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Trophic niche structure of invertebrate-eating bats and birds in West African rice agroecosystems revealed by DNA metabarcoding

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Author Contributions: AR originally formulated the idea and developed the methodology, CM, ST, ML, RL, RR, JP, AR, PL, PC and TG conducted field work, VM performed all laboratory analyses, VM, PC, TG and AR conducted data curation, TG performed the data analyses and wrote the manuscript draft, all authors contributed to review and editing of the final manuscript.

Abstract

Knowledge of animal community diets is essential for understanding ecosystem functioning. Bats and birds are important groups of invertebrate predators, managing their populations. However, the diets of West African species and the mechanisms shaping them remain poorly understood. In this study, we investigated these mechanisms in agricultural landscapes of Guinea-Bissau using metabarcoding and next-generation sequencing. Specifically, we asked: 1) How do dietary breadth and composition vary among predator species and between bats and birds 2) How does dietary overlap vary within and between guilds? (3) To what extent is dietary dissimilarity associated with phylogeny?

We analysed the diet of 13 bat and eight bird species. Results revealed that Hemiptera (18.5%); Coleoptera (16.6%), Blattodea (15.8%), Lepidoptera (15.5%) and Orthoptera (11.4%) were the most consumed orders, with termites (Blattodea, Termitidae) standing out (8.2%). Based on OTU richness and sample-based rarefaction, all predators exhibited broad niches (99.7 ± 37.4 OTUs per predator species, on average), with bats generally exhibiting broader niches. Bats' and birds' diets differed significantly (ANOSIM R = 0.61, p = 0.001), possibly driven by differences in foraging periods. At the OTU level, birds displayed significant dietary segregation (O_{birds} = 0.05, p = 0.017), whereas some bats displayed significant dietary overlap (O_{bats} = 0.23, p = 0.001), indicating low interspecific competition. However, we found no strong correlation between diet dissimilarity and phylogeny.

These findings provide insight into niche partitioning and may inform future assessments on the importance of the ecological role of bats and birds in West African agroecosystems.

Key words

Dietary overlap; Community ecology; Niche partitioning; Ecosystem services; Biodiversity conservation

Introduction

Diet is a fundamental component of animal ecology because it defines the resources that organisms use and therefore constrains the ecological niche they can occupy (McCann 2007). Dietary studies provide insights into species' energetic requirements, ecological roles, and the trophic interactions that structure communities. Additionally, studies of trophic niches provide essential insights into resource partitioning and coexistence, particularly in species-rich assemblages where multiple consumers exploit overlapping prey pools (Schoener 1974; Novella-Fernandez et al. 2020). However, trophic niches are rarely structured along a single ecological axis; instead, multiple mechanisms may operate simultaneously and at different hierarchical levels within predator assemblages (Chesson 2000; McGill et al. 2006)

Bats and birds are two major groups of aerial insectivorous that exert strong top-down effects on invertebrate communities, thereby influencing ecosystem functioning across terrestrial ecosystems (Kunz et al. 2011; Nyffeler et al. 2018). Their trophic ecology has been shown to vary widely among species, shaped by morphological, behavioural, and environmental differences (Salinas-Ramos et al. 2015; Maine and Boyles 2015; Mansor et al. 2018; Davies et al. 2022). Although regional context modifies prey availability and predator foraging opportunities, a consistent global pattern is that insectivorous bats generally display broader diets than most birds (Maas et al. 2016). This difference is frequently attributed to their nocturnal activity, the greater taxonomic diversity of nocturnal arthropods, and the broad range of foraging strategies adopted by bats (Maas et al. 2016; Wong and Didham 2024). Temporal segregation of foraging activity therefore represents one important axis of niche differentiation among aerial predators (Kronfeld-Schor and Dayan 2003), but its relative contribution remains unclear when considered alongside other ecological and evolutionary factors. Evolutionary history may also contribute to trophic divergence, with more distantly related species often differing in diet due to morphological constraints, sensory adaptations, and distinct ancestral foraging strategies (Van Cakenberghe et al. 2002; Brändle et al. 2002; Carrillo-Araujo et al. 2015). Conversely, closely related species may display similar diets unless competition or behavioural differentiation promotes trophic segregation (Schoener 1974; Stevens and Willig 2000), as predicted by traditional niche theory (Macarthur and Levins 1967). Nevertheless, dietary similarity does not necessarily scale linearly with phylogenetic distance, particularly in highly mobile and opportunistic predators, where behavioural plasticity and fluctuating resource availability may override evolutionary proximity.

Tropical systems, characterised by high arthropod diversity and pronounced seasonal variability, provide a valuable context in which to examine how multiple ecological axes structure trophic niches (Novotny and Miller 2014). Agricultural mosaics such as rainfed rice systems combine high productivity with marked temporal changes in prey availability (Lawler 2001), while still maintaining diverse predator communities (Chaves et al. 2026). These landscapes therefore offer an opportunity to examine how temporal activity, trophic strategy, and evolutionary history interact in shaping dietary patterns within and between predator guilds.

Thus, trophic differentiation in aerial predator assemblages may emerge from distinct ecological axes operating at different hierarchical levels. Temporal activity may structure broad guild-level segregation, whereas within-guild dietary patterns may be shaped by behavioural and ecological traits rather than by phylogenetic relatedness alone. At the same time, substantial dietary overlap may arise where multiple predators exploit a broadly shared prey pool, making it important to distinguish between differences in prey composition and complete trophic segregation.

In this study, we used DNA metabarcoding and next-generation sequencing (NGS) to examine trophic niche structure in a community of invertebrate-eating bats and birds foraging in West African rice landscapes. Specifically, we addressed the following questions: 1) How do dietary breadth and composition vary among predator species and between major predator guilds (here defined as nocturnal insectivorous bats and predominantly diurnal birds)? 2) How does dietary overlap vary within and between guilds? (3) To what extent is dietary dissimilarity associated with phylogenetic distance across the assemblage?

We hypothesized that trophic niches in this assemblage are structured hierarchically along multiple ecological axes. Specifically, we predict that (i) all predator species exhibit relatively broad arthropod diets consistent with the high prey diversity characteristic of tropical ecosystems (Novotny and Miller 2014); (ii) temporal activity patterns contribute to trophic differentiation between major predator guilds, leading to differences in dietary composition between nocturnal bats and diurnal birds; (iii) phylogenetic relatedness does not consistently predict dietary similarity, either within guilds or across the assemblage, suggesting that ecological and behavioural traits mediate trophic overlap at finer scales.

Materials and methods

Study area

The study was conducted in the Oio region of northern Guinea-Bissau (Figure 1), an area characterised by a Guinean maritime climate with two distinct seasons, a rainy season from May to November, and a dry season from December to April (FAO and ICRISAT 2019). Mean annual air temperature is about 28°C with little seasonal variation and annual precipitation ranges from 1200 to 1400 mm (Catarino et al. 2001; Climate Change Knowledge Portal 2023). The dominant vegetation is savannah woodland, a secondary formation largely shaped by human interventions such as fires and shifting agriculture (Catarino et al. 2008). The wider landscape also includes extensive cashew orchards, small villages (*tabancas*) and mosaics of smallholder agricultural plots.

Our work focused on freshwater lowland rainfed rice fields within the Mansabá sector (12° 20' 0.314" N, 15° 10' 57.474" W; Figure 1), locally known as *bolanhas*. These fields occupy former wet grass savannahs that flood during the rainy season (Catarino et al. 2008), creating seasonally inundated habitats that support high invertebrate and vertebrate diversity (Lawler 2001). These rice systems comprise actively cultivated paddies interspersed with fallow areas and isolated trees and are bordered by savannah woodlands and cashew orchards. Invertebrate communities in these landscapes include numerous species that are often considered important rice pests (Heinrichs and Barrion 2004), some of which can cause substantial crop damage (Oerke 2006; Waddington et al. 2010).

In Guinea Bissau, rice cultivation is a central component of rural livelihoods, and rice fields cover approximately 21% of the country's harvested area (FAO and ICRISAT 2019). Reflecting its importance, rice production has expanded over recent decades (Djata et al. 2003; USDA 2024), a trend mirrored across several African countries (Seck et al. 2012).

Bat and bird sampling

Fieldwork was conducted from June to December in 2021 and 2022, spanning the entire rice growth cycle, except for August when sampling was suspended due to heavy rainfall. Captures were performed using 12 m mist nets (Ecotone, 712/2P). On average, five nets were deployed per sample session (range: 1-8), positioned along rice field margins, near isolated trees, and close to water bodies to maximize capture success for both bats and birds. Nets were operated from 07:00 to 11:00 and from 17:00 to 22:00, covering the main activity periods of both groups.

Captured animals were kept in single-use paper bags for at least 30 minutes to allow for faecal sample collection. Faecal pellets were collected from the holding bags, with up to three pellets obtained per individual. Each pellet was placed in a separate 2 ml tube containing 96% ethanol. Captured individuals were then identified to the lowest taxonomic level possible, and standard morphometric measurements were taken. Bird measurements included wing, weight, and tarsus, while bat measurements included forearm length, weight, and sexual characteristics. When possible, sex and age were also determined. Bird identification followed Borrow and Demey (2014), with nomenclature following Clements (2007). Bat identification followed Happold and Happold (2013), with nomenclature following Simmons and Cirranello (2025). When field identification was uncertain, it was confirmed through molecular techniques (see Section "Laboratory procedures"). All captures and handling procedures were conducted under permits issued by the Instituto da Biodiversidade e Áreas Protegidas (IBAP), the national regulatory authority in Guinea-Bissau, and complied with applicable ethical guidelines for the use of wild animals in research.

Laboratory procedures

We individually processed and extracted the DNA of 665 faecal pellets, of which 526 belonged to bats and 139 to birds. The number of individuals and pellets analysed was determined by balancing the maximization diet estimation accuracy with the associated costs (Mata et al. 2019). DNA extraction from bat faecal samples followed the protocol described by (Gonçalves et al. 2024). Initially, 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) was added to each sample, followed by homogenization with a sterile spatula, vertexing, and incubation in a dry bath for 30 min at 56°C. Samples were vortexed again for 1 minute and centrifuged at 12,000 × g for 30 seconds. Up to 500 μL of supernatant was then transferred to a new tube, and 25 uL of OB Protease was added. The remaining steps followed the E.Z.N.A. Tissue Kit (Omega Bio-Tek, Georgia, USA) protocol, except that DNA was eluted twice in 50 μL to create two extracts. For bird faecal samples, we followed the manufacturer's protocol from the Stool DNA Isolation Kit (Norgen Biotek Corporation, Ontario, Canada). Extractions were conducted in batches of 23 samples, each including one negative control without faecal sample. The extracted DNA was placed in 96-well plates along with the negative controls, following the order of extraction. The last well in each plate was left empty for negative control of the polymerase chain reaction (PCR).

The prey DNA was amplified using the FwhF2-R2n COI primers (Vamos et al. 2017), modified to include Illumina adaptors (FwhF2: 5' - TCGTCGGCAGCGTCAGATGTGTATAAGAGACAGGGDACWGGWTGAACWGTWTAYCCHCC - 3'; FwhR2n: 5' – GTCTCGTGGGCTCGGAGATGTGTATAAGAGACAGGTRATWGCHCCDGCTARWACWGG - 3'). These primers have proven effective in amplifying a broad range of arthropods and perform well with degraded DNA (Elbrecht et al. 2019; Mata et al. 2021; da Silva et al. 2024). The PCR reaction mixture consisted of 5 μL of Qiagen Multiplex Master Mix, 0.3 μL of each primer at 10 nmol/L, 3.4 μL of water, and 1 μL of extracted DNA. The cycling conditions included 15 minutes at 95°C, followed by 40 cycles of 30 seconds denaturation at 95°C, 30 seconds of annealing at 50°C, and 30 seconds elongation at 72°C, concluding with a final elongation step of 10 minutes at 72°C.

The field IDs of bats and birds were verified by amplifying a small fragment of the COI gene using the FwhF1-R1 primers (Vamos et al. 2017), also modified with Illumina adaptors (FwhF1: 5' - TCGTCGGCAGCGTCAGATGTGTATAAGAGACAGYTCHACWAAYCAYAARGAYATYGG - 3'; FwhR1: 5' - GTCTCGTGGGCTCGGAGATGTGTATAAGAGACAGARTCARTTWCCRAAHCCHCC - 3'). This step confirmed the identity of cryptic species, as the Fwh2 primers often fail to detect vertebrate taxa. The PCR conditions for this amplification were the same as those used for the prey DNA. After amplification, the PCR products were diluted 1:4. A second PCR was performed to add 7bp long indexes along with the Illumina P5 and P7 sequencing adaptors. The PCR mix and cycling parameters were similar to the first PCR, but KAPA HiFi HotStart ReadyMix (Rocher, Basel, Switzerland) was used with eight cycles of denaturation and annealing at 55°C, and extension. The indexed PCR products were purified using Agencourt AMpure XP beads (Beckman Coulter, Brea, California, USA) at a 1:0.8 ratio. The purified products were quantified using an Epoch Microplate Spectrophotometer (Agilent, California, USA), diluted to a concentration of 15 nM, and pooled per maker. Each library was individually quantified using qPCR (KAPA Library Quant Kit qPCR Mix; Rocher), diluted to 4 nM, and sequenced on a MiSeq targeting a depth of 30,000 reads for Fwh2 and 4000 reads for Fwh1.

Bioinformatic analysis

The software Flash was used to merge paired reads (Magoč and Salzberg 2011) , considering a minimum expected overlap of 10 and maximum of 250 bp. Obitools commands ‘ngsfilter,’ ‘obiuniq,’ and ‘obigrep’ (Boyer et al. 2016) were employed to, respectively, remove primer sequences, dereplicate reads within each sample, and discard singletons per sample. VSEARCH was then applied, using the ‘--cluster_unoise’ command to denoise reads with default parameters (--unoise_alpha 2 --minsize 8) while filtering for sequences without the expected length (--minseqlength 195 --maxseqlength 215), the ‘--uchime3_denovo’ command to remove chimeric sequences with default parameters, the ‘--cluster_size’ command to cluster at 99% similarity (--id 0.99), and the ‘--useach_global’ option to map reads back to the retained OTUs (operational taxonomic units), using a 99 % identity threshold (-id.99) (Rognes et al. 2016). Next, LULU was used to merge similar OTUs (>84% similarity) with high levels of co-occurrence (>95%; Frøslev et al. 2017). OTUs not matching the expected length (within 205 ± 3 bp; Vamos et al. 2017) were excluded. To account for potential contamination, the number of reads from extraction and PCR negative controls was subtracted from associated samples.

The resulting OTUs were compared to the BOLD database using BOLDigger v2.1.1 (on 10–02–2025; Buchner and Leese 2020) and identifications were manually curated. OTUs sequences were than manually compared with BOLD hits, complemented with comparation with NCBI hits (in February 2025) and identified to the lowest possible taxonomic level based on the following thresholds: 98.5 % for species level, 97 % for genus, 95 % for family, and 90 % for order. When OTUs had similar identities across multiple species, genera, or other taxonomic ranks, the broadest level of classification was selected, following a least common ancestor approach. Due to the incompleteness of COI databases for West Africa, particularly on invertebrates and bats, OTUs not identifiable to species level were named as the lowest taxonomic rank identified followed by their OTU number (e.g. Aranea OTU1021, *Scotophilus* OTU2). OTUs were categorized as dietary (e.g., most arthropods) or non-dietary (e.g., vertebrates, fungi, internal and external parasites, OTUs only identified to class level).

It's important to acknowledge the limitations of DNA metabarcoding, particularly the potential for detecting secondary ingestion. This can occur when prey species consumed by arthropod predators, which are then eaten by bats and birds, are detected (da Silva et al. 2019; Deagle et al. 2019). However, since the DNA from the prey gut contents is usually present in smaller quantities and more prone to degradation, the likelihood of amplification during PCR is lower (Mata et al. 2021). Additional filtering was applied to exclude samples containing fewer than 100 dietary reads and to discard diet OTUs accounting for less than 1% of the total reads per sample, thereby minimizing the effects of secondary ingestion (Deagle et al. 2019).

Data analysis

Predators represented by fewer than seven sampled individuals were excluded from the analysis. While this sample size is below optimal levels for a detailed diet characterisation (Mata et al. 2019), this threshold was chosen to retain a broader representation of bird species, particularly insectivorous species, and to allow meaningful comparisons with bats.

Diet breadth and sample coverage for each predator species were assessed using the iNEXT function from the iNEXT package (Hsieh et al. 2016). Rarefaction and sample coverage curves were generated from sample-based incidence data using Hill number species richness ($q=0$), with 1000 bootstrap replicates. Curves were calculated for three taxonomic prey levels (OTU, family, and order), along with 95% confidence intervals. To allow direct comparison of diet breadth among predators, we extracted richness estimates standardised to 14 individuals. This value corresponds to twice the minimum number of individuals sampled for any included predator species, including the species with the lowest sample coverage, and represents a compromise between maximising species inclusion and ensuring comparable sampling effort across predators (Chao et al. 2014).

Diet composition was analysed using occurrence-based metrics due to the high dietary richness and potential recovery bias associated with differential digestion of prey (Deagle et al. 2019). The weighted percent of occurrence (wPOO) was calculated following Deagle et al. (2019) at three prey taxonomic levels (OTU, family, and order). This metric was calculated for all predator individuals combined, for birds and bats separately, and for each predator species. OTUs that could not be assigned to family or order were retained in the dietary matrices as missing values (NA) at those taxonomic levels.

Dietary differences between predators were visualised using non-metric multidimensional scaling (NMDS) using the metaMDS function from the vegan package (Oksanen et al. 2022). Differences in dietary composition were tested using analysis of similarities (ANOSIM) with the anosim function from the same package, using 999 permutations. Species-level NMDS and ANOSIM analyses were based on wPOO data and distances were calculated with the Bray-Curtis index, while individual-level analysis used prey occurrence data and distances were calculated with the Jaccard index. For individual-level analysis, OTUs found in only a single individual's diet were excluded. This approach reduces noise associated with extremely rare prey while preserving individual-level dietary variation.

To further mitigate the influence of zero inflation associated with rare prey items, dietary overlap was quantified using Pianka's index, which emphasises shared prey items by placing greater weight on their presence rather than their absence (Pianka 1973). Pianka's index and its statistical significance were computed using wPOO values and the niche_null_model function from the EcoSimR package (Gotelli et al. 2015), with 1000 randomisations, and using the RA3 as randomisation algorithm. This algorithm reshuffles the prey species wPOO within each predator, while retaining the observed diet breadth. For each predator pair, analysis was restricted to prey taxa detected in the diet of at least one of the two predators, thereby avoiding the zero inflation that would arise from a community-wide prey matrix.

Differences in prey consumption between bats and birds at the prey order level were assessed using chi-square tests. Specifically, we compared the number of bat and bird individuals consuming each prey order. Adjusted p-values were obtained using the Benjamini–Hochberg false discovery rate (FDR) correction for multiple comparisons. Differences in predator and prey composition among rice fields were assessed using ANOSIM with 999 permutations. Predator composition was analysed using occurrence data and distances were calculated with the Jaccard index, while prey composition was based on daily prey wPOO and distances were calculated with the Bray-Curtis index.

To examine the relationship between phylogeny and diet, the correlation between diet dissimilarities and phylogenetic distances was assessed with a multiple regression on distance matrices (MRM) using the MRM function from the ecodist package (Goslee and Urban 2007). For each predator group, 1000 phylogenetic trees were sampled. Bird trees were retrieved from BirdTree (Jetz et al. 2012) using the tree source "Ericson All Species", and bat trees were retrieved from VertLife (Upham et al. 2019) using the tree source "Mammals birth-death node-dated completed trees". For predators identified only to the genus level, a congeneric species known to occur in the study area and with similar morphological traits was used as a proxy. We then computed the average phylogenetic distance for each predator pair, based on the 1000 trees. Diet dissimilarity was calculated for each predator pair as $D = 1 - O$, where D is the dissimilarity index and O is Pianka's index.

To account for variation in sampling effort, we included the minimum sample size of each pair of predators in the regression. As a sensitivity analysis, we performed the MRM with different pools of species, assessing the influence of phylogenetic distant species (e.g., *Ispidina picta*), and the influence of species with very small and very large sample sizes for both bats and birds.

All graphs were generated using the ggplot function from the ggplot2 package (Wickham 2016), and all analyses were performed in the R statistical environment (R Core Team 2024). Statistical significance was set at α = 0.05.

Results

We analysed the diets of 471 individuals, comprising 334 bats and 137 birds, across 13 species of bats and eight species of birds. DNA metabarcoding of 665 faecal samples revealed 3371 occurrences of 1304 different arthropod prey OTUs, spanning 144 families and 22 orders. Only 10.1% of prey OTUs are identified at the species level.

The average number of individuals sampled per predator species was 22,4 (± 10.3, 95% CI). *Scotophilus* sp. was the most sampled taxon, with 106 individuals (Table 1). In contrast, *Nycteris* cf. *hispida*, *Prinia subflava*, and *Scotoecus albofuscus* were each represented by seven individuals. All these species exhibited sample coverage values above 22%, with the exception of *N.* cf. *hispida,* which showed an exceptionally low sample coverage (0.05%), indicating that its detected diet represents only a small fraction of its total prey richness. Accordingly, results involving this species should be interpreted with caution, particularly in analyses of dietary composition and overlap.

Diet breadth and composition

On average, each predator species consumed 99.7 ± 37.4 different OTUs, with values ranging from 28 in *P. subflava* and *Uraeginthus bengalus* to 369 prey OTUs in *Scotophilus* sp. (Table 1).

The most frequently consumed prey orders were Hemiptera, Coleoptera, Blattodea, Lepidoptera, and Orthoptera (Figure 2; Online resource 1). When considering bats alone, the same orders dominated the diet and showed similar relative importance. In contrast, bird diets were dominated by Lepidoptera, with Aranea showing higher representation compared to bats (Figure 2; Online resource 1). At the family level, Termitidae was the most frequently detected family. However, only 69.1% of prey OTUs could be identified to family level (Online resource 2). The most frequently detected prey species was *Macrotermes bellicosus*, a termite species (Online resource 3). The consumption of this and other highly represented termite species, such as *Microtermes* sp. showed a seasonal peak in June and July.

With the exception of *N.* cf. *hispida*, which exhibited an exceptionally low sample coverage (0.05 ± 0.05%), rarefaction analysis revealed that sample coverage at the OTU level ranged from 15.0 ± 14.2% in *Lagonosticta senegala* to 70.2 ± 3.0% in *Scotophilus* sp. (Table 1). Using richness estimates standardised to 14 individuals, nearly all predator species consumed more than 40 different prey OTUs (Table 1 and Figure 3). We observed a high proportion of rare OTUs in predator diets: about 60.8% of prey OTUs in bats and 72.5% in birds were detected in the diet of only a single individual.

Using diet breadth standardized at 14 samples, bats generally exhibited broader niche breadths than birds at the OTU level (Figure 3). However, this pattern was not evident at higher prey taxonomic levels, where confidence intervals overlapped extensively among most predator species (Figure 3). Additionally, we found no significant differences in dietary breadth between granivorous and insectivorous birds (Figure 3), although sample sizes were limited.

Uraeginthus bengalus showed the narrowest niche breadth at the OTU level (34.33 ± 11.25 prey OTUs) with Blattodea (family Termitidae) comprising almost half of its diet (Figure 2) with *Odontotermes* sp., accounting for 26.7% of it. Despite consuming a limited number of OTUs, these prey spanned a diversity of families and orders similar to those exploited by other predators (Figure 3). Among bats, *Glauconycteris variegata* showed the narrowest niche breadth across all prey taxonomic levels (Figure 3), feeding primarily on Lepidoptera, Blattodea, Orthoptera, and Hemiptera (Figure 2). In contrast, *L. senegala* showed the broadest niche breadth among birds at the OTU level, with a mean number of prey taxa (74.54 ± 17.18) comparable to that of bats, although its confidence intervals were wide and overlapped with those of other bird species. *Euplectes franciscanus* was the bird species consuming the highest richness of prey orders and was the only predator detected consuming Ephemeroptera, Zygentoma, and Gastropoda.

Diet overlap and phylogenetic relationships

We detected compositional differences among rice fields for both prey (ANOSIM R = 0.34, p = 0.001) and predator assemblages (ANOSIM R = 0.44, p = 0.001) indicating moderate spatial structuring of predator and prey assemblages across the study area. This spatial heterogeneity warrants caution when interpreting dietary overlap, as differences among predators may partly reflect variation in prey assemblages across fields, even though all dietary analyses integrate individuals sampled across multiple fields.

Despite some overlap, dietary composition differed between bats and birds, as shown by NMDS (Figure 4), which was supported by ANOSIM analysis (ANOSIM R = 0.61, p = 0.001). Differences between the two predator groups were also evident in the distribution of prey orders. When comparing prey order consumption between bats and birds, Hygrophila, Aranea, Odonata, Hymenoptera, and Lepidoptera, were significantly more consumed by birds, while Dermaptera, Psocodea, Coleoptera, Blattodea and Hemiptera were mainly consumed by bats (Online resource 4).

At the individual level, NMDS revealed a substantial overlap among predator species; however, ANOSIM indicated a significant, albeit weak, differentiation among species overall ($R_{all} = 0.20$, $p = 0.001$), within bats ($R_{Bats} = 0.19$ $p = 0.001$), and within birds ($R_{Birds} = 0.11$, $p = 0.001$). This apparent overlap was likely influenced by the high proportion of rare OTUs, which generated extensive zero inflation even after excluding prey detected in only a single individual predator.

When reducing the influence of joint absences using Pianka's index, overall dietary overlap among predators was low but significant ($O_{all} = 0.11$, $p = 0.001$). Overlap was more pronounced among bat species ($O_{Bats} = 0.23$, $p = 0.001$), with several pairs of bat species showing higher overlap than expected by chance (Figure 5). In contrast, bird species showed significant dietary segregation ($O_{Birds} = 0.05$, $p = 0.017$), with most pairwise comparisons showing lower overlap than expected (Figure 5). Pairwise dietary overlap among birds was comparable to that observed between bat and bird species. However, a small number of bird species pairs within the same family (e.g., Ploceidae and Estrildidae) showed non-significant Pianka's index values (Figure 5).

Pianka's index also revealed relatively high dietary overlap among a group of morphological and phylogenetic similar pipistrelloid bats (*Neoromicia somalica*, *Pseudoromicia rendalli*, and *Afronycteris nanus*) (Figure 5). However, this overlap was strongly influenced by the high consumption of seasonally abundant termites (*M. bellicosus* and *Microtermes sp.*). When these prey were excluded, overlap values decreased overall; however, only the overlap between *N. somalica* and *P. rendalli* was no longer significant ($O_{Neo\ som-Afr\ nan} = 0.39$, $p_{Neo\ som-Afr\ nan} = 0.028$; $O_{Neo\ som-Pse\ ren} = 0.34$, $p_{Neo\ som-Pse\ ren} = 0.174$; $O_{Pse\ ren-Afr\ nan} = 0.42$, $p_{Pse\ ren-Afr\ nan} = 0.008$). Conversely, two species from distinct suborders *Macronycteris gigas* and *Mops condylurus*, showed the highest overlap ($O = 0.72$, $p < 0.001$) which remained high even after excluding termites ($O = 0.63$, $p = 0.005$).

Despite the higher overlap among some closely related species, no significant correlation was detected between phylogenetic distance and diet dissimilarity at OTU prey level, for both predator groups ($R^2_{Bats} = 0.04$, $p_{Bats} = 0.28$; $R^2_{Birds} = 0.06$, $p_{Birds} = 0.31$). However, for birds, when removing the *I. picta* from the analysis, this relation became significant ($\beta = 0.0009$; $R^2 = 0.35$; $p = 0.01$). For birds, the minimum sample size in each predator pair explained part of dietary variation ($\beta = -0.01$; $R^2 = 0.21$; $p = 0.02$), with lower dissimilarity (higher overlaps) being correlated with higher minimum sample sizes.

Discussion

In this study, we applied DNA metabarcoding to examine the dietary breadth, composition, and trophic overlap in a community of invertebrate-eating bats and birds foraging in lowland rainfed rice fields in West Africa. By integrating diet data across multiple predator species and taxonomic groups, our results provide one of the first metabarcoding-based community-level assessments of trophic resource use by flying vertebrates in African agricultural landscapes. Overall, we found broad and relatively generalised diets across predators, differences in dietary composition between bats and birds, reduced dietary overlap among birds, and moderate overlap among some bat species. These patterns emerge from a spatially heterogeneous landscape in which both prey and predator assemblages vary among rice fields and therefore represent integrated trophic relationships across multiple foraging contexts rather than field-specific interactions.

Diet breadth and prey use

Both bats and birds displayed broad diets characterised by high prey richness and a large proportion of rare prey items. This pattern is consistent with expectations for tropical systems, where high arthropod diversity and strong temporal variation in prey availability thought to favour generalised foraging patterns (Novotny and Miller 2014). Bats generally showed broader dietary breadths than birds at the OTU level, in line with previous studies suggesting that nocturnal insectivorous predators often exploit a wider range of prey taxa than diurnal predators (Maas et al. 2016; Wong and Didham 2024). This difference may reflect a combination of higher nocturnal insect activity in warmer environments, reduced visual constraints, and flexible foraging strategies in bats (Boonman et al. 2013; Kirkpatrick et al. 2018; Wong and Didham 2024). At coarser taxonomic levels (family and order), however, niche breadth estimates converged across predators, with extensive overlap in confidence intervals. This indicates that differences between bats and birds are driven primarily by fine-scale prey selection rather than by the exploitation of fundamentally different prey groups (Heim et al. 2021; Chaves et al. 2026). Similarly, we detected no significant differences in dietary breadth between granivorous and insectivorous birds, although this result should be interpreted cautiously given the limited sample sizes for some insectivorous species.

A high proportion of rare OTUs (prey items recorded only once) was detected in both bat and bird diets. These results suggest that some bird species may exhibit broader diets than often assumed, while reinforcing the generally broad dietary character of bats (Maas et al. 2016). Although consistent with previous metabarcoding studies (Garfinkel et al. 2022; Bookwalter et al. 2023), the high number of rare OTUs may also partly reflect unequal and, in some cases, low sample coverage, which can bias the detection of infrequently consumed prey, particularly in birds. Rare prey items should thus be interpreted cautiously; nevertheless, their prevalence, together with the consumption of prey during seasonal peaks is consistent with, and may reflect, opportunistic foraging behaviour reported in other systems (Mwansat et al. 2015; Andriollo et al. 2021).

The general patterns of prey order importance for bats and birds were consistent with general knowledge for other world regions (Kunz et al. 2011; Nyffeler et al. 2018). Among the most frequently detected prey items, termites (Blattodea; Termitidae) and ants (Hymenoptera; Formicidae) emerged as major components of bats' and birds' diets. Ant and termite abdomens, rich in fat (Eklöf and Rydell 2017), are a critical food source in the tropics for many animals, including bats and birds (Redford 1987; Korb and Salewski 2001). For example, *U. bengalus* showed the highest termite consumption, consistent with previous observations that termites are vital to the diet of nestlings of this species (Hamed and Evans 1983). Other predators such as *G. variegata*, and *P. rendalli*, consumed termites seasonally (e.g. *M. bellicosus* and *Microtermes sp.*), exhibiting temporal shifts in diet corresponding to known termite reproductive periods, typically peaking between late June and early July when alate termites emerge shortly after the first heavy rains (Mitchell 2008; Manzoor and Mir 2010).

The marked contribution of termite taxa to predator diets suggests that temporally abundant prey can strongly influence observed dietary patterns, including increasing apparent overlap among species. Chaves et al. 2026 also reported the consumption of agricultural pests by these predators foraging in rice fields. The combination of broad diets and the consumption of pest taxa indicates a potential contribution of these predators in pest suppression, including rice pests, which often exhibit periodic peaks of abundance similar to termites (Heinrichs 1994). This potential role cannot be directly quantified from dietary data alone; however it suggests that these predators may contribute to pest management in West African rice fields, as already documented for other regions and cropping systems (Díaz-Siefer et al. 2022; Tuneu-Corral et al. 2023).

However, several limitations constrain inference on predator diet and pest control potential, including incomplete diet characterisation, as evidenced by low sample coverage for some species, incomplete reference databases, which resulted in a low proportion of OTUs identified to the species level (10,1%), and limited ecological knowledge of many invertebrate taxa in the region. Despite these limitations, the frequent detection of diverse arthropod taxa, including pest species (Chaves et al. 2026), highlights the ecological relevance of bats and birds within these agroecosystems.

Overall, the broad diets of flying vertebrates in West African rice fields likely reflect a combination of diverse prey assemblages and the flexible foraging strategies (MacArthur and Pianka 1966; Pyke 2019). Although both groups exhibited broad dietary patterns, some species showed more restricted prey use, suggesting some degree of trophic differentiation. These dietary differences likely stem from a combination of behavioural, morphological, and temporal factors, although their relative importance cannot be disentangled with the present data

Diet overlap and phylogenetic relationships

We observed differences in dietary composition between bats and birds, consistent with differences in foraging period and prey activity patterns. Diurnal birds consumed a higher proportion of typically diurnal prey orders such as Odonata and Hymenoptera (Corbet 1980; Wong and Didham 2024), whereas bats primarily consumed nocturnal or crepuscular taxa such as Dermaptera, Coleoptera, Blattodea, and

Hemiptera (Rankin and Palmer 2009; Wong and Didham 2024). Therefore, temporal segregation likely represents an important axis of niche differentiation between these two predator groups.

Within groups, patterns of dietary overlap differed markedly between bats and birds. Bird species exhibited low dietary overlap, with most species' pairs showing lower overlap than expected by chance. Only a small number of within-family comparisons yielded non-significant Pianka's index values, indicating neither overlap nor clear segregation. Despite the very low overlap values, the analysis of correlation between diet dissimilarity and phylogenetic distances revealed a weak relationship only after excluding *I. picta*, a phylogenetically distant species. This suggests that phylogeny may contribute to dietary dissimilarity, although this result is sensitive to species composition. However, dietary dissimilarity is also influenced by sample sizes. Therefore, these results may reflect a combination of ecological differences and sampling effects, rather than clear phylogenetic structuring (Deagle et al. 2019; Mata et al. 2019). Overall, the relationship between phylogeny and diet remains inconclusive in this system.

The low overlap among bird species may also reflect a greater diversity in foraging strategies, as this study included exclusively insectivorous, primarily granivorous, and granivorous-insectivorous bird species (Owiunji and Plumptre 1998; Billerman et al. 2022). Even among exclusively insectivorous, we examined highly aerial foragers, such as *H. lucida* (Turner and Rose 1989), and ground-foraging species such as *P. subflava* and *I. picta* (Ryan and Dean 2020; Woodall 2021).

Bat species showed higher dietary overlap than birds, particularly among morphologically and phylogenetically similar pipistrelloid species. This overlap was also partially driven by the high consumption of termites (*M. bellicosus* and *Microtermes* sp.). The high importance of these prey species, as measured by wPOO, is influenced by the feeding behaviour of individuals exploiting swarming termites or other temporally abundant prey, which can inflate their apparent contribution to the overall diet. Although these termites were a significant component of the bat diet, the relatively high dietary overlap observed between bats, particularly between closely related species, does not necessarily indicate low competition, as overlap in resource use does not directly translate into competitive interactions (Schoener 1974). Instead, this pattern may reflect shared exploitation of abundant prey resources and similar foraging strategies (Findley and Black 1983; Schoeman and Jacobs 2011; Dammhahn and Goodman 2014; Blanch et al. 2023). Several factors may contribute to this pattern, including the high mobility and extensive home ranges of bats (Fenton 1990), and variation in habitat use and resource distribution (Stevens and Willig 2000). Competition for food resources might only be evident when food is scarcer (Roeleke et al. 2018) probably during the dry season. Population regulation from predation or disturbances may also contribute to reduced density, reducing competition (Bloch et al. 2011). However, the relative importance of these mechanisms cannot be determined from the present data.

Despite the higher overlap among some closely related bat species, no significant relationship was detected between phylogenetic distance and diet dissimilarity. The lack of correlation likely reflects a combination of limited statistical power, diet variability, and potential uncertainty in phylogenetic relationships (López-Aguirre et al. 2023). The high overlap between *Macronycteris gigas* and *Mops condylurus*, two species from distinct suborders, further illustrates that dietary similarity can occur among distantly related taxa.

Overall, while temporal foraging behaviour plays a key role in structuring dietary differences between bats and birds, our findings suggest that niche partitioning is a more complex process influenced by multiple factors, including morphology, behaviour, and habitat use. These factors, alongside foraging time, likely shape the dietary overlap observed within and between these predator groups.

Conclusions

Our findings highlight variation in diet breadth and overlap among invertebrate-eating flying vertebrates foraging in lowland rainfed rice fields. The observed differences in dietary composition, shaped by dietary preferences and foraging strategies, underscore the importance of preserving diverse communities of birds and bats within these agroecosystems. At the same time, dietary overlap among some bat species suggests shared use of available prey resources. Moreover, the generalised diets of these predators, together with the consumption of pest taxa, indicate a potential role in the regulation of invertebrate populations. The critical importance of rice in global food security (Maclean et al. 2002), and the harm that chemical pesticides pose to human health and wildlife (Ansari et al. 2014), highlight the need to better understand the ecological roles of these invertebrate-eating predators in rice systems.

Key measures to foster the presence of birds and bats in agroecosystems, while aligning with sustainable agricultural practices, might include maintaining patches of native vegetation (Horgan et al. 2017) and isolated trees within the rice fields (Fernandes 2024), providing permanent drinking water sources during the dry season, ensuring adequate roosting sites, and reducing agrochemical usage (Tuneu-Corral et al. 2023). However, some of these predators can also affect crops directly (de Mey et al. 2012; Downs and Hart 2020) or influence other trophic interactions, including mesopredator regulation (Sottomayor et al. 2024). Therefore, further studies are needed to provide a deeper understanding of the true ecological roles of these bats and birds.

Given the high environmental variability across seasons, further studies focusing on temporal variation in dietary composition and overlap would help to better characterize the trophic structure of these predator communities in West African agroecosystems. Advancing this understanding will be essential for integrating ecological knowledge into the sustainable management of tropical agroecosystems.

Acknowledgements

We would like to express our deepest gratitude to the rural communities in which this project took place, especially the farmers who allowed us to conduct our fieldwork in their rice fields. The logistics of the fieldwork were supported by the KAFO Peasant Federation in Guinea-Bissau. Special thanks to KAFO’s secretary-general Sambú Seck, and also to all the staff at KAFO’s Djalicunda centre for their support and for the warm welcome they gave us.

Funding

This study was funded by Fundação para a Ciência e Tecnologia, I.P./MCTES through national funds (PIDDAC) via project PTDC/ASP-AGR/0876/2020 (DOI: 10.54499/ PTDC/ASP-AGR/0876/2020) VM was also funded through individual contracts (2020.02547.CEECIND/ CP1601/CP1649/CT0004)

Conflicts of interest

The authors declare that they have no conflict of interest.

Ethics approval

All applicable institutional and/or national guidelines for the care and use of animals were followed.

Availability of data and material

The datasets used and analysed during the current study are available from the corresponding author on reasonable request.

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Tables

Table 1 – Predator species and prey diversity. The table lists predator species grouped into bats and birds, showing sample size (the number of individual predators analysed), the total number of different prey taxa (OTU) found, the number of prey found in the diet of 14 individuals (mean ± 95% CI), and the sample coverage for each species (mean ± 95% CI). Abbreviations used for species names are in the "Acronym" column.

Predator species	Acronym	Group	Sample size	No of prey OTUs	No of prey OTUs for 14 individuals	Sample Coverage
Afronycteris nanus	*Afr nan*	Bat	36	126	61.11 ± 7.28	0.60 ± 0.06
Euplectes franciscanus	*Eup fra*	Bird	13	58	61.95 ± 14.29	0.22 ± 0.14
Glauconycteris variegata	*Gla var*	Bat	11	38	44.48 ± 9.34	0.54 ± 0.16
Hipposideros caffer / ruber	*Hip caf/rub*	Bat	34	242	120.60 ± 10.59	0.50 ± 0.06
Hirundo lucida	*Hir luc*	Bird	8	31	49.18 ± 15.06	0.27 ± 0.20
Ispidina picta	*Isp pic*	Bird	9	39	55.08 ± 13.83	0.30 ± 0.20
Lagonosticta senegala	*Lag sen*	Bird	10	55	74.54 ± 17.18	0.15 ± 0.14
Macronycteris gigas	*Mac gig*	Bat	10	52	68.34 ± 14.84	0.36 ± 0.14
Mops condylurus	*Mop con*	Bat	41	185	82.98 ± 7.65	0.62 ± 0.05
Neoromicia somalica	*Neo som*	Bat	23	106	73.36 ± 9.77	0.56 ± 0.08
Nycteris cf. *hispida*	*Nyc cf his*	Bat	7	49	95.69 ± 25.67	0.05 ± 0.05
Pipistrellus sp.	*Pip sp*	Bat	13	78	82.21 ± 12.26	0.52 ± 0.10
Ploceus cucullatus	*Plo cuc*	Bird	71	202	53.75 ± 5.33	0.53 ± 0.06
Ploceus melanocephalus	*Plo mel*	Bird	8	29	45.69 ± 13.85	0.31 ± 0.20
Prinia subflava	*Pri sub*	Bird	7	28	47.45 ± 14.55	0.29 ± 0.23
Pseudoromicia rendalli	*Pse ren*	Bat	18	128	104.28 ± 13.99	0.41 ± 0.08
Scotoecus albofuscus	*Scoe alb*	Bat	7	72	123.59 ± 25.69	0.33 ± 0.13
Scotoecus sp.	*Scoe sp*	Bat	19	128	103.21 ± 12.41	0.59 ± 0.07
Scotophilus leucogaster	*Scop leu*	Bat	9	51	73.49 ± 16.69	0.30 ± 0.15
Scotophilus sp.	*Scop sp*	Bat	106	369	83.51 ± 5.19	0.70 ± 0.03
Uraeginthus bengalus	*Ura ben*	Bird	11	28	34.33 ± 11.25	0.33 ± 0.19

Figure legends

Figure 1 – Location of the study site in Guinea-Bissau. The map on the left shows the location of sampling points and respective rice fields. The map was built under the coordinate reference system EPSG:4326 – WGS 84 on 22 November 2024. Insets include a map with the location of the study area in the context of West Africa and the location of Oio Region and Mansabá Sector in Northern Guinea-Bissau (top-right). The pictures on the right show typical lowland rainfed smallholder rice fields, namely Demba Só (centre) and Mambonco (bottom).

Figure 2 – Weighted percentage of occurrence (wPOO) of arthropod orders in the diet of bats and birds from lowland rainfed rice fields of Guinea Bissau. The first column on the left represents the combined diet of all species, while the second and third columns represent the diets of all bat species combined and all bird species combined, respectively. The following columns represent the diet of each species with bats labelled in red, and birds labelled in blue. Predator species acronyms are listed in Table 1.

Figure 3 – Niche breadth estimates (taxon richness) for the 21 bat and bird species from lowland rainfed rice fields of Guinea Bissau. Estimates are represented by black dots and coloured bars represent the 95% lower and upper confidence intervals. Niche breadth was estimated at different prey taxonomic levels (OTU, Family, Order) for each species. Estimates were calculated for 14 individuals and were generated from sample-based incidence data, using Hill number species richness (q=0), and 1000 bootstraps. Bats bars are in red, while birds are in blue. Predator species acronyms are listed in Table 1.

Figure 4 – NMDS ordination of molecular bat and bird diets (at the OTU prey level) from lowland rainfed rice fields of Guinea Bissau. The diamonds represent predator species, bats are labelled in red, while birds are labelled in blue. Polygons represent the convex hulls enclosing 95% of data points. Smaller dots represent prey species coloured by their respective order, and larger dots are the centroids of each prey order. The ordination is calculated with Jaccard distance. The ordination stress level is indicated in the panel. Predator species acronyms are listed in Table 1.

Figure 5 – Pianka’s pairwise overlap of molecular bat and bird diets (at the OTU level) from lowland rainfed rice fields of Guinea Bissau. The pair comparisons that show higher overlap values than expected by chance are coloured in green and the ones that show lower values than expected by chance are

coloured in red. Values close to expectations are coloured in grey. Bats are labelled in red, while birds are labelled in blue. Predator species acronyms are listed in Table 1.

Figures

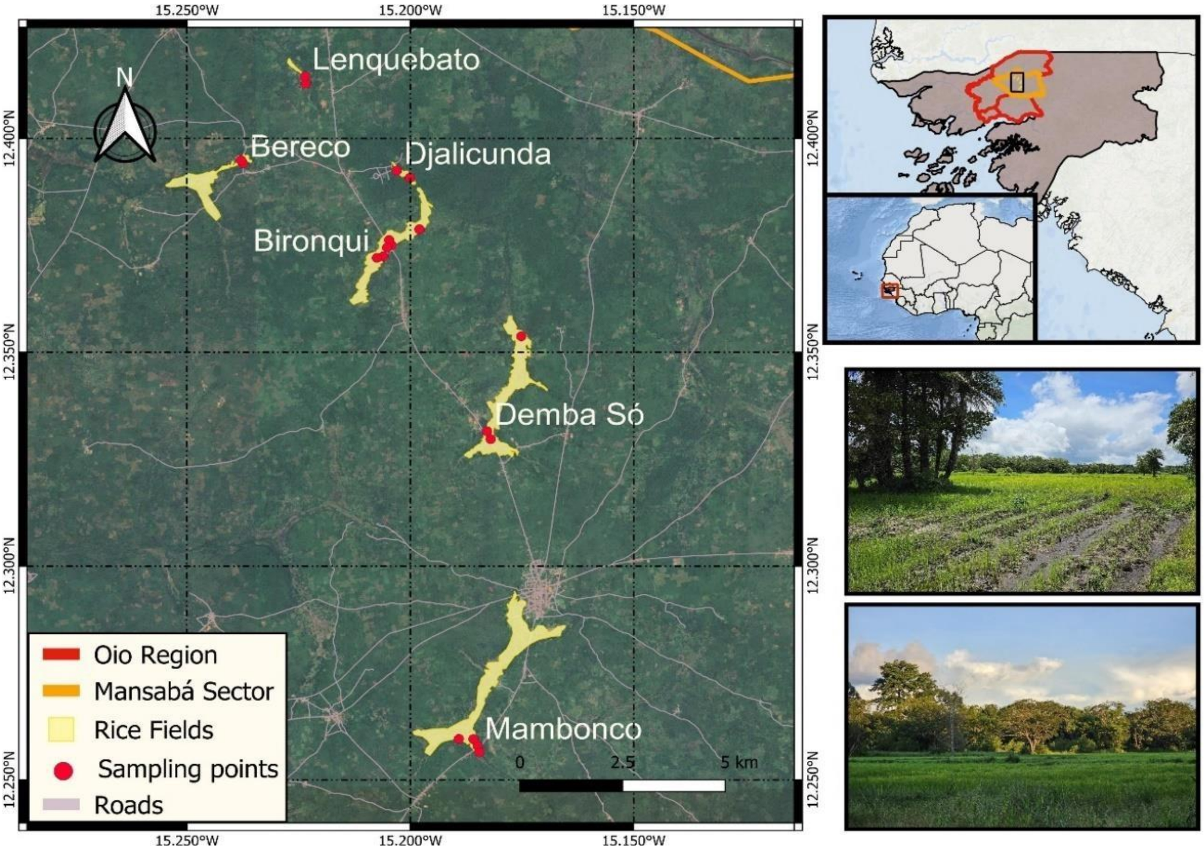
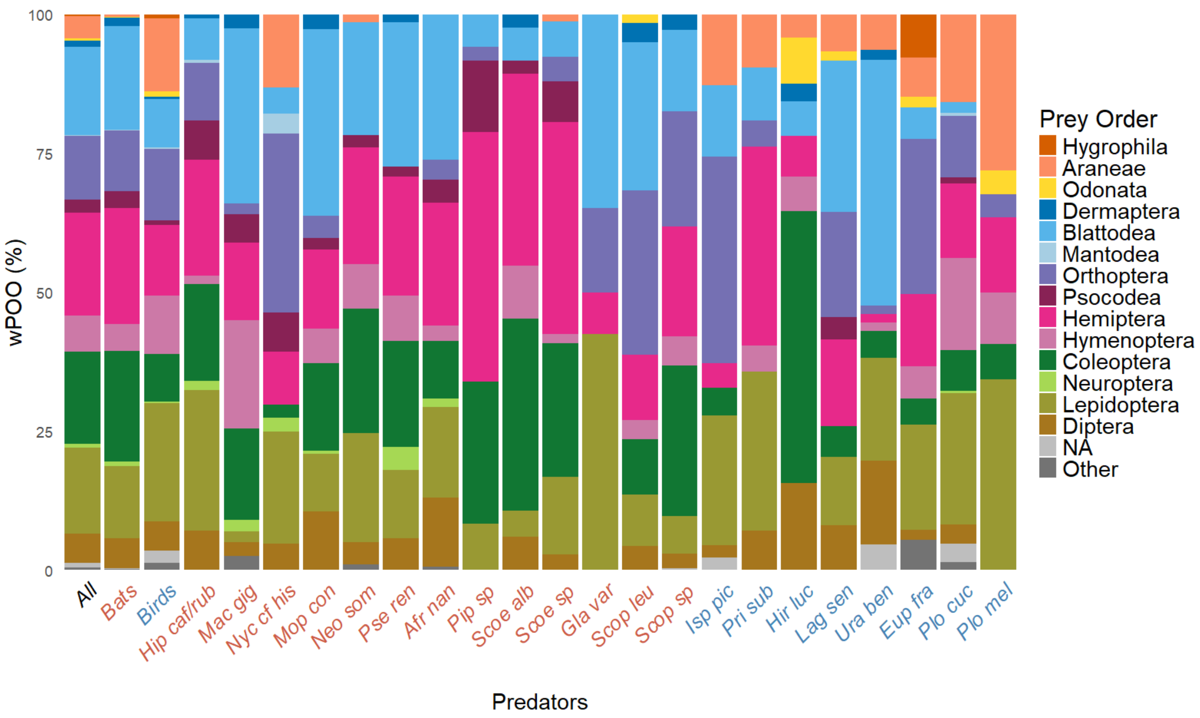
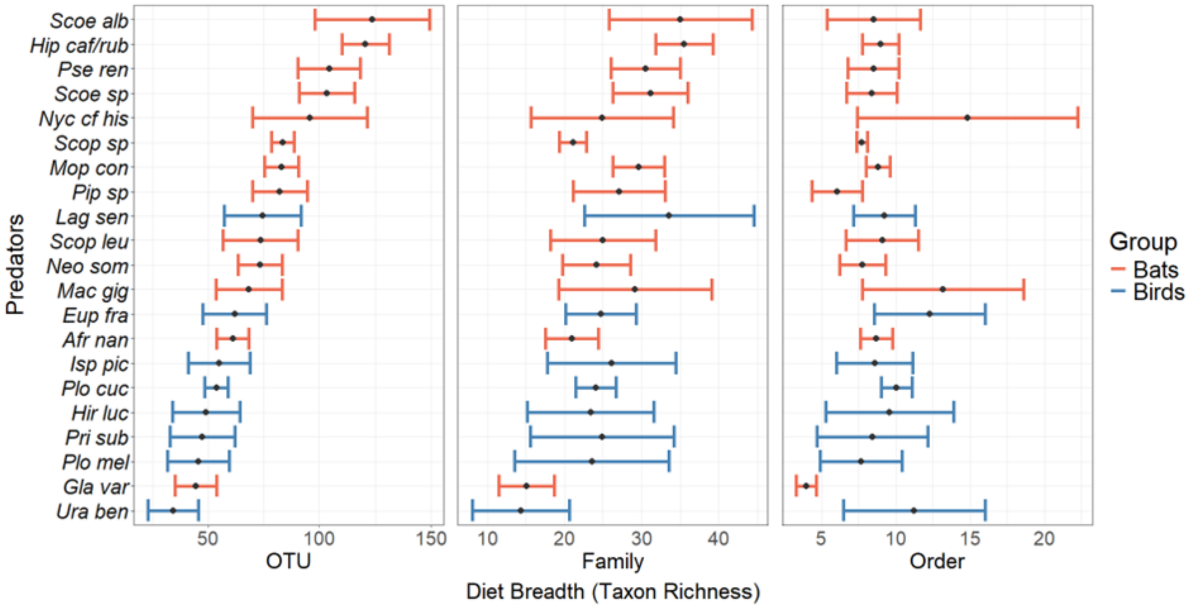


Figure 1


wPOO (%)
100
75
50
25
0
All
Bats
Birds
Hip caf/rub
Mac gig
Nyc cf his
Mop con
Neo som
Pse ren
Afr nan
Pip sp
Scoe alb
Scoe sp
Gla var
Scop leu
Scop sp
Isp pic
Pri sub
Hir luc
Lag sen
Ura ben
Eup fra
Plo cuc
Plo mel
Predators
Prey Order
Hygrophila
Araneae
Odonata
Dermaptera
Blattodea
Mantodea
Orthoptera
Psocodea
Hemiptera
Hymenoptera
Coleoptera
Neuroptera
Lepidoptera
Diptera
NA
Other

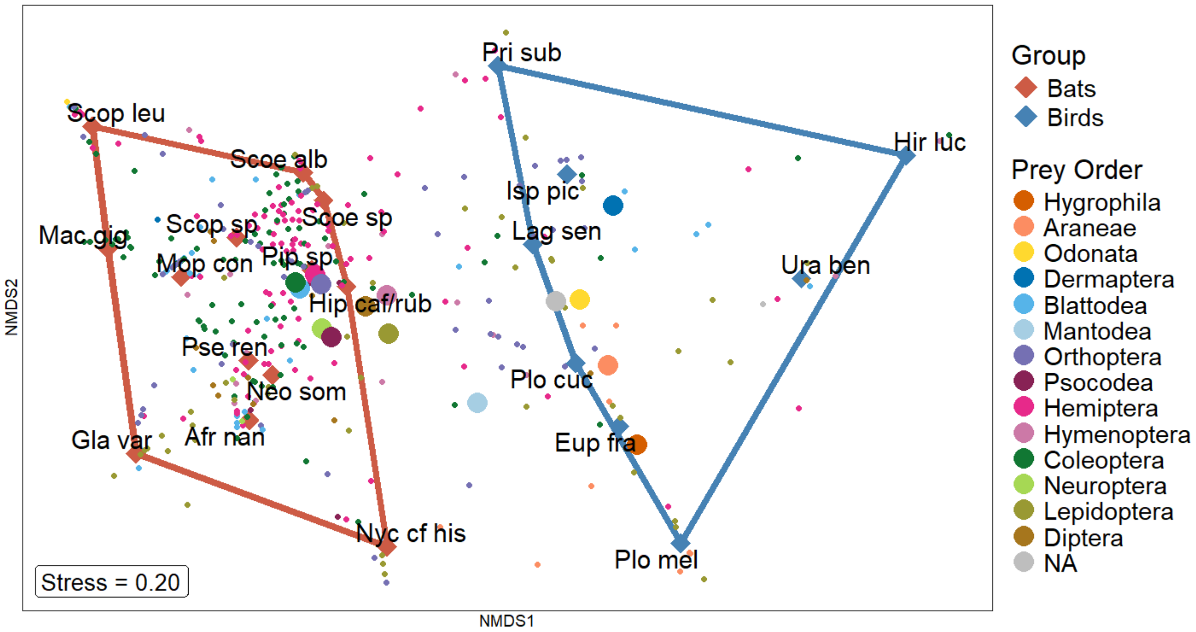
832 Figure 2



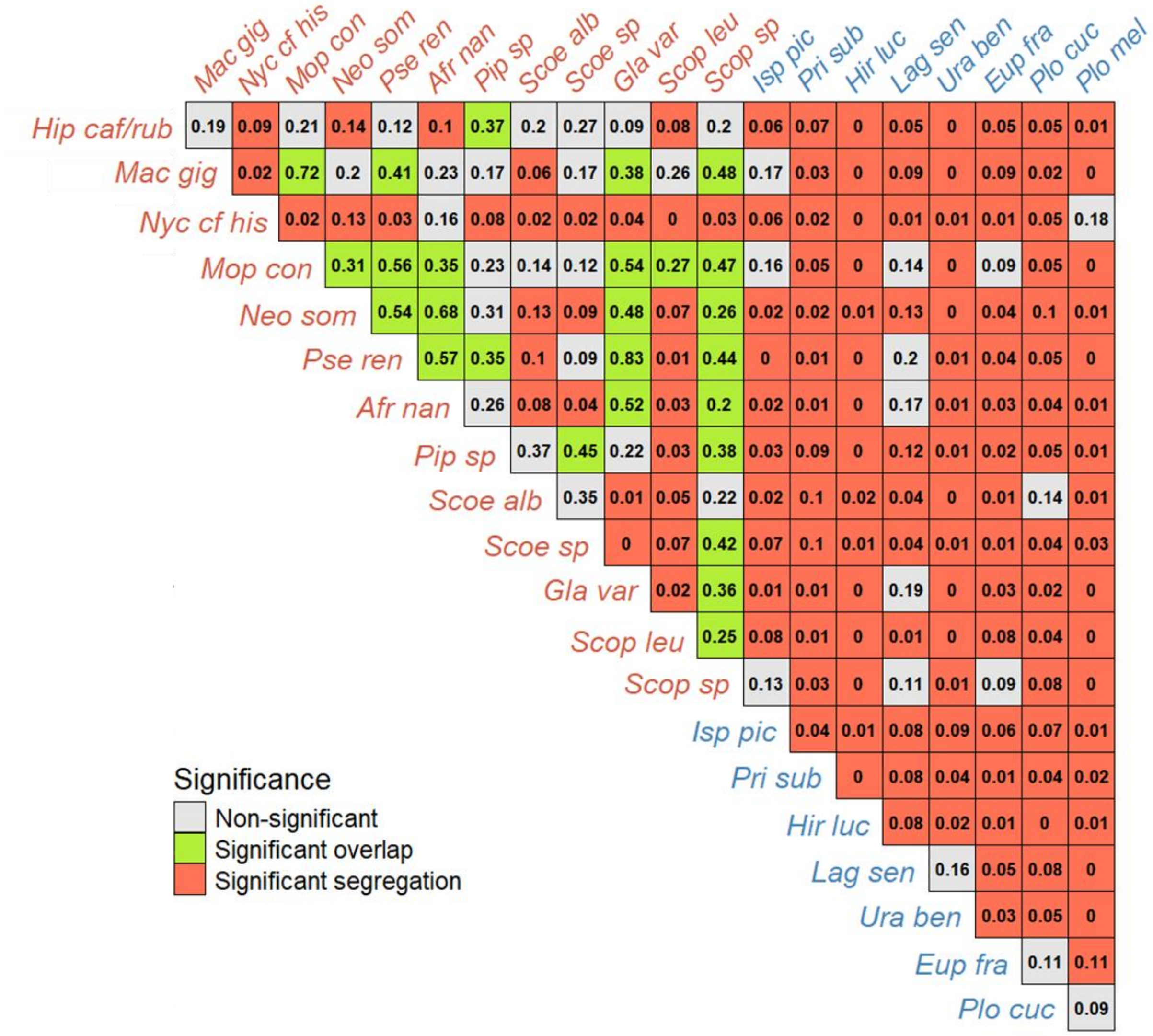
Scoe alb
Hip caf/rub
Pse ren
Scoe sp
Nyc cf his
Scop sp
Mop con
Pip sp
Lag sen
Scop leu
Neo som
Mac gig
Eup fra
Afr nan
Isp pic
Plo cuc
Hir luc
Pri sub
Plo mel
Gla var
Ura ben
Predators
50
100
150
OTU
10
20
30
40
Family
5
10
15
20
Order
Diet Breadth (Taxon Richness)
Group
Bats
Birds

Figure 3

835



836 Figure 4



	Mac gig	Nyc cf his	Mop con	Neo som	Pse ren	Afr nan	Pip sp	Scoe alb	Scoe sp	Gla var	Scop leu	Scop sp	Isp pic	Pri sub	Hir luc	Lag sen	Ura ben	Eup fra	Plo cuc	Plo mel
Hip caf/rub	⬜ 0.19	🟥 0.09	⬜ 0.21	🟥 0.14	⬜ 0.12	🟥 0.1	🟩 0.37	⬜ 0.2	⬜ 0.27	⬜ 0.09	🟥 0.08	⬜ 0.2	🟥 0.06	🟥 0.07	🟥 0	🟥 0.05	🟥 0	🟥 0.05	🟥 0.05	🟥 0.01
Mac gig		🟥 0.02	🟩 0.72	⬜ 0.2	🟩 0.41	⬜ 0.23	⬜ 0.17	🟥 0.06	⬜ 0.17	🟩 0.38	⬜ 0.26	🟩 0.48	⬜ 0.17	🟥 0.03	🟥 0	🟥 0.09	🟥 0	🟥 0.09	🟥 0.02	🟥 0
Nyc cf his			🟥 0.02	🟥 0.13	🟥 0.03	⬜ 0.16	🟥 0.08	🟥 0.02	🟥 0.02	🟥 0.04	🟥 0	🟥 0.03	🟥 0.06	🟥 0.02	🟥 0	🟥 0.01	🟥 0.01	🟥 0.01	🟥 0.05	⬜ 0.18
Mop con				🟩 0.31	🟩 0.56	🟩 0.35	⬜ 0.23	⬜ 0.14	⬜ 0.12	🟩 0.54	🟩 0.27	🟩 0.47	⬜ 0.16	🟥 0.05	🟥 0	⬜ 0.14	🟥 0	⬜ 0.09	🟥 0.05	🟥 0
Neo som					🟩 0.54	🟩 0.68	⬜ 0.31	🟥 0.13	🟥 0.09	🟩 0.48	🟥 0.07	🟩 0.26	🟥 0.02	🟥 0.02	🟥 0.01	🟥 0.13	🟥 0	🟥 0.04	🟥 0.1	🟥 0.01
Pse ren						🟩 0.57	🟩 0.35	🟥 0.1	⬜ 0.09	🟩 0.83	🟥 0.01	🟩 0.44	🟥 0	🟥 0.01	🟥 0	⬜ 0.2	🟥 0.01	🟥 0.04	🟥 0.05	🟥 0
Afr nan							⬜ 0.26	🟥 0.08	🟥 0.04	🟩 0.52	🟥 0.03	🟩 0.2	🟥 0.02	🟥 0.01	🟥 0	⬜ 0.17	🟥 0.01	🟥 0.03	🟥 0.04	🟥 0.01
Pip sp								⬜ 0.37	🟩 0.45	⬜ 0.22	🟥 0.03	🟩 0.38	🟥 0.03	🟥 0.09	🟥 0	🟥 0.12	🟥 0.01	🟥 0.02	🟥 0.05	🟥 0.01
Scoe alb									⬜ 0.35	🟥 0.01	🟥 0.05	⬜ 0.22	🟥 0.02	🟥 0.1	🟥 0.02	🟥 0.04	🟥 0	🟥 0.01	⬜ 0.14	🟥 0.01
Scoe sp										🟥 0	🟥 0.07	🟩 0.42	🟥 0.07	🟥 0.1	🟥 0.01	🟥 0.04	🟥 0.01	🟥 0.01	🟥 0.04	🟥 0.03
Gla var											🟥 0.02	🟩 0.36	🟥 0.01	🟥 0.01	🟥 0	⬜ 0.19	🟥 0	🟥 0.03	🟥 0.02	🟥 0
Scop leu												🟩 0.25	🟥 0.08	🟥 0.01	🟥 0	🟥 0.01	🟥 0	🟥 0.08	🟥 0.04	🟥 0
Scop sp													⬜ 0.13	🟥 0.03	🟥 0	⬜ 0.11	🟥 0.01	⬜ 0.09	🟥 0.08	🟥 0
Isp pic														🟥 0.04	🟥 0.01	🟥 0.08	🟥 0.09	🟥 0.06	🟥 0.07	🟥 0.01
Pri sub															🟥 0	🟥 0.08	🟥 0.04	🟥 0.01	🟥 0.04	🟥 0.02
Hir luc																🟥 0.08	🟥 0.02	🟥 0.01	🟥 0	🟥 0.01
Lag sen																	⬜ 0.16	🟥 0.05	🟥 0.08	🟥 0
Ura ben																		🟥 0.03	🟥 0.05	🟥 0
Eup fra																			⬜ 0.11	🟥 0.11
Plo cuc																				⬜ 0.09

Figure 5

Online Resources

Online resource 1 – Weight percentage of occurrence (wPOO) of the prey orders consumed by all individual predators, and by bats and birds separately.

Prey Orders	wPOO (%)
All	
Hemiptera	18,58
Coleoptera	16,62
Blattodea	15,84
Lepidoptera	15,51
Orthoptera	11,45
Diptera	6,45
Hymenoptera	5,34
Araneae	4,12
Psocodea	2,34
Dermaptera	1,20
NA	0,71
Neuroptera	0,59
Odonata	0,33
Hygrophila	0,21
Mantodea	0,19
Ephemeroptera	0,11
Trichoptera	0,11
Decapoda	0,10
Lithobiomorpha	0,07
Phasmatodea	0,05
Scolopendromorpha	0,04
Zygentoma	0,04
Bats	
Hemiptera	20,96
Coleoptera	19,89
Blattodea	18,75
Lepidoptera	13,10
Orthoptera	10,91
Diptera	5,37
Hymenoptera	4,82
Psocodea	2,93
Dermaptera	1,56
Neuroptera	0,76
Araneae	0,45
Trichoptera	0,15
Mantodea	0,13
NA	0,10
Scolopendromorpha	0,06
Odonata	0,04
Birds	
Lepidoptera	21,39
Araneae	13,07
Hemiptera	12,77
Orthoptera	12,74

Hymenoptera	10,41
Blattodea	8,75
Coleoptera	8,64
Diptera	5,25
NA	2,20
Odonata	1,03
Psocodea	0,90
Hygrophila	0,73
Ephemeroptera	0,36
Decapoda	0,33
Dermaptera	0,33
Mantodea	0,33
Lithobiomorpha	0,24
Neuroptera	0,18
Phasmatodea	0,18
Zygentoma	0,15

Online resource 2 – Weight percentage of occurrence (wPOO) of the main prey families (over 1% of wPOO) consumed by all individual predators, and by bats and birds separately.

Prey Families	wPOO (%)
All	
NA	18,19
Termitidae	8,20
Carabidae	5,23
Formicidae	4,57
Ectobiidae	4,47
Cicadellidae	4,06
Gryllidae	3,50
Rhyparochromidae	3,12
Erebidae	2,70
Pentatomidae	2,57
Tettigoniidae	2,23
Acrididae	2,18
Hydrophilidae	1,66
Gelechiidae	1,62
Scarabaeidae	1,47
Gracillariidae	1,43
Araneidae	1,41
Noctuidae	1,31
Delphacidae	1,27
Cydnidae	1,23
Chrysomelidae	1,16
Staphylinidae	1,16
Myopsocidae	1,15
Trigonidiidae	1,09
Limoniidae	1,03
Cicadidae	1,02
Bats	
NA	17,20

Termitidae	8,65
Carabidae	7,32
Ectobiidae	5,78
Cicadellidae	4,97
Gryllidae	4,29
Rhyparochromidae	3,99
Formicidae	3,25
Pentatomidae	2,88
Hydrophilidae	1,90
Acrididae	1,83
Scarabaeidae	1,76
Erebidae	1,72
Cydnidae	1,69
Delphacidae	1,66
Tettigoniidae	1,62
Gelechiidae	1,53
Staphylinidae	1,50
Trigonidiidae	1,46
Myopsocidae	1,43
Limoniidae	1,40
Nitidulidae	1,29
Chrysomelidae	1,12
Elateridae	1,08
Birds	
NA	20,60
Formicidae	7,80
Termitidae	7,11
Erebidae	5,07
Araneidae	4,16
Gracillariidae	3,93
Tettigoniidae	3,70
Cicadidae	3,50
Acrididae	3,03
Noctuidae	2,64
Cicadellidae	1,85
Gelechiidae	1,83
Pentatomidae	1,80
Gryllidae	1,58
Pisauridae	1,40
Salticidae	1,33
Geometridae	1,31
Ectobiidae	1,28
Chrysomelidae	1,26
Curculionidae	1,21
Ceratopogonidae	1,16
Hydrophilidae	1,06
Notodontidae	1,05
Rhyparochromidae	1,00

Online resource 3 – Weight percentage of occurrence (wPOO) of the main prey species (over 1% of wPOO) consumed by all individual predators, and by bats and birds separately.

Prey Species	wPOO (%)
All	
Macrotermes bellicosus	4.69
Ectobidae sp.	2.55
Oecophyla loginoda	1.57
Paraphonus	1.52
Microtermes sp.	1.29
Platymestopus vestitus	1.25
Pentatomidae sp.	1.02
Bats	
Macrotermes bellicosus	6,46
Ectobiidae sp.	3,39
Parophonus sp.	2,15
Microtermes sp.	1,78
Platymetopus vestitus	1,76
Pentatomidae sp.	1,29
Cicadellidae sp.	1,12
Lepidoptera sp.	1,06
Birds	
Oecophylla longinoda	4,47
Cicadidae sp.	3,26
Erebidae sp.	2,17
Odontotermes sp.	1,95
Gracillariidae sp.	1,67
Lepidoptera sp.	1,58
Gelechiidae sp.	1,57
Odontotermes latericius	1,36
Diplopoda sp.	1,36
Orthoptera sp.	1,10
Lepidoptera sp.	1,08
Ancistrotermes cavithorax	1,05
Odontotermes nilensis	1,03

Online resource 4 – Distribution of prey orders consumed by predators, showing the total number of predator individuals analysed and the number and percentage of bird and bat individuals consuming each prey order. Adjusted p-values were obtained from chi-squared tests assessing differences between bird and bat frequencies for each prey order, with correction for multiple comparisons using the Benjamini–Hochberg false discovery rate (FDR).

Prey Orders	Number of predator individuals	Number of bird individuals	Number of bat individuals	Percentage of Birds	Percentage of bats	Adjusted p-value
Araneae	57	52	5	96,2	3,8	6,9E-27
Blattodea	192	29	163	30,3	69,7	2,2E-07
Coleoptera	238	34	204	28,9	71,1	9,7E-12
Decapoda	2	2	0	100,0	0,0	1,5E-01
Dermaptera	25	2	23	17,5	82,5	4,7E-02
Diptera	86	22	64	45,6	54,4	5,0E-01
Ephemeroptera	1	1	0	100,0	0,0	3,6E-01
Hemiptera	258	52	206	38,1	61,9	1,4E-05
Hygrophila	3	3	0	100,0	0,0	4,8E-02
Hymenoptera	95	38	57	61,9	38,1	2,5E-02
Lepidoptera	207	75	132	58,1	41,9	9,2E-03
Lithobiomorpha	1	1	0	100,0	0,0	3,6E-01
Mantodea	4	2	2	70,9	29,1	6,4E-01
NA	11	10	1	96,1	3,9	1,2E-04
Neuroptera	11	1	10	19,6	80,4	3,2E-01
Odonata	6	5	1	92,4	7,6	2,5E-02
Orthoptera	141	46	95	54,1	45,9	3,6E-01
Phasmatodea	1	1	0	100,0	0,0	3,6E-01
Psocodea	34	4	30	24,5	75,5	4,6E-02
Scolopendromorpha	1	0	1	0,0	100,0	1,0E+00
Trichoptera	2	0	2	0,0	100,0	1,0E+00
Zygentoma	1	1	0	100,0	0,0	3,6E-01