# Responses of insectivorous bat assemblages to land-use change in the endemic-rich island of São Tomé, Gulf of Guinea

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# Resumo

A alteração do uso do solo é uma das causas principais da perda de biodiversidade em todo o mundo, cujos impactos são ainda mais dramáticos nas ilhas oceânicas tropicais, caracterizadas por níveis elevados de endemismos. A Ilha de São Tomé, localizada no Golfo da Guiné, tem experienciado uma significativa desflorestação impulsionada pela agricultura. No entanto, pouco se sabe sobre a influência de diferentes tipos de uso do solo nas assembleias de vertebrados nativos da ilha. Para abordar esta falta de conhecimento, realizamos um estudo acústico em toda a ilha das assembleias de morcegos insectívoros em 115 pontos de amostragem em diferentes tipos de cobertura do solo da ilha: floresta primária, floresta secundária, plantações de sombra, plantações de óleo de palma, agricultura de pequena escala e áreas urbanas. Com base em 19.744 registos de passagens de morcegos de cinco taxa diferentes, examinamos a assembleia geral de morcegos (riqueza de espécies, atividade como proxy de abundância e composição), bem como as respostas específicas das espécies à mudança no uso do solo. Verificámos que a riqueza de espécies foi relativamente consistente na maioria dos usos do solo, exceto na floresta primária, que apresentou a menor riqueza de espécies. Além disso, a atividade geral dos morcegos foi mais elevada em habitats antropogénicos. Também foi possível observar respostas específicas das espécies, com *Hipposideros ruber* e *Macronycteris thomensis* a serem encontrados quase exclusivamente em áreas florestais, enquanto *Chaerephon* spp. estava fortemente associado a áreas urbanas. Por fim, foi possível perceber que a altitude teve um efeito negativo na atividade da maioria das espécies. Este trabalho fornece as primeiras informações sobre os efeitos da mudança no uso do solo nos morcegos insectívoros desta ilha tropical.

Palavras-chave: Morcegos insulares, Chiroptera, Alteração do uso do solo, Florestas tropicais, Bioacustica, Ilha de São Tomé

# Abstract

Land use change is the main driver of biodiversity loss worldwide, whose impacts are even more dramatic across tropical oceanic islands characterised by high levels of endemisms. The Island of São Tomé, located in the Gulf of Guinea, has experienced significant agriculture-driven deforestation. Yet, little is known about the influence of different humanised land use types on the island's native vertebrate assemblages. To address this knowledge gap, we conducted an island-wide acoustic survey of insectivorous bat assemblages across 115 sites throughout the island's main land cover types: old-growth forest, regrowth forest, shaded plantations, oil palm plantations, small-scale agriculture, and urban areas. Based on 19,744 bat passes recorded from five taxa, we examined bat overall assemblage (species richness, activity as a proxy of abundance, and composition), and species-specific responses to land use change. We found that species richness was relatively consistent across most land uses except for old-growth forest which exhibited the lowest species richness. Additionally, general bat activity (number of bat passes) was higher in anthropogenic habitats. Furthermore, we found species-specific responses with *Hipposideros ruber* and *Macronycteris thomensis* being almost exclusively found in forested areas, while *Chaerephon* spp. was highly associated with urban areas. We also found that altitude had a negative effect on most species' activity. Our study provides the first insights into the effects of land-use change on insectivorous bats of this tropical, endemic-rich island.

Keywords: Island bats, Chiroptera, Land use change, Tropical forests, Bioacoustic, São Tomé Island

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# List of Abbreviation

| | |
|---|---|
| NMDS | NON-METRIC MULTIDIMENSIONAL SCALING |
| PCA | PRINCIPAL COMPONENT ANALYSIS |
| SD | STANDARD DEVIATION |

# Introduction

As the main drivers for biodiversity loss are experiencing a rise in intensity, the global species loss is predicted to continue at the current, or even accelerated rates (Pereira et al. 2010, Ceballos et al. 2015). Among these drivers, changes in land use are of significant concern, particularly in tropical regions as those comprisethe most diverse terrestrial ecosystems (Myers et al. 2000, Lee and Jetz 2008; Gibson et al. 2011). This conversion is primarily driven by the ongoing growth ofthe human population and the resulting increased demand for food, leading to the conversion of land for agriculture and pastures, often destroying biodiversity-rich old- growth forests (Laurance et al. 2014). Indeed, land use change has a great negativeeffect on tropical biodiversity (Sala et al. 2000). Although this impact varies amongspecies groups,human-altered habitats typically harbour lower levels of speciesdiversity and inflated abundances of generalist species (Scales and Marsden 2008,Newbold et al. 2014).

Islands are important areas for biodiversity conservation, often harbouring a greater number of endemic species compared to equivalent mainland areas (Fernandez-Palacios et al. 2021). They have been significantly impacted by historical and contemporary human-induced changes in land use, and their relatively smaller size places them in a more vulnerable position to habitat disturbance (Myers et al. 2000,Norder et al. 2020, Nogué et al. 2021). Indeed, most threatened species worldwide are restricted to islands (Triantis et al. 2010; Leclerc et al. 2018). Insular endemic species are particularly threatened as their often higher habitat specialisation and unique adaptation and interspecific interactions aggravates the impacts of land usechange and other anthropogenic stressors such as invasive species and climate change(de Lima 2012; Fernandez-Palacios et al. 2021). For instance, Maas et al. (2009) foundthat despite no pronounced changes in bird species richness on the island of Sulawesi,Indonesia, endemic species presented a decline in abundance over the years and therewas a significant species turnover that resulted in an increase in the abundance of widespread birds, associated with more open habitats.

Present in every continent except for Antarctica, bats comprise one of the most taxonomically diverse mammalian orders, encompassing over 1400 species (Tsang et al. 2016; Simmons and Cirranello et al. 2023). Due to their ability to fly, they can disperse over water and are often the only native mammals in many insular ecosystems (Fleming and Racey 2009). About 60% of all bat species are present on islands, and roughly 25% are island endemics (Jones et al. 2009). Bats play a crucial role in ecosystem functioning, further providing valuable ecosystem services such as pest control, facilitating seed dispersal, and promoting pollination (Williams-Guillén et al. 2016; Florens et al. 2017; Kemp et al. 2019; Nóbrega et al. 2023). In light of their ecological significance, it is noteworthy that island endemic bat populations are substantially more threatened than their non-insular counterparts (Conenna et al. 2017).

The responses exhibited by bats to land use change are often species-specific, being frequently modulated by ecological traits such as differences in echolocation, diet and morphological characteristics (Davies et al. 2016; Núñez et al., 2019). Notwithstanding the scarcity of studies in the Paleotropics and in particularly in Africa (Meyer et al. 2016), in mainland areas, species richness tends to peak in unfragmented primary forest (Meyer et al. 2016; Rocha et al. 2017) but significant levels of batdiversity can still be found in humanised habitats such as agricultural landscapes (Mendenhall et al 2014; Williams-Guillen et al 2016), agroforestry systems (Faria et al. 2006; Pardini et al. 2009) and urbanised areas (Jung and Kalko 2011; Russo and Ancillotto 2015). Indeed, some agroforestry systems such as shade plantations present high levels of bat diversity, richness, and abundance (Faria et al. 2006). Likewise, although urban areas often harbour a subset of the original species diversity, numerous species (particularly of open space foragers such as the members of the family Molossidae) exhibit high levels of adaptability to urban environments, utilising human-made infrastructures as roosting sites and taking advantage of arthropod prey that is attracted by streetlights (Jung and Kalko 2011; Ancillotto et al. 2015; Lopez-Baucells et al. 2017). Yet, in oceanic islands, characterised by a reduced species pool, compared with mainland areas, the scarcity of studies analysing the responses of bats to land use change precludes similar generalisations. This is aggravated by the idiosyncratic responses detected in the few studies that have conducted robust island-wide bat surveys in these understudied ecosystems (Conenna et al. 2017). For instance, Ferreira et al. (2022) used low-cost acoustic detectors to conduct an island-wide survey of aerial insectivorous bats in the Macaronesian island of Madeira and reported that while the activity of *Pipistrellus maderensis* was positively associated with the cover of primary forest (*Laurisilva)*, the activity of *Nyctalus leisleri verrucosus* was negatively affected by the same land cover.

These contrasting responses to the same land use type were likely explained by reduced manoeuvrability of the open space forager *N. l. verrucosus,* in relation to the edge space forager *P. maderensis* (Ferreira et al. 2022). Around one quarter of the island-restricted bats are assessed as threatened (Critically Endangered, Endangered, or Vulnerable) by the IUCN and a substantial fraction of the remaining are classified as Data Deficient (IUCN, 2023). A better understanding of how insular bats are affected by habitat change, the key driver of bat population declines and extinction (Frick et al. 2020), is thus paramount to prevent that more species follow the fate of the endemic Christmas Island pipistrelle *Pipistrellus murrayi*, declared extinct in 2009 (Conenna et al. 2017).

The oceanic tropical island of São Tomé, located in the Gulf of Guinea, Central West Africa, harbours seven aerial insectivorous bat species, of which three are endemic (Rainho et al. 2022). Two bat species, *Hipposideros ruber* and *Macronycteris thomensis*, belong to the Hipposideridae family. *Macronycteris thomensis*, is an endemic species found throughout the island and while it has been detected in underground roosts, its biology remains poorly known (Rainho et al. 2022). *Hipposideros ruber* is a small leaf-nosed bat particularly associated with primary and secondary forest, which forages by hawking and gleaning in cluttered habitats (Rainho et al. 2010). In São Tomé, this species presents the unusual diurnal activity, a behaviour currently undescribed for mainland populations (Russo et al. 2011). *Taphozous mauritianus* is the only representative of the family Emballonuridae on the island. While it is commonly found across sub-Saharan Africa, on the island of São Tomé, it seems to be limited to the northern coast. This open space forager has been classified as Endangered on the island due to its restricted habitat area and few known locations (Rainho et al. 2010, Rainho et al. 2022). The Molossidae family is represented in São Tomé Island by two species: *Chaerephon pumilus*, commonly known as the little free-tailed bat, and the endemic *Chaerephon tomensis*. *Chaerephon pumilus* is a habitat generalist with a wide distribution across Africa (Mickleburgh 2019). On São Tomé, this species was captured in shade cocoa and coconut plantations and roosts across large sections of island (Rainho et al. 2022). On the other hand, *C. tomensis* is much rarer, and recent trapping efforts failed to detect its presence. However, Rainho et al. (2010) detected through acoustic sampling, two different groups of vocalisations belonging to *Chaerephon* spp, while one of these corresponds to *C. pumilus,* the other may be indicative of the presence of *Chaerephon tomensis*, although further confirmation is required. Another rare species found on the island belongs to the genus *Myotis* within the Vespertilionidae family. The individuals captured in São Tomé are likely to be *M.* cf. *tricolor* but they presented considerable differentiation from *Myotis tricolor* individuals captured in the African mainland, including differences in echolocation calls, morphology and genetics (Rainho

et al. 2022). Notably, this species has only been detected in two locations (Rainho et al. 2010). Finally, the only representative of the family Miniopteridae is the endemic *Miniopterus newtoni*. This species is widely distributed across the island, occupying both forested and urbanised areas. It forms sizable colonies alongside other species, using caves and tunnels as roosting sites (Rainho et al. 2010).

Here, we use the endemic-rich island of São Tomé as a case study to investigate the responses of insectivorous bats to a gradient of land use types, ranging from old-growth forests to agricultural and urban areas. Capitalising on low-cost passive acoustic recorders, we address the following questions: How does land cover type affect:
a) assemblage-level species richness, activity (proxy of abundance) and assemblage composition? We anticipate that species richness, and activity inanthropogenic habitats with higher vegetation complexity (e.g., shade plantations), will be more similar to that of old-growth forests, than in less vegetated habitats (urban areas), and species composition would be consequently different along that gradient; b) species-level responses? We anticipate that species-specific activity is associated with the foraging guild: forest foragers showing higher activity in forests and shaded plantations, and edge and open-space foragers in plantations, agricultural and urban areas.

# 1. Material and Methods

## 1.1. Study area

The study was conducted on the island of São Tomé, part of the Democratic Republic of São Tomé and Príncipe (Fig. 1). Located in the Gulf of Guinea, this oceanic island, with a total area of 857 km2, has a rugged topography with numerous peaks above 1000 m, distributed across the island, except for the flatter northeast areas. The highest peak is Pico of São Tomé which reaches around 2024 m of altitude (Ceríaco et al. 2022). It has a tropical humid climate with two distinct seasons. The dry season (or “gravana”) occurs from June to mid-September, while the rainy season extends throughout the rest of the year, except for a shorter period of the dry season, also called “gravanito”, that lasts only for a few weeks anywhere between mid-December and mid-March (Ceríaco et al. 2022). The annual average rainfall varies across the territory, reaching around 7000 mm in the southwest while reaching less than 600 mm in the northeast. The average annual temperature also varies across the country reaching around 18ºC at higher altitudes and 30ºC closer to the sea level (NBSAP 2015). Over time the island's original cover has suffered significant anthropogenic change. Yet, substantial sections of the island are still covered by old-growth forest with high tree density, with an intermediate density of understory vegetation and epiphytes, primarily found in the rugged high-altitude areas. Old-growth forest (ca. 26.4% of the island) further tends to be surrounded by secondary regrowth forests (ca. 30.5%), resulting from agricultural abandonment and characterised by the presence of non-endemic and smaller trees. Organic shaded plantations of cocoa and coffee encompass areas where these crops (ca. 28.5%) are cultivated beneath the canopy of typically non-native trees. Other land cover types on the island (ca. 14.5%) include urban areas, organic oil palm plantations, small-scale agriculture, while the once dry forest on the northern coast gave place to anthropogenic savannas (Soares et al. 2022).

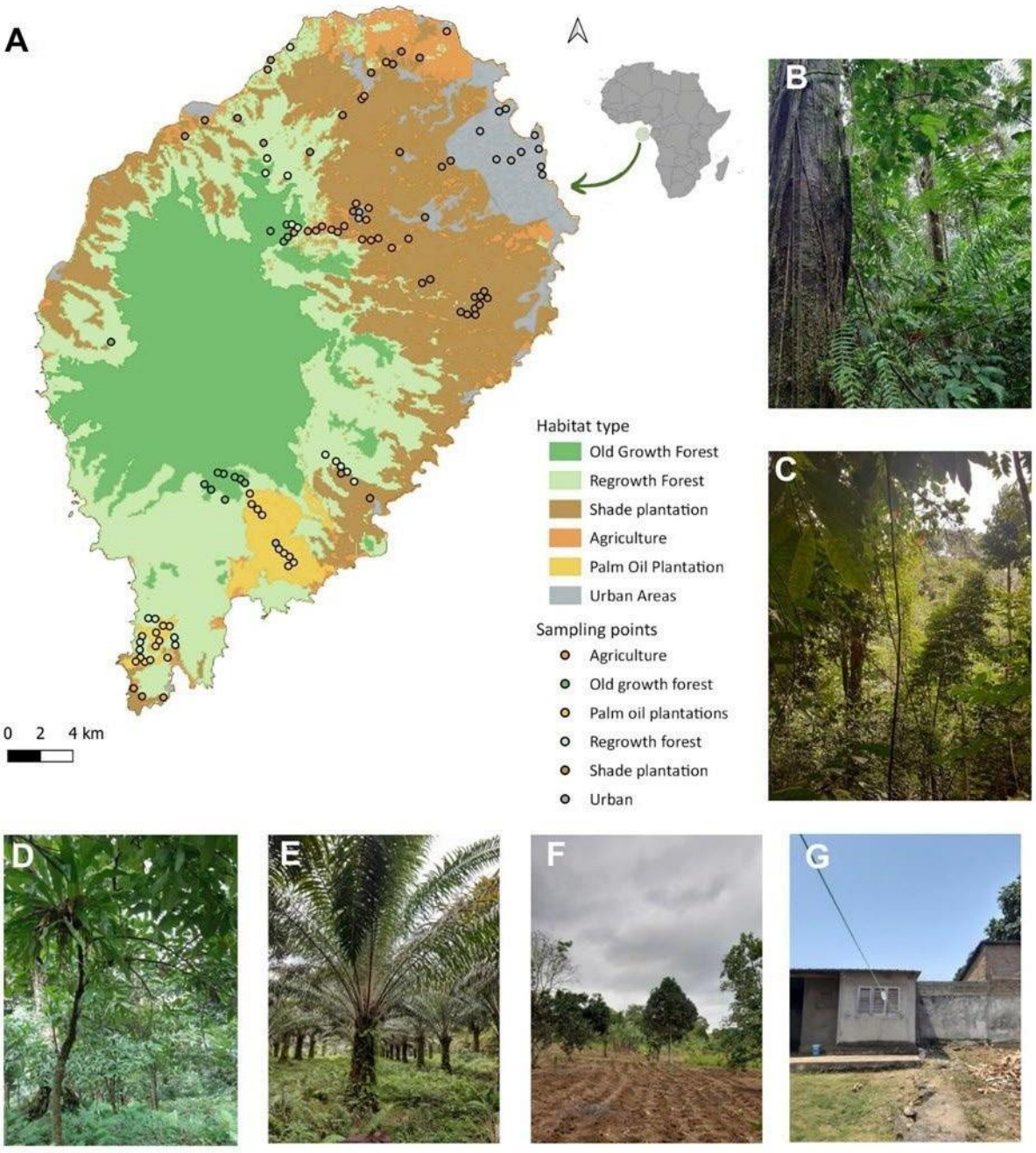


Figure 1 - A. Map of São Tomé, displaying the 115 sampling points coloured according to the main land cover types: B. old-growth forest; C. secondary regrowth forest; D. shaded plantation; E. palm oil plantation; F. agriculture; G. urban areas.

## 1.2. Data collection

We conducted an island-wide acoustic survey from August 2022 to September 2022 (dry season) using AudioMoth® recorders (Hill et al. 2018). To ensure representation of all major land cover types existing on the island — old-growth and regrowth forests, shade

and palm oil plantations, and agriculture and urban areas — sampling sites were tentatively stratified according to land cover type (according to what was logistically possible given site accessibility), with the help of geographic information system (GIS) data obtained from Soares et al. (2020). One AudioMoth recorder was deployed in each of the 115 sampling sites (old-growth: 13; regrowth: 17; shade plantation: 29; oil palm plantations: 20; agriculture: 24; urban areas: 13) (Fig.1A). The type of land cover was assessed at the sampling site considering what was the percentage of each land cover type within a 100-meter radius.

AudioMoth recorders were programmed to record for one minute every five minutes, for two consecutive days and nights, at mid-gain, with a 384 kHz sample rate. The recorders were placed between 1.5 and 2 m above the ground, attached to trees. Contiguous sampling sites were at least 250 m apart from each other. Each recorder was placed inside a plastic box for water protection, with an opening covered by a membrane that allowed the microphone to properly record. Additionally, we did a description of each sampling site's land cover type following these variables: the number of trees with > 10 cm of diameter at breast height (DBH), the height of the five nearest tallest trees, number of stems, lianas (using a categorical scale ranging from 0 (no lianas) to 3 (maximum liana density), number of oil or coconut palm trees, percentage of canopy cover and, vegetation cover at 0, 1, 2, 8, 16 and 32 m, all within a 10 m radius.

## 1.3. Bioacoustic analysis

To analyse our recordings, we used the Kaleidoscope software (Wildlife Acoustics, USA). We first split the recordings into 5-second WAV files (Torrent et al. 2018) and thenwe filtered the recordings for the frequency range between 8 and 250 kHz and a pulse length ranging from 2 to 500 milliseconds. This allowed us to separate the recordings with no pulses into a 'noise' folder that was no longer analysed. Recordings that contained a bat-pass, defined as two or more pulses of a species detected in a 5-s recording (Millon et al. 2015), were then manually classified to the species or genus level, whenever the former was not possible. This classification was carried out by examining the following call parameters: frequency of maximum energy (FmaxE), start (Fmax), and end (Fmin) frequencies, duration of the call, and inter-pulse interval (Russo and Jones 2002). Information on these parameters was retrieved from Rainho et al. (2022) (Table S1 and Fig. S1).

## 1.4. Data analysis

Bat activity, given by the number of bat passes, was used as a proxy for bat abundance (Kunz et al. 2009). Assemblage composition was examined using a Non-metric Multidimensional Scaling (NMDS) ordination based on a Bray-Curtis similarity matrix, considering the number of bat passes per site. Differences between habitats were evaluated using a Permutational Multivariate Analysis of Variance (PERMANOVA). These two analyses were performed using the "vegan" package in R (Oksanen et al. 2022). We also conducted pairwise comparisons to investigate which land cover types differed from each other, using the package "RVAideMemoire" in R (Herve 2023).

Spatial autocorrelation between sampling sites and bat activity was inspected through a Mantel test using the R package "ade4" (Dray 2023). No spatial autocorrelation ($p > 0.05$). To examine the effects of land cover type and altitude on bat species richness, total activity, and species-specific activity, we applied Generalised Linear Mixed-effects Models (GLMMs), as well as Linear Mixed-effects Models (LMMs), using the R package "lme4" (Bates et al. 2023). To account for natural variability in bat activity between sampling sites closer to each other, a random term indicating the date the sampling site had been surveyed was used. The distribution family for each of the response variables was a Poisson distribution for species richness and activity of *Miniopterus newton*, negative binomial for total activity and activity of *Hipposideros ruber* and *Macronycteris thomensis* and normal distribution for *Chaerephon* spp ($\log_{10}$ x). The species *Taphozous mauritianus* was excluded from the species-specific analyses due to the low number of detections (n = 23). Additionally, we used Tukey tests for the GLMMs, to examine which habitats were significantly different from each other, using Package "multcomp" in R (Torsten Hothorn et al. 2023).

Altitude values (meters above sea level) were standardised to a mean of zero and a standard deviation of one. To improve model fitting, we excluded an outlier from the model on the total bat activity. This outlier corresponded to the urban land cover type and exhibited a substantially higher bat activity (1706 bat passes) compared to the rest (mean ± SD = 158.22 ± 163.05 bat passes). We suspect that the high value observed for bat activity in this sampling site is due to its proximity to a roosting site. All local-scale variables (Table S2) were summarised in a Principal Component Analysis (PCA) (Fig. S2). The primary axis obtained from the PCA was initially considered as a potential

predictor. However, due to the strong correlation observed between the first axis of the PCA and a numerical transformation of the land cover type variable that ranged from one to five, in which one is the least disturbed and five the most (old-growth forest: 1; regrowth forest: 2; shade plantation: 3; oil palm plantation: 4; agriculture: 5; urban areas: 5) ($r$ > 80%), we opted to not include the first axis of the PCA in further analysis. All analyses were performed in R 4.1.2 software (R Core Team 2022).

# 2. Results

We detected a total of 19,744 bat passes from five different taxa. The most commonly recorded bats belonged to the genus *Chaerephon*, with a total of 10 789 bat passes; from these, 9 099 were confirmed *C. pumilus*, while the remainder could include records of the rare and little known *C. tomensis* endemic. The endemic *Miniopterus newtoni* was the second most commonly recorded species (8,030 bat passes) and the most widespread distributed (100 sampling sites), followed by the other endemic *Macronycteris thomensis* (703 bat passes, 42 sampling sites), *Hipposiderus ruber* (191 detections, 39 sampling sites) and *Taphozous mauritianus* (23 bat passes, 9 sampling sites). The *Hipposiderus ruber* and the endemic *Miniopterus newtoni* were the only species detected in every land cover type (Fig. 2A). The number of taxa recorded across the different land cover types varied between one in old-growth, regrowth, shade and oil palm plantations and agriculture and five in regrowth, shade and oil palm plantations, agriculture and urban (mean ± SD = 3.15 ± 1.19), and species activity between one in old-growth and regrowth and 800 in shade plantations (mean ± SD = 171.69 ± 217.22).

## 2.1. Assemblage-wide responses

In the ordination diagram, old-growth and secondary regrowth forests clustered nearby, away from the remaining anthropogenic land cover types (Fig. 2B). Assemblage composition differed across the different land cover types ($F$ = 12.098; $R^2$ = 0.359; $P$ = 0.001), with the multiple comparisons test revealing that all pairs of land cover types differed in bat composition, except between shade plantations and agricultural areas that showed similar assemblages (Table S3). Species richness varied little between habitats (Fig. S3); however, old-growth forests presented the lowest richness values, harbouring between one and two species (Table S4, Fig. S3). Bat activity was higher in all the anthropogenic habitats than in old-growth forests, with a noticeable trend for even higher bat activity in the more disturbed habitats (Fig. 3A, Table S4). Indeed, palm oil plantations and agriculture areas had the highest effect on activity (β =2.788, P < 0.001; β =2.685, P < 0.001) (Table S4). Lastly, altitude was found to have an overall negative effect on bat activity (β = -0.411, P = 0.005) (Table S4).

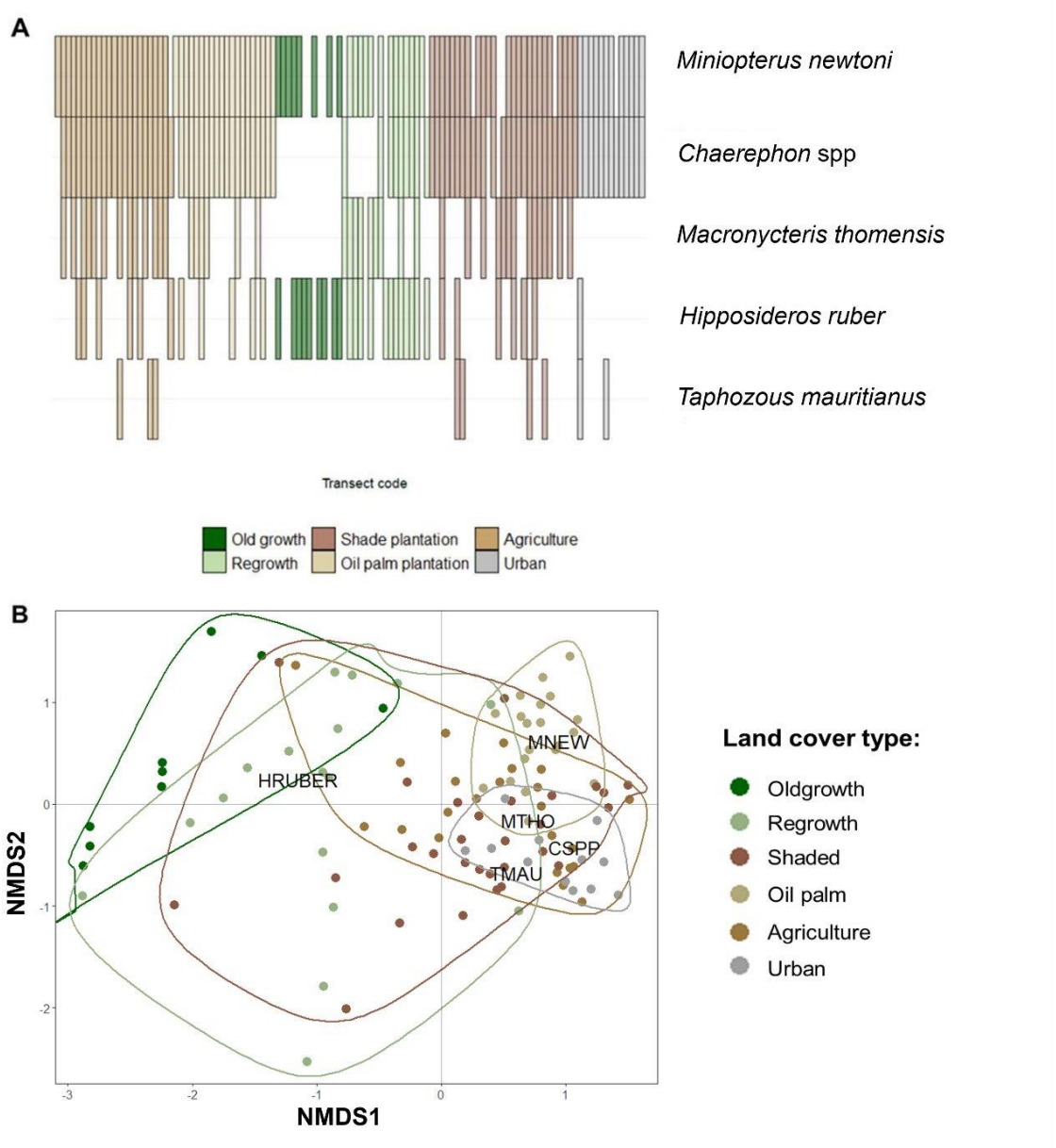


Figure 2 - A. Species detected at each sampling point; Each rectangle corresponds to a species detection, coloured according to land cover type. B. Arrangement of the sampling sites and species along the axes of a non-metric multidimensional scaling (NMDS) based on a Bray-Curtis similarity matrix. NMDS had a stress value of 0.145. CSPP- *Chaerephon spp*; HRUBER- *Hipposideros ruber*; MNEW- *Miniopterus newtoni*; MTHO- *Macronycteris thomensis*; TMAU- *Taphozous mauritianus*.

## 2.2. Species-specific responses

Urban areas had a higher effect on *Chaerephon* spp. activity than in any other land cover type (β = 1.527, P < 0.001[6]) (Fig. 2B and 3B; Table S5), whereas *Miniopterus newtoni,*, displayed a particularly strong association with oil palm plantations (β = 2.058, P< 0.001) (Fig. 2A, 3D, Table S4 and S5). *M. newtoni* was negatively influenced by urban areas (Table S5) and altitude (β= -0.10205, P= 0.0102) (Table S4). The endemic *Macronycteris thomensis* was not detected in old-growth forest and urban areas (Fig. 2A) and, similarly to all other bat species, was negatively influenced by altitude (β = -0.616, P < 0.001) (Table S4). *M. thomensis* activity in all habitats was significantly different from old growth forest, with regrowth forest having the highest effect (β= 23.646P < 0.001) (Fig.3E; Table S5). *Hipposideros ruber* was positively influenced by old-growth and regrowth forest and negatively affected by urban areas (β= -3.336, P= 0.008) (Fig. 3C; Table S4).

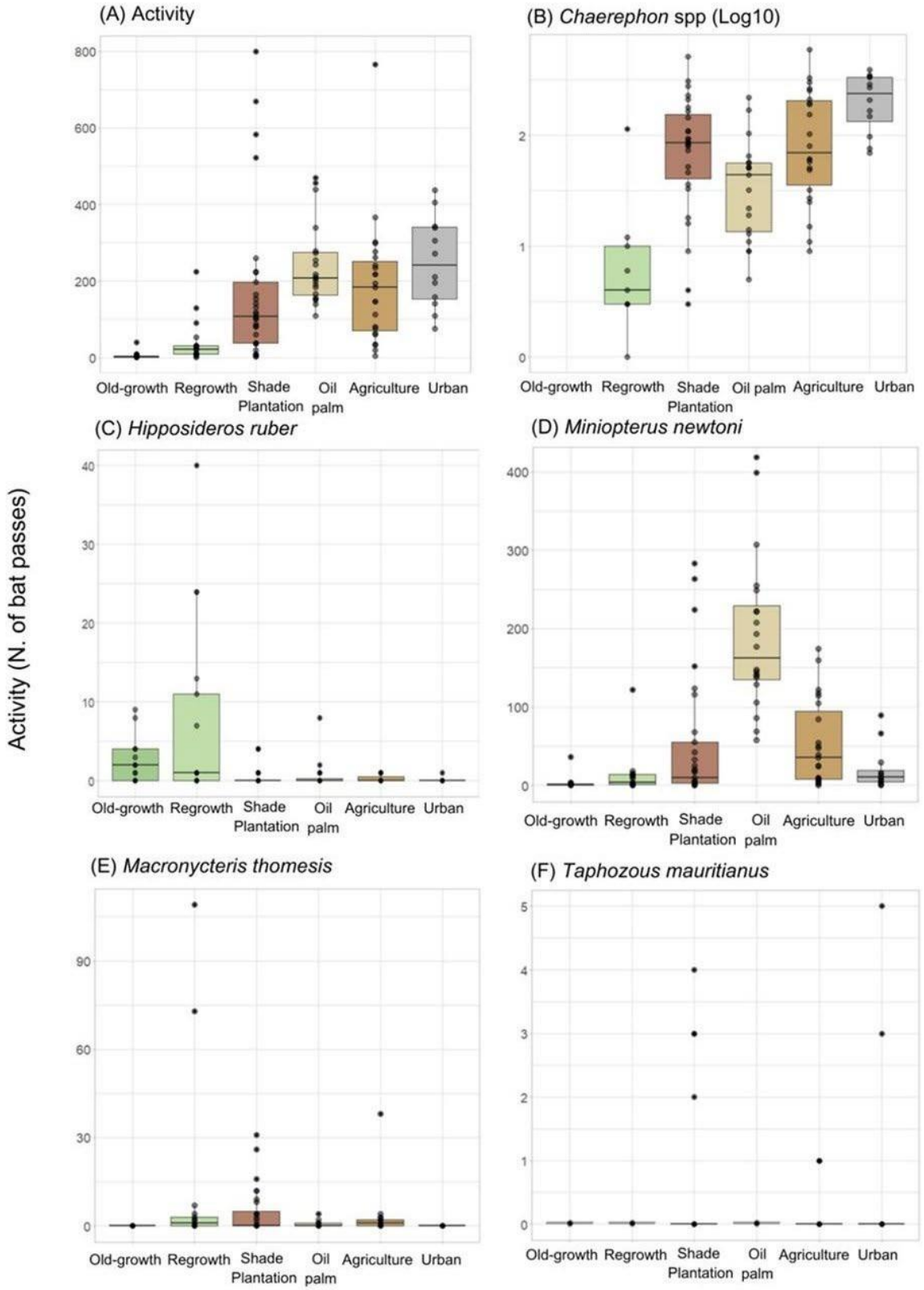
(A) Activity
(B) Chaerephon spp (Log10)
(C) Hipposideros ruber
(D) Miniopterus newtoni
(E) Macronycteris thomesis
(F) Taphozous mauritianus
Old-growth
Regrowth
Shade Plantation
Oil palm
Agriculture
Urban
Activity (N. of bat passes)
Land use type

Figure 3 - (A) Total activity (number of bat passes) and activity of (B) *Chaerephon* spp., (C) *Hipposideros ruber*, (D) *Miniopterus newtoni*, (E) *Macronycteris thomesis* and (F) *Taphozous mauritianus* across land cover type. Each box corresponds to a land cover, the line refers to the median activity, and the box represents the interquartile range.

# Discussion

While land use change continues to threaten the native habitats in the island of São Tomé, previous studies pointed in the direction of mostly detrimental effect on endemic birds (Rocha 2008; de Lima et al. 2013), but on endemic amphibians, human-modified landscapes have shown potential for their conservation (Strauß et al. 2018). In this study, despite a previous assessment on the distribution of bat species across the island (Rainho et al. 2010), we offer the first insights on the impact of land use change on insectivorous bats.

Overall, the number of bat species has not been negatively affected by land use change and the total species activity even increased over the gradient of increasing intensity in the land use change. Yet, species-specific analysis unveiled a negative effect of land use change on forest foragers and a positive effect on open-area foragers. Our results therefore show that insectivorous bat responses to land use change are modulated by their foraging guild. Altitude had a negative effect on the total batactivity, which might further contribute to the relatively low bat activity observedin the old-growth forests, which were at higher altitude (mean ± sd: 666.23 ± 475.47),than the rest of the habitat types (350.10 ± 374.31). Of the species that had previously been detected on the island, we were unable to detect *Myotis* cf. *tricolor* and had a very reduced number of detections of *Taphozous mauritianus.*

Bat species richness did not show much variation across different land cover types. Somewhat unexpectedly, the lowest levels of species richness were found in old-growth forests. However, when considering the overall composition of bat communities, there were notable differences among land cover types. Forested habitats, including old-growth and regrowth areas, displayed similar compositions, while the remaining habitats also exhibited comparable assemblage compositions distinct from the forested ones. These similarities may be linked to specific echolocation and morphological traits that influence species' ability to thrive in particular habitats (Jung and Threlfall 2016, Huanget al. 2019; Núñez et al. 2019). For instance, when considering their foraging guild, we can observe two forest forager species (*H. ruber* and *M. thomensis*), two open space foragers

(*Chaerephon* spp. and *T. mauritianus*) and a clutter-edge forager (*M. newtoni*). When comparing our results for bat species richness with the results reported by de Lima (2013) for bird species richness on the island it is possible to see a similar pattern of increased richness with land use intensity. Bat activity was consistently higher across all anthropogenic land cover types when compared to old-growth forest. Notably, a clear trend emerged, showing elevated activity levels in more disturbed habitats, particularly in oil palm plantations and agricultural areas. Monocultural agroforestry systems do not configure as the most suited habitat for insectivorous bats. Such habitats often have low arthropod diversity due to pesticide application (Lawer and Darkoh 2016). However, in São Tomé, bats displayed the opposite response, with increased activity in oil palm plantations. Agricultural uses with reduced pesticide input are known to be beneficial to insectivorous bats (Williams-Guillén et al. 2016), in particular to gleaning species,which are generally more vulnerable to habitat modification (Puig-Montserrat et al. 2021; Ancillotto et al. 2023; but see Froidevaux et al. 2017). Accordingly, the higher levels of bat activity detected over agricultural areas can likely be attributed tothe island's predominant agricultural practices, which are largely conducted withoutthe heavy use of pesticides, leading to a potential greater availability of prey (Bengtsson et al. 2005). This abundance of food resources likely explains the higher bat activity levels observed in these areas, but more studies on arthropod abundancein these different habitats would be required.

Open space foragers with constant and quasi-constant frequencies and narrow wings (Jung and Kalko 2011), such as *Chaerephon* spp. tend to be habitat generalists and to benefit from less cluttered environments (Torrent et al., 2018; López-Bosch et al. 2022). Species within the Molossidae family, to which they belong, seem to benefitprofit from urban environments, utilising man-made structures for roosting (Razafindrakoto et al 2017; López-Baucells et al. 2017) and taking advantage of the increased availability of arthropod prey attracted to streetlights (Jung and Threlfall 2016) and the eventual increased abundance of arthropods, including agricultural pests, in agroecosystems (Kemp et al. 2019; Weier et al. 2021). However, molossids do not seem to have a preference for either natural or urban environments across different continents, which could be due to their capacity to fly for long distances and thus be less affected by anthropogenic pressures (Jung and Kalko 2011, Jung and Threlfall 2016, Kemp et al. 2019). Our findings, with *Chaerephon* spp. being detected across various habitats, except for old-growth forests, and exhibiting a strong association with urban areas, support this. The lackof detection of *Chaerephon* spp. in old-growth forests might

relate to the incapacity to detect high flying animals, above the tree canopy (Duchamp et al. 2006). Moreover, despite our findings indicating *Chaerephon* spp. as the most frequently detected and exhibiting a degree of adaptability to anthropogenic influences, we cannot conclusively confirm the detection of the endemic *C. tomensis*. Consequently, it is of paramount significance to conduct further investigations into the presence of this species, to comprehensively assess its current status, particularly as it has been poorly detected thus far (Rainho et al. 2022). Trying to be certain of the species echolocation call characteristics would be a priority as it would facilitate whole island surveys using automatic recording units.

Hipposiderids are narrow space foragers, adapted to forest habitats (Monadjem et al. 2020) and *Hipposideros ruber*, with its echolocation call structure that beginswith constant frequency and is followed by a frequency modulated section, is no exception (Rainho et al. 2022). This type of echolocation call is better suited to highly cluttered habitats such as forested areas (Denzinger and Schnitzler 2013). Our findings align with previous records for this species on the African mainland (Mande et al. 2023), supporting that the species is highly associated with both old-growth and regrowth forests. Furthermore, our results indicate a negative effect on activity of the more open land cover types, which could reflect the poor performance of their high frequency echolocation calls in detecting prey in more open areas. Additionally, this particular species is predominantly linked to lowland forest ecosystems on the mainland (Monadjem et al. 2017). Given that the majority of the surveyed old-growth forest areas were situated at higher altitudes, that could explain the low levels ofactivity of this species on old-growth forest. The endemic *Macronycteris thomensis*,has a similar echolocation call structure to *H. ruber* but with a lower frequency. *Macronycteris* sp. are known to be less tolerant to cluttered spaces and for being more adapted to mid-storey flights (Mande et al. 2023). During our surveys, we were unable to detect this species in old-growth forest. Other than reflecting that the species is not present in old-growth habitats, this was likely due to our inability to survey more core areas of the Obô Natural Park, where the most pristine old-growth forest is located (Soares et al. 2022), and to a combination of probable low natural abundance of this species in its native habitat and low detectability of its low intensity echolocation calls, particularly in highly cluttered spaces. Furthermore, as expected for a forest- associated species, it was not detected in urban areas. Instead, it was particularly active in regrowth forest, which seems to be the preferred land cover type for this endemic species. This result thus aligns with previous research supporting the conservation potential of regrowth areas for reverting faunal declines in modified tropical landscapes (Barlow et al. 2007; Chazdon 2019), particularly for forest-associated bats (Farneda et al. 2018, 2022; Rocha et al. 2018; López-Baucells et al.

2022; Yoh et al. 2022). The non-detection of *Macronycteris thomensis* in old-growth might also be influenced by the fact that the species was found to be negatively influenced by altitude, and the old-growth sites sampled during this study, where predominantly at higher altitudes (where the largest expanses of old-growth forest are currently located in São Tomé; Soares et al. 2022). Altitude was also found to influence the activity levels of other forest-associated island insectivorous bats (e.g., *Plecotus austriacus* in Madeira Island; Ferreira et al. 2022), suggesting a strong modulating effect over the habitat preferences of insular species.

The endemic *Miniopterus newtoni* has low duty cycle frequency-modulated echolocation calls, characteristic of the clutter-edge space foraging guild (Denzinger and Schnitzler 2013, Taylor et al. 2013). This species was detected across all land cover types, but it displayed a higher association with oil palm plantations. Although the conversion of native habitats to oil palm plantations has largely negative impacts on native biodiversity (Wilcove and Koh 2010; Azhar et al 2015; Freudman et al 2015), some species - including bats (Mullin et al. 2020) - do benefit or are able to persist in these highly modified anthropogenic habitats. Conversely, urban areas and higher altitudes had a negative impact on its activity. This preference for oil palm plantations may be attributed to greater prey availability. It is worth noting that, unlike other studies where insect and bat activity decreased in oil palm plantations due to agrochemical usage (Lawer and Darkoh 2016), as mentioned before, the production here is mostly organic (Socfin 2022), potentially resulting in a higher abundance of insects. The proximity of these plantations with old growth forest and being a clutter-edge forager might indicate that this species can profit from both land cover types.

It is important to note that we did not account for possible differences in detectability between the different species. High levels of clutter, like the ones found in forests, often result in lower levels of detection since calls can be deflected by vegetation and by forcing species to fly over the clutter (Kaiser and O'Keefe 2015, Duchamp et al. 2006). So, it is possible that our low levels of detection in old-growth forest could also be explained by these factors.

Conservation implications

The loss of forest cover in the tropics continues to intensify with expanding agriculture (Laurance et al. 2014), especially placing forest-dependent species at risk. This seems to be the case of the insectivorous bats of São Tomé Island, namely the species

*Hipposideros ruber* and *Macronycteris thomensis,* which were mainly detected in forested habitats. Our findings suggest that conservation efforts should place a higher priority on preserving bat species that inhabit forest environments, given the inability of these species to thrive elsewhere (Muñoz-Torrent et al. 2022). To address this concern,it is essential to protect and consider the regrowth forests surrounding the old-growth protected areas as potential means to mitigate species declines in altered tropical landscapes (Chazdon 2019). Furthermore, given that agricultural areas,including small-scale agriculture, palm oil and shaded plantations represent habitatswith considerable insectivorous bat use, and that to date these constitute biological agriculture, it is imperative to continue promoting the avoidance of the usage of pesticides. For instance, the endemic species *Miniopterus newtoni* exhibited elevated activity levels within oil palm plantations, possibly attributed to a greater prey abundance resulting from the limited pesticide application in these plantations on the island. Given the ability of some species to thrive in agricultural areas, our findings further shed light on the potential of insectivorous bats to act as pest suppressors (Kemp et al. 2019). Likewise, the potential of insectivorous bats to act as an important suppressor ofzoonotic diseases is illustrated by the total bat activity being the highest in urban areas.Maintaining the heterogeneous mosaic of land use types — including the irreplaceablenative forests — in São Tomé Island, as well as in other tropical oceanic islands, willcontinue to allow maximising bat diversity in the whole island, with potentially importantbenefits for local communities.

# Conclusion

The observed associations between the insectivorous bats of São Tomé and the island's different land cover types aligned with the bat species foraging guilds. Overall, bat activity was higher in human-modified habitats, indicating that similarly to what was found in other native taxa such as birds and amphibians (de Lima et al. 2013; Strauß et al. 2018; Soares et al. 2022), multiple bat species exhibit some degree of adaptability to human-altered habitats of São Tomé. Since insectivorous bats, including multiple

island-restricted species, are known to consume insect disease vectors and agriculture and forestry arthropod pests (Kemp et al. 2019; Nobrega et al. 2023; Toneu-Corral et al. 2023), their persistence in humanised landscapes is likely to bring considerable benefits for local populations. However, certain species, especially those highly specialised in forested environments, including some endemic species (e.g. *Macronycteris thomensis*), were negatively impacted by more disturbed land cover types such as palm oil plantations and urban areas. Alarmingly, others still, such as *M*. cf. *tricolor* were not even detected. This, combined with the acute lack of knowledge of the São Tomé collared fruit bat *Myonycteris brachycephala*, an endemic, non-echolocating bat only known from two localities and with no recent detections (Rainho et al. 2022), makes it evident that more research is needed to support the conservation of bats in this endemic-rich island.

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# Attachments

Table S1. Echolocation call characteristics of the bat species in São Tomé (adapted from Rainho et al. (2022)).

| Species | Call type | Fmin (kHz) | Fmax (kHz) | FmaxE (KHz) | Duration (ms) | Interval (ms) |
|---|---|---|---|---|---|---|
| *Hipposideros ruber* | CF-FM | 139.7 ±0.2 139.3-139.8 | 141.5±0.4 140.8-141.9 | 140.9±0.3 140,4–141,1 | 5.9±0.2 5,7 – 6,1 | 14.1 ±4.2 10.4-22.1 |
| *Macronycteris thomensis* | CF-FM | 66.0 ±0.8 64.3-66.8 | 68.0±1.0 66.8-70.2 | 67.2±0.4 66,4 – 68,0 | 20.7±4.0 15,6 – 28,6 | 66.8 ±17.4 43.2-106.4 |
| *Myotis tricolor* | FM | 39.3±2.0 36.6-41.6 | 117.3±3.3 112.0-120.8 | 78.4±2.1 76,4 – 81,8 | 1.84±0.1 1,74 – 1,92 | 82.7±16.2 58.4-102.6 |
| *Miniopterus newtoni* | FM | 50.3±1.3 47.8-52.2 | 101.7±16.7 69.6-119.0 | 55.9±2.7 53,2 – 61,0 | 4.8±2.1 2,3–7,8 | 61.4±23.6 31.8-105.7 |
| *Taphozous mauritianus* | QFC | 24.2±0.7 23.4-25.2 | 31.9±0.6 31.4-32.5 | 28.3±0.2 28,1 – 28,4 | 14.8±1.7 12,8 – 16,8 | 77.4±6.4 70.7-86.4 |
| *Chaerephon pumilus* | QFC | 24.9±2.7 19.8-29.4 | 36.0±8.7 24.7-51.5 | 28.4±2.3 23,4 – 31,5 | 13.6±3.0 8,1–18,6 | 258.4±156.5 62.8-472.0 |
| *Rousettus aegyptiacus* | FM | 9.3±2.4 4.1-11.9 | 110.5±48.0 | - | 0.33±0.12 0.2-0.5 | 122.5±28.7 0.2-0.5 |

| | | | | | | |
|---|---|---|---|---|---|---|
| | | | 44.0-150.0 | | | |
| *Chaerephon* spp. | QFC | 21.0±1.1 19.0-22.4 | 23.0±1.1 20.4-25.5 | 22.1±1.0 19.9-24.1 | 16.3±1.7 12.7-19.9 | 350.7±97.2 137.0-558.5 |

Table S2. Summary of local-scale variables. T = number of trees (DBH ≥ 10 cm), HT = Tree hight (m), S = number of woody stems (DBH < 10 cm), P = number of palms, C = percent canopy cover, L = number of lianas, VC = vegetation cover at 0, 1, 2, 4, 8, 16, and 32 m. Results are presented as mean ± SD.

| **Habitat category** | **Old-growth forest** | **Regrowth forest** | **Shade plantation** | **Oil palm plantation** | **Agriculture** | **Urban area** |
|---|---|---|---|---|---|---|
| **T** | 22.05 ± 11.25 | 20.96 ± 11.44 | 5.70 ± 4.22 | 0.05 ± 0.22 | 3.65 ± 4.23 | 3.69 ± 2.53 |
| **HT** | 24.13 ± 9.97 | 17.24 ± 6.19 | 11.67 ± 4.58 | 17 | 9.08 ± 6.23 | 6.43 ± 2.96 |
| **S** | 64.14 ± 28.87 | 48.39 ± 27.49 | 3.76 ± 6.83 | 0.10 ± 0.45 | 1.70 ± 3.21 | 1.46 ± 1.66 |
| **P** | 1.09 ± 3.65 | 8.17 ± 10.92 | 1.55 ± 2.31 | 17.10 ± 2.79 | 1.43 ± 2.57 | 1.46 ± 3.20 |
| **C** | 69.77 ± 16.29 | 70.22 ± 18.80 | 44.09 ± 22.55 | 50.50 ± 15.38 | 20.78 ± 22.14 | 14.00 ± 14.45 |
| **L** | 0.68 ± 1.04 | 0.43 ± 0.74 | 0.06 ± 0.35 | 0 | 0 | 0 |

| | | | | | | |
|---|---|---|---|---|---|---|
| **VC 0m** | 55.45 ± 19.57 | 48.04 ± 21.78 | 23.18 ± 21.64 | 68.75 ± 15.72 | 45.87 ± 31.79 | 9.23 ± 10.17 |
| **VC 1m** | 57.73 ± 19.62 | 52.61 ± 19.99 | 30.00 ± 16.54 | 19.50 ± 9.16 | 28.61 ± 26.25 | 9.62 ± 5.94 |
| **VC 2m** | 46.82 ± 20.27 | 48.70 ± 13.67 | 45.61 ± 14.35 | 13.75 ± 3.93 | 14.57 ± 15.59 | 9.38 ± 7.95 |
| **VC 4m** | 52.95 ± 14.69 | 52.39 ± 13.39 | 41.21 ± 15.56 | 35.50 ± 22.76 | 10.63 ± 12.90 | 9.23 ± 8.38 |
| **VC 8m** | 51.14 ± 13.71 | 42.17 ± 18.21 | 13.48 ± 9.39 | 5.25 ± 1.12 | 4.22 ± 6.10 | 5.00 ± 7.36 |
| **VC 16m** | 21.82 ± 13.76 | 20.87 ± 17.49 | 3.18 ± 4.81 | 0.25 ± 1.12 | 1.09 ± 3.68 | 0 |
| **VC 32m** | 6.14 ± 8.44 | 0.65 ± 2.29 | 0 | 0 | 0 | 0 |

Table S3. Results of the pairwise comparisons of species composition of insectivorous bats surveyed across 115 sampling sites in São Tomé Island. Pairwise comparisons were performed using a PERMANOVA of assemblage composition (NMDS). Significant differences are highlighted in bold (P < 0.05).

| | Regrowth | Agriculture | Old growth | Palm oil | Shade |
|---|---|---|---|---|---|
| Agriculture | **0.0012** | - | - | - | - |
| Old growth | **0.0012** | **0.0012** | - | - | - |
| Palm oil | **0.0012** | **0.0012** | **0.0012** | - | - |
| Shade | **0.0012** | 0.4350 | **0.0012** | **0.0012** | - |
| Urban | **0.0012** | **0.0075** | **0.0012** | **0.0012** | **0.0046** |

Table S4. Generalised Linear Models (GLMMs) explaining bat species richness, total activity, and species-specific activity. For each model, we indicate the estimate, standard error, Z- or T- value, and P-value. For *Chaerephon* spp. ($log_{10}x$) a linear model was used instead of a GLMMs (see methods).

| **Response variable** | **Predictor** | **Estimate** | **Std. error** | **Z / T value** | **P value** |
|---|---|---|---|---|---|
| | Intercept | 0.339 | 0.247 | 1.37 | 0.171 |
| | Regrowth | 0.751 | 0.284 | 2.642 | **0.008** |
| | Shade | 0.904 | 0.270 | 3.349 | **0.001** |
| Richness | Oil palm | 0.766 | 0.288 | 2.662 | **0.008** |
| | Agriculture | 1.041 | 0.266 | 3.92 | **< 0.001** |
| | Urban | 0.759 | 0.301 | 2.518 | **0.012** |
| | Altitude | -0.090 | 0.067 | -1.352 | 0.176 |
| | Intercept | 2.415 | 0.403 | 5.995 | **< 0.001** |
| | Regrowth | 1.392 | 0.424 | 3.287 | **0.001** |

| Response variable | Predictor | Estimate | Std. error | Z / T value | P value |
|---|---|---|---|---|---|
| Activity (N. of bat passes) | Shade | 2.225 | 0.534 | 4.17 | **< 0.001** |
| | Oil palm | 2.788 | 0.459 | 6.063 | **< 0.001** |
| | Agriculture | 2.685 | 0.514 | 5.22 | **< 0.001** |
| | Urban | 2.393 | 0.619 | 3.862 | **< 0.001** |
| | Altitude | -0.411 | 0.146 | -2.81 | **0.005** |
| *Chaerephon* spp. ($log_{10}x$) | Intercept | 0.494 | 0.228 | 2.164 | **0.037** |
| | Regrowth | 0.162 | 0.242 | 0.670 | 0.504 |
| | Shade | 0.916 | 0.264 | 3.465 | **0.001** |
| | Oil palm | 1.017 | 0.262 | 3.877 | **< 0.001** |
| | Agriculture | 1.246 | 0.244 | 5.115 | **< 0.001** |
| | Urban | 1.527 | 0.320 | 4.769 | **< 0.001** |
| | Altitude | -0.176 | 0.094 | -1.868 | 0.069 |
| *Hipposideros ruber* | Intercept | 0.883 | 0.509 | 1.736 | 0.083 |
| | Regrowth | 1.098 | 0.633 | 1.735 | 0.083 |
| | Shade | -1.744 | 0.672 | -2.596 | **0.009** |
| | Oil palm | -1.257 | 0.731 | -1.721 | 0.085 |
| | Agriculture | -2.278 | 0.707 | -3.223 | **0.001** |
| | Urban | -3.336 | 1.253 | -2.664 | **0.008** |
| | Altitude | 0.085 | 0.219 | 0.390 | 0.697 |
| | Intercept | 1.962 | 0.342 | 5.74 | **< 0.001** |

| Response variable | Predictor | Estimate | Std. error | Z / T value | P value |
|---|---|---|---|---|---|
| *Miniopterus newtoni* | Regrowth | 0.390 | 0.187 | 2.088 | **0.037** |
| | Shade | 1.795 | 0.204 | 8.783 | **< 0.001** |
| | Oil palm | 2.058 | 0.177 | 11.621 | **< 0.001** |
| | Agriculture | 0.845 | 0.188 | 4.493 | **< 0.001** |
| | Urban | -0.530 | 0.214 | -2.478 | **0.013** |
| | Altitude | -0.102 | 0.039 | -2.569 | **0.010** |
| *Macronycteris thomensis* | Intercept | -21.899 | 0.070 | -310.803 | **< 0.001** |
| | Regrowth | 23.646 | 0.071 | 331.636 | **< 0.001** |
| | Shade | 22.756 | 0.071 | 320.842 | **< 0.001** |
| | Oil palm | 20.250 | 0.071 | 284.265 | **< 0.001** |
| | Agriculture | 21.090 | 0.071 | 296.481 | **< 0.001** |
| | Urban | 0.219 | 0.072 | 3.067 | **0.002** |
| | Altitude | -0.616 | 0.072 | -8.616 | **< 0.001** |

Table S5. Tukey post-hoc pairwise comparisons for the effect of different land cover types on bat activity, and species-specific activity. For each pairwise comparison, we indicate the estimate, standard error, Z-value, and P-value.

| Response variable | Comparison | Estimate | Std. error | Z value | P value |
|---|---|---|---|---|---|
| **Activity (N. of bat passes)** | Regrowth - Old growth | 1.392 | 0.424 | 3.287 | 0.012 |
| | Shade - Old growth | 2.225 | 0.534 | 4.170 | < 0.001 |
| | Oil palm - Old growth | 2.788 | 0.460 | 6.063 | < 0.001 |
| | Agriculture - Old growth | 2.685 | 0.514 | 5.220 | < 0.001 |
| | Urban - Old growth | 2.393 | 0.620 | 3.862 | 0.001 |
| | Shade - Regrowth | 0.833 | 0.377 | 2.211 | 0.217 |
| | Oil palm - Regrowth | 1.395 | 0.326 | 4.286 | < 0.001 |
| | Agriculture - Regrowth | 1.293 | 0.378 | 3.421 | 0.007 |
| | Urban - Regrowth | 1.000 | 0.482 | 2.076 | 0.282 |
| | Oil palm - Shade | 0.562 | 0.371 | 1.515 | 0.633 |

| Response variable | Comparison | Estimate | Std. error | Z value | P value |
|---|---|---|---|---|---|
| | Agriculture - Shade | 0.460 | 0.326 | 1.410 | 0.702 |
| | Urban - Shade | 0.168 | 0.375 | 0.446 | 0.997 |
| | Agriculture - Oil palm | -0.102 | 0.371 | -0.276 | 1.000 |
| | Urban - Oil palm | -0.395 | 0.443 | -0.891 | 0.943 |
| | Urban - Agriculture | -0.293 | 0.366 | -0.800 | 0.964 |
| | Regrowth - Old growth | 0.227 | 0.242 | 0.939 | 0.933 |
| | Shade - Old growth | 1.063 | 0.257 | 4.138 | < 0.001 |
| | Oil palm - Old growth | 1.136 | 0.258 | 4.408 | < 0.001 |
| | Agriculture - Old growth | 1.297 | 0.245 | 5.297 | < 0.001 |
| | Urban - Old growth | 1.838 | 0.281 | 6.547 | < 0.001 |
| | Shade - Regrowth | 0.836 | 0.184 | 4.555 | < 0.001 |

| Response variable | Comparison | Estimate | Std. error | Z value | P value |
|---|---|---|---|---|---|
| ***Chaerephon* spp.** | Oil palm - Regrowth | 0.908 | 0.193 | 4.714 | **< 0.001** |
| | Agriculture - Regrowth | 1.069 | 0.190 | 5.642 | **< 0.001** |
| | Urban - Regrowth | 1.611 | 0.237 | 6.797 | **< 0.001** |
| | Oil palm - Shade | 0.072 | 0.218 | 0.332 | 0.999 |
| | Agriculture - Shade | 0.233 | 0.181 | 1.288 | 0.783 |
| | Urban - Shade | 0.775 | 0.231 | 3.359 | **0.009** |
| | Agriculture - Oil palm | 0.161 | 0.202 | 0.797 | 0.966 |
| | Urban - Oil palm | 0.703 | 0.242 | 2.908 | **0.040** |
| | Urban - Agriculture | 0.542 | 0.183 | 2.961 | **0.034** |
| | Regrowth - Old growth | 0.390 | 0.187 | 2.088 | 0.262 |
| | Shade - Old growth | 1.795 | 0.204 | 8.783 | **<0.001** |

| Response variable | Comparison | Estimate | Std. error | Z value | P value |
|---|---|---|---|---|---|
| | Oil palm - Old growth | 2.058 | 0.177 | 11.621 | **<0.001** |
| | Agriculture - Old growth | 0.845 | 0.188 | 4.493 | **<0.001** |
| | Urban - Old growth | -0.530 | 0.214 | -2.478 | 0.113 |
| | Shade - Regrowth | 1.404 | 0.121 | 11.591 | **<0.001** |
| ***Miniopterus newtoni*** | Oil palm - Regrowth | 1.668 | 0.073 | 22.700 | **<0.001** |
| | Agriculture - Regrowth | 0.455 | 0.098 | 4.620 | **<0.001** |
| | Urban - Regrowth | -0.921 | 0.136 | -6.761 | **<0.001** |
| | Oil palm - Shade | 0.264 | 0.114 | 2.318 | 0.164 |
| | Agriculture - Shade | -0.949 | 0.091 | -10.480 | **<0.001** |
| | Urban - Shade | -2.325 | 0.125 | -18.629 | **<0.001** |
| | Agriculture - Oil palm | -1.213 | 0.081 | -14.930 | **<0.001** |

| Response variable | Comparison | Estimate | Std. error | Z value | P value |
|---|---|---|---|---|---|
| | Urban - Oil palm | -2.589 | 0.125 | -20.767 | **<0.001** |
| | Urban - Agriculture | -1.376 | 0.101 | -13.625 | **<0.001** |
| | Regrowth - Old growth | 23.646 | 0.071 | 331.636 | **<0.001** |
| | Shade - Old growth | 22.756 | 0.071 | 320.842 | **<0.001** |
| | Oil palm - Old growth | 20.250 | 0.071 | 284.265 | **<0.001** |
| | Agriculture - Old growth | 21.090 | 0.071 | 296.481 | **<0.001** |
| | Urban - Old growth | 0.219 | 0.072 | 3.067 | **0.023** |
| | Shade - Regrowth | -0.890 | 0.101 | -8.853 | **<0.001** |
| ***Macronycteris thomensis*** | Oil palm - Regrowth | -3.396 | 0.101 | -33.741 | **<0.001** |
| | Agriculture - Regrowth | -2.556 | 0.101 | -25.359 | **<0.001** |
| | Urban - Regrowth | -23.427 | 0.101 | -232.397 | **<0.001** |

| Response variable | Comparison | Estimate | Std. error | Z value | P value |
|---|---|---|---|---|---|
| | Oil palm - Shade | -2.505 | 0.101 | -24.923 | **<0.001** |
| | Agriculture - Shade | -1.665 | 0.100 | -16.582 | **<0.001** |
| | Urban - Shade | -22.536 | 0.101 | -223.765 | **<0.001** |
| | Agriculture - Oil palm | 0.840 | 0.101 | 8.351 | **<0.001** |
| | Urban - Oil palm | -20.031 | 0.101 | -198.450 | **<0.001** |
| | Urban - Agriculture | -20.871 | 0.101 | -206.920 | **<0.001** |

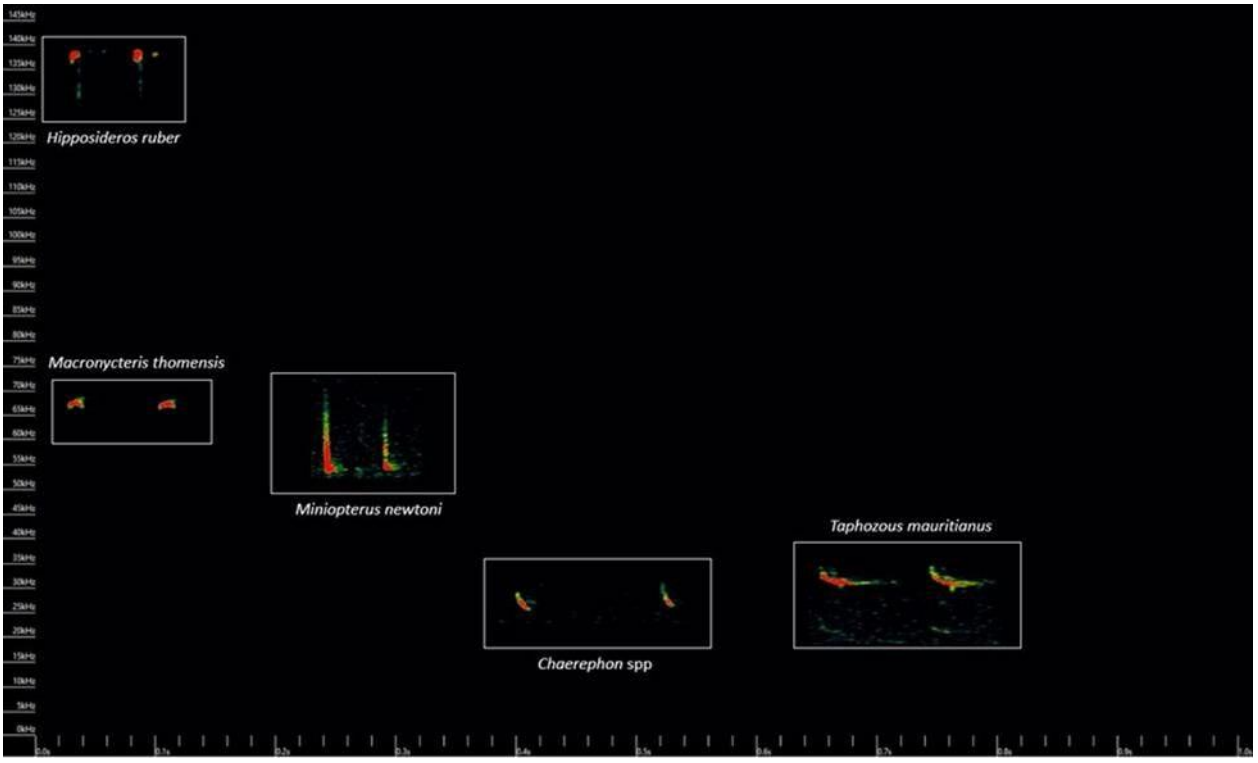


Figure S1. Sonogram illustrating the echolocation calls from each of the bat taxa recorded across 115 sampling sites in the São Tomé Island, including *Hipposiderus ruber*, *Macronycteris thomensis*, *Miniopterus newtoni*, *Chaerophon* spp. and *Taphozous mauritianus*.

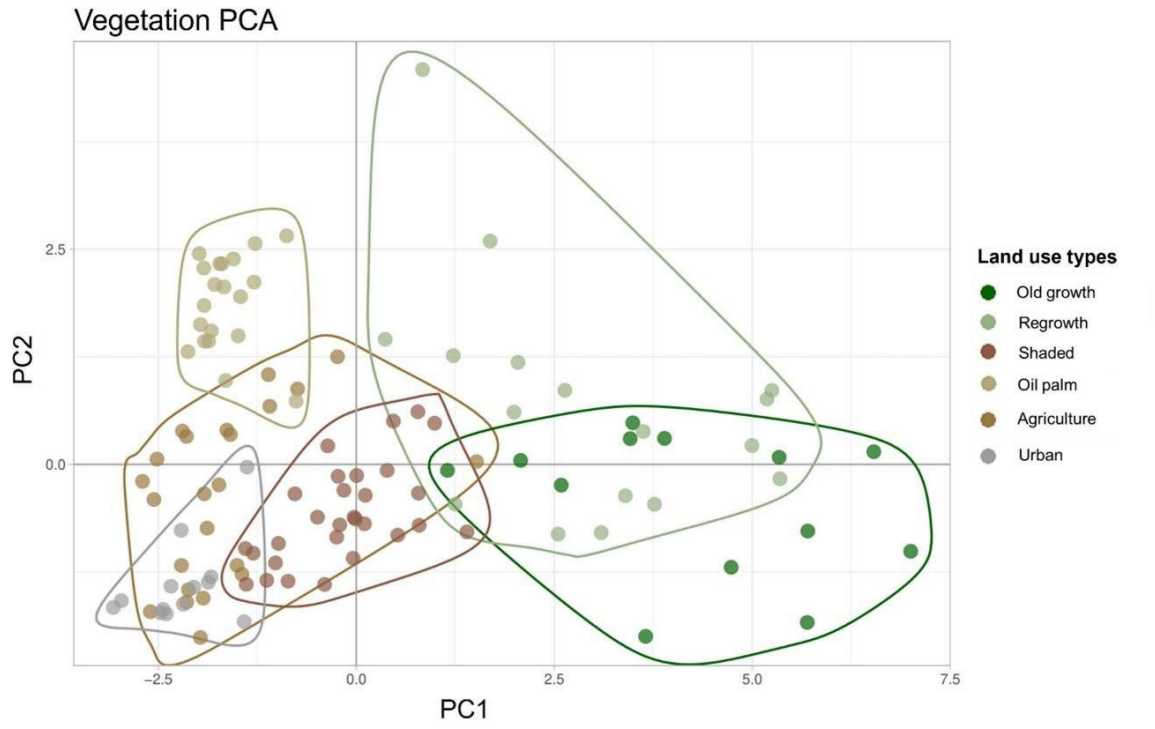


Figure S2. Principal components analysis (PCA) examining the variation between vegetation structure variables.

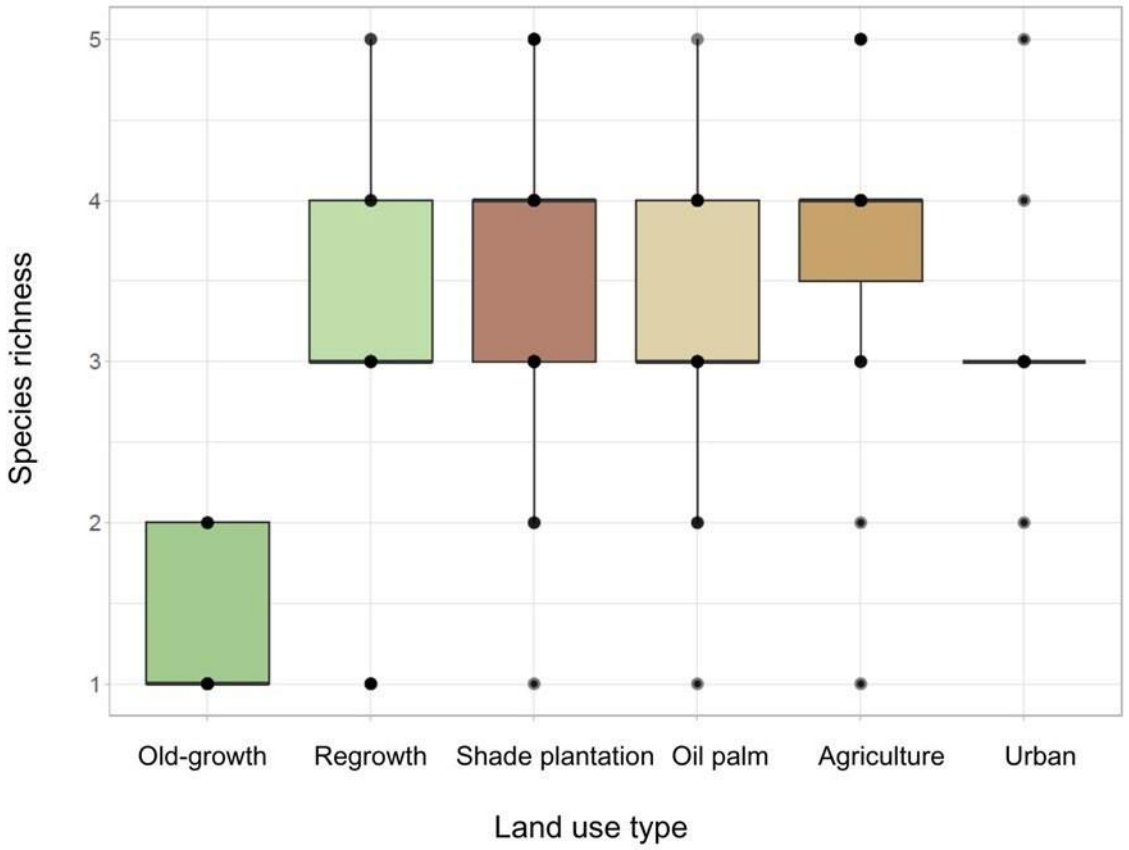


Figure S3. Species richness across land cover type. Each box corresponds to a land cover, the line refers to the median activity, and the box represents the interquartile range.