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Carolina Ribeiro

Universidade de Lisboa

Patrícia A.P. Chaves

Universidade de Lisboa

Paula Lopes

Universidade de Lisboa

Gonçalo A. Fernandes

Universidade de Lisboa

Sérgio Timóteo

University of Coimbra

Ricardo Rocha

University of Oxford

Christoph F.J. Meyer

University of Salford

Vanessa A. Mata

CIBIO - Centro de Investigação em Biodiversidade e Recursos Genéticos

Jorge M. Palmeirim

Universidade de Lisboa

Ana Rainho

`amrainho@ics.ulisboa.pt`

Universidade de Lisboa

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Carolina Ribeiro¹; Patrícia A.P. Chaves¹; Paula Lopes^{1,2}; Gonçalo A. Fernandes¹; Sérgio Timóteo³; Ricardo Rocha⁴; Christoph F.J. Meyer⁵; Vanessa A. Mata^{6,7}; Jorge M. Palmeirim¹ and Ana Rainho^{1,8}

1. CE3C - Centre for Ecology, Evolution and Environmental Changes & CHANGE - Global Change and Sustainability Institute, Departamento de Biologia, Faculdade de Ciências, Universidade de Lisboa, 1749-016 Lisbon, Portugal

2. SPEA - Portuguese Society for the Study of Birds, 1700-031 Lisboa, Portugal

3. Centre for Functional Ecology, Associate Laboratory TERRA, Department of Life Sciences, University of Coimbra, Calçada Martim de Freitas, 3000-456 Coimbra, Portugal.

4. Department of Biology, University of Oxford, 11a Mansfield Rd, OX1 3SZ, Oxford, UK5.

5. ERIC - Environmental Research and Innovation Centre, Faculty of Health, Community and Life Sciences, University of Salford, Salford, M5 4WT, UK

6. CIBIO - Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO - Laboratório Associado, , Campus de Vairão, 4485-661 Vairão, Portugal.

7. BIOPOLIS - Program in Genomics, Biodiversity and Land Planning, Campus de Vairão, 4485-661 Vairão, Portugal

8. ICS - Instituto de Ciências Sociais, Universidade de Lisboa, Av. Professor Aníbal de Bettencourt 9, 1600-189 Lisboa, Portugal

Corresponding author: Ana Rainho (amrainho@ics.ulisboa.pt)

Carolina Ribeiro <https://orcid.org/0009-0009-2805-7053>

Patrícia A.P. Chaves <https://orcid.org/0000-0001-6571-0191>

Paula Lopes <https://orcid.org/0009-0007-1073-594X>

Gonçalo A. Fernandes <https://orcid.org/0000-0001-8605-6248>

Sérgio Timóteo <https://orcid.org/0000-0003-2417-3259>

Ricardo Rocha <https://orcid.org/0000-0003-2757-7347>
Christoph F.J. Meyer <https://orcid.org/0000-0001-9958-8913>
Vanessa A. Mata <https://orcid.org/0000-0003-3005-9030>
Jorge M. Palmeirim <https://orcid.org/0000-0003-4734-8162>
Ana Rainho <https://orcid.org/0000-0001-8826-9458>

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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).

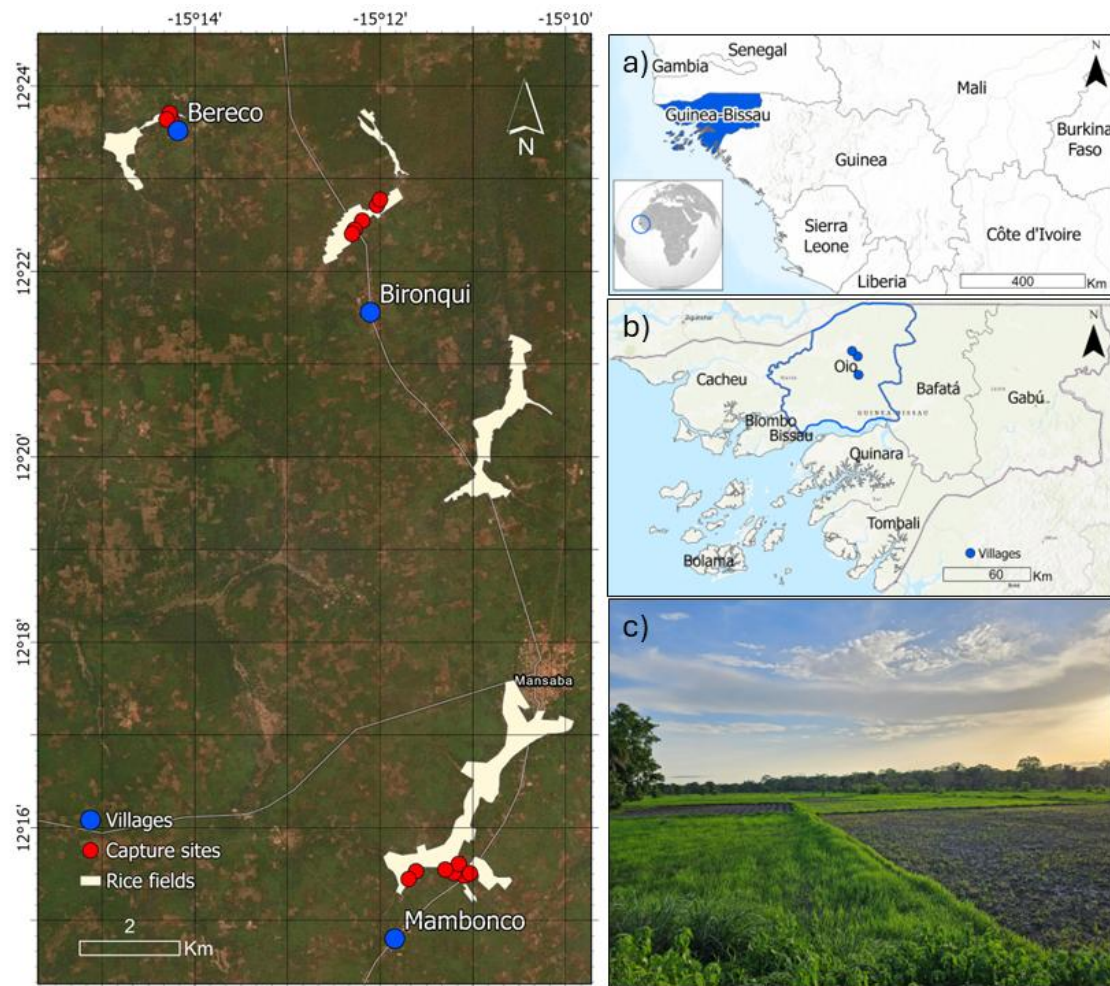


Fig. 1 Location and context of the study area in Guinea-Bissau. The main map (left) shows the rice fields, nearby villages, and capture locations where at least one individual of the three focal bat species was recorded and included in the dietary study. Insets on the right show (a) the location of Guinea-Bissau 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, NOAA, 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 $12,000 \times g$ 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; Roche), 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 $\geq 99\%$ for species, $\geq 97\%$ for genus, $\geq 95\%$ for family, and $\geq 90\%$ 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 $\times$ 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: $wPOO \sim \text{Species} + s(\text{month}, \text{by} = \text{Species})$ 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 ($wPOO \sim s(\text{month})$) were fitted for species $\times$ 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 $\pm$ 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.

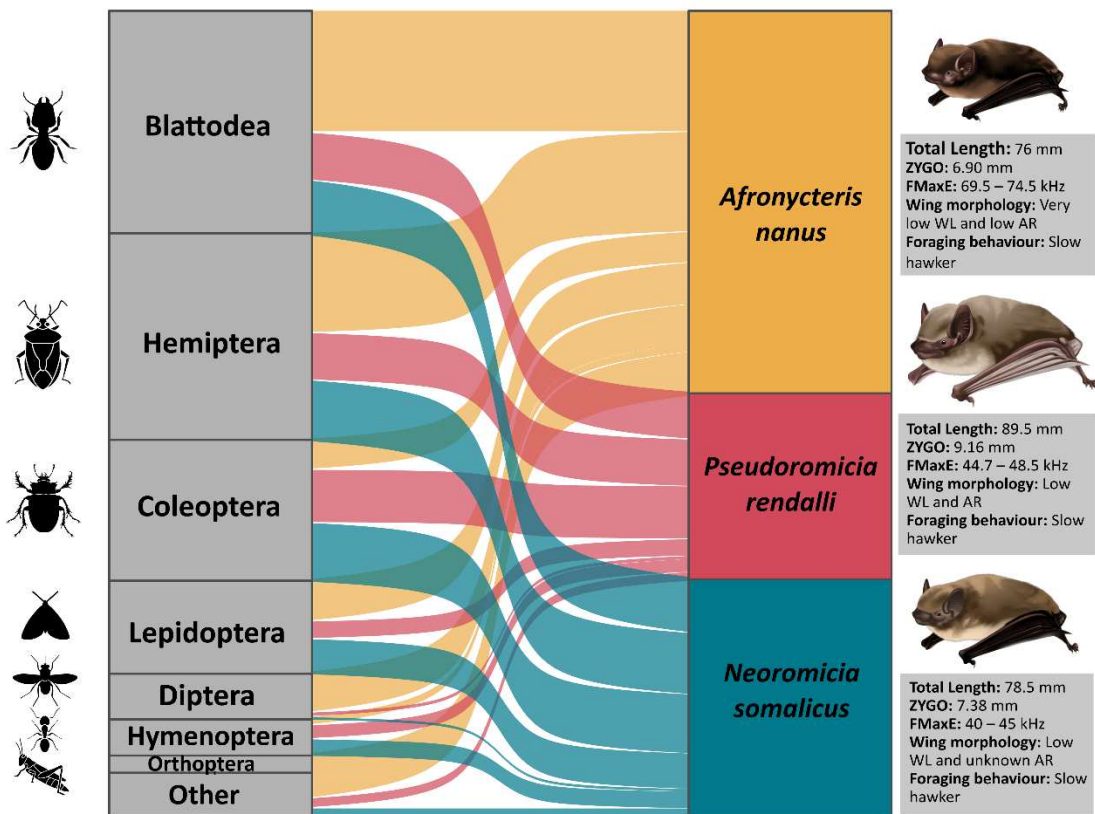


Fig. 2 Dietary interactions between the top seven consumed prey orders – Blattodea, Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera, Orthoptera, and Other (includes the orders Araneae, Crassiditellata, Dermaptera, Neuroptera, Psocodea, Scolopendromorpha, and Trichoptera) – and the three Pipistrelle-like 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).

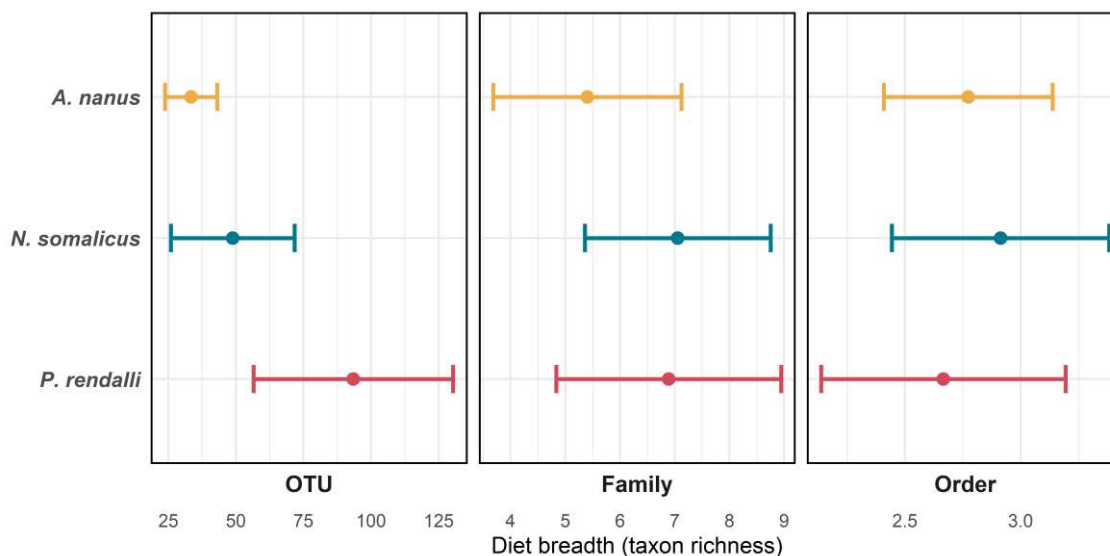


Fig. 3 Estimated dietary breadth of the three bat species at three prey taxonomic levels (OTU, family, and order). Points represent estimated prey richness (Hill number, $q = 0$), and horizontal bars indicate 95% confidence intervals based on 1,000 bootstrap replicates. A target sample coverage of 0.40 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

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

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

3.2. Diet Overlap

NMDS ordination (stress = 0.127; Fig. 4) showed substantial overlap in dietary composition among the three bat species, although their distributions in ordination space were not identical. Several of the dominant prey orders, including Hemiptera, Lepidoptera and Blattodea, occupied 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.

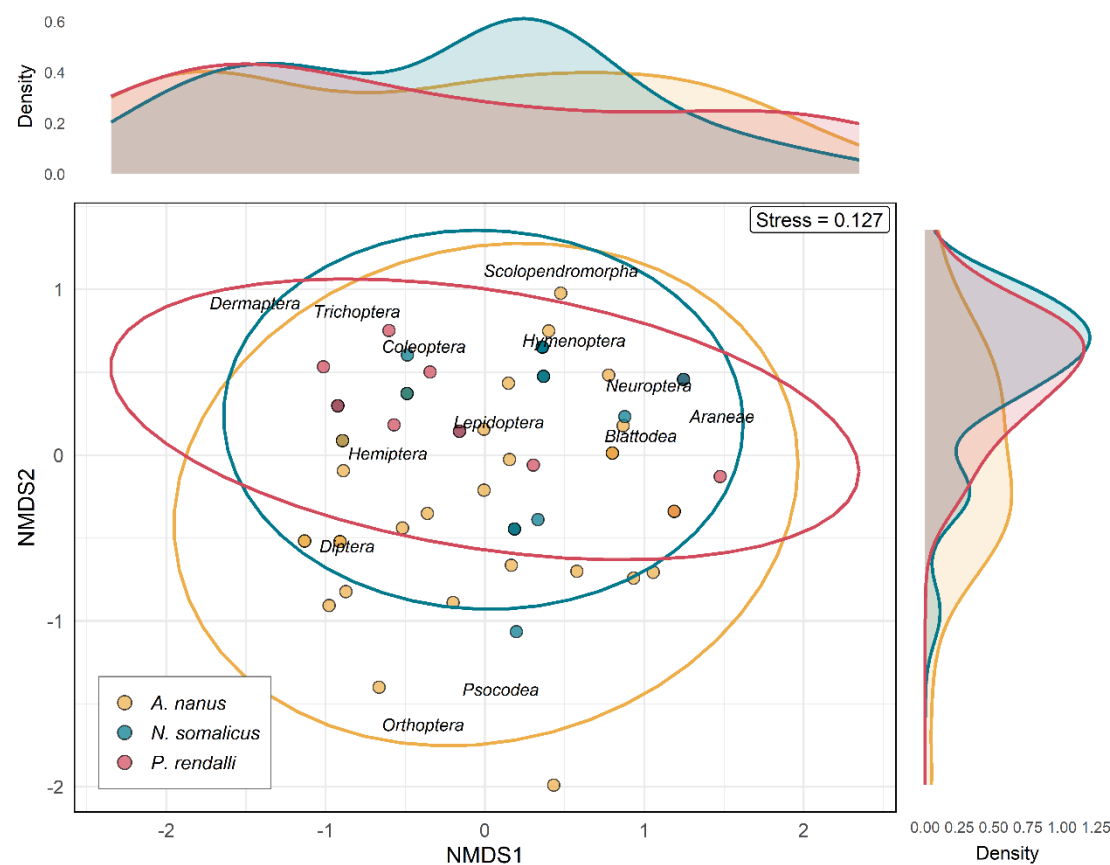


Fig. 4 Non-metric multidimensional scaling (NMDS) ordination of dietary composition of *Afronycteris nanus*, *Neoromicia somalicus*, and *Pseudoromicia rendalli*, based on Jaccard dissimilarities calculated from presence–absence of prey orders detected in individual faecal samples ($k = 2$; stress = 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).

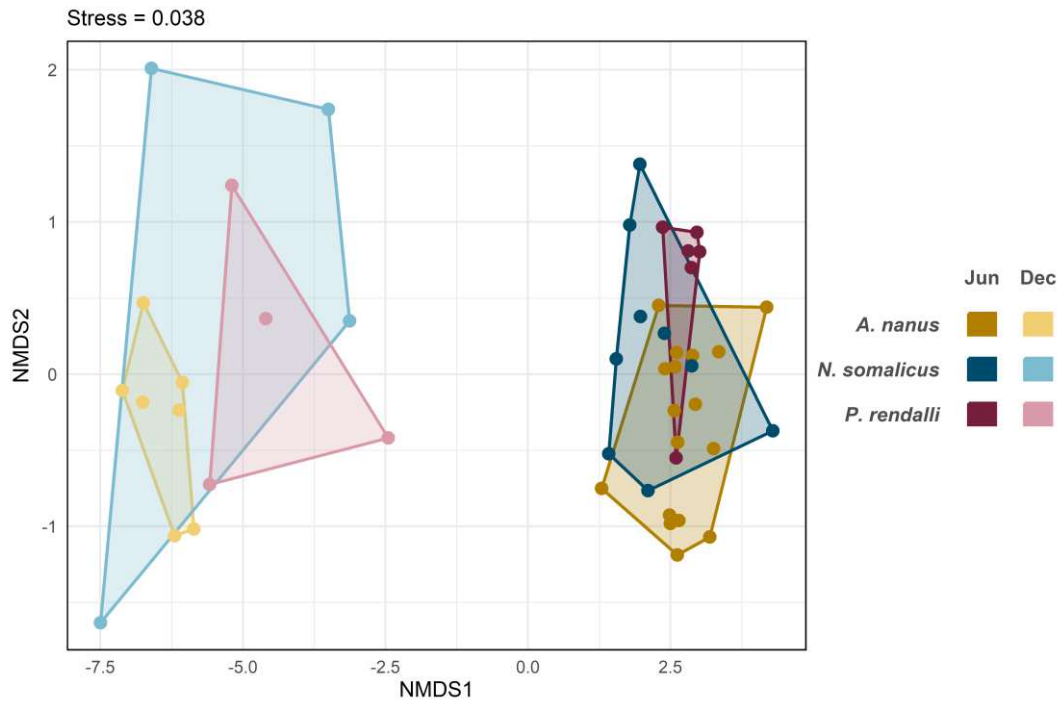


Fig. 5 Non-metric multidimensional scaling (NMDS) ordination of dietary composition of *Afronycteris nanus*, *Neoromicia somalicus*, and *Pseudoromicia rendalli* sampled in June and December at Bironqui, based on Jaccard dissimilarities calculated from presence–absence of prey OTUs detected in individual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

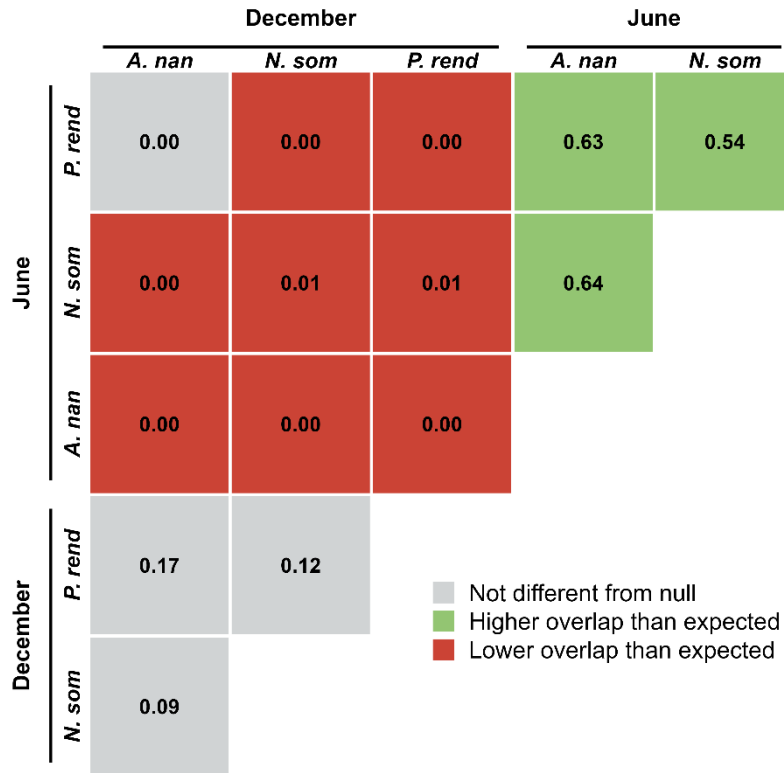


Fig. 6 Pairwise dietary overlap among *A. nanus*, *N. somalicus*, and *P. rendalli* sampled at Bironqui in June and December, quantified using Pianka's index based on OTU-level prey occurrence (Table S10). Each cell shows the observed Pianka overlap index for a species–month pair. Green cells indicate 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).

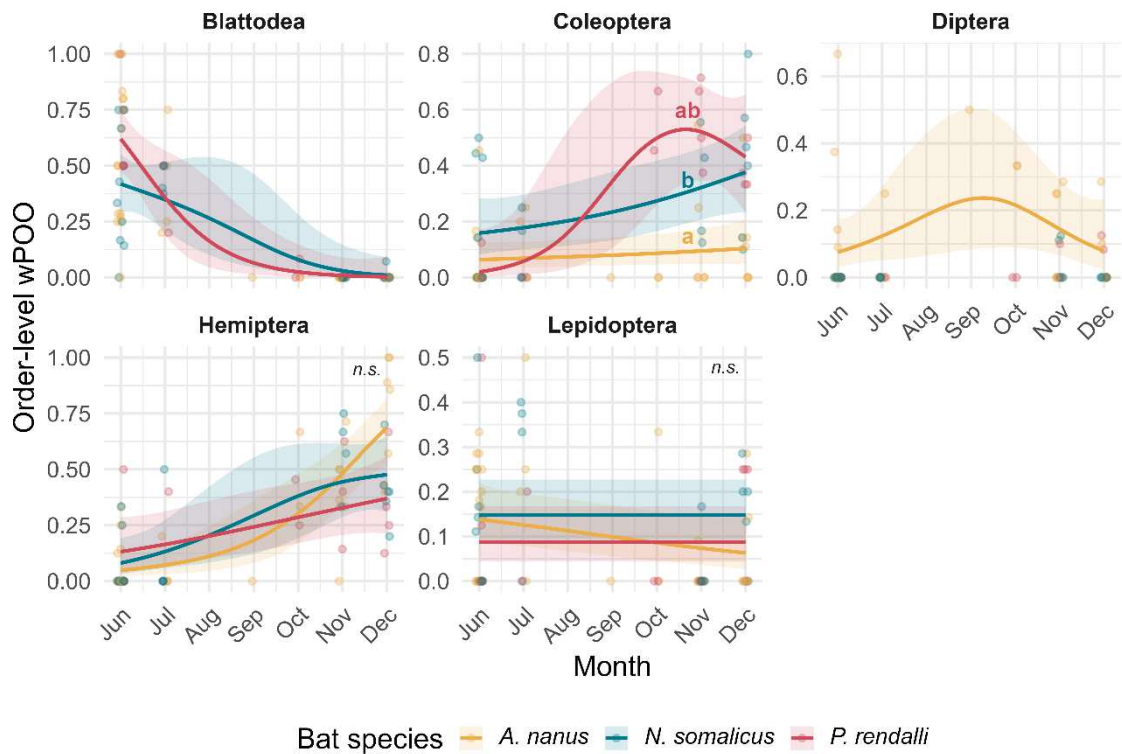


Fig. 7 Temporal variation in the dietary contribution of major arthropod orders to the diets of *Afronycteris nanus*, *Neoromicia somalicus*, and *Pseudoromicia rendalli* between June and December. Dietary contribution is expressed as order-level weighted proportion of occurrence (wPOO). Lines represent 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).

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

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

4.2. Temporal restructuring of trophic niches

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

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

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

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

Taken together, these results indicate that interspecific differences were subtle across complementary aspects of diet, whereas temporal variation more strongly reshaped trophic 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.

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