

Activity patterns of tropical insectivorous bats across a gradient of habitat disturbance in São Tomé and Príncipe, Central West Africa

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2022/2023

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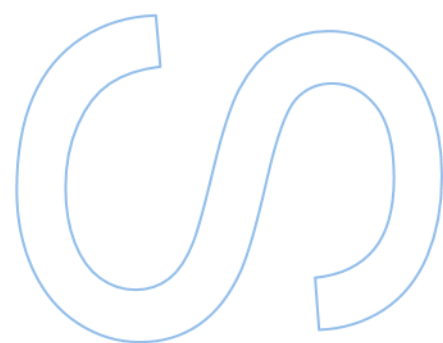
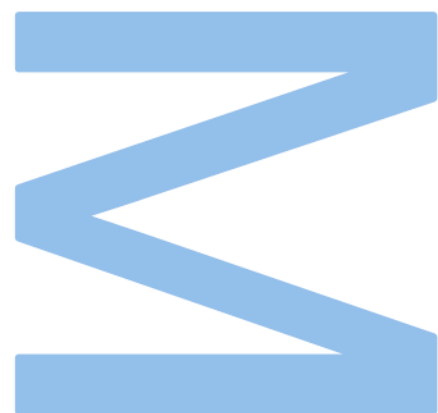
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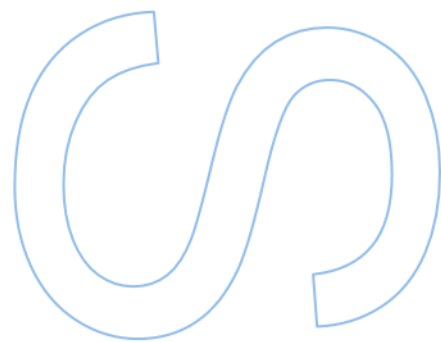
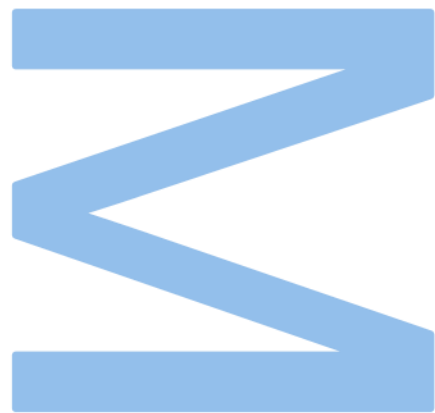
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Acknowledgements

Quero começar por agradecer aos meus orientadores, Filipa Palmeirim, Vanessa Mata e Ricardo Rocha e a todo o TROPIBIO. A vossa orientação e apoio constantes foram essenciais para a realização desta tese. Obrigada!

Também gostaria de expressar o meu agradecimento à Associação Monte Pico e à Fundação Príncipe por nos terem acompanhado nos trabalhos de campo.

À Patrícia Guedes, que nos recebeu em São Tomé, o meu sincero agradecimento pela simpatia e pelo bom-humor!

Quero também agradecer à Natalie Yoh, que partilhou connosco o conhecimento que nos deu as bases necessárias para a realização desta tese. Foi essencial!

Aos meus pais e ao meu irmão Peter, porque mesmo que se esqueçam repetidamente sobre o que é esta tese, eles nunca pararam de me apoiar.

Ao jet sete e às fãs do triangle chest, o meu agradecimento por estarem sempre presentes.

Um agradecimento especial à Maria e Mariana por me acompanharem neste percurso de mestrado!

À Ana Fernandes, com quem trabalhei, acima de tudo taciturnamente, durante este ano de tese!

À Leandra e à Catarina por serem as minhas almosts vozes de consciência e emotional support.

À minha professora do ensino secundário, Armanda Figueiredo, que teve a grande sua influência no meu gosto pela biologia.

Ao António, Silvestre e Tico, por me fazerem companhia nas tardes de trabalho em casa.

E ao nosso Bô.

Resumo

As perturbações humanas no habitat têm um impacto significativo na biodiversidade, afetando a composição, a riqueza e a abundância das espécies. No entanto, as respostas comportamentais à mudança de habitat, como alterações nos padrões de atividade e na partição ao longo do eixo temporal, permanecem pouco investigadas, especialmente para espécies insulares. Neste estudo, avaliamos os efeitos dos habitats humanizados mais comuns nos padrões de atividade de morcegos insetívoros nas ilhas de São Tomé e Príncipe. Utilizando gravadores acústicos AudioMoth, amostramos seis espécies de morcegos em florestas, plantações de sombra e de óleo de palma, áreas agrícolas e urbanas. Nos vários habitats de ambas as ilhas, observamos diferenças significativas na sobreposição temporal ao nível da assembleia, sendo estas tendências próprias para cada ilha e habitat. Por exemplo, em São Tomé, a maior sobreposição ocorreu em áreas de floresta, enquanto no Príncipe foi onde a sobreposição foi mais baixa. A maioria das espécies apresentou um padrão de atividade bimodal. As variações nos padrões de atividade dentro das espécies foram mais pronunciadas entre florestas e áreas agrícolas ou urbanas, em comparação com florestas e plantações de sombra. Os padrões de atividade de *Chaerephon pumilus* e *Hipposideros ruber* diferiram nos tipos de habitat homólogos de cada ilha, sendo que *Hipposideros ruber* exibiu atividade diurna em São Tomé. Este estudo contribui para uma maior compreensão dos efeitos da alteração do uso do solo em morcegos insetívoros insulares, como os morcegos de São Tomé e Príncipe.

Palavras-chave: Padrão de atividade; morcegos; São Tomé e Príncipe; sobreposição temporal; uso do solo.

Abstract

Human-induced habitat disturbances have a significant impact on biodiversity, by impacting species richness, abundance, and assemblage composition. Yet, behavioural responses to habitat change, such as alterations in activity patterns and partitioning along the temporal niche axis remain poorly investigated, especially for data deficient insular species. Here, we evaluate the effects of the most common humanized habitats on the activity patterns of insectivorous bats in the islands of São Tomé and Príncipe. Using AudioMoth acoustic recorders we sampled six insectivorous bat species across forests, shaded and oil palm plantations, as well as agricultural and urban areas. In the various habitats of both islands, we observed significant differences in temporal overlap at the assemblage level, with these trends being specific to each island and habitat type. For instance, in São Tomé, the highest degree of overlap occurred in forests, while in Príncipe, it was the lowest. Most species displayed a bimodal activity pattern. The variations in activity patterns within species were more pronounced between forests and agricultural or urban areas, compared to forests and shade plantations. Additionally, the activity patterns of *Chaerephon pumilus* and *Hipposideros ruber* differed within homologous habitat types in both islands, with *Hipposideros ruber* exclusively exhibiting diurnal activity in São Tomé. Our study contributes to a more comprehensive understanding of the effects of land-use change on insular insectivorous bats and we provide much-needed information about the poorly known bats of the Gulf of Guinea Oceanic Islands.

Keywords: Activity pattern; bats; São Tomé and Príncipe; temporal overlap; land-use.

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List of Abbreviations

FCUP	FACULTY OF SCIENCES OF THE UNIVERSITY OF PORTO
UP	UNIVERSITY OF PORTO
A.S.L.	ABOVE SEA LEVEL
CPUM	<i>Chaerephon pumilus</i>
CSPS	<i>Chaerephon</i> sp.
HRUBER	<i>Hipposideros ruber</i>
MNEW	<i>Miniopterus newtoni</i>
MTHO	<i>Macronycteris thomensis</i>
PSC	<i>Pseudoromicia principis</i>
OLD	FORSTS
SHADE	SHADE PLANTATIONS
PALM	OIL PALM PLANTATIONS
AGRIC	AGRICULTURAL AREAS
URB	URBAN AREAS
C	CANOPY COVER
T	NUMBER OF TREES
VC	VEGETATION COVER

Introduction

Animals exhibit remarkable behavioural adaptations that allow them to thrive in diverse environments (Hedenström, 2008; Mazza et al., 2020; Tranquillo et al., 2023). The ability to adjust their temporal activity is particularly intriguing, as species can modify diel activity patterns how they distribute their activity throughout the diel cycle in response to environmental cues and physiological needs (Ikeda et al., 2016; Monterroso et al., 2014). This plasticity manifests in various ways, with some species being nocturnal, primarily active at night, while others are diurnal, predominantly active during the day. Additionally, certain animals are crepuscular, displaying heightened activity levels during the twilight hours of dawn and dusk (Chen & Seybold, 2014; Meliane et al., 2023; Refinetti, 2008; Vallejo-Vargas et al., 2022).

Analysing species activity patterns yields valuable insights into their behaviour and ecological dynamics, encompassing their daily and seasonal activities (Bridges et al., 2004; Ferreira et al., 2017), foraging tactics (Laidlaw & Wan Noordin, 1998), and interactions (Gelmi-Candusso et al., 2023). These analyses further aid in unravelling factors influencing species' temporal niche of communities (Mariton et al., 2023) and enable the assessment of a species' adaptability in response to environmental changes caused by human activities. For instance, in the presence of increased human activity, animals often decrease their level of activity (Oberosler et al., 2017). In some mammals, for example, this shift leads to a more nocturnal behaviour (Bogdan et al., 2016; Gaynor et al., 2018). Considering the significant influence of the environment on animal behaviours, it becomes crucial to understand the effects of human-induced habitat changes on species' activity patterns. This can be achieved, for example, by quantifying the temporal overlap coefficient, a coefficient that indicates the degree of temporal overlap among species (Ridout & Linkie, 2009).

Human activities that transform and degrade native habitats comprise the most widespread causes of biodiversity loss on the planet (Chapin Iii et al., 2000; Lambin et al., 2003). This matter becomes particularly alarming when considering tropical forests, which act as epicentres for global biodiversity (Gibson et al., 2011). The depletion of these ecosystems can significantly amplify the rates at which species disappear worldwide (Pimm et al., 1995) and, concurrently, erode the capacity of these forests to furnish indispensable ecosystem services to human communities (Daily, 1997; Watson et al., 2018). In particular, the persistence of biodiversity hinges significantly on tropical island ecosystems (Fernández-Palacios et al., 2021). Largely due to their isolation,

these islands harbour a disproportionate number of endemic species in relation to equivalent mainland areas, which are often acutely sensitive to human stressors, such as land-use change and, invasive species (Hoekstra et al., 2005; Kier et al., 2009; Maas et al., 2009; Waltert et al., 2011).

Human-induced habitat changes, including agricultural expansion, and urbanization, are recognized as major threats to overall biodiversity, including bats (Frick et al., 2018). These alterations have profound implications for bat behaviour and activity patterns, disrupting roosting sites and limiting foraging opportunities (Appel et al., 2021; Voigt & Kingston, 2016). Notably, bats are a highly species-rich group comprising over 1,400 species (Simmons & Cirranello, 2020), with approximately 60% of them inhabiting islands (Conenna et al., 2017). Worldwide, these species offer essential ecosystem services, such as natural pest and zoonotic disease suppression through the predation of insects, which yields significant economic and health benefits (Florens et al., 2017; Kemp et al., 2019; Nóbrega et al., 2023; Tuneu-Corral et al., 2023). Island-dwelling bats are also sensitive to shifts in land-use (Ferreira et al., 2022), which alongside their ecological diversity, abundance, and ease of sampling makes them valuable indicator species for studying the impacts of habitat disturbance on insular ecosystems (Conenna et al., 2017; Jones et al., 2009).

Island bats are poorly studied in relation to their mainland counterparts (Conenna et al., 2017). Yet, an increasing number of studies supports that species richness and activity levels - two widely employed indicators of bat sensitivity to habitat disturbance - are significantly impacted by land-use changes (Davies et al., 2016; Ferreira et al., 2022). However, to date, research on the insular bat responses to land-use change largely has overlooked behavioural alterations, including changes in activity patterns and temporal niche partitioning, which could potentially offer a more nuanced and sensitive insight into how species respond to habitat conversion. In fact, studies in mainland areas have identified substantial shifts in the activity pattern of bats in relation to agriculture (Presley et al., 2009a), logging (Castro-Arellano et al., 2009; Presley et al., 2009b), urbanisation (Montaño-Centellas et al., 2015) and forest fragmentation (Appel et al., 2021). Island bats are equally likely to exhibit shifts in their activity patterns due changes in their local biotic and abiotic conditions. However, insular bats often present distinctive activity patterns in relation to their mainland counterparts. For instance, insular bats tend to have more prevalent diurnal habits, due to the absence of diurnal birds of prey (e.g., hawks and falcons) that can effectively hunt them during

daytime (Chua & Aziz, 2018; Moore, 1975; Russo et al., 2011). It is therefore unclear how human-driven habitat changes might impact their diel temporal dynamics.

Ecological traits such as wing morphology and echolocation call design often modulate the habitat preferences and foraging behaviour of insectivorous bats (Siemers et al., 2001). Bats are categorised into distinct functional groups based on these traits (Denzinger & Schnitzler, 2013). For example, clutter foragers like the Hipposideridae, characterised by constant frequency (CF) calls and broad wings (Monadjem et al., 2010; Taylor et al., 2013), are specialised for forested environments and exhibit reduced activity in open habitats (Williams-Guillén & Perfecto, 2011) such as agricultural and urban areas (Jung & Threlfall, 2016). Conversely, open-space foragers like the Molossidae, known for their long, narrow wings and quasi-constant frequency (QCF) calls (Denzinger & Schnitzler, 2013), demonstrate higher overall activity levels in regions with simpler or absent vertical forest strata (Williams-Guillén & Perfecto, 2011), such as open agricultural spaces and urban areas (Avila-Flores & Fenton, 2005). Clutter-edge foragers, like Vespertilionidae and Miniopteridae, identified by frequency-modulated (FM) calls and broader wings (Denzinger & Schnitzler, 2013), tend to forage near the edges of clutter, including forest edges and gaps (Monadjem et al., 2020), occasionally transitioning between these areas and open habitats (Fenton, 1990).

The oceanic islands of São Tomé and Príncipe, located in the Gulf of Guinea, host eight insectivorous bat species, four of which are endemic to these islands (Rainho et al., 2022). São Tomé is home to three endemic species, namely: *Chaerephon tomensis* - a poorly known species from Molossidae family (Monadjem et al., 2019), for which no information is currently available regarding its roosting sites or preferred habitats (Rainho et al., 2022; Rainho et al., 2010). The endemic *Macronycteris thomensis* is widespread across São Tomé (Rainho et al., 2010), and belongs to the Hipposideridae family (Monadjem et al., 2017a). While limited information exists about this species, Rainho et al. (2022) suggest that its biology could resemble that of its close relative, *Macronycteris gigas*, found on the nearby island of Bioko. The endemic *Miniopterus newtoni*, a member of the Miniopteridae family (Juste, 2019), is abundant throughout São Tomé (Rainho et al., 2010) and occupies both human-altered habitats and old-growth lowland forests (Juste, 1990, as cited in Rainho et al., 2022). *Pseudoromicia principis* is endemic to the island of Príncipe belongs to the Vespertilionidae family (Juste et al., 2023) and is an abundant and versatile species, found in urban, agricultural, and forested areas (Rainho et al., 2022). The *Myotis tricolor* from the Vespertilionidae family (Monadjem & Jacobs, 2017), is found in São Tomé and has a

single known roosting site in a sea cave (Rainho et al., 2010). On the mainland, this species is linked to mountainous areas where it roosts in caves and is recognized as a clutter-edge forager (Monadjem et al., 2020). The *Chaerephon pumilus*, from the Molossidae family (Mickleburgh et al., 2019), is found in both islands, São Tomé and Príncipe (Rainho et al., 2022), and inhabits a range of habitats from semi-arid to humid forests (Bouchard, 1998). This species forages in open spaces and roosts within cracks in rocks or trees, as well as in buildings (Monadjem et al., 2020). The *Hipposideros ruber* from the Hipposideridae family (Monadjem, 2017a), is common in São Tomé and Príncipe (Rainho et al., 2022), this species prefers lowland tropical moist forests but is less common in drier and less forested regions (Rainho et al., 2010). This species utilises diverse roosting sites, from caves to abandoned buildings, and additionally uses artificial tunnels in São Tomé (Rainho et al., 2022). Regarding its foraging behaviour, *H. ruber* is known to forage in narrow spaces (Happold, 2013). Additionally, this species displays diurnal activity, although Russo et al. (2011) indicated that the individuals remain more active during the night. Additionally, *Taphozous mauritanus*, which belongs to the Emballonuridae family (Monadjem et al., 2017b), is found in the less forested northern area of São Tomé and has only been acoustically detected in Príncipe (Rainho et al., 2010). This species is an open-space forager, and, in other regions of Africa, this species tends to inhabit savanna woodlands, deliberately avoiding densely forested interiors (Monadjem et al., 2020).

Anthropogenic land-uses, such as agriculture and urbanisation, have significantly transformed the native landscapes in São Tomé and Príncipe (de Lima et al., 2013; Lima, 2012; Strauß et al., 2018), as in many other regions (Dauby et al., 2022; Muñoz-Torrent et al., 2022). Agriculture has held historical significance in this country, commencing with a focus on sugar cane and subsequently transitioning to cocoa and coffee cultivation (Jones et al., 1991). Presently, the scenario is further compounded by the extensive spread of oil palm plantations in São Tomé, which span extensive areas and encourage monoculture practices (Eyzaguirre, 1986). Although the distribution of species across the island is known (Rainho et al., 2010), the responses of bats to these land-use changes are poorly understood (but see Rainho et al. (2010) and Rainho et al. (2022)).

Our knowledge of the activity patterns of insular bats remains scarce, hindering our ability to understand the behavioural responses of this important group to human-induced habitat changes in island ecosystems. The primary objective of this thesis is to use acoustic data to identify and compare the activity patterns within and between insectivorous bat species across different habitat types - old-growth forests, oil palm plantations, agricultural areas, and urban areas - in both São Tomé and Príncipe islands. For this, we investigated the hourly activity patterns of six species, by examining the temporal overlap among all detected species within each of the surveyed habitat types, as well as the temporal overlap within the same species but between habitat types. Specifically, we address the following questions:

1) Does species' temporal overlap in activity change between habitats? Bats utilise temporal partitioning as a strategy to alleviate interspecific competition (Lambert et al., 2018). Therefore, in habitats with an anticipated higher species richness such as forests and shade plantations, we predict reduced species' temporal overlap.

2) How does the diel activity of each species characterises (i.e., time and distribution of the species activity peaks) and whether does that vary between habitats? After characterising diel species activity, we hypothesise that bat activity patterns vary between habitat types and, as shifts in the activity patterns of mainland bats have been observed to be more pronounced in habitats that exhibit particularly contrasting structural differences (Montaño-Centellas et al., 2015; Presley et al., 2009a), we anticipate that urban and agricultural areas will manifest the most distinct activity patterns in comparison to forest.

3) How do the activity patterns of the same species compare between analogous habitats in São Tomé and Príncipe islands? Using *Chaerephon pumilus* and *Hipposideros ruber* as case studies, we anticipate that due to the intrinsic environmental conditions of each island, the activity patterns are likely to be distinct. This may involve changes in the timing and frequency of activity peaks, especially for *Hipposideros ruber*, which is anticipated to be more responsive to alterations in habitat.

1. Materials and Methods

1.1. Study area

The study was conducted in São Tomé and Príncipe, a democratic state comprising two main islands (São Tomé and Príncipe), as well as several smaller islets. This nation is located in the Gulf of Guinea, off the western equatorial coast of Central Africa

(Figure 1). Both islands experience two distinct dry and rainy seasons. São Tomé has average annual temperatures of 27 °C near the sea level and 21 °C at higher

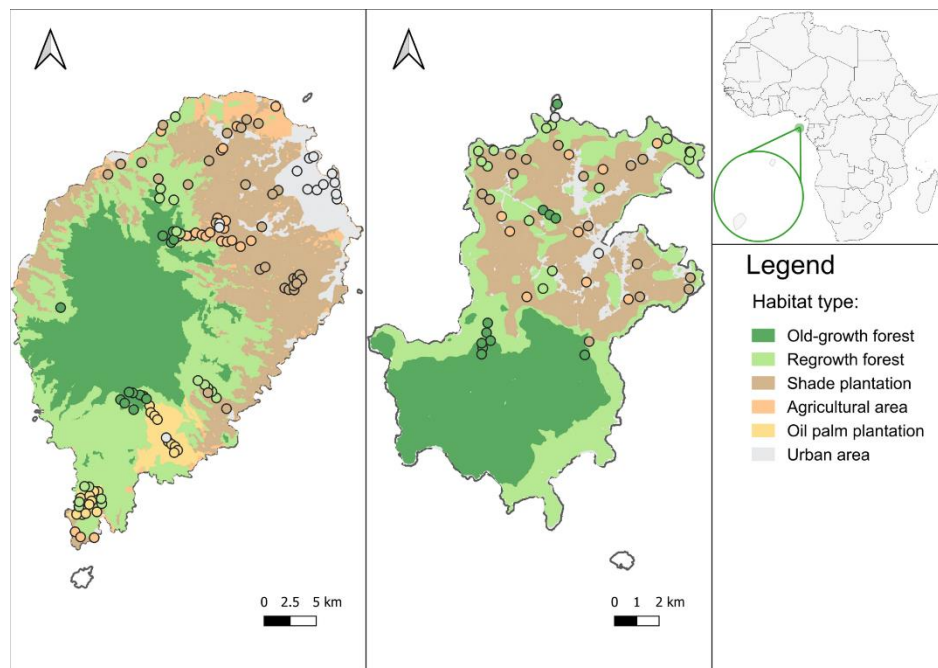


Figure 1 - Land cover and location of all sample sites on São Tomé and Príncipe adapted from Soares et al. (2020).

elevations. Príncipe experiences an average annual temperature of 26 °C, with minor fluctuations between coastal and mountainous regions. On both islands, the average annual precipitation ranges from 900 mm in the northeast to around 6000 mm in the south (Lima & Oliveira, 2017). Both islands have rugged mountainous topography, with São Tomé's highest point being Pico de São Tomé at 2024 m above sea level (a.s.l.) and Príncipe's highest point being Pico do Príncipe at 948 m a.s.l.. São Tomé and Príncipe are known for their diverse ecosystems, particularly the tropical forests that fall within the ecoregion of São Tomé, Príncipe, and Annobón moist lowland forests.

Moreover, São Tomé and Príncipe are home to the Ôbo Natural Park, a significant conservation area established in both islands. The park covers c.a. 235 km² on São Tomé Island (27% of the island area) and 65 km² on Príncipe Island (46%), encompassing extensive portions of the islands' old-growth forests and serves as a vital habitat for numerous endemic and endangered species (e.g., *Bostrychia bocagei* and *Lanius newtoni*; BirdLife International, 2014).

Both islands are occupied by a number of habitat types encompassing a range of human-disturbance intensities, including old-growth forests, regrowth forests, shaded plantations, oil palm plantations (only in São Tomé Island), agricultural areas, and

urban areas. In this study, bats were surveyed across each of these habitats throughout each island (Figure 1). Old-growth forests are the least disturbed areas on the islands, covered by native forest vegetation. While they may have experienced alterations or disturbances in the past, these areas are largely characterised by relatively low levels of known human intervention. Regrowth forests are predominantly composed of introduced species, resulting from the regrowth of vegetation after the removal of pre-existing old-growth forests. Shade plantations represent areas where shade-grown crops of mainly cocoa and coffee are cultivated beneath the canopy of taller exotic trees. Oil palm plantations consist of palm tree monocultures specifically cultivated for organic oil production. Agricultural areas were characterised by landscapes managed by humans for farming activities, cultivating crops like banana trees, cassava, carrots, and tomatoes. Urban areas encompass developed regions with human settlements, infrastructure, and modified landscapes.

1.2. Sampling design

The acoustic data collection was conducted between August and early September 2022 on both São Tomé and Príncipe. This time period was selected to avoid the rainy season, which has the potential to impact both bat activity and the performance of the recording equipment. The objective of the survey was to cover as much area of each island as possible, however, due to difficulties in accessing more remote areas, sampling did not cover each island entirely (Figure 1). Sampling sites were selected to capture the heterogeneity of habitats across the country as effectively as possible and were spaced at least 250 m apart from each other to avoid pseudoreplication.

We deployed AudioMoth acoustic recorders (Hill et al., 2018) at each sampling point for a minimum duration of two days and two nights (48 h) before being relocated to another site. The microphones of the recording devices were positioned perpendicular to the ground at a height of 2 m, fixed on trees. AudioMoths were configured to record 1 min every 5 min at a sample rate frequency of 384 kHz for a continuous 24-hour period. A total of 202 sites were initially sampled, but only 166 sites were used in the analysis. São Tomé comprised a total of 115 sites. Of these, 13 were situated in old-growth forests, 17 in regrowth forests, 29 in shade plantations, 20 in oil palm plantations, 23 in agricultural areas, and 13 in urban areas. Similarly, Príncipe had a total of 51 sites. Among these, 11 were in old-growth forests, 14 in regrowth forests, 15 in shade plantations, 9 in agricultural areas, and 2 in urban areas.

The canopy cover was estimated at each site (Table S 1; Table S 2) through visual assessment by determining the percentage of cover above the AudioMoth. The old-growth forests and regrowth forests represented relatively undisturbed areas with similar canopy cover (Table S 1; Table S 2). Therefore, and due to the low number of bat detections in old-growth forests alone, we have decided to merge these two categories for the analysis, now referring to them simply as forests.

1.3. Bioacoustic analysis

Bat activity was measured using a "bat pass", representing a sequence of two echolocation pulses emitted by an individual bat of a specific species within a five-second audio file 5). The original one-minute recordings obtained from the AudioMoths were divided into five-second files using Kaleidoscope v.5.3.8 software (Wildlife Acoustics, USA). This division allowed for the isolation of files containing bat passes, while files without any bat passes were automatically sorted into a separate "noise" folder. To select files containing bat passes, specific signal detection parameters were established in Kaleidoscope. The detection range for frequencies was set between 8 and 250 kHz. Additionally, the minimum and maximum durations of detection pulses were set between 2 and 500 milliseconds. The software was configured to consider a maximum inter-syllable gap of 500 milliseconds, and a minimum of two pulses were required for detection.

Species were identified by analysing echolocation call characteristics, including minimum and maximum pulse frequency, peak frequency, call duration, and the interval between pulses. The characteristics of the echolocation call for each species were sourced from Rainho et al. (2010), with specific information about *P. principis* obtained from Juste et al. (2023). Due to the similarity in echolocation characteristics between *C. tomensis* and *C. pumilus*, identifying *C. tomensis* is challenging (Rainho et al., 2022). Consequently, when we identify *Chaerephon* sp., it could refer to either *C. pumilus* or *C. tomensis*. Using Kaleidoscope, echolocation calls were manually identified, resulting in a total of 45,410 bat passes identified to either the species or genus level (24,414 in São Tomé and 20,996 in Príncipe). Furthermore, social calls and feeding buzzes were also identified manually. However, they were not used in the analysis for this study. Although some research incorporates social calls to examine community activity levels (Springall et al., 2019), relating specific social calls to individual species is challenging. Bat activity for each species per night was quantified by summing the total number of bat passes for each hour.

To ensure robust data representation, only species detected in at least 10% of the surveyed nights (Alberto, 2012) were considered in subsequent analysis. Additionally, the recommendation of Lashley et al. (2018) was adhered to, whereby species required a minimum of 100 independent detections per habitat to be included.

1.4. Activity patterns

For this study, we employed *circular* statistical analyses, starting by converting the time data into a radian scale, ranging from zero hours (0) to 24 hours (2π). To address the first and second questions, the diel activity patterns of each bat species in each habitat type were assessed via Kernel density functions. A k_{max} value of 3 was selected, as it has been shown to provide robust estimates for both unimodal and bimodal activity distributions, and an adjust factor of 1 was applied for bandwidth scalar adjustment (Ridout & Linkie, 2009). Both of these parameters interact to define the width of the kernel used for density estimation. A careful choice of k_{max} and adjust is essential to ensure that the resulting density curve accurately represents the underlying patterns in the data while avoiding undue influence from noise or oversmoothing (Ridout & Linkie, 2009). These choices facilitated the use of the overlap estimator Δ_4 for further consideration. To enable the analysis, the times of recording were transformed into a radians scale and treated as part of a continuous circular distribution.

1.5. Quantifying the overlap coefficient

For the first question, we investigated whether bat populations segregate their activity across different habitats on each island. This involved calculating the average overlap coefficient for each specific habitat. This was determined by comparing the activity patterns of every pair of bat species within the same habitat type. Furthermore, we analysed the overlap coefficient for each pair of compared habitat types to understand variations in activity patterns within distinct habitats for each species. Regarding the second question, the overlap coefficients were also determined to compare the diel activity patterns of each species between habitat types, including shade plantations, agricultural areas, urban areas, and oil palm plantations (São Tomé only) in relation to forests. In addressing the third question, we compared the activity patterns between the two islands for both *H. ruber* and *C. pumilus*. It's important to note that due to a limited number of detections in forests on both islands for *H. ruber*, we did not apply the data selection criteria for this species in this habitat.

The overlap coefficients (Δ), ranging from 0 to 1, quantify the extent of overlap in activity patterns between species. A value of 0 means the activity patterns are

completely dissimilar, while a value of 1 indicates complete overlap. The confidence intervals with 95% certainty were estimated using the bootstrap technique with 9,999 resamples, following the methodology outlined by Ridout and Linkie (2009). For these calculations, we used the *overlap* package in R (Meredith et al., 2014; Ridout & Linkie, 2009). We followed Ridout and Linkie (2009) for the selection of the most appropriate overlap coefficient estimator. Ridout and Linkie (2009) considered three options: Dhat1, Dhat4, and Dhat5, each with distinct overlap measurement methods, of which Dhat1 emerged as well-suited for smaller sample sizes, while Dhat5 presented higher susceptibility to inconsistent results due to minor data variations makes this estimator less suitable for robust outcomes. Factoring these considerations, we selected Dhat4 as our preferred estimator due to more consistent performance across sample sizes, particularly when exceeding 50 observations.

1.6. Characterisation of each species diel activity

Additionally for the second question, to help characterize the activity pattern we performed Rayleigh and Hermans-Rasson tests for each dataset (each species on each habitat for São Tomé and Príncipe). This analysis assesses whether bat activity displays non-random or uniformly distributed patterns. The Rayleigh test evaluates whether there's a significant deviation from uniformity in the overall distribution, while the Hermans-Rasson test is particularly useful for identifying complex patterns, especially in cases with multimodal activity patterns (Landler et al., 2019). According to Landler et al. (2019), while the Rayleigh test determines if the distribution significantly deviates from uniformity, it's important to note that in cases of multimodal distributions, this test may not reject the null hypothesis of uniform distribution due to its lower sensitivity to this type of pattern. This highlights the necessity of also applying the Hermans-Rasson's test. Unlike the Rayleigh test, the Hermans-Rasson's test directly assesses the presence of multimodal distributions. Consequently, if the result of the Hermans-Rasson's test is significant, it indicates that the null hypothesis is rejected, signifying the presence of a multimodal distribution. Consequently, both the Rayleigh and Hermans-Rasson's tests were performed using the *circular* package (Lund et al., 2017) in R. It's worth noting that the code for the Hermans-Rasson's test, incorporated in this package, was provided by Landler et al. (2019).

2. Results

We recorded a total of 45,410 bat passes, with 24,414 in São Tomé and 20,996 in Príncipe. On São Tomé, the most frequently detected bat species was *Miniopterus newtoni*, with 10,949 detections, followed by *C. pumilus* with 10,436 detections, *Chaerephon* sp. with 1,834 detections, *M. thomensis* with 986 detections, and finally *H. ruber* with 209 detections. On Príncipe, *P. principis* was the most commonly detected species with 18,172 detections, followed by *C. pumilus* with 2,685 detections, and *H. ruber* with 139 detections.

2.1. Temporal overlap between species in each of the habitat types on São Tomé island

In São Tomé, oil palm plantations comprised the habitat type in which the species detected (*C. pumilus*, *Chaerephon* sp. and *M. newtoni*) had the highest average coefficient of temporal overlap ($\Delta 4 \sim 0.70$). This coefficient was lower for species found in agricultural areas (*C. pumilus*, *Chaerephon* sp. and *M. newtoni*; $\Delta 4 = 0.61$) and urban areas (*C. pumilus*, *Chaerephon* sp. and *M. newtoni*; $\Delta 4 = 0.57$), and particularly lower for species detected in shade plantations (*C. pumilus*, *Chaerephon* sp., *M. newtoni* and *M. thomensis*; $\Delta 4 = 0.36$), and forest (*C. pumilus*, *Chaerephon* sp., *M. newtoni* and *M. thomensis*; $\Delta 4 = 0.28$; Figure 2). By visually examining the peaks of activity frequency, we observed that in forests species had their highest temporal overlap peak during the predawn period (Figure 2A), whereas in all other habitat types (Figure 2B, 2C, 2D and 2E), they had their highest peak during the late evening period (around 8 PM). In forests, shade plantations, and agricultural areas (Figure 2A, 2B and 2D), all species showed a pattern of overall decreasing activity after the first peak as midnight approached, followed by an increase in overall activity as dawn approached. However, this pattern did not apply to *M. thomensis* (only detected in forests and shade plantations), which exhibited a peak of activity around midnight (Figure 2A and 2B), nor to *H. ruber* (only detected in forests), which displayed increased diurnal activity with the highest peaks of activity during daylight hours (Figure 2A). In oil palm plantations, all detected species exhibited decreased activity as midnight approached (Figure 2C). However, in this habitat type, *Chaerephon* sp. and *C. pumilus* showed two clear peaks of activity prior to midnight, while *M. newtoni* only exhibited one clear peak around that same period. In urban areas, *Chaerephon* spp. showed a decrease in activity as midnight approached, while *Miniopterus newtoni* appeared to be active all night without any clear isolated peak of activity frequency (Figure 2E).

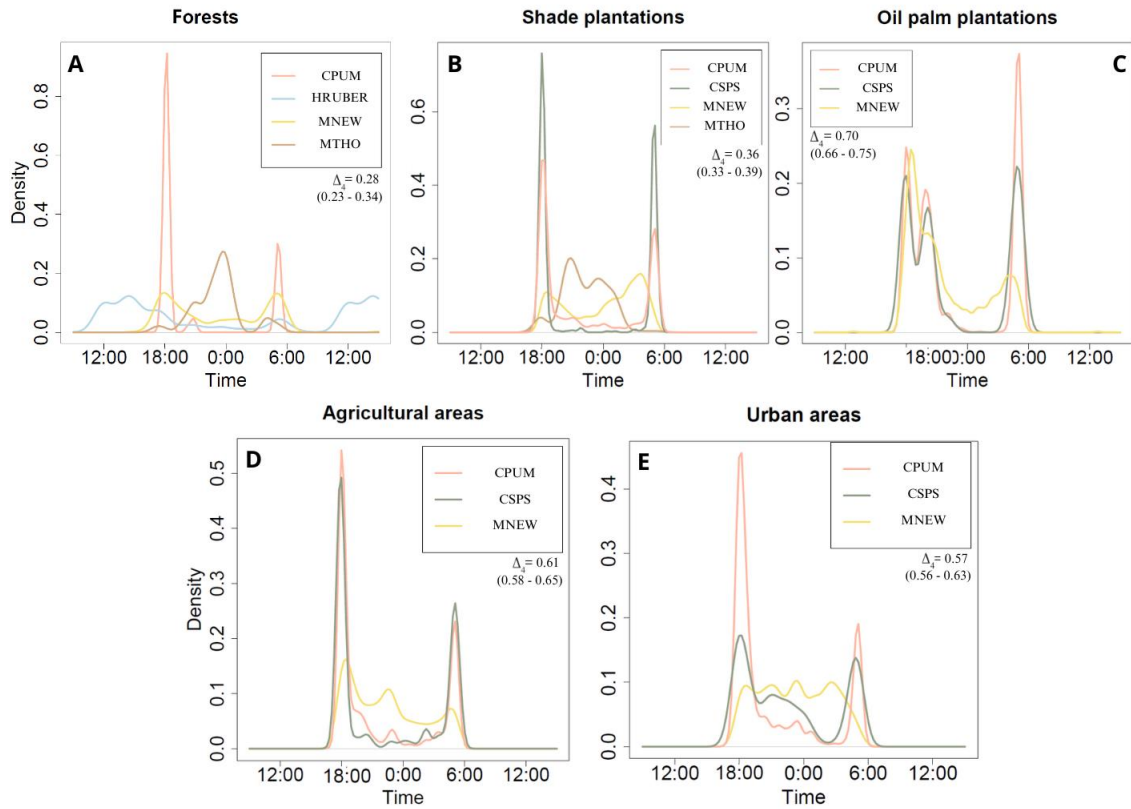


Figure 2 - Overlapping species activity curves for each habitat on São Tomé. These curves were generated using the *overlap* package with the kernel density function *densityPlot*. The overlap coefficients (Δ_4) were calculated using the *overlapEst* function with the *Dhat4* parameter. The corresponding confidence intervals were determined using the *bootCI* function with the estimator *basic0* from the same package, employing 9999 bootstrap estimations. Abbreviations: CPUM - *Chaerephon pumilus*; CSPS - *Chaerephon* sp.; HRUBER - *Hipposideros ruber*; MNEW - *Miniopterus newtoni*; MTHO - *Macronycteris thomensis*.

The confidence intervals for the overlap coefficients of each habitat showed differences between them, except for the coefficients obtained for forests and shade plantations, as well as the coefficients of agricultural and urban areas (Table 1).

Table 1 - Statistical significance of the difference in temporal overlap coefficients of each habitat on São Tomé. Abbreviations: Old - forests; Shade - shade plantations; Palm - oil palm plantations; Agric - agricultural areas; Urb - urban areas; * - Significantly different.

São Tomé	Old	Shade	Palm	Agric
Shade	-			
Palm	*	*		
Agric	*	*	*	
Urb	*	*	*	-

2.2. Temporal overlap between species in each of the habitat types on Príncipe island

On Príncipe, we observed that the two species detected in forests exhibited the highest average overlap coefficient ($\Delta_4 \sim 0.83$), indicating a strong temporal overlap in their activity patterns. In contrast, these same species in shade plantations, urban areas, and agricultural areas showed a lower overlap coefficients of approximately 0.77, 0.75, and 0.47, respectively (Figure 3).

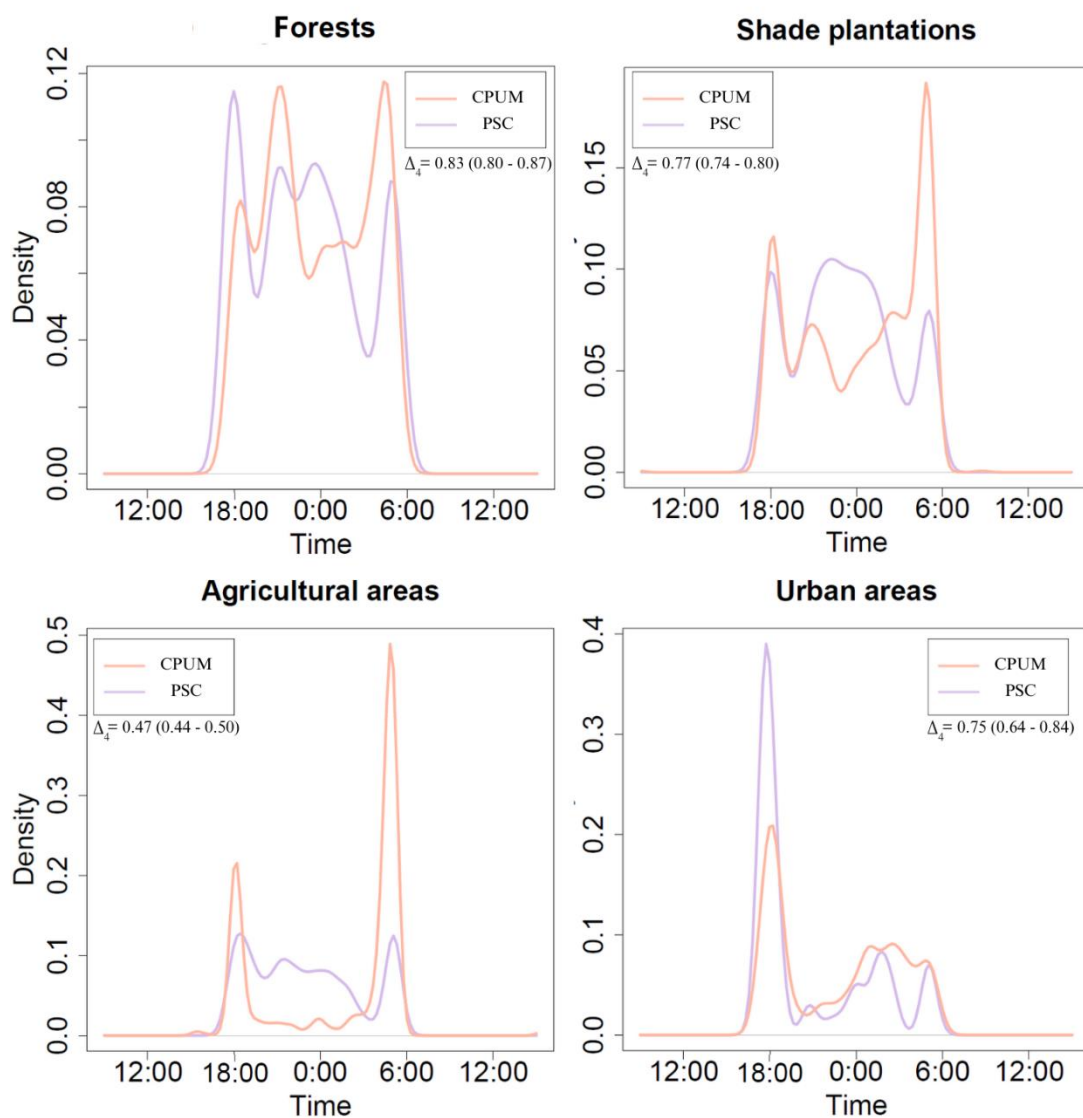


Figure 3 - Overlapping species activity curves for each habitat on Príncipe. These curves were generated using the *overlap* package with the kernel density function *densityPlot*. The overlap coefficients (Δ_4) were calculated using the *overlapEst* function with the *Dhat4* parameter. The corresponding confidence intervals were determined using the *bootCI* function with the estimator *basic0* from the same package, employing 9999 bootstrap estimations. Abbreviations: CPUM - *Chaerephon pumilus*; PSC - *P. principis*.

We found that in forests, the peak of higher temporal overlap occurred during the late evening, specifically around 9 PM. In shade plantations, agricultural and urban areas, overlap peaked shortly after sunset. In forests, shade plantations and agricultural areas, *C. pumilus* displayed a consistent trend of declining activity as midnight approached, followed by an increase in activity towards dawn. At the species level, neither *P. principis* nor *C. pumilus* exhibited high activity around midnight in urban areas. Notably, in urban areas, each species exhibited distinct activity patterns in relation to their activity patterns in other habitat types (Figure 3).

The confidence intervals for the overlap coefficients revealed that the coefficients of agricultural areas differed from all other habitats, whereas forests, shade plantations, and urban areas did not show significant differences from one another (Table 2).

Table 2 - Statistical significance of the difference in temporal overlap coefficients of each habitat on Príncipe. Abbreviations: Old - forests; Shade – shade plantations; Palm – oil palm plantations; Agric – agricultural areas; Urb – urban areas; * - Significantly different.

São Tomé	Old	Shade	Agric
Old			
Shade	-		
Agric	*	*	
Urb	-	-	*

2.3. Temporal overlap between habitat types for each species on São Tomé island

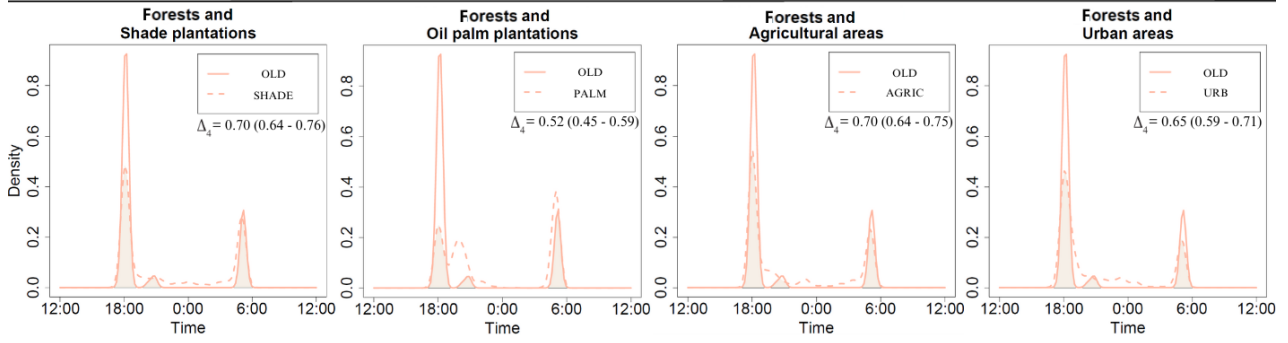
In São Tomé island, the observed overlap coefficients between forests and shade plantations showed lower values for *M. newtoni* ($\Delta 4 \sim 0.69$) and *M. thomensis* ($\Delta 4 \sim 0.69$) compared to *C. pumilus* ($\Delta 4 \sim 0.70$) (Figure 4). In the case of forests with oil palm plantations, *C. pumilus* had a lower coefficient ($\Delta 4 \sim 0.52$) than *M. newtoni* ($\Delta 4 \sim 0.71$). Similarly, when comparing forests and agricultural areas, *C. pumilus* exhibited a lower overlap coefficient ($\Delta 4 \sim 0.70$) than *M. newtoni* ($\Delta 4 \sim 0.76$). Notably, between forests and urban areas, *M. newtoni* and *C. pumilus* showed relatively small differences their overlap coefficients, with the former having a slightly lower value ($\Delta 4 \sim 0.64$) compared to the latter ($\Delta 4 \sim 0.65$).

Regarding *C. pumilus*, the confidence intervals for the overlap coefficients indicated that the coefficient between forests and oil palm plantations was different from the overlap coefficient between forests and shade plantations (Table 3). Additionally, the overlap coefficient between forests and oil palm plantations was different from the

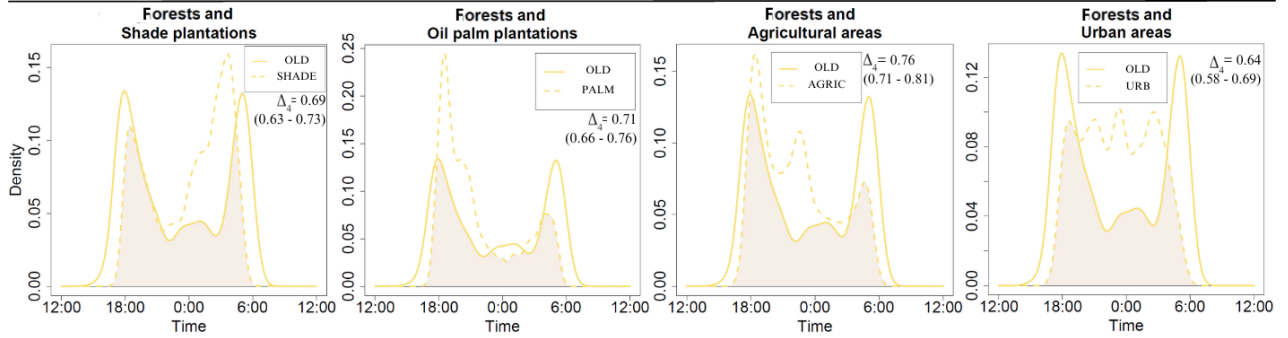
overlap coefficients of forests and agricultural areas, as well as forests and oil palm plantations and forests and urban areas. For *M. newtoni*, the overlap coefficient between forests and agricultural areas was different from the overlap coefficient between forests and urban areas (Table 3).

With the exception of the Rayleigh test for *M. newtoni* in forest, all other Rayleigh and Hermans-Rasson's tests provided statistical evidence to support the deviation from an uniform distribution (Table 4). Both *C. pumilus* and *Chaerephon* sp. exhibited bimodal activity patterns in all habitats (Figure 4). The species *M. newtoni* also showed a bimodal distribution in forests, oil palm plantations, and shade plantations, but it displayed a more consistent activity pattern in urban areas. In agricultural areas, *M. newtoni* demonstrated a gradual decrease in activity throughout the night, with three distinct peaks observed: the first peak occurred shortly after sunset, the second approached midnight, and the third occurred shortly before sunrise. As for *M. thomensis*, it displayed bimodal activity distributions throughout the night in both forests and shade plantations.

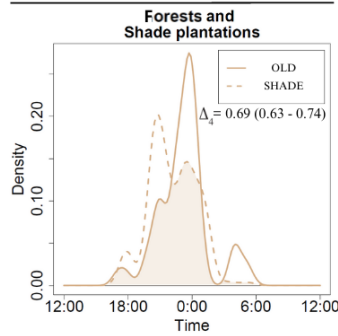
Chaerephon pumilus



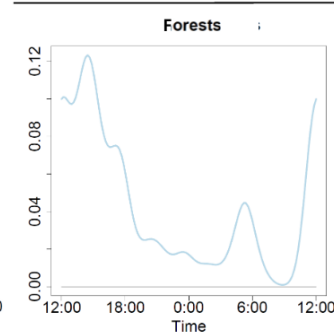
Miniopterus newtoni



Macronycteris thomensis



Hipposideros ruber



Chaerephon sp.

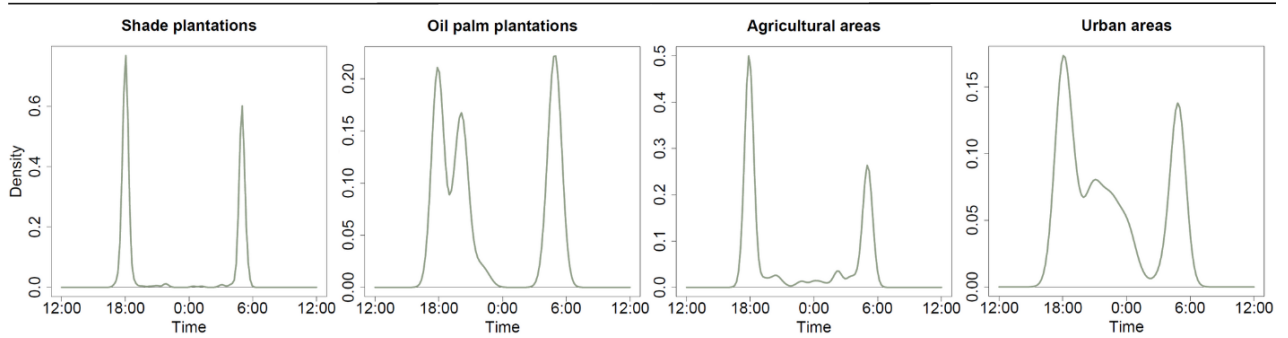


Figure 4 - Temporal activity patterns for five species in São Tomé. *Chaerephon sp.* and *Hipposideros ruber* do not show overlap due to insufficient detections in old-growth forest or in all other habitats, respectively. Abbreviations: OLD – forests; SHADE – shade plantations; PALM – oil palm plantations; AGRIC – agricultural areas; URB – urban areas.

Table 3 - Statistical significance of the difference in temporal overlap coefficients between habitat comparisons on São Tomé. Abbreviations: Old vs Shade – overlap between forests and shade plantations; Old vs Palm – overlap between forests and oil palm plantations; Old vs Agric – overlap between forests and agricultural areas; Old vs Urb – overlap between forests and urban areas; * - Significantly different.

São Tomé	Old vs Shade	Old vs Palm	Old vs Agric
<i>Chaerephon pumilus</i>			
Old vs Palm	*		
Old vs Agric	-	*	
Old vs Urb	-	*	-
<i>Miniopterus newtoni</i>			
Old vs Palm	-		
Old vs Agric	-	-	
Old vs Urb	-	-	*

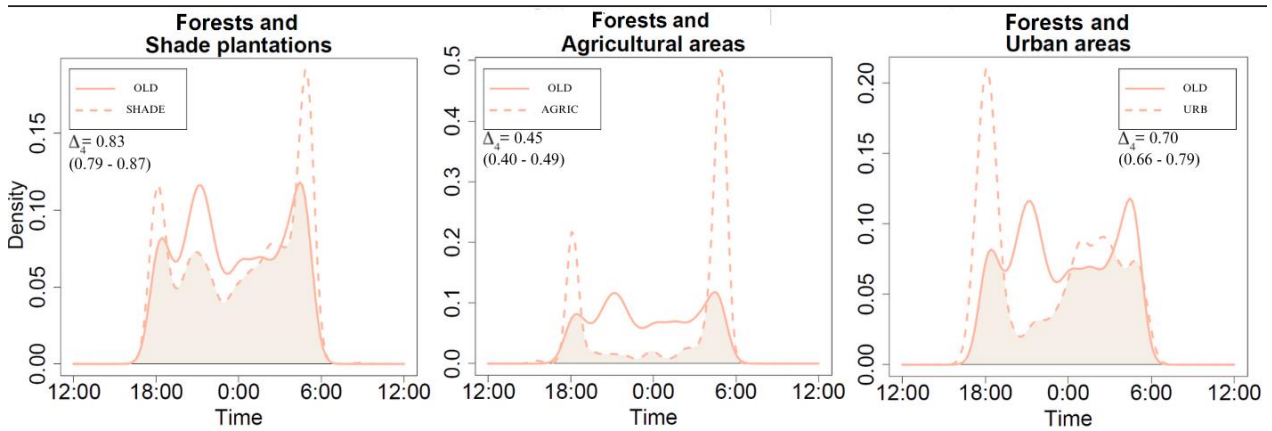
Table 4 - Rayleigh and Hermans-Rasson's tests performed for each habitat on each detected species in São Tomé. n – number of detections; r – Rayleigh test statistics; T – Hermans-Rasson statistics; P – p-value; Sig. – Statistical significance; * - statistically significant (p < 0.005).

São Tomé	n	Rayleigh test		Hermans-Rasson's test			
		r	P	Sig.	T	P	Sig.
<u>Forest</u>							
<i>Chaerephon pumilus</i>	158	0.537	<0.001	*	313.867	0.0001	*
<i>Hipposideros ruber</i>	133	0.621	<0.001	*	147.836	0.0001	*
<i>Miniopterus newtoni</i>	226	0.084	0.142	-	164.807	0.0001	*
<i>Macronycteris thomensis</i>		0.372	<0.001	*	323.589	0.0001	*
<u>Shade plantation</u>							
<i>Chaerephon pumilus</i>	2904	0.364	<0.001	*	2858.192	0.0001	*
<i>Chaerephon sp.</i>	527	0.140	<0.001	*	854.281	0.0001	*
<i>Miniopterus newtoni</i>	1530	0.187	<0.001	*	1025.887	0.0001	*
<i>Macronycteris thomensis</i>		0.476	<0.001	*	517.588	0.0001	*
<u>Oil palm plantation</u>							
<i>Chaerephon pumilus</i>	1003	0.352	<0.001	*	982.651	0.0001	*
<i>Chaerephon sp.</i>	133	0.264	<0.001	*	149.285	0.0001	*
<i>Miniopterus newtoni</i>	5699	0.417	<0.001	*	5874.101	0.0001	*
<u>Agricultural area</u>							
<i>Chaerephon pumilus</i>	3008	0.447	<0.001	*	3389.982	0.0001	*
<i>Chaerephon sp.</i>	3008	0.219	<0.001	*	732.561	0.0001	*
<i>Miniopterus newtoni</i>	1229	0.331	<0.001	*	739.221	0.0001	*
<u>Urban area</u>							
<i>Chaerephon pumilus</i>	3323	0.551	<0.001	*	3818.618	0.0001	*
<i>Chaerephon sp.</i>	551	0.316	<0.001	*	360.728	0.0001	*
<i>Miniopterus newtoni</i>	1408	0.158	<0.001	*	783.312	0.0001	*

2.4. Temporal overlap between habitat types for each species on Príncipe

When comparing the data from forests and shade plantations on Príncipe, the overlap coefficient was lower for *C. pumilus* ($\Delta_4 \sim 0.83$) compared to *P. principis* ($\Delta_4 \sim 0.93$) (Figure 5). Similarly, for forests and agricultural areas, the overlap coefficient was lower for *C. pumilus* ($\Delta_4 \sim 0.45$) than *P. principis* ($\Delta_4 \sim 0.91$). In terms of forests and urban areas, *P. principis* had the lowest value of this coefficient ($\Delta_4 \sim 0.60$) when compared to *C. pumilus* ($\Delta_4 \sim 0.70$) (Figure 5).

Chaerephon pumilus



Pseudoromicia principis

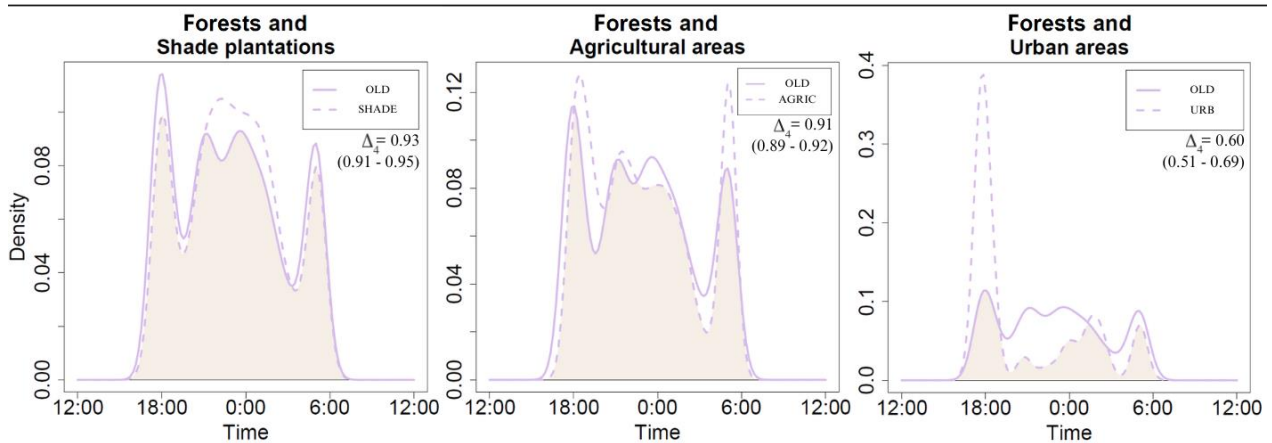


Figure 5 - Temporal activity pattern for three species of São Tomé. Abbreviations: OLD – forests; SHADE – shade plantations; AGRIC – agricultural areas; URB – urban areas.

Regarding *C. pumilus*, the confidence intervals of the overlap coefficients show that the coefficient between forests and agricultural areas differ significantly from the coefficients between forests and shade plantations, forests and urban areas, and forests and shade plantations (Table 5). For *P. principis*, the overlap coefficient of forests and urban areas was significantly different from the coefficient of forests and shade plantations. Additionally, the coefficient of forests and urban areas was different from the coefficient of forests and agricultural areas (Table 5).

Table 5 - Statistical significance of the difference in temporal overlap coefficients between habitat comparisons on Príncipe. Abbreviations: Old vs Shade – overlap between forests and shade plantations; Old vs Agric – overlap between forests and agricultural areas; Old vs Urb – overlap between forests and urban areas; * - Significantly different.

	Príncipe	Old vs Shade	Old vs Agric
<i>Pseudoromicia principis</i>			
Old vs agric		-	
Old vs urb		*	*
<i>Chaerephon pumilus</i>			
Old vs agric		*	
Old vs urb		*	*

The non-uniform distribution observed in both species on Príncipe was supported by statistical evidence from the Rayleigh and Hermans-Rasson's tests (Table 6). *Chaerephon pumilus* exhibited a bimodal distribution of activity in all habitat types, except for shade plantations, where it displayed three prominent peaks. The first peak occurred during sunset, followed by a second peak in the late evening (around 9 PM), and the third and highest peak occurred during sunrise (Figure 5). *Pseudoromicia principis* exhibited a similar pattern with three peaks in forests, shade plantations, and agricultural areas, which is supported by the high overlap coefficient. The first peak occurred at sunset, followed by a second peak starting in the late evening (around 9 PM) and extending into the late night (around 3 AM). The third peak occurred just before sunrise. The activity pattern of this species in urban areas showed the most distinct variation compared to other habitats, as indicated by the decreased overlap coefficient between urban areas and the activity pattern observed in forests, despite also displaying three prominent peaks. In both species, the non-uniform distribution observed was supported by the statistical evidence provided by the Rayleigh and Hermans-Rasson's tests (Table 6).

Table 6 - Rayleigh and Hermans–Rasson’s tests performed for each habitat on each detected species on Príncipe. n – number of detections; r – Rayleigh test statistics; T – Hermans-Rasson statistic; P – p-value; Sig. – Statistical significancy; * - statistically significant (p < 0.005).

Príncipe	n	Rayleigh test			Hermans-Rasson’s test		
		r	P	Sig.	T	P	Sig.
<u>Forests</u>							
<i>Pseudoromicia principis</i>	3797	0.176	0.000	*	1825.636	0.0001	*
<i>Chaerephon pumilus</i>	516	0.084	0.026	*	282.000	0.0001	*
<u>Shade plantation</u>							
<i>Pseudoromicia principis</i>	7888	0.157	0.000	*	3226.261	0.0001	*
<i>Chaerephon pumilus</i>	1114	0.138	0.000	*	615.761	0.0001	*
<u>Agricultural area</u>							
<i>Pseudoromicia principis</i>	4742	0.209	0.000	*	2112.116	0.0001	*
<i>Chaerephon pumilus</i>	848	0.368	0.000	*	1155.568	0.0001	*
<u>Urban area</u>							
<i>Pseudoromicia principis</i>	111	0.441	0.000	*	101.494	0.0001	*
<i>Chaerephon pumilus</i>	206	0.139	0.019	*	112.776	0.0001	*

2.5. Temporal overlap variation of *Hipposideros ruber* and *Chaerephon pumilus* between São Tomé and Príncipe

The overlap coefficient ($\Delta 4$) of *H. ruber* between São Tomé and Príncipe forests was 0.43 (Figure 6). In the case of São Tomé, the species exhibited a bimodal activity pattern with both diurnal and nocturnal activity. The species showed two distinct peaks, with the first peak occurring around 3 PM, followed by a decrease in activity until the second peak, which occurred near sunrise (Figure 6). However, in Príncipe, *H. ruber* was largely nocturnal but with a similarly bimodal activity pattern. The first peak occurred soon after sunset, with a slight decrease when approaching midnight, an abrupt decrease soon after midnight, and, when approaching the sunrise, a sharp increase in activity, leading to the specie’s highest peak of activity.

Hipposideros ruber

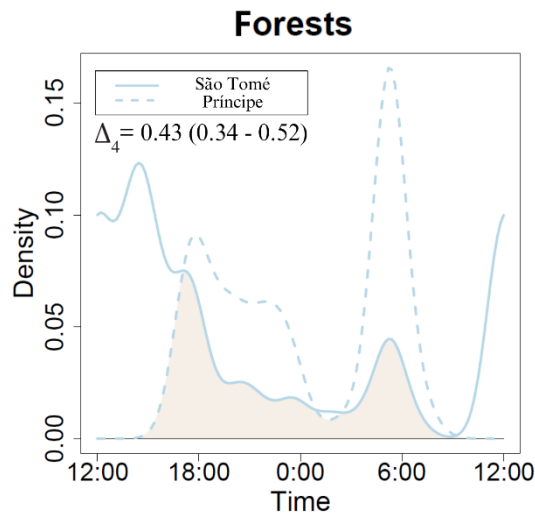


Figure 6 - Overlap of temporal activity patterns on São Tomé and Príncipe for *Hipposideros ruber* in forests.

The overlap coefficient (Δ_4) of *C. pumilus* between São Tomé and Príncipe in forests was 0.23 (Figure 7A), whereas in shade plantations (Figure 7B), agricultural areas (Figure 7C) and urban areas (Figure 7D) it was 0.60, 0.60 and 0.63, respectively.

Chaerephon pumilus

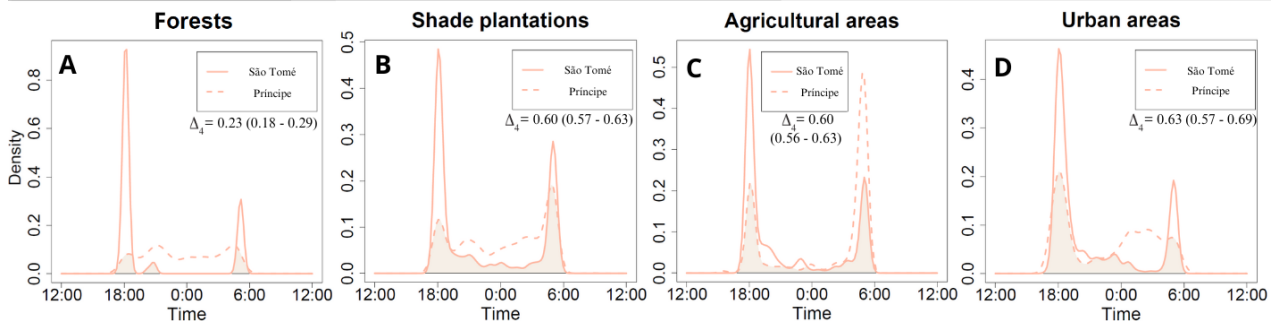


Figure 7 - Overlap of temporal activity patterns on São Tomé and Príncipe for *Chaerephon pumilus* in all habitat types common to both islands.

In forests, activity in São Tomé is concentrated around two peaks, while in Príncipe, the species' activity appears more evenly distributed throughout the night (Figure 7A). In shade plantations, while species' activity in São Tomé is mostly concentrated around peaks, with minimal activity during the remaining hours, in Príncipe, activity is also concentrated around peaks but with considerable more activity during the other periods of the night (Figure 7B). In agricultural areas, both islands show concentrated activity around two peaks. However, in São Tomé, the first peak near sunset is higher than the second peak near sunrise. Conversely, in Príncipe, the higher peak occurs near sunrise (Figure 7C). In urban areas, São Tomé exhibits more concentrated activity

around the peaks near sunset and sunrise. However, on Príncipe, activity increases after midnight and displays a more consistent pattern, tapering off near sunrise (Figure 7D).

Discussion

Human-induced habitat change is one of the conspicuous features of Anthropocene insular landscapes (Fernández-Palacios et al., 2021). Yet, behavioural responses to habitat change in island ecosystems remains poorly investigated as previous research mostly examined responses in terms of occupancy and abundance metrics. Here, we have used the tropical islands of São Tomé and Príncipe as case studies to evaluate the circadian rhythms of insectivorous bats across a gradient of native and anthropogenic habitats. We found that most species presented a bimodal activity pattern, with within-species differences in activity patterns being on average more contrasting between forests and agricultural and urban areas, than between old-growth and shade plantations. At the assemblage level temporal overlap varied considerably across the different habitats of both islands. However, assembly-wise patterns of temporal overlap across habitat types were island-specific, with old-growth presenting the greatest degree of overlap in São Tomé, but the lowest one in Príncipe. Likewise, the activity patterns of the two species studied in both islands varied between the same habitat types of São Tomé and Príncipe with *Hipposideros ruber* presenting diurnal activity only in the former.

Assemblage-level temporal overlap across habitat types

The temporal activity patterns of insectivorous bats are known to exhibit significant variability (Fenton et al., 1977; Rocha et al., 2020), influenced by factors such as food availability, moonlight, cloud and canopy cover and interspecific competition (Appel et al., 2019; Meyer et al., 2004; Rivero-Monteagudo & Mena, 2023; Vásquez et al., 2020).

In São Tomé, but not so much in Príncipe, we noted a potential reliance on time partitioning as a mechanism for coexistence. For instance, in the shade plantations of São Tomé, we detected a temporal overlap coefficient of 0.36 vs 0.77 in Príncipe, whereas in forests these values were 0.28 and 0.83 respectively for São Tomé and Príncipe. Lower overlap coefficients suggest that species co-occurring in each habitat exhibit differing activity peaks, possibly to mitigate interspecific competition (Delaval et al., 2005; Fern et al., 2018; Kronfeld-Schor & Dayan, 2003). The differences found for

the more species-rich habitats of São Tomé, in relation to the same habitat types in the nearby island of Príncipe, aligns with the notion that in environments with greater species diversity, time partitioning emerges as a strategy to alleviate competitive pressures (Adams & Thibault, 2006; Razgour et al., 2011). Príncipe is home to only four species of insectivorous bats, whereas in São Tomé seven are currently known (Rainho et al., 2022). This lower species diversity in Príncipe may translate into reduced interspecific competition for food or roosting sites, thus leading to a less pronounced reliance on time partitioning. However, in Príncipe, the low overlap coefficient in agricultural areas (0.47) suggests that time partitioning might be a factor influencing temporal coexistence in this habitat for the two species detected.

In São Tomé, we observed evidence of potential time partitioning. Habitats with fewer highly active species (three species each in oil palm plantations, agricultural areas, and urban areas) exhibited higher temporal coefficient overlaps (0.70, 0.61, and 0.57, respectively) compared to habitats with more highly active species (four species each in forests and shade plantations), which had coefficient overlaps of 0.28 and 0.36, respectively. This aligns with the findings of Razgour et al. (2011) and Adams and Thibault (2006), who demonstrated that sometimes, with the presence of competitors, insectivorous bat species may shift their activity peaks. On Príncipe, forests, shade plantations, and urban areas displayed higher overlap coefficients (0.83, 0.77, and 0.75, respectively), significantly differing from the lower overlap coefficient observed in agricultural areas (0.47). Given that the active species are consistent across all habitats, competition may not be the driving factor behind these overlap coefficients on this island. Instead, the lower coefficient could be attributed to differences in prey availability, leading to less similarity in activity patterns.

Species-specific temporal overlap across habitat types

Human activities can significantly impact wildlife behaviour, leading some species to adjust their activity patterns in a habitat-specific manner, modulated by factors such as prey availability, predation risk (Appel et al., 2023) or competition (Adams & Thibault, 2006). Bats, being nocturnal, are especially impacted by artificial light at night (Stone et al., 2015). These light-induced behavioural shifts alter the spatial and temporal activity patterns of bats. Light-sensitive species tend to avoid illuminated areas, leaving these resources available for more light-tolerant species (Rowse et al., 2016). In São Tomé, we observed a significant difference in activity patterns for the species *M. newtoni* between forests and urban areas. This aligns with previous findings that urban

environments pose unique challenges and opportunities compared to natural forest settings (Jung & Threlfall, 2016). This can be possibly explained by prey availability. If prey is scarce, this species may need to sustain a uniform level of activity throughout the night to meet its nutritional needs. Given that urban areas are open habitats, this species might be disadvantaged when competing with *C. tomensis* and *C. pumilus*, which, as molossids, are specialized foragers in such environments (Avila-Flores et al., 2023). This competition could further drive *M. newtoni* to forage in a more continuous manner throughout the night. Conversely, another plausible explanation is that this species could be targeting insect species that remain active and abundant throughout the entire night. This constant activity might serve to lower intraspecific competition in these areas. In forests, *M. newtoni* starts its activity earlier and ends it later compared to other habitats. This aligns with the observations of Russo et al. (2007), who noted that bats in closed canopy habitats tend to initiate activity earlier than those in open habitats. Even in the absence of prevalent predators, this pattern may persist, as observed in these bats. In closed canopy habitats, bats may extend their period of activity because the canopy darkens the environment. Conversely, as a clutter-edge species, foraging success in forests may be more challenging. This could require an adjustment in its active period to capture more prey, either to compensate for interspecific competition or to overcome its lower adaptability to forage in cluttered environments. This might lead to extended foraging periods to meet its nutritional needs.

For *C. pumilus* in São Tomé, the activity pattern in oil palm plantations differs significantly from that in forests. This shift could be due to reduced prey availability in oil palm plantations. Forest conversion to oil palm plantations results in biodiversity loss (Koh & Wilcove, 2008), impacting arthropods negatively in terms of abundance and composition (Alonso-Rodríguez et al., 2017), as higher management intensity and changes in landscape structure in agricultural areas are linked to lower arthropod species richness (Hendrickx et al., 2007). Given that *C. pumilus* belongs to the Molossidae family and is better adapted to open spaces (Russo & Ancillotto, 2015), the increase in human disturbance may not alter its activity pattern as much as more forest-associated species, as reflected by the similar overlap coefficients observed in shade plantations, agricultural areas, and urban areas (0.70, 0.70, 0.65, respectively). The activity patterns of *M. thomensis* in forests and shade plantations highly overlap, indicating a substantial similarity. This can be attributed to the presence of only two nocturnal raptors on the island, one of which (*Tyto alba thomensis*), favours open areas

(Melo et al., 2022), resulting in similar predation pressures in both habitats. Moreover, this species belongs to Hipposideridae family, which is typically associated with forested environments. Additionally, the comparable canopy cover in both habitats (Table S 1) further contributes to this pattern similarity.

In Príncipe, *C. pumilus* exhibits a distinct activity pattern in agricultural areas compared to forests. Presley et al. (2009a) also observed differing activity patterns in these habitat types. Unlike our findings, the bats avoided flying during twilight in agricultural areas due to high predation risk from diurnal predators. In our case, the predator is nocturnal, but similar to Presley et al. (2009a), *C. pumilus* may have adjusted its activity pattern in agricultural areas to minimize predation risk, which is higher in open habitats than in forests. Therefore, the species shows two activity peaks during twilight periods, with reduced activity throughout the rest of the night in agricultural areas, as opposed to a more evenly distributed activity in forests. As an open-space forager without specialization for clutter-edge areas like forests and shade plantations, this species might face a disadvantage in capturing prey while flying in more cluttered environments and require increased activity throughout the night to meet its nutritional needs in forests and shade plantations. Consequently, the activity patterns in these habitats (forests and shade plantations) overlap to a greater extent. For *P. principis*, the most distinct activity pattern from the one observed in forests was found in urban areas. The patterns observed in shade plantations and agricultural areas more closely resembled those of forests, supported by the high overlap coefficient. The bats that belong to Vespertilionidae, as is the case of this species, can easily adapt to urban areas (Ancillotto et al., 2015; Ferreira et al., 2022; Russo & Ancillotto, 2015; Tomassini et al., 2014). However, it is important to note that the sampled forests sites were not too far from disturbed habitats. This is a limitation of the study design due to restricted access in the southern part of the island, where extensive forests are located.

Differences in bat activity patterns between the islands of São Tomé and Príncipe

There is a notable contrast in the activity patterns of *H. ruber* on the forests of the island of São Tomé and the island of Príncipe, supported by the low overlap coefficient (0.43). Bats are typically nocturnal, primarily to evade predation by diurnal bird predators (Speakman, 1990, 1991). Therefore, the detected diurnal activity in *H. ruber* in São Tomé, previously reported by Russo et al. (2011) is a somewhat unusual behaviour, even for insular bats. This diurnal activity in São Tomé is likely due to the

absence of effective diurnal aerial predators (e.g., hawks and falcons; de Lima & Melo, 2021) on this island (Russo et al., 2011). On the other hand, and despite the similar lack of diurnal aerial predators on Príncipe (de Lima & Melo, 2021), *H. ruber* maintains its mostly nocturnal behaviour in this island, similar to its counterparts in the African mainland (Nkrumah et al., 2016). The contrast might also stem from the higher species diversity on São Tomé compared to Príncipe. In response, these bats may have shifted their activity to daytime as a strategy to avoid predators and reduce competition. This behavioural distinction holds significant implications for *H. ruber's* conservation, potentially indicating specialized ecological roles or adaptations specific to each island's environment. Further studies probing into the drivers of these behavioural disparities and their implications for the species' ecological niche and conservation status could provide invaluable insights for future conservation strategies. Understanding the reasons behind such distinct activity patterns — whether linked to the absence of diurnal predators, competition avoidance, prey availability, or a combination of factors — would be particularly enlightening.

In terms of *C. pumilus*, all habitats differ; however, with the exception of forests, all habitat types exhibit high temporal overlap coefficients. This difference between the two islands may be attributed to lower inter-specific competition for food resources on Príncipe compared to São Tomé. With fewer species competing for limited resources, *C. pumilus* may not have had as great a need to maximize prey capture early in the night (resulting in a peak at dusk, as observed in São Tomé). Instead, it may have distributed its feeding activity more evenly throughout the night.

Conclusion

While native habitats continue to be converted into human-use land at unprecedented rates (Millennium ecosystem assessment, 2005), our understanding of how biodiversity can cope with such changes remains limited, particularly in tropical ecosystems. Indeed, while most studies have focused on metrics quantifying biodiversity, relatively little attention has been paid to behavioural changes (Frey et al., 2017). In that regard, my study carried out in the endemic-rich islands of São Tomé and Príncipe suggested that insectivorous bats adapt their activity patterns across the gradient of increasing intensity of land-use change. In particular, we found that (i) temporal overlap within species assemblages varies considerably across different habitats on both islands, with island-specific patterns; (ii) most species exhibit a bimodal activity pattern, with more pronounced differences in activity patterns between forests and agricultural/urban

areas compared to forests and shade plantations; and (iii) the activity patterns of the studied species differ between equivalent habitats on the two islands, with *Hipposideros ruber* exhibiting diurnal activity only in São Tomé. These findings provide evidence that human-induced habitat change not only alters species diversity patterns but also influences the behavior of the remaining species. Nonetheless, it is important to acknowledge a potential limitation in our study, particularly in urban areas, where the sample size was relatively small on Príncipe and the additional absence of sampling sites in the southern part of this island. This reduced sample size may have introduced a bias into our results. Therefore, future studies should aim to address these challenges. Additionally, efforts should be made to gather information on other species that may not have been adequately detected in this study and assess their activity patterns. Another important area of study is understanding the insect species on which each insectivorous bat species preys upon. By conducting these investigations, we can gain a clearer understanding of the ecology of each bat species, ultimately leading to more effective conservation strategies.

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Attachments

VEGETATION STRUCTURE OF SÃO TOMÉ

Habitat type	C	T	VC
Old-growth forest	69.77 ± 16.29	22.05 ± 11.25	292.05 ± 42.93
Regrowth forest	70.22 ± 18.80	20.96 ± 11.44	265.43 ± 43.39
Shade plantation	44.09 ± 22.55	5.70 ± 4.22	156.66 ± 36.07
Oil palm plantation	50.50 ± 15.38	0.05 ± 0.22	143.00 ± 29.44
Agricultural area	20.78 ± 22.14	3.65 ± 4.23	104.99 ± 46.47
Urban area	14.00 ± 14.45	3.69 ± 2.53	42.46 ± 18.06

Table S 1 – Vegetation structure of São Tomé. Abbreviations: C – canopy cover; T – number of trees; VC – vegetation cover.

VEGETATION STRUCTURE OF PRÍNCIPE

Habitat type	C	T	VC
Old-growth forest	85.42 ± 7.53	11.67 ± 3.55	210.41 ± 43.03
Regrowth forest	80.00 ± 9.26	10.00 ± 7.79	158.34 ± 35.69
Shade plantation	49.67 ± 25.03	6.33 ± 5.11	123.99 ± 38.00
Agricultural area	22.50 ± 20.85	4.00 ± 4.14	108.0 ± 39.67
Urban area	47.50 ± 67.18	5.00 ± 7.07	25.0 ± 17.33

Table S 2 - Vegetation structure of Príncipe. Abbreviations: C – canopy cover; T – number of trees; VC – vegetation cover.