Department of **BIOLOGY**

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1. Abstract

Cattle farming is a major driver of deforestation, forest degradation, and biodiversity loss, while also supporting national food security and economic development. Balancing these outcomes is a challenge, particularly in Brazil where cattle farming drives >70% of deforestation. The ecological impacts of deforestation have been studied using bats as bioindicators, though specific effects of cattle farming on Amazonian biodiversity remains poorly understood. This study investigates the responses of aerial insectivorous bats (AIBs) to beef-production in the Brazilian Amazon. Using bioacoustic data from farms in Mato Grosso, bat activity, sonotype (species) richness and evenness, and composition were compared between forest and pastures at assemblage-level, ensemble-level and individual sonotype. Diversity metrics were calculated using Hill numbers, and Generalised Additive Models were fitted to test the differences between forest and pasture, and the influence of landscape variables (forest cover, patch density, and edge density) at 0.5, 1.5, and 3 km scales. Bat activity and sonotype richness were significantly higher in pastures than forests, potentially due to higher insect densities. This pattern was driven by open-space and edge foragers, suggesting that cattle landscapes favour disturbance-tolerant AIB sonotypes although forest foragers exhibited some plasticity by having higher activity in pastures. Assemblages in forest sites had more evenly distributed activity and were more compositionally variable than pastures, suggesting a greater presence of specialist species. The effects of landscape-scale composition and configuration were ensemble-specific and scale-dependent, with flexible-forest sonotypes relying on forest cover and connectivity at the largest scale. These findings highlight the importance of maintaining forest patches and landscape heterogeneity in cattle-farming areas to preserve Amazonian bat diversity and their associated ecosystem services.

2. Introduction

Food production is a major driver of environmental change, pushing the Earth's system beyond its planetary boundaries (Campbell et al., 2017). Beef production in particular has one of the most significant environmental footprints, with cattle farming being a leading cause of deforestation, fragmentation and forest degradation (Halpern et al., 2022). It is a major contributor to large-scale land-use change, biodiversity loss and carbon emissions, as well as contributing to spillover of zoonotic disease (Foley et al., 2005). However, in the context of growing global food security concerns (Guiné, 2024), cattle farming also plays an important role in supporting nutritional needs and economic stability across the globe (Opadoyin Tona, 2022). It is therefore essential to develop informed and effective policies that preserve the benefits of beef production, while addressing the long-term environmental impacts of deforestation caused by cattle farming.

Brazil is the world's second biggest producer and exporter of beef, with a still-growing industry (FAO, 2025). While this expansion supports both national and global food and economic security, it also contributes significantly to deforestation. Brazil has experienced one of the greatest rates of primary forest loss worldwide (Turubanova et al., 2018), with cattle farming alone accounting for >70% of the country's deforestation (Pendrill et al., 2019). In response to this loss, Brazil has implemented legislative measures aimed at reducing deforestation and protecting native vegetation. The most significant of these is the Forest Code requiring the establishment of Permanent Preservation Areas (Áreas de Preservação Permanente) and Legal Forest Reserves (Reserva Legal) on private land (Chiavari and Lopes, 2015). Legal Forest Reserves require landowners to designate and maintain a proportion of natural forest on their land, the size of this depending on the biome in which they are present (Chiavari and Lopes, 2015). Alongside legislative efforts, several studies have proposed that intensification of cattle farming could reduce deforestation (Cohn et al., 2014; Garcia et al., 2017; Stabile et al., 2020). By increasing productivity on existing pasture, intensification could enable the continued growth of beef production without the need for further forest clearance and the associated environmental impacts. A study by Garcia et al. (2017) concluded that sustainable intensification may also produce social benefits, such as an increase in contract workers and training. Nevertheless, the effects of intensification on biodiversity, especially within the Amazonian biome, remains largely understudied. If intensification is to be use as a tool to reduce deforestation, then the effect that pastures have on biodiversity in a beef-production landscape must be explored.

Bats are a well-suited taxa to study the impacts that deforestation and land-use change have on biodiversity and ecosystem functioning within the Neotropics (Jones et al., 2009). With over 160 species present within the Amazon basin (López-Baucells et al., 2016), bats represent a wide diversity of feeding guilds, foraging strategies, dispersal capabilities, and manoeuvrability (Patterson et al., 2003). In addition, they provide many ecosystem services such as seed dispersal, pollination, and insect pest control, while also being sensitive to a variety of anthropogenic stressors (Kunz et al., 2011). These attributes, combined with bats local abundance as well as their (relative) easiness to sample, make them a good taxa for bioindication.

The impacts of deforestation on bats have been widely studied both in Brazil and across the tropics (reviewed, respectively by Mendes and Srbek-Araujo, 2021 and Meyer et al., 2016), demonstrating that landscape composition and configuration can greatly influence their activity and diversity. Within these studies, landscape composition is defined as the proportion of different land-use types (e.g. forest, pasture, urban areas) in the landscape, with landscape configuration being the distribution them – e.g. number of habitat patches (patch density) or amount of borders between land-use types (edge density) (Fahrig, 2005).

Responses of bats to landscape composition and configuration have been found to vary in a species-specific and feeding ensemble-specific manner at different spatial scales, likely driven by differences in ecological traits such as dietary habits, body size, and home range (Meyer et al., 2016; Rocha et al., 2017; Pinto and Keitt, 2008). However, there has been little research into how bat populations respond to changes in habitat configuration in tropical beef producing landscapes. Studies conducted in other regions indicate that livestock grazing may favour some bat species by maintaining semi-open habitats (López-González et al., 2015), attracting insect prey (Shiel et al., 1991) and providing access to drinking water (Ciechanowski, 2002). Recent studies in Italy have demonstrated that some insectivorous bat species are active around livestock, with activity levels rising with larger herd sizes (Ancillotto et al., 2017; Ancillotto et al., 2021). However, aerial insectivorous bats (AIBs) remain particularly understudied in Brazil, as the traditional sampling method of using mist nests is ineffective for capturing these species (Carvalho et al., 2023). Acoustic surveys are better suited for detecting AIBs, but these are often more costly, technical, and require an acoustic library of echolocation calls for species identification. As a result, despite considerable advances in our understanding of Neotropical AIB echolocation and greater availability of affordable passive acoustic recorders (Arias-Aguilar et al., 2018; López-Baucells et al., 2021), how insectivorous bats respond to all human-modified landscapes in Brazil is still poorly understood.

Specific traits of bats, such as their echolocation, alongside their wing morphology and feeding strategies, influence their habitat use and their ability to persist in human-modified landscapes (Schnitzler and Kalko, 2001, Bader et al., 2015 and Colombo et al., 2023). Different AIB foraging ensembles are often distinguished by these characteristics, with a particular emphasis on their echolocation calls. AIBs echolocation calls can be identified through the variation in their echolocation call characteristics, such as call shape (Figure 1) and peak frequency. Bat species that forage in open spaces, open-space bats, emit low frequency quasi-constant frequency (qCF) calls or low frequency FM-qCF calls that have a short frequency modulated (FM) component and a long qCF component, enabling them to detect prey in large spaces and navigate greater distances (Schnitzler and Kalko, 2001). Edge foragers similarly use FMqCF calls but at a medium frequency with a short qCF component, enabling them to forage effectively in both cluttered and open environments (Schnitzler and Kalko, 2001). Bat species that preferentially forage in forest interiors - forest specialists – use short broadband FM or long constant frequency (CF) calls that are adapted for navigation and foraging in cluttered forest environments created by dense vegetation (Schnitzler and Kalko, 2001). Some forest foragers are known for their plasticity in foraging. where they often exploit different types of forest habitat - these species are known as flexible-forest foragers (as defined by Yoh et al., 2022). Within all these foraging ensembles, some species have very similar echolocation calls, preventing reliable species level identification. To address this, bat calls are classified into sonotypes, where species with indistinguishable echolocation calls are grouped together (see Table 1).



The few recent studies on AIBs within the Brazilian Amazon have found that different foraging ensembles have specific responses to fragmentation and land-use change, reflecting their adaptations to specific habitat types. For example, in a study Rowley et al. (2024) looked at differences between continuous forest and secondary regrowth forest, open-space sonotypes were found to respond negatively to vegetation structure, and some flexible-forest sonotypes showed no habitat preference to different forest types. While Yoh et al. (2022), in a study looking at edge effects across primary and secondary forest, found that sonotype responses were in line with their ensemble classifications – with forest bats being more sensitive to edges habitats than edge foragers. However, there have been no studies exploring the differences in responses of these ensembles to forest composition and configuration in a beef-production landscape.

Within this study I use bioacoustic data to assess AIB responses to pasture and forest composition and configuration across multiple spatial scales within the beef production landscape of Mato Grosso in the Brazilian Amazon. This state housed over 30 million individual cattle in 2017 (Vale et al., 2019), making it particularly relevant for livestock production at both the national and international scales. Specifically, I will address the following objectives:

- How does AIB assemblage activity, sonotype diversity and composition differ between forest and pasture on cattle farms? Based on previous research on how habitat disturbance affects Brazilian bat assemblages (Mendes and Srbek-Araujo, 2021), I expect activity, sonotype richness and evenness, and assemblage composition to differ between pastures and forests, with the former exhibiting higher bat activity but lower sonotype richness (Ancillotto et al., 2017).
- 2. Do different AIB ensembles and sonotypes respond differently to forest and pasture?

As echolocation characteristics are related to how bats navigate different levels of vegetation clutter (Jones and Rayner, 1989), I predict 'open-space bats' and 'edge bats' will show higher activity and sonotype richness in pastures, while 'forest bats' and 'flexible-forest bats' will have higher activity and sonotype richness in forests.

3. Do assemblage-level and ensemble-specific responses change across gradients of landscape composition and configuration?

Based on previous studies of livestock-associated bats, I anticipate that AIB activity will decrease with increasing forest cover, due to higher activity levels in pasture areas where cattle are present (Ancillotto et al., 2017; Ancillotto et al., 2021). In contrast, sonotype richness is expected to increase with forest cover, as it is primarily influenced by landscape-scale forest availability (Ancillotto et al., 2017; Ancillotto et al., 2021).

3. Methods

3.1 Study Area

This study was conducted in the north of the state of Mato Grosso, Bazil ~ 56° - 57.6° W and 9.4° - 10.2° S. The area is classified mostly as a binary landscape, containing Amazonian forest fragments and cattle pasture (**Figure 2B**). Annual rainfall within this region varies from 2000 to 2400 mm, with the dry season being between May and September. The mean annual temperature is 25.8°C, ranging from 24.5°C in January to 29°C in September.



Figure 2 – **A)** Map of study area in the north of Mato Grosso, showing forest pasture, water and other land-use types and all sampling sites within the study ('other' includes agriculture and non-vegetated areas) **B)** Location of study area in relation to the rest of Mato Grosso state in Brazil, South America **C)** Example of buffer sizes 0.5, 1.5, and 3.0 km around a forest site.

Fieldwork was carried out by Brazilian collaborators from September to November in 2023. They sampled twenty cattle farms within the area (**Figure 2A**), which were recruited with the support of a local veterinarian to select a diverse and representative range of farms. Due to the Forest Code, these farms all contained forest reserves alongside pastures, but the age and quality of these fragments are unknown.

3.2 Bioacoustic surveys

At each farm a total of six acoustic SongMetre mini-bat (SSMB) recorders were deployed for 24 hours. Three recorders were placed in pasture and three were placed in the interior of forest reserves (**Figure 2A**). They were set up to record 5 second clips at a sampling rate of 384kHz when triggered and recording from 30 minutes before sunset until 30 minutes after sunrise. Three of the 120 sites had to be removed from the analysis due to either missing acoustic data or lack of coordinates, making the analysis impossible.

3.3 Bioacoustic analysis

Prior to bioacoustic analysis, I compiled a list of bat species known to occur within the wider study area (**Table 1**), as well as their call characteristics and sonotype (using classifications by López-Baucells et al. (2016) and Arias-Aguilar et al. (2018)). Echolocation calls were analysed and identified using Kaleidoscope-5.6.8 software (Wildlife Acoustics Inc., 2024), based on the detection of a "bat pass" – defined as two or more pulses (calls) of a single sonotype present within a 5 second recording (Torrent et al., 2018) – as a classification unit. I limited the analysis to between 18:00 and 22:00 due to the size of the dataset. However, this temporal window is anticipated to detect ~90% of bat species present at a site in Amazonian AIB assemblages (López-Baucells et al., 2021).

Sonotypes were classified into foraging ensembles using previous classifications from Rowley et al. (2024), Yoh et al. (2022), Falcão et al. (2021), and Estrada-Villegas et al. (2010). Namely, sonotypes were classified as: open-space, edge, forest, flexible-forest and water (see **Table 1**). Due to their dependence on water bodies and distance to water, water sonotypes (species which preferentially/exclusively forage over bodies of water) were only used in the analysis of assemblage-level activity, sonotype diversity, and composition.

Family	Potential Species Present	Sonotype	Ensemble
Mormoopidae	Pteronotus gymnontus	Pte gym	Flexible-Forest
	Pteronotus rubiginosus	Pte rub	Flexible-Forest
	Pteronotus personatus	Pte per	Flexible-Forest
Noctilionidae	Noctilio albiventris	Noc alb	Water
	Noctilio leporinus	Noc lep	Water
Emballonuridae	Saccopteryx canescens	Emballonuridae I	Edge
	Saccopteryx gymnura		
	Centronycteris maximiliani	Emballonuridae II	Edge

Table 1 – Family and scientific name of potential species present in each sonotype, sonotype name, and feeding ensemble classification

	Centronycteris centralis				
	Saccopteryx bilineata	Sac bil/lep	Edge		
	Saccopteryx leptura				
	Peropteryx trinitatis	Per tri	Edge		
	Peropteryx macrotis	Per mac	Edge		
	Peropteryx kappleri	Per kap	Edge		
	Cormura brevirostris	Cor bre	Edge		
	Rhynchonycteris naso	Rhy nas	Open-Space		
	Diclidurus ingens	Dic ing	Open-Space		
	Diclidurus albus	Dic spp.	Open-Space		
	Diclidurus scutatus				
Molossidae	Molossus Molossus	Molossus I	Open-Space		
	Neoplatymops mattogrossensis				
	Molossus currentium	Molossus II	Open-Space		
	Molossus rufus				
	Nyctinomops macrotis	Molossidae D	Open-Space		
	Nyctinomops laticaudatus				
	Tadarida brasiliensis				
	Eumops auripendulus				
	Eumops glaucinus				
	Eumops hansae				
	Cynomops planirostris				
	Cynomops paranus				
	Cynomops abrasus				
	Molossops neglectus	Mol neg	Open-Space		
	Promops centralis	Pro cen	Open-Space		
	Promops nasutus	Pro nas	Open-Space		
Vespertilionidae	Lasiurus ega	Vespertilionidae I	Forest		
	Rhogeessa io	Vespertilionidae II	Forest		
	Lasiurus blossevillii				
	Myotis nigricans	Myo nig	Forest		
	Myotis riparius	Myo rip	Forest		
	Eptesicus brasiliensis	Eptesicus I	Forest		
	Eptesicus chiriquinus				
	Eptesicus furinalis				

3.4 Activity, sonotype diversity, and assemblage composition

Sonotype activity is determined as the total number of bat passes per site and is used as a proxy for species abundance, as proposed by Miller (2001). Activity was calculated for the whole assemblage, each ensemble and each sonotype. Sonotype diversity at each site was

calculated using Hill numbers of orders q = 0 and q = 1, representing sonotype richness and Shannon diversity (sonotype evenness) respectively, using the "iNEXT" R package. Hill numbers express diversity as the effective number of species rather than raw index values, allowing for direct and meaningful comparisons between diversity metrics. This method for calculating sonotype richness and evenness was used for assemblage-level and ensemblelevel diversity at each site.

I tested for spatial autocorrelation with Morgan's I test using the "spdep" R package, and detected significant spatial autocorrelation for activity, sonotype richness and evenness, indicating that these values are not spatially independent. To account for this, I used Generalised Additive Models (GAMs) with a smoothing term for longitude and latitude to reduce spatial autocorrelation in model residuals, using "mgcv" R package. GAMs were fitted at both the assemblage-level and ensemble-level to determine the differences of activity, sonotype richness, and evenness between forest and pasture sites. The assumption of normally distributed residuals was tested using the "DHARMa" R package and was not met for activity. Consequently, the log-transformed activity was used in these and all subsequent GAMs. As at a few sites recording did not start until after 18:00, I also included an offset term within all models to account for unequal sampling effort. For this offset term, I used the base-10 log of the minutes sampled at each site to reduce skew.

Differences in assemblage composition between forest and pasture sites, were characterized through a Non-Metric Multidimensional Scaling (NMDS) ordination based on a Bray-Curtis similarity matrix of species abundance data at each sampling site, using the "vegan" R package. To determine the differences between land-use types, I used a PERMANOVA (Permutational Multivariate Analysis of Variance) with 999 permutations, using the adonis() function. As PERMANOVA results may be influenced by differences in within-group variability (multivariate dispersion), I conducted a test for homogeneity of multivariate dispersions (PERMDISP) using the betadisper() function, followed by a permutation test (permutest()) with 999 permutations.

3.5 Landscape variables

Landscape variables (*forest cover*, *forest patch density* and *edge density*) were obtained from land-use data from MapBiomass Brazil Land cover and use (Collection 9) (MapBiomas Project, 2025) using the software QGIS v3.40 (QGIS.org, 2025) (**Figure 2C**). Forest patches contained all forest land-use types within MapBiomass (forest formation, savanna formation and floodable forest), with an edge being the boundary of forest patches.

Forest cover was determined using the calculation:

Forest cover (%) =
$$\frac{\text{total area of forest patches}}{\text{total area of buffer}} \times 100$$

Forest patch density was determined using the calculation:

Forest patch density (per ha) =
$$\frac{number of forest patches}{total area of forest in buffer} \times 10,000$$

Edge density was determined using the calculation:

$$Edge \ density \ (per \ ha) = \frac{total \ length \ of \ forest \ patch \ edges}{total \ area \ of \ buffer} \times \ 10,000$$

Each landscape variable was extracted from three buffer sizes around each sampling site, with radii of 0.5, 1.5 and 3 km (see **Figure 2C**). As not much is known about the home ranges of species in this study, to select these scales I took into consideration the buffer sizes used in other AIB studies within the Brazilian Amazon (e.g. López-Baucells et al.; 2022; Rowley et al., 2024).

As collinearity is often a problem with landscape variables, I ran variance inflation factor (VIF) calculations on these variables at each spatial scale, using "car" R package. VIFs for all predictors ranged from 1.05 to 1.80, which is below the commonly used thresholds of 5-10, indicating no problematic multicollinearity.

3.6 Modelling influence of landscape structure

I analysed the effect of percentage forest cover, patch density and edge density at each scale (0.5, 1.5 and 3 km) on a) log activity, sonotype richness, and evenness at the assemblage level, and b) the log activity, sonotype richness, and evenness of each ensemble, namely: open-space, edge, forest and flexible-forest.

To do this, I fitted 45 GAMs including fixed terms for forest cover, patch density, and edge density, an offset term for sampling effort and a smooth term for longitude and latitude. Models including all these terms always had the lowest Akaike's Information Criterion (AIC) and so every model was structured the same, which allowed for comparison across diversity metrics, ensembles and spatial scales.

4. Results

I identified 65,559 bat passes from 27 different sonotypes across 5 families (**Table 2**). In forests, 12,190 total bat passes were recorded, and 53,369 were recorded in pastures. In total, I identified nine open-space sonotypes with 41,054 bat passes, seven edge sonotypes with 16,345 bat passes, five forest sonotypes with 7,181 bat passes, three flexible-forest sonotypes with 845 bat passes, and two water sonotypes with 125 bat passes (**Table 2**). Open-space foragers represented >60% of total bat passes recorded.

	Forest	Pasture	Total
Open-Space Foragers			
Molossidae D	1068	21773	22841
Molossus I	515	4763	5278
Molossus II	1156	10871	12027
Mol neg	0	2	2
Pro cen	56	409	465
Pro nas	0	38	38
Rhy nas	0	29	29
Dic ing	1	186	187
Dic spp.	12	175	187
Open-Space Total	2808	38246	41054
Edge Foragers			
Emballonuridae I	38	11	49
Emballonuridae II	537	105	642
Sac bil/lep	2673	3322	5995
Per tri	1191	1009	2200
Per mac	222	1291	1513
Per kap	1076	4332	5408
Cor bre	386	161	547
Edge Total	6123	10231	16354
Forest Foragers			
Vespertilionidae I	40	129	169
Vespertilionidae II	10	59	69
Myo nig	400	455	855
Myo rip	975	48	1023
Eptesicus I	1188	3877	5065
Forest Total	2613	4568	7181
Flexible-Forest Foragers			
Pte gym	29	85	114
Pte rub	537	64	601

Table 2 – Number of bat passes recorded in forest and pasture sites for each sonotype, with total bat passes for each foraging ensemble and the assemblage

Pte per	76	54	130
Flexible-Forest Total	642	203	845
Water Foragers (excluded)			
Noc alb	4	120	124
Noc lep	0	1	1
Water Total	4	121	125
Total (Assemblage)	12190	53369	65559

4.1 Assemblage activity, sonotype diversity, and composition

Both activity and sonotype richness were significantly higher in pasture sites than in forest sites (**Figure 3A and 3B**) – log-transformed activity increased by 1.73 (\pm 0.24 SE, p < 0.001), and sonotype richness increased by 4.34 (\pm 0.90 SE, p < 0.001) in pastures (**Appendix I**). However, sonotype evenness was not significantly different in either forest or pasture sites (estimate = -0.10 ± 0.29 SE, p = 0.735) (**Figure 3B**). The smooth term for geographic coordinates had a significant but minimal effect on log-transformed activity as edf = 0.86 (F = 6.1, p = 0.009) (**Appendix I**).

The NMDS ordination had a stress value of 0.218, indicating it provided a reliable representation of community structure (**Figure 3C**). The PERMANOVA indicated a significant difference in bat assemblage composition between land-use types ($R^2 = 0.171$, p = 0.001). However, PERMDISP was also significant ($R^2 = 0.171$, p = 0.001) indicating differences in variability within each land-use type. Upon visualisation of the NMDS, forest sites appear to be more heterogenous than pasture sites (**Figure 3C**).

4.2 Ensemble-level activity and sonotype diversity

In pasture sites, open-space foragers were the ensemble with the highest activity (71.8%), followed by edge foragers (19.2%), forest foragers (8.6%) and finally flexible-forest foragers (0.4%). In forest sites, edge foragers had the highest activity (50.2%), followed by open-space foragers (23.0%), forest foragers (21.4%), and finally flexible-forest foragers (5.3%).

Log-transformed activity was significantly higher in pasture sites for three ensembles (**Figure 4A**): open-space (estimate = 2.82 ± 0.25 SE, p < 0.001), edge (estimate = 0.73 ± 0.26 SE, p < 0.006) and forest (estimate = 0.76 ± 0.29 SE, p = 0.01) (**Appendix III**). However, activity was significantly higher in forest sites for flexible-forest foragers (**Figure 4A**) (estimate = -0.68 ± 0.31 SE, p = 0.03). The smooth term for geographic coordinates had a significant but minimal effect on sonotype richness for edge ensemble as edf = 0.94 (F = 14.5, p < 0.001) (**Appendix IV**).



Figure 3 – **A)** Assemblage-level activity (number of bat passes) across forest and pasture. Box plots show median and interquartile range of land-use type sampling sites. Significance (***, p < 0.001) from log-transformed activity GAMs. **B)** Assemblage-level sonotype richness and evenness (as effective number of species) across forest and pasture. Box plots show median and interquartile range of land-use type sampling sites. Richness significance (***, p < 0.001) from GAM. **C)** NMDS ordination based on Bray–Curtis dissimilarity, with sites coloured by land-use type. 95% confidence ellipses around group centroids illustrate variation in assemblage composition within each land-use type.

Sonotype richness is significantly higher in pasture sites for all four ensembles (**Figure 4B**): open-space (estimate = 1.48 ± 0.19 SE, p < 0.001), edge (estimate = 0.88 ± 0.28 SE, p = 0.002), forest (estimate = 0.92 ± 0.25 SE, p < 0.001) and flexible-forest (estimate = 0.50 ± 0.17 SE, p = 0.004) (**Appendix III**). The smooth term for geographic coordinates had a significant but minimal effect on sonotype richness for edge ensemble as edf = 0.86 (F = 6.2, p = 0.008) (**Appendix IV**).

Sonotype evenness was significantly higher in pasture sites only for edge (estimate = 0.75 ± 0.17 SE, p < 0.001) and flexible-forest foragers (estimate = 0.65 ± 0.18 SE, p < 0.001) (Figure 4B, Appendix III). However, there was no significant difference for both open-space and forest ensembles (Figure 4B, Appendix III).



p < 0.05, *** p < 0.001) (O = Open-Space, E = Edge, F = Forest, F-F = Flexible-Forest)

4.3 Sonotype activity

The most common sonotype was open-space *Molossidae D*, with a total of 22,841 bat passes present in 91.5% of (or 108) sites (**Figure 5**, **Table 2**). The least common sonotype was the water forager *Noctilio leporinus*, which was only detected once at a single site (**Table 2**).

Sonotypes that had >75% of their calls in pasture sites included all nine open-space sonotypes, the edge sponotypes *Peropteryx macrotis* and *Peropteryx kappleri* and the forest sonotypes *Eptesicus I*, *Vespertilionidae I* and *II* (Figure 5). Sonotypes that have >75% of their calls in forest sites included the edge sonotypes *Emballonuridae I* and *II*, the forest sonotype *Myotis riparius*, and the flexible-forest sonotype *Pteropnotus rubiginosus* (Figure 5).



4.4 Influence of landscape variables on responses

At the assemblage level forest cover had a significant negative effect on activity and sonotype richness at 0.5km (**Figure 6**, **Appendix V**). Conversely, edge density had a significant positive effect on sonotype richness at 1.5km and evenness at both 0.5 and 1.5km scales (**Figure 6**, **Appendix V**). No landscape variables were significant at 3km (**Figure 6**, **Appendix V**).

For open foragers, forest cover had a significant negative effect on activity and sonotype richness at 0.5km and across all scales for sonotype evenness (**Figure 7**, **Appendix VII**). For edge foragers, edge density had a significant positive effect for all three metrics at 0.5km and for activity and richness at 1.5km (**Figure 7**, **Appendix VII**). Forest cover was not a significant variable for edge foragers. However, forest cover did have a significant negative effect on activity and sonotype richness for forest foragers at the 0.5km scale (**Figure 7**, **Appendix VII**). Furthermore, for this ensemble, edge density had a significant positive effect on sonotype evenness at 0.5km and 1.5km scales and sonotype richness at 1.5km scale. No landscape variables were significant at 3km for open-space, edge and forest ensembles

(Figure 7, Appendix VII). Lastly, for flexible-forest foragers, forest cover had a significant positive effect on sonotype richness and sonotype evenness at 3km scale (Figure 7, Appendix VII). Edge density had a significant positive effect on activity at 0.5km but a negative effect on sonotype richness and sonotype evenness at 3km scale (Figure 7, Appendix VII).



and evenness modelled as a function of patch density, edge density and forest cover. Repeated and coloured by buffer sizes. Shown are the standard errors of each coefficient estimate. Fill denotes significance, with only significant terms being filled in.



5. Discussion

Neotropical bats are known to respond to changes in forest cover at the landscape-scale. Yet, to date, these dynamics had not been explored in the context of beef-producing landscapes (reviewed in Meyer et al., 2016). My analysis adds to this by revealing that patterns of bat activity, species richness and evenness varied between forest and pastures in the Amazonian beef-production landscape of north Mato Grosso, at both assemblage- and ensemble-level. Moreover, these patterns are affected by landscape-level variables in a scale dependent manner. Nevertheless, it is important to note that differences in detectability between structurally complex forests and open pastures may have contributed to these observed patterns (see **5.6**).

5.1 Differences in bat assemblage responses in forest vs pasture

As anticipated, total activity was higher in pasture than in forest. This pattern aligns with Ancillotto et al. (2017), who found that AIBs preferentially foraged over livestock, likely in response to a greater abundance of insects. In my study, this elevated activity in pasture is primarily driven by open-space foragers that represent >60% of total bat passes. However, edge foraging sonotypes, which are the most active ensemble in forest sites, also have higher activity in pastures. Together, these patterns suggest that this beef-production landscape acts as a trait-mediated environmental filter, selectively benefiting the disturbance-tolerant sonotypes of open and edge foragers which then dominate the assemblage.

Contrary to my prediction, sonotype richness was higher in pastures than in forests. This unexpected pattern again likely reflects the increased activity of open-space and edge ensembles within the landscape, which seem to preferentially forage over pastures. This pattern of sonotype richness is consistent with Torrent et al. (2018), one of the few Neotropical studies comparing bat assemblages between open-space areas (lakes) and cluttered forests. They found higher activity and richness above lakes – including for some strict forest-foraging species – which they also partly attributed to higher insect densities in the open-space of lakes. However, my results do differ from a study by Silva-Souza et al. (2022), that despite having higher bat passes and richness in pastures compared to semideciduous forest, found no significant difference between the two. Yet, Silva-Souza et al.'s study took place in a rocky agropastoral landscape – comparing eucalyptus forest monocultures and horse and cattle pastures to fragmented semideciduous forest – between Atlantic Forest and Cerrado biomes. Differences in our results may be due to the differences in the landscape studied or the level of grazing intensity or number of animals on the pastures which determine insect populations.

Despite the significant differences between forest and pasture for activity and richness, sonotype evenness did not differ significantly. This suggests that activity in pastures is less evenly distributed between sonotypes than in forests – as despite supporting more sonotypes and greater activity, the effective number of species when calculated for evenness, is no different. Therefore, pastures may be dominated by a few active and many low-activity sonotypes that inflate richness without increasing evenness. In contrast, forest patches – despite having fewer overall passes and less sonotypes – support a more balanced distribution across foraging ensembles. This suggests that forest assemblages are made up of sonotypes with relatively balanced activity levels, which therefore may be forest

specialist species. Rocha et al. (2017) also found more even communities in forest interiors than forest edges, suggesting that intact forest structure and resource heterogeneity prevent skewed activity distributions, and facilitate even activity across sonotypes.

Assemblage structure of AIBs is known to differ between open and cluttered habitats (Kemp et al., 2019). As expected, assemblage composition was significantly different between forest and pasture, with forest assemblages being more heterogeneous and showing greater variation across sites. Conversely, assemblages in pasture were more uniform and so are likely dominated by a consistent group of sonotypes as discussed above. Again, this suggests that forest sites support more variable and potentially specialist communities in comparison to the more homogenized assemblage of disturbance-tolerant sonotypes in pastures.

5.2 Differences in ensemble responses in forest vs pasture

The patterns found for open-space ensembles – higher activity and richness in pastures – align with my expectations. This is because Molossidae, the family that contains the majority of open-space foragers in this study, are known to be tolerant to fragmentation and less sensitive to anthropogenic disturbances (see Estrada-Villegas et al., 2010 and Kemp et al., 2019 respectively) due to the adaptation of their echolocation and functional traits to open-space foraging (Núñez et al., 2019). Molossids have fast economic flight and, because of their large body size and long narrow wings, have restricted mobility in cluttered environments, making flying in forest habitats (such as those in this study) metabolically costly (Dennis Castillo-Figueroa, 2020). That emballonurids included in the open-space ensemble (e.g. *Diclidurus* genus), have low frequency calls and larger body sizes than other emballonurids (Jung et al., 2007), suggests that these sonotypes also have metabolic costs associated with flying in forest habitats.

Open-space foragers have the second highest activity and richness for forests sites, which may indicate – due to trait-mediated environmental filtering – that they are particularly abundant in this pasture-dominated landscape. However, it is possible that some open-space sonotypes were detected by recorders in forest sites despite these bats actually flying in open areas within or above the canopy, or even in the surrounding pasture. This is plausible given that molossid echolocation calls are powerful and adapted to travel long distances in open environments (Schnitzler and Kalko, 2001). Additionally, many of the forest patches here are relatively small, making it possible that calls from open-space foragers could be picked up by detectors positioned within or beneath the canopy. Another potential explanation is that cattle grazing may have opened up the forest understory, creating conditions more suitable for open-space foraging – molossids in particular are known to be more active in forests where vegetation is sparse (Rowley et al., 2024; Núñez et al., 2019).

The patterns of high activity and richness in both forest and pasture for the edge ensemble were expected. However, these foragers also exhibited greater activity and diversity in pastures compared to forest. Emballonurids (the family in this ensemble), tend to exploit forest gaps and even open landscapes (Jung et al., 2007), and this may facilitate pasture foraging. In line with our findings, Azofeifa et al. (2019) found that Venezuelan rice fields act as key feeding grounds for these bats, and – with open areas adjacent to roosts – this environment is similar to that of pasture. The flexibility of edge-foraging sonotypes to navigate and feed in both cluttered and open environments likely underpins their preference of pasture sites in this study – again supporting Ancillotto et al.'s (2017) conclusion that pastures with their high insect densities, may offer rich foraging opportunities.

Although comprising only a small fraction of bat passes, forest and flexible-forest ensembles exhibited some unexpected patterns. Forest foragers showed significantly higher activity and richness in pastures, while flexible-forest foragers (despite having greater activity in forests) also showed higher richness in pastures. This could reflect habitat spillover driven by the increased foraging opportunities livestock provide, resulting in forest foragers having a plastic use of the landscape, exploiting pasture resources while relying on forests for roosting. Similar flexibility of the forest ensemble has been reported by Rocha et al. (2017) between old-growth forests and secondary regrowth forests, as well as by Torrent et al. (2018) between open-space lakes and surrounding forest. Indeed, a study by Siemers et al. (2001) found that *Myotis nigricans* can alter their echolocation and forage in uncluttered environments, demonstrating their capacity for greater activity in pasture. However, despite this acoustic plasticity, forest sonotypes are adapted to cluttered environments and may be outcompeted in open habitats, with their smaller size and slower flight making them more vulnerable to predation. This likely contributes to the beef-production landscape appearing to favour the disturbance-tolerant open-space and edge ensembles. In contrast, due to their lower activity in pastures, the flexible-forest ensemble may be less plastic with their landscape resource use than previously thought. Our results here align with Núñez et al. (2019), who reported higher abundances of *Pteronotus* species in forest interiors than in recently cleared zones or edge habitats, suggesting they are particularly vulnerable to landuse change (see 5.3).

5.3 Differences in sonotype-specific activity between forest vs pasture

Molossidae D represents a large proportion of open-space activity (~55%) and of total recorded activity (~35%) (**Table 2**). However, this sonotype is made up of nine species, meaning that this may be due to the cumulative abundance of multiple disturbance-tolerant species (see **Table 1**).

Unlike all open-space sonotypes and some edge sonotypes (Peropteryx macrotis and Peropteryx kappleri), the fact that forest sonotypes Eptesicus I, Vespertilionidae I and II had >75% of their calls in pasture sites is unexpected. However, the *Eptesicus I* sonotype has similar echolocation characteristics to the North American species Eptesicus fuscus (Arias-Aguilar et al., 2018), which is known to forage in open spaces and cluttered forest (Simmons et al., 2001). Surlykke and Moss (2000) found that E. fuscus varies elements of its echolocation – such as signal duration, interpulse interval, and minimum frequency – between open and cluttered environments. Due to their similarity, it is possible that species in Eptesicus I may share this acoustic dexterity of Eptesicus fuscus, allowing them to forage regularly in pastures. The species Lasiurus eqregius was excluded from this study due to its rarity in the South Brazilian Amazon, but it is classified within the Vespertilionidae I sonotype (López-Baucells et al., 2016). However, L. egregius is primarily associated with open habitats such as swamps and grasslands, but its echolocation call structure, duration, and frequency – along with its wing morphology – suggest adaptations for flying in cluttered environments (López-Baucells et al., 2014). This apparent mismatch indicates that other species within Vespertilionidae I and II may also be capable of using open-space habitats. potentially by adjusting their call structure, which may explain their high activity levels in pasture sites.

Sonotypes with >75% of their activity in forests – such as *Emballonuridae* II, *Pteropnotus rubiginosus* and *Myotis riparius* – may be particularly vulnerable to anthropogenic land-use change. Indeed, Rowley et al. (2024) also found the activity of *Centronycteris maximiliani* (a

species classified in *Emballonuridae II*) to be higher in continuous forest compared to fragments and secondary forest, indicating that this species may be particularly sensitive to forest fragmentation and reliant on intact forest conditions for foraging or roosting. Furthermore, De Oliveira et al. (2015) found that Pteropnotus rubiginosus (formerly Pteropnotus parnellii 55) showed higher activity in forest sites with greater insect mass and richness, independent of land-use type. Although this suggests that the activity of P. rubiginosus is influenced by insect availability, my findings may indicate that this is not the case in pastures. Given that the echolocation and wing morphology of *P. rubiginosus* has adaptations suited to foraging in cluttered environments, it may be less able to exploit insect prey in open habitats like pasture - even if insect abundance is high - potentially limiting its activity in these sites, making it vulnerable in beef-producing landscapes. Furthermore, in my study, Myotis riparus being the least plastic forest sonotype (Figure 5) does not align with most literature surrounding this species, where it is often found in edge fragments and human-disturbed environments (Rowley et al., 2024; Novaes et al., 2017). Conversely, my results are consistent with the findings of Morris et al. (2010), where Myotis species consistently foraged within forest interiors and avoided edges, suggesting that this species is more dependent on forest resources than other forest foragers, thereby making it vulnerable within beef-producing landscapes.

5.4 Influence of landscape variables on responses

The assemblage-level relationships with landscape variables are likely shaped by patterns seen for each foraging ensemble. This is probably driven by open-space foragers due to their prevalence, as well as that of edge foragers in forest sites.

Despite this relationship not being as predicted, the open-space ensemble's consistent negative relationship across all metrics with forest cover aligns with their adaptation to open, human-modified habitats (Kemp et al., 2019; Castro-Fernandes et al., 2025). However, their relationship with activity and richness only being significant at the smallest scale and becoming less negative at larger scales (**Figure 7**), indicates that these bats still utilise forests across a broader landscape, most likely for roosting. This pattern is also seen at the assemblage-level, as well as being mirrored by forest foragers for both activity and richness. This suggests that forest foragers use pastures at only the smallest scale (likely for foraging) and are still reliant on larger landscape scale forest cover, a pattern also observed for other forest associated bats in disturbed landscapes (Rocha et al., 2017).

The edge ensemble's consistent positive relationship with edge density is expected due to their affinity with forest edges. However, for richness and evenness, and activity respectively, forest and flexible-forest ensembles also have a positive relationship with edge density at the small or medium scales. This was also seen at the assemblage level for both sonotype richness and evenness. These results are somewhat unexpected due to the association of edge density with forest fragmentation. While this might reflect that at smaller scales ensembles may benefit from edges (e.g. due to increased foraging opportunities and connectivity between roosts (Kalda et al., 2015)) – at larger scales, a higher edge density may be associated with unfavourable levels of fragmentation, therefore resulting in a negative relationship.

Flexible-forest foragers, as expected, are uniquely positively associated with forest cover for richness and evenness, but negatively with edge density. While this is in line with the ensemble's association with forest, it is interesting that significance was only detected at the largest scale used within this study (3km). This suggests that flexible-forest species (the least plastic of all four ensembles investigated), respond more strongly to larger landscape

scale forest amount and configuration. This has strong implications for conservation, indicating that this ensemble may require a greater level of habitat connectivity across the landscape to thrive.

5.5 Implications for conservation

My findings demonstrate that forest habitats, despite lower overall bat activity and richness, support assemblages with more even activity across sonotypes and greater heterogeneity, likely indicating the presence of specialist species. It is therefore essential that conservation efforts, such as the Forest Code, continue to preserve intact forest patches within cattle-producing landscapes to maintain these specialist and forest-dependent sonotypes. Furthermore, sonotypes identified as particularly vulnerable within this landscape – such as *Emballonuridae I* and *II, Myotis riparius*, and *Pteronotus rubiginosus* – should be explicitly targeted by conservation efforts. Protecting and restoring the intact forest habitats required by these vulnerable species will be critical to their persistence in increasingly human-modified landscapes.

Additionally, the high bat activity and sonotype richness in pastures, particularly benefiting open-space and edge foraging bats alongside some forest sonotypes, suggests that implementing biodiversity-friendly cattle management practices – such as reduced pesticide use – can maintain insect abundance and therefore support bat populations. Furthermore, a study by Puig-Montserrat et al. (2015) demonstrated that increasing bat populations in rice paddies in Northeastern Iberia (through deploying bat boxes), led to decreased insect pest levels. This highlights the ecosystem service potential of bats in agricultural landscapes, implying that reducing pesticide use could simultaneously decrease cattle pest abundance and increase bat populations.

The diversity of ensemble responses to landscape variables further emphasizes the importance of landscape heterogeneity in sustaining diverse and complex bat populations. Conservation strategies should therefore aim to maintain or restore a mosaic of habitat types alongside grazing pasture – such as forest and transitional edges – to support a wider range of bat ensembles and overall biodiversity.

5.6 Caveats and future study

Detectability of bat calls varies considerably between cluttered forests and open pastures, biasing acoustic activity and richness estimates. In forests, understory vegetation and the canopy can attenuate and scatter echolocation calls, reducing the effective range of passive acoustic recorders (López-Baucells et al., 2021). This is exacerbated in more dense vegetation. In contrast, in the open space of pastures, calls propagate with less obstruction, so recorders are effective at detecting calls at greater distances. Due to this, activity and number of species recorded can become artificially inflated in open habitats, even if actual activity and richness are similar or lower than that of forests. Therefore, the patterns observed in this study may be due to or exaggerated by this difference in detectability.

As my analysis focuses solely on the first four hours after sunset, any temporal nuances throughout the night may be overlooked. The finding of López-Baucells et al. (2021) that this sampling window captures ~90% of species still suggests that ~10% may have been undetected. These may be the rarest species with specialised habitat requirements making them particularly vulnerable to land-use change. Furthermore, studies of activity patterns of AIBs find that species stagger their activity temporally to avoid competition (see Rivero-

Monteagudo and Mena, 2023) and also change their activity patterns depending on land-use type (Araújo-Fernandes et al., 2025). Consequently, some species may be more active later than 22:00 and could be underrepresented within this analysis, making them appear much rarer than they are. Due to this, further study of this data looking at the entire night should be undertaken to determine if and how this temporal variability effects the results shown here.

The next steps for this research would be to assess the individual responses of sonotypes to landscape-scale variables, specifically sonotypes highlighted here to be more vulnerable. This would enable a more accurate understanding of the responses of AIB assemblages within beef-production landscapes and better inform future policy. To further this, the responses of assemblages, ensembles and sonotypes to intensification variables should be investigated. Alongside the bioacoustic data used in this study, detailed surveys were also conducted at each farm, including information on cattle farming practices such as number of the cattle and number of days cattle are kept outside. Modelling the responses of AIBs to these beef-production variables would allow for a better understanding of how assemblages respond to intensification. Which would, in turn, help produce better informed policies to support and enact sustainable intensification of beef-production, aimed at reducing deforestation in the Amazon.

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8. Appendix

Appendix I – Generalised Additive Models (GAMs) explaining assemblage-level AIB activity, sonotype richness and evenness. For each model predictor, I show the estimate, standard error, t-value and P-value. Significant P-values are in bold.

Response Variable	Predictor	Estimate	SE	t value	P value
Activity	Intercept (Forest)	17.688	6.251	2.83	0.006
	Pasture	1.727	0.237	7.286	<0.001
Richness	Intercept (Forest)	25.741	18.175	1.416	0.159
	Pasture	4.343	0.897	4.841	<0.001
Evenness	Intercept (Forest)	8.694	5.918	1.469	0.145
	Pasture	-0.099	0.291	-0.339	0.735

Appendix II – Output of the smooth term for geographic coordinates of the models described in Appendix I. I show the effective degrees of freedom (edf), reference degrees of freedom (Ref. df), F-statistic, and P-value. Significant P-values are in bold.

Response Variable	edf	Ref.df	F	P-value
Activity	0.860	1	6.155	0.009
Richness	0.507	1	1.029	0.157
Evenness	0.510	1	1.04	0.156

Appendix III – Generalised Additive Models (GAMs) explaining ensemble-level AIB activity, sonotype richness and evenness. For each model predictor, I show the estimate, standard error, *t*-value and P-value. Significant P-values are in bold.

Ensemble	Response Variable	Predictor	Estimate	SE	t value	P value
	Activity	Intercept (Forest)	6.747	5.305	1.272	0.206
	-	Pasture	2.824	0.250	11.298	<0.001
Open-	Richness	Intercept (Forest)	0.713	0.141	5.041	<0.001
Space		Pasture	1.476	0.195	7.580	<0.001
	Evenness	Intercept (Forest)	4.883	3.136	1.557	0.122
		Pasture	0.084	0.133	0.634	0.527
	Activity	Intercept (Forest)	28.723	7.195	3.992	<0.001
		Pasture	0.732	0.261	2.811	0.006
Edge	Richness	Intercept (Forest)	19.483	7.384	2.639	0.010
		Pasture	0.878	0.278	3.152	0.002
	Evenness	Intercept (Forest)	-0.308	0.120	-2.576	0.011
		Pasture	0.755	0.170	4.440	<0.001
	Activity	Intercept (Forest)	-2.348	4.469	-0.525	0.601
		Pasture	0.764	0.289	2.641	0.010
Forest	Richness	Intercept (Forest)	-0.098	0.189	-0.520	0.604
		Pasture	0.917	0.252	3.637	<0.001
	Evenness	Intercept (Forest)	-0.439	0.145	-3.037	0.003
		Pasture	0.002	0.193	0.009	0.993
	Activity	Intercept (Forest)	-0.408	0.216	-1.886	0.064
		Pasture	-0.683	0.306	-2.232	0.029
Flexible-	Richness	Intercept (Forest)	-1.145	0.117	-9.767	<0.001
		Pasture	0.493	0.166	2.971	0.004
	Evenness	Intercept (Forest)	-1.225	0.129	-9.482	<0.001
		Pasture	0.647	0.183	3.542	0.001

Appendix IV – Output of the smooth term for geographic coordinates of the models described in Appendix III. I show the effective degrees of freedom (edf), reference degrees of freedom (Ref. df), F-statistic, and P-value. Significant P-values are in bold.

Ensemble	Response Variable	edf	Ref.df	F	P-value
0	Activity	0.563	1	1.288	0.133
Open- Space –	Richness	0.000	1	0	0.661
	Evenness	0.693	1	2.260	0.0738
Edge	Activity	0.935	1	14.470	<0.001
	Richness	0.862	1	6.247	0.008
	Evenness	0.000	1	0	0.801
	Activity	0.280	1	0.389	0.242
Forest	Richness	0.000	1	0	0.323
	Evenness	0.000	1	0	0.594
	Activity	0.000	1	0	0.861
Flexible-	Richness	0.000	1	0	0.873
	Evenness	0.000	1	0	0.672

Appendix V – Generalised Additive Models (GAMs) explaining relationships of assemblagelevel AIB activity, sonotype richness and evenness to landscape variables forest cover, patch density and edge density at each buffer size (0.5, 1.5, and 3 km). For each model predictor, I show the estimate, standard error, t-value and P-value. Significant P-values are in bold. The intercept (baseline) is the model's predicted response when all predictors are set to their average (mean) value after standardization with the function scale().

Buffer Size	Response Variable	Predictor	Estimate	SE	t value	P value
	Activity	Intercept (Baseline)	29.663	8.209	3.613	<0.001
		Forest Cover	-0.674	0.147	-4.588	<0.001
		Patch Density	0.062	0.143	0.436	0.664
0.5 km		Edge Density	0.172	0.150	1.150	0.253
		Intercept (Baseline)	56.648	28.038	2.020	0.046
	Sonotype	Forest Cover	-1.622	0.555	-2.923	0.004
	Richness	Patch Density	0.191	0.541	0.353	0.725
1	-	Edge Density	0.736	0.566	1.302	0.196
_		Intercept (Baseline)	18.043	8.269	2.182	0.031
	Sonotype	Forest Cover	-0.070	0.160	-0.440	0.661
	Evenness	Patch Density	-0.087	0.155	-0.562	0.576
		Edge Density	0.415	0.163	2.548	0.012
	Activity	Intercept (Baseline)	17.943	7.544	2.379	0.019
		Forest Cover	-0.303	0.181	-1.672	0.097
		Patch Density	-0.014	0.179	-0.081	0.936
_		Edge Density	0.277	0.144	1.923	0.057
		Intercept (Baseline)	9.688	0.501	19.333	<0.001
1.5 km	Sonotype	Forest Cover	-0.084	0.623	-0.135	0.893
	Richness	Patch Density	-0.036	0.629	-0.058	0.954
-		Edge Density	1.065	0.511	2.085	0.039
		Intercept (Baseline)	2.827	1.347	2.099	0.038
	Sonotype	Forest Cover	0.099	0.178	0.554	0.580
	Evenness	Patch Density	0.158	0.180	0.877	0.382
		Edge Density	0.384	0.146	2.628	0.010
		Intercept (Baseline)	13.407	7.431	1.804	0.074
	Activity	Forest Cover	-0.102	0.184	-0.557	0.579
		Patch Density	-0.094	0.176	-0.537	0.593
¢2		Edge Density	0.163	0.153	1.066	0.289
		Intercept (Baseline)	9.698	0.501	19.358	<0.001

3.0 km	Sonotype	Forest Cover	0.922	0.620	1.488	0.140
	Richness	Patch Density	0.169	0.611	0.276	0.783
	~	Edge Density	0.496	0.520	0.954	0.342
Sonotype Evenness	Intercept (Baseline)	9.441	6.604	1.430	0.156	
	Sonotype	Forest Cover	0.111	0.183	0.607	0.545
	Evenness	Patch Density	0.316	0.177	1.790	0.076
		Edge Density	0.098	0.153	0.641	0.523

Appendix VI – Output of the smooth term for geographic coordinates of the models described in Appendix V. I show the effective degrees of freedom (edf), reference degrees of freedom (Ref. df), F-statistic, and P-value. Significant P-values are in bold.

Buffer Size	Response Variable	edf	Ref.df	F	P-value
	Activity	0.913	1	10.517	<0.001
0.5 km	Richness	0.737	1	2.809	0.054
	Evenness	0.777	1	3.492	0.037
1.5 km	Activity	0.796	1	3.897	0.029
	Richness	<0.001	1	<0.001	0.376
	Evenness	0.024	1	0.025	0.314
3.0 km	Activity	0.660	1	1.942	0.089
	Richness	<0.001	1	<0.001	0.864
	Evenness	0.516	1	1.068	0.153

Appendix VII – Generalised Additive Models (GAMs) explaining relationships of ensemblelevel AIB activity, sonotype richness and evenness to landscape variables forest cover, patch density and edge density at each buffer size (0.5, 1.5, and 3 km). For each model predictor, I show the estimate, standard error, t-value and P-value. Significant P-values are in bold. The intercept (baseline) is the model's predicted response when all predictors are set to their average (mean) value after standardization with the function scale().

Ensemble	Buffer Size	Response Variable	Predictor	Estimate	SE	t value	P value
			Intercept (Baseline)	23.309	9.967	2.339	0.021
			Forest Cover	-1.091	0.189	-5.765	<0.001
		Activity	Patch Density	0.055	0.186	0.299	0.766
			Edge Density	0.104	0.194	0.537	0.592
	3		Intercept (Baseline)	10.945	7.407	1.478	0.143
		Sonotype	Forest Cover	-0.769	0.161	-4.782	<0.001
Open-Space	0.5 km	Richness	Patch Density	0.028	0.159	0.176	0.861
			Edge Density	0.075	0.164	0.456	0.649
		Sonotype Evenness	Intercept (Baseline)	11.703	4.747	2.465	0.015
			Forest Cover	-0.188	0.088	-2.129	0.036
			Patch Density	-0.101	0.087	-1.170	0.245
			Edge Density	0.109	0.090	1.206	0.231
			Intercept (Baseline)	4.949	5.509	0.898	0.371
			Forest Cover	-0.286	0.244	-1.171	0.244
		Activity	Patch Density	0.020	0.245	0.082	0.935
			Edge Density	0.344	0.198	1.741	0.015 0.036 0.245 0.231 0.371 0.244 0.935 0.084 <0.001 0.447 0.390
	*		Intercept (Baseline)	1.498	0.159	9.437	<0.001
Open-Space	1.5 km	Sonotype	Forest Cover	-0.151	0.198	-0.763	0.447
Open-Opace		Richness	Patch Density	0.173	0.200	0.863	0.390
			Edge Density	0.207	0.162	1.281	0.203
	,		Intercept (Baseline)	10.164	4.322	2.352	0.020
		Sonotype	Forest Cover	-0.231	0.102	-2.277	0.025
		Evenness	Patch Density	-0.027	0.100	-0.271	0.787

			Edge Density	-0.010	0.080	-0.124	0.901	
			Intercept (Baseline)	1.997	0.196	10.166	<0.001	
		Activity	Forest Cover	0.071	0.244	0.290	0.772	
		Activity	Patch Density	-0.096	0.240	-0.398	0.691	
			Edge Density	0.163	0.204	0.799	0.426	
			Intercept (Baseline)	1.498	0.161	9.288	<0.001	
Open-Space	3.0 km	Sonotype	Forest Cover	0.080	0.200	0.400	0.690	
open-opace	5.0 Km	Richness	Patch Density	0.143	0.197	0.723	0.471	
			Edge Density	0.055	0.167	.167 0.329 0		
			Intercept (Baseline)	14.632	4.562 3.208	0.002		
		Sonotype	Forest Cover	-0.222	0.098	-2.274	0.025	
		Evenness	Patch Density	0.084	0.093	0.901	0.369	
			Edge Density	-0.088	0.081	-1.081	0.282	
		Activity	Intercept (Baseline)	47.465	8.960	5.297	<0.001	
			Forest Cover	-0.263	0.158	-1.669	0.098	
			Patch Density	0.166	0.154	1.073	0.286	
			Edge Density	0.355	0.161	2.201	0.030	
			Intercept (Baseline)	38.765	9.452	4.101	<0.001	
Edge	0.5 km	Sonotype	Forest Cover	-0.248	0.168	-1.472	0.144	
		Richness	Patch Density	0.158	0.165	0.958	0.340	
			Edge Density	0.365	0.172	2.117	0.037	
			Intercept (Baseline)	10.723	5.656	1.896	0.061	
		Sonotype	Forest Cover	-0.217	0.110	-1.982	0.050	
		Evenness	Patch Density	-0.071	0.108	-0.663	0.509	
			Edge Density	0.120	0.112	1.074	0.286	
			Intercept (Baseline)	36.762	8.387	4.383	<0.001	
		Activity	Forest Cover	-0.075	0.187	-0.402	0.688	
			Patch Density	-0.019	0.184	-0.104	0.917	

			Edge Density	0.355	0.148	2.405	0.018
			Intercept (Baseline)	25.634	8.444	3.036	0.003
Edgo	15 km	Sonotype	Forest Cover	0.016	0.193	0.083	0.934
Eage	1.5 KIII	Richness	Patch Density	-0.110	0.191	-0.575	0.566
			Edge Density	0.451	0.153	2.948	0.004
			Intercept (Baseline)	1.205	2.573	0.468	0.641
		Sonotype	Forest Cover	0.007	0.122	0.056	0.955
		Evenness	Patch Density	-0.127	0.123	-1.030	0.305
-			Edge Density	0.237	0.099	2.396	0.018
			Intercept (Baseline)	36.294	8.861	4.096	<0.001
		Activity	Forest Cover	-0.145	0.187	-0.773	0.441
			Patch Density	-0.078	0.177	-0.438	0.662
			Edge Density	0.251	0.155	1.618	0.109
		Sonotype Richness	Intercept (Baseline)	19.471	8.615	2.260	0.026
Edge	3.0 km		Forest Cover	0.107	0.194	0.550	0.583
	0.0 111		Patch Density	-0.140	0.185	-0.755	0.452
			Edge Density	0.311	0.161	1.927	0.056
		Sonotype Evenness	Intercept (Baseline)	-0.055	0.099	-0.552	0.582
			Forest Cover	0.076	0.123	0.618	0.538
			Patch Density	-0.083	0.121	-0.683	0.496
			Edge Density	0.132	0.103	1.289	0.200
			Intercept (Baseline)	1.672	3.519	0.475	0.636
		Activity	Forest Cover	-0.541	0.177	-3.049	0.003
		ourity	Patch Density	-0.029	0.177	-0.165	0.869
			Edge Density	0.097	0.180	0.538	0.591
			Intercept (Baseline)	9.383	7.127	1.317	0.191
Forest	0.5 km	Sonotype	Forest Cover	-0.578	0.153	-3.774	<0.001
. 0.001	0.0 KII	Richness	Patch Density	0.011	0.151	0.072	0.943

		×9	Edge Density	0.290	0.156	1.854	0.067
			Intercept (Baseline)	10.668	5.760	1.852	0.067
		Sonotype	Forest Cover	-0.191	0.111	-1.720	0.088
		Evenness	Patch Density	0.056	0.109	0.510	0.611
(S-			Edge Density	0.294	0.113	2.590	0.011
			Intercept (Baseline)	0.399	0.161	2.480	0.015
		Activity	Forest Cover	-0.221	0.201	-1.101	0.273
		Activity	Patch Density	0.266	0.290 0.156 1.854 0.067 10.668 5.760 1.852 0.067 -0.191 0.111 -1.720 0.088 0.056 0.109 0.510 0.611 0.294 0.113 2.590 0.011 0.399 0.161 2.480 0.015 -0.221 0.201 -1.101 0.273 0.266 0.203 1.312 0.192 0.196 0.164 1.196 0.234 0.017 0.142 0.120 0.905 -0.190 0.177 -1.077 0.284 0.058 0.179 0.322 0.748 0.350 0.144 2.420 0.017 -0.186 1.755 -0.106 0.916 -0.037 0.126 -0.290 0.773 0.148 0.127 1.165 0.247 0.218 0.103 2.115 0.037 0.216 0.202 -1.070 0.287 0.214	1.312	0.192
			Edge Density	0.196			
			Intercept (Baseline)	0.017		0.905	
Forest	15 km	Sonotype	Forest Cover	-0.190	0.177	-1.077	0.284
Forest	1.5 Kii	Richness	Patch Density	0.058	0.179	0.322	0.748
			Edge Density	0.350	0.144	2.420	0.017
		Sonotype	Intercept (Baseline)	-0.186	1.755	-0.106	0.916
			Forest Cover	-0.037	0.126	-0.290	0.773
		Evenness	Patch Density	0.148	0.127	1.165	0.247
40)-			Edge Density	0.218	0.103	2.115	0.037
		A	Intercept (Baseline)	1.195	2.801	0.427	0.670
			Forest Cover	-0.216	0.202	-1.070	0.287
		Activity	Patch Density	0.214	0.198	1.080	120 0.905 077 0.284 322 0.748 420 0.017 106 0.916 290 0.773 165 0.247 115 0.037 427 0.670 070 0.282 437 0.663 117 0.907 122 0.903 572 0.568 260 0.210 012 <0.001
			Edge Density	-0.074	0.168	-0.437	0.663
			Intercept (Baseline)	0.017	0.145	0.117	0.907
Forest	2.0 km	Sonotype	Forest Cover	0.022	0.180	0.122	0.903
Forest	3.0 km	Richness	Patch Density	0.102	0.178	0.572	0.568
			Edge Density	0.190	0.151	1.260	0.210
			Intercept (Baseline)	-0.713	0.102	-7.012	<0.001
		Sonotype	Forest Cover	0.158	0.126	1.248	0.214
		Evenness	Patch Density	0.160	0.124	1.290	0.200

			Edge Density	0.157	0.105	1.489	0.139
			Intercept (Baseline)	6.756	5.900	1.145	0.255
		Activity	Forest Cover	0.182	0.124	1.463	0.146
		Activity	Patch Density	-0.043	0.123	-0.349	0.728
			Edge Density	0.438	0.127	3.451	<0.001
			Intercept (Baseline)	3.042	3.767	0.808	0.421
Flexible-	0.5 km	Sonotype	Forest Cover	-0.041	0.083	-0.489	0.626
Forest	0.0 Km	Richness	Patch Density	0.013	0.082	0.153 0	0.879
			Edge Density	0.137	0.085 1.618	1.618	0.109
			Intercept (Baseline)	4.181	4.041	1.035	0.303
		Sonotype Evenness	Forest Cover	-0.039	0.085	-0.460	0.646
			Patch Density	0.012	0.083	0.145	0.885
			Edge Density	0.141	0.086	1.634	0.105
		Activity	Intercept (Baseline)	-1.424	0.116	-12.223	<0.001
			Forest Cover	0.167	0.145	1.146	0.254
			Patch Density	0.042	0.147	0.283	0.778
			Edge Density	0.204	0.119	1.718	0.089
		18	Intercept (Baseline)	0.529	2.913	0.182	0.856
Flexible-	1.5 km	Sonotype	Forest Cover	0.081	0.107	0.756	0.451
Forest	LU KIII	Richness	Patch Density	-0.045	0.107	-0.425	0.672
			Edge Density	0.001	0.086	0.016	0.988
			Intercept (Baseline)	2.171	3.728	0.582	0.562
		Sonotype	Forest Cover	0.072	0.113	0.641	0.523
		Evenness	Patch Density	-0.069	0.112	-0.619	0.537
			Edge Density	-0.024	0.090	-0.263	0.793
			Intercept (Baseline)	3.978	5.297	0.751	0.454
		Activity	Forest Cover	-0.026	0.149	-0.173	0.863
	Activity	Activity	Patch Density	-0.093	0.144	-0.647	0.519

Flexible-			Edge Density	-0.153	0.124	-1.230	0.221
			Intercept (Baseline)	0.692	3.035	0.228	0.820
	20 km	Sonotype	Forest Cover	0.221	0.103	2.143	0.034
Forest	3.0 KIII	Richness	Patch Density	0.022	0.100	0.219	0.827
		×2	Edge Density	-0.175	0.086	-2.037	0.044
			Intercept (Baseline)	1.335	3.440	0.388	0.699
		Sonotype	Forest Cover	0.243	243 0.108 2.252	2.252	0.026
		Evenness	Patch Density	0.023	0.105	0.218	0.828
			Edge Density	-0.181	0.090	-2.017	0.046

Appendix VIII – Output of the smooth term for geographic coordinates of the models described in Appendix VII. I show the effective degrees of freedom (edf), reference degrees of freedom (Ref. df), F-statistic, and P-value. Significant P-values are in bold.

Ensemble	Buffer Size	Response Variable	edf	Ref.df	F	P-value
		Activity	0.821	1	4.587	0.020
Open- Space	0.5km	Richness	0.620	1	1.631	0.108
		Evenness	0.857	1	5.972	0.010
0		Activity	0.223	1	0.288	0.259
Open- Space	1.5km	Richness	<0.001	1	<0.001	0.550
opuoo		Evenness	0.844	1	5.412	0.013
		Activity	<0.001	1	<0.001	0.575
	3.0 km	Richness	<0.001	1	<0.001	0.636
		Evenness	0.910	1	10.135	0.001
Edge		Activity	0.963	1	26.320	<0.001
	0.5km	Richness	0.940	1	15.740	<0.001
		Evenness	0.785	1	3.644	0.034
		Activity	0.946	1	17.670	<0.001
	1.5km	Richness	0.893	1	8.322	0.003
		Evenness	0.193	1	0.240	0.268
		Activity	0.939	1	15.413	<0.001
	3.0 km	Richness	0.817	1	4.462	0.021
		Evenness	<0.001	1	<0.001	0.550
		Activity	0.111	1	0.125	0.291
	0.5km	Richness	0.633	1	1.723	0.102
		Evenness	0.797	1	3.929	0.029
		Activity	<0.001	1	<0.001	0.856
Forest	1.5km	Richness	<0.001	1	<0.001	0.912
		Evenness	0.083	1	0.091	0.299
		Activity	0.075	1	0.081	0.301
	3.0 km	Richness	<0.001	1	<0.001	0.848
		Evenness	<0.001	1	<0.001	0.583
		Activity	0.660	1	1.937	0.090
	0.5km	Richness	0.598	1	1.491	0.118
		Evenness	0.670	1	2.026	0.085
		Activity	<0.001	1	<0.001	0.585
Flexible-	1.5km	Richness	0.329	1	0.490	0.225
TOTESt		Evenness	0.494	1	0.976	0.163
-		Activity	0.510	1	1.040	0.156
	3.0 km	Richness	0.345	1	0.527	0.219
		Evenness	0.407	1	0.685	0.197

9. Management Report

This study differs somewhat to my research proposal titled *The Impact of Beef-Production on Aerial Insectivorous Bats in the Brazilian Cerrado.* The main difference is that the echolocation call identification was done manually instead of using a machine learning tool, which resulted in a change of study area and the lack of some analysis I originally set out to do.

The change to manual identification was due to a staffing change over the summer just before the start of my project, where my original co-supervisor who was developing a machine learning tool to identify Brazilian bat calls was no longer in the lab group. As a result, I had to learn how to manually identify these calls, which is a skill that takes a long time to develop. I had to research and familiarise myself with the diverse echolocation call characteristics of all 31 sonotypes in my study area, as well as any common 'noise' such as insects which cannot easily be distinguished when starting. To do this, I also had to develop confidence in using Kaleidoscope-5.6.8 software, for which I had a two-day workshop on in October yet was based on two different bat species from the Azores.

Due to the size of the datasets and the slow pace of identifying while learning, I no longer had the time to classify all audio recordings for the Brazilian Cerrado and so instead shared the task of manual identification of Brazilian Amazon with a fellow MBiol student who was using the same data. Despite two of us doing this, it still took up until the beginning of February to classify all ~78,000 files, which often had 3 or more sonotypes in them making them difficult to interpret. In my research proposal, the bioacoustic analysis was planned to be finished by the end of Michaelmas week 6 and instead lasted until almost two months later (week 3/4 Hilary). As a result of this, all subsequent analysis was pushed back.

As well as this set back, obtaining landscape variables from QGIS took longer than expected as I had to learn how to use this new software alone. As a result, by the time I had all my data ready for analysis (bioacoustic and landscape) it was Hilary week 6/7. This left me with a lot less time for statistical analysis than planned, despite already starting data preparation and aspects of my analysis once I had finished my bioacoustic analysis. Due to this, I did not have the time to complete some analysis that I set out to do in my research proposal, such as determining sonotype-specific responses to landscape structure, and modelling the responses of all levels (assemblage, ensemble, and sonotype) to variables of livestock production. As I could not carry out the latter in time, I was not able to relate the responses of aerial insectivorous bats to intensification of beef-production as I originally set out to do.

Overall, I was able to complete most of my planned analyses in the absence of a machinelearning tool for Brazilian bat calls. Moreover, I developed a strong, transferable skill set in manual sonotype identification using Kaleidoscope and in landscape analysis with QGIS.