotypes and environmental variables in my results are therefore unlikely to be representative of all sonotypes that use CF calls.

In line with similar studies, sonotypes with high-frequency calls were associated with forest according to the RLQ analysis (Wordley et al., 2017; Threlfall et al., 2011; Hanspach et al., 2012). High-frequency calls have short wavelengths, enabling bats to discriminate even very

small insect prey in cluttered environments (Altringham 2011). However, they attenuate more quickly compared to those of lower frequency (Jung et al., 2007). Therefore, open-space foragers typically use low-frequency calls which travel further (Denzinger & Schnitzler, 2013). In my study, the calls with lowest frequency were predominantly from the Molossidae, which were also most strongly associated with pasture cover and qCF calls. This suggests the Molossidae's low-frequency qCF calls help them to forage and persist in these open, cattle-dominated landscapes. Conversely, sonotypes with high-frequency calls adapted to cluttered environments, such as the Vespertilionids and Mormoopids, may be more vulnerable to land-use change.

The RLQ analysis revealed an association between sonotypes' preferred foraging strata of the forest and their sensitivity to land-use change: above-canopy sonotypes were associated with fragmented pastureland whereas canopy and understory sonotypes were associated with forest. Above-canopy sonotypes forage across open-spaces for widely distributed resources (Marques et al., 2016; Meyer & Kalko, 2008). They are consequently well-adapted to pastoral landscapes. In contrast, sonotypes which forage primarily in the forests' understory, or to a lesser extent canopy, are adapted to cluttered environments and may therefore be more vulnerable to forest loss and fragmentation (Díaz-B et al., 2023). However, following Yoh et al (2022)'s classification of sonotypes' vertical strata, twelve sonotypes were classified as 'canopy foragers' whereas only four (all Molossidae) and three (all Mormoopidae) sonotypes were classified as 'above-canopy' and 'understory' foragers respectively. This resulted in less statistical power to study the association between above-canopy and understory foraging, and vulnerability to land-use change.

### **Environmental variables**

The proportion of native vegetation in a landscape is an important predictor of bat activity (Mancini et al., 2024) and functional diversity (García-Morales et al., 2016; Jakobsson et al., 2020). Areas with less forest are likely to hold fewer appropriate roosting sites and reduced prey availability for bats (Meyer & Kalko, 2008; Estrada-Villegas et al., 2010). In line with my hypothesis, environments with less forest and more pastureland favoured bats with high mobility that can travel large distances to roosting sites (high relative wing loading and aspect ratio) and with low-frequency qCF calls that are suited to open-space foraging (e.g. the Molossidae). In contrast, more forested sites were associated with sonotypes with high manoeuvrability (low relative wing loading and aspect ratio), and high-frequency FM calls suited for clutter-space foraging (e.g. the Vespertilionidae).

In this study, patch density is a measure of how fragmented the forest habitat is within each sampling buffer. Habitat fragmentation tends to alter the structure and functioning of biodiversity in resulting patches (Haddad et al., 2015). In bats, sonotypes appear to respond in different ways depending on their functional traits (Meyer & Kalko, 2008). In this study, clutter-space foragers, particularly from the Vespertilionidae family, were identified as most sensitive to habitat fragmentation. Their low relative wing loading and aspect ratio wings mean travelling between patches is very energetically costly, likely reducing their ability to persist in habitats where resources are more widely distributed (Estrada-Villegas et al., 2010).

Water bodies are an important drinking and foraging resource for bats, particularly in arid environments or during dry seasons (Torrent et al., 2018; Korine et al., 2016), and AIBs frequently forage over water due to the increased densities of insects (López-González et al., 2015). Díaz-B et al. (2023) found that mobile, open-space foragers were associated with more distant water bodies. Such sonotypes can travel greater distances and so may not be limited to forage within a certain area around water sources, compared to less flight-efficient sonotypes. Contrastingly, my study found that sonotypes with lower mobility were associated with further distances to water. This could be explained by a flaw in my methodology: I identified water sources using Google-Earth pro. Most water identified was in open pastureland, and any water in forest that was hidden beneath the canopy would have been missed. Therefore, these results must be interpreted with caution. Future studies may need to map water sources themselves when in the region for greater accuracy.

### **Potential impacts and recommendations**

Changes to bat community composition have important ecological consequences. As vulnerable sonotypes decline, so too will the ecosystem services they provide (Brasileiro et al., 2022; Kemp et al., 2019). The loss of insectivorous bats will likely alter baseline insect populations, potentially leading to increases in pest species that were previously suppressed. For example, *Myotis nigricans* (Vespertilionidae) is a key predator of insect pests in rice crops, and *Eptesicus furinalis* (Vespertilionidae) and *Pteronotus gymnonotus* (Mormoopidae) have been reported to forage in crops such as coffee, banana, and pineapple (Azofeifa et al., 2019). As these sonotypes were all identified as vulnerable to land-use change in this study, the ecosystem services they provide may also be at risk in increasingly deforested and fragmented landscapes. If agricultural pests are no longer effectively controlled by bats, farmers may face higher economic costs from increased crop damage and the need for alternative pest-control measures. This highlights the critical importance of maintaining a functionally diverse bat community to preserve insect suppression, widely recognised as one

of the most valuable ecosystem services bats provide to humans (Moir et al., 2021; Boyles et al., 2013).

Currently, data on the diets of AIBs is sparse. Future studies should consider whether the sonotypes which are particularly vulnerable to land-use change are those responsible for consuming and thus controlling the insects which damage crops or transmit infections to livestock or humans (e.g. Ancillotto et al., 2021). Furthermore, the relationship between functional traits, agricultural expansion and the spread of zoonotic diseases, of which bats are often a vector, is also poorly understood in this landscape (White & Razgour, 2020). With the increasing proximity of bats to agriculture, future studies should consider how trait-mediated shifts in bat communities may influence the risk of zoonotic disease outbreaks.

Given the findings from this study, I recommend that conservation efforts prioritise the sonotypes identified as most vulnerable, primarily the clutter-space foragers from the Vespertilionidae and Mormoopidae families. From the analyses with environmental variables, I recommend that land managers not only maintain as much forest cover as possible (40% is the optimal amount recommended by Arroyo-Rodríguez et al., 2020), but also minimise levels of habitat fragmentation. Incentives encouraging neighbouring farms to maintain a single forest patch rather than having separate forested reserves could help to preserve vulnerable species and thus functional diversity in these agricultural landscapes. Through these approaches, the ecological functions and services that bats provide may be safeguarded, supporting both biodiversity conservation and the sustainability of agricultural landscapes.

## Conclusion

Habitat loss and fragmentation are reshaping Amazonian bat communities in profound ways (Farneda et al., 2024). Whilst some sonotypes appear able to exploit modified landscapes, others face an increased risk of local extinction. My findings indicate that sonotypes with low relative wing loading and aspect ratio, and high-frequency FM/CF-FM calls (mostly from the Vespertilionidae and Mormoopidae families) are especially vulnerable to livestock-associated land-use change. These results align with other studies on AIBs whilst providing the first insight into the functional response of AIBs to cattle-dominated landscapes in the Brazilian Amazon. Such traits, whilst advantageous in cluttered habitats such as forests, leave bats poorly suited to the increasingly open and fragmented landscapes driven by cattle farming. In contrast, sonotypes from the Molossidae family, adapted for flight in open spaces, appear readily able to persist and even benefit from such environmental changes. This knowledge can help prioritise conservation towards sonotypes and ecosystem services identified as at greatest risk of being lost, hence increasing the sustainability of agriculture for the future.

## Acknowledgments

First and foremost, I would like to thank my wonderful supervisor Ricardo Rocha, who has provided me with invaluable support and opportunities; I've thoroughly enjoyed being a part of your team!

A huge thank you to Harriet Bartlett, Filipa Palmeirim and Adrià López-Baucells for all of their time and guidance.

Thank you, Rosie, for being such a great companion throughout this project; I feel so lucky to have worked alongside you.

I would also like to thank Eva Nobrega, who showed me the ropes of bioacoustic data collection and analysis, and to the OxTec team, for their frequent insights and discussions.

And finally, thank you to my parents, for their endless enthusiasm and encouragement, and who have so patiently listened to me ramble about bats for a year straight.

## Bibliography

- Aharon, G., Sadot, M., & Yovel, Y. (2017). Bats Use Path Integration Rather Than Acoustic Flow to Assess Flight Distance along Flyways. *Current Biology*, 27(23), 3650-3657.e3. <https://doi.org/10.1016/j.cub.2017.10.012>
- Aleixandre-Benavent, R., Aleixandre-Tudó, J. L., Castelló-Cogollos, L., & Aleixandre, J. L. (2018). Trends in global research in deforestation. A bibliometric analysis. *Land Use Policy*, 72, 293–302. <https://doi.org/10.1016/j.landusepol.2017.12.060>
- Altringham, J. D. (2011). *Bats : from evolution to conservation* (2nd ed.). Oxford University Press.
- Alvarado, F., Escobar, F., Williams, D. R., Arroyo-Rodríguez, V., & Escobar-Hernández, F. (2018). The role of livestock intensification and landscape structure in maintaining tropical biodiversity. *Journal of Applied Ecology*, 55(1), 185–194. <https://doi.org/10.1111/1365-2664.12957>
- Ancillotto, L., Festa, F., De Benedetta, F., Cosentino, F., Pejic, B., & Russo, D. (2021). Free-ranging livestock and a diverse landscape structure increase bat foraging in mountainous landscapes. *Agroforestry Systems*, 95(2), 407–418. <https://doi.org/10.1007/s10457-021-00591-0>
- Arias-Aguilar, A., Hintze, F., Aguiar, L. M. S., Rufay, V., Bernard, E., & Pereira, M. J. R. (2018). Who's calling? Acoustic identification of Brazilian bats. In *Mammal Research* (Vol. 63, Issue 3, pp. 231–253). Springer Berlin Heidelberg. <https://doi.org/10.1007/s13364-018-0367-z>
- Arroyo-Rodríguez, V., Fahrig, L., Tabarelli, M., Watling, J. I., Tischendorf, L., Benchimol, M., Cazetta, E., Faria, D., Leal, I. R., Melo, F. P. L., Morante-Filho, J. C., Santos, B. A., Arasa-Gisbert, R., Arce-Peña, N., Cervantes-López, M. J., Cudney-Valenzuela, S., Galán-Acedo, C., San-José, M., Vieira, I. C. G., ... Tscharrntke, T. (2020). Designing optimal human-modified landscapes for forest biodiversity conservation. In *Ecology Letters* (Vol. 23, Issue 9, pp. 1404–1420). Blackwell Publishing Ltd. <https://doi.org/10.1111/ele.13535>
- Azofeifa, Y., Estrada-Villegas, S., Mavárez, J., & Nassar, J. M. (2019). Activity of Aerial Insectivorous Bats in Two Rice Fields in the Northwestern Llanos of Venezuela. *Acta Chiropterologica*, 21(1), 149–163. <https://doi.org/10.3161/15081109ACC2019.21.1.012>
- Bader, E., Jung, K., Kalko, E. K. V., Page, R. A., 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>
- Benjamini, Y., & Hochberg, Y. (1995). Controlling the False Discovery Rate: a Practical and Powerful Approach to Multiple Testing. In *J. R. Statist. Soc. B* (Vol. 57, Issue 1). <https://academic.oup.com/jrsssb/article/57/1/289/7035855>

- Boyles, J. G., Cryan, P. M., McCracken, G. F., & Kunz, T. H. (2011). Economic Importance of Bats in Agriculture. *Science*, 332(6025), 41–42. <https://doi.org/10.1126/science.1201366>
- Boyles, J. G., Sole, C. L., Cryan, P. M., & McCracken, G. F. (2013). On Estimating the Economic Value of Insectivorous Bats: Prospects and Priorities for Biologists. In *Bat Evolution, Ecology, and Conservation* (pp. 501–515). Springer New York. [https://doi.org/10.1007/978-1-4614-7397-8\\_24](https://doi.org/10.1007/978-1-4614-7397-8_24)
- Brasileiro, L. A. M., Machado, R. B., & Aguiar, L. M. S. (2022). Ecosystems Services Provided by Bats Are at Risk in Brazil. *Frontiers in Ecology and Evolution*, 10. <https://doi.org/10.3389/fevo.2022.852177>
- Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., Narwani, A., Mace, G. M., Tilman, D., Wardle, D. A., Kinzig, A. P., Daily, G. C., Loreau, M., Grace, J. B., Larigauderie, A., Srivastava, D. S., & Naeem, S. (2012). Biodiversity loss and its impact on humanity. *Nature*, 486(7401), 59–67. <https://doi.org/10.1038/nature11148>
- Carvalho, W. D., Miguel, J. D., da Silva Xavier, B., López-Baucells, A., de Castro, I. J., Hilário, R. R., de Toledo, J. J., Rocha, R., & Palmeirim, J. M. (2023). Complementarity between mist-netting and low-cost acoustic recorders to sample bats in Amazonian rainforests and savannahs. *Community Ecology*, 24(1), 47–60. <https://doi.org/10.1007/s42974-022-00131-5>
- Chambers, C. L., Cushman, S. A., Medina-Fitoria, A., Martínez-Fonseca, J., & Chávez-Velásquez, M. (2016). Influences of scale on bat habitat relationships in a forested landscape in Nicaragua. *Landscape Ecology*, 31(6), 1299–1318. <https://doi.org/10.1007/s10980-016-0343-4>
- Chiavari, J., Lopes, C. L., & de Alcantara Machado, L. (2023). *The Brazilian Forest Code: The Challenges of Legal Implementation* (pp. 295–314). [https://doi.org/10.1007/978-3-031-29853-0\\_15](https://doi.org/10.1007/978-3-031-29853-0_15)
- Cisneros, L. M., Fagan, M. E., & Willig, M. R. (2015). Effects of human-modified landscapes on taxonomic, functional and phylogenetic dimensions of bat biodiversity. *Diversity and Distributions*, 21(5), 523–533. <https://doi.org/10.1111/ddi.12277>
- Colombo, G. T., Di Ponzio, R., Benchimol, M., Peres, C. A., & Bobrowiec, P. E. D. (2023). Functional diversity and trait filtering of insectivorous bats on forest islands created by an Amazonian mega dam. *Functional Ecology*, 37(1), 99–111. <https://doi.org/10.1111/1365-2435.14118>
- Denzinger, A., & Schnitzler, H. U. (2013). Bat guilds, a concept to classify the highly diverse foraging and echolocation behaviors of microchiropteran bats. *Frontiers in Physiology*, 4 JUL. <https://doi.org/10.3389/fphys.2013.00164>
- Díaz-B, C. A., Otálora-Ardila, A., Valdés-Cardona, M. C., López-Arévalo, H. F., & Montenegro, O. L. (2023). Bat functional traits associated with environmental, landscape, and conservation variables in Neotropical dry forests. *Frontiers in Forests and Global Change*, 6. <https://doi.org/10.3389/ffgc.2023.1082427>

- Ding, J., Gu, H., Zhang, K., Lin, A., Feng, J., & Liu, Y. (2024). Adaptive adjustment of the FM component of calls in CF-FM bats is not involved in avoidance of conspecific jamming. *Animal Behaviour*, 216, 97–105. <https://doi.org/10.1016/j.anbehav.2024.07.021>
- Dray, S., Choler, P., Dolédec, S., Peres-Neto, P. R., Thuiller, W., Pavoine, S., & Ter Braak, C. J. F. (2014). Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation. *Ecology*, 95(1), 14–21. <https://doi.org/10.1890/13-0196.1>
- Dray, S., & Dufour, A. (2007). *The ade4 package: Implementing the duality diagram for ecologists*. <https://cran.r-project.org/web/packages/ade4/index.html>.
- Estrada-Villegas, S., Meyer, C. F. J., & Kalko, E. K. V. (2010). Effects of tropical forest fragmentation on aerial insectivorous bats in a land-bridge island system. *Biological Conservation*, 143(3), 597–608. <https://doi.org/10.1016/j.biocon.2009.11.009>
- FAO. (2023). *Land statistics and indicators 2000–2021*. <https://doi.org/10.4060/cc6907en>
- Farneda, F. Z., Otálora-Ardila, A., Meyer, C. F. J., López-Arévalo, H. F., Gómez-Posada, C., & Polanía, J. (2024). Multiple dimensions of phyllostomid bat biodiversity across ecosystems of the Orinoco Llanos. *Animal Conservation*. <https://doi.org/10.1111/acv.12941>
- Farneda, F. Z., Rocha, R., López-Baucells, A., Groenenberg, M., Silva, I., Palmeirim, J. M., Bobrowiec, P. E. D., & Meyer, C. F. J. (2015). Trait-related responses to habitat fragmentation in Amazonian bats. *Journal of Applied Ecology*, 52(5), 1381–1391. <https://doi.org/10.1111/1365-2664.12490>
- Ferreira, D. F., Gibb, R., López-Baucells, A., Nunes, N. J., Jones, K. E., & Rocha, R. (2022). Species-specific responses to land-use change in island insectivorous bats. *Journal for Nature Conservation*, 67. <https://doi.org/10.1016/j.jnc.2022.126177>
- Frank, H. K., Frishkoff, L. O., Mendenhall, C. D., Daily, G. C., & Hadly, E. A. (2017). *Phylogeny, Traits, and Biodiversity of a Neotropical Bat Assemblage: Close Relatives Show Similar Responses to Local Deforestation*. <https://doi.org/10.5061/dryad.mb552>
- Frick, W. F., Kingston, T., & Flanders, J. (2020). A review of the major threats and challenges to global bat conservation. In *Annals of the New York Academy of Sciences* (Vol. 1469, Issue 1, pp. 5–25). Blackwell Publishing Inc. <https://doi.org/10.1111/nyas.14045>
- Froidevaux, J. S. P., Zellweger, F., Bollmann, K., & Obrist, M. K. (2014). Optimizing passive acoustic sampling of bats in forests. *Ecology and Evolution*, 4(24), 4690–4700. <https://doi.org/10.1002/ece3.1296>
- Garbino, G., Gregorin, R., Lima, I., Loureiro, L., Moras, L., & Moratelli, R. (2022). *Updated checklist of Brazilian bats: version 2020*. Brazilian Bat List Committee — CLMB Brazilian Society for the Study of Chiropterans (Sbeq).
- García-Morales, R., Moreno, C. E., Badano, E. I., Zuria, I., Galindo-González, J., Rojas-Martínez, A. E., & Ávila-Gómez, E. S. (2016). Deforestation impacts on bat functional diversity in tropical landscapes. *PLoS ONE*, 11(12). <https://doi.org/10.1371/journal.pone.0166765>

- Gonçalves-Souza, T., Chase, J. M., Haddad, N. M., Vancine, M. H., Didham, R. K., Melo, F. L. P., Aizen, M. A., Bernard, E., Chiarello, A. G., Faria, D., Gibb, H., de Lima, M. G., Magnago, L. F. S., Mariano-Neto, E., Nogueira, A. A., Nemésio, A., Passamani, M., Pinho, B. X., Rocha-Santos, L., ... Sanders, N. J. (2025). Species turnover does not rescue biodiversity in fragmented landscapes. *Nature*. <https://doi.org/10.1038/s41586-025-08688-7>
- Guillerme, T., Cardoso, P., Jørgensen, M. W., Mammola, S., & Matthews, T. J. (2025). The what, how, and why of trait-based analyses in ecology. *Ecography*. <https://doi.org/10.1111/ecog.07580>
- Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., Lovejoy, T. E., Sexton, J. O., Austin, M. P., Collins, C. D., Cook, W. M., Damschen, E. I., Ewers, R. M., Foster, B. L., Jenkins, C. N., King, A. J., Laurance, W. F., Levey, D. J., Margules, C. R., ... Townshend, J. R. (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*, *1*(2). <https://doi.org/10.1126/sciadv.1500052>
- Hanspach, J., Fischer, J., Ikin, K., Stott, J., & Law, B. S. (2012). Using trait-based filtering as a predictive framework for conservation: A case study of bats on farms in southeastern Australia. *Journal of Applied Ecology*, *49*(4), 842–850. <https://doi.org/10.1111/j.1365-2664.2012.02159.x>
- Heinrich, V. H. A., Dalagnol, R., Cassol, H. L. G., Rosan, T. M., de Almeida, C. T., Silva Junior, C. H. L., Campanharo, W. A., House, J. I., Sitch, S., Hales, T. C., Adami, M., Anderson, L. O., & Aragão, L. E. O. C. (2021). Large carbon sink potential of secondary forests in the Brazilian Amazon to mitigate climate change. *Nature Communications*, *12*(1). <https://doi.org/10.1038/s41467-021-22050-1>
- Hending, D., Andrianiaina, A., Rose, M., Rowlands, A., Storm, S., Holderied, M. W., & Cotton, S. (2023). Vanilla Bats: Insectivorous Bat Diversity in the Vanilla Agroecosystems of Northeastern Madagascar. *Acta Chiropterologica*, *24*(2), 363–378. <https://doi.org/10.3161/15081109ACC2022.24.2.007>
- Henle, K., Davies, K. F., Kleyer, M., Margules, C., & Settele, J. (2004). Predictors of species sensitivity to fragmentation. In *Biodiversity and Conservation* (Vol. 13).
- Jakobsson, S., Wood, H., Ekroos, J., & Lindborg, R. (2020). *Contrasting multi-taxa functional diversity patterns along vegetation structure gradients of woody pastures*. <https://doi.org/10.1007/s10531-020>
- Jones, G., Jacobs, D., Kunz, T., Willig, M., & Racey, P. (2009). Carpe noctem: the importance of bats as bioindicators. *Endangered Species Research*, *8*, 93–115. <https://doi.org/10.3354/esr00182>
- Jung, K., Kalko, E. K. V., & Von Helversen, O. (2007). Echolocation calls in Central American emballonurid bats: Signal design and call frequency alternation. *Journal of Zoology*, *272*(2), 125–137. <https://doi.org/10.1111/j.1469-7998.2006.00250.x>
- Kemp, J., López-Baucells, A., Rocha, R., Wangenstein, O. S., Andriatafika, Z., Nair, A., & Cabeza, M. (2019). Bats as potential suppressors of multiple agricultural pests: A case study from Madagascar. *Agriculture, Ecosystems and Environment*, *269*, 88–96. <https://doi.org/10.1016/j.agee.2018.09.027>

- Kinap, N. M., Farneda, F. Z., Rabelo, R. M., Bernard, E., & Bobrowiec, P. E. D. (2024). Functional diversity and trait-environment relationships of bat assemblages in an Amazonian forest-savannah mosaic. *Biodiversity and Conservation*, *33*(10), 2757–2774. <https://doi.org/10.1007/s10531-024-02880-3>
- Korine, C., Adams, R., Russo, D., Fisher-Phelps, M., & Jacobs, D. (2016). Bats and Water: Anthropogenic Alterations Threaten Global Bat Populations. In *Bats in the Anthropocene: Conservation of Bats in a Changing World* (pp. 215–241). Springer International Publishing. [https://doi.org/10.1007/978-3-319-25220-9\\_8](https://doi.org/10.1007/978-3-319-25220-9_8)
- Kunz, T. H., de Torrez, E. B., Bauer, D., Lobo, T., & Fleming, T. H. (2011). Ecosystem services provided by bats. In *Annals of the New York Academy of Sciences* (Vol. 1223, Issue 1, pp. 1–38). Blackwell Publishing Inc. <https://doi.org/10.1111/j.1749-6632.2011.06004.x>
- Kuschnig, N., Cuaresma, J. C., Krisztin, T., & Giljum, S. (2021). Spatial spillover effects from agriculture drive deforestation in Mato Grosso, Brazil. *Scientific Reports*, *11*(1), 21804. <https://doi.org/10.1038/s41598-021-00861-y>
- Lapola, D. M., Pinho, P., Barlow, J., Aragão, L. E. O. C., Berenguer, E., Carmenta, R., Liddy, H. M., Seixas, H., Silva, C. V. J., Silva-Junior, C. H. L., Alencar, A. A. C., Anderson, L. O., Armenteras, D., Brovkin, V., Calders, K., Chambers, J., Chini, L., Costa, M. H., Faria, B. L., ... Walker, W. S. (2023). The drivers and impacts of Amazon forest degradation. *Science*, *379*(6630). <https://doi.org/10.1126/science.abp8622>
- Laurance, W. F., Sayer, J., & Cassman, K. G. (2014). Agricultural expansion and its impacts on tropical nature. *Trends in Ecology & Evolution*, *29*(2), 107–116. <https://doi.org/10.1016/j.tree.2013.12.001>
- López-Baucells, A., Rowley, S., Rocha, R., Bobrowiec, P. E. D., Palmeirim, J. M., Farneda, F. Z., & Meyer, C. F. J. (2022). Interplay between local and landscape-scale effects on the taxonomic, functional and phylogenetic diversity of aerial insectivorous neotropical bats. *Landscape Ecology*, *37*(11), 2861–2875. <https://doi.org/10.1007/s10980-022-01493-x>
- López-Baucells, A., Yoh, N., Rocha, R., Bobrowiec, P. E. D., Palmeirim, J. M., & Meyer, C. F. J. (2021). Optimizing bat bioacoustic surveys in human-modified Neotropical landscapes. *Ecological Applications*, *31*(6). <https://doi.org/10.1002/eap.2366>
- López-Baucells, Rocha, Bobrowiec, Bernard, Palmeirim, & Meyer. (2016). *Field Guide to the Bats of the Amazon*. [www.tropicalconservation.net](http://www.tropicalconservation.net)
- López-Bosch, D., Rocha, R., López-Baucells, A., Wang, Y., Si, X., Ding, P., Gibson, L., & Palmeirim, A. F. (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*(2), 208–221. <https://doi.org/10.1002/rse2.237>
- López-González, C., Gómez-Ruiz, E. P., Lozano, A., & López-Wilchis, R. (2015). Activity of insectivorous bats associated with cattle ponds at la Michilía biosphere reserve, Durango, Mexico: Implications for conservation. *Acta Chiropterologica*, *17*(1), 117–129. <https://doi.org/10.3161/15081109ACC2015.17.1.010>

- Luo, B., Leiser-Miller, L., Santana, S. E., Zhang, L., Liu, T., Xiao, Y., Liu, Y., & Feng, J. (2019). Echolocation call divergence in bats: a comparative analysis. *Behavioral Ecology and Sociobiology*, 73(11). <https://doi.org/10.1007/s00265-019-2766-9>
- Mancini, M. C. S., Bobrowiec, P. E. D., Oliveira, L. L., Del Sarto Oliveira, L. L., & Gregorin, R. (2024). Better together: integrating mist-nets and bioacoustics reveals large-scale native vegetation as a key predictor of bat community conservation in a fragmented landscape. *Biodiversity and Conservation*, 33(4), 1503–1521. <https://doi.org/10.1007/s10531-024-02813-0>
- Marinello, M. M., & Bernard, E. (2014). Wing morphology of neotropical bats: A quantitative and qualitative analysis with implications for habitat use. *Canadian Journal of Zoology*, 92(2), 141–147. <https://doi.org/10.1139/cjz-2013-0127>
- Marques, J. T., Ramos Pereira, M. J., & Palmeirim, J. M. (2016). Patterns in the use of rainforest vertical space by Neotropical aerial insectivorous bats: All the action is up in the canopy. *Ecography*, 39(5), 476–486. <https://doi.org/10.1111/ecog.01453>
- Meyer, C. F. J., & Kalko, E. K. V. (2008). Assemblage-level responses of phyllostomid bats to tropical forest fragmentation: Land-bridge islands as a model system. *Journal of Biogeography*, 35(9), 1711–1726. <https://doi.org/10.1111/j.1365-2699.2008.01916.x>
- Miatta, M., Bates, A. E., & Snelgrove, P. V. R. (2021). Incorporating Biological Traits into Conservation Strategies. *Downloaded from Www.Annualreviews.Org. Guest (Guest*, 49, 58. <https://doi.org/10.1146/annurev-marine-032320>
- Moir, M., Richards, L. R., Rambau, R. V., & Cherry, M. I. (2021). Functional diversity and trait filtering of insectivorous bats relate to forest biogeography and fragmentation in South Africa. *Journal of Biogeography*, 48(5), 1170–1182. <https://doi.org/10.1111/jbi.14069>
- Mouillot, D., Graham, N. A. J., Villéger, S., Mason, N. W. H., & Bellwood, D. R. (2013a). A functional approach reveals community responses to disturbances. In *Trends in Ecology and Evolution* (Vol. 28, Issue 3, pp. 167–177). <https://doi.org/10.1016/j.tree.2012.10.004>
- Mouillot, D., Graham, N. A. J., Villéger, S., Mason, N. W. H., & Bellwood, D. R. (2013b). A functional approach reveals community responses to disturbances. *Trends in Ecology & Evolution*, 28(3), 167–177. <https://doi.org/10.1016/j.tree.2012.10.004>
- Norberg, & Rayner. (1987). *Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation*. <https://royalsocietypublishing.org/>
- Núñez, S. F., López-Baucells, A., Rocha, R., Farneda, F. Z., Bobrowiec, P. E. D., Palmeirim, J. M., & Meyer, C. F. J. (2019). Echolocation and Stratum Preference: Key Trait Correlates of Vulnerability of Insectivorous Bats to Tropical Forest Fragmentation. *Frontiers in Ecology and Evolution*, 7. <https://doi.org/10.3389/fevo.2019.00373>
- Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., & Wagner, H. (2020). *Vegan: Community Ecology Package*. <https://Cran.r- Proj e Ct.Org/Web/Packa Ges/Vegan/ Index.Html>.

- Otálora-Ardila, A., Farneda, F. Z., Meyer, C. F. J., López-Arévalo, H. F., Polanía, J., & Gómez-Posada, C. (2024). Trait-mediated filtering predicts phyllostomid bat responses to habitat disturbance in the Orinoco Llanos. *Biodiversity and Conservation*, 33(4), 1285–1302. <https://doi.org/10.1007/s10531-024-02792-2>
- Pavan, A. C., Bobrowiec, P. E. D., & Percequillo, A. R. (2018). Geographic variation in a South American clade of mormoopid bats, *Pteronotus* (Phyllostodia), with description of a new species. *Journal of Mammalogy*, 99(3), 624–645. <https://doi.org/10.1093/jmammal/gyy048>
- Pavoine, S. (2020). adiv: An r package to analyse biodiversity in ecology. *Methods in Ecology and Evolution*, 11(9), 1106–1112. <https://doi.org/10.1111/2041-210X.13430>
- Püttker, T., Crouzeilles, R., Almeida-Gomes, M., Schmoeller, M., Maurenza, D., Alves-Pinto, H., Pardini, R., Vieira, M. V., Banks-Leite, C., Fonseca, C. R., Metzger, J. P., Accacio, G. M., Alexandrino, E. R., Barros, C. S., Bogoni, J. A., Boscolo, D., Brancalion, P. H. S., Bueno, A. A., Cambui, E. C. B., ... Prevedello, J. A. (2020). Indirect effects of habitat loss via habitat fragmentation: A cross-taxa analysis of forest-dependent species. *Biological Conservation*, 241. <https://doi.org/10.1016/j.biocon.2019.108368>
- Quintanilla, M., León, A. G., Josse, C., & Romo, Z. (2022). *The Amazon against the clock: a Regional Assessment on Where and How to protect 80% by 2025*. <https://amazonia80x2025.earth/>
- Ricotta, C., de Bello, F., Moretti, M., Caccianiga, M., Cerabolini, B. E. L., & Pavoine, S. (2016). Measuring the functional redundancy of biological communities: a quantitative guide. *Methods in Ecology and Evolution*, 7(11), 1386–1395. <https://doi.org/10.1111/2041-210X.12604>
- Rowley, S., López-Baucells, A., Rocha, R., Bobrowiec, P. E. D., & Meyer, C. F. J. (2024). Secondary forest buffers the effects of fragmentation on aerial insectivorous bat species following 30 years of passive forest restoration. *Restoration Ecology*. <https://doi.org/10.1111/rec.14093>
- Silva, I., Rocha, R., López-Baucells, A., Farneda, F. Z., & Meyer, C. F. J. (2020). Effects of forest fragmentation on the vertical stratification of neotropical bats. *Diversity*, 12(2). <https://doi.org/10.3390/d12020067>
- Simoës, R., Picoli, M. C. A., Camara, G., Maciel, A., Santos, L., Andrade, P. R., Sánchez, A., Ferreira, K., & Carvalho, A. (2020). Land use and cover maps for Mato Grosso State in Brazil from 2001 to 2017. *Scientific Data*, 7(1). <https://doi.org/10.1038/s41597-020-0371-4>
- Spera, S. A., Cohn, A. S., Vanwey, L. K., Mustard, J. F., Rudorff, B. F., Risso, J., & Adami, M. (2014). Recent cropping frequency, expansion, and abandonment in Mato Grosso, Brazil had selective land characteristics. *Environmental Research Letters*, 9(6). <https://doi.org/10.1088/1748-9326/9/6/064010>
- Strand, J., Soares-Filho, B., Costa, M. H., Oliveira, U., Ribeiro, S. C., Pires, G. F., Oliveira, A., Rajão, R., May, P., van der Hoff, R., Siikamäki, J., da Motta, R. S., & Toman, M. (2018). Spatially explicit valuation of the Brazilian Amazon Forest's Ecosystem

- Services. *Nature Sustainability*, 1(11), 657–664. <https://doi.org/10.1038/s41893-018-0175-0>
- Suárez-Castro, A. F., Mayfield, M. M., Mitchell, M. G. E., Cattarino, L., Maron, M., & Rhodes, J. R. (2020). Correlations and variance among species traits explain contrasting impacts of fragmentation and habitat loss on functional diversity. *Landscape Ecology*, 35(10), 2239–2253. <https://doi.org/10.1007/s10980-020-01098-2>
- Threlfall, C., Law, B., Penman, T., & Banks, P. B. (2011). Ecological processes in urban landscapes: Mechanisms influencing the distribution and activity of insectivorous bats. *Ecography*, 34(5), 814–826. <https://doi.org/10.1111/j.1600-0587.2010.06939.x>
- Torrent, L., López-Baucells, A., Rocha, R., Bobrowiec, P. E. D., & Meyer, C. F. J. (2018). The importance of lakes for bat conservation in Amazonian rainforests: an assessment using autonomous recorders. *Remote Sensing in Ecology and Conservation*, 4(4), 339–351. <https://doi.org/10.1002/rse2.83>
- Violle, C., Reich, P. B., Pacala, S. W., Enquist, B. J., & Kattge, J. (2014). The emergence and promise of functional biogeography. In *Proceedings of the National Academy of Sciences of the United States of America* (Vol. 111, Issue 38, pp. 13690–13696). National Academy of Sciences. <https://doi.org/10.1073/pnas.1415442111>
- White, R. J., & Razgour, O. (2020). Emerging zoonotic diseases originating in mammals: a systematic review of effects of anthropogenic land-use change. In *Mammal Review* (Vol. 50, Issue 4, pp. 336–352). Blackwell Publishing Ltd. <https://doi.org/10.1111/mam.12201>
- Wolf, A. A., Funk, J. L., Selmants, P. C., Morozumi, C. N., Hernández, D. L., Pasari F □, J. R., Zavaleta, E. S., Pacala, S. W., Designed, E. S. Z., Performed, E. S. Z., & Ana-Lyzed Data, J. L. F. (2021). *Trait-based filtering mediates the effects of realistic biodiversity losses on ecosystem functioning*. 118. <https://doi.org/10.1073/pnas.2022757118/-/DCSupplemental>
- Wordley, C. F. R., Sankaran, M., Mudappa, D., & Altringham, J. D. (2017). Bats in the Ghats: Agricultural intensification reduces functional diversity and increases trait filtering in a biodiversity hotspot in India. *Biological Conservation*, 210, 48–55. <https://doi.org/10.1016/j.biocon.2017.03.026>
- WWF. (2022). *WWF 2022*.
- Yoh, N., Clarke, J. A., López-Baucells, A., Mas, M., Bobrowiec, P. E. D., Rocha, R., & Meyer, C. F. J. (2022). Edge effects and vertical stratification of aerial insectivorous bats across the interface of primary-secondary Amazonian rainforest. *PLoS ONE*, 17(9 September). <https://doi.org/10.1371/journal.pone.0274637>
- Yoh, N., Syme, P., Rocha, R., Meyer, C. F. J., & López-Baucells, A. (2020). Echolocation of Central Amazonian ‘whispering’ phyllostomid bats: call design and interspecific variation. *Mammal Research*, 65(3), 583–597. <https://doi.org/10.1007/s13364-020-00503-0>
- Zalles, V., Hansen, M. C., Potapov, P. V., Stehman, S. V., Tyukavina, A., Pickens, A., Song, X. P., Adusei, B., Okpa, C., Aguilar, R., John, N., & Chavez, S. (2019). Near doubling of

Brazil's intensive row crop area since 2000. *Proceedings of the National Academy of Sciences of the United States of America*, 116(2), 428–435.  
<https://doi.org/10.1073/pnas.1810301115>

Zarin, D. J., Harris, N. L., Baccini, A., Aksenov, D., Hansen, M. C., Azevedo-Ramos, C., Azevedo, T., Margono, B. A., Alencar, A. C., Gabris, C., Allegretti, A., Potapov, P., Farina, M., Walker, W. S., Shevade, V. S., Loboda, T. V., Turubanova, S., & Tyukavina, A. (2016). Can carbon emissions from tropical deforestation drop by 50% in 5 years? *Global Change Biology*, 22(4), 1336–1347. <https://doi.org/10.1111/gcb.13153>

# Management report

## **Supervisor revisions**

At the beginning of Michalemas term, the co-supervisor I had been assigned changed departments and was no longer available to co-supervise my project. My supervisor tried but was unable to find another person to fill in as a suitable co-supervisor. I therefore reached out to other researchers for meetings and advice when necessary, for instance for queries that my supervisor was unable to advise on, such as the bioacoustic analysis.

## **Bioacoustic identifications**

For the bioacoustic identification portion of the project, I worked alongside another Master's student. We divided the dataset equally and supported each other with identifications when necessary. We received the bioacoustic data from Harriet Bartlett and the researchers in Brazil in the 1<sup>st</sup> week of Michaelmas term. In preparation, we met with Eva Nobrega during 0<sup>th</sup> week, who introduced us to Kaleidoscope software and demonstrated how to identify call characteristics using European bat species as examples.

When we began identifying the data, we faced significant challenges. The dataset included over 28 sonotypes, and neither I nor the other Master's student had prior experience in identifying bat echolocation calls. Furthermore, no one in Oxford knew how to identify Brazilian bat calls, so we had no one to consult with any queries apart from the guide we were using (López-Baucells et al., 2016) and each other. In 7<sup>th</sup> week, we had a valuable meeting with Adrià López-Baucells, an expert in Neotropical bat bioacoustics. He addressed several of our questions and confirmed that we were identifying calls accurately. After completing my identifications in 2<sup>nd</sup> week of Hilary term, I revisited and revised the first several weeks of IDs, as by this point, my knowledge and understanding had improved considerably, allowing me to correct previous misidentifications.

## **Data analysis**

In 5<sup>th</sup> week of Hilary, we began cleaning the data in R studio, which contained over 60,000 bat identifications. Once the data were processed, I ran RLQ and fourth corner analyses and decided which model would be best to determine the differences in alpha diversity between forest and pasture, as this had not been done before by my supervisor or any other papers I had come across. I decided to use mixed beta regression models due to the structure of my response variables (limited between 0 and 1) and the need to account for between-farm variation. Running the RLQ analysis was relatively straightforward, but interpreting the results proved more difficult due to the limited number of published studies explaining its outputs. Despite this, I carefully read through the available literature (publications, author guides, and

R studio package descriptions) and came to understand the ecological interpretations of my results.

### **Thesis write-up**

In 7<sup>th</sup> week of Hilary, I began to write up my thesis. My supervisor provided feedback on my introduction and methods as I wrote them. As I knew he was going to Borneo at the start of 2<sup>nd</sup> week of Trinity, I sent him a draft of the full thesis at the start of the 1<sup>st</sup> week of Trinity, and he provided me with comments on the Wednesday before submission.

### **Technological issues**

Throughout Hilary term, I encountered several technological difficulties that impacted my work. Firstly, my original laptop performed an unprompted factory reset. All my work had been backed up, but the software used to perform acoustic analyses and coding had to be re-installed and set up, which took more time than necessary due to the way in which software had to be installed (it was a chromebook so I had to code apps to install them, which was a laborious process). I purchased a new laptop and continued to use the faulty one in the time before it arrived. The new laptop arrived, and I set this up with all the necessary software, but it too proved faulty, so had to be returned after less than a week. I bought a third laptop, where the same problem ensued, and I am now using the 4<sup>th</sup> laptop of the year. I lost considerable time searching for suitable laptops, checking reviews, ordering them, and setting up the necessary software.

## Appendix

- 1) Photos of data collection
- 2) Photos of echolocation calls
- 3) Estimating wing morphology values
- 4) Landscape variable calculations
- 5) Trait values
- 6) Environmental variables values

### Photos of data collection



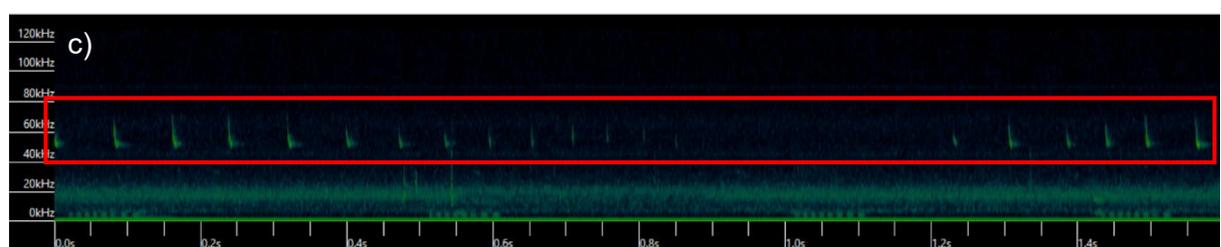
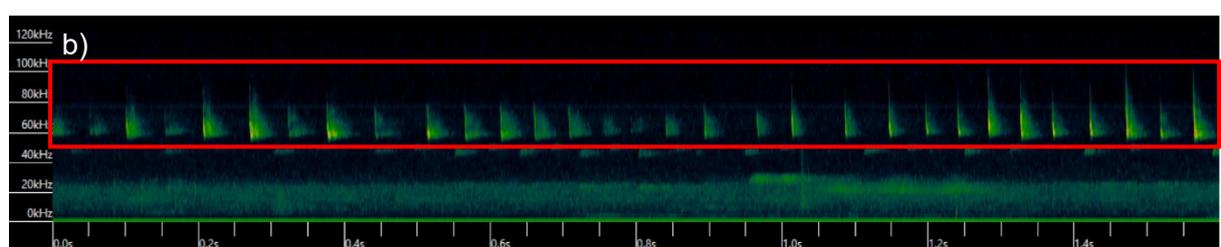
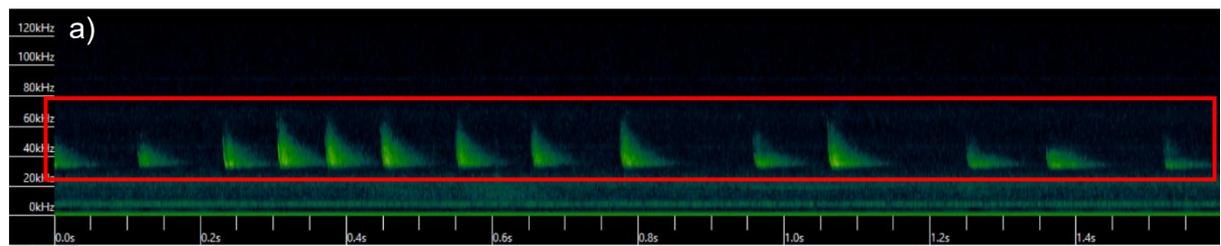
**Figure A1:** Photos of the detectors being deployed in Brazil, by Harriet Bartlett and researchers from the University of Sao Paulo and the University of Passo Fundo, Brazil

## Photos of echolocation calls

Below are examples of each classification of echolocation call, and of the difficulties encountered when identifying Molossidae D. Photos were taken from my bioacoustic analysis in Kaleidoscope. Example calls are outlined in a red box.

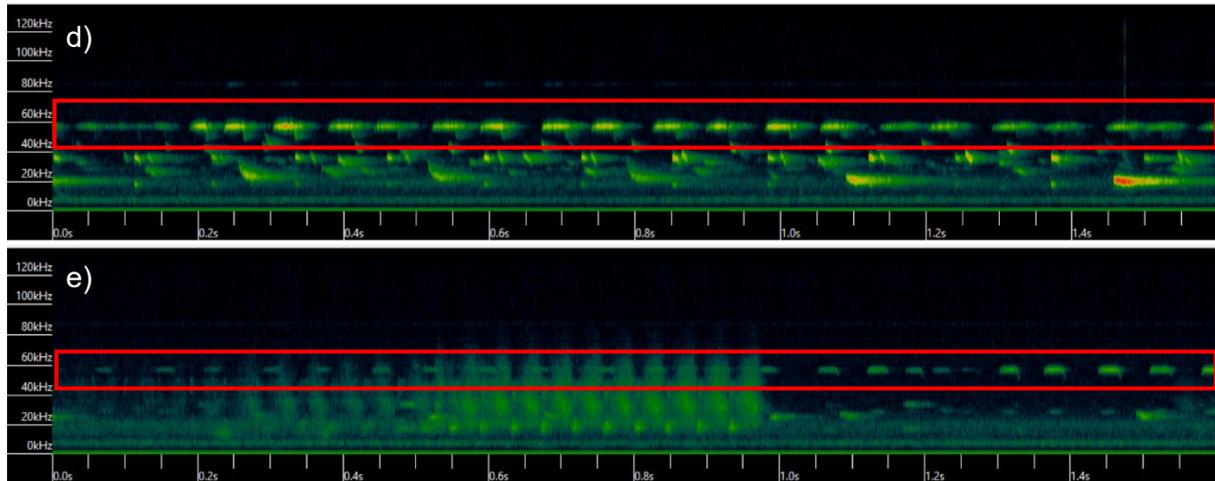
### Frequency-modulated (FM) calls

Classified as (a) *Eptesicus I.*, (b) *Myotis nigricans*, and (c) *Myotis riparius*



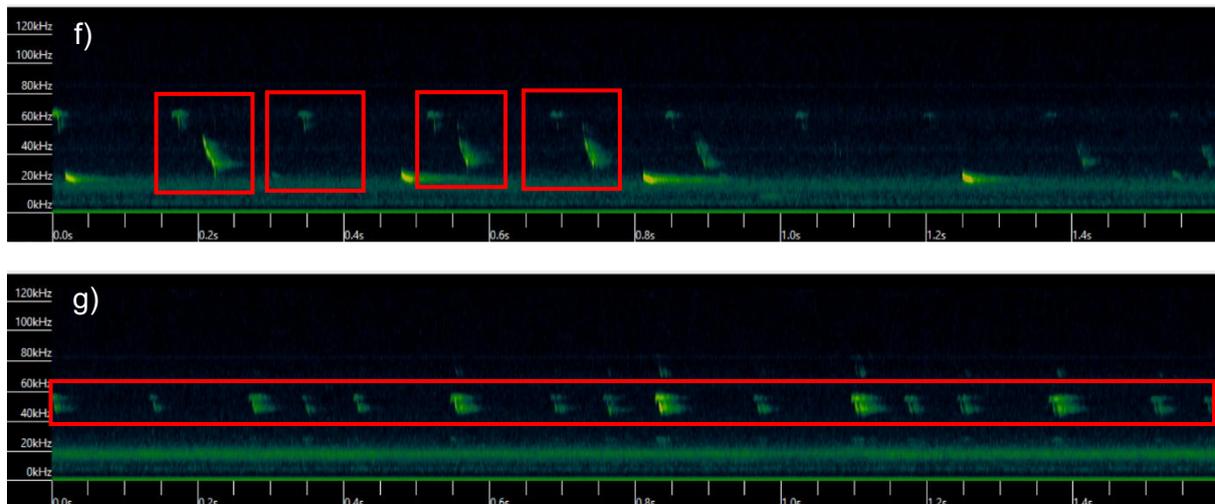
## Constant-frequency (CF) calls

Classified as (d&e) *Pteronotus rubiginosus*



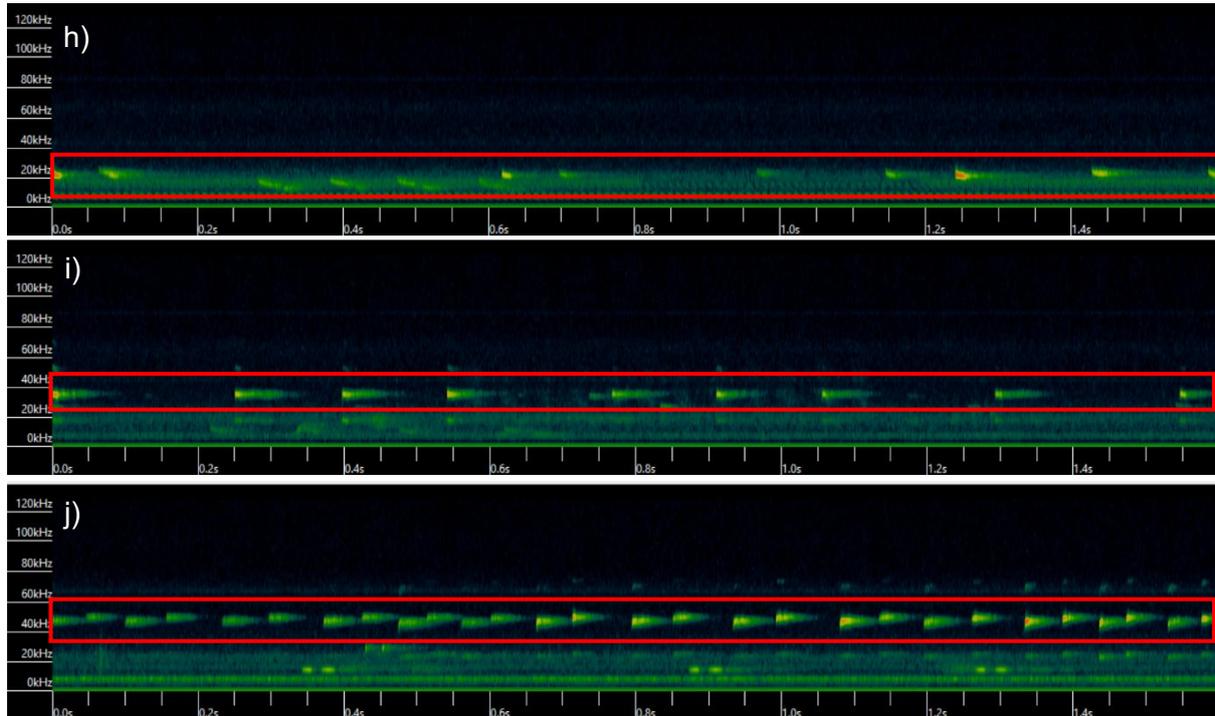
## Constant-frequency frequency-modulated (CF-FM) calls

Classified as (f) *Noctilio albiventris* and (g) *Pteronotus gymnonotus*



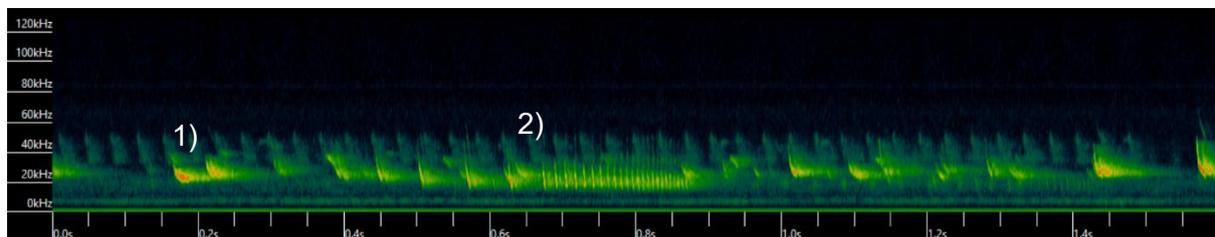
## Quasi-constant frequency (qCF) calls

Classified as (h) Molossidae D, (i) *Peropteryx kappleri*, and (j) *Saccopteryx billineata/leptura*



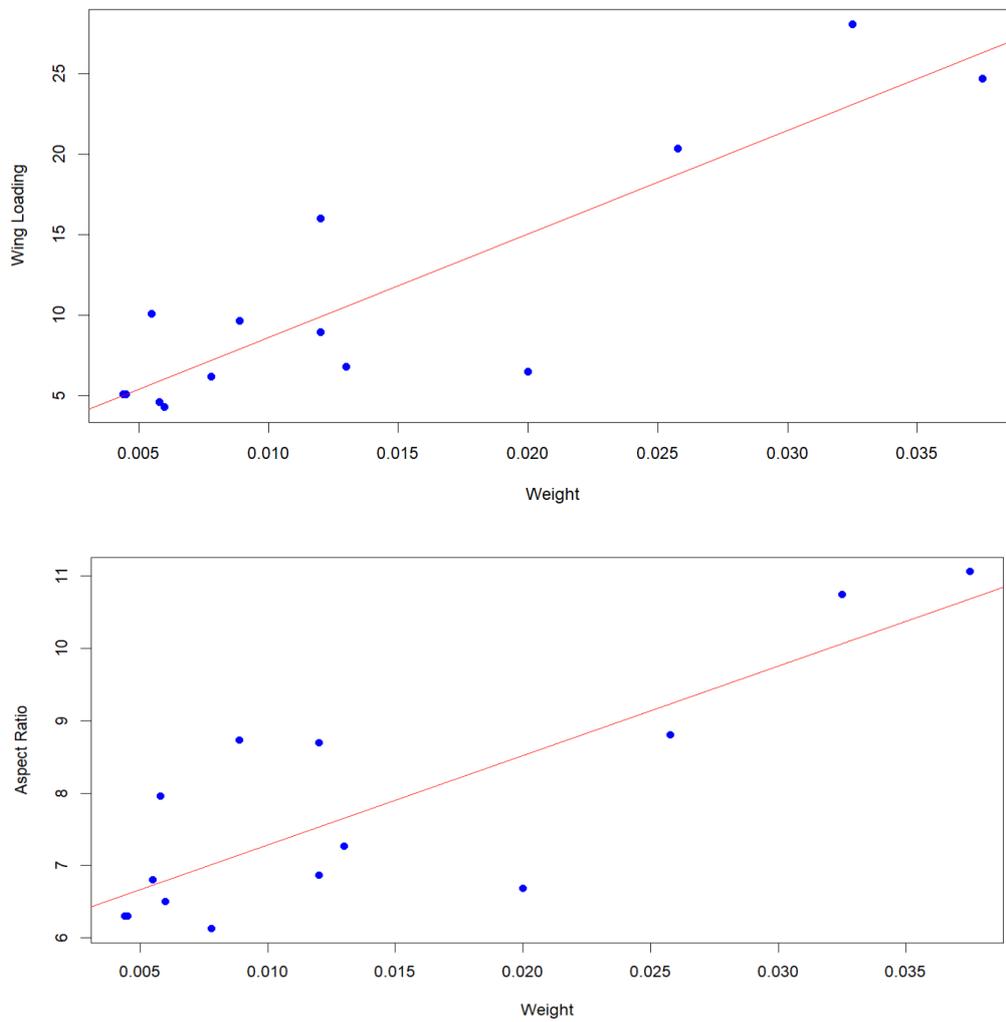
## Difficulties identifying Molossidae D call shape

Whilst Molossidae D's calls mostly appeared qCF, they were prone to turning FM as the bat approaches their prey. As shown in this example, at the beginning of the image (Figure A2), the Molossidae D's call is qCF shaped (1). However, as the bat approaches an insect towards the middle of the picture, the pulses get closer together and the shape becomes increasingly FM (2). Call shapes are identified as the search-phase call rather than when approaching prey or during social calls, so the most important call shape here is the qCF shape shown towards the beginning of the image.



**Figure A2:** Molossidae D's qCF call morphing into an FM call as it approaches an insect

## Estimating wing morphology values



**Figure S3:** Linear regression demonstrating the relationship between body mass and (a) relative wing loading (rWL) and (b) aspect ratio (AR) of the AIBs included in the analysis. Equations of the regression were used to estimate values of rWL and AR for *Noctilio albus*, *Saccopteryx canescens*, and *Peropteryx trinitatis*.  $rWL = 642.732 * Weight + 2.187$ , adjusted  $R^2 = 0.7558$ ;  $AR = 123.4593 * Weight + 6.0485$ , adjusted  $R^2 = 0.6503$ .

## Landscape variable calculations

Landscape variables were calculated in QGIS using land-use data from MapBiomass Brazil (Land cover and use, Collection 9).

Forest and pasture cover was calculated as follows:

$$\text{Land-use cover} = \text{Total area of land-use pixel} / \text{Buffer area}$$

Forest patch density was calculated as follows:

$$\text{Forest patch density (patches per ha)} = (\text{number of forest patches} / \text{total area of forest in buffer (m}^2\text{)}) * 10,000$$

Edge density was calculated as follows:

$$\text{Edge density (meters per ha)} = (\text{total length of forest patch edges (m)} / \text{buffer area (m}^2\text{)}) * 10,000$$

## Trait values

Relative wing loading = Wing loading (adult mass multiplied by gravitational acceleration divided by wingspan) divided by mass raised to a third:  $rWL = (Mg/S)/mass^{1/3}$

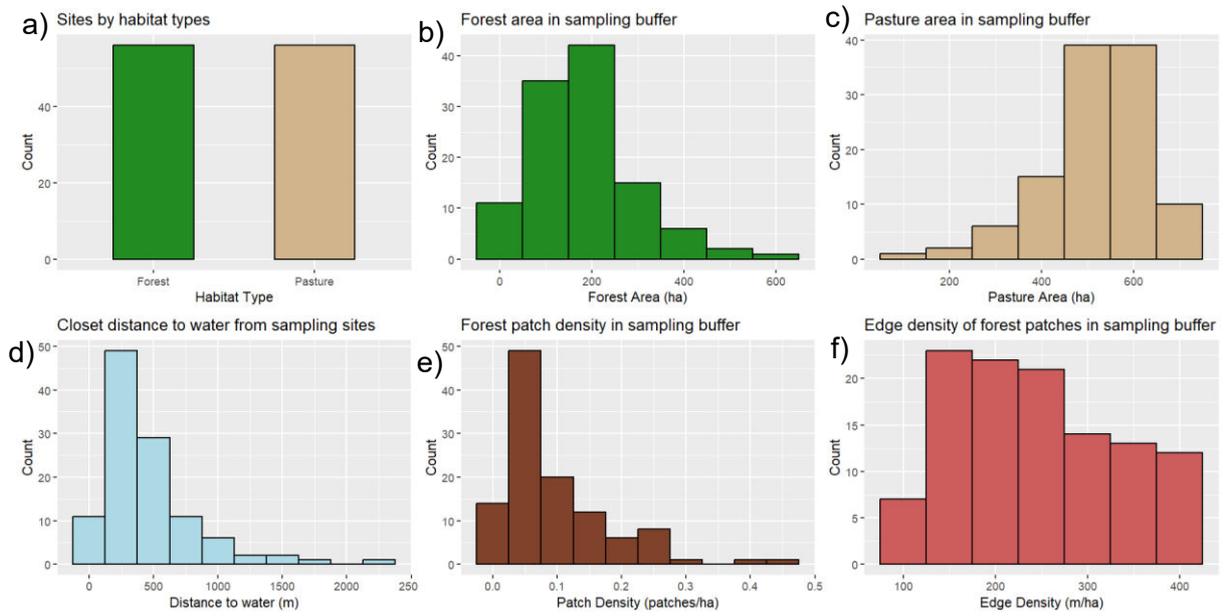
Aspect ratio = The square of the adult wingspan, divided by the area of the wing:  $AR = B^2/S$

**Table A1:** Values of the functional traits for each of the 19 species/sonotypes included in the analysis

SPS	Species	Frequency	Call_structure	Weight	AR	WL	VertS	FA_smallest*
E2	Centronycteris maximiliani/centralis	40	QCF	5.8	7.9575	4.61	2	41.5
CB	Cormura brevirostris	28	QCF	8.9	8.73	9.66	2	41
EP	Eptesicus brasiliensis	32	FM	12	6.8648	8.94	2	40
M1	Molossus molossus	38.25	QCF	12	8.7	16	3	37
MN	Myotis nigricans	60	FM	4.5	6.3	5.1	2	30
MR	Myotis riparius	50	FM	4.4	6.3	5.1	2	31
PK	Peropteryx kappleri	31	QCF	8.1	7.3268	6.66	2	43
PM	Peropteryx macrotis	38	QCF	5.5	6.8	10.1	2	43
P	Promops sp.	32.25	QCF	37.5	11.0626	24.7	3	48
PG	Pteronotus gymnonotus	55	CF-FM	13	6.4883	6.46	1	50
PG	Pteronotus gymnonotus	55	CF-FM	13	8.0428	7.1	1	50
P5	Pteronotus parnelli 55	55	CF	20	6.68	6.48	1	50
PP	Pteronotus personatus	68.5	CF-FM	7.5	6.7	5.97	1	40
S	Saccopteryx bilineata	43.5	QCF	9.3	4.5373	4.62	2	40.5
S	Saccopteryx bilineata	43.5	QCF	9.3	8.1719	7.66	2	40.5
S	Saccopteryx leptura	51.5	QCF	4.8	5.6774	6.25	2	40.5
MD	Eumops hansae	20	QCF	16.5	8.6961	22.49	3	44.22222222
MD	Eumops auripendulus	20	QCF	32	10.6799	19.89	3	44.22222222
MD	Eumops maurus	20	QCF	22	8.4748	13.13	3	44.22222222
MD	Cynomops sp	20	QCF	32.55	7.3659	25.96	3	44.22222222
M2	M2	32.5	QCF	32.5	10.0647	22.79	3	41.5
M2	M2	32.5	QCF	32.5	11.0626	38.01	3	41.5
M2	Molossus ater	32.5	QCF	32.5	11.1	23.4	3	41.5
RN	Rhynchonycteris naso	98.88	CF-FM	6	6.5	4.3	2	35
N.A	Noctilio albus	73.06	CF-FM	25.7	9.22	18.71	2	54
E1	Saccopteryx canescens	54	QCF	5	6.67	5.4	2	35
PT	Peropteryx trinitatis	43.63	QCF	6	6.79	6.04	2	36

\* Lowest values from the range of FA values were used from Lopez-Baucells et al (2016)

## Environmental variables values



**Figure A4:** Values of the six environmental variables included in the analysis (a) Habitat type (either forest or pasture), (b) Forest area in the sampling buffer (ha), (c) Pasture area in the sampling buffer (ha), (d) The closest distance to water from each of the sampling sites, (e) the patch density of forest in the sampling buffer, and (f) the edge density of forest patches in the sampling buffer