Temporal niche partitioning promoting a dynamic bat coexistence

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A - Research concept and design, B - Collection and/or assembly of data, C - Data analysis and interpretation, D - Writing the article, E - Critical revision of the article, F - Final approval of the article

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Abstract:
Temporal niche partitioning is a key evolutionary mechanism that facilitates species coexistence, yet knowledge gaps remain, particularly concerning nocturnal partitioning. We investigate nocturnal niche partitioning in a bat community along an altitudinal gradient by mist-netting bats over 151 nights across six years and 53 sampling sites. In total, 20 cooccurring species were detected with overlapping activity windows. Activity patterns were characterized by three main features: number of activity peaks, their timing, and intensity, which in turn shaped species composition throughout the night. Species sharing habitats (i.e. syntopic species, e.g. *M. bechsteinii*, *P. auritus* and *M. escalerai*) cooccur with up to 50%-60% temporal niche overlap. Other sympatric cryptic species (e.g., *M. myotis*/*blythii*) may exhibit higher temporal overlap if they show significant differences in foraging habitats or prey preferences. Temporal partitioning is affected by morphological traits, with larger species generally peaking later in the night, and by different responses to environmental factors. These include, for example, moon illumination or tree layer, which affect predation risk, resource availability (prey, roosts), and thermoregulation, which in turn reflect on activity patterns. This is the first study to describe nocturnal niche partitioning in an insectivorous bat community along an environmental gradient, providing a novel perspective into how behavioural traits and environmental factors shape species coexistence. This study shows that temporal niche partitioning across the night is an important complementary mechanism for sustaining diverse and dynamic bat communities.

Keywords: Niche overlap, Bat ecology, Activity patterns, Competitive exclusion, Environmental gradients.

Received: 2025-10-27
Revised: 2026-05-18
Accepted: 2026-06-01
Final review: 2026-04-10

Short title
Temporal niche partitioning and dynamic bat coexistence

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Abstract

Temporal niche partitioning is a key evolutionary mechanism that facilitates species coexistence, yet knowledge gaps remain, particularly concerning nocturnal partitioning. We investigate nocturnal niche partitioning in a bat community along an altitudinal gradient by mist-netting bats over 151 nights across six years and 53 sampling sites. In total, 20 cooccurring species were detected with overlapping activity windows. Activity patterns were characterized by three main features: number of activity peaks, their timing, and intensity, which in turn shaped species composition throughout the night. Species sharing habitats (i.e. syntopic species, e.g. *M. bechsteinii*, *P. auritus* and *M. escalerai*) cooccur with up to 50%-60% temporal niche overlap. Other sympatric cryptic species (e.g., *M. myotis/blythii*) may exhibit higher temporal overlap if they show significant differences in foraging habitats or prey preferences. Temporal partitioning is affected by morphological traits, with larger species generally peaking later in the night, and by different responses to environmental factors. These include, for example, moon illumination or tree layer, which affect predation risk, resource availability (prey, roosts), and thermoregulation, which in turn reflect on activity patterns. This is the first study to describe nocturnal niche partitioning in an insectivorous bat community along an environmental gradient, providing a novel perspective into how behavioural traits and environmental factors shape species coexistence. This study shows that temporal niche partitioning across the night is an important complementary mechanism for sustaining diverse and dynamic bat communities.

Keywords

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Introduction

The coexistence of competitor species poses challenges to the central Ecology theory whereby two species sharing a limiting resource cannot coexist indefinitely (Chesson, 2000;

Macarthur and Levins, 1967). Nevertheless, potentially competing species may coexist, primarily through niche partitioning, which enables them to exploit shared resources differently to reduce direct competition.

The concept of ecological niche partitioning has been the focus of sustained investigation since Darwin's time. A substantial body of research has employed a variety of models and empirical evidence to understand how species diversity is preserved (Chesson, 2000). Patterns of niche partition among co-existing sympatric species have been frequently observed in diverse ecological communities, from large terrestrial vertebrates (e.g. Shao et al., 2021), to epipelagic fish (e.g. Ceia et al., 2023), bumblebees (e.g. Scriven et al., 2016), and seabirds (e.g. Petalas et al., 2021).

Niche partitioning, by definition, is a mechanism that can take several forms, including resource, spatial, and temporal partitioning (Lange et al., 2021; Schoener, 1974). Resource partitioning refers to the use of different resources or subsets of a shared resource pool, such as prey of different sizes (Pianka, 1974; Shao et al., 2021). Spatial partitioning occurs when species exploit different areas within a habitat, as seen in seabird species that forage in distinct oceanic zones (Gulka et al., 2019). Temporal partitioning involves differences in activity patterns across time, whether daily, seasonally or even at broader temporal scales, allowing species to minimise competition by using shared resources at different times. For example, different mosquito species exhibit activity peaks at distinct times, thereby reducing competition for resources (Marini et al., 2017). Similar cases were reported, for example, among some felid species in Borneo carnivores, where clear temporal niche partitioning was observed between two sympatric felid species that share morphological and ecological similarities (Nakabayashi et al., 2021) or among vertebrate scavengers (Cunningham et al., 2019; Olea et al., 2022).

These partitioning strategies are not mutually exclusive; they often interact in complex and dynamic ways, promoting biodiversity and ecosystem stability (Chesson, 2000; Schoener, 1974; Wang et al., 2024). For example, ant and spider species combine spatial and temporal mechanisms when foraging at different times and on different branches of extrafloral nectary-bearing plants to reduce direct competition, despite occupying the same trophic level (Lange et al., 2021). Such behavioural flexibility highlights how species can coexist even within overlapping ecological niches (Dickson, 2012; Kalka et al., 2008).

Understanding how niche partitioning functions within the same trophic guild or ecological community is crucial for assessing species’ behavioural trade-offs, resource preferences and responses to environmental features. Temporal partitioning, in particular, must be interpreted in relation to the environmental conditions under which species interactions take place. Evidence suggests that variation in activity timing may be driven more by shared environmental responses than by interspecific competition (Kalyuzhny et al., 2019). Evaluating how environmental factors influence species’ presence and behaviour is key to uncovering the mechanisms that enable coexistence (Appel et al., 2017). Mountains offer exceptional conditions for studying species' resource exploitation patterns across environmental gradients. Their pronounced altitudinal stratification creates steep climatic and ecological gradients over relatively short distances, enabling the observation of ecological processes at multiple scales, while also supporting high concentrations of endemic species and providing critical refugia for lowland species threatened by anthropogenic climate change (Rahbek, Borregaard, Antonelli, et al., 2019). Accounting for approximately one-third of the terrestrial biodiversity (Spehn et al., 2011), mountain ecosystems encompass a wide range of vegetation types (Körner, 2004) and topographic features, resulting in highly diverse and dynamic biophysical environments. This strong climatic stratification (Jansen, 2002) provides an exceptional setting for testing ecological hypotheses, such as temporal niche partitioning of tabanid flies in montane cloud forests (e.g., Cárdenas, 2016), and diel and spatial niche partitioning of mesocarnivores along altitudinal gradients (Tsunoda et al., 2022).

In this context, insectivorous bats are a particularly compelling group for examining coexistence mechanisms, as they are globally distributed, occupy a high trophic level, and play essential roles in ecosystems, such as regulating insect populations (Dickson, 2012; Jones et al., 2009; Kalka et al., 2008). Given the growing impacts of anthropogenic pressures, including climate change (Mas et al., 2022), habitat degradation (Napal et al., 2013), and biodiversity loss (Rioux et al., 2022), it is increasingly important to understand the patterns of niche partitioning to predict species and community responses and to design effective conservation strategies. Although several insectivorous bat species are known to share habitats, most studies focus on resource-level, spatial, and acoustic space partitioning (Salinas-Ramos et al., 2020). In contrast, temporal niche partitioning, particularly in relation to daily patterns, has received less attention (Hickey et al., 1996; Mohan et al., 2021) even though it may be key to understanding how sympatric species avoid competition (Lear et al., 2021). For instance, Adams and Thibault (2006) demonstrated that certain bat species can adjust their drinking times according to the presence and abundance of competing bat species. Such behavioural flexibility helps reduce competition for key resources such as water, especially under stressful conditions. Moreover, in environmental limiting scenarios, bats' activity patterns may represent a balance between the selection of available resources and constraints imposed by competition (Razgour, Korine, et al., 2011). In a heterogeneous landscape, bat temporal activity can be influenced by multiple environmental axes, such as insect abundance and/or diversity over different habitats and time (Beilke et al., 2021). Insectivorous bats tend to forage during or after nocturnal insect activity peaks (Rydell et al., 1996), with strong variation across species due to prey availability, seasonality, habitat preferences, and interspecies interactions (Agosta et al., 2005; Jachowski et al., 2014; Kalcounis et al., 1999; Kunz, 1973; Razgour, Korine, et al., 2011). The approach used to identify bats' peak activity is not consensual because it depends on the environmental conditions of each case study (Adams et al., 2015). Some studies use arbitrary activity levels

(Broders, 2003; Brooks and Ford, 2005), activity plots (Hayes, 1997), the number of calls above a certain threshold (Gorresen et al., 2008) or at a certain percentile threshold (Adams et al., 2015; Mariton et al., 2023).

While most studies exploring temporal partitioning focus on seasonal or annual dynamics, fine-scale patterns, such as those during nocturnal activity, have received less attention. Progress has been made in understanding environmental influences on insectivorous bats (Appel et al., 2017, 2019; Raposeira et al., 2023), which exhibit evolutionary adaptations such as echolocation, thermoregulation and wing morphology, enabling bats to thrive in diverse environments (Fenton and Simmons, 2015; Noberg and Rayner, 1987; Ruf and Geiser, 2015). These adaptations highlight bats' ecological success. However, much remains to be understood about how bat species share or partition resources during the night in the same region, emphasising the need for further research into their ecological interactions and behavioural strategies.

In this study, we investigated fine-scale nightly activity patterns of Iberian insectivorous bat species across an environmental resource gradient in Portugal's central mountains. The bat activity patterns were assessed by capture sessions. We hypothesised that, during the species co-occurrence in their activity period (Raposeira et al., 2023), variation in activity patterns may be influenced by species-specific traits as body size and diet (Cano and Murillo-García, 2021; Jones and Rydell, 1994), as well as environmental factors (Raposeira et al., 2023), through which temporal niche partitioning plays an important role in promoting species coexistence. We addressed three main hypotheses: (1) cooccurring species exhibit different levels of overnight temporal activity overlap. (2) Temporal activity overlap varies among species pairs. (3) Biological and/or environmental factors mediate bat activity patterns, which reflect evolutionary strategies of temporal niche partitioning to favour species coexistence. We expect differences in peak activity patterns among species that occupy the same space simultaneously. Furthermore, we anticipate that morphological traits and environmental features influence temporal activity overlap, enabling species to exploit resources more effectively and minimizing competition.

Materials and Methods

Study area

The study was conducted in the Portuguese part of the Iberian Central Range (Serra da Estrela, Lousã, Malcata, Caramulo and Beira Baixa). This region is influenced by two major bioclimates: Temperate (colder and humid - north-south influence over the mountain chain) and Mediterranean (southeast-northwest influence over the mountain chain) (Jansen, 2002). The selected study area, which totals ca. 682 000 ha (maximum altitude 1993 m a.s.l.), encompasses a wide range of habitat diversity and biogeographical strata in a relatively small area (Fig. 1) (Raposeira et al., 2023).

Data collection

We carried out 151 capture nights at 53 sampling sites between May 2014 and October 2019 to cover the region’s diverse habitats and environmental gradient, with an altitudinal range of 357 - 1,978 m a.s.l. Thirty-three sites were sampled systematically across years and seasons to capture inter- and intra-annual environmental variability (mean distance between sampling sites: 3.88±3.68 km, minimum 0.57 km and maximum 55.13 km), while an additional 20 sites were sampled non-systematically (mean distance between sampling sites 9.76 ±14.61 km, minimum 1.11 km and maximum 13.28 km) to increase coverage for rarer species and habitats (Fig. 1). At each site, bats were captured with mist-nets that were set at the same locations. Bats were captured in free-flight using a series of individual mist-nets set with a cumulative total length of 142 m per site (height of each net 2.6 m and a mesh size of 3.81 cm), near water spots, foraging areas, and feeding perches (Raposeira et al., 2023), to cover the widest variety of activity zones. At each sampling site, an arrangement of mist nets—triple-high, double, and/or single—was selected based on local conditions, ensuring a consistent total netting area of 369.2 m² per site per night. Each mist-net set consisted of a combination of individual nets of varying lengths (6–18 m) and heights (2.6–8 m) (Raposeira et al., 2023). Nets were opened at sunset and monitored every 20 minutes for at least the first five hours of activity, and were closed if no bats were captured during three consecutive checks (which means that each site/day was effectively sampled for at least 6 hours or until bat activity drastically declined). Mist-netting procedures followed the best-practice guidelines (Kurta et al., 1988; U.S. Fish and Wildlife Service, 2007; Weller et al., 2007; MacCarthy et al., 2006). However, the survey durations depended on weather conditions (Erickson and West, 2002). Bats were identified with the support of a morphological identification guide (Dietz and Helversen, 2004).

During bat trapping sessions, altitude was recorded using a GPS and temperature was measured at the beginning and end of each session with a Kestrel 3000-pocket weather meter. Night cooling was calculated as the difference between the initial and final temperature of the session. The tree layer was visually estimated as the percentage of trees taller than 2 m within a 200 m radius, following Raposeira et al. (2023). The forearm length of each bat was measured using a digital calliper.

Data analysis

The sampling unit in the analyses was the number of bats of a given species captured in each 20-minute interval, used as a proxy for bat activity, using the same netting effort across all sampling sites, from sunset to the end of activity. To analyse if cooccurring species exhibit different levels of overnight temporal activity overlap, we identified the most active period for each species. The time interval was defined as the time interval when captures reached ≥50% of the maximum number of captures per species and period unit (Adams et al. 2015). This threshold has been widely used in previous studies to identify peak drinking and foraging times and to evaluate temporal niche partitioning (e.g. Adams and Thibault, 2006; Lear et al., 2021; Swift, 1980).

To analyse if temporal activity overlap varies among species pairs, we calculated the proportion of peak activity overlap between species pairs across the study area, Kernel estimators were applied using the R package ‘overlap’ (Ridout and Linkie, 2009). Following Meredith and Ridout (2021), and based on the recommendations by Ridout and Linkie (2009), the choice of overlap estimator was determined by the size of the smaller of the two samples. Estimator $\widehat{\Delta}_1$ was used when the smallest sample was < 50, as it performs more reliably with small samples. Estimator$\widehat{\Delta}_4$ was used on the other cases as it provides better-adjusted estimates for larger samples. Confidence intervals (95%) (by bootstrap method to estimate standard errors) of the activity overlap between two species were generated using 10,000 new observations through ‘randomly resampling observations with replacement from the original sample’ (Meredith and Ridout, 2021). Species with overlap coefficients ≤0.3 were considered to have low overlap, while those with overlap ≥0.7 were classified as having high overlap. Although universal thresholds were not found for overlap coefficients, similar qualitative classifications have been applied in previous ecological studies to describe temporal segregation (Ridout & Linkie, 2009; Monterroso et al., 2014). These thresholds were not used as strict statistical cut-offs but rather as descriptive guidelines.

To assess whether phylogenetic relatedness influenced temporal overlap patterns, a Spearman rank correlation was computed between phylogenetic proximity and coefficient overlap, which revealed no such correlation (see *Supplementary information (SI)–Table S2,* Fig. *S2*). Phylogenetic proximity was not taken into account in all further analyses.

To evaluate the influence of environmental, morphological, and temporal variables on bat activity patterns at the community level, a Generalised Additive Mixed model (GAMM) was computed using the ‘mgcv’ package in R (Wood, 2017) . The time of bat capture after sunset was the response variable. Moon illumination, altitude, tree layer, night cooling and length of bat's forearm in interaction with species were the smoothed terms analysed. These environmental and morphological variables were selected because they have been previously shown to significantly influence bat activity, highlighting their relevance within the scope of this study (Appel et al., 2019; Noberg and Rayner, 1987; Raposeira et al., 2023). Year and sampling site type (water spot, foraging site and feeding perch) were included as random effects, and month as a cyclic smoothed term. Moon illumination was calculated considering cloud cover (TCC, %), following Pajot, et al. (2021). Cloud cover data were downloaded from Copernicus platform (https://cds.climate.copernicus.eu/) as NetCDF file, using 'ERA5 hourly data on single levels from 1959 to present' dataset, with a spatial resolution of 0.25° × 0.25° and temporal resolution of 1 hour (Hersbach et al., 2018).

To reduce multicollinearity among predictors, Spearman correlation analyses were performed between explanatory variables. Highly and moderately collinear variables ($|\rho|>0.4$) were excluded, retaining only those with the strongest statistical relevance for further analysis (*appendix SI* - Fig. S13). To determine the contribution of each predictor to the model, a likelihood ratio test was used to compar models with and without the predictor. Predictors with p-values ≤ 0.05 were considered significant and were included in the final model. Model selection was based on Akaike Information Criterion (AIC) and log-likelihood values. Due to the absence of temperature data before 2017, analyses of GAMM were restricted to the 2017–2019 interval. As a complementary analysis, Spearman rank correlations were computed between each environmental variable and bat activity (number of captures per each 20-minute sampling unit) for each species (*appendix SI* - Fig. S8 - S12). All statistical analyses were conducted in R 4.2.1 version (R Core Team, 2024).

Bat capture and handling followed all relevant guidelines and regulations and were approved by the Ethical committee at the ICNF (Instituto da Conservação da Natureza e das Florestas). This study was also carried out in compliance with the ARRIVE guidelines (https://arriveguidelines.org/).

Results

Over 859 hours (51,559 min.) of sampling, we captured 1,722 bats representing 20 species (Table 1). The number of captures per 20-minute session ranged from 1 to 17 individuals, with a mean and standard deviation of 2.25 ± 1.95 individuals per session. Species with fewer than five captured individuals (*Miniopterus schreibersii* and *Tadarida teniotis*) were excluded from subsequent analyses, since this small number of observations provides limited data to define activity patterns and ensure statistical robustness. Nights with only one species detected (19 nights across seven sites, representing 12.60% of the total) were also excluded, as they do not provide relevant information on species temporal cooccurrences.

Nocturnal niche partitioning

Regarding nocturnal activity, bat species exhibited distinct patterns, with varying numbers of activity peaks and, in some cases, limited overlap in peak activity times (Fig. 2). The number of peaks ranged widely, from a single peak (four species, e.g. *Myotis escalerai*) to six peaks (two species – *Myotis daubentonii* and *Plecotus auritus*). *Myotis escalerai*, *Myotis mystacinus*, *Pipistrellus pipistrellus* and *Eptesicus serotinus* showed a unimodal activity pattern, with one peak frequently occurring soon after sunset. *Myotis bechsteinii*, *Myotis emarginatus* and *Pipistrellus pygmaeus* displayed a bimodal pattern, while the remaining 13 species exhibited multimodal activity (Table 1 and Fig. 2).

Larger species (*Myotis myotis*, *Nyctalus lasiopterus*, *Nyctalus leisleri*, *Eptesicus serotinus*) generally reached their first peak starting at least 40 minutes after sunset, except for *Myotis blythii* and *Rhinolophus ferrumequinum* reached theirs earlier (Table 1 and Fig. 2). In general, smaller species (*Pipistrellus pipistrellus, Pipistrellus kuhlii, Hypsugo savii, Myotis mystacinus*) reached their first activity peak around 20 minutes after sunset.

Pipistrellus pipistrellus, *Pipistrellus pygmaeus, Pipistrellus kuhlii*, *Hypsugo savii*, *Rhinolophus euryale*, *Myotis escalerai*, and *Myotis mystacinus* were mostly active during the early part of the night (within the first 150 minutes after sunset) (Fig. 2). In contrast, *Myotis emarginatus*, *Plecotus auritus*, *Myotis daubentonii* and *Nyctalus leisleri* remained active over longer periods, with *M. emarginatus* activity peaking only around 500 minutes (~8h) after sunset. *M. emarginatus* was part of a small group of species with late activity peaks, alongside *Myotis bechsteinii and Rhinolophus hipposideros*.

Temporal overlap among species pairs

Of 190 potential species pairs, cooccurrence (i.e., species recorded on the same night and site) was confirmed for 158 pairs (83.2%). For most species, peak activity occurred during the first part of the night (0 - 360 min.; 18:00 – 00:00 GMT), except for *Myotis emarginatus*, whose highest peak occurred in the second part of the night (361 – 600 min.; 01:00 – 05:00 GMT) (Fig. 2). Among the 158 cooccurring pairs, only 28.5% (45 species pairs) were captured within the same 20 minutes period at the same site. The average temporal overlap between bat species was approximately 0.6, with minimum and maximum values of 0.1 and 0.9, respectively (Δ-overlap coefficient). Overall, 44.9 % of cooccurring species pairs (71 pairs) showed high overlap (Δ ≥0.7), while 17.7% (28 pairs) showed low overlap (Δ ≤ 0.3) (Table 2).

Myotis emarginatus showed the lowest overlap with other cooccurring species (15 species, Table 2, *appendix SI* -Table S1, Fig. S1). In addition, *Myotis bechsteinii* also exhibited a clear pattern of low overlap with two species, *Myotis escalerai* (Δ-0.3) and *Pipistrellus pipistrellus* (Δ-0.2). Similarly, *Rhinolophus hipposideros* displayed limited overlap with five species (*Rhinolophus euryale* (Δ-0.3), *Plecotus austriacus* (Δ-0.3), *P. pipistrellus* (Δ-0.1), *M. escalerai* (Δ-0.1) and *Eptesicus serotinus* (Δ-0.3)) (Fig. 2 and Table 2, *appendix SI* -Table S1, Fig. S1).

Among the remaining six species pairs with low activity overlap, two involved *Myotis escalerai* (with *Plecotus auritus* and *Nyctalus lasiopterus*, in addition to the previously mentioned associations with *R. hipposideros* and *Myotis bechsteinii*). *N. lasiopterus* also showed reduced overlap (in addition to *M. escalerai*) with *Pipistrellus pipistrellus* and *Hypsugo savii,* while *P. auritus* exhibited low overlap with *P. pipistrellus* and *Pipistrellus pygmaeus* (in addition to *M. escalerai*) (Table 2, *see SI* -Table S1, Fig.S1).

Biological and environmental factors

We tested the influence of biological and environmental variables on the presence of each species in 20-minute periods after sunset throughout the night in the overall study area. Across the study period, moon illumination ranged from 0 to 0.73, sampling site altitude from 386 to 1,978 m a.s.l., the tree layer from 0 to 98%, and night cooling from -4.50 to 11.30ºC (Table 1). All species were sampled during the main periods of their annual life cycle, between May and October (Raposeira et al., 2023).

The best-fitting model included the interaction between forearm length and species, moon illumination, altitude, tree layer, night cooling, and month of capture as smoothed terms (Table 3, *see appendix SI*– Fig.S13). All smoothed terms that were significant in the model were also influenced by moon illumination, month and night cooling. The interaction between forearm length (FA), used as a proxy for body size, and species showed a significant effect for *Eptesicus serotinus*, *Myotis daubentonii*, *M. emarginatus*, *M. mystacinus*, *Nyctalus leisleri*, *Plecotus auritus*, *Pipistrellus pipistrellus*, *Rhinolophus euryale*, *R. hipposideros, Hypsugo savii and Barbastella barbastellus*. This result highlights the role of morphological traits in shaping the timing of activity, with larger species tending to be active later and smaller species active earlier, responding differently to environmental conditions and ecological circumstances (*appendix SI* – e.g. Fig.S3, Table S3).

Beyond morphological traits, several environmental factors also influenced the timing and intensity of bat activity. At higher altitudes, bat activity extended later into the night *(appendix SI* - Fig. S4). This was evident for some species such as *Myotis daubentonii* and *Myotis escalerai (appendix SI* - Fig. S8).

Overall, increased moon illumination shifted bat community activity towards later nocturnal periods *(appendix SI* - Fig. S3). This pattern was significant for some species such as *Barbastella barbastellus, Myotis emarginatus* and *Myotis escalerai (appendix SI* - Fig. S10). Tree layer appeared to have the opposite effect: in more forested areas, bat activity was generally higher during the early part of the night and decreased as the night progressed *(appendix SI* - Fig. S5). However, this pattern was only statistically significant for *Rhinolophus euryale* and *Rhinolophus ferrumequinum* in Spearman correlation *(appendix SI* - Fig. S9). A similar pattern was observed in relation to night cooling, where greater night-time temperature decreases were generally associated with reduced activity throughout the night across the overall bat community (the only exceptions being *Barbastella barbastellus*, and *Rhinolophus hipposideros* (*appendix SI* - Fig. S7 and S11).

Activity patterns throughout the night also changed significantly along the season for several bat species, reflecting variations in environmental conditions and bats' biological cycle. Overall, bat activity tended to increase later in the night as the season progressed (August and September) (*appendix SI* – Fig. S6). Some examples of this were *Myotis daubentonii* and *Plecotus auritus* (*appendix SI* – Fig. S12). Finally, among the variables with random effects, the type of sampling site showed a small but significant contribution to explaining the model's variance.

Most bat species exhibited early-night activity peaks and moderate to high temporal overlap. However, several species—most notably *Myotis emarginatus*, *Myotis bechsteinii*, and *Rhinolophus hipposideros*—showed clear evidence of temporal partitioning, with reduced overlap relative to other species. Activity patterns also varied with body size, with larger species tending to peak later after sunset than smaller ones. Some species were mostly active during the early part of the night, while others kept active later into the night.

Discussion

Our study provides evidence that several bat species exhibit high temporal niche partitioning as a mechanism to reduce interspecific competition. Divergence in nocturnal peak activity was particularly clear in *Myotis emarginatus*, whose activity scarcely overlapped with any other species, strongly indicating temporal partitioning. In contrast, varying degrees of temporal overlap were observed among other species: *Rhinolophus hipposideros* overlapped with six species, *Pipistrellus pipistrellus* with five, *Myotis escalerai* and *Plecotus auritus* with four, and *Nyctalus lasiopterus* and *Myotis bechsteinii* with three. These differences reflect species-specific strategies for resource use. To our best knowledge, this is the first study to characterize nocturnal temporal niche partitioning within an insectivorous bat community across an environmental gradient, relating to potential species-specific behavioural traits, such as opportunism or caution. The observed patterns suggest that temporal partitioning is not random but shaped by the interplay of multiple factors. Behavioural mechanisms, combined with biophysical factors, competition, predation risk, and habitat characteristics, appear to mediate activity patterns and thus promote coexistence (Beilke, et al. 2021). Together, these findings support the hypothesis that temporal niche partitioning allows species sharing the same space to reduce competitive pressures, when necessary, while exploiting complementary ecological opportunities.

Nocturnal niche partitioning

The activity patterns identified in this study were characterized by three main features that differentiated species throughout the night: 1) the number of activity peaks, corresponding to three types of peak activity (unimodal, bimodal and multimodal), 2) the period of the night in which these peaks occurred, and 3) the intensity of each species activity peaks, in relation to other active species throughout the night. The combination of these features allows species to modulate their activity patterns in relation to biotic and abiotic drivers and to the other bat species. Consistent with previous studies, *Eptesicus serotinus* exhibited a unimodal activity pattern throughout the night (Catto et al., 1995; Mariton et al., 2023). However, some species, such as *Barbastella barbastellus*, showed a multimodal pattern, and *Pipistrellus pipistrellus* a unimodal pattern, contrary to what has been reported in other studies (Hillen et al., 2010; Mariton et al., 2023; Tillon, 2015). This may suggest that some species can shift their activity patterns according to the local environmental characteristics (e.g. prey availability, predation risk, competition or environmental conditions), beyond their energy needs.

Temporal overlap among species pairs

Previous studies have analysed the activity patterns of most species included in this study, highlighting diverse foraging behaviours and prey preferences (Jones and Rydell, 1994; Mariton et al., 2023). For instance, *Rhinolophus* sp. detects fluttering moths in narrow habitats, while narrow-space gleaners such as *Plecotus auritus*, *Myotis emarginatus*, *Myotis bechsteinii and Myotis escalerai* primarily feed on moths and flightless or diurnal arthropods. Edge-space gleaners like *Plecotus austriacus* forage mostly on moths, whereas trawlers such as *M. daubentonii* feed on arthropods over water. In contrast, aerial hawkers such as *Barbastella barbastellus*, *Pipistrellus kuhlii*, *Pipistrellus pipistrellus*, *Pipistrellus pygmaeus* and *Hypsugo savii* and also open space foragers like *Nyctalus leisleri*, *Eptesicus serotinus* (dipterians), and *Nyctalus lasiopterus* (moths and small birds) capture prey on the wing (Anderson and Racey, 1991; Novella-Fernandez et al., 2020; Rydell et al., 1996; Starik et al., 2021; Voigt et al., 2021). There are also studies describing the temporal partitioning among bats throughout the night as a mechanism for optimising resource exploitation and minimising interspecific competition (Adams and Thibault, 2006; Razgour, et al., 2011). The novelty of our study lies in the finding that temporal niche partitioning patterns vary depending on the cooccurring species and simultaneously on morphological and environmental factors.

Our results show that several syntopic species (those cooccurring at the same location and time) seem to avoid high temporal overlap (>50–60% of activity peaks). This pattern appeared to be more pronounced in forest-dwelling bats such as *Myotis bechsteinii*, *Barbastella barbastellus*, *Plecotus auritus* and *Myotis escalerai*, as well as in *Rhinolophus hipposideros* and *Rhinolophus euryale.* Such a pattern suggests that coexistence may be facilitated by fine-scale temporal niche partitioning, whereby species tolerate the presence of other syntopic species provided that activity peaks do not overlap to an extent that could intensify competition for prey resources. (Andreas et al., 2013; Hillen and Veith, 2013). These findings were consistent with previous studies demonstrating niche partitioning at the micro-scale of roost selection or prey type/percentage (Hillen and Veith, 2013; Novella-Fernandez et al., 2020). This suggests that temporal partitioning complements spatial and trophic differentiation as a mechanism to minimise competition in syntopy, similar to what has been observed in spiders and ants, that partition foraging space and time on the same extrafloral nectary-bearing plants (Lange et al., 2021).

In addition to partial temporal niche partitioning between the two syntopic narrow gleaners (*P. auritus* and *Myotis escalerai*), these species can share the same roosts and foraging habitats within the study area. Previous studies conducted within the same region reported differences in prey species between them, although both tend to favour similar prey orders (Lepidoptera, Diptera, Aracnedae) (Mata et al., 2021; Novella-Fernandez et al., 2020; Razgour, et al., 2011). Nevertheless, regional dietary variation is likely, particularly in the case of *M. escalerai*, which has shown regional differences in dietary patterns in the presence of its cryptic species *M. crypticus* (Novella-Fernandez et al., 2020).

The low temporal overlap between *Rhinolophus euryale* and *Rhinolophus hipposideros* suggests that these species also exhibit temporal niche partitioning, possibly as a consequence of their frequent occurrence along the same environmental gradient (Raposeira et al., 2023). This finding aligns with previous studies on trophic niche partition, although both species predominantly consume lepidoptera, *R. hipposideros* tends to feed predominantly on small moths, whereas *R. euryale* prefers medium-sized ones (Andreas et al., 2013). This indicates that these species may rely on multiple mechanisms (temporal, spatial, and trophic) to facilitate their coexistence.

When we compare sympatric cryptic species such as *Pipistrellus pipistrellus*/*P. pygmaeus*, *Plecotus auritus*/*P. austriacus* and *Myotis myotis*/*M. blythii* they showed no more than 50% overlap in their peak activity patterns except for *M. myotis*/*M. blythii,* which exhibited an 80% overlap. This might be explained by the level of partitioning in different niche axes, as despite their morphological similarity, these species pairs may differ in foraging habitats and prey preferences (Mckay, 2020). In the case of *P. pipistrellus*/*P. pygmaeus*, both consume Diptera (Barlow, 1997) but select different habitat types: *P. pipistrellus* uses a wide range of habitats, from deciduous woodlands to pasture, whereas *P. pygmaeus* preferentially forages in riparian habitats (Davidson-Watts and Jones, 2006). This aligns with our findings, as *P. pygmaeus* seems to use limited altitudinal, tree layer, and night cooling ranges, and does not tolerate moon luminosity as well as *P. pipistrellus*. Similarly, according to Razgour et al. (2011), *P. auritus* and *P. austriacus* show a large dietary overlap, but differ in their habitat preferences, with *P. austriacus* primarily associated with grasslands and *P. auritus* with woodlands. This highlights that temporal niche partitioning may become particularly important when spatial and/or dietary overlap is only partial. For *M. myotis/M. blythii* pair, previous studies suggest a limited overlap in both habitat use and diet, with *M. myotis* feeding mainly on Coleoptera in orchards, stream margins, and pastures and *M. blythii* on Orthoptera in grasslands, similar to patterns described for sympatric fish species (Arlettaz et al., 1997; Knickle and Rose, 2014). This suggests that high temporal overlap may occur when spatial or dietary divergences reduce competition, as reported in mixed colonies of *M. myotis/M. blythii* (Arlettaz et al., 1997).

The activity pattern of *Myotis emarginatus* was unique among the species analysed. Its limited temporal overlap with most other species was not explained by the variables included in this study. This pattern could be driven not by competitive exclusion but by co-evolution and adaptation to the activity rhythms of its preferred prey. For example, the stable fly *Stomoxys calcitrans*, which is documented as a preferential prey for *M. emarginatus* (Vallejo et al., 2019, 2023), may influence its activity peak (at the end of the night). However, the activity patterns of these insects also vary greatly (Schofield and Brady, 1996), which may depend on local or seasonal environmental conditions (Semelbauer et al., 2018). Further studies are needed to better understand this pattern.

In the case of *Nyctalus lasiopterus,* none of the three species with which it showed reduced temporal overlap (*Pipistrellus pipistrellus*, *Hypsugo savii* and *Myotis escalerai*), shares the same foraging strategy (Kipson et al. 2018, Novella-Fernandez et al. 2020, Popa-Lisseanu et al. 2009). Moreover, in most cases, they do not share the same prey preference, *P. pipistrellus* primarily feeds on Diptera, *H. savii* on Formicoidea and *M. escalerai* in Lepidoptera, suggesting limited overlap in insect prey (Kipson et al. 2018, Novella-Fernandez et al. 2020, Tobisch et al. 2025). Being an aerial-hawking species, *N. lasiopterus* preferably eats Lepidopterans and migratory songbirds (Smirnov and Vekhnik, 2013; Stidsholt et al., 2025). However, information remains scarce regarding interspecific interactions, mechanisms of coexistence, and species-specific behavioural traits that could explain the limited overlap observed.

Temperament of bat species, i.e., behavioural characteristics such as caution vs. opportunism, may also influence temporal niche partitioning; however, little is known about the topic. Evidence suggests that temperament differences can reflect in different predator-avoidance strategies, which are among the socioecological factors that more strongly shape behaviours (Sussman et al., 2013). For example, Sussman (2013) identified that rhesus macaques are more aggressive and unsociable in the presence of humans, long-tailed macaques are more cautious and fearful, and pigtailed macaques are more sociable with humans and less aggressive than the other species. In our results, the rare or inconspicuous species *Myotis bechsteinii* exhibited reduced temporal overlap with the more abundant *Pipistrellus pipistrellus*. This pattern may reflect behavioural adjustments in response to the presence of a dominant species. However, this interpretation should be treated with caution, as it may also be influenced by intraspecific variability or other ecological factors. Further studies are needed to confirm this pattern.

Biological and environmental factors

Differences between species regarding moon illumination, altitude and tree layer also suggest that environmental conditions influence each species differently. On the other hand, the combination of these environmental features at a given time can create opportunities for temporal and spatial niche differentiation. In addition to behavioural traits such as temperament, but also competition, prey preferences and their foraging behaviour (Jones and Rydell, 1994), it is documented that bat activity may also be differently influenced by moon illumination and cloud cover during the night (Appel et al., 2017), as well as by their morphological characteristics and biophysical preferences, particularly regarding altitude and tree layer, which are strongly associated to different habitat types (Raposeira et al., 2023).

Temporal niche partitioning is a dynamic process which varies among species, across different environmental conditions and throughout the night. There is no direct and exclusive correlation between temporal niche partitioning and phylogenetic relatedness, as temporal partition can be closely related to other forms of resource partitioning. Several interacting factors, such as biophysical conditions (e.g. temperature, moonlight), seasonal fluctuations in prey abundance, the biological cycle of the species and habitat preferences, can influence these patterns. Our findings indicate that bat activity is strongly influenced by temporal and environmental predictors. These results are consistent with the documented effects of lunar illumination on bat activity patterns and the importance of nocturnal temperature dynamics for insect prey abundance and bat energetic needs (Appel et al., 2017, 2019).

Our study revealed that the higher activity associated with moon illumination observed in some bats occurred during the latter part of the night. This pattern may be partly explained by a greater predation risk for bats earlier in the night, particularly under higher luminosity conditions, delaying bat activity as a predation avoidance strategy (Kelm et al., 2023). This could be relevant, for example, for *Myotis daubentonii, Myotis emarginatus* and *Rhinolophus euryale.* Regarding altitude, the fact that some bats increase their activity at higher elevations later in the night may reflect the location of their roosts at lower altitudes. These bats may require some time to reach higher areas, where insect abundance is likely greater, but roosts' availability is lower. This can be, for instance, the case of *Myotis daubentonii,* as also documented in Raposeira et al. (2023) for the same study area. As for the tree layer, the tendency of the bat community to be more active in forested areas during the early hours of the night may be related to the protection that dense vegetation provides against predators, particularly during the period of highest predator activity at the onset of the night (Kelm et al., 2023). However, only *Rhinolophus euryale* and *Rhinolophus ferrumequinum* showed this preference clearly.

During summer nights with moderate cooling, less cold-tolerant bats reduce or cease foraging due to increased thermoregulatory costs and decreased insect availability (Czenze et al., 2024; Fjelldal et al., 2023). *Myotis emarginatus* is one such example, having been documented as less tolerant to night cooling (Raposeira et al. 2023). However, this creates temporal niche opportunities for some bats (Downs et al., 2016; Russo and Jones, 2003; Toshkova et al., 2023), likely benefiting from reduced competition and access to cold-active prey (Dietz et al., 2009) as it is the case of *Barbastella barbastellus* (Górska et al., 2025). Together, these findings indicate that cold-tolerant bats can extend their foraging into cooler conditions, supporting the concept of temporal niche exploitation. Regarding the monthly pattern, the higher activity observed later in the night during June, August, and September may be related to seasonal aspects of the bats' biological cycle. In June, this increase could be associated with the need to obtain more food resources to support newborns, whereas in August and September, it may reflect the mating period (Raposeira et al., 2023).

Forearm length (FA) showed species-specific effects, highlighting the role of morphological traits in shaping the timing of activity, with larger and smaller species responding differently to environmental conditions and ecological opportunities. Larger species, being more conspicuous and visible to nocturnal predators, tend to begin their nightly activity later, avoiding the earliest hour when predator activity peaks and the risk of predation is highest, whereas smaller species can afford to be active earlier in the night. Beyond directly influencing bat behaviour, predation pressure may also act as a selective force shaping bat morphology, including traits such as body size and colouration (Horta et al., 2022).

Nevertheless, the observed patterns of temporal niche partitioning suggest that bat species within the community interact in response to environmental pressures and resource availability in their habitat. This balance of interactions with the environment is essential for maintaining overall biodiversity and promoting community stability by facilitating the coexistence of bat species. Without such coexistence mechanisms, some bat species could be driven to extinction by global stressors, including habitat homogenization, driven by land abandonment, wildfires, or biotic invasions.

Limitations and future directions

The mist netting survey method has inherent limitations, like any other method, as they sample only a fraction of the bat community (Flaquer et al., 2007; MacCarthy et al., 2006). Capture probability is not uniform across species and is strongly influenced by flight behaviour, echolocation abilities, habitat structure, and vertical space use. For instance, high-altitude, or net-avoiding species are typically underrepresented, whereas low-flying species are more frequently captured (O’Shea et al., 2003). However, previous studies have quantified mist-netting biases and detection probabilities. For instance, MacCarthy et al. (2006) reported that a considerable proportion of bats either avoided nets or escaped prior to checks. Therefore, our results should be interpreted as reflecting relative patterns of bat activity among captured individuals rather than absolute measures of species presence or absence. While detectability constraints may influence species representation, they are unlikely to obscure the general temporal patterns described here. Although bats were not individually marked, tissue samples were collected from all captured individuals for complementary analyses. The small biopsy mark on the wing membrane remained visible for at least one year, allowing the identification of previously sampled individuals. Consequently, bats recaptured during the same night were released without additional registration. Furthermore, considering that the healing time of a wing biopsy punch is approximately four weeks (Faure et al., 2009), it was also possible to infer whether a capture event had occurred recently based on the appearance of the biopsy mark.

Additionally, we were unable to account for the potential effect of roost proximity on capture times, since most roosts, particularly those of forest species, are unknown. It is possible that species roosting farther from the sampling sites arrived later in the night than those roosting nearby. However, this effect can be minimised by the extensive sampling across multiple nights, sites, and habitats. Nonetheless, future studies combining roost monitoring with temporal activity data would be valuable to disentangle this effect. Furthermore, our approach did not provide direct insights into the prey species consumed during the sampled period, limiting conclusions about dietary overlap. Consequently, the reasons why some bat species exhibit high temporal overlap while others show minimal overlap remain unclear in some cases, reflecting a significant gap in our understanding of interspecific interactions among coexisting bat species. Further research is needed to identify the mechanisms underlying temporal niche partitioning, particularly those related to behavioural ecology and interspecific temperament. Integrating behavioural observations, diet analyses, and fine-scale activity data will be essential to increase our knowledge of bat communities' coexistence. Nevertheless, the analyses of multiple drivers of temporal partitioning are a correlation-based approach, making it difficult to establish definitive cause–and-effect relationships. Still, despite these limitations, our study provides valuable insights into the factors shaping temporal niche partitioning in bat communities, highlighting patterns of coexistence that can guide future ecological research and conservation efforts.

Conclusions

Understanding the drivers of temporal niche partitioning, including interspecific relationships, is fundamental to advance our knowledge of community ecology and predict the consequences of environmental change. This study demonstrates that temporal niche partitioning throughout the night is a key mechanism promoting coexistence in bat communities.

The comparison of our results with existing literature suggests that some species can adjust their activity throughout the night, balancing the search for resources with energetic needs, predation risk, competition, and interspecific behaviour. Beyond competition for space and prey, our findings highlight that temporal niche partitioning is modulated by morphological traits, with larger species generally peaking later, and by different responses to environmental factors, such as moon illumination, altitude or tree layer, which affect activity in response to predation risk, resource availability (prey, roosts), thermoregulation, energy balance, and the biological cycle.

Species can coexist in syntopy (i.e., at the same time and place) as long as their activity patterns overlap in relatively low (c. 60% of the time). Behavioural characteristics associated with species temperament can also influence temporal niche partitioning. Sympatric cryptic species can co-occur with high overlap when the foraging habitats or prey diverge, whereas temporal partitioning becomes increasingly important when this divergence is only partial. Ultimately, our study underscores that the coexistence of bat species is shaped by the interplay of morphological, behavioural and environmental factors, and that understanding these multi-dimensional interactions is crucial for predicting how bat communities—and biodiversity in general—respond to ongoing environmental change.

Acknowledgements

This work was supported by Portuguese Foundation for Science and Technology (FCT) with a Ph.D. grant (SFRH/BD/124367/2016) and by Bat Conservation International with a Student Scholarship (grant number SS1805) (H. Rap.). P. Hor. was funded by FCT with a PhD grant (SFRH/BD/117979/2016). This research was supported under the scope of the FCT project PTDC/BIA-ECO/31731/2017. The authors thank the reviewers for their constructive comments and suggestions, which helped improve the quality and clarity of the manuscript.

Conflict of interest statement

All authors declare no competing interests

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Table 1 –Characterisation of each captured bat species sample size, biometry, environmental features, and activity patterns.

			Environmental features				Activity pattern					
Species	n	Forearm length (FA) range (mm)	Moon illumination range (0 - 1)	Altitude range of captures (m a.s.l.)	Tree layer (TreeL) range (0 - 1)	Night cooling range (°C)	Range of capture months	Range of captures (min. after sunset)	Timing of first peak activity (min.)	Timing of highest peak activity (min.)	Timing of last peak activity (min.)	Number of peak activities
Rhinolophus ferrumequinum - Rfer	91	49.30 - 58.70	0 - 0.46	425 - 962	0.20 - 0.94	0 - 5.10	05 - 10	19 - 500	20	60 - 180	260	3
Rhinolophus hipposideros - Rhip	12	36.03 - 39.20	0 - 0.63	675 - 955	0.45 - 0.94	0 - 3.50	05 - 09	60 - 400	160	160	400	3
Rhinolophus euryale - Reur	37	42.85 - 48.70	0 - 0.70	551 - 806	0.20 - 0.94	0 - 3.60	05 - 10	19 - 340	20	20 - 60	220	3
Barbastella barbastellus - Bbar	77	29.70 - 42.02	0 - 0.52	492 - 1862	0 - 0.94	-1.90 - 5.00	05 - 10	20 - 580	20 - 80	120	180 - 200	3
Plecotus auritus - Paur	257	31.70 - 42.45	0 - 0.73	658 - 1978	0 - 0.94	-1.90 - 5.00	05 - 10	20 - 540	60	120	400 - 420	6
Plecotus austriacus - Paus	110	33.12 - 43.13	0 - 0.58	425 - 1978	0 - 0.94	-0.60 - 8.80	05 - 10	20 - 540	20 - 60	20 - 60	220	3
Myotis bechsteinii - Mbec	11	39.87 - 44.05	0 - 0.40	658 - 1436	0.45 - 0.9	0.60 - 8.80	06 - 10	60 - 500	100	100 and 180	180	2
Myotis escalerai - Mesc	164	35.77 - 41.25	0 - 0.38	386 - 1862	0 - 0.94	-0,60 - 8.80	05 - 10	0 - 540	40 - 80	40 - 80	40 - 80	1
Myotis daubentonii - Mdau	92	30.80 - 40.01	0 - 0.55	432 - 1436	0.10 - 0.75	-1.90 - 5.80	06 - 10	20 - 580	20 - 40	20 - 40	340 - 360	6
Myotis emarginatus - Mema	30	35.50 - 43.02	0 - 0.41	425 - 1837	0 - 0.94	0 - 5.10	05 - 10	19 - 500	100	500	500	2
Myotis mystacinus - Mmys	12	34.00 - 44.5	0 - 0.46	955 - 1436	0.70 - 0.70	-1.90 - 5.80	06 - 10	20 - 540	60	60	60	1
Myotis myotis - Mmyo	34	56.76 - 64.09	0 - 0.55	425 - 1862	0 - 0.94	-1.90 - 5.00	05 - 10	20 - 540	60	60	220	3
Myotis blythii - Mbly	8	55.17 - 61.80	0 - 0.27	887 - 1122	0.20 - 0.70	0.70 - 2.00	05 - 09	20 - 260	20	140 and 200	260	5
Pipistrellus pipistrellus - Ppip	266	25.61 - 33.33	0 - 0.52	386 - 1862	0 - 0.94	-4.50 - 6.00	05 - 10	0 - 460	20 - 80	20 - 80	20 - 80	1
Pipistrellus pygmaeus - Ppyg	7	29.13 - 31.06	0 - 0	432 - 1084	0 - 0.70	1.80 - 5.00	06 - 08	40 - 300	60	60	140	2

Pipistrellus kuhlii - Pkuh	28	27.71 - 36.60	0 - 0.58	608 - 1084	0 - 0.90	0 - 4.90	05 - 10	0 - 500	20 - 120	20 - 120	220	2
Hypsugo savii - Hsav	178	31.32 - 38.46	0 - 0.61	581 - 1862	0 - 0.98	-0.39 - 6.30	05 - 10	0 - 480	20	60 - 120	160	3
Eptesicus serotinus - Eser	98	42.23 - 57.68	0 - 0.51	425 - 1862	0 - 0.98	-0.60 - 6.30	06 - 10	19 - 520	40 - 160	40 - 160	40 - 160	1
Nyctalus leisleri - Nlei	190	39.83 - 53.42	0 - 0.73	581 - 1436	1 - 0.98	-1.90 - 11.30	05 - 10	0 - 560	60 - 220	60 - 220	380 - 400	3
Nyctalus lasiopterus - Nlas	20	61.24 - 66.03	0 - 0.37	866 - 1434	0 - 0.80	-4.50 - 11.30	05 - 08	60 - 520	80	220	300	5

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Table 2 – Coefficient of overnight activity overlap across captured bat species. The cross represents the cooccurrence of species at least in one night in the same sampling site. Confidence intervals of overlap coefficients are included in Table S1 (*SI appendix*).

	R. ferrumequinum	*R. hipposideros*	*R. euryale*	*B. barbastellus*	*P. auritus*	*P. austriacus*	*N. leisleri*	*N. lasiopterus*	*P. pipistrellus*	*P. pygmaeus*	*P. kuhlii*	*H. savii*	*E. serotinus*	*M. bechsteinii*	*M. daubentonii*	*M. emarginatus*	*M. escalerai*	*M. mystacinus*	*M. myotis*	*M. blythii*	Mean overlap	Maximum overlap	Nº overlapping species
R. ferrumequinum		0.5	0.7		0.6	0.8	0.9		0.5	0.5	0.7		0.7	0.7	0.8	0.2	0.5		0.8		0.6	0.9	14
R. hipposideros	x		0.3	0.4	0.8	0.3	0.6		0.1		0.4		0.3		0.6	0.1	0.1	0.4	0.5	0.6	0.4	0.8	15
R. euryale	x	x		0.7	0.4	0.9	0.6		0.7				0.7			0.3	0.8				0.6	0.9	10
B. barbastellus		x	x		0.5	0.8	0.7	0.5	0.6	0.6	0.7	0.6	0.7	0.6	0.7	0.2	0.5	0.7	0.8		0.6	0.8	17
P. auritus	x	x	x	x		0.5	0.7	0.8	0.2	0.2	0.5	0.4	0.4	0.5	0.7	0.2	0.2	0.4	0.5	0.6	0.5	0.8	19
P. austriacus	x	x	x	x	x		0.7	0.4	0.7	0.7	0.8	0.8	0.7	0.5	0.7	0.3	0.7	0.8	0.8	0.7	0.7	0.9	19
N. leisleri	x	x	x	x	x	x		0.7	0.4		0.7	0.6	0.7	0.7	0.8	0.2	0.4	0.7	0.8	0.9	0.7	0.9	18
N. lasiopterus				x	x	x	x		0.2		0.5	0.3	0.4		0.7		0.2				0.5	0.8	10
P. pipistrellus	x	x	x	x	x	x	x	x		0.5	0.6	0.6	0.5	0.2	0.5	0.3	0.8	0.6	0.5	0.4	0.5	0.8	19
P. pygmaeus	x			x	x	x			x		0.9	0.8	0.8	0.7	0.6	0.3	0.6		0.9		0.6	0.9	13
P. kuhlii	x	x		x	x	x	x	x	x	x		0.8	0.9	0.7	0.7	0.3	0.6	0.9	0.8	0.8	0.7	0.9	18
H. savii				x	x	x	x	x	x	x	x		0.8	0.5	0.6	0.4	0.7	0.8	0.8	0.6	0.6	0.8	16
E. serotinus	x	x	x	x	x	x	x	x	x	x	x	x		0.6	0.7	0.3	0.5	0.8	0.8	0.8	0.6	0.9	19
M. bechsteinii	x			x	x	x	x		x	x	x	x	x			0.2	0.3	0.6	0.7		0.5	0.7	14
M. daubentonii	x	x		x	x	x	x	x	x	x	x	x	x			0.2	0.5	0.7	0.7		0.6	0.9	16
M. emarginatus	x	x	x	x	x	x	x		x	x	x	x	x	x	x		0.4	0.3	0.3		0.3	0.4	17
M. escalerai	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x			0.6	0.5	0.5	0.8	18
M. mystacinus		x		x	x	x	x		x		x	x	x	x	x	x			0.9	0.8	0.6	0.9	14
M. myotis	x	x		x	x	x	x		x	x	x	x	x	x	x	x	x	x		0.8	0.7	0.9	17
M. blythii		x			x	x	x		x		x	x	x				x	x	x		0.7	0.9	11

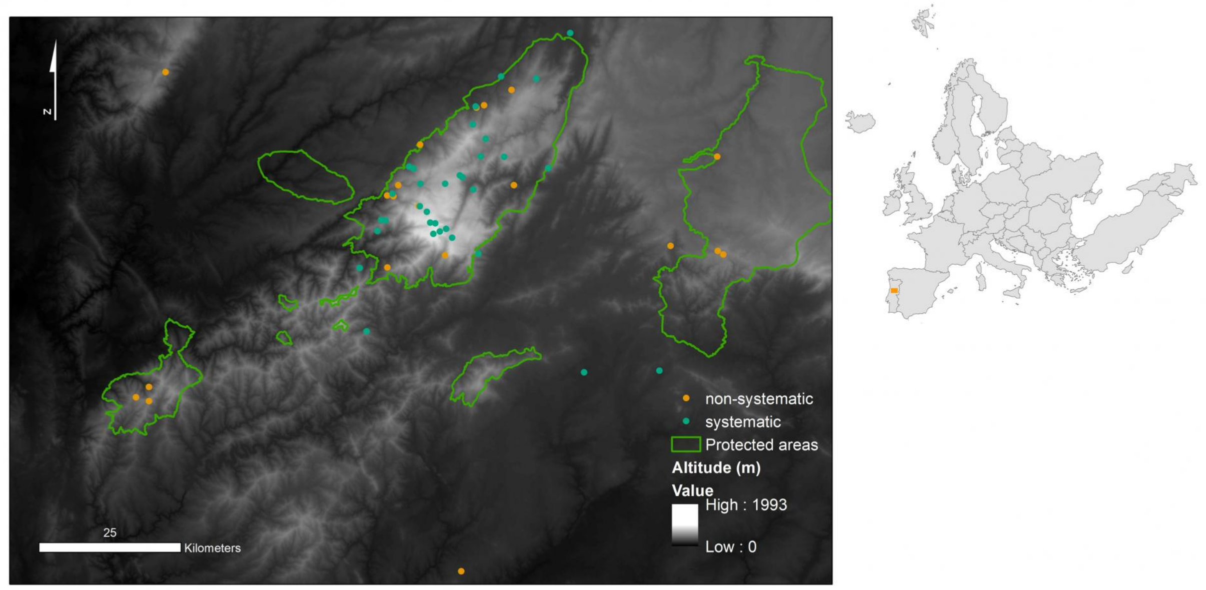
Colour gradient
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0

Table 3 – Model selection results for the Generalised Additive Mixed Models (GAMMs) used to assess temporal patterns of bat activity throughout the night (*Min_capture_after_sunset*). Models are ranked according to Akaike's Information Criterion (AIC), with the most parsimonious model (lowest AIC) shown in bold. All explanatory variables were included as smooth terms (denoted as s()), and forearm length (*FA*) was included as a smooth term in interaction (×) with species. *Moon_illu* – moon illumination; *NC* – night cooling; *TreeL* – tree layer cover; *Alt* – altitude at capture site; *Month* – month of capture; *d.f.* – degrees of freedom.

model (description)	AIC	ΔAIC	d.f.	log likelihood	R^2
Min_capture_after_sunset ~ s(FA x Species) + s(Moon_illu) + s(Alt) + s(TreeL) + s(Month) + s(NC)	**16468.88**	**-**	**117.26**	**-8129.19**	**0.30**
Min_capture_after_sunset ~ s(FA x Species) + s(Moon_illu) +s(NC)+s(Month)+s(Alt)	16494.31	25.43	104.67	-8149.74	0.29
Min_capture_after_sunset ~ s(FA x Species) + s(Moon_illu) +s(NC)+s(Alt)	16609.44	115.13	100.63	-8212.17	0.25
Min_capture_after_sunset ~ s(FA x Species) + s(Moon_illu) +s(NC)+s(Month)	16634.23	24.79	87.68	-8235.56	0.23
Min_capture_after_sunset ~ s(FA x Species) + s(Moon_illu) +s(NC)+s(TreeL)	16711.63	77.40	87.24	-8276.00	0.20

Fig. 1 – Spatial distribution of sampling sites across the altitudinal gradient of the study area, distinguishing between systematic and non-systematic sampling locations. All sampling sites were located in the Portuguese part of the Iberian Central Range.

Fig. 2 – Number of individuals captured of each bat species per 20-minute unit after sunset. Species were plotted by phylogenetic distance. The dashed line in 50% is the level at which we considered the peak activity. Species abbreviations are described in Table 1.



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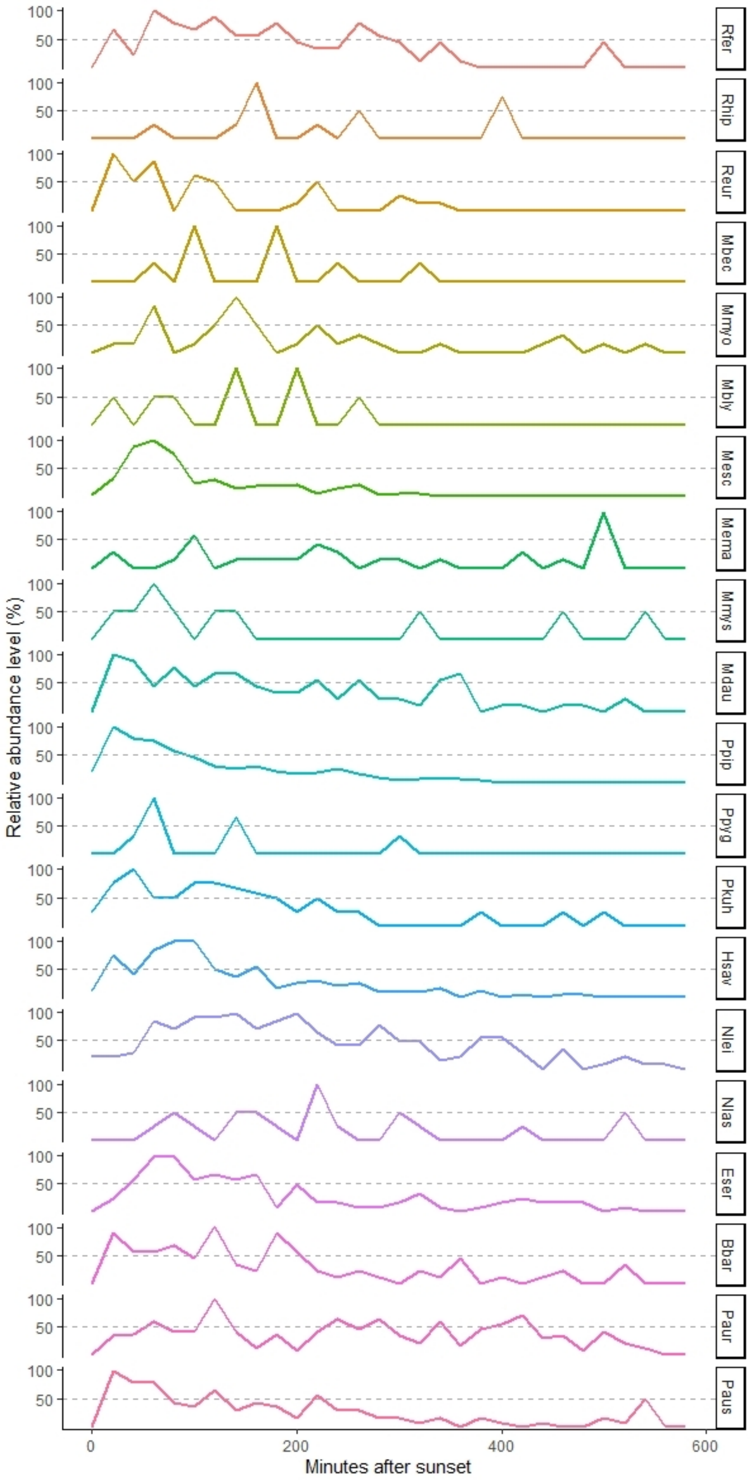

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Figure 1 – Spatial distribution of sampling sites across the altitudinal gradient of the study area, distinguishing between systematic and non-systematic sampling locations. All sampling sites were located in the Portuguese part of the Iberian Central Range.

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Figure 2 – Number of individuals captured of each bat species per 20-minute unit after sunset. Species were plotted by phylogenetic distance. The dashed line in 50% is the level at which we considered the peak activity. Species abbreviations are described in Table 1.

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