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Habitat use and diel activity of insectivorous bats across land-cover types on an Afrotropical oceanic island

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Abstract

Tropical island biodiversity is declining at alarming rates. Yet, understanding how species are coping with such disturbance remains limited for Afrotropical islands. Here, we examined habitat use and diel activity of insectivorous bats across different land-cover types covering the endemic-rich Princípe Island, Central West Africa. We acoustically surveyed insectivorous bats across 48 sites throughout old-growth forests, secondary re-growth forests, cocoa shaded plantations, and horticultures. Based on 17,527 bat passes, we were able to record all four insectivorous bat species known to occur on Princípe, including the recently described *Pseudoromicia principis*, the most frequently recorded species. *Taphozous mauritianus*, a data deficient open-space forager, was the least recorded species. Overall, insectivorous bat activity was comparable across secondary re-growth forests, cocoa shaded plantations, and horticultural areas. Although overall activity was lower in old-growth forests, *Hipposideros ruber*—a forest specialist—was found exclusively in old-growth and secondary re-growth forests. Diel activity patterns of *Mops pumilus* varied between forests and non-forest habitats, whereas those of *P. principis* remained similar. Inter-specific activity overlap decreased towards more altered land-cover types. Our findings emphasize that conserving the remaining forests, along with the current mosaic of land-cover types, is needed to maintain Príncipe's complete insectivorous bat assemblages.

KEYWORDS

Chiroptera, endemic species, Gulf of Guinea, human-modified landscapes, land-use change, passive acoustic monitoring, São Tomé and Princípe, tropical forests

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1 | INTRODUCTION

Land-use change is the primary driver of biodiversity loss worldwide (Caro et al., 2022). This is especially concerning in the humid tropics, where deforestation—primarily due to agricultural expansion—continues to erode vast tracts of native habitat in the most rich biodiverse locations (Hansen et al., 2020). The situation is even more critical on tropical oceanic islands, as their often high levels of endemism (Fernández-Palacios et al., 2021), greater physical and behavioral specialization among species (Kier et al., 2009), and heightened exposure to natural hazards (Gonçalves, Farooq, et al., 2024) make their unique biota particularly vulnerable to habitat disturbance.

The effects of land-use change on biodiversity can be complex, depending on both the intrinsic species traits (Newbold et al., 2016) and the degree of structural and compositional change in relation to the baseline habitat (Barlow et al., 2007). Following anthropogenic disturbance, while some disturbance-sensitive species might undergo extinction (Palmeirim et al., 2017), the persisting species can adjust their habitat use and behavior in the novel environmental conditions (Mazza et al., 2020; Tranquillo et al., 2023). More profoundly altered habitats also tend to have more contrasting conditions, including variations in resource availability, microclimate, light duration (e.g., increased exposure in newly open areas), human presence, shifts in species composition (Fletcher Jr et al., 2024), and greater inter- and intraspecific competition (Monterroso et al., 2014). These factors might synergistically act to promote species changes in habitat use (Ferreira et al., 2022). Similarly, species diel activity is also affected by such physical and biological factors (Abrahams et al., 2025; Ikeda et al., 2016), which are typically altered following human-induced disturbance in the environment, thereby affecting species diel activity patterns. For instance, in more open habitats with higher light duration, nocturnal species might delay their activity (Russo et al., 2007). Likewise, temporal partitioning in human-disturbed habitats where fewer competing species co-exist might allow for lower interspecific competition (Lambert et al., 2018). Understanding how species cope with land-use change remains a cornerstone to outline evidence-based management actions, which is not trivial given the accelerated pace of land-use change across tropical islands (Wood et al., 2017).

On oceanic islands, bats often comprise the only native mammal species (Nóbrega et al., 2023), with ca. 25% of all bat species occurring on islands being island-endemics (Conenna et al., 2017). Despite the high conservation concern of insular bats, bat responses to land-use change have rarely been explored on Afrotropical islands (but see e.g., Kemp et al., 2019 and Mandl et al., 2022). Overall, bat responses to land-use change are typically driven by features such as their diet, morphology, behavior, and echolocation call characteristics (Davies et al., 2016; Núñez et al., 2019; Wordley et al., 2017). In aerial insectivorous bats, echolocation characteristics are intrinsically linked to their habitat affinities and foraging strategies, and according to those, aerial insectivorous bats are often categorized into three main foraging guilds: forest, edge, and open-space foragers (Schnitzler & Kalko, 2001; Yoh et al., 2022). Forest foragers, which emit long constant frequency (CF) calls or very short, broadband frequency-modulated (FM) calls, are generally the most vulnerable to land-use changes that reduce habitat clutter (Rowley et al., 2024). In contrast, edge foragers use quasi-constant frequency (QCF) or combined FM–QCF calls, while open-space foragers typically emit low-frequency FM–QCF calls with a narrow FM component followed by a long QCF element (Hazard et al., 2023). As such, edge forager bats might benefit from the creation of edges, while open-area forager bats might benefit from the removal of the tridimensionality habitat complexity (López-Bosch et al., 2021; Mendes & Srbek-Araujo, 2021). In addition, some bat species are particularly adaptable to human-altered environments, often taking advantage of buildings, bridges, and other structures as alternative roost sites (López-Baucells et al., 2017). Examples of such synanthropic species include *Mops pumilus*, an open-space forager that has been associated with anthropogenic structures such as houses, churches, and warehouses, which provide suitable roosting sites in the absence of natural cavities on the Afrotropical São Tomé Island (Rainho et al., 2010).

In the Atlantic coast of Central Africa, Príncipe Island (139 km^2) is part of the Cameroon volcanic line in the so-called Gulf of Guinea (Ceríaco, Santos, Lima, et al., 2022). Despite the relatively short distance from mainland Africa (220 km), it remained isolated throughout its geological history, possibly starting approximately 31 Ma years ago (Ceríaco, Santos, Viegas, et al., 2022). As a result, Príncipe is characterized by exceptional levels of endemism, including eight endemic bird species (29% of the native species), three of amphibians (100%), eight of reptiles (67%) and two of mammals (29%) (Ceríaco, Santos, Viegas, et al., 2022). The island has been permanently colonized by humans since the 15th century, and ca. 25% of its area remains covered by old-growth forests (Dauby et al., 2022). The rest of the island consists of a mosaic of land-cover types, dominated by abandoned plantations that have regenerated into secondary re-growth forests, shaded cocoa plantations, small horticulture holdings, and urban areas (Dauby et al., 2022). Nonetheless, despite the island's relevance for conservation and its high degree of anthropogenic influence, the impacts of land-use change on Príncipe's native fauna remain largely unexplored (but see Dallimer & King, 2008 and Rebelo et al., 2024). Yet, in São Tomé Island, within the same archipelago and partially overlapping in its bat fauna, insectivorous bat activity—including the activity of forest foragers—and species richness were higher on human-altered land-cover types (Castro-Fernandes et al., 2025). In addition, changes in diel activity patterns in relation to old-growth forests were more substantial in habitats with greater structural contrast to forests (Araújo-Fernandes et al., 2025).

In this study, we use a space-for-time approach to unveil the responses of insectivorous bats to historical land-use changes. To do so, we examine how insectivorous bats utilize the various land-cover types across the endemic-rich Príncipe Island—a comparatively small but older island compared to the nearby oceanic São Tomé Island (Ceríaco, Santos, Lima, et al., 2022). The island's insectivorous bat assemblage is composed of four species: *Hipposideros ruber* (a Hipposideridae and forest forager), *Pseudoromicia principis* (an endemic Vespertilionidae and edge forager recently described by Juste et al., 2023), *Mops pumilus* (formerly *Chaerephon pumilus*; a Molossidae and open-space forager), and *Taphozous mauritianus* (an Emballonuridae and open-space forager) (Rainho et al., 2022). Specifically, we analyzed habitat use and diel activity patterns of each species across the island's four predominant land-cover types: old-growth forests, secondary re-growth forests, cocoa shaded plantations, and horticultures. Given the diversity of foraging preferences among Príncipe's insectivorous bats, we expected considerable changes in species composition between land-cover types due to species-specific responses. As observed in São Tomé Island (Castro-Fernandes et al., 2025), we anticipate *H. ruber* to be mostly associated with forested land-covers, while the remaining species are likely to exhibit higher activity in more altered land-covers such as horticultures, where synanthropic species are likely to benefit from human-associated foraging and roosting resources (López-Baucells et al., 2017; Russo & Ancillotto, 2015). We further expected diel activity patterns to vary most between forested habitats and horticultures, given structural contrast between these habitats, likely resulting in differing light conditions and arthropod diversity (Araújo-Fernandes et al., 2025; Montaño-Centellas et al., 2015; Presley et al., 2009). Within the same land-cover, overlap in interspecific bat activity is expected to be lower in land-covers where multi-species activity is higher, comprising a temporal partitioning strategy to reduce interspecific competition (Lambert et al., 2018). We note that different echolocation calls have different detection ranges, that is, higher frequencies have shorter detection ranges, and more complex habitats further reduce detectability (Russo et al., 2018). Therefore, we additionally anticipate old-growth forests will have lower detection ranges for *H. ruber* and *P. principis* than secondary re-growth and other land-use types. Given this limitation and restricted sampling (see sections 2.2 and 4.1), results for this habitat type should be interpreted with caution.

2 | METHODS

2.1 | Study area

The study was conducted on Príncipe Island, one of the two main islands comprising the Democratic Republic of São Tomé and Príncipe, off the western equatorial coast of Central Africa (Figure 1). With a human population of ca. 8,000 people, Príncipe Island experiences an average annual temperature of 26°C, with minor fluctuations between coastal and mountainous regions (highest point at 948 m a.s.l). The average annual precipitation ranges from 1000 mm in the northeast to around 3000 mm in the south (Ceríaco, Santos, Lima, et al., 2022).

Príncipe Island is covered by old-growth forests (ca. 32% of the island area), re-growth forests (ca. 27%), agricultural areas including shaded plantations and horticultures (altogether accounting for ca. 30%) and, to a lesser extent, urban areas (ca.9%) (Soares, 2019). Old-growth forests comprise the least disturbed land cover, composed of native forest vegetation. While old-growth forest may have experienced alterations in the past, these areas are now largely characterized by known human intervention and mostly located within the limits of the Ôbo Natural Park, a significant conservation area covering 65 km^2 (46% of the island's area). Secondary re-growth forests largely result from re-growth following the abandonment of cocoa plantations and, despite being dominated by native vegetation, include the presence of introduced tree species (e.g., *Annona reticulata*, *Pachira aquatica*, *Cinnamomum verum*, and *Mangifera indica*; Figueiredo et al., 2011). Part of these forests is also within the limits of the Natural Park. Shaded plantations comprise agroforestry systems where (mostly) cocoa grows under the canopy of predominantly exotic trees. Horticultures refer to small-holding fields growing banana, cassava, carrots, and tomatoes, among others.

2.2 | Acoustic surveys

Insectivorous bats were acoustically surveyed across 48 sampling sites: 11 sites in old-growth forests, 13 in

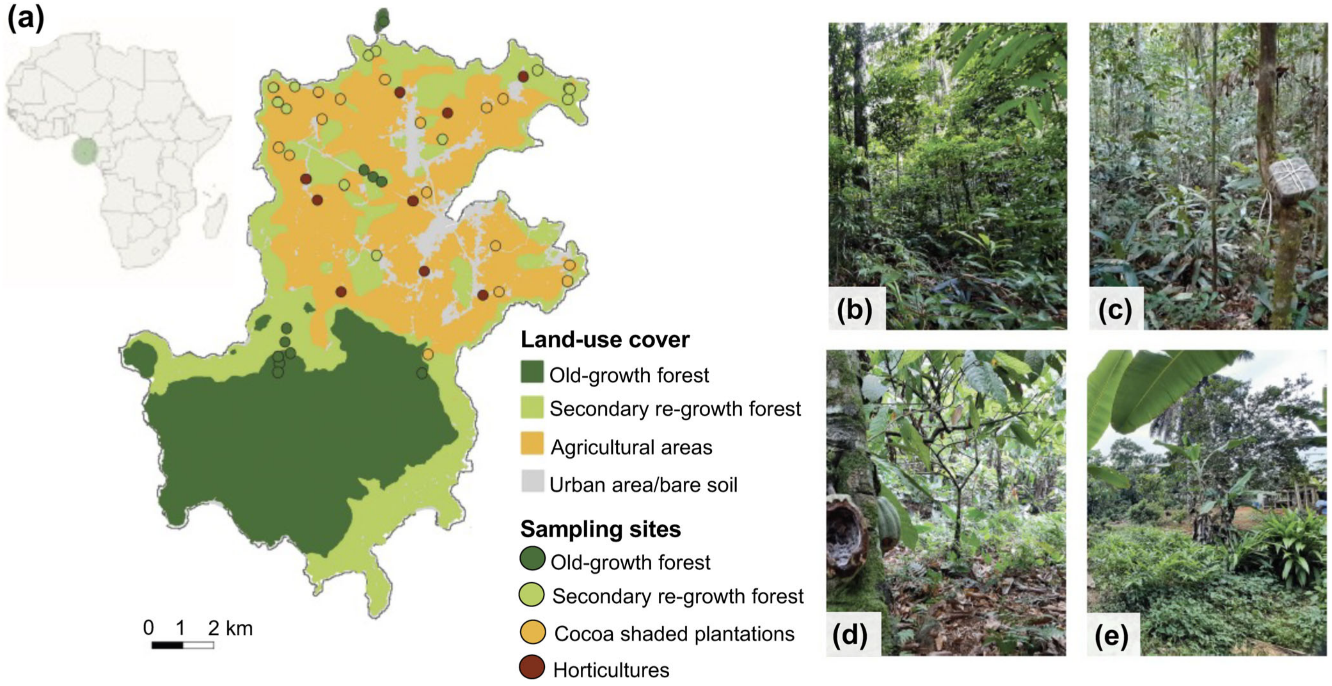

FIGURE 1 (a) Sampling sites across Princípe Island, West Central Africa. Each of the 48 sampling sites is color-coded according to the land-cover type: (b) old-growth forest, (c) secondary re-growth forest, (d) cocoa shaded plantation, and (e) horticultures. Land-cover types shown in this map were adapted from Soares (2019). Agricultural areas include both cocoa shaded plantations and horticultures.

secondary re-growth forests, 15 in cocoa shaded plantations, and nine in horticultures (Figure 1). Sampling occurred between the 1st and the 11th of August 2022. Between two and 12 sites spatially closer were simultaneously sampled (see detailed information on the sampling sites and data collected in Palmeirim et al., 2024). This period was selected to avoid heavy rain during the surveys, which have the potential to impact both bat activity and the performance of the recorders. The sampling site location aimed to cover as much area of the island as possible. However, due to difficulties in accessing more remote areas, sampling for old-growth forests was geographically restricted (Figure 1). Following López-Baucells et al. (2021) and Sugai et al. (2019), recommending at least 200 to 300 m spacing between detectors in tropical forests to reduce overlap of detection ranges, sampling sites were at least 250 m apart from each other. As used in previous studies (e.g., Ferreira et al., 2022; Mullin et al., 2020), this spacing between sampling sites, additionally boosted by the altitudinal differences in the rough terrain, aimed to minimize simultaneously recording the same individual bats. Each sampling site was surveyed using one AudioMoth acoustic device (Hill et al., 2018), which was attached to a tree trunk at ~2 m height. Therefore, our survey focuses on understory bat activity and may underestimate bat activity in the canopy for forested habitats. Acoustic devices were set to record 1 min every 5 min at a sample rate frequency of 384 kHz for 48 h including during the day as *H. ruber* is known to exhibit diurnal flight (Russo et al., 2011).

2.3 | Bioacoustic analysis

Bat activity was measured using a "bat pass", representing a sequence of two or more echolocation pulses emitted by a specific species within a five-second audio file (López-Baucells et al., 2019). The original 1-min recordings obtained from the acoustic devices were divided into five-second files using Kaleidoscope v.5.3.8 software (Wildlife Acoustics, USA). This division allowed for the isolation of files likely containing bat passes, while additional files were automatically sorted into a separate "noise" folder. To select files containing bat passes, specific signal detection parameters were established in Kaleidoscope. This included setting the detection range for frequencies between 8 and 250 kHz, and the minimum and maximum durations of detection pulses between 2 and 500 ms. The software was configured to consider a maximum inter-syllable gap of 500 ms, and a minimum of two pulses was required for detection. Because this noise filtering approach may lead to the under detection of low-intensity calls (Perea & Tena, 2020), we manually filtered all the noise files obtained in the old-growth forest sites. As we did not find bat pulses in the noise files of those sites, we did not go through the noise files regarding the remaining sampling sites.

Species were then identified by analyzing the characteristics of the echolocation call, namely the call shape, 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 regarding *P. principis* obtained from Juste et al. (2023). Species were manually identified using Kaleidoscope. Social calls and feeding buzzes were not identified to the species level and thus were not considered in this study.

2.4 | Data analysis

2.4.1 | Habitat use

Species activity was examined at the assemblage and species-specific levels, and it was given by the number of bat passes (Kunz et al., 2009). Species composition across the different land covers 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). We tested whether species composition varied between land covers using a Permutational Multivariate Analysis of Variance (PERMANOVA). Complementarily, we applied a Permutational Analysis of Multivariate Dispersions (PERMDISP) to compare the dispersion in species composition between land covers. These analyses were carried out using the *vegan* R package (Oksanen et al., 2013).

To examine the effects of land covers and altitude on overall bat species activity and species-specific activity, we applied Generalized Linear Mixed-effects Models (GLMMs), using the *lme4* R package (Bates et al., 2015). A random term indicating the date the sampling site had been surveyed was used to account for natural variability in bat activity between sampling sites spatially closer, including any pseudo-replication effect arising from recording the same individual in adjacent sampling sites, which have been simultaneously sampled, in addition to climate conditions (e.g., rain and wind). Altitude was standardized to a mean of zero and a standard deviation of one. The distribution family used in each model varied according to the response variable: Poisson for overall activity and negative binomial for *P. principis*, *M. pumilus*, and *H. ruber*, while *T. mauritianus* was only detected in three sites and so excluded from subsequent analysis. We further examined the residuals of each model using the *DHARMa* R package (Hartig, 2022).

2.4.2 | Diel activity patterns

To assess diel activity patterns, the number of bat passes recorded per species per land-cover type was summed for each hour. Following the recommendations of Lashley et al. (2018), to ensure robust data representation, only species detected in at least 10% of the surveyed nights with a minimum of 100 independent detections per land-cover type were considered in subsequent analysis. As such, we were not able to include *T. mauritianus* nor *H. ruber*. The low number of bat detections in old-growth forests precluded us from including this land-cover type separately. Alternatively, following Rocha et al. (2020) and Araújo-Fernandes et al. (2025), we merged old-growth forests and re-growth forests in the diel activity pattern analysis. The old-growth forests and re-growth forests represented relatively similar canopy cover (mean ± SD: 85.42 ± 7.53% in old-growth forests and 80.00 ± 9.26% in secondary re-growth forests; Table S1), and only minor differences in the diel activity patterns would be expected between the two land-cover types. When old-growth forests and re-growth forests are considered together, we refer to them simply as "overall forests".

We used circular statistics that required converting time data into a radian scale, spanning from 0 (0) to 24 h (2π). To visualize diel activity patterns and subsequently calculate the overlap coefficients, we employed Kernel density functions. To do so, we used a smoothing parameter for Kernel density estimation (i.e., $k_{\max}$) with a value of "three" (Ridout & Linkie, 2009; Rivero-Monteagudo & Mena, 2023). This value is known for robust estimates in both unimodal and bimodal activity distributions. We further applied an adjustment factor of one for bandwidth scalar adjustment. These parameters interact to determine the width of the Kernel used for density estimation and later pattern display. The careful choice of $k_{\max}$ and adjustment is crucial to accurately represent underlying patterns while avoiding undue influence from noise or over-smoothing (Rivero-Monteagudo & Mena, 2023).

We then estimated overlap coefficients (Δ) that quantified (1) overlap between intraspecific activity between overall forest and the remaining land-cover types, and (2) overlap between interspecific species activity within the same land-cover. We considered three options of overlap coefficients, namely Dhat1 ($\Delta1$), Dhat4 ($\Delta4$), and Dhat5 ($\Delta5$), each with distinct overlap measurement methods. Following Ridout and Linkie (2009), we selected Dhat4 due to its more consistent performance across sample sizes. This overlap coefficient ranged from

0, meaning no overlap in diel species activity, to 1, indicating complete overlap. The confidence intervals with 95% certainty were estimated using the bootstrap technique with 9999 resamples (Ridout & Linkie, 2009). For these calculations, we used the *overlap* R package (Meredith & Ridout, 2014). To ascertain whether the two activity sets under comparison originated from identical distributions, we conducted a probability test using the 'compareCkern' function from the *Activity* package (Rowcliffe et al., 2014). All analyses were performed in R 4.1.2 software (R Core Team, 2022).

3 | RESULTS

We recorded a total of 17,527 bat-passes from four species: the endemic edge-forager *Pseudoromicia principis* was the most detected species (15,165 bat-passes, 86.42%), followed by the open-space forager *Mops pumilus* (2307 bat-passes, 13.16%), the forest forager *Hipposideros ruber* (48 detections, 0.27%), while *Taphozous mauritianus* was the least detected (7 detections, 0.04%). The two species *Pseudoromicia principis* and *Mops pumilus* were present in the four land-cover types surveyed, while *H. ruber* was restricted to either old-growth or secondary re-growth forest (Figure 2a). As *T. mauritianus* was only detected in three sites within shaded plantations (Figure 2a), this species was not included in subsequent analyses.

3.1 | Habitat use

Species composition was similar across land-cover types (Figure 2b and Table S2). Despite the apparent lower variation in species composition in horticultures, no differences in the species composition dispersion were observed (Figure 2b and Table S2). Overall, there was no difference in overall bat activity (Figure 3a and Table S4) or for the most detected species, *P. principis* (Figure 3b and Tables S3 and S4), across secondary re-growth forests, cocoa shaded plantations, and horticultures. However, we detected lower bat activity overall in old-growth forests compared to the other habitat types (Table S3). The activity of the open-space forager *M. pumilus* was lower in both forest types (old-growth and re-growth forests) compared to either shaded plantations or horticultures (Figure 3c and Tables S3 and S4). Lastly, *H. ruber* was similarly active in both land-use types where it was recorded, namely: old-growth and secondary re-growth forests (Figure 3d and Tables S3 and S4). Altitude had no effect on overall activity or any species-specific bat activity (Table S3).

3.2 | Activity patterns

Species-specific activity patterns varied between forest and human-altered land covers differently for *P. principis* and *M. pumilus* (Figure 4). Indeed, the overlap in the activity of *P. principis* between overall forests (i.e., considering together

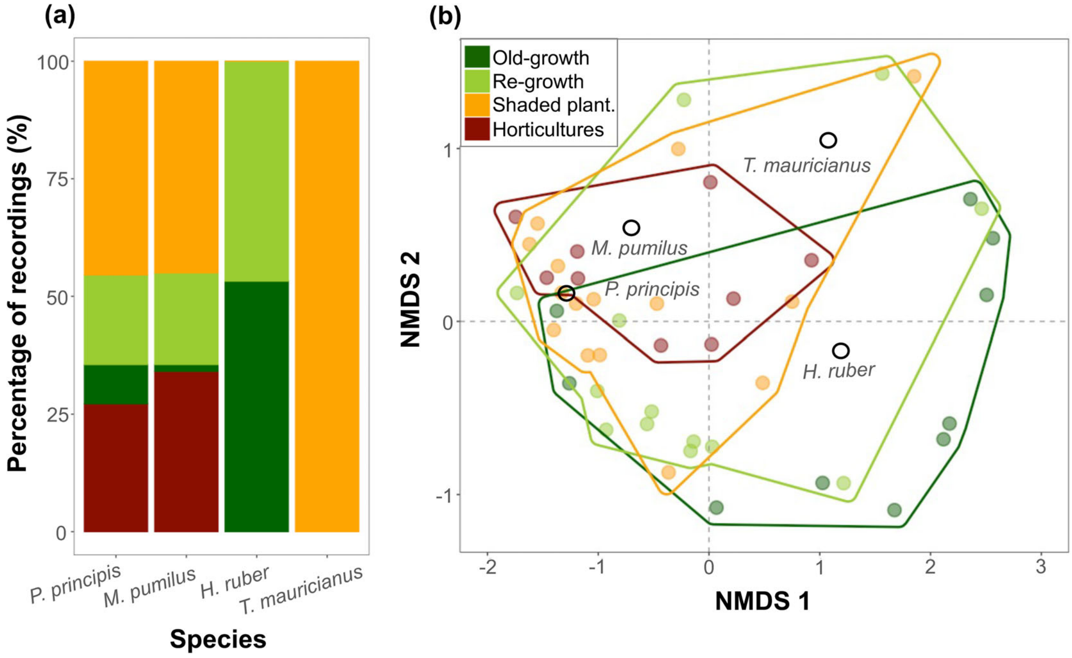

FIGURE 2 (a) Proportion (%) of the number of records for each of the four insectivorous bat species (i.e., *Pseudoromicia principis, Mops pumilus, Hipposideros ruber and Taphozous mauritianus*) recorded across the 48 sampling sites surveyed across all four major land-cover types in Príncipe: Old-growth forest, re-growth forest, cocoa-shaded plantations, and horticultures. (b) Non-Metric Multi-Dimensional Scaling (NMDS) ordination plot denoting both sampling sites and species. In (b), sampling sites are represented by circles, color-coded according to land-cover type.

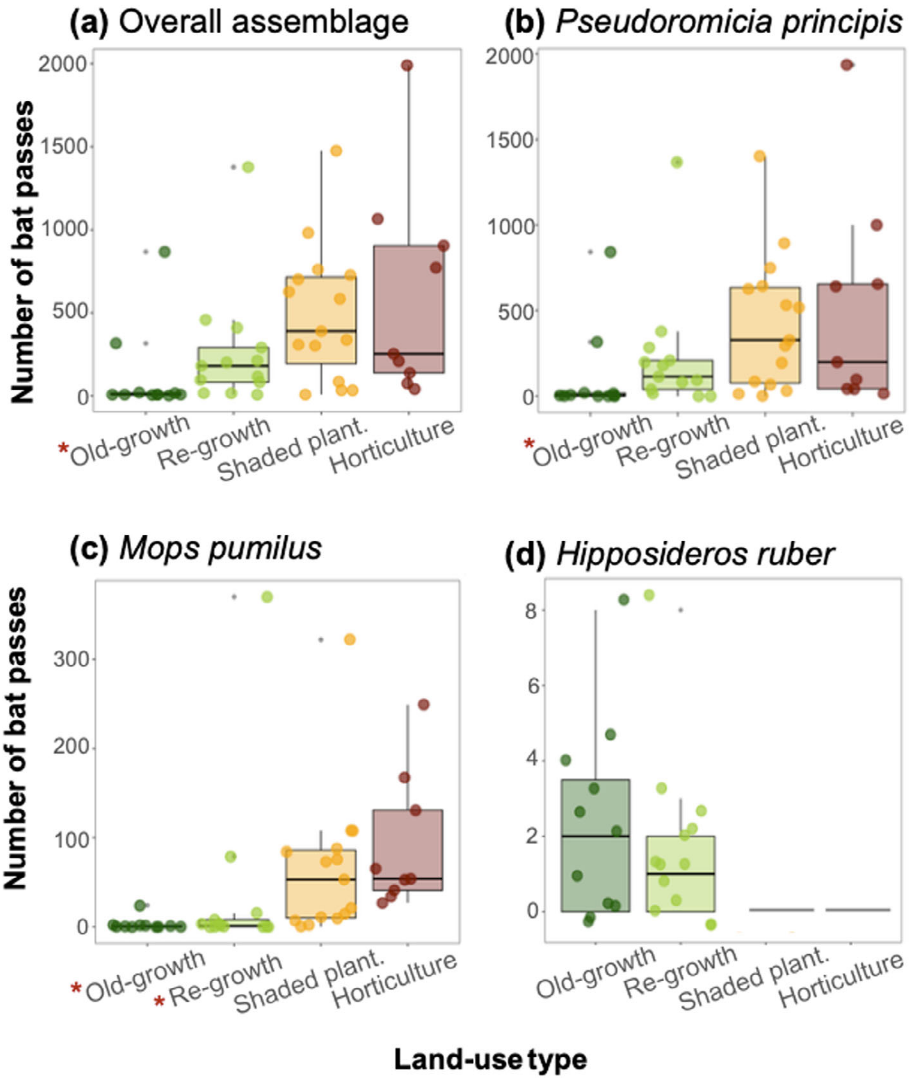

FIGURE 3 (a) Overall bat activity and species-specific activity of (b) *Pseudoromicia principis*, (c) *Mops pumilus*, and (d) *Hipposideros ruber* as denoted by the number of bat passes recorded across each of the four major land-cover types in Príncipe: Old-growth forest, re-growth forest, cocoa shaded plantations, and horticultures. Red asterisks indicate land-cover types with a significantly lower number of bat passes in relation to the remaining land-cover types.

old-growth and secondary re-growth forests) and shaded plantations was as high as 0.94 (0.92–0.96) (Figure 4a) and 0.90 (0.88–0.91) between overall forests and horticultures (Figure 4b). On the contrary, the overlap in the activity of *M. pumilus* decreased from 0.80 (0.76–0.85) between overall forests and shaded plantations (Figure 4c) to 0.44 (0.40–0.48) when considering overall forests and horticultures. In horticultures, *M. pumilus* presented two sharp activity peaks at dusk and dawn (Figure 4d). Diel activity tended to be more uniform in forests. Overall, forests had the highest overlap in activity across species with an overlap of 0.84 (0.80–0.88) (Figure 5a), which decreased to 0.73 (0.70–0.76) (Figure 5b) in shaded plantations and to 0.47 (0.45–0.50) in horticultures (Figure 5c).

4 | DISCUSSION

The exceptionally high biodiversity on islands, including a disproportionate number of threatened species (Ricketts et al., 2005), makes understanding the effects of land-use change in insular ecosystems critical to averting the ongoing defaunation crisis (Fernández-Palacios et al., 2021). The current lack of knowledge is particularly acute on Afrotropical islands (Conenna et al., 2017; de Lima et al., 2011), many of which—such as the ones located in the Gulf of Guinea—host exceptional levels of endemicity. Princípe Island's bats were found to have rather species-specific responses to the different land-cover types. The forest forager *H. ruber* was exclusively found in forested habitats, highlighting the importance of these habitats for specialist species. In contrast, *P. principis*, *M. pumilus*, and *T. mauritianus* were predominantly detected in shaded plantations and horticultural areas, indicating a greater flexibility in habitat use. The endemic *P. principis* exhibited little variation in diel activity patterns across land-cover types, whereas the diel activity patterns of *M. pumilus* varied between forests and non-forest land-covers. This suggests that although both

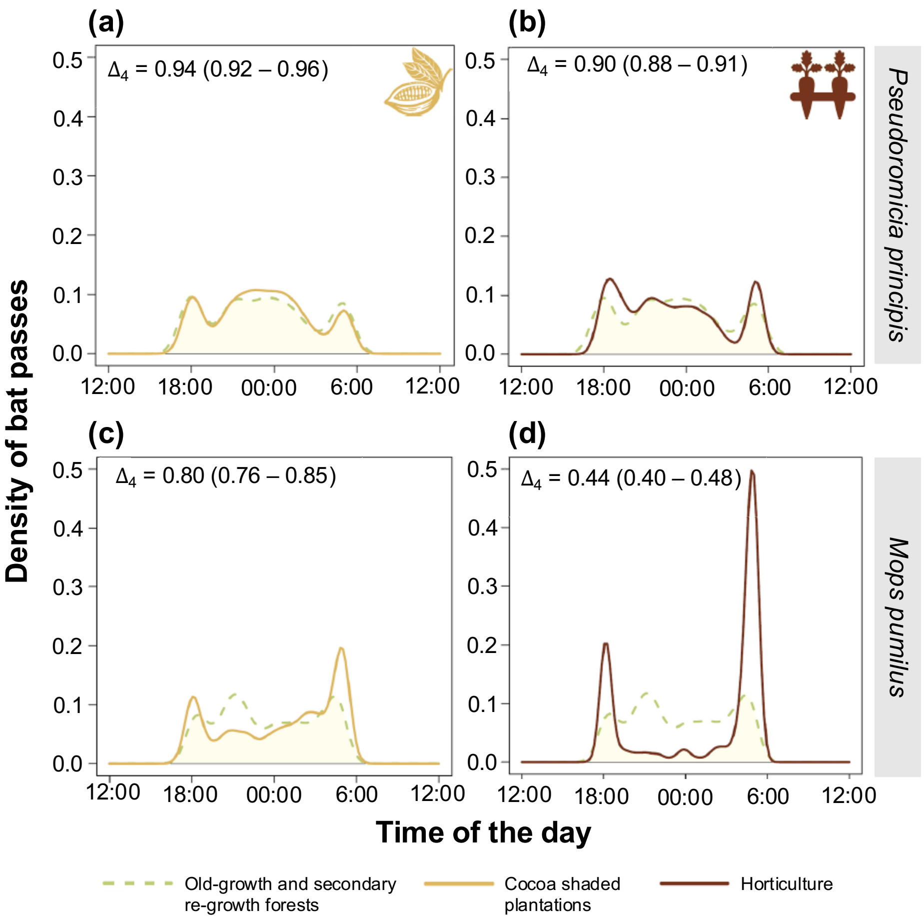

FIGURE 4 Comparison of the diel activity patterns of (a–b) *Pseudoromicia principis*, (c–d) *Mops pumilus*, between (a, c) forests (including old-growth and secondary re-growth forests) and cocoa shaded plantations, and between (b, d) forests and horticultures. For each comparison, the overlap coefficient and its confidence intervals are provided. All *p*-values testing the probability that two or more distributions deriving from the same distribution were below 0.001.

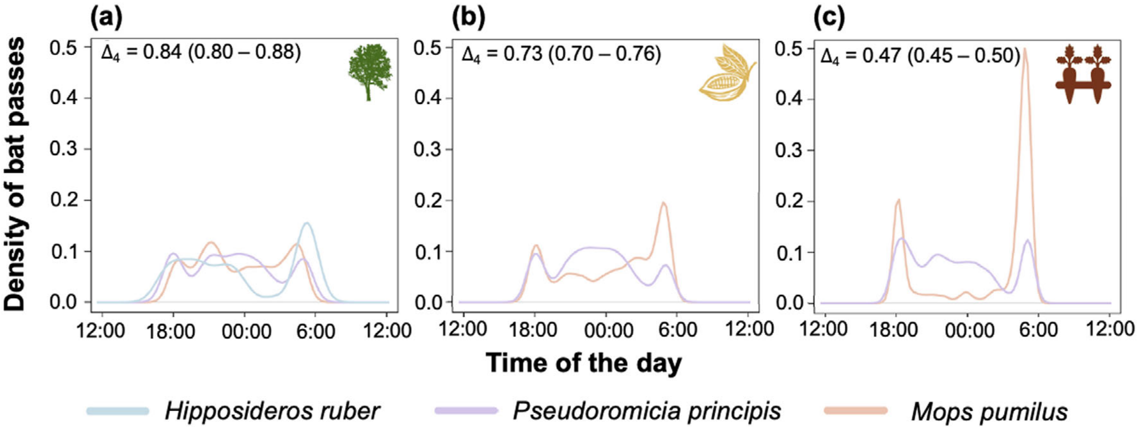

FIGURE 5 Comparison of the diel activity patterns of the species co-existing in each land-cover type, including (a) forests (including both old-growth and secondary re-growth forests), (b) cocoa shaded plantations, and (c) horticultures. For each comparison, the overlap coefficient and its confidence intervals are provided. All *p*-value testing the probability that two or more distributions deriving from the same distribution were below 0.001. Due to the low number of records, *Hipposiderus ruber* diel activity is presented in (a) but it was excluded from the analysis.

species have similar levels of activity across the habitats, their habitat use may diverge due to specificities associated, for example, to foraging, roosting, or dissimilar predation risks.

4.1 | Habitat use

The two most abundant species we detected, *P. principis* and *M. pumilus*, were mainly recorded in cocoa-shaded plantations and horticultures. Both species are well-adapted to exploit resources in more open spaces, but are less able to forage in structurally complex vegetation characteristic of mature forest. While several studies have reported negative effects of habitat modification on island bats (e.g., Davies et al., 2016; Ferreira et al., 2022; Moseley et al., 2022), our findings are consistent with those observed for insectivorous bat assemblages in the nearby São Tomé Island, where overall activity was higher in the same non-forest land-cover types (Castro-Fernandes et al., 2025). Likewise, a higher species richness and abundance of (non-endemic) birds (de Lima et al., 2013; Soares et al., 2020), as well as a higher abundance of amphibians (Strauß et al., 2018), were also reported for the anthropized habitats of São Tomé and elsewhere across the tropics (e.g., Kemp et al., 2019; Silva-Souza et al., 2022). Therefore, human modification may be negative for some species, while also creating opportunities for other species. For example, secondary re-growth forests are broadly characterized by the presence of fruiting trees, which might boost overall insect availability and increase prey for *P. principis* and *M. pumilus*. Further research is needed to assess activity in relation to prey availability across these landscapes.

As already observed on São Tomé Island (Castro-Fernandes et al., 2025), shaded plantations and horticultures exhibited the highest activity of insectivorous bats. Shaded plantations, resembling agroforests, involve cocoa cultivation beneath the canopy of predominantly exotic trees (de Lima et al. 2013). Horticultures consist mainly of smallholding fields, typically forming heterogeneous mosaics of diverse crops such as banana, pineapple, and cassava. Both habitat types are characterized by low-intensity management, with minimal to no use of pesticides or fertilizers. Organic management practices are known to benefit arthropods, eventually contributing to a reasonable prey availability for insectivorous bats (Williams-Guillén et al., 2016). The molossid *M. pumilus* is particularly well adapted to fly in open areas due to the high aspect ratio (long and narrow) of its wings (Jung and Kalko, 2011) and, as a result, broadly benefits from some less structurally complex habitat types (Russo and Ancillotto, 2015). In fact, molossids often tend to comprise the most recorded bats in horticultures (Kemp et al., 2019). This species adaptability to humanized habitats might further relate to their roost plasticity ranging from house roofs to tree cavities, palm leaves, and rocky crevices (Rainho et al., 2022). Molossids are known to play an important role as suppressors of agricultural pests (e.g., Wanger et al., 2014); thus, *M. pumilus* may be benefiting from an increased abundance of pest arthropods in the island's agricultural matrix.

The Princípe endemic *P. principis* is known to be relatively abundant in forest, horticultures, and urban areas (Rainho et al., 2022). This small vespertilionid is an edge forager—a guild that is typically flexible in its foraging and echolocation behavior, frequently switching between open and clutter-edge habitats (Fenton, Fenton et al., 1990). It is likely that these characteristics enable *P. principis* to thrive, not only along forest edges, but also in human-altered land covers, thereby explaining its island-wide distribution.

The open-space forager *T. mauritianus* was only recorded seven times in three sites located within shaded plantations. Despite being relatively rare on Princípe, this species is not known to be highly sensitive to land-use change. Noteworthy, although an efficient island colonizer (Bonaccorso, 2019), the presence of *T. mauritianus* was only recently confirmed in Princípe (Rainho et al., 2022).

The forest forager *H. ruber* was restricted to both old-growth and secondary re-growth forests (but see Rainho et al., 2022). Forest specialists, such as *H. ruber*, tend to have short, broad wings and emit high-frequency, broadband echolocation calls, which attenuate quickly but offer more detailed information—traits that are particularly well-suited for navigating and hunting in cluttered environments (Denzinger and Schnitzler, 2013; Mande et al., 2023). These specializations, along with additional life-history traits (e.g., reliance on tree roosts), mean these species are unable to persist in non-forest habitats. Therefore, for *H. ruber* to persist, it is vital to preserve both old-growth and secondary re-growth forests—the two land-cover types where the species was detected.

An important caveat to our findings is that bat calls are harder to detect in cluttered environments (Duchamp et al., 2006), which might have also contributed to the lower overall bat activity recorded in both old-growth and secondary re-growth forests compared to more open habitats. Similarly, higher frequency calls attenuate more quickly than lower frequency calls, therefore reducing the detectability of forest specialist species two-fold (Russo et al., 2018). Another consideration is vertical stratification exhibited across species (see e.g., Marques et al., 2016; Yoh et al., 2022). *M. pumilus* forages above the tree canopy (Duchamp et al., 2006), which might have impacted the species' detection in forest sites as we deployed detectors solely in the understory. In addition, due to logistic constraints, the south of the Island—covered by old-growth forest—was not surveyed in this study. While it is possible that additional surveys in the south of the island might allow a more solid view on the old-growth use by insectivorous bats, we note that the findings of this study—regarding general activity responses to habitat cover—were in line with those reported for the nearby São Tomé Island (Castro-Fernandes et al., 2025).

4.2 | Diel activity patterns

While *P. principis* maintained similar uniform diel activity patterns across overall forests (i.e., including both old-growth and secondary re-growth forests) and non-forest habitats, *M. pumilus* differed from uniform diel activity in overall forests to a diel activity characterized by dusk and dawn peaks in non-forested habitats, most pronounced in horticultures. The dusk and dawn activity peaks of *Mops pumilus* in horticultural areas may reflect responses to variations in light levels (Russo et al., 2007) or arthropod diversity and activity (Montaño-Centellas et al., 2015; Presley et al., 2009). Alternatively, these patterns could reflect its synanthropic associations. Horticultural areas are often located near human settlements, and since *M. pumilus* frequently roosts in anthropogenic structures (Rainho et al., 2022), the elevated activity at these times may correspond to patterns of roost emergence and return.

Interspecific competition typically intensifies in more species-rich habitats, potentially leading to temporal displacement in habitat use as a mechanism to reduce niche overlap (Lambert et al., 2018). Based on this, we expected lower temporal overlap among species in forests and shaded plantations, due to greater species diversity. However, our findings revealed the opposite pattern: greater temporal overlap occurred in the more species-rich forests and shaded cocoa plantations, and overlap was lower in horticultural areas. This differs from patterns in the nearby island of São Tomé—in which overlap was lowest in forest and greater in palm oil plantations (a habitat not present in Princípe) and horticultural areas (Araújo-Fernandes et al., 2025)—and might suggest that either interspecific competition might be avoided due to mechanisms other than temporal partitioning, for example, differences in prey preferences (Gonçalves, Nóbrega, et al., 2024) or that it is not required due to sufficient prey availability. Future research should therefore aim to disentangle the diet composition and prey availability across habitats to better understand the mechanisms facilitating bat coexistence on the island. Noteworthy, bats might vary their activity patterns between old-growth and secondary re-growth forests, which we could not analyze due to limited bat records from old-growth forests. As such, our results are likely to more strongly reflect the diel activity patterns for secondary re-growth forests, and we thus urge caution when interpreting these results.

Furthermore, we did not observe any diurnal activity of *H. ruber* on Princípe during our study period. This contrasts with findings from São Tomé, where the species is largely active during both the day and night (Araújo-Fernandes et al., 2025; Rainho et al., 2022; Russo et al., 2011). Both islands lack specialized diurnal avian bat predators; thus, this disparity in behavior is rather intriguing and requires further study as it might signal more significant population-level differences.

4.3 | Implications for conservation

Forest conversion into working landscapes is a major driver of the contemporary biodiversity crisis (Caro et al., 2022)—particularly for oceanic islands (Fernández-Palacios et al., 2021). On Princípe, where only 25% of the old-growth forest cover persists (Dauby et al., 2022), the extant insectivorous bat fauna is persisting under the current land-cover configuration. To sustain current bat activity levels, conservation efforts must prioritize the protection and restoration of old-growth and re-growth forests. Indeed, the forest forager *H. ruber* was restricted to both old-growth and secondary re-growth forests, emphasizing the role forested habitats play in preserving island-wide integrity of bat assemblages. We also recommend promoting biodiversity-friendly agricultural practices by continuing the use of established low-intensity management practices. In addition, given the particularly high activity of insectivorous bats in both shaded plantations and small-holdings horticultures, we highlight the need to understand their potential role as pest suppressors (Ferreira et al., 2023; Kemp et al., 2019). In summary, preserving a mosaic of land-cover types that includes old-growth and secondary re-growth forests would help ensure the long-term survival of bat species in Princípe, a strategy that may also be effective on other human-populated tropical oceanic islands.

AUTHOR CONTRIBUTIONS

Ricardo Rocha, Patrícia Guedes, Yodiney Dos Santos, and João C. Alves collected the data; Ana Catarina Araújo-Fernandes and Ana Sofia Castro-Fernandes processed the acoustic data under the supervision of Natalie Yoh; Ana Filipa Palmeirim led the analysis and the writing, and all the co-authors contributed with comments and revisions to drafts of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The dataset on insectivorous bat records used in this study is available in Palmeirim et al. (Palmeirim et al., 2024); https://doi.org/10.3897/BDJ.12.e131955.

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