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Abstract

Trophic differentiation among sympatric species is often treated as relatively stable, yet seasonal changes in resources may reorganize how species share their trophic niche. We examined whether trophic relationships among three sympatric pipistrelle-like bats, *Afronycteris nanus, Neoromicia somalicus*, and *Pseudoromicia rendalli*, were persistent or changed through time in West African rice agroecosystems. Using DNA metabarcoding of faecal samples from 78 individuals, we identified 244 prey OTUs spanning 13 arthropod orders. Diets were broad and consistent with generalist insectivory, with Blattodea, Hemiptera, and Coleoptera contributing most across species. Despite this similarity, OTU-level dietary composition differed significantly among species, although species identity explained only a small proportion of variation. Dietary overlap was moderate (Pianka = 0.491–0.602) and higher than expected under a null model. Temporal variation was stronger than interspecific differentiation. Diets in June (early wet season) and December (dry season) were strongly differentiated, and interspecific overlap shifted from high in June (0.543–0.642) to lower in December (0.095–0.173), while within-species overlap between periods was near zero. Seasonal change did not simply strengthen or weaken a fixed pattern of trophic segregation: the configuration of dietary similarity was reorganized through time, as species pairs differing significantly in dietary composition changed between June and December. Temporal changes in major prey orders were largely shared among species, with little evidence for consistently divergent species-specific trajectories. Together, these results show that trophic differentiation among these morphologically similar bats is modest overall, but temporal variation can reorganize the configuration of trophic similarity among species.

Keywords: DNA metabarcoding; dietary overlap; trophic niche; insectivorous bats; seasonal dynamics; Guinea-Bissau.

1. Introduction

Dietary studies are crucial to understanding ecosystem structure, function, and species interactions (Nielsen et al. 2018; Liu et al. 2021). By revealing patterns of resource use and niche differentiation at intra- and interspecific levels, dietary analyses provide key insights into the processes shaping community composition and trophic interactions (Salinas-Ramos et al. 2015; Nielsen et al. 2018). Consequently, they are essential not only for informing management and conservation strategies but also for understanding the ecological mechanisms that allow ecologically similar species to coexist within biological communities (Sousa et al. 2019; Liu et al. 2021).

A key question in dietary ecology is how closely related species coexist in the same environment despite overlapping ecological requirements. According to niche differentiation theory, coexistence can be promoted when species differ in resource use along one or multiple niche dimensions, thereby reducing the potential for competitive exclusion (MacArthur & Levins 1967; Pianka 1973; Krüger et al. 2014; Salinas-Ramos et al. 2015). Yet coexistence does not necessarily require strong or persistent trophic segregation. Closely related species may share substantial portions of their dietary niche, particularly when resources are abundant, while maintaining more subtle differences in prey use (Schoener 1974; Salinas-Ramos et al. 2015). In insectivorous bats, such differences have frequently been associated with functional traits including body size, echolocation characteristics and foraging behaviour (Stevens & Willig 2000; Schoeman & Jacobs, 2011; Dammhahn & Goodman 2014; Blanch et al. 2023).

Trophic niche relationships can also change through time. Dietary breadth, composition and overlap provide complementary information on trophic niche structure, but estimates based on a restricted period may obscure temporal changes in the relationships among coexisting species (Langley et al. 2026). Seasonal variation in prey abundance, accessibility and community composition can alter both the resources used by individual species and the degree of overlap among them. Consequently, species that are trophically similar during a given period may become more differentiated during another period (Falke et al. 2020). Considerable dietary overlap among

bat species is commonly reported, particularly during periods of high resource availability (Salinas-Ramos et al. 2015; Andriollo et al. 2021; Srilopan et al. 2025), but overlap alone cannot distinguish between species with consistently similar trophic niches and those whose dietary relationships are reorganized through time. Accounting simultaneously for dietary breadth, composition, overlap, and temporal variation is therefore important for evaluating whether trophic differentiation is persistent or seasonally dynamic.

Although insectivorous bats are generally considered dietary generalists (Maas et al. 2016; Salinas-Ramos et al. 2015), growing evidence suggests that prey use varies with species-specific traits, seasonality and habitat characteristics, resulting in subtle but ecologically meaningful niche differentiation among species (Salinas-Ramos et al. 2015; Kolkert et al. 2020; Andriollo et al. 2021; Maine & Boyles, 2015). This temporal dimension may be particularly relevant in strongly seasonal environments, where changes in rainfall, vegetation and arthropod communities can substantially alter both the composition and accessibility of potential prey over relatively short periods (Zahn et al. 2007; Salinas-Ramos et al. 2015).

Despite growing global interest in bat diets, the feeding ecology of closely related bats in African agricultural landscapes remains poorly understood (Xavier et al. 2023). Here, we investigated three morphologically similar vesper bats: *Afronycteris nanus*, *Neoromicia somalicus*, and *Pseudoromicia rendalli*, occurring sympatrically in smallholder rice fields in Guinea-Bissau. Rice cultivation in this region follows a pronounced seasonal cycle, with major changes in water availability and vegetation structure from sowing through crop development to harvest, accompanied by temporal changes in arthropod communities (Sottomayor et al. 2024; Lopes et al. 2026a). Together, these environmental and agricultural changes can alter the abundance and accessibility of potential prey, providing a strong temporal context in which to examine trophic relationships among insectivorous bats.

Recent taxonomic revisions have recognised *Afronycteris*, *Neoromicia*, and *Pseudoromicia* as distinct genera within the tribe Vespertilionini, while also highlighting their close evolutionary and morphological affinities (Monadjem et al. 2020; 2021; Zhukova et al. 2025; Torrent et al.

2025). Their morphological similarity and sympatric occurrence provide an opportunity to examine how persistent dietary differentiation and temporal changes in resource use jointly structure trophic relationships among ecologically similar species (Novella-Fernandez et al. 2020; Dai et al. 2023). We investigated trophic niche structure among these three coexisting species by assessing whether they differed in dietary breadth and prey use, the extent to which their diets overlapped, and whether these patterns changed over the rice cultivation cycle.

Given their morphological similarity and overlapping geographic ranges, we expected the three bat species to show broadly similar diets and considerable dietary overlap, while retaining subtle differences in prey composition consistent with trophic differentiation (MacArthur & Levins 1967; Salsamendi et al. 2012; Krüger et al. 2014; Salinas-Ramos et al. 2015). Because prey communities and environmental conditions change through the rice cultivation cycle, we further expected the degree and configuration of dietary overlap among species to vary through time, as observed in other seasonally dynamic predator assemblages (Falke et al. 2020; Langley et al. 2026).

2. Methodology

2.1. Study Area

This study was conducted in the Oio region, northern Guinea-Bissau (12°20'0.314"N, 15°10'57.474"W; Fig. 1). The climate is tropical humid maritime, with distinct rainy (June – November) and dry (December – May) seasons. Rice cultivation follows this marked seasonality, with sowing starting in July, following the first heavy rains, crop growth and maturation occurring throughout the rainy season, and harvest taking place in December, when dry-season conditions are already established. The landscape is dominated by smallholder rice fields interspersed with cashew orchards, secondary forest patches, and human settlements. Further details of the study landscape and rice agroecosystem are provided in Chaves et al. (2024), Sottomayor et al. (2024), and Lopes et al. (2026a).

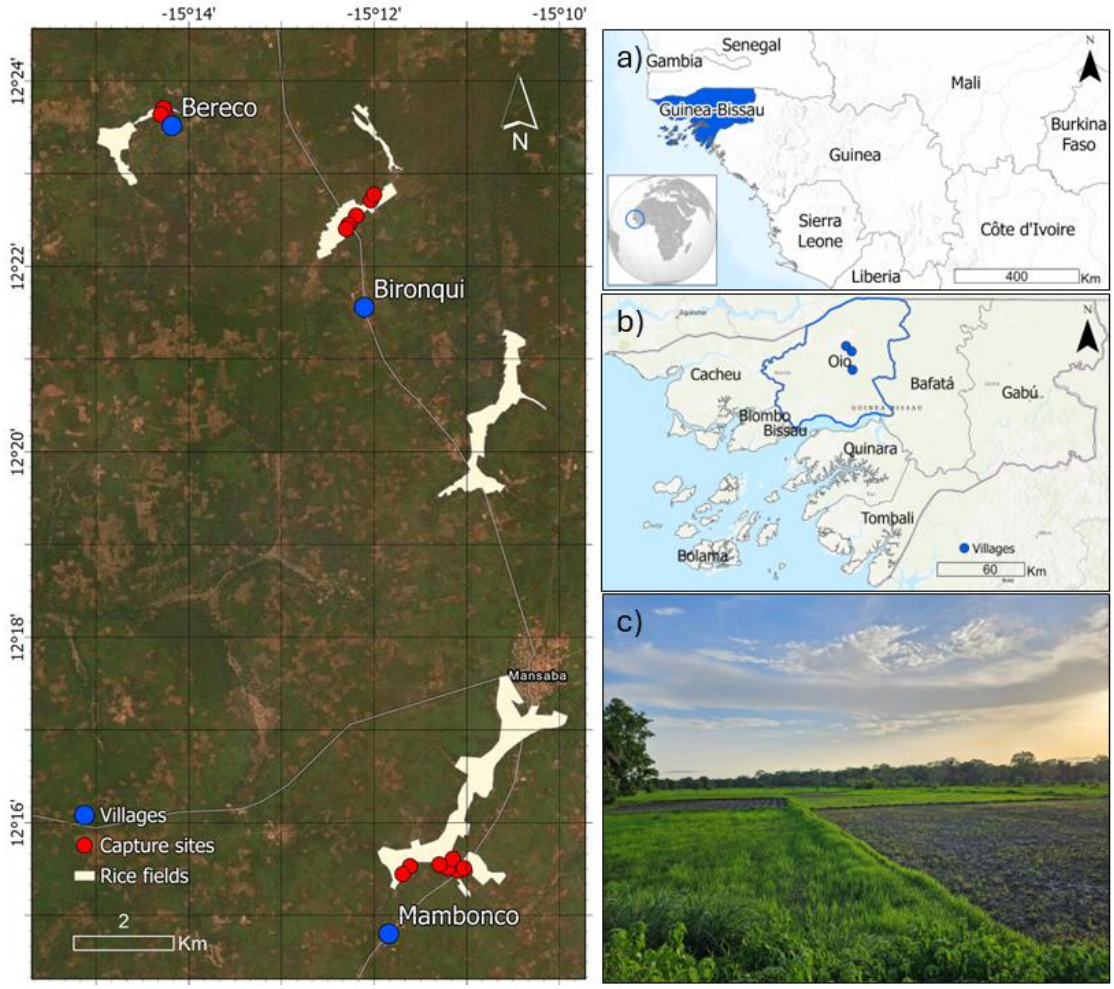


Fig. 1 Location and context of the study area in Guinea-Bissau. The main map (left) shows the rice fields, nearby villages, and capture locations where at least one individual of the three focal bat species was recorded and included in the dietary study. Insets on the right show (a) the location of Guinea-Bissau within West Africa, (b) the location of the study area within Oio Region and Mansabá Sector, and (c) a view of part of the rice fields at Bironqui. Source: Esri, TomTom, Garmin, FAO, NOOA, USGS, EarthStar Geographics

2.2. Bat sampling

Bats were captured in rice fields from October to December 2021 and from June to December 2022, encompassing the rice-growing cycle from sowing to harvest and the transition from the wet season to the dry season (Lopes et al. 2026b). No capture sessions were conducted in August

because heavy rains made fieldwork impractical. Sampling was conducted across multiple rice-field sites as part of the broader field study (Chaves et al. 2026), but faecal samples included in the present analysis originated from rice fields near Bironqui, Bereco and Mambonco (Fig. 1).

Bats were captured using 12-meter mist nets (Ecotone, 712/2P), with one to eight nets set along field margins, near isolated trees, and close to water sources to maximize capture success. Sampling effort and capture success varied across sites and months, resulting in an unbalanced number of individuals available for dietary analysis. Bats were captured from sunset until 22:00 and held individually for 30 minutes in single-use paper bags, placed inside breathable cotton bags, to collect faecal samples. The use of individual disposable paper bags minimized the risk of cross-contamination among samples. Food-passage studies in vespertilionid bats indicate rapid digestion, with marked food detectable in faeces within tens of minutes after ingestion (Grant, 1988; Staliński, 1994), suggesting that pellets collected shortly after capture largely reflect recent foraging. Faecal pellets were stored in 96% ethanol.

All bats were identified morphologically following Happold and Happold (2013), with species identity subsequently validated through DNA barcoding of faecal samples (see Sections 2.3 and 2.4). Taxonomy followed Simmons and Cirranello (2025). Animals were captured and samples transported under licences issued by the Guinea-Bissau Institute of Biodiversity and Protected Areas (IBAP).

2.3. Laboratory Procedures

DNA was extracted individually from 78 faecal pellets following the protocol described by Gonçalves et al. (2024). Each sample was homogenised in 650 µL of lysis buffer (0.1 M Tris-HCl, 0.1 M EDTA, 0.01 M NaCl, 1% N-lauroylsarcosine, pH 7.5-8; Maudet et al. 2002) and incubated in a dry bath at 56°C for 30 minutes. The samples were vortexed for 1 minute before centrifugation at 12,000 × g for 30 seconds, and the supernatant was mixed with 25 µL of OB Protease. DNA purification followed the E.Z.N.A. Tissue DNA Kit protocol (Omega Bio-Tek, Georgia, USA), except that DNA was eluted twice in 50 µL, producing two eluates per sample.

Extractions were performed in batches of 23 samples, with one extraction blank per batch. One negative PCR control was included per PCR plate.

Prey DNA was amplified using the FwhF2-R2n COI primers (Vamos et al. 2017), modified to incorporate Illumina adaptors. These primers successfully amplify a wide range of arthropods and perform well with degraded DNA (Elbrecht et al. 2019; Mata et al. 2021; da Silva et al. 2024). Each PCR reaction contained 5 µL Qiagen Multiplex Master Mix, 0.3 µL of each primer (10 nmol/L), 3.4 µL water, and 1 µL of extracted DNA. Amplification consisted of an initial denaturation at 95°C for 15 min, followed by 40 cycles of 95°C for 30 s, 50°C for 30 s and 72°C for 30 s, with a final extension at 72°C for 10 min.

Morphological identification of bats species was validated using FwhF1–R1 primers (Vamos et al. 2017) under the same amplification conditions. This marker was used because the FwhF2–R2n primers frequently fail to amplify vertebrate DNA. Following amplification, the PCR products were diluted 1:4. A second PCR was performed to add 7bp-long indices to the Illumina P5 and P7 sequencing adaptors. Indexing PCRs (8 cycles and annealing at 55°C) were performed with KAPA HiFi HotStart ReadyMix (Roche, Basel, Switzerland). Amplified products were purified using Agencourt AMpure XP beads (Beckman Coulter, Brea, California, USA) at a 1:0.8 ratio. Purified products were quantified with an Epoch Microplate Spectrophotometer (Agilent, California, USA), diluted to 15 nM, and pooled by marker. Libraries were quantified by qPCR (KAPA Library Quant Kit qPCR Mix; Rocher), diluted to 4 nM, and sequenced on an Illumina MiSeq at a target depth of 30,000 reads for FwhF2-R2n and 4000 reads for FwhF1–R1.

2.4. Bioinformatic Analysis

Paired-end reads were merged using FLASH (Magoč & Salzberg, 2011), considering a minimum expected overlap of 10 bp and a maximum of 250 bp. The OBItools commands ngsfilter, obiuniq, and obigrep (Boyer et al. 2016) were used to remove primer sequences, dereplicate reads per sample, and remove singletons per sample, respectively. VSEARCH (Rognes et al. 2016) was

then used to denoise sequences using cluster_unoise with default parameters (unoise_alpha = 2, minsize = 8), while retaining sequences within the expected length range (fwh1: 150-200bp; fwh2: 203-208bp); remove chimeras using uchime3_denovo; cluster sequences at 99% similarity using cluster_size; and map reads back to the retained operational taxonomic units (OTUs) at 99% identity using usearch_global. Finally, LULU (Frøslev et al. 2017) was used to curate the OTU table using default parameters (minimum_ratio = 1, minimum_match = 84, minimum_relative_cooccurrence = 0.95). Read counts detected in extraction and PCR negative controls were subtracted from the corresponding samples to account for potential contamination.

OTUs were compared against the BOLD database using BOLDigger v2.1.1 (Buchner & Leese, 2020), and taxonomic assignments were manually curated using BOLD and complementary matches from NCBI with >90% query coverage. OTUs were assigned to the lowest reliable taxonomic level using sequence-similarity thresholds of ≥99% for species, ≥97% for genus, ≥95% for family, and ≥90% for order. When similarly ranked matches corresponded to different taxa, assignments followed a least-common-ancestor approach. OTUs were classified as dietary (primarily arthropods) or non-target (e.g. fungi and internal or external parasites), with non-target OTUs excluded from subsequent analyses.

To minimise the inclusion of poorly represented sequences potentially arising from sequencing artefacts or secondary ingestion, OTUs contributing <1% of the total dietary reads within each sample were discarded (Deagle et al. 2019; da Silva et al. 2019). Samples containing fewer than 100 dietary reads after filtering were also excluded to ensure sufficient sequencing depth for dietary characterisation.

2.5. Data analysis

All analyses were conducted in R (R Core Team, 2025), with figures produced primarily using ggplot2 (Wickham, 2016). Statistical significance was assessed at $\alpha = 0.05$. ChatGPT (OpenAI)

was used to assist with reviewing and refining R code; all modifications and resulting analytical outputs were reviewed and verified by the authors.

Because read abundance in DNA metabarcoding data does not reliably reflect prey biomass or abundance owing to variation in DNA content, digestion rates and primer biases, dietary composition was summarised using presence/absence and weighted proportion of occurrence (wPOO), an occurrence-based index that accounts for the relative contribution of each prey taxon within individual samples before summarising diet across samples (Deagle et al. 2019).

Dietary breadth was compared among species using coverage-based rarefaction and extrapolation of Hill numbers ($q = 0$) with iNEXT (Hsieh et al. 2016), separately at OTU, family and order levels. A target sample coverage of 0.40 was selected based on the lowest OTU-level coverage observed among species (*P. rendalli*) and used for standardization across taxonomic resolutions (Chao et al. 2014). This target was attainable for all species at OTU and family levels. At order level, however, the minimum coverage attainable for *N. somalicus* and *P. rendalli* was already higher than the target (0.52 and 0.45, respectively), and estimates for these species were therefore obtained at these minimum attainable coverage levels. Estimates and 95% confidence intervals were based on 1,000 bootstrap replicates.

Dietary contributions of major prey orders were visualised with a bipartite Sankey diagram based on weighted proportion of occurrence (wPOO), using ggalluvial (Brunson & Read, 2017). Rare orders (Araneae, Crassiclitellata, Dermaptera, Neuroptera, Psocodea, Scolopendromorpha and Trichoptera) were grouped as “Other” for visualisation.

Prey richness per individual was analysed separately at OTU, family and order levels using generalized linear mixed models in glmmTMB (Brooks et al. 2017), with bat species as a fixed effect and month–year as a random intercept. OTU richness was fitted with a negative-binomial distribution, family richness with Poisson, and order richness with a Conway–Maxwell–Poisson (COM-Poisson) distribution, all using log links. Species effects were tested by likelihood-ratio comparison of models with and without the species term. Pairwise comparisons were obtained

from estimated marginal means using emmeans (Lenth, 2021) with Tukey adjustment. Model diagnostics were assessed with DHARMa (Hartig, 2024), including tests of residual uniformity, dispersion, and zero inflation.

Overall dietary composition was visualised using non-metric multidimensional scaling (NMDS; metaMDS in vegan; Oksanen et al. 2018) based on the presence–absence of prey orders and Jaccard dissimilarities, with two dimensions and up to 100 random starts. Marginal kernel densities represented distributions along NMDS axes, and prey-order scores were plotted in the ordination space. Differences in OTU-level dietary composition were tested using PERMANOVA (adonis2 function in vegan) with binary Jaccard dissimilarities and 999 permutations. Bat species and month were included as additive predictors and tested marginally. Pairwise species comparisons retained month as a covariate and used Holm-adjusted P-values. Homogeneity of multivariate dispersion among species was assessed with the betadisper function in vegan and 999-permutation tests.

Trophic overlap was quantified at the OTU level using Pianka's index (Pianka, 1973), calculated from proportional OTU occurrence distributions pooled within each bat species. Significance was assessed with a randomization algorithm 3 (RA3) null model implemented with custom R code, in which resource-use values were randomly reassigned among prey categories independently within each predator group while preserving its observed utilisation distribution. For each pairwise comparison, 999 randomisations were performed, with directional upper- and lower-tail probabilities calculated using an add-one correction.

Seasonal analyses were restricted to June (wet season) and December (dry season), the only months with sufficient representation of all three species, and to Bironqui to avoid spatial confounding. Temporal NMDS used OTU-level presence–absence data, binary Jaccard dissimilarities, two dimensions and up to 100 random starts, with convex hulls representing species–month groups. Temporal PERMANOVA included species and month as additive predictors, with 999 permutations and marginal tests. Multivariate dispersion was assessed separately for bat species and month using betadisper, and pairwise species comparisons were

conducted within each month with Holm adjustment. Temporal changes in trophic overlap were evaluated using Pianka's index for the six species–month combinations at Bironqui. All 15 pairwise comparisons were calculated, comprising within-month interspecific, within-species temporal, and between-species/between-month contrasts, and significance was assessed using the same RA3 procedure.

Temporal changes in the contribution of major prey orders were analysed with generalized additive models (GAMs) using mgcv (Wood, 2025). OTU-level wPOO values were summed within each individual and prey order, with undetected orders assigned wPOO = 0 and values of 1 retained. Analyses included Blattodea, Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera and Orthoptera.

Bat species × prey order combinations were considered adequately represented when the order occurred in at least five bat individuals, was detected in at least three sampled months, and occurred in at least two individuals in at least two of those months. For orders meeting these criteria in all three bat species, joint quasibinomial GAMs with logit link were fitted as: wPOO ~ Species + s(month, by = Species) using shrinkage cubic regression splines and REML. Basis dimension was constrained by the number of sampled months. Bat species differences in mean dietary contribution across the sampling period were evaluated with estimated marginal means averaged equally across sampled months and Tukey-adjusted pairwise comparisons. Differences in temporal trajectories were tested by comparing each joint model with a reduced model containing the same species effect and a single shared temporal smooth, using an F test.

For orders that did not meet these criteria across all three bat species, single-species GAMs (wPOO ~ s(month)) were fitted for species × order combinations that met the criteria individually. These models were used only to assess within-species temporal variation. Model performance was summarised using adjusted R^2 and percentage deviance explained, and diagnostics were assessed with gam.check.

To assess whether spatial and interannual imbalance sampling influenced temporal patterns, we repeated the analyses using restricted datasets. The June–December PERMANOVA and temporal Pianka analyses were repeated using only 2022 samples from Bironqui, thereby holding both site and year constant. GAMs were refitted using Bironqui-only samples to remove spatial heterogeneity, 2022-only samples to remove interannual variation, and 2022 Bironqui-only samples to hold both site and year constant.

3. Results

We analysed faecal samples from 78 individual bats: 37 *A. nanus*, 23 *N. somalicus*, and 18 *P. rendalli.* The distribution of samples across months and years is provided in Table S1. DNA metabarcoding revealed 492 prey occurrences, corresponding to 244 unique OTUs from 13 arthropod orders, 51 families, and 27 genera. Only 5.3% of OTUs were confidently identified to species level.

3.1. Dietary Breadth and Composition

Across the three focal species, individual bats contained 6.31 ± 0.72 prey OTUs (mean ± 95% CI). The greatest dietary contributions were from Blattodea (27.6%), Hemiptera (25.6%), Coleoptera (17.5%), Lepidoptera (11.5%), and Diptera (5.7%) (Fig. 2). Termitidae (19.4%) and Cicadellidae (13.2%) were the most represented families, and *Macrotermes* (10.8%) and *Microtermes* (8.4%) made the largest contributions among identified genera (Table S2). Seven potential agricultural pest arthropods were detected in the diets (Table S3).

Afronycteris nanus consumed 110 OTUs from 10 orders, *N. somalicus* 100 OTUs from 9 orders, and *P. rendalli* 93 OTUs from 8 orders. Despite this variation in observed richness, the three species relied broadly on the same dominant prey orders, particularly Blattodea, Hemiptera and Coleoptera, although their relative contributions differed (Fig. 2). Blattodea (31.5%) and Hemiptera (26.0%) contributed most to the diet of *A. nanus*; Hemiptera (25.6%), Coleoptera (24.7%) and Blattodea (23.2%) contributed similarly to that of *N. somalicus*; and Coleoptera

(28.0%), Blattodea (25.2%) and Hemiptera (24.9%) dominated the diet of *P. rendalli*. Termitidae was among the most represented prey families across all three species.

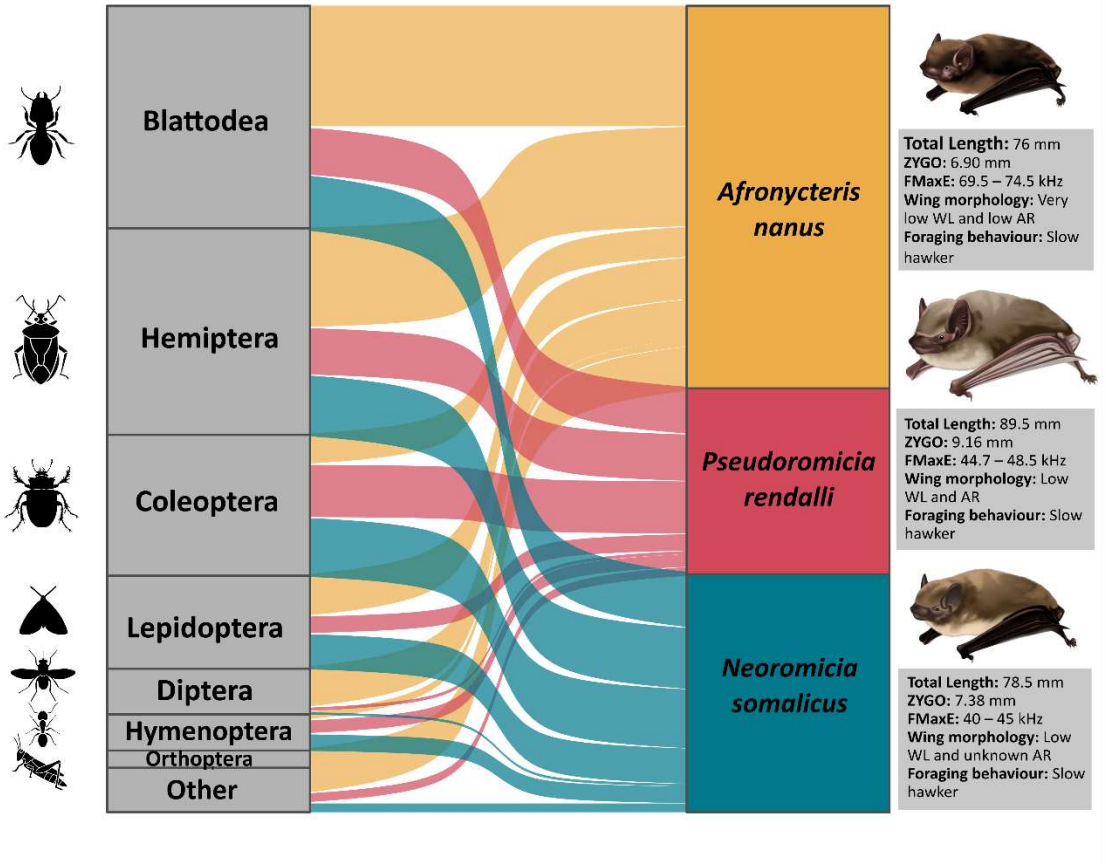


Fig. 2 Dietary interactions between the top seven consumed prey orders – Blattodea, Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera, Orthoptera, and Other (includes the orders Araneae, Crassiclitellata, Dermaptera, Neuroptera, Psocodea, Scolopendromorpha, and Trichoptera) – and the three Pipistrelle-like bats – *Afronycteris nanus*, *Neoromicia somalicus*, and *Pseudoromicia rendalli*, ordered by total prey consumption - using wPOO based on DNA metabarcoding data. Nodes on opposing axes represent prey order groups and predator species, respectively. The width of each connecting link is scaled according to the wPOO value, reflecting the relative dietary contribution of each prey group. Measurements abbreviations: ZYGO – zygomatic breadth (mm); FMaxE – frequency of maximum energy (kHz; Table S4); WL – wing-loading; AR – aspect ratio. Sources: Norberg & Rayner 1987; Goodman & Ranivo 2004; Lausen

& Barclay 2005; Schoeman & Jacobs 2008; Wilson & Mittermeier 2019; Monadjem et al. 2010a, 2010b; Patterson & Webala 2012; Bates et al. 2013; Happold & Happold 2013; Monadjem et al. 2013; Naidoo et al. 2013; Decher et al. 2015; Kangoyé et al. 2015; Monadjem et al. 2021; Taylor et al. 2022; Grunwald et al. 2023; Grunwald et al. 2025; Taylor-Boyd et al. 2025. Bat illustrations by Catarina Covas.

Coverage-based estimates of dietary breadth, expressed as estimated richness ($q = 0$), varied in magnitude among species and taxonomic levels (Fig. 3; sample-size-based rarefaction/extrapolation curves in Fig. S1). At the OTU level, estimated richness was highest for *P. rendalli* (93.4 OTUs, 95% CI: 56.5–130.3), followed by *N. somalicus* (48.8 OTUs, 25.9–71.8) and *A. nanus* (33.5 OTUs, 23.8–43.1), although uncertainty was considerable, particularly for *P. rendalli*. At the family level, estimated richness was highest for *N. somalicus* (7.1 families, 5.4–8.8), closely followed by *P. rendalli* (6.9 families, 4.8–8.9), and lowest for *A. nanus* (5.4 families, 3.7–7.1). Estimated order richness was similar among species (2.7–2.9 orders).

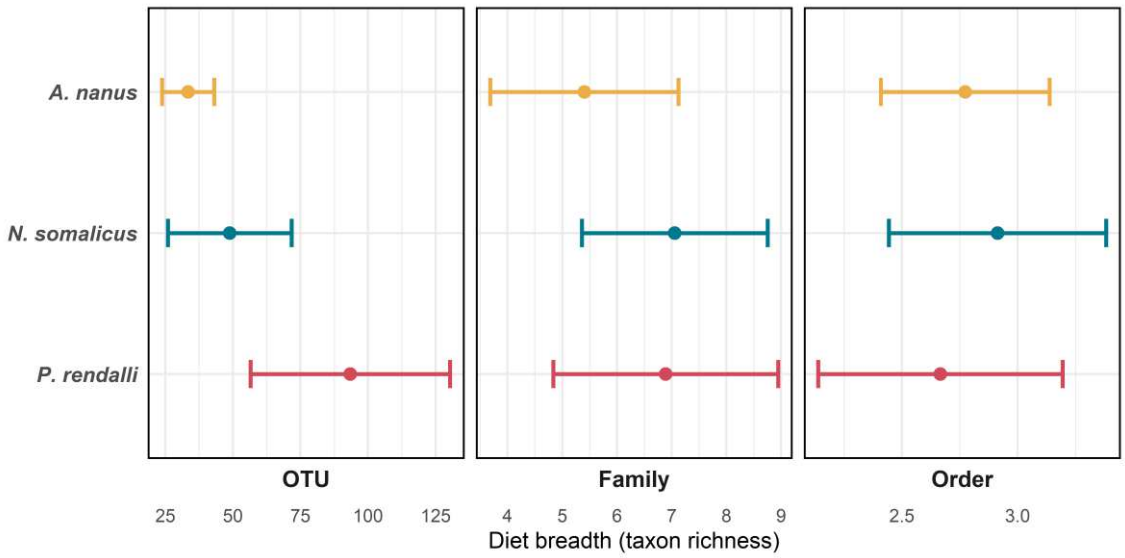


Fig. 3 Estimated dietary breadth of the three bat species at three prey taxonomic levels (OTU, family, and order). Points represent estimated prey richness (Hill number, q = 0), and horizontal bars indicate 95% confidence intervals based on 1,000 bootstrap replicates. A target sample coverage of 0.40 was used to account for differences in sampling completeness. This target was attained for all OTU- and family-level estimates; at the order level, the minimum attainable

384 coverage was 0.52 for *Neoromicia somalicus* and 0.45 for *Pseudoromicia rendalli*. Colours
385 represent bat species.

386

387 In contrast to these species-level estimates, the number of prey OTUs detected per individual did
388 not differ among bat species after accounting for temporal variation (negative-binomial GLMM:
389 $\chi^2 = 2.04$, df = 2, $P = 0.360$; Table S5). Thus, the higher estimated OTU-level dietary breadth of
390 *P. rendalli* did not reflect greater prey richness within individual bats, but rather greater variation
391 in prey taxa detected across individuals. Family richness per individual differed significantly
392 among species (Poisson GLMM: $\chi^2 = 10.55$, df = 2, $P = 0.005$; Table S5), with *N. somalicus*
393 showing greater richness than *A. nanus* (estimated marginal means: 4.15 vs 2.62 families per
394 individual; Tukey-adjusted $P = 0.005$; Table S6), whereas *P. rendalli* did not differ significantly
395 from either species. Order richness per individual did not differ among bat species (COM-Poisson
396 GLMM: $\chi^2 = 1.77$, df = 2, $P = 0.413$; Table S5).

397

398 **3.2. Diet Overlap**

399 NMDS ordination (stress = 0.127; Fig. 4) showed substantial overlap in dietary composition
400 among the three bat species, although their distributions in ordination space were not identical.
401 Several of the dominant prey orders, including Hemiptera, Lepidoptera and Blattodea, occupied
402 relatively central positions within the shared dietary space, whereas less frequently detected

orders such as Dermaptera, Psocodea, Orthoptera and Scolopendromorpha were positioned toward its periphery.

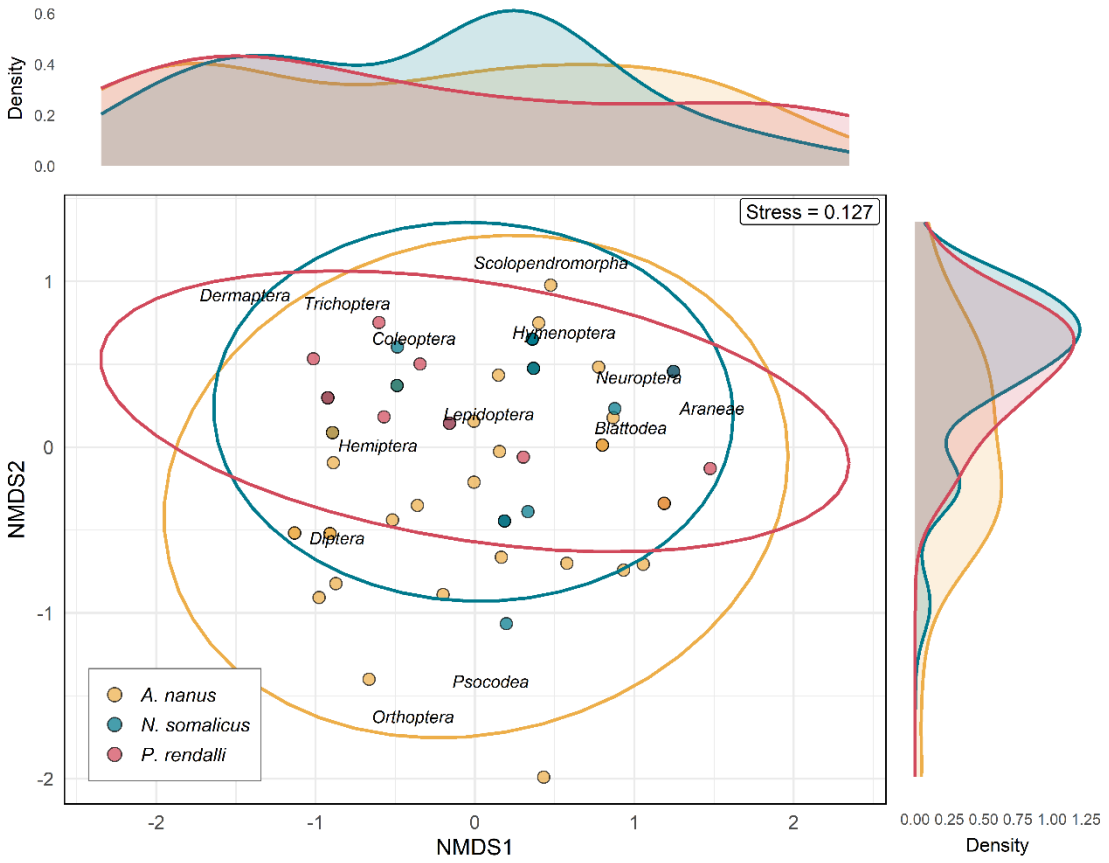
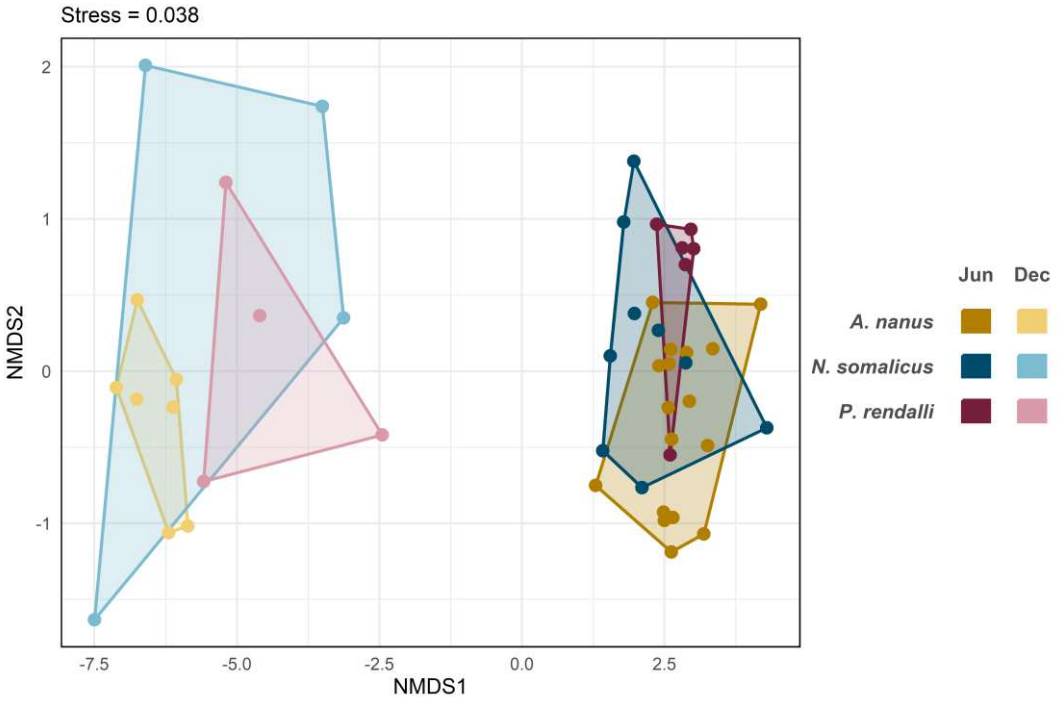


Fig. 4 Non-metric multidimensional scaling (NMDS) ordination of dietary composition of *Afronycteris nanus*, *Neoromicia somalicus*, and *Pseudoromicia rendalli,* based on Jaccard dissimilarities calculated from presence–absence of prey orders detected in individual faecal samples (k = 2; stress = 0.127). Points represent individual bats, with closer points indicating more similar dietary composition. Arthropod-order labels represent their scores in the NMDS ordination and indicate their association with the distribution of individual diets. Ellipses represent 95% confidence regions for each bat species. Marginal density plots show the distribution of individuals of each species along NMDS axes 1 and 2. Colours represent bat species

PERMANOVA indicated significant differences in OTU-level dietary composition among bat species after accounting for month (F = 1.92, R^2 = 0.042, P = 0.001), while month explained a

substantially larger proportion of variation (F = 3.31, R^2 = 0.183, P = 0.001). Multivariate dispersion did not differ among species (PERMDISP: F = 0.059, P = 0.947), indicating that the observed compositional differences were not attributable to unequal within-species dispersion. Pairwise PERMANOVA detected significant differences in OTU-level dietary composition among all three species pairs, although effect sizes were small: *A. nanus* vs *N. somalicus* (R^2 = 0.026, Holm-adjusted P = 0.020), *A. nanus* vs *P. rendalli* (R^2 = 0.034, Holm-adjusted P = 0.003), and *N. somalicus* vs *P. rendalli* (R^2 = 0.040, Holm-adjusted P = 0.020; Table S7). Despite these compositional differences, Pianka's index indicated substantial dietary overlap among all species pairs (0.491–0.602), with overlap significantly higher than expected under the RA3 null model in every comparison (all directional $P \leq 0.003$; Table S8), showing that the three species differed in prey composition while still sharing a substantial proportion of their dietary resources.

Temporal NMDS ordination showed pronounced separation in dietary composition between June (wet season) and December (dry season) (stress = 0.038; Fig. 5). In June, the three bat species occupied largely overlapping regions of ordination space, whereas their distributions were more separated in December. PERMANOVA confirmed significant effects of both species (F = 1.97, R^2 = 0.074, P = 0.001) and month (F = 6.13, R^2 = 0.115, P = 0.001) on OTU-level dietary composition. Multivariate dispersion did not differ significantly among species (PERMDISP: F = 0.30, P = 0.710) or between months (F = 3.78, P = 0.061). Pairwise PERMANOVA revealed significant interspecific differences within both months, but the pattern changed seasonally: in June, *P. rendalli* differed from both *A. nanus* and *N. somalicus*, whereas in December *A. nanus* differed from both the other species (Table S9). Pianka's index nevertheless indicated substantial dietary overlap among species in June (0.543–0.642), with all pairwise overlaps significantly higher than expected under the RA3 null model. In December, overlap among species was much smaller (0.095–0.173) and did not differ significantly from null expectations (Fig. 6; Table S10). Within each species, dietary overlap between June and December was very low (0–0.012) and significantly lower than expected under the null model (Fig. 6; Table S10).



443

444 **Fig. 5** Non-metric multidimensional scaling (NMDS) ordination of dietary composition of
445 *Afronycteris nanus*, *Neoromicia somalicus*, and *Pseudoromicia rendalli* sampled in June and
446 December at Bironqui, based on Jaccard dissimilarities calculated from presence–absence of prey
447 OTUs detected in individual faecal samples (k = 2; stress = 0.038). Points represent individual
448 bats, with closer points indicating more similar dietary composition. Convex hulls encompass
449 individuals belonging to each species–month combination and illustrate the extent and overlap of
450 their dietary composition in ordination space. Colours distinguish bat species, while darker and
451 lighter shades indicate June and December, respectively

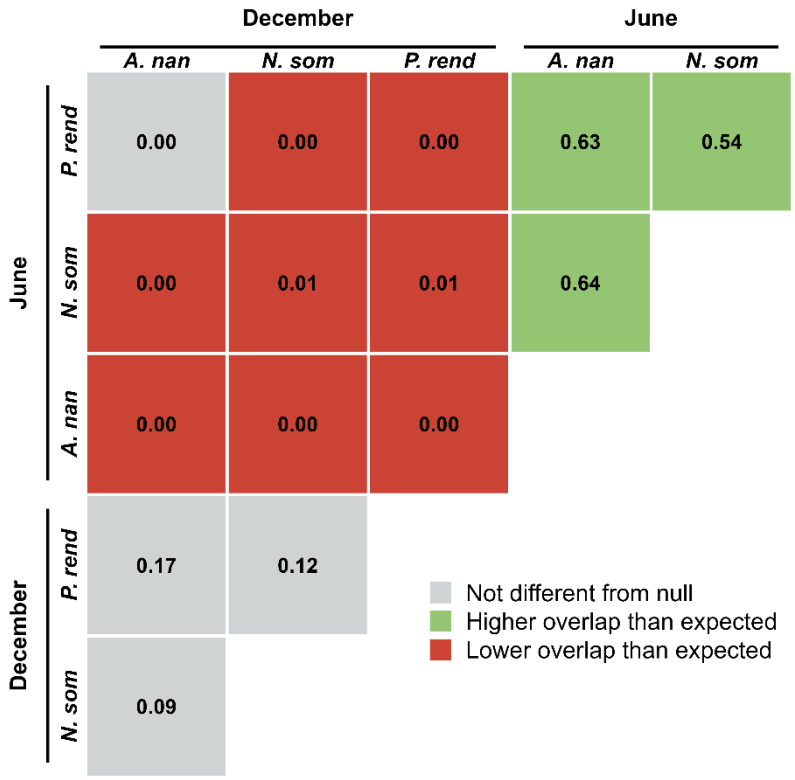


Fig. 6 Pairwise dietary overlap among *A. nanus*, *N. somalicus*, and *P. rendalli* sampled at Bironqui in June and December, quantified using Pianka's index based on OTU-level prey occurrence (Table S10). Each cell shows the observed Pianka overlap index for a species–month pair. Green cells indicate overlap significantly higher than expected under an RA3 null model (upper-tail $P < 0.05$), red cells indicate overlap significantly lower than expected (lower-tail $P < 0.05$), and grey cells indicate no significant departure from the null expectation

3.3. Temporal Variation in Prey Consumption

Temporal changes in prey use differed markedly among arthropod orders (Fig. 7; Tables S11 and S12). Joint three-species GAMs could be fitted for Coleoptera, Hemiptera and Lepidoptera (Table S11). Coleoptera increased through the rice cultivation cycle in *N. somalicus* and *P. rendalli*, with significant temporal smooths in both species ($P = 0.017$ and $P = 0.004$, respectively), whereas no significant temporal trend was detected for *A. nanus* ($P = 0.169$). Hemiptera increased over the sampling period in all three bat species, with significant temporal variation in *A. nanus* ($P <$

0.001), *N. somalicus* ($P < 0.001$), and *P. rendalli* ($P = 0.024$). By contrast, Lepidoptera showed no significant temporal trend in any species (all $P > 0.06$). Among the joint three-species models, model fit was strongest for Hemiptera (adjusted $R^2 = 0.579$; 53.3% deviance explained) and Coleoptera (adjusted $R^2 = 0.485$; 44.8% deviance explained), but weak for Lepidoptera (adjusted $R^2 = 0.031$; 6.5% deviance explained).

For prey orders that could not support a joint three-species model, Blattodea declined markedly through the sampling period in both *N. somalicus* ($P = 0.003$) and *P. rendalli* ($P = 0.001$) (Fig. 7; Table S11). Diptera showed an apparent increase midway through the rice cultivation cycle in *A. nanus*, although the temporal smooth was not significant ($P = 0.141$). Hymenoptera and Orthoptera had insufficient temporal representation for GAM analysis.

Based on estimated marginal means from the joint GAMs (Table S13), *N. somalicus* had a significantly higher dietary contribution of Coleoptera than *A. nanus* (estimated contrast *A. nanus* − *N. somalicus* = −1.317, SE = 0.407, Tukey-adjusted $P = 0.005$; Fig. 7; Table S14), whereas *P. rendalli* did not differ significantly from either species. No significant interspecific differences were detected for Hemiptera or Lepidoptera (all Tukey-adjusted $P > 0.05$; Table S14). Formal

comparisons of species-specific temporal trajectories were not significant after Holm correction for Coleoptera, Hemiptera or Lepidoptera (all adjusted $P \geq 0.091$; Table S15).

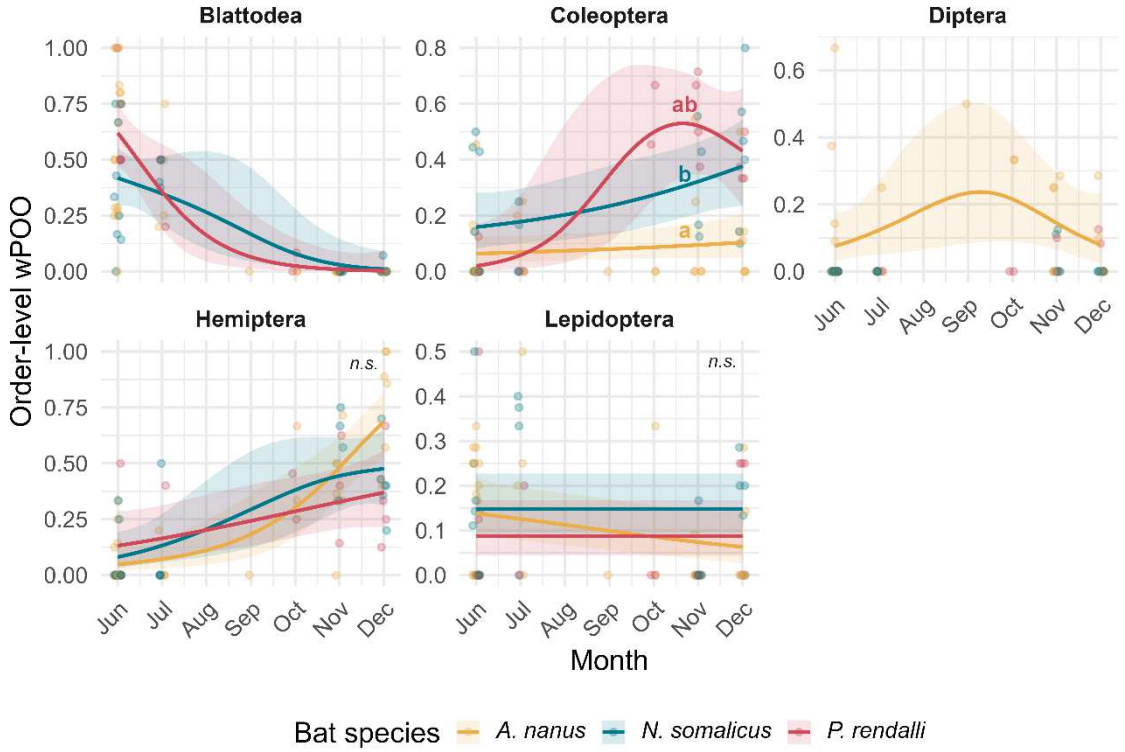


Fig. 7 Temporal variation in the dietary contribution of major arthropod orders to the diets of *Afronycteris nanus*, *Neoromicia somalicus*, and *Pseudoromicia rendalli* between June and December. Dietary contribution is expressed as order-level weighted proportion of occurrence (wPOO). Lines represent fitted generalized additive models (GAMs), with shaded areas indicating 95% confidence intervals; points represent individual bats. For prey orders with sufficient temporal replication in all three bat species, joint models were used to estimate species-specific temporal trends and test interspecific differences in mean dietary contribution. Species sharing at least one letter did not differ significantly, whereas species with no letters in common differed significantly (Tukey-adjusted $P < 0.05$); "n.s." indicates no significant interspecific differences (Table S12). For prey orders lacking sufficient replication for a three-species comparison, temporal trends are shown only for species with adequate data, and no interspecific significance annotation is provided

Sensitivity analyses supported the main temporal patterns: restricting the June–December comparison to 2022 samples from Bironqui retained a strong month effect on diet composition (PERMANOVA: $R^2 = 0.131$, $P = 0.001$), while restricted GAMs produced broadly consistent temporal trajectories (Table S16; Fig. S2).

4. Discussion

Our results reveal substantial trophic similarity among three sympatric pipistrelle-like bats but also show that this similarity is neither total nor temporally stable. The three species shared the same major prey groups and overlapped considerably in diet, yet complementary dietary metrics revealed subtle interspecific differences. At the same time, temporal variation explained substantially more variation in dietary composition than bat species identity, and the configuration of overlap among species differed markedly between seasons. Together, these findings indicate that trophic differentiation in this assemblage of closely related and morphologically similar bats is both multidimensional and temporally dynamic: species differences emerge across complementary dimensions of diet, while temporal variation exerts a stronger influence on overall dietary structure than persistent species identity.

4.1. Dietary similarity and the scale of trophic differentiation

The broad prey spectrum shared by *A. nanus*, *N. somalicus* and *P. rendalli* is consistent with the generalist insectivory reported for other African vespertilionids (Monadjem et al. 2010b; Happold & Happold 2013; Nsengimana et al. 2023; Van Cakenberghe & Seamark 2024). Among the three focal species, such generalism was accompanied by marked temporal flexibility in prey use, which may be advantageous in seasonal environments where prey communities change substantially over short periods (Wilson & Mittermeier 2019; Salinas-Ramos et al. 2015). Termites were especially prominent in all three diets, consistent with their high energetic value, seasonal mass emergences and documented importance to other African insectivorous bats

(Mitchell 2008; Eklöf & Rydell 2017; Monadjem et al. 2010b; Van Cakenberghe & Seamark 2024).

The prominence of Blattodea, Hemiptera and Coleoptera contrasts with the Lepidoptera- and Diptera-dominated diets reported for many insectivorous bats in Africa (Waghiiwimbom et al. 2019; Nsengimana et al. 2023). *A. nanus* diets in Rwanda were dominated by Lepidoptera and Diptera (Nsengimana et al. 2023), whereas Diptera were dominant in Cameroon (Waghiiwimbom et al. 2019). This difference is unlikely to reflect the metabarcoding primer alone, as the same FwhF2–R2n primer set has recovered markedly different prey assemblages in other bat studies, including diets dominated by Diptera or Lepidoptera (Nóbrega et al. 2023; Gonçalves et al. 2024; Srilopan et al. 2025). Instead, the prevalence of termites and rice-associated hemipterans in our samples suggests that local prey communities and the strongly seasonal agricultural landscape may contribute substantially to the distinctive dietary composition observed (Aizpurua et al. 2018; Aihartza et al. 2023).

Broad dietary similarity, however, did not imply complete trophic equivalence. Dietary differentiation depended on both taxonomic resolution and the dietary metric considered. Differences in dietary breadth were most evident at the OTU level, whereas individual prey richness differed at the family level but not consistently at broader or finer resolutions. OTU-level composition also differed significantly among species, although the effect was small and occurred within substantial dietary overlap. Substantial dietary overlap does not necessarily imply ecological equivalence or preclude coexistence, as closely related species may share much of their trophic niche while differing more subtly in prey use or along other niche dimensions (Schoener 1974; Salinas-Ramos et al. 2015; Rainho et al. 2023). These patterns indicate that dietary breadth, richness, composition and overlap capture complementary aspects of trophic differentiation rather than a single gradient from similarity to segregation. Accordingly, the apparent degree of niche differentiation among generalist predators can shift with both the metric used to characterise diet and the taxonomic resolution at which prey is identified (Razgour et al. 2011; Kent et al. 2026).

548 Differences in morphology, echolocation and foraging behaviour could contribute to the subtle
549 interspecific differences observed. *A. nanus*, for example, is the smallest of the three species and
550 uses substantially higher-frequency echolocation calls (FMaxE ≈ 70–75 kHz) than *N. somalicus*
551 (40–45 kHz) or *P. rendalli* (≈45–49 kHz; Table S4). Across aerial-hawking vespertilionids, higher
552 call frequencies are generally associated with smaller body size and shorter-range, finer-resolution
553 acoustic sampling, which may favour detection of smaller prey or prey encountered in more
554 structurally complex space (Thiagavel et al. 2017; Jung et al. 2014). Such trait differences could
555 explain some of the fine-scale dietary variation observed here (Neuweiler & Covey 2000; Fenton
556 et al. 2016; Leiser-Miller & Santana 2021; Villalobos-Chaves & Santana 2022; Zhu et al. 2024).
557 However, they were not tested directly and should not be interpreted as evidence of trait-mediated
558 specialization. Instead, the species appear to occupy broadly similar trophic space while differing
559 more subtly in how that shared resource base is used, as reported for other sympatric insectivorous
560 bat assemblages (Vesterinen et al. 2018; Andriollo et al. 2021).

561 The prominence of Blattodea, Hemiptera and Coleoptera also gives this shared trophic niche an
562 applied dimension. These groups contain numerous crop-associated insects, including important
563 rice pests (Heinrichs et al. 2017; Sottomayor et al. 2024; Chaves et al. 2026), and all three bat
564 species consumed at least some of the seven potential pest species detected (Table S3), including
565 the African warlike termite *Macrotermes bellicosus* and the rice gall midge *Orseolia oryzae*.
566 These records demonstrate direct trophic links with agricultural pests, although they do not
567 quantify the magnitude of any resulting pest-suppression service. They nevertheless complement
568 growing evidence that insectivorous bats can contribute to the consumption of crop pests in
569 agricultural landscapes (Cohen et al. 2020; Liu et al. 2023; Nsengimana et al. 2023).

570

571 **4.2. Temporal restructuring of trophic niches**

572 The strongest pattern in the study was not simply that diets changed through time, but that
573 seasonality altered the trophic relationships among species. The identity of the most differentiated

574 species pairs changed between June and December, showing that temporal change did not merely
575 strengthen or weaken a fixed pattern of niche partitioning. Instead, the configuration of dietary
576 similarity itself was reorganized through time. Similar seasonal reconfigurations of dietary
577 relationships have been attributed to changes in resource availability interacting with species-
578 specific foraging strategies in other predator assemblages (Falke et al. 2020; Enomoto et al. 2023).

579 The order-level GAM trajectories suggest that much of the temporal restructuring among the three
580 focal species reflected shared responses rather than consistently divergent species-specific shifts.
581 Several major prey groups changed markedly over time, but temporal trajectories did not differ
582 significantly among species. Thus, although pairwise overlap and OTU-level composition
583 changed through time, broad temporal changes in prey use were often shared among the three
584 bats. This suggests that temporal dynamics in the resource landscape may exert a stronger
585 influence on overall diet structure than persistent species-specific differences in prey use, as
586 observed in other bat assemblages (Andriollo et al. 2021; Aihartza et al. 2023).

587 The independent yellow-sticky-trap survey provides useful context for this interpretation. Flying-
588 insect abundance and composition varied strongly throughout the rice cultivation cycle in the
589 same landscape (Fig. S3; Fernandes et al. 2025). The early importance of Blattodea in bat diets
590 coincided with a pronounced June peak in trap captures, consistent with mass termite swarming
591 at the onset of the rainy season (Mitchell 2008). This agreement suggests that some dietary shifts
592 may track conspicuous seasonal resource pulses. However, the relationship was not universal:
593 Hemiptera declined markedly in trap captures after June while their dietary contribution increased
594 through the rice cultivation cycle in all three bat species. Dietary change therefore did not simply
595 mirror overall insect abundance, indicating that temporal trophic dynamics cannot be reduced to
596 passive tracking of prey phenology alone and may also reflect differences in prey accessibility or
597 selection (Pereira et al. 2002; Rainho et al. 2010; Vesterinen et al. 2016; Johnston & Fenton 2001).

598 Taken together, these results indicate that interspecific differences were subtle across
599 complementary aspects of diet, whereas temporal variation more strongly reshaped trophic
600 relationships among the three focal species.

4.3. Limitations and future directions

Several limitations should be considered when interpreting these results. DNA metabarcoding provides high taxonomic resolution but does not reliably quantify prey biomass or the number of prey individuals consumed, because sequence recovery is affected by differential digestion, primer bias and variation in mitochondrial DNA copy number among taxa (Deagle et al. 2019; Elbrecht et al. 2019). Incomplete reference databases for West African arthropods also constrained taxonomic assignment, with only a small proportion of prey OTUs identified confidently to species level. In addition, the insect data from yellow sticky traps were used only as contextual information because the survey was conducted independently of bat sampling and sampled only a subset of the flying arthropod community, rather than providing spatially and temporally matched estimates of prey availability to bats. Consequently, temporal changes in diet cannot be attributed directly to changes in prey abundance, nor can we distinguish effects of prey availability from prey accessibility, prey choice or changes in bat foraging behaviour (Rainho et al. 2010; Vesterinen et al. 2016; Johnston & Fenton 2001). Sex-specific differences in habitat use and diet may also contribute to temporal variation in prey use, but could not be examined in the present study (Lintott et al. 2014; Mata et al. 2019). Sampling was also uneven across months, years and sites, with most samples originating from Bironqui and from 2022. Despite limited representation of some species–month combinations, sensitivity analyses restricting the data by site and year supported the main temporal patterns.

Future studies should therefore combine dietary metabarcoding with concurrent, taxonomically resolved sampling of potential prey and direct information on bat behaviour and habitat use (Aihartza et al. 2023). Integrating these data with morphological and echolocation traits would also allow explicit tests of whether the subtle interspecific dietary differences observed here are associated with functional differences among species (Villalobos-Chaves & Santana 2022). Extending sampling more evenly across seasons, years and sites would be particularly valuable for determining whether the strong temporal restructuring documented between the wet and dry

seasons is recurrent and whether the degree of dietary overlap among species changes consistently with seasonal resource dynamics. Such an integrated approach would help distinguish shared responses to changing prey communities from genuine species-specific prey preferences and provide a stronger basis for understanding how trophic interactions contribute to coexistence in seasonal tropical agroecosystems.

Conclusion

The three sympatric pipistrelle-like bats shared a broad trophic niche, with modest interspecific differentiation that varied with the dietary metric and taxonomic resolution considered. Temporal variation, however, strongly restructured prey use and interspecific overlap through the rice cultivation cycle, including changes in the relative contribution of major prey orders. Together, these findings show that trophic relationships among ecologically similar predators are multidimensional and temporally dynamic and are best characterised by combining complementary measures of dietary breadth, composition and overlap at multiple levels of taxonomic resolution.

References

Aihartza J, Vallejo N, Aldasoro M, García-Mudarra JL, Goiti U, Nogueras J, Ibáñez C (2023) Aerospace-foraging bats eat seasonably across varying habitats. Scientific Reports 13:19576. https://doi.org/10.1038/s41598-023-46939-7

Aizpurua O, Budinski I, Georgiakakis P, Gopalakrishnan S, Ibañez C, Mata VA, Rebelo H, Russo D, Szodoray-Parádi F, Zhelyazkova V, Zrncic V, Gilbert MTP, Alberdi A (2018) Agriculture shapes the trophic niche of a bat preying on multiple pest arthropods across Europe: Evidence from DNA metabarcoding. Molecular Ecology 27:815-825. https://doi.org/10.1111/mec.14474

Andriollo T, Michaux J, Ruedi M (2021) Food for everyone: Differential feeding habits of cryptic bat species inferred from DNA metabarcoding. Molecular Ecology 30:4584-4600. https://doi.org/10.1111/mec.16073

655 Bates PJ, Cameron K, Pearch MJ, Hayes B (2013) A review of the bats (Chiroptera) of the
656 Republic of Congo, including eight species new to the country. Acta Chiropterologica
657 15:313-340. https://doi.org/10.3161/150811013x678955
658 Blanch E, López-Baucells A, Mata VA, Flaquer C, López-Bosch D (2023) To share or not to
659 share: DNA metabarcoding reveals trophic niche overlap between sympatric trawling
660 bats. European Journal of Wildlife Research 69:90. https://doi.org/10.1007/s10344-023-
661 01712-z
662 Boyer F, Mercier C, Bonin A, Le Bras Y, Taberlet P, Coissac E (2016) OBITOOLS: A UNIX-
663 inspired software package for DNA metabarcoding. Molecular Ecology Resources
664 16:176-182. https://doi.org/10.1111/1755-0998.12428
665 Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ,
666 Mächler M, Bolker BM (2017) glmmTMB balances speed and flexibility among
667 packages for zero-inflated generalized linear mixed modeling. The R Journal 9:378.
668 https://doi.org/10.32614/rj-2017-066
669 Brunson JC, Read QD (2017) ggalluvial: Alluvial plots in "ggplot2". CRAN: Contributed
670 Packages. https://doi.org/10.32614/cran.package.ggalluvial
671 Chao A, Gotelli NJ, Hsieh TC, Sander EL, Ma KH, Colwell RK, Ellison AM (2014) Rarefaction
672 and extrapolation with Hill numbers: A framework for sampling and estimation in species
673 diversity studies. Ecological Monographs 84:45-67. https://doi.org/10.1890/13-0133.1
674 Chaves P, Schaafsma M, Dabo D, Lomba JZ, Mane F, de Lima RF, Palmeirim JM, Rocha R, Seck
675 S, Biai J, Timóteo S, Meyer CFJ, Rainho A (2024) Friend or foe? Attitudes of rice farmers
676 toward wild animals in West Africa. Ecology and Society 29:24.
677 https://doi.org/10.5751/ES-15486-290424
678 Chaves PAP, Mata VA, Lopes P, Camará M, Coimbra D, Dabo D, de Lima RF, Lecoq M,
679 Fernandes G, Guedes P, Lacerda I, Massaad M, Meyer CFJ, de Oliveira RN, Palmeirim
680 JM, Rocha R, Biai J, Sottomayor M, Gonçalves T, Ferreira S, Rainho A, Timóteo S (2026)
681 Ecological networks reveal strong pest suppression complementarity between birds and
682 bats within rice-dominated agroecosystems in West Africa. Agriculture, Ecosystems &

683 Environment 396:110020. https://doi.org/10.1016/j.agee.2025.110020
684 Cohen Y, Bar-David S, Nielsen M, Bohmann K, Korine C (2020) An appetite for pests:
685 Synanthropic insectivorous bats exploit cotton pest irruptions and consume various
686 deleterious arthropods. Molecular Ecology 29:1185-1198.
687 https://doi.org/10.1111/mec.15393
688 da Silva, L. P. Mata, V. A. Lopes, P. B. Pereira, P. Jarman, S. N. Lopes, R. J. & Beja, P. (2019).
689 Advancing the integration of multi-marker metabarcoding data in dietary analysis of
690 trophic generalists. *Molecular Ecology Resources*, *19*(6), 1420–1432.
691 https://doi.org/10.1111/1755-0998.13060
692 da Silva LP, Mata VA, Lopes PB, Pereira P, Jarman SN, Lopes RJ, Beja P (2019) Advancing the
693 integration of multi-marker metabarcoding data in dietary analysis of trophic generalists.
694 Molecular Ecology Resources 19:1420-1432. https://doi.org/10.1111/mec.17324
695 Dai W, Li A, Chang Y, Liu T, Zhang L, Li J, Leng H, Li Z, Jin L, Sun K, Feng J (2023) Diet
696 composition, niche overlap and partitioning of five sympatric rhinolophid bats in
697 southwestern China during summer. Frontiers in Ecology and Evolution 11:1108514.
698 https://doi.org/10.3389/fevo.2023.1108514
699 Dammhahn M, Goodman SM (2014) Trophic niche differentiation and microhabitat utilization
700 revealed by stable isotope analyses in a dry-forest bat assemblage at Ankarana, northern
701 Madagascar. Journal of Tropical Ecology 30:97-109.
702 https://doi.org/10.1017/S0266467413000825
703 Deagle BE, Thomas AC, McInnes JC, Clarke LJ, Vesterinen EJ, Clare EL, Kartzinel TR, Eveson
704 JP (2019) Counting with DNA in metabarcoding studies: How should we convert
705 sequence reads to dietary data? Molecular Ecology 28:391-406.
706 https://doi.org/10.1111/mec.14734
707 Elbrecht V, Braukmann TWA, Ivanova NV, Prosser SWJ, Hajibabaei M, Wright M, Zakharov EV,
708 Hebert PDN, Steinke D (2019) Validation of COI metabarcoding primers for terrestrial
709 arthropods. PeerJ 7:e7745. https://doi.org/10.7717/peerj.7745
710 Falke LP, Henderson JS, Novak M, Preston DL (2020) Temporal shifts in intraspecific and

711 interspecific diet variation among 3 stream predators. Freshwater Science 39:115-125.
712 https://doi.org/10.1086/707599.
713 Fernandes GA, Massaad M, Chaves PAP, Rainho A (2025) Tree and landscape characteristics
714 outweigh insect abundance in driving bat activity in West African rice fields. Agriculture,
715 Ecosystems & Environment 393:109774. https://doi.org/10.1016/j.agee.2025.109774
716 Frøslev TG, Kjøller R, Bruun HH, Ejrnæs R, Brunbjerg AK, Pietroni C, Hansen AJ (2017)
717 Algorithm for post-clustering curation of DNA amplicon data yields reliable biodiversity
718 estimates. Nature Communications 8:1188. https://doi.org/10.1038/s41467-017-01312-x
719 Gonçalves A, Nóbrega EK, Rebelo H, Mata VA, Rocha R (2024) A metabarcoding assessment of
720 the diet of the insectivorous bats of Madeira Island, Macaronesia. Journal of Mammalogy
721 105:524-533. https://doi.org/10.1093/jmammal/gyae033
722 Goodman SM, Ranivo J (2004) The taxonomic status of Neoromicia somalicus malagasyensis.
723 Mammalian Biology 69:434-438. https://doi.org/10.1078/1616-5047-00166
724 Grant JD (1988) Food-passage time in Nyctophilus gouldi (Microchiroptera: Vespertilionidae).
725 Journal of Mammalogy 69:653-655. https://doi.org/10.2307/1381367
726 Grunwald AL, Demos TC, Nguéagni Y, Tchamba MN, Monadjem A, Webala PW, Peterhans JC,
727 Patterson BD, Ruedas LA (2023) A review of bats of the genus Pseudoromicia
728 (Chiroptera: Vespertilionidae) with the description of a new species. Systematics and
729 Biodiversity 21:2156002. https://doi.org/10.1080/14772000.2022.2156002
730 Grunwald AL, Demos TC, Atagana PJ, Volk CM, Monadjem A, Okono FPM, Ngueagni Y, Merrill
731 RT, Bevers I, Armstrong KD, Kilber EE, Talla A, Fils EMB, Patterson BD, Ballhorn DJ,
732 Ruedas LA (2025) Uncovering the diversity of bats in the Mbam Minkom Massif,
733 Cameroon: Insights into the importance of tropical inselbergs. Acta Chiropterologica
734 26:275-314. https://doi.org/10.3161/15081109ACC2024.26.2.011
735 Happold M, Happold D (eds) (2013) Mammals of Africa: Hedgehogs, shrews and bats.
736 Bloomsbury Publishing, London. https://doi.org/10.5040/9781472926944.0390
737 Hartig F (2024) DHARMa: Residual diagnostics for hierarchical (multi-level/mixed) regression
738 models. R package version 0.4.7. https://github.com/florianhartig/dharma.

739 Heinrichs EA, Sy AA, Akator SK, Oyediran I (1997) Seasonal occurrence of rice yellow mottle
740 virus in lowland rice in Cote d'Ivoire. International Journal of Pest Management 43:291-
741 297. https://doi.org/10.1080/096708797228591
742 Heinrichs EA, Nwilene FE, Stout MJ, Hadi BAR, Freitas T (2017) Rice insect pests and their
743 management. Burleigh Dodds Science Publishing.
744 https://doi.org/10.4324/9781351114240
745 Hsieh TC, Ma KH, Chao A (2016) iNEXT: An R package for rarefaction and extrapolation of
746 species diversity (Hill numbers). Methods in Ecology and Evolution 7:1451-1456.
747 https://doi.org/10.1111/2041-210x.12613
748 Johnston DS, Fenton MB (2001) Individual and population-level variability in diets of pallid bats
749 (*Antrozous pallidus*). Journal of Mammalogy 82:362-373. https://doi.org/10.1644/1545-
750 1542(2001)082<0362:iaplvi>2.0.co;2
751 Kent CM, Powell S, Sherry TW (2026) Multispecies niche overlap: Moving beyond pairwise
752 metrics to understand community-wide similarities in resource use. Ecology and
753 Evolution 16:e73886. https://doi.org/10.1002/ece3.73886.
754 Kolkert H, Andrew R, Smith R, Rader R, Reid N (2020) Insectivorous bats selectively source
755 moths and eat mostly pest insects on dryland and irrigated cotton farms. Ecology and
756 Evolution 10:371-388. https://doi.org/10.1002/ece3.5901
757 Krüger F, Clare EL, Greif S, Siemers BM, Symondson WOC, Sommer RS (2014) An integrative
758 approach to detect subtle trophic niche differentiation in the sympatric trawling bat
759 species *Myotis dasycneme* and *Myotis daubentonii*. Molecular Ecology 23:3657-3671.
760 https://doi.org/10.1111/mec.12512.
761 Langley I, Hammond PS, Thompson PM, Pierce GJ, Wilson LJ, Hall AJ, Hastie GD, Russell DJ
762 (2026) Temporal changes in the dietary niche of sympatric seals provides insight into the
763 role of competition in population declines. Oikos 2026:e11875.
764 https://doi.org/10.1002/oik.11875
765 Lausen CL, Barclay RMR (2005) *Pipistrellus nanus*. Mammalian Species 784:1-7.
766 https://doi.org/10.1644/784.1

767 Lenth RV (2021) emmeans: Estimated marginal means, aka least-squares means. R package
768 version 1.8.5. https://cran.r-project.org/package=emmeans
769 Lintott PR, Bunnefeld N, Fuentes-Montemayor E, Minderman J, Mayhew RJ, Olley L, Park KJ
770 (2014) City life makes females fussy: Sex differences in habitat use of temperate bats in
771 urban areas. Royal Society Open Science 1:140200. https://doi.org/10.1098/rsos.140200
772 Liu G, Zhang S, Zhao X, Li C, Gong M (2021) Advances and limitations of next generation
773 sequencing in animal diet analysis. Genes 12:1854.
774 https://doi.org/10.3390/genes12121854
775 Liu Y, Si M, Huang Z, Feng J, Jiang T (2023) Bats are sentinels for invasive pest surveillance
776 based on DNA metabarcoding. Ecological Indicators 152:110354.
777 https://doi.org/10.1016/j.ecolind.2023.110354
778 Lopes P, Lacerda I, Chaves P, de Lima RF, Camará M, Lecoq M, Palmeirim JM, Rainho A (2026a)
779 Landscape context outweighs field-scale features in structuring bird communities in West
780 African smallholder rice agroecosystems. Web Ecology 26:103-118.
781 https://doi.org/10.5194/we-26-103-2026
782 Lopes P, Lacerda I, Chaves P, de Lima R, Camará M, Lecoq M, Rainho A, Palmeirim J (2026b)
783 Bird community dynamics across the rice cycle in small-scale rainfed floodplain fields in
784 West Africa. Ibis 168: 1611-1628. https://doi.org/10.1111/ibi.70077
785 Maas B, Karp DS, Bumrungsri S, Darras K, Gonthier D, Huang JC, Lindell CA, Maine JJ, Mestre
786 L, Michel NL, Morrison EB, Perfecto I, Philpott SM, Şekercioğlu ÇH, Silva RM, Taylor
787 PJ, Tscharntke T, Van Bael SA, Whelan CJ, Williams-Guillén K (2016) Bird and bat
788 predation services in tropical forests and agroforestry landscapes. Biological Reviews
789 91:1081-1101. https://doi.org/10.1111/brv.12211
790 MacArthur R, Levins R (1967) The limiting similarity, convergence, and divergence of coexisting
791 species. The American Naturalist 101:377-385. https://doi.org/10.1086/282505
792 Magoč T, Salzberg SL (2011) FLASH: Fast length adjustment of short reads to improve genome
793 assemblies. Bioinformatics 27:2957-2963. https://doi.org/10.1093/bioinformatics/btr507
794 Maine JJ, Boyles JG (2015) Land cover influences dietary specialization of insectivorous bats

795 globally. Mammal Research 60:343-351. https://doi.org/10.1007/s13364-015-0243-z
796 Maudet C, Miller C, Bassano B, Breitenmoser-Würsten C, Gauthier D, Obexer-Ruff G, Michallet
797 J, Taberlet P, Luikart G (2002) Microsatellite DNA and recent statistical methods in
798 wildlife conservation management: Applications in alpine ibex [*Capra ibex* (*ibex*)].
799 Molecular Ecology 11:421-436. https://doi.org/10.1046/j.0962-1083.2001.01451.x
800 Mata, V. A., Amorim, F., Corley, F. V. M., McCracken, G. F., Rebelo, H. & Beja, P. (2016).
801 Female dietary bias towards large migratory moths in the European free-tailed bat
802 (*Tadarida teniotis*). *Biology Letters,*12 (3):
803 20150988. https://doi.org/10.1098/rsbl.2015.0988
804 Mata VA, Amorim F, Corley FVM, McCracken GF, Rebelo H, Beja P (2016) Female dietary bias
805 towards large migratory moths in the European free-tailed bat (Tadarida teniotis). Biology
806 Letters 12:20150988. https://doi.org/10.1002/eap.2457
807 Mitchell JD (2008) Swarming flights of the fungus-growing termite, *Macrotermes natalensis*
808 (Haviland) (Isoptera: Macrotermitinae), and the environmental factors affecting their
809 timing and duration. African Entomology 16:143-152. https://doi.org/10.4001/1021-
810 3589-16.2.143
811 Monadjem A, Ellstrom M, Maldonaldo C, Fasel N (2010a) The activity of an insectivorous bat
812 *Neoromicia nana* on tracks in logged and unlogged forest in tropical Africa. African
813 Journal of Ecology 48:1083-1091. https://doi.org/10.1111/j.1365-2028.2010.01219.x
814 Monadjem A, Taylor PJ, Cotterill FPD, Schoeman MC (2010b) Bats of Southern and Central
815 Africa: A biogeographic and taxonomic synthesis. Wits University Press
816 Monadjem A, Richards L, Taylor PJ, Stoffberg S (2013) High diversity of pipistrelloid bats
817 (Vespertilionidae: Hypsugo, Neoromicia, and Pipistrellus) in a West African rainforest
818 with the description of a new species. Zoological Journal of the Linnean Society 167:191-
819 207. https://doi.org/10.1111/j.1096-3642.2012.00871.x
820 Monadjem A, Richards LR, Decher J, Hutterer R, Mamba ML, Guyton J, Naskrecki P, Markotter
821 W, Wipfler B, Kropff AS, Dalton DL (2020) A phylogeny for African Pipistrellus species
822 with the description of a new species from West Africa (Mammalia: Chiroptera).

823 Zoological Journal of the Linnean Society 191:548-574.
824 https://doi.org/10.1093/zoolinnean/zlaa068
825 Monadjem A, Demos TC, Dalton DL, Webala PW, Musila S, Kerbis Peterhans JC, Patterson BD
826 (2021) A revision of pipistrelle-like bats (Mammalia: Chiroptera: Vespertilionidae) in
827 East Africa with the description of new genera and species. Zoological Journal of the
828 Linnean Society 191:1114-1146. https://doi.org/10.1093/zoolinnean/zlaa087
829 Naidoo S, Vosloo D, Schoeman MC (2013) Foraging at wastewater treatment works increases the
830 potential for metal accumulation in an urban adapter, the banana bat (*Neoromicia nana*).
831 African Zoology 48:39-55. https://doi.org/10.1080/15627020.2013.11407567 .
832 Nielsen JM, Clare EL, Hayden B, Brett MT, Kratina P (2018) Diet tracing in ecology: Method
833 comparison and selection. Methods in Ecology and Evolution 9:278-291.
834 https://doi.org/10.1111/2041-210X.12869
835 Nóbrega EK, Toshkova N, Gonçalves A, Reis A, Soto EJ, Ruiz SP, Mata VA, Rato C, Rocha R
836 (2023) Insights into the habitat associations, phylogeny, and diet of *Pipistrellus*
837 *maderensis* in Porto Santo, northeastern Macaronesia. Web Ecology 23:87-98.
838 https://doi.org/10.5194/we-23-87-2023.
839 Norberg U, Rayner J (1987) Ecological morphology and flight in bats (Mammalia; Chiroptera):
840 Wing adaptations, flight performance, foraging strategy and echolocation. Philosophical
841 Transactions of the Royal Society of London B, Biological Sciences 316:335-427.
842 https://doi.org/10.1098/rstb.1987.0030
843 Novella-Fernandez R, Ibañez C, Juste J, Clare EL, Doncaster CP, Razgour O (2020) Trophic
844 resource partitioning drives fine-scale coexistence in cryptic bat species. Ecology and
845 Evolution 10:14122-14136. https://doi.org/10.1002/ece3.7004
846 Nsengimana O, Walker FM, Webala PW, Twizeyimana I, Dusabe MC, Sanchez DE, Sobek CJ,
847 Ruhagazi D, Iribagiza P, Muvunyi R, Medellin RA (2023) Our good neighbours:
848 Understanding ecosystem services provided by insectivorous bats in Rwanda. PLOS
849 ONE 18:e0287536. https://doi.org/10.1371/journal.pone.0287536
850 Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB,

Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2018) vegan: Community ecology package. R package version 2.4-6. https://CRAN.R-project.org/package=vegan

Patterson BD, Webala PW (2012) Keys to the bats (Mammalia: Chiroptera) of East Africa. Fieldiana Life and Earth Sciences 6:1-60. https://doi.org/10.3158/2158-5520-12.6.1

Pereira MJR, Rebelo H, Rainho A, Palmeirim JM (2002) Prey selection by *Myotis myotis* (Vespertilionidae) in a Mediterranean region. Acta Chiropterologica 4:183-193. https://doi.org/10.3161/001.004.0207

Pianka ER (1973) The structure of lizard communities. Annual Review of Ecology and Systematics 4:53-74. https://doi.org/10.1146/annurev.es.04.110173.000413

R Core Team (2025) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Rainho A, Augusto AM, Palmeirim JM (2010) Influence of vegetation clutter on the capacity of ground foraging bats to capture prey. Journal of Applied Ecology 47:850-858. https://doi.org/10.1111/j.1365-2664.2010.01820.x

Rainho A, Ferreira DF, Makori B, Bartonjo M, Repas-Gonçalves M, Kirakou S, Maghuwa F, Webala PW, Tomé R (2023) Guild vertical stratification and drivers of bat foraging in a semi-arid tropical region, Kenya. Biology 12:1116. https://doi.org/10.3390/biology12081116

Razgour O, Clare EL, Zeale MRK, Hanmer J, Schnell IB, Rasmussen M, Gilbert TP, Jones G (2011) High-throughput sequencing offers insight into mechanisms of resource partitioning in cryptic bat species. Ecology and Evolution 1:556-570. https://doi.org/10.1002/ece3.49

Roeleke M, Johannsen L, Voigt CC (2018) How bats escape the competitive exclusion principle: Seasonal shift from intraspecific to interspecific competition drives space use in a bat ensemble. Frontiers in Ecology and Evolution 6:101. https://doi.org/10.3389/fevo.2018.00101

Rognes T, Flouri T, Nichols B, Quince C, Mahé F (2016) VSEARCH: A versatile open-source tool for metagenomics. PeerJ 4:e2584. https://doi.org/10.7717/peerj.2584

879 Salinas-Ramos VB, Herrera Montalvo LG, León-Regagnon V, Arrizabalaga-Escudero A, Clare
880 EL (2015) Dietary overlap and seasonality in three species of mormoopid bats from a
881 tropical dry forest. Molecular Ecology 24:5296-5307. https://doi.org/10.1111/mec.13386
882 Salsamendi E, Garin I, Arostegui I, Goiti U, Aihartza J (2012) What mechanism of niche
883 segregation allows the coexistence of sympatric sibling rhinolophid bats? Frontiers in
884 Zoology 9:30. https://doi.org/10.1186/1742-9994-9-30
885 Schoeman MC, Jacobs DS (2008) The relative influence of competition and prey defences on the
886 phenotypic structure of insectivorous bat ensembles in Southern Africa. PLoS ONE
887 3:e3715. https://doi.org/10.1371/journal.pone.0003715
888 Schoeman MC, Jacobs DS (2011) The relative influence of competition and prey defences on the
889 trophic structure of animalivorous bat ensembles. Oecologia 166:493-506.
890 https://doi.org/10.1007/s00442-010-1854-3
891 Schoener TW (1974) Resource partitioning in ecological communities: Research on how similar
892 species divide resources helps reveal the natural regulation of species diversity. Science
893 185:27-39. https://doi.org/10.1126/science.185.4145.27
894 Simmons NB, Cirranello AL (2025) Bat species of the world: A taxonomic and geographic
895 database. Version 1.9. Accessed 11 June 2025
896 Sottomayor M, Palmeirim AF, Meyer CFJ, de Lima RF, Rocha R, Rainho A (2024) Nature-based
897 solutions to increase rice yield: An experimental assessment of the role of birds and bats
898 as agricultural pest suppressors in West Africa. Agriculture, Ecosystems & Environment
899 370:109067. https://doi.org/10.1016/j.agee.2024.109067
900 Sousa LL, Silva SM, Xavier R (2019) DNA metabarcoding in diet studies: Unveiling ecological
901 aspects in aquatic and terrestrial ecosystems. Environmental DNA 1:199-214.
902 https://doi.org/10.1002/edn3.27
903 Srilopan S, Mata VA, Bumrungsri S (2025) DNA metabarcoding reveals insights into diet
904 partitioning and pest suppression by open space bats in agricultural landscapes. Acta
905 Chiropterologica 26:171-187. https://doi.org/10.3161/15081109acc2024.26.2.003
906 Staliński J (1994) Digestion, defecation and food passage rate in the insectivorous bat *Myotis*

907 *myotis*. Acta Theriologica 39:1-11. https://doi.org/10.4098/at.arch.94-1
908 Stevens RD, Willig MR (2000) Density compensation in New World bat communities. Oikos
909 89:367-377. https://doi.org/10.1034/j.1600-0706.2000.890218.x
910 Taylor PJ, Matamba E, Steyn JN, Nangammbi T, Zepeda-Mendoza ML, Bohmann K (2017) Diet
911 determined by next generation sequencing reveals pest consumption and opportunistic
912 foraging by bats in macadamia orchards in South Africa. Acta Chiropterologica 19:239-
913 254. https://doi.org/10.3161/15081109acc2017.19.2.003
914 Taylor PJ, Strydom E, Richards L, Markotter W, Toussaint DC, Kearney T, Cotterill FP, Howard
915 A, Weier SM, Keith M, Neef G, Mamba ML, Magagula S, Monadjem A (2022)
916 Integrative taxonomic analysis of new collections from the Central Angolan Highlands
917 resolves the taxonomy of African pipistrelloid bats on a continental scale. Zoological
918 Journal of the Linnean Society 196:1570-1590.
919 https://doi.org/10.1093/zoolinnean/zlac071
920 Taylor-Boyd H, Fuentes-Montemayor E, Monadjem A, Cooper-Bohannon R, Montauban C, Mata
921 VA, Rebelo H, Kangwa B, Mateke C, Park K (2025) Acoustic parameters of bat
922 echolocation calls in Zambia: A collaborative effort to develop a call library for non-
923 invasive research and monitoring. Acta Chiropterologica 27:111-124.
924 https://doi.org/10.3161/15081109acc2025.27.1.010
925 Torrent L, Juste J, Garin I, Aihartza J, Dalton DL, Mamba M, Tanshi I, Powell LL, Padidar S,
926 Garcia Mudarra JL, Richards L, Monadjem A (2025) Taxonomic revision of African
927 pipistrelle-like bats with a new species from the West Congolean Rainforest. Zoological
928 Journal of the Linnean Society 204:zlaf020. https://doi.org/10.1093/zoolinnean/zlaf020
929 Vamos EE, Elbrecht V, Leese F (2017) Short COI markers for freshwater macroinvertebrate
930 metabarcoding. Metabarcoding and Metagenomics 1:e14625.
931 https://doi.org/10.3897/mbmg.1.14625
932 Vesterinen EJ, Ruokolainen L, Wahlberg N, Peña C, Roslin T, Laine VN, Vasko V, Sääksjärvi IE,
933 Norrdahl K, Lilley TM (2016) What you need is what you eat? Prey selection by the bat
934 *Myotis daubentonii*. Molecular Ecology 25:1581-

1594. https://doi.org/10.1111/mec.13564

Vesterinen EJ, Puisto AIE, Blomberg AS, Lilley TM (2018) Table for five, please: Dietary partitioning in boreal bats. Ecology and Evolution 8:10914-10937. https://doi.org/10.1002/ece3.4559

Villalobos-Chaves D, Santana SE (2022) Craniodental traits predict feeding performance and dietary hardness in a community of Neotropical free-tailed bats (Chiroptera: Molossidae). Functional Ecology 36:1690-1699. https://doi.org/10.1111/1365-2435.14063.

Waghiiwimbom MD, Eric-Moise BF, Jules AP, Tamesse JL (2019) The diet composition of four vesper bats (Chiroptera: Vespertilionidae) from the Centre Region of Cameroon (Central Africa). International Journal of Natural Resource Ecology and Management 4:153-163. https://doi.org/10.11648/j.ijnrem.20190406.11.

Wickham H (2016) ggplot2: Elegant graphics for data analysis, 2nd edn. Springer, Cham. https://doi.org/10.1007/978-3-319-24277-4

Wilson DE, Mittermeier RA (eds) (2019) Handbook of the mammals of the world, volume 9: Bats. Lynx Edicions, Barcelona

Wood S (2025) mgcv: Mixed GAM computation vehicle with automatic smoothness estimation. Version 1.9-3. https://doi.org/10.32614/CRAN.package.mgcv

Xavier BS, Rainho A, Santos AM, Vieira MV, Carvalho WD (2023) Global systematic map of research on bats in agricultural systems. Frontiers in Ecology and Evolution 11:1214176. https://doi.org/10.3389/fevo.2023.1214176.

Zahn A, Rodrigues L, Rainho A, Palmeirim JM (2007) Critical times of the year for *Myotis myotis*, a temperate zone bat: roles of climate and food resources. Acta Chiropterologica 9:115-125. https://doi.org/10.3161/1733-5329(2007)9[115:CTOTYF]2.0.CO;2

Zhu D, Liu Y, Gong L, Si M, Wang Q, Feng J, Jiang T (2024) The consumption and diversity variation responses of agricultural pests and their dietary niche differentiation in insectivorous bats. Animals 14:815. https://doi.org/10.3390/ani14050815

Zhukova SS, Yuzefovich AP, Lebedev VS, Kruskop SV (2025) Reassessment of the taxonomic borders within Pipistrellus (Chiroptera, Vespertilionidae, Pipistrellini). Diversity 17:317.

963 https://doi.org/10.3390/d17050317.

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