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Responses of insectivorous bats to different types of land-use in an endemic-rich island in Central West Africa

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ABSTRACT

Land-use change underpins the ongoing biodiversity crisis. Although such impacts are particularly acute across endemic-rich oceanic islands, little is known for afro-tropical islands. Here we assessed insectivorous bat responses to different land-use types of the island of São Tomé, in Central West Africa. Since its human colonization in the mid-15th century, São Tomé lost over 70 % of its native habitat, mostly to shaded and oil palm plantations, agriculture, and urban areas, while part of that was abandoned allowing secondary forests to re-grow. Using passive acoustic monitoring, we surveyed insectivorous bats in 115 sites across each land-use type over one month. We then examined bat species richness and activity, and species-specific activity. Based on 5520 h of recordings, we obtained 19,744 bat passes from five of the six taxa known to occur on the island, three of which are endemics. Both species richness and activity were highest in the four non-forest land-use types, with activity further decreasing with altitude. Species-specific responses corresponded to foraging guild: the forest foragers *Hipposideros ruber* and *Macronycteris thomensis* showed higher activity in forests and shaded plantations, the activity of the open-space foragers *Chaerephon* spp. peaked in urban areas, while that of the edge forager *Miniopterus newtoni* was highest in oil palm plantations. The island's insectivorous bats are persisting despite land-use change, including island endemics. Maintaining the mosaic of land-use types, including native forests, is likely to help sustain insectivorous bat diversity in this tropical island.

1. Introduction

Owing to remarkably high levels of species endemism, islands hold a disproportionate share of the planet's biodiversity (Fernández-Palacios et al., 2021). Nevertheless, despite their pivotal role in the fate of biodiversity in the Anthropocene, island biodiversity continues to decline at alarming rates largely driven by human-induced land-use and the spread of non-native taxa (Russell and Kueffer, 2019).

Land-use change – largely driven by the ongoing human population growth and associated demand for commodities (Laurance et al., 2014) – exerts far-reaching impacts on biological communities. Due to the often-small size of most islands, the impacts of land-use change are especially pronounced on insular ecosystems, as it often affects substantial sections of the landscape, acting synergistically with other drivers of global change (e.g., invasive species; Didham et al., 2007). This, coupled with the distinctive adaptations of insular biodiversity to the island's native vegetation and the tendency that island taxa tend to exhibit greater physical and behavioural specialisation compared to their mainland counterparts (Kier et al., 2009), contributes to the diminished resilience of insular biodiversity to anthropogenic disturbance (Russell and Kueffer, 2019; Leclerc et al., 2018; Matthews et al., 2022).

In the aftermath of land-use change, species diversity is expected to depend on the quality of the novel habitat (Watling et al., 2011), which

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is generally higher in land-use types characterised by a lower structural and compositional contrast with the native habitat (Barlow et al., 2007). As such, converting old-growth forest into agricultural or urban areas is often anticipated to have a more detrimental effect on species diversity than the conversion of the former into forested habitats, such as secondary re-growth or shaded plantations (Rocha et al., 2018; Almeida-Maués et al., 2022). Moreover, while species richness often declines under land-use change (Sala et al., 2000), that is not always the case as species turnover might offset such decline (Palmeirim et al., 2017). In fact, while some more sensitive species undergo local extinction, others might thrive in novel habitats (Newbold et al., 2014). Understanding the drivers behind the response of different species to land-use change is paramount for outlining efficient management actions, which is not trivial given the accelerated pace of land-use change across tropical islands (Wood et al., 2017).

Although several studies have examined bat responses to land-use change, including in oceanic islands (e.g., Ferreira et al., 2022; Davies et al., 2016), research into the impacts of land-use change in tropical insular bats is still scarce, with African islands being particularly underrepresented (Meyer et al., 2016). Yet, in many insular ecosystems, native mammal assemblages are often restricted to bats (Fleming and Racey, 2009), with roughly 25 % of all bat species occurring in islands being island-endemics (Conenna et al., 2017). Moreover, insular bats play a crucial role in ecosystem functioning, providing valuable ecosystem services such as seed dispersal and insect suppression (Maas et al., 2016; Florens et al., 2017; Nóbrega et al., 2023).

Bat responses to land-use change are largely determined by their echolocation call characteristics, diet, and morphology (Davies et al., 2016; Wordley et al., 2017; Núñez et al., 2019). The characteristics of the echolocation calls – produced by insectivorous bats to navigate their surroundings and locate food – are adapted to the species foraging preferences and greatly influence their capacity to forage in more or less cluttered habitats (Denzinger and Schnitzler, 2013). Aerial insectivorous bats can be divided into three main foraging-habitat guilds based on the shape of the echolocation call, namely: forest, edge and open-space foragers (Denzinger and Schnitzler, 2013; Schnitzler and Kalko, 2001; Yoh et al., 2022). Although within guild responses to habitat change can further be species-specific (e.g., Estrada-Villegas et al., 2010; Rowley et al., 2024), narrow space forager forest bats, emitting constant frequency (CF) or frequency-modulated (FM) calls, tend to be the most sensitive to land-use changes, particularly when those include a decrease in the habitat clutter (Ferreira et al., 2022; López-Bosch et al., 2021). Yet, although some studies report higher bat diversity in undisturbed native habitats (Farneda et al., 2020), several modified land-use types have been noted to retain equivalent or even greater bat diversity at the assemblage-level. These disturbed habitats might not only harbour existing forest specialist species but also edge/open species that are typically not found in old-growth forest habitats (Mendes and Srbek-Araujo, 2021). Additionally, human-associated resources often create new foraging and roosting opportunities that certain synanthropic species are able to exploit (Voigt et al., 2016).

Here, we examined the responses of insectivorous bats to land-use change in the endemic-rich island of São Tomé, Central West Africa. São Tomé was human-colonised in the mid-15th century, leading to the substantial replacement of the lowland forests by cocoa and coffee plantations, largely shaded by exotic trees (Muñoz-Torrent et al., 2022). In addition to the remaining old-growth forests, the island hosts considerable expanses of secondary re-growth (in areas of abandoned cocoa/coffee plantations), shaded plantations (mostly cocoa but limited shade coffee persists), organic oil palm plantations as well as small-scale agricultural and urban areas (Dauby et al., 2022). A total of seven insectivorous bat species occur in São Tomé, including two forest foragers (*Macronycteris thomensis* and *Hipposideros ruber*), three open-space foragers (*Chaerephon pumilus*, *C. tomensis* and *Taphozous mauritianus*) and two edge foragers (*Miniopterus newtoni* and *Myotis* cf. *tricolor*). From these, three species—including one species in each foraging guild — are endemic to the island (Rainho et al., 2022). Using passive acoustic detectors, we surveyed bats across the main land-use types and assessed the effects of land-use and altitude on insectivorous bats at both (1) the assemblage-level, considering species richness and activity, and (2) the species-level, considering species-specific activity. Given the even distribution of the bat species within foraging guilds, we do not anticipate species richness to peak at any land-use type. Yet, we expect bat activity to be greater in some anthropogenic land-use types such as agricultural and urban areas, where synanthropic species are likely to benefit from human-associated foraging/roosting resources (Russo and Ancillotto, 2015; Williams-Guillén et al., 2016; Lopez-Baucells et al., 2017). Species-specific activity is expected to be associated with foraging guild, with forest foragers exhibiting higher activity in forests and shaded plantations, and edge and open-space foragers in plantations, agricultural and urban areas (Jung and Kalko, 2010; Ferreira et al., 2022; Rowley et al., 2024).

2. Material and methods

2.1. Study area

The study was conducted on the São Tomé Island, part of the Democratic Republic of São Tomé and Príncipe (Fig. 1). Located in the Gulf of Guinea, 255 km west of Gabon, São Tomé (857 km^2) has a rugged topography with numerous peaks above 1000 m, with the highest reaching 2024 m asl (Ceríaco et al., 2022). The island's climate is tropical humid, and it has a dry season from June to mid-September and a rainy season extending for the remaining months (Ceríaco et al., 2022). Annual average rainfall reaches 7000 mm in the southwest and 600 mm in the northeast of the island. The average annual temperature varies between 18 °C and 30 °C at the highest and lowest altitudes, respectively (NBSAP, 2015).

Originally, São Tomé Island was characterised by dense tropical forest in the south part and drier forest in the north (Ceríaco et al., 2022). Following the colonization by the Portuguese in 1485, a considerable amount of the lowland forest has been converted into 'human-useful' land-use types (Soares et al., 2020). Yet, more than a quarter of the island (ca. 26 %; mostly in the rugged high-altitude areas) is still occupied by old-growth forest. Secondary re-growth forests, resulting mostly from the abandonment of cocoa farms and characterised by non-native trees cover ca. 30 % of the landscape, while organic shaded plantations of cocoa and coffee —where these crops are cultivated beneath the canopy of typically non-native tree species—encompasses ca. 26 % of the island. Organic oil palm plantations which, despite considerable expansion in recent years (Oyono et al., 2014), have been present since the Portuguese colonization era, and occupy an area of ca. 3 % in the southern part of the island. Furthermore, small-scale agriculture covers ca. 8 % of the island, and urban areas, including the island's capital (the city of São Tomé) and its surroundings, as well as multiple other smaller cities on both the south and north coast, occupy ca. 6 % of the island. The once-dry forest on the northern coast gave place to anthropogenic savannas (Soares et al., 2022), a land-use type that was not considered in this study because the sites had just been burned at the time sampling was taking place.

2.2. Sampling design and data collection

Bat acoustic surveys were carried out between August and September 2022, during the dry season. The sampling period was chosen to avoid severe storms typical of the region, preventing rain-induced deterioration of acoustic recordings and ensuring accurate detection of bat activity, which tends to decrease during heavy rain due to reduced insect activity and echolocation interference (Griffin, 1971; Parsons et al., 2003). To ensure data representativity for each of the major land-use types present on the island, sampling sites were tentatively stratified according to the availability of each land-use type. In total, we surveyed

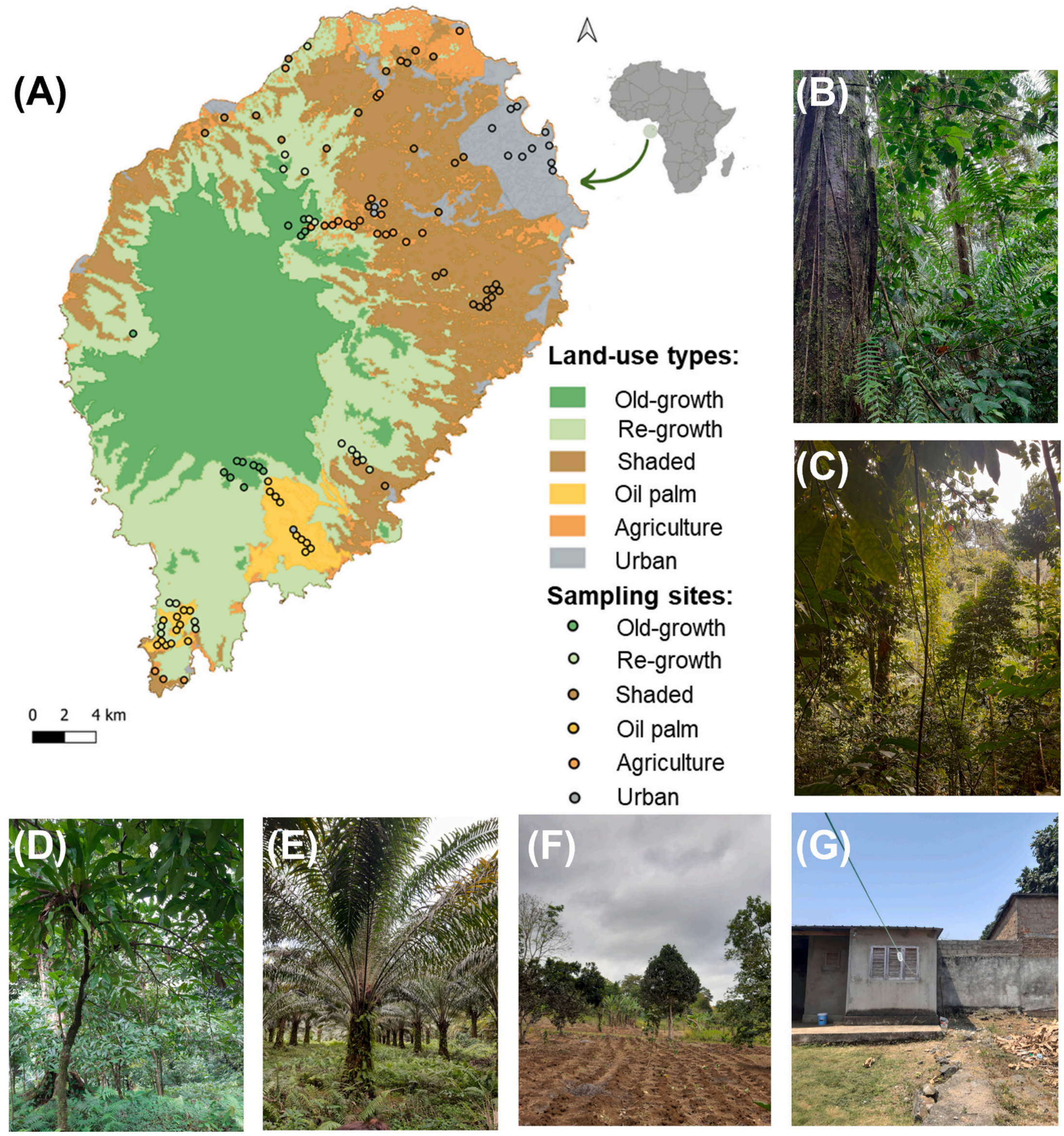


Fig. 1. (A) Sampling sites across São Tomé, West Central Africa. Each of the 115 sampling sites is color-coded according to the land-use type. The island area is also covered according to the same main land-use types: (B) old-growth forest, (C) secondary re-growth forest, (D) shaded plantation, (E) oil palm plantation, (F) agricultural area and (G) urban area. Land-use types shown in this map were adapted from Soares et al. (2020).

115 sites, including 13 sites in old-growth forests, 17 in secondary re-growth forests, 29 in shaded plantations, 20 in oil palm plantations, 23 in small-scale agricultural areas and 13 in urban areas (Fig. 1A).

Each sampling site was surveyed by deploying one AudioMoth recorder (Hill et al., 2018) programmed to record for one minute every five minutes, for two consecutive days and nights, at mid-gain with a 384 kHz sample rate. Diurnal recording was intended to capture the diurnal activity of *Hipposideros ruber* (Russo et al., 2011). Recorders were attached to an available vertical structure, between 1.5 and 2 m above the ground. Spatially contiguous sampling sites were at least 250 m apart from each other, to minimise simultaneously recording the same individual (Ferreira et al., 2022; Mullin et al., 2020; Yoh et al., 2022). Up to a total of 20 spatially aggregated sampling sites were surveyed at the same time.

2.3. Acoustic analysis

Using the Kaleidoscope Version 5.4.7 (Wildlife Acoustics, USA), we first split the recordings into 5 s WAV files (López-Bosch et al., 2021). We then filtered the recordings for a frequency range between 8 and 250 kHz and for pulses ranging from 2 to 500 milliseconds. Files outside of these parameters were considered 'noise' and removed from subsequent analysis. Recordings that contained one 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. This classification was carried out by examining the following call parameters: frequencies of maximum energy (F_{maxE}) and minimum energy (F_{min}), call duration and inter-pulse interval (Russo and Jones, 2002). Information on each of these parameters has been locally obtained for each of the species by Rainho et al. (2022) (Fig. S1). Echolocation calls were mostly identified at the species level. However, the two *Chaerephon* species were considered at the genus level, as although we were able to identify *C. pumilus* in 84 % of the 10,789 *Chaerephon* bat passes, for the remaining we were not able to distinguish between *C. pumilus* and *C. tomensis* due to overlap in the echolocation call parameters (Rainho et al., 2022). Yet, to maximise readability, we refer to species richness, activity, composition, and species-specific activity, rather than taxa.

2.4. Environmental variables

To understand how insectivorous bats respond to land-use change, we considered the land-use type (i.e., old-growth forest, secondary re-growth forest, shaded plantations, oil palm plantations, agricultural areas and urban areas) and altitude. Land-use information was obtained from Soares et al. (2020) geographic information system (GIS) data. In addition to land-use type, we considered the altitude of each sampling site obtained from a digital elevation model (DEM) from the Shuttle Radar Topographic Mission (SRTM) (Jarvis et al., 2008). Although we measured several local habitat characteristics, including tree density, tree height, canopy cover and overall vegetation obstruction at different heights (Table S1), those characteristics were generally similar for sampling sites of the same land-use type (Fig. S2). Accordingly, to minimise redundancy in the models performed, we did not include local habitat characteristics in the subsequent analysis. We also quantified the cover of the different land-use types within circular buffers of three different radii (i.e., 250, 500, and 750 m) centred in each sampling site. However, we observed limited heterogeneity in terms of land-use types within buffers. Indeed, buffers were predominantly covered by the land-use type where the sampling site was located, with the only exception being the buffers corresponding to the sites located within agricultural areas (Fig. S3). For this reason, we opted to simply use the main land-use as a categorical variable in the subsequent analyses, instead of incorporating the information from the circular buffers.

2.5. Data analysis

We first examined species composition across the different land-use types using a Non-Metric Multidimensional Scaling (NMDS) ordination based on a Bray-Curtis similarity matrix, considering the number of bat passes per site for each species (stress: 0.147). The sum of all-species bat passes per site comprised overall bat activity which was used as a proxy for species abundance (Kunz et al., 2009). We assessed spatial autocorrelation through Moran's I test using the 'spdep' R package (Bivand et al., 2024). Spatial autocorrelation was detected for all response variables, namely bat species richness, overall activity, and species-specific activity. To account for this, we applied Generalized Additive Models (GAM) with a smoothing term including the geographic coordinates, to evaluate the effects of land-use type and altitude on bat species richness, overall activity, and species-specific activity. GAM were run using the 'mgcv' R package (Wood, 2023). Altitude was standardised to a mean of zero and a standard deviation of one. The distribution family used in each model varied according to the response variable: a Gaussian distribution was used for species richness, activity of *Miniopterus newtoni* ($\log_{10} x$) and *Chaerephon* spp. ($\log_{10} x$); a negative binomial for total activity, activity of *Hipposideros ruber* and *Macronycteris thomensis*. We were not able to run the model for the activity of one species, *Taphozous mauritianus*, due to its low number of detections ($N = 23$). Using the models' output, we conducted post-hoc *t*-tests to compare each response variable between pairs of land-use types other than those including old-growth forests (Table S5). In addition, since *Macronycteris thomensis* was not detected in any of the old-growth forest or urban sites, we removed these two land-use types from the modelling of this species activity. Finally, to improve the fitting of the model regarding overall bat activity, we excluded the site 'STU2' located in an urban area (AICc = 1314 and 1293, including and excluding the outlier, respectively). This site exhibited substantially higher bat activity (1706 bat passes) compared to the averaged bat activity per site in each of the remaining land-use types (mean ± SD = 158.22 ± 163.05 bat passes), which might be due to the proximity to a roosting site. This site was therefore considered to be an outlier and removed from subsequent analysis. Additionally, we removed a site located in a shaded plantation for the species-specific analysis of *Macronycteris thomensis* (STS6) (AICc = 384 and 360, including and excluding the outlier, respectively). We evaluated the residuals of each model using the DHARMa package in R (Hartig, 2022) and found no violations of the model assumptions. All analyses were performed using R version 4.1.2 (R Core Team, 2022).

3. Results

In total, we detected 19,744 bat passes from five taxa. Two taxa were notably more commonly recorded, namely the *Chaerephon* spp. with 54.6 % of the detections (10,789 bat passes), and the endemic *Miniopterus newtoni* with 40.7 % (8030 bat passes), while *Taphozous mauritianus* was the least detected species (23 bat passes). Overall, bat activity varied per land-use type between zero and 800 bat passes (mean ± SD: 158.2 ± 162.3) in the old-growth and shaded plantations, respectively. The number of species varied between one and five (3 ± 1), with *Miniopterus newtoni* and *Hipposideros ruber* being the only species detected in every land-use type (Fig. 2A). Overall, secondary re-growth forests and shaded plantations were quite broad in terms of their species compositions, whereas oil palm plantations and urban areas presented lower variation that did not overlap with that of old-growth forests (Fig. 2B).

3.1. Assemblage-level responses

Species richness and bat activity were both lowest in old-growth forests, which harboured fewer species (one or two) and had reduced bat activity compared to non-forest land-use types, including shaded plantations ($\beta = 1.025$, $P = 0.040$), oil palm plantations ($\beta = 2.694$, $P < 0.001$), agricultural ($\beta = 1.947$, $P < 0.001$), and urban areas ($\beta = 2.056$, $P = 0.002$) (Fig. 3A–B, Tables S3 and S5). Geographic coordinates also affected bat activity ($X^2 = 43.42$, $P < 0.001$) (Table S4). Bat activity was negatively affected by altitude ($\beta = -0.884$, $P = 0.003$) (Fig. 4, Tables S3).

3.2. Species-level responses

The activity of *Chaerephon* spp. was higher in oil palm plantations ($\beta = 0.758$, $P = 0.003$), agricultural ($\beta = 0.654$, $P = 0.018$), and urban areas ($\beta = 1.076$, $P = 0.003$) when compared to either old-growth or secondary re-growth forests (Fig. 5A, Table S3 and S5). The geographic coordinates affected this species activity ($F = 3.82$, $P < 0.001$) (Table S4). The activity of *M. thomensis*, a forest forager —not recorded in old-growth forests or urban areas—was lower in shaded plantations ($\beta = -2.551$, $P = 0.021$), oil palm plantations ($\beta = -2.797$, $P = 0.003$) and agricultural areas ($\beta = -2.840$, $P = 0.006$) in comparison to that in secondary re-growth forests. The geographic coordinates also affected this species activity ($X^2 = 26.73$, $P = 0.024$) (Fig. 5B, Tables S3–S4). The activity of the forest forager *H. ruber* was associated with forest land-use types, being lower in agricultural areas ($\beta = -2.187$, $P = 0.010$) and urban areas ($\beta = -3.329$, $P = 0.040$), compared to old-growth forests, and lower in any land-use type (except in old-growth forests) than in secondary re-growth forests (Shaded: $t = 2.233$, $P = 0.028$; oil palm: $t = 2.245$, $P = 0.027$; agricultural: $t = 2.753$, $P = 0.007$; urban: $t = 2.370$, $P = 0.020$) (Fig. 5C, Tables S3 and S5). The edge forager *M. newtoni* exhibited higher activity in all land-use types except re-growth forests (Shaded: $\beta = 1.085$, $P = 0.031$; agricultural: $\beta = 1.429$, $P = 0.003$; urban: $\beta = 1.079$, $P = 0.044$), with activity peaking in oil palm plantations ($\beta = 1.702$, $P < 0.001$) (Fig. 5D, Table S3).

4. Discussion

Here we provide the first assessment of how insectivorous bats respond to land-use change in tropical endemic-rich islands. Overall, and in line with studies of continental bat assemblages elsewhere in the tropics (e.g., Wordley et al., 2017; Kemp et al., 2019; Rowley et al., 2024), we found that the secondary re-growth forests, agricultural and

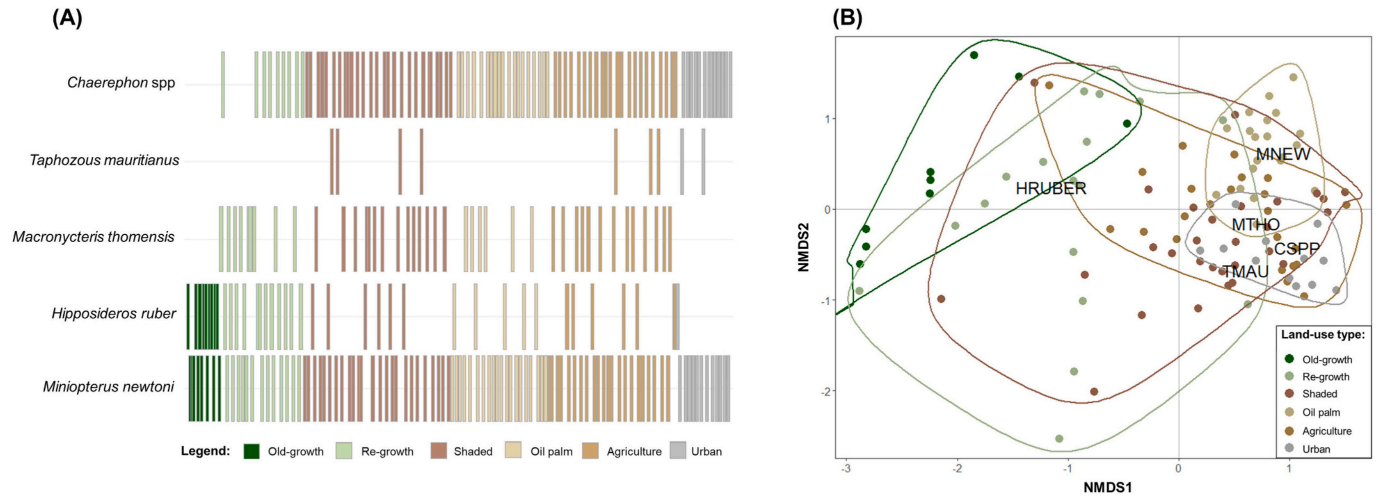
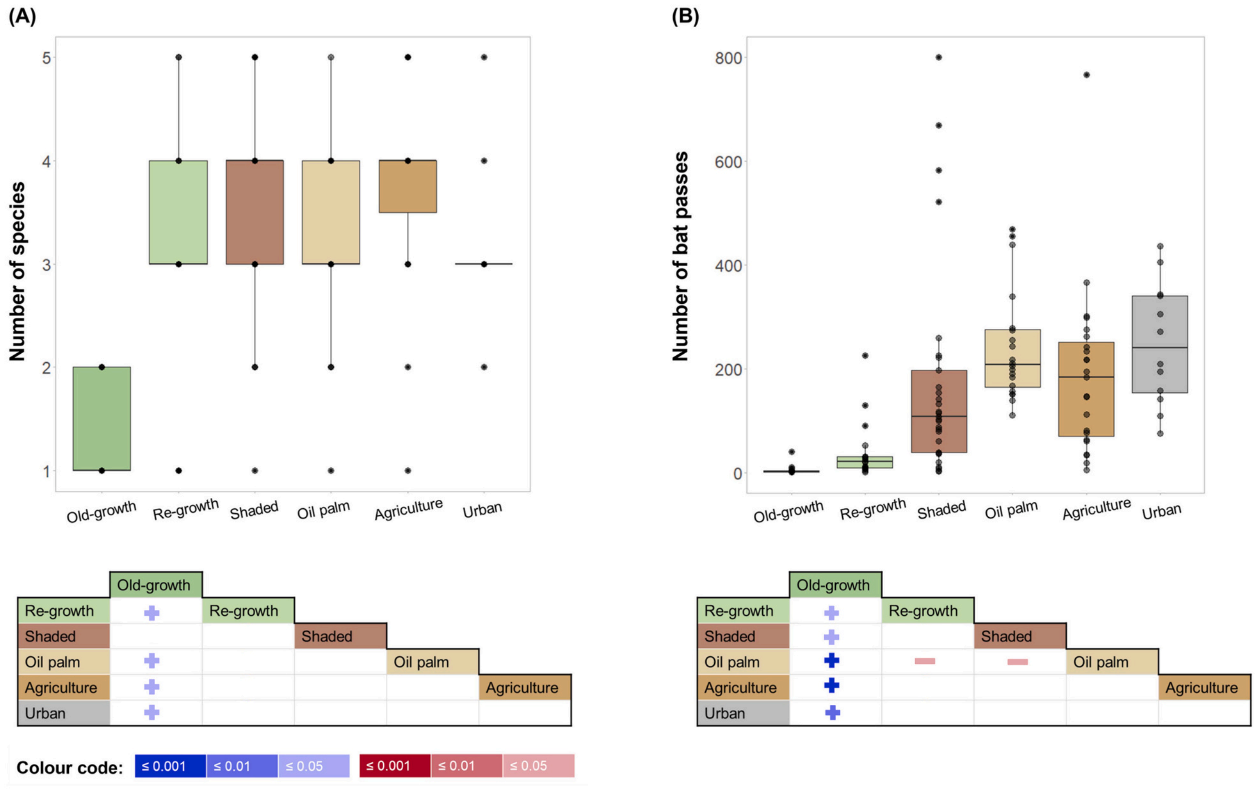


Fig. 2. (A) Bat species detected at each of the 115 sampling sites surveyed across all six land-use types in São Tomé. Each bar corresponds to a species presence at a given site, coloured according to land cover type. (B) Non-Metric Multi-Dimensional Scaling (NMDS) ordination plot denoting both sampling sites and species. Sampling sites are represented by circles, color-coded according to land-use type. CSPP – *Chaerephon* spp.; HRUBER – *Hipposideros ruber;* MNEW – *Miniopterus newtoni*; MTHO – *Macronycteris thomensis*; TMAU – *Taphozous mauritianus*.



	Old-growth	Re-growth	Shaded	Oil palm	Agriculture
Re-growth	+				
Shaded					
Oil palm	+				
Agriculture	+				
Urban	+				

	Old-growth	Re-growth	Shaded	Oil palm	Agriculture
Re-growth	+				
Shaded	+				
Oil palm	+	−	−		
Agriculture	+				
Urban	+				

Fig. 3. (A) Species richness and (B) activity (number of bat passes) across each of the land-use types in São Tomé. Each boxplot refers to the median activity, and the whiskers refer to the interquartile range. The plus sign represents a positive T-value and the minus sign a negative T-value (Table S5), the intensity in which each sign is coloured varies according to *P*-value: $0.05 \geq P > 0.01$, $0.01 \geq P > 0.001$ and $P \leq 0.001$.

urban areas support the majority of São Tomean insectivorous bat species diversity. This aligns with findings for other São Tomean vertebrates (Soares et al., 2022), indicating that although old-growth specialists —such as *Hipposideros ruber* and several of the island's endemic birds (de Lima et al., 2013)—are heavily impacted by land-use change, at least some species are capable of persisting and even flourishing, in the island's novel land-use types.

4.1. Insectivorous bat assemblage-level responses to land-use type

Our results are consistent with other studies on gradients of land-use intensity within tropical landscapes (Meyer et al., 2016) and island systems (Ferreira et al., 2022). Those studies show that insectivorous bat assemblages are highly responsive to land-use change (Fig. 3), including that assemblages are more dissimilar to forest in land-uses with reduced vegetation cover (Fig. 2B). Species activity was higher in non-forest land-use types than in old-growth (Fig. 3B). While it is important to

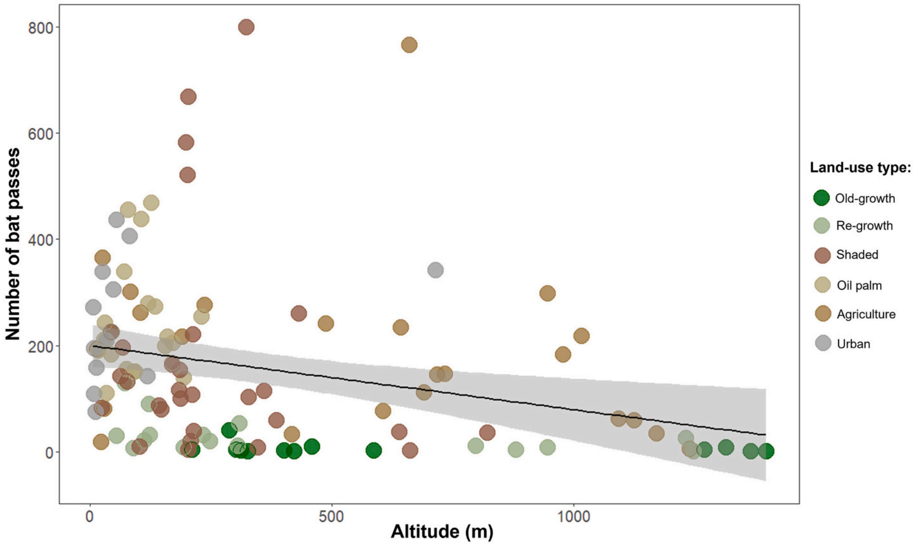


Fig. 4. Relationship between bat activity (number of bat passes) and altitude (expressed in meters). The line indicates model adjusted fit, and the shaded area represents the 95 % confidence region. Sampling sites are represented by circles, color-coded according to land-use type.

acknowledge a potential methodological bias affecting species detectability between land-use types, e.g., bat calls are less likely to be detected in cluttered environments compared to open spaces (Duchamp et al., 2006), this issue does not fully account for the observed results. Indeed, our findings are consistent with previous studies showing a higher abundance of amphibians (Strauß et al., 2018) and both abundance and species richness of birds (de Lima et al., 2013; Soares et al., 2020) across the anthropogenic land-use types of São Tomé.

Secondary re-growth is one of the most prevalent types of forest cover throughout the tropics and provides key habitat to numerous forest-dwelling species (Chazdon, 2019). Although its conservation value for insectivorous bats is not well understood in the Afro- and Asian-tropics, an increasing body of literature from the American tropics suggests that re-growth has considerable "rescue" potential for old-growth specialists affected by forest loss (Yoh et al., 2022; López-Baucells et al., 2022; Rowley et al., 2024). Likewise, shaded plantations, with substantial structural heterogeneity, provide a quality habitat for numerous insectivorous bats (Williams-Guillén and Perfecto, 2011; Wordley et al., 2015; Huang et al., 2019). In our study, re-growth and shaded plantations, alongside agricultural areas, were the only habitats to overlap with old-growth in assemblage similarity (Fig. 2B). Accordingly, this indicates that they can – to some extent – buffer the consequences of old-growth forest loss for São Tomean insectivorous bats, similar to the island's native birds (de Lima et al., 2013).

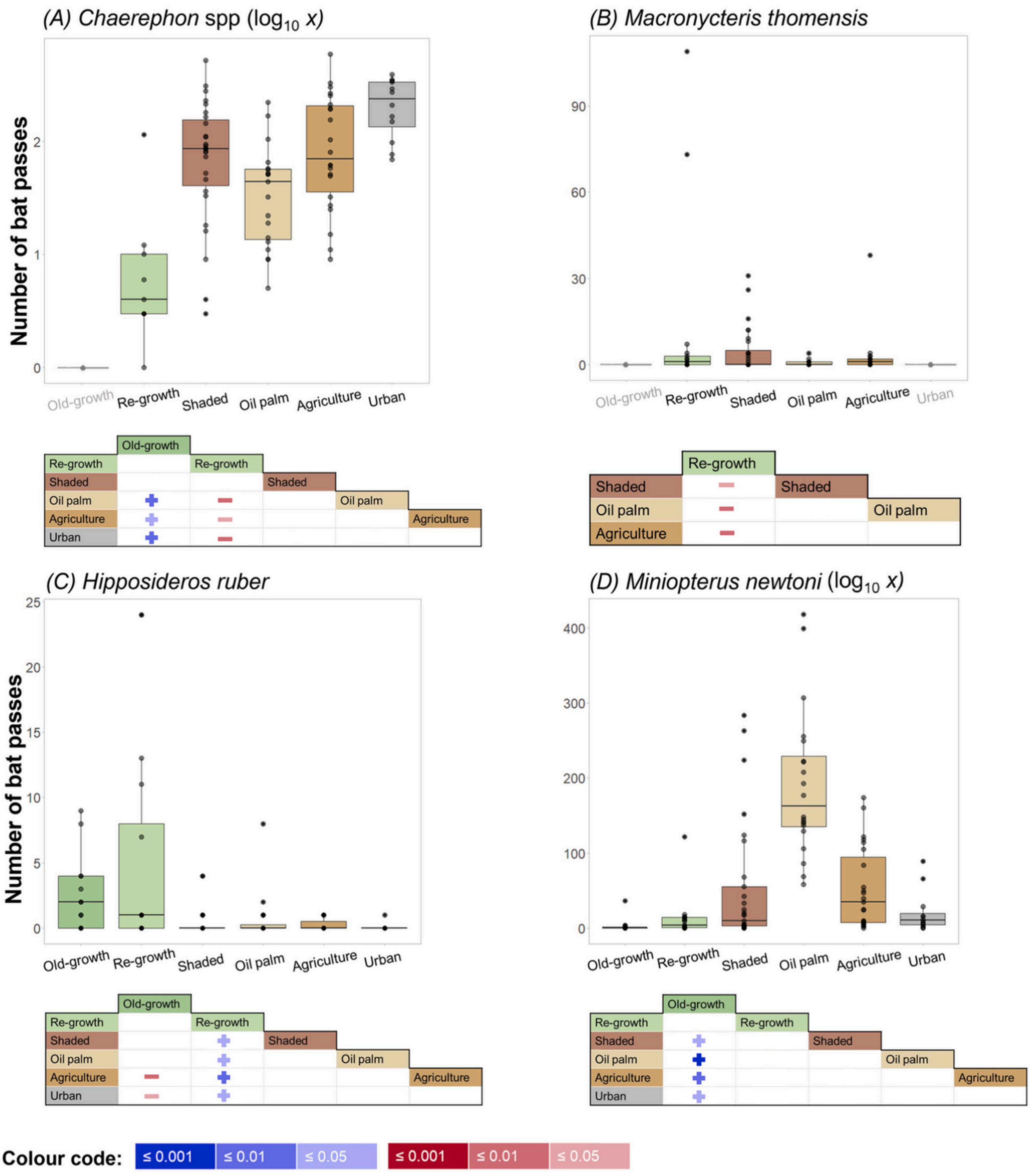
Changes in arthropod diversity and abundance resulting from agricultural activities can be influenced by the adopted pest management practices (Bommarco et al., 2011) and the physical structure of the agricultural habitats replacing native vegetation (Barnes et al., 2017). Other than taking place on an island where the main agricultural land-use types still retain substantial forest cover, our case study has the particularity of being carried out on an island where – despite limited data – agriculture is largely practised with little or no pesticide input. Abstaining from pesticide use is known to benefit insectivorous bats (Williams-Guillén et al., 2016), particularly 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 potential for increased prey availability might explain the higher bat activity in agricultural areas. However, further studies quantifying arthropod abundance would be required to confirm this hypothesis.

Although the conversion of native habitats to oil palm plantations has largely negative impacts on biodiversity (Wilcove and Koh, 2010; Azhar et al., 2015; Freudmann et al., 2015), some species, including bats, are able to persist or even thrive therein given certain conditions (e.g., Mullin et al., 2020). In our study, oil palm was only second to urban areas in terms of bat activity. This suggests that, in São Tomé, oil palm plantations seem to provide suitable foraging, or other resources of benefit to some of the island's insectivorous bats. Insect and bat activity in oil palm plantations are impacted by agrochemical usage (Lawer and Darkoh, 2016). We remark that oil palm production in São Tomé is currently organic (Socfin, 2022), which might have buffered its impacts.

4.2. *Species-level responses to land-use type*

The open-space forager *Chaerephon* spp. was particularly active in non-forest habitats, peaking in urban and agricultural areas (Fig. 5A). Indeed, throughout the tropics, molossids are among the most common urban bats (Russo and Ancillotto, 2015) and they often tend to be the most recorded group in agricultural landscapes, where they act as important pest suppressors of agricultural pests (Wanger et al., 2014; Kemp et al., 2019). Their high aspect ratio (long and narrow) wings equip them well to fly in open urban landscapes (Jung and Kalko, 2011) and they are able to roost in a wide array of human-structures (Lopez-Baucells et al., 2017). Still, although we can confidently say that *Chaerephon* spp. exhibits a high degree of adaptability to anthropogenic habitats in São Tomé, currently we are not able to expand specifically on the responses to land-use of the endemic *Chaerephon tomensis*, classified as Endangered by the IUCN Rest List (Monadjem et al., 2019). The overlap in echolocation call characteristics between this species and *C. pumilus* invalidates acoustic surveys (Rainho et al., 2022), and as such alternative methods (such as roost surveys) are needed to investigate the spatiotemporal dynamics of this poorly known species. Moreover, it is possible that *Chaerephon* spp. might have been under-detected in old-growth forests using our ground-level survey method as these high-flying bats commute and forage above the tree canopy in cluttered environments (Duchamp et al., 2006).

Forest bats, such as *Macronycteris thomensis* and *H. ruber*, tend to have short broad wings and higher frequency, broadband echolocation calls (with faster attenuation but capable of providing more information), which are particularly well-suited to flight and prey capture in cluttered environments (Denzinger and Schnitzler, 2013; Mande et al., 2023). The endemic *M. thomensis* was not detected in old-growth forest, but was particularly active in re-growth forests and shaded plantations (Fig. 5B). Conversely, while detected across all habitats, *H. ruber* was mostly active



(A)

	Old-growth	Re-growth	Shaded	Oil palm	Agriculture
Re-growth					
Shaded					
Oil palm	+	−			
Agriculture	+	−			
Urban	+	−			

(B)

	Re-growth	Shaded	Oil palm
Shaded	−		
Oil palm	−		
Agriculture	−		

(C)

	Old-growth	Re-growth	Shaded	Oil palm	Agriculture
Re-growth					
Shaded		+			
Oil palm		+			
Agriculture	−	+			
Urban	−	+			

(D)

	Old-growth	Re-growth	Shaded	Oil palm	Agriculture
Re-growth					
Shaded	+				
Oil palm	+				
Agriculture	+				
Urban	+				

Fig. 5. Species-level activity across each of the six land-use types in São Tomé: (A) *Chaerephon* spp., (B) *Macronycteris thomensis* (C) *Hipposideros ruber*, (D) *Miniopterus newtoni.* Each boxplot refers to the median activity, and the whiskers refer to the interquartile range. The plus sign represents a positive T-value and the minus sign a negative T-value (Table S5), the intensity in which each sign is coloured varies according to P-value: $0.05 \geq P > 0.01$, $0.01 \geq P > 0.001$ and $P \leq 0.001$.

in old- and re-growth forests, while being virtually absent from shaded plantations (Fig. 5C). While emphasizing the idiosyncratic responses of island insectivorous bats to land-use change (Ferreira et al., 2022), this highlights the conservation potential of these habitats in modified tropical landscapes (Chazdon, 2019), particularly for forest-associated bats (Farneda et al., 2020; Rowley et al., 2024).

The wing and echolocation traits of edge foragers allow this guild to exploit habitats with varying degrees of vegetation clutter (Denzinger and Schnitzler, 2013). In line with this, the endemic *Miniopterus newtoni* was detected across all land-use types, exhibiting particularly high levels of activity in the agricultural land-uses, peaking in oil palm plantations (Fig. 5D). *Miniopterus* spp. were among the most detected bats in Malagasy agricultural areas, where they were found to consume important agricultural pests (Kemp et al., 2019). *Miniopterus newtoni* might be providing similar ecosystem services to São Tomean farmers, highlighting the need for more research into the trophic ecology of insular bats.

Unfortunately, our data was too sparse to investigate how *Taphozous mauritianus* responds to the different land-uses and we were not able to detect *Myotis* cf. *tricolor*. The former is relatively common across sub-

Saharan Africa, being present in multiple islands (Monadjem and Jacobs, 2017). However, based on genetic, molecular and echolocation differentiation, *Myotis* cf. *tricolor* seems to present some degree of differentiation from mainland forms (Rainho et al., 2022). Despite one known roost location with several hundreds of individuals, the species has only been recorded acoustically once (Rainho et al., 2022), suggesting alternative survey approaches may be needed to monitor this species. Furthermore, the spatial aggregation of some of the land-use types in São Tomé comprised a limitation in our study. For instance, old-growth forests are located in the south-central portion of the island whereas oil palm plantations, despite being relatively extensive, only occur in the south of the island. Moreover, spatial location significantly influenced the variation of species richness, bat activity, *Chaerephon* spp., and *Macronycteris thomensis* making it difficult to attribute the observed responses to land-use changes or spatial factors. Nonetheless, the results observed in this study largely align with expectations for each foraging guild and overall bat activity. Additionally, the acoustic survey carried out lasted for a short period (ca. 1 month). As bat activity may change substantially with season, lunar phase, and across the years, our research does not capture any potential temporal variability in the response of insectivorous bats to land-use change (Appel et al., 2019; Torrent et al., 2018).

4.3. Conservation implications

Insectivorous bat activity was higher in anthropogenic land-use types of lower altitude. Despite that, our findings also highlight the critical role of native habitats in maintaining the integrity of bat assemblages across the whole island, particularly in conserving forest specialist species—an important consideration given the rapid ongoing forest conversion in São Tomé (Muñoz-Torrent et al., 2022). Additionally, we note that we were unable to detect one of the previously identified insectivorous bats (*Myotis* cf. *tricolor*) and we cannot infer responses for the threatened *Chaerephon tomensis*. Nonetheless, multiple bat species, including the endemics, seem to be able to persist, and even thrive with some levels of human-disturbance, similar to non-endemic birds and amphibians (de Lima et al., 2013; Strauß et al., 2018; Soares et al., 2022). The non-forest land-uses including small-scale agricultural areas, biological oil palm and cocoa shaded plantations, supported a particularly high insectivorous bat activity. Given the low management intensity of these land-use types, we recommend maintaining such biodiversity-friendly management. We further highlight the potential role of insectivorous bats as pest suppressors in these agricultural areas (Kemp et al., 2019; Gonçalves et al., 2024). Quantifying the ecosystem services provided by bats can help demonstrate how conserving forest habitats for these species can provide additional benefits to local communities. Moreover, maintaining the mosaic of the different land-use types, including native forests, would allow to maximise the persistence of bat diversity in São Tomé, as might also be the case across other tropical oceanic islands.

CRediT authorship contribution statement

Ana Sofia Castro-Fernandes: Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis, Data curation. **Ana Catarina Araújo-Fernandes:** Writing – review & editing, Data curation. **Patrícia Guedes:** Writing – review & editing, Data curation. **José Cassari:** Data curation. **Vanessa A. Mata:** Writing – review & editing, Supervision. **Natalie Yoh:** Writing – review & editing, Supervision, Formal analysis. **Ricardo Rocha:** Writing – review & editing, Supervision, Methodology, Data curation. **Ana Filipa Palmeirim:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Data curation, Conceptualization.

Declaration of Generative AI and AI-assisted technologies in the writing process

The corresponding author confirms on behalf of all authors that during the preparation of this work the authors did not use any AI tool.

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Declaration of competing interest

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2024.110910.

Data availability

The dataset on insectivorous bat records used in this study is available in Palmeirim et al. (2024).

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