UNIVERSIDADE DE LISBOA
FACULDADE DE CIÊNCIAS
DEPARTAMENTO DE BIOLOGIA ANIMAL

Bats, Birds, and Bugs: Metabarcoding trophic niches of invertebrate-eating flying vertebrates in West African lowland rice fields

Tiago Morais Gonçalves

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Doutora Ana Rainho

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Resumo

A dieta constitui uma parte essencial da ecologia animal. O estudo da dieta permite perceber como os diferentes elementos de uma comunidade interagem entre si, e como se influenciam na exploração dos recursos. O estudo da dieta pode também ser utilizado como ferramenta para desvendar importantes serviços de ecossistemas – benefícios proporcionados pelos ecossistemas naturais direta ou indiretamente ao ser humano – fornecidos pelas diferentes espécies, tais como provisão de recursos ou regulação do meio ambiente. Os morcegos e as aves são dois importantes grupos de predadores de invertebrados. Estes grupos podem ter um efeito de controlo sobre as suas presas e, por isso, um grande valor económico e social para o ser humano, uma vez que algumas espécies de invertebrados podem ter efeitos bastante nefastos na ausência de controlo, como é o caso de pragas agrícolas e vetores de doenças. A dieta destes predadores pode variar bastante de acordo com a espécie, o habitat e a sazonalidade. Portanto, perceber como varia a sua dieta é extremamente importante tanto para o conhecimento das comunidades faunísticas de forma holística como pela relevância que a conservação destas espécies tem para a humanidade.

O arroz é uma das principais fontes de alimento em todo o mundo. Na África Ocidental e, em particular, na Guiné-Bissau, o arroz tem uma importância fundamental na alimentação das pessoas, sendo a sua principal fonte de alimento. Para além disto, a produção de arroz tem também uma grande importância na paisagem do país, correspondendo a cerca de 21% da sua área cultivada. Estes arrozais são também importantes para as comunidades de invertebrados, especialmente durante a estação das chuvas devido ao seu alagamento, constituindo importantes locais de reprodução e de alimentação. Alguns destes invertebrados podem constituir também importantes pragas do arroz, afetando significativamente a sua produção. Deste modo, os arrozais da Guiné-Bissau constituem um importante local para o estudo da dieta dos predadores destes invertebrados, bem como da importância que estes predadores podem ter para a segurança alimentar das pessoas.

Neste estudo, foram utilizadas técnicas de *metabarcoding* e *next-generation sequencing* (NGS) para melhorar o conhecimento a cerca da partição do nicho ecológico numa comunidade de vertebrados voadores comedores de invertebrados que se alimentam em campos de arroz de pequenos proprietários. Considerámos três dos mecanismos que determinam a partilha de recursos em predadores simpátricos - especialização da dieta, sobreposição da dieta e caraterísticas funcionais - para responder às seguintes questões: 1) como é que a amplitude e composição da dieta variam entre diferentes espécies e grupos de predadores? 2) como é que a dieta se sobrepõe entre espécies e como é que as distâncias filogenéticas influenciam estas sobreposições? 3) como é que a diversidade funcional influência a variação da amplitude e composição da dieta entre os predadores?

Prevemos que os três mecanismos contribuam para a partilha de recursos e para a baixa competição pelos recursos das presas nesta comunidade. Espera-se que todas as espécies apresentem dietas amplas, devido à elevada diversidade de invertebrados geralmente observada nos trópicos. Espera-se que os morcegos apresentem dietas mais amplas do que as aves, tanto devido à atividade noturna geralmente mais elevada dos invertebrados, como ao carácter mais generalista dos morcegos. Esperamos também que os predadores apresentem diferenças substanciais na composição da dieta, devido a fatores como a utilização diferente do tempo e do microhabitat. Espera-se que espécies semelhantes morfológica, comportamental e filogeneticamente apresentem uma segregação alimentar ainda maior, no entanto, espera-se que os morcegos apresentem baixa competição trófica interespecífica. O tamanho, as caraterísticas de ecolocalização e a estratégia de alimentação são caraterísticas que limitam a capacidade dos morcegos de capturar presas e, portanto, devem ser importantes fatores de composição da dieta neste grupo. Da mesma forma, espera-se que a espessura do bico e o nicho trófico - invertívoro vs. granívoro - sejam os principais fatores que determinam as diferenças na dieta das aves.

Os morcegos e as aves foram recolhidos em arrozais do sector de Mansabá, região de Oio, no norte da Guiné-Bissau. Estes animais foram capturados com redes de nevoeiro em 2021 e 2022 entre junho e dezembro, exceto em agosto. As suas fezes foram recolhidas e armazenadas em álcool a 96%. Estas amostras foram posteriormente analisadas com *metabarcoding* e NGS, através da amplificação do gene *COI*. As unidades taxonómicas operacionais (OTUs) resultantes foram comparadas com as bases de dados BOLD e NCBI para identificação até ao menor nível taxonómico possível. Para este trabalho, foram apenas consideradas espécies de predadores com mais de 7 indivíduos amostrados. Para comparação da amplitude da dieta entre predadores, extraímos os valores das curvas de rarefação para 14 indivíduos, para 3 níveis taxonómicos de presa (OTU, Família e Ordem). Para a análise da composição da dieta, calculámos a percentagem de ocorrência ponderada (wPOO) para cada taxa de presa na dieta dos diferentes predadores. As diferenças na composição entre predadores foram posteriormente analisadas através *non-metric multidimensional scaling* (NMDS) e *analysis of similarities* (ANOSIM). A sobreposição da dieta entre pares de predadores foi analisada através do índice de Pianka. As distâncias filogenéticas foram obtidas online no sítio TimeTree. Posteriormente, calculámos a correlação entre a sobreposição da dieta e as distâncias filogenéticas. Os caracteres funcionais dos diferentes predadores foram compilados através de medições no campo e fontes publicadas. De forma a perceber como estas diferentes características podem explicar a variação na composição da dieta, modelámos as distâncias derivadas do NMDS com as características funcionais. Para perceber quais os taxa de invertebrados que têm maior influência na dieta dos predadores ao nível da amplitude e composição de presas recorremos a modelos lineares generalizados (GLMs).

Foram analisados 454 indivíduos, 328 morcegos e 126 aves, pertencentes a 13 espécies de morcegos e oito espécies de aves. Hemiptera (20.6%), Blattodea (17.7%), Coleoptera (14.1%), Lepidoptera (12.9%), and Orthoptera (11.3%), foram as principais ordens de presas consumidas, com as térmitas (Blattodea, Termitidae) a ter um papel de destaque na dieta destes predadores. Considerando apenas a dieta das aves, as aranhas compõem também grande parte da sua dieta. Foram encontradas 53 potenciais pragas agrícolas e oito potenciais vetores de doenças humanas, animais e vegetais. Todas as espécies de predadores apresentam uma grande amplitude de dieta com uma elevada percentagem de OTUs apenas encontradas na dieta de um indivíduo. Os morcegos apresentam, tendencialmente, maior amplitude que as aves ao nível da OTU. As aves e os morcegos apresentam uma segregação significativa da sua dieta, possivelmente justificada pela segregação temporal nos seus períodos de atividade. Considerando as sobreposições entre os diferentes pares de espécies, não encontrámos qualquer sobreposição significativa entre aves e morcegos. Várias espécies de morcegos mostram uma sobreposição significativa da dieta com algumas destas sobreposições a ser fortemente influenciadas pelo consumo de algumas espécies de térmitas. Apesar disto, um grupo de espécies Pipistreloide (*Neoromicia somalica*, *Pseudoromicia rendalli*, e *Afronycteris nanus*) apresentou uma sobreposição significativa da sua dieta. A sobreposição da dieta entre morcegos e especificamente entre espécies morfologicamente, comportamentalmente e filogeneticamente semelhantes vai ao encontro do padrão de baixa competição interespecífica na dieta, mencionado em estudos prévios. Contrariamente, nenhum par de aves revelou uma sobreposição significativa da dieta. Quer em aves quer em morcegos, não foi encontrada qualquer relação entre a sobreposição da dieta e as distâncias filogenéticas. Considerando os dois grupos de predadores em conjunto, a variação da dieta de aves e morcegos, quer na amplitude, quer na composição foi mais bem explicada pela sua distinção taxonómica do que por qualquer caracter destas espécies. Quando considerados em separado, apesar de nenhum caracter ser significativo, a variação da dieta dos morcegos foi mais bem explicada pela densidade de habitat e pela estratégia de caça. Estes dois caracteres influenciam principalmente o consumo de Araneae, Psocodea, Blattodea, e as famílias Erebidae e Limoniidae. No caso das aves, o peso e a grossura do bico são as características que melhor explicam a variação da dieta. Estes caracteres influenciam sobretudo o consumo de Araneae, em particular, da família Salticidae.

Estes resultados revelam a complexidade das interações entre espécies de predadores e entre predadores e presas, bem como a importância que os invertebrados assumem na dieta destes predadores. Por outro lado, mostram a importância que estes predadores podem ter no controlo das diversas espécies de invertebrados, incluindo potenciais pragas e vetores de doenças. As aves e os morcegos parecem ter um papel complementar no controlo de invertebrados possivelmente devido aos diferentes períodos de atividade. De um modo geral, todas as espécies parecem ter dietas muito diferentes, ainda que haja alguma sobreposição entre algumas espécies de morcegos. Posto isto, torna-se essencial a conservação de uma comunidade diversa de aves e morcegos de modo que se possa melhor aproveitar os potenciais serviços de ecossistemas que estes providenciam. Isto é especialmente importante em zonas, como a Guiné-Bissau e, no geral, a Africa Ocidental, onde o acesso a formas alternativas de combate a estes invertebrados, como os pesticidas, é difícil, devido ao baixo poder económico, e, ao mesmo tempo, apresenta um perigo à biodiversidade e ao ambiente, devido ao uso indiscriminado amplificado pela ausência de controlo e regulamentação ao uso destas substâncias.

Palavras-chave: Conservação da biodiversidade; Diversidade funcional; Ecologia trófica; Predação de invertebrados; Serviços ecossistémicos

Abstract

The knowledge about the diet of animal communities is essential to understand how communities function. Bats and birds are two important groups of invertebrate predators, suppressing their populations. However, the diet and the factors shaping it remain poorly understood for West African species. In this study, we investigated these mechanisms in agricultural landscapes of Guinea-Bissau using metabarcoding and next-generation sequencing. Specifically, we aimed to answer the following questions: 1) how do dietary breadth and composition vary among predator species and groups? 2) how does dietary overlap vary, and how do phylogenetic distances influence these overlaps? 3) how does functional diversity influence dietary breadth and composition among predators?

We analysed the diet of 13 bat and eight bird species. Results revealed that Hemiptera (20.6%), Blattodea (17.7%), Coleoptera (14.1%), Lepidoptera (12.9%), and Orthoptera (11.3%) were the most consumed invertebrate orders, with termites (Blattodea, Termitidae) representing a significant component. We found 53 potential crop pests and eight potential human, animal, and plant disease vectors in the diet of both bats and birds. All predators have broad niches, with bats generally exhibiting wider ones. There was a distinct trophic segregation between bats and birds, which is possibly explained by the differences in foraging periods. Some bat species displayed significant dietary overlaps, which indicate a low level of interspecific competition. However, we found no correlation between diet overlap and phylogenetic distance. Habitat density preference and foraging strategies were the only traits explaining bats' diet, mainly by influencing the consumption of Araneae, Psocodea, and Blattodea. While weight and beak depth significantly shaped birds' diet, especially the consumption of Araneae.

These findings highlight the importance of species-specific traits in shaping trophic niches and inform strategies to enhance the role of bats and birds in the provision of ecosystem services such as pest and disease vector suppression.

Keywords: Biodiversity conservation; Ecosystem services; Functional diversity; Invertebrate predation; Trophic ecology

Index

List of figures

List of tables

List of Abbreviations

AIC – Akaike information criterion

ANOSIM – Analyses of similarity

BOLD – Barcode of Life Data System

CI – Confidence interval

COI – Mitochondrial *cytochrome oxidase I*

DNA – Deoxyribonucleic acid

EPSG – European Petroleum Survey Group

FAO – Food and Agriculture Organization of the United Nations

GLM – Generalised linear models

IBAP – Institute for Biodiversity and Protected Areas

ICRISAT – International Crops Research Institute for the Semi-arid Tropics

NCBI – National Center for Biotechnology Information

NGS – Next generation sequencing

NMDS – Non-metric multidimensional scaling

OTU – Operational taxonomic unit

PCR – Polymerase chain reaction

USDA – United States Department of Agriculture

WGS – World Geodetic System

wPOO – Weighted percentage of occurrence

1. Introduction

Diet is a central part of animal ecology and a key determinant of the ecological niche that different species occupy (McCann 2007). Dietary studies provide insights into species' fundamental resource requirements and their ecological roles, both as consumers and food resources. Additionally, the study of the trophic niche of a community can unveil the biotic interactions that shape resource use among species (Nielsen et al. 2018). For example, dietary studies inform how predators partition resources and how predator-prey dynamics influence both groups (Schoener 1974; Sheppard and Harwood 2005).

Bats and birds are two important predators of invertebrates, playing critical roles in ecosystem processes (Kunz et al. 2011; Nyffeler et al. 2018). Previous studies of their dietary ecology highlight that dietary breadth and composition are highly variable, influenced by species-specific traits, seasonal changes, and habitat characteristics (Salinas-Ramos et al. 2015; Maine and Boyles 2015; Mansor et al. 2018; Davies et al. 2022). For instance, invertivorous (i.e. species that feed on invertebrates) bats tend to exhibit more generalist diets than invertivorous gleaning birds, likely due to differences in prey availability between day and night and bats' more opportunistic foraging behaviour (Maas et al. 2016; Wong and Didham 2024). These patterns align with optimal foraging theory, which predicts that resource availability influences dietary specialization and generalization (MacArthur and Pianka 1966; Pyke 2019). Furthermore, evolutionary history further contributes to dietary differences, with distantly related species often displaying greater differences in resource use (Van Cakenberghe et al. 2002; Brändle et al. 2002; Carrillo-Araujo et al. 2015). Conversely, phylogenetically and ecologically similar sympatric species may exhibit competition driven dietary segregation (Macarthur and Levins 1967) or alternatively, show lower abundances if competition persists (Root 1973; Stevens and Willig 2000).

Despite this, some studies argue that direct competition has a limited role in dietary differentiation among bat species. This may be due to their high vagility, extensive home ranges, and seasonal variation in prey availability which reduce the likelihood of resource limitation (Findley and Black 1983; Stevens and Willig 2000; Schoeman and Jacobs 2011; Dammhahn and Goodman 2014; Blanch et al. 2023). In addition to competition, functional traits - morphological and behavioural characteristics influencing prey acquisition – are key drivers of dietary variation. However, how these traits drive the dietary breadth or composition of bats and birds is still not fully understood. This is especially true for the understudied African species. In bats, traits such as body size, echolocation characteristics, cranial and dental morphology, jaw structure, and foraging strategy have been shown to drive prey selection (Bogdanowicz et al. 1999; Emrich et al. 2014; Weterings and Umponstira 2014; Villalobos-Chaves and Santana 2022; Ancillotto et al. 2023). Similarly, in birds, beak morphology strongly correlates to dietary preferences, distinguishing, for instance invertivorous and granivorous species (Brandl et al. 1994; Grant and Grant 2006). Among granivores, beak thickness correlates strongly with seed hardness (Hau and Wikelski 2001). However, the relationship between beak morphology and feeding ecology remains contested in some studies (Bright et al. 2016; Van Wassenbergh and Baeckens 2019), and evidence for correlations between body size and dietary breadth in birds have also yielded conflicting results: while some works show significant relations (Schluter and Grant 1984; Brändle et al. 2002), others reported no significant association (Brandl et al. 1994).

By consuming substantial amounts of invertebrates, bats and birds play a critical role in suppressing pest populations, an ecosystem service that benefits several agricultural crops and supports human health by reducing vectors of human disease (Whelan et al. 2008; Maas et al.

2016; Puig-Montserrat et al. 2020; Díaz-Siefer et al. 2022; Tuneu-Corral et al. 2023). Thus, understanding the factors driving dietary variation among these predator groups is essential for preserving or even optimising their contributions to these ecosystem services.

In Guinea-Bissau, freshwater lowland rice fields occupy areas that originally consisted of wet grass savannahs, known locally as *lala*, which flood during the rainy season (Catarino et al. 2008). These flooded areas support high biodiversity, functioning as key breeding and feeding habitats for invertebrates and vertebrates (Lawler 2001). Some invertebrates inhabiting rice fields can also be important rice pests (Heinrichs and Barrion 2004), severely damaging rice production (Oerke 2006; Waddington et al. 2010). Rice fields form a prominent part of the landscape, covering approximately 21% of the country's harvested area (FAO and ICRISAT 2019). Reflecting its dietary significance to people, rice production has recently expanded in the region (Djata et al. 2003; USDA 2024), a trend also observed in other countries across Africa (Seck et al. 2012). Understanding the dietary ecology of invertebrate-eating predators foraging in these fields is critical for food security and pest management.

In this study, we used metabarcoding and next-generation sequencing (NGS) to explore the ecological niche partitioning in a community of invertebrate-eating flying vertebrates foraging in smallholder rice fields. We focus on three key mechanisms driving resource partitioning in sympatric predators – diet breadth, diet overlap and the influence of functional traits – to answer the following questions: 1) how do dietary breadth and composition vary among predator species and groups? 2) how does dietary overlap vary, and how do phylogenetic distances influence these overlaps? 3) how does functional diversity influence dietary breadth and composition among predators?

We predict that all three mechanisms contribute to resource partitioning, leading to low competition for prey resources in this community. All species are expected to exhibit broad diets, reflecting the high invertebrate diversity characteristic of tropical ecosystems (Novotny and Miller 2014). Bats are anticipated to have broader diets than birds due to the typically higher nocturnal activity of invertebrates (Wong and Didham 2024), and their generalist foraging strategies (Maas et al. 2016). We also expect substantial differences in dietary composition among predators, driven by distinct circadian activity and microhabitat use (Mansor and Mohd Sah 2012; Emrich et al. 2014). Morphologically, behaviourally, and phylogenetically similar species are predicted to exhibit higher dietary segregation (Macarthur and Levins 1967). However, bats are expected to show low interspecific trophic competition (Fenton 1990). Functional traits such as body size, echolocation characteristics and foraging strategy are anticipated to significantly shape dietary composition in bats (Emrich et al. 2014; Ancillotto et al. 2023). In birds, dietary variation is likely driven by beak thickness and trophic niche (invertivore vs. granivore; Brandl et al. 1994).

2. Methods

2.1. Study area

The study area is located in the region of Oio in northern Guinea-Bissau (Figure 2.1). It is characterized by a Guinean maritime climate (FAO and ICRISAT 2019) with two distinct seasons, a rainy season from May to November, and a dry season from December to April. The mean annual air surface temperature is 27.96°C with little variation throughout the year, and annual precipitation varies between 1200 to 1400 mm (Catarino et al. 2001; Climate Change

Knowledge Portal 2023). The dominant vegetation is a savannah woodland, a secondary formation largely shaped by human interventions such as fires and shifting agriculture (Catarino et al. 2008). The landscape also includes rice, cashew fields and small villages (locally called *tabancas*). Our work focused on the lowland rainfed rice fields, which consisted of rice-paddies, fallow land, and isolated trees (Figure 2.1). The rice fields were bordered by woodlands and cashew orchards, while human settlements were scattered along the main roads.

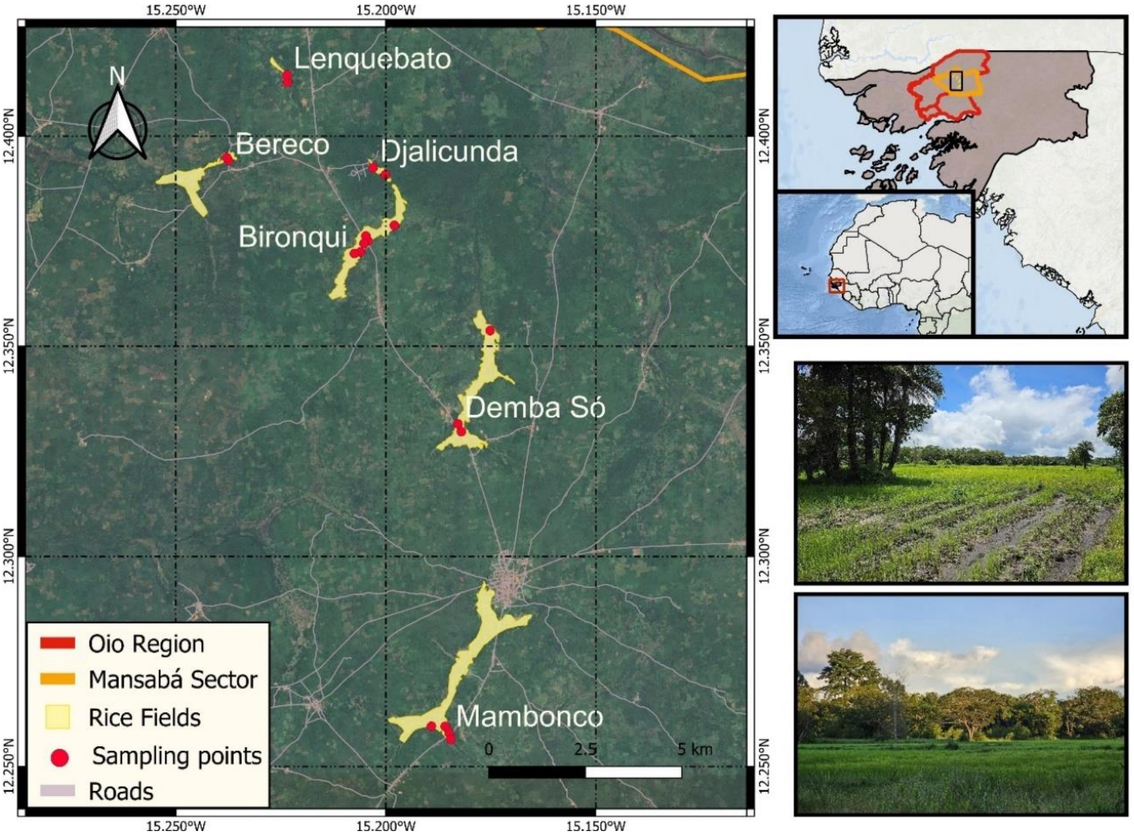


Figure 2.1. – Location of the study site in Guinea-Bissau. The map on the left shows the location of sampling points and respective rice fields. The map was built under the coordinate reference system EPSG:4326 – WGS 84 on 22 November 2024. Insets include a map with the location of the study area in 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 Mamboncо (bottom).

2.2. Bat and bird sampling

The sampling sites were located across various rice fields within the Mansabá sector (12° 20' 0.314" N, 15° 10' 57.474" W; Figure 2.1). Fieldwork was conducted from June to December in 2021 and 2022, excluding August due to the heavy rain, spanning the entire rice growth cycle.

Captures were performed using 12 m mist nets (Ecotone, 712/2P), with an average of five nets, ranging from one to eight, used per sample session. Nets were deployed near field edges, isolated trees, and water sources to maximize capture success. Captures took place from 7 to 11 a.m. and from 5 to 10 p.m. Captured animals were kept in single-use paper bags for at least 30 minutes before being identified and measured. Bird identification followed Borrow and Demey (2014) with nomenclature based on Clements (2007). Bat identification followed Happold and Happold (2013) and nomenclature was based on Simmons and Cirranello (2024). When field identification was uncertain, it was confirmed through molecular techniques (see Section Laboratory procedures). 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. Faecal pellets were collected with a maximum of three samples per individual and placed in 2 ml tubes filled with 96% alcohol, one pellet per tube.
All captures were conducted under the license issued by the Institute for Biodiversity and Protected Areas (IBAP), the regulatory authority in Guinea-Bissau.

2.3. Laboratory procedures

We individually processed and extracted the DNA of 664 faecal pellets, of which 537 belonged to bats and 127 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. 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). 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 and annealing at 55°C. 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 30k reads for Fwh2 and 4k reads for Fwh1.

2.4. Bioinformatic analysis

The software Flash was used to merge paired reads (Magoč and Salzberg 2011). Obitools commands ‘ngsfilter,’ ‘obiuniq,’ and ‘obigrep’ (Boyer et al. 2016) were employed to 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, the ‘—uchime3_denovo’ command to remove chimeric sequences, the ‘—cluster_size’ command to cluster at 99% similarity, and the ‘—usearch_global’ option to map reads back to the retained OTUs (operational taxonomic units) (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 and NCBI databases for identification to the lowest taxonomic level possible. When OTUs had similar identities across multiple species, genera, or other taxonomic ranks, the broadest level of classification was selected. OTUs were categorized as dietary (e.g., most arthropods) or non-dietary (e.g., predators, fungi, internal and external parasites).

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).

2.5. Data analysis

When predators were identified only at the genus level, we used OTUs to differentiate between potential species. Predators with less than seven sampled individuals were excluded from the analysis. While this sample size is not optimal for robust diet characterization (Mata et al. 2019), it was selected to include a larger number of bird species, particularly invertivores, to enable 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), and 1000 bootstraps. Curves were calculated for three taxonomic prey levels (OTU, Family, and Order), along with 95% confidence intervals. To compare diet breadth across predators, we extracted values from the curves for 14 individuals (twice the sample size of the species with the lowest number of individuals; Chao et al. 2014).

To quantitatively analyse the diet composition, we used occurrence data due to the high dietary richness and potential recovery bias from differential digestion (Deagle et al. 2019). The weighted percent of occurrence (wPOO) was calculated following Deagle et al. (2019). Dietary differences between predators were visualised using non-metric multidimensional scaling (NMDS) with Jaccard distance, using the metaMDS function from *vegan* package (Oksanen et al. 2022). Dissimilarities in diet were assessed with the anosim function from the same package, using 999 permutations. For species-level NMDS and ANOSIM, we used wPOO, while for individual-level analysis, we used prey occurrence data, excluding OTUs found only in a single individual's diet. To mitigate potential issues in NMDS and ANOSIM caused by the high proportion of absences linked to rare prey items in some predator diets, we performed a pairwise predator diets comparison using Pianka's index. This index emphasizes the relative abundances of shared prey, placing greater weight on their presence rather than their absence (Pianka 1973). Pianka's index was computed using wPOO and the niche.overlap function from the *spaa* package (Zhang 2016). Overlap significance was tested with the niche_null_model function from *EcoSimR* package (Gotelli et al. 2015) with 1000 repetitions.

To analyse how phylogenetic distance influences the dietary overlap, we calculated Spearman's correlation with cor function in R (R Core Team 2024). Phylogenetic distances between predators were obtained from TimeTree (Kumar et al. 2022). For predators identified only to the genus level, we used a species from that genus known to occur in the study area. When phylogenetic distance for a species was unavailable, we used data from a closely related species from the same genus.

We analysed how functional traits influenced predators' niche breadth using univariate Generalised Linear Models (GLMs) with glm function in R (R Core Team 2024). Dietary breadth at the three prey taxonomic levels (OTU, Family, and Order) was modelled as a function of the predators' functional traits, using the Gaussian family and "log" as link function, except when considering the diet of both predator groups at the OTU level, for that case the Gamma family with "log" as link function performed better, based on Akaike information criterion (AIC). We compiled functional traits related to morphology, habitat and foraging behaviour from field measurements and published sources (Monadjem et al. 2010; Borrow and Demey 2014; Tobias et al. 2022; Cosentino et al. 2023) (for further details, see Table S1 in the Supplementary Information section). Correlations between functional traits were assessed using Spearman's correlation with cor function in R (R Core Team 2024), and one of the variables with correlations exceeding 0.75 were discarded (Alberdi et al. 2020; Smeraldo et al. 2021).

We examined the dietary composition distances of bats and birds, derived from the NMDS, to understand how functional traits account for the differences in diet between these groups. Predators not identified to the species level were excluded from the ordination. This analysis was performed using the envfit function from the *vegan* package (Oksanen et al. 2022) with 999 permutations. To identify which prey orders and families most influence the relation between dietary composition and functional traits, we performed univariate GLMs for all prey orders and for families with an average wPOO higher than 1%. The prey consumption of the different taxa was modelled as a function of the predators' functional traits, using the quasibinomial distribution family with "logit" as link function using the glm function in R (R Core Team 2024). This family is suitable for modelling proportions and accounts for overdispersion (Shoukri and Aleid 2022).

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). For all analyses the significance level was set at 0.05.

3. Results

We analysed the diets of 454 individuals, comprising 328 bats and 126 birds, across 13 species of bats and eight species of birds. DNA metabarcoding of 664 faecal samples revealed 3229 occurrences of 1252 different arthropod prey OTUs, spanning 134 families and 18 orders. Only 11% of prey OTUs are identified at the species level.

The average number of individuals sampled per predator species was 21.62 (± 9.92, 95% CI). *Scotophilus* sp. was the most sampled taxon with 103 individuals (Table 3.1). In contrast, *Hirundo lucida*, *Nycteris* cf. *hispida*, *Ploceus melanocephalus*, *Prinia subflava*, and *Scotoecus albofuscus* were each represented by seven individuals.

3.1. Diet breadth and composition

On average, each predator species consumed 96.67 ± 34.32 different OTUs, with values ranging from a total of 18 in *Uraeginthus bengalus* to 351 prey OTUs in *Scotophilus* sp. (Table 3.1). The average number of OTUs per individual predator ranged from 2.3 ± 0.92 invertebrate OTUs in *U. bengalus* to 12.43 ± 3.31 in *S. albofuscus* (Table 3.1; rarefaction and sample coverage curves are available from Figure S1 to S6 in the Supplementary Information section).

Table 3.1 – 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 average prey taxa consumed per individual predator (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	Avg. no of prey OTUs per indiv. predator	Sample Coverage
Afronycteris nanus	*Afr nan*	Bat	34	118	6.50 ± 0.92	0.63 ± 0.06
Euplectes franciscanus	*Eup fra*	Bird	12	54	5.17 ± 2.57	0.24 ± 0.15
Glauconycteris variegata	*Gla var*	Bat	11	40	5.18 ± 2.24	0.52 ± 0.15
Hipposideros caffer / ruber	*Hip caf/rub*	Bat	34	239	10.29 ± 2.38	0.49 ± 0.06
Hirundo lucida	*Hir luc*	Bird	7	29	5.00 ± 2.24	0.35 ± 0.22
Ispidina picta	*Isp pic*	Bird	9	35	4.56 ± 1.77	0.33 ± 0.20
Lagonosticta senegala	*Lag sen*	Bird	9	53	6.00 ± 2.22	0.04 ± 0.09
Macronycteris gigas	*Mac gig*	Bat	10	53	6.80 ± 2.86	0.36 ± 0.14
Mops condylurus	*Mop con*	Bat	41	181	7.85 ± 1.92	0.62 ± 0.06
Neoromicia somalica	*Neo som*	Bat	23	107	7.70 ± 1.51	0.57 ± 0.08
***Neoromicia* sp.**	*Neo sp*	Bat	13	81	9.08 ± 3.39	0.52 ± 0.10
Nycteris* cf. *hispida	*Nyc cf his*	Bat	7	52	7.57 ± 5.41	0.04 ± 0.09
Ploceus cucullatus	*Plo cuc*	Bird	65	183	4.25 ± 0.65	0.47 ± 0.07
Ploceus melanocephalus	*Plo mel*	Bird	7	28	4.71 ± 1.71	0.26 ± 0.19
Prinia subflava	*Pri sub*	Bird	7	29	4.86 ± 1.45	0.34 ± 0.23
Pseudoromicia rendalli	*Pse ren*	Bat	17	125	9.71 ± 3.68	0.37 ± 0.08
Scotoecus albofuscus	*Scoe alb*	Bat	7	73	12.43 ± 3.31	0.32 ± 0.13
***Scotoecus* sp.**	*Scoe sp*	Bat	18	124	11.78 ± 2.64	0.61 ± 0.07
Scotophilus leucogaster	*Scop leu*	Bat	10	63	7.5 ± 3.92	0.27 ± 0.12
***Scotophilus* sp.**	*Scop sp*	Bat	103	345	7.08 ± 0.73	0.69 ± 0.03
Uraeginthus bengalus	*Ura ben*	Bird	10	18	2.30 ± 0.92	0.31 ± 0.21

The average prey wPOO for each predator species showed that Hemiptera, (20.6%), Blattodea (17.7%), Coleoptera (14.1%), Lepidoptera (12.9%), and Orthoptera (11.3%), were the most consumed prey orders (Figure 3.1). When considering bats alone, the principal orders consumed, and their relative importance were practically the same as when considering both predator groups. When considering only birds' diet, Hemiptera (17.5%) and Blattodea (15.6%) continued to be the most consumed orders, followed by Orthoptera (14.2%), Lepidoptera (13.0%), and Araneae (12.3%).

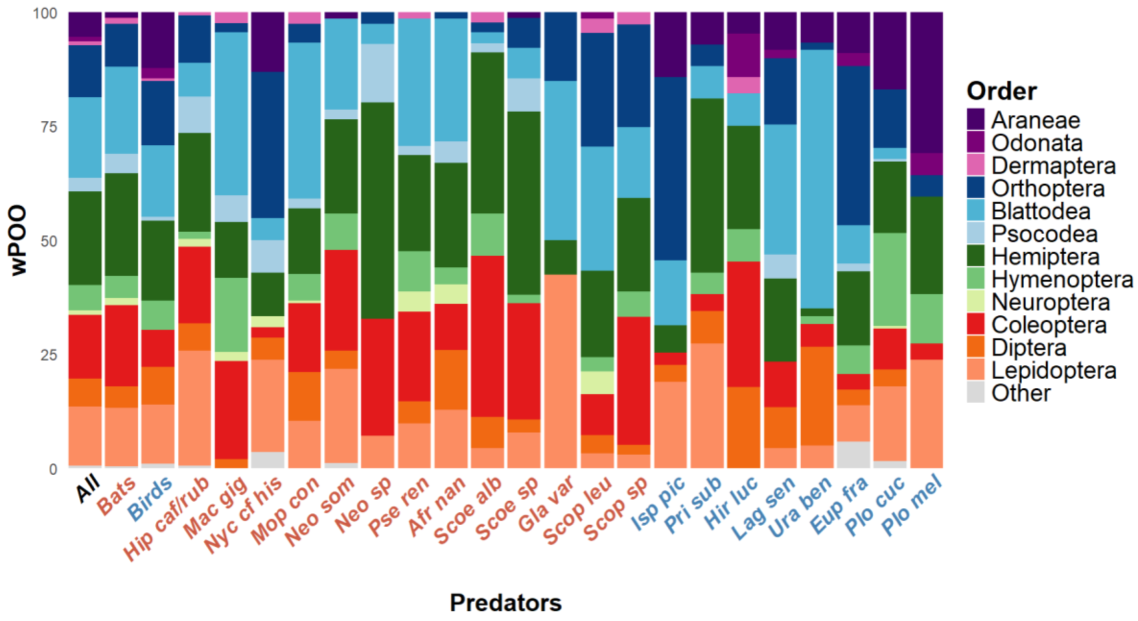


Figure 3.1 – Weighted percentage of occurrence (wPOO) of arthropod orders in the diet of bats and birds from lowland rainfed rice fields of Guinea Bissau. The first column on the left represents the combined diet of all species, while the second and third columns represent the diets of all bat species 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 3.1.

While the occurrence of Hemiptera reflected the consumption of different families and species, Blattodea was primarily represented by the families Termitidae and Ectobiidae, averaging 13.27% and 6.05% of the diet of each predator species, making them the first and the third most consumed prey families. The most frequently consumed prey species were also from these two families: *Macrotermes bellicosus* (4.63 %, average wPOO per predator species), *Ectobidae* sp. (2.62%), *Odontotermes* sp. (1.27%), and *Microtermes* sp. (1.20%).

Additionally, we found 53 potential crop pests and eight potential human, animal, and crop disease vectors both in bird and bat diets. All predator species, except *Nycteris* sp., consumed potential crop pests or disease vectors. About 42.5% of all individuals studied consumed at least one pest or disease vector species. This included 43.6% of bat individuals and 39.7% of bird individuals. Among birds, a smaller proportion of granivorous individuals (37.9%) consumed pests or disease vectors compared to invertivorous individuals (47.8%). A detailed description of all predators' consumption of potentially harmful invertebrate species is available in Table S2 in the Supplementary Information section.

Prey consumption showed a seasonal pattern. Termites, such as *M. bellicosus* and *Microtermes* sp., peaked in predators' diets during June and July. In contrast, other species, like *Platymetopus vestitus*, and *Carabidae* sp. appeared in predators' diet only towards the end of the year (see Figure S7 in the Supplementary Information section).

Rarefaction analysis revealed that sample coverage at the OTU level ranged from 4.16 ± 9.51% in *Lagonosticta senegala* to 69.45 ± 3.47% in *Scotophilus* sp. (Table 3.1). With 14 samples per predator species, nearly all predators consumed over 40 different OTU prey (Figure 3.2). We observed a high proportion of rare OTUs in the diets: about 60.5% of prey OTUs in bats and 73% in birds were detected in the diet of only one individual predator.

Bats generally exhibited a broader niche breadth than birds at the OTU level, though this pattern disappeared at higher prey taxonomic levels (Figure 3.2). Additionally, using 14 samples, we found no significant differences in the dietary breadth between granivorous and invertivorous birds, except for *U. bengalus* at OTU prey level. However, granivore’s sample coverages tended to be smaller.

Figure 3.2 – 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 3.1.

Uraeginthus bengalus showed the narrowest niche breadth at the OTU level (24.17 ± 9.57 preyed OTUs) with Blattodea constituting more than half of the diet of this species (Figure 3.1). Despite preying on a relatively, limited number of OTUs, these belong to a diverse range of families and orders similar to those targeted by other predators (Figure 3.2). Among bats, *Glauconycteris variegata* has the narrowest niche breadth across all prey taxonomic levels, particularly at the family and order level (Figure 3.2). This species fed mostly on insects from the orders Lepidoptera and Blattodea (Figure 3.1). In contrast, *Lagonosticta senegala* showed the broadest niche breadth among birds at the OTU level, with a mean number of prey taxa (81.48 ± 23.79) comparable to that of bats, though it also presents a large confidence interval, overlapping with other birds. *Euplectes franciscanus* was the bird species with the highest diversity of orders consumed. It was also the only sampled predator species consuming the orders Ephemeroptera and Zygentoma, and Gastropoda species.

3.2. Diet overlap and phylogenetic relationships

Despite some overlap, a clear separation existed between the dietary composition of birds and bats (Figure 3.3A). This separation is supported by ANOSIM analysis (ANOSIM R = 0.59, p-value = 0.001). The distribution of prey orders also evidenced the difference between the two predator groups. When comparing the consumption of prey orders between bats and birds, the majority of Aranea (96.2 %), Odonata (92.9 %), and Hymenoptera (64.4 %) was consumed by birds, while Dermaptera (89.8 %), Neuroptera (83.3 %), Psocodea (75.4%), Coleoptera (70.7 %) and Blattodea (67.5%) were mainly consumed by bats.

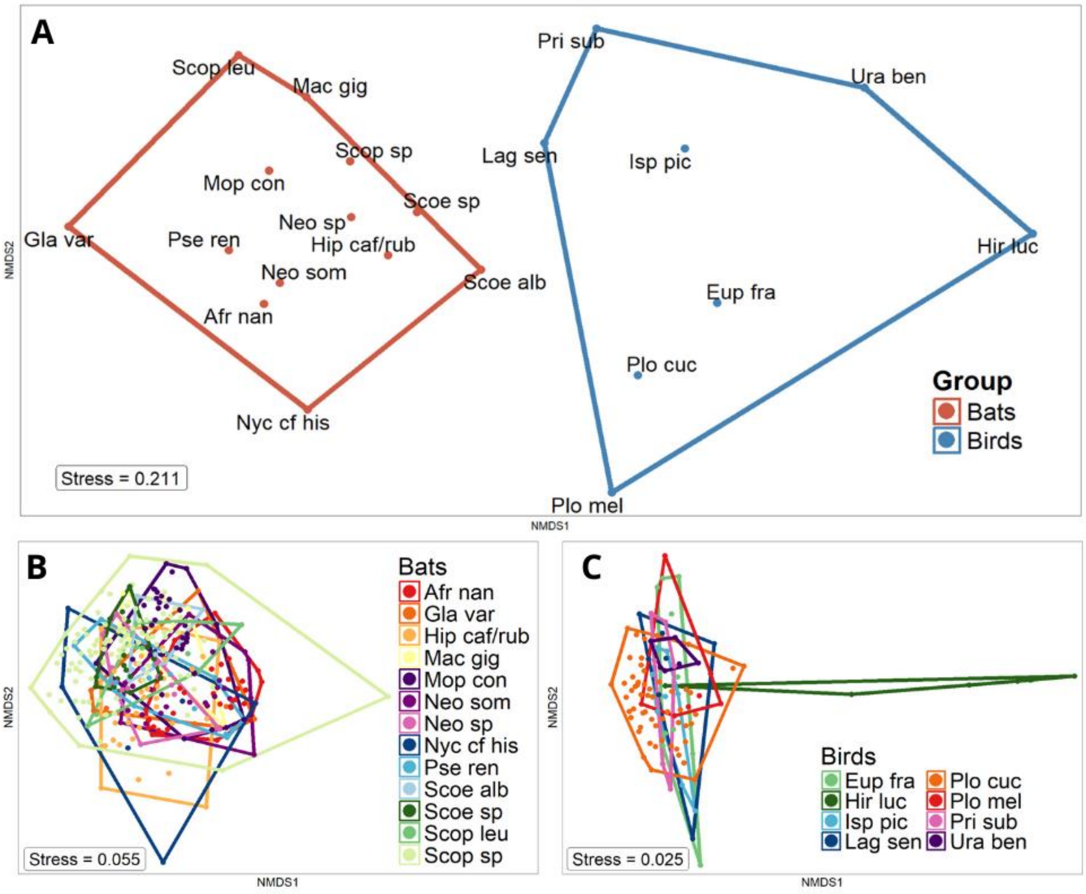
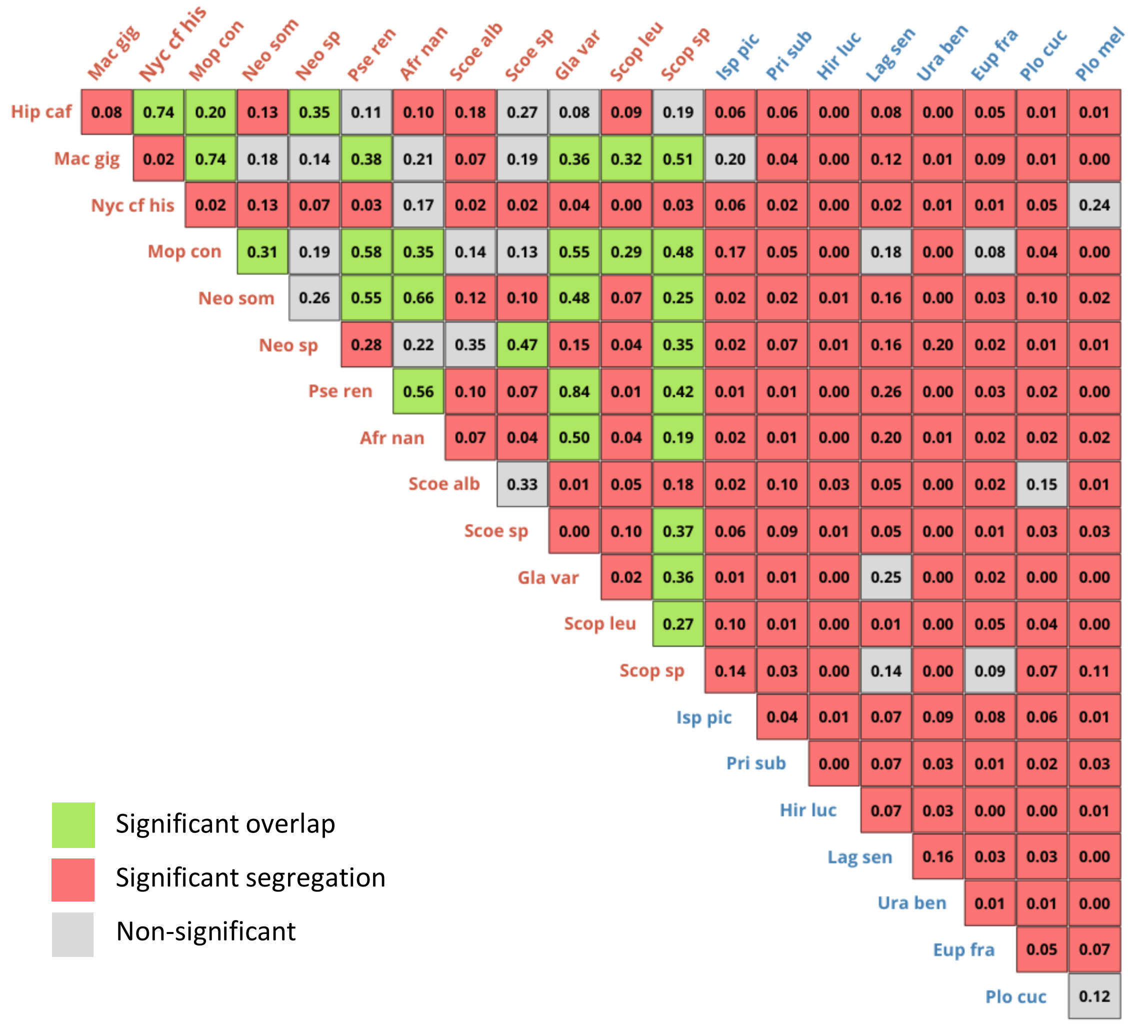


Figure 3.3 – NMDS ordination of molecular bat and bird diets (at the OTU prey level) from lowland rainfed rice fields of Guinea Bissau. The ordination is calculated with Jaccard distance. Polygons represent the convex hulls enclosing 95% of data points. A: NMDS ordination of bat and bird diets, with each dot representing the diet of a predator species. B: NMDS ordination of bats' diets where each polygon represents a species, and each dot represents an individual. C: NMDS ordination of birds' diets, where each polygon represents a species, and each dot represents an individual. The ordination stress level is indicated in the respective panel. Predator species acronyms are listed in Table 3.1.

When examining the diet composition of bats and birds separately, most species within each predator group exhibited a high degree of diet overlap (Figure 3.3B, and C). The great exception was *H. lucida* in relation to all other birds (R = 0.07, p = 0.001; Figure 3.3C). The high overlap observed between the other species appeared to be strongly influenced by the large number of rare OTUs, leading to an inflation in similarity due to the high proportion of zeros. ANOSIM analyses confirmed a significant, albeit small, difference between species diet (R_{bats} = 0.20 p = 0.001; R_{birds} = 0.13, p = 0.01).

By reducing the inflated similarity due to absences, Pianka's index revealed a significant, albeit small, dietary overlap between bat species ($O_{bats} = 0.27$, $p = 0.001$), with several pairs of bat species showing a higher overlap than expected by chance (Figure 3.4). In contrast, Pianka´s index showed significant dietary segregation between bird species ($O_{birds} = 0.04$, $p = 0.001$), with all species showing a smaller pairwise overlap than would be expected by chance (Figure 3.4). In fact, the pairwise overlap in diet composition between birds appeared to be as low as the overlap between bat and bird species. Besides the segregation between all bird species, the overlaps between the *H. lucida* and the other bird species were, on average, slightly smaller than the overlaps between the other birds.



	Mac gig	Nyc cf his	Mop con	Neo som	Neo sp	Pse ren	Afr nan	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	🟥 0.08	🟩 0.74	🟩 0.20	🟥 0.13	🟩 0.35	⬜ 0.11	🟥 0.10	🟥 0.18	⬜ 0.27	⬜ 0.08	🟥 0.09	⬜ 0.19	🟥 0.06	🟥 0.06	🟥 0.00	🟥 0.08	🟥 0.00	🟥 0.05	🟥 0.01	🟥 0.01
Mac gig		🟥 0.02	🟩 0.74	⬜ 0.18	⬜ 0.14	🟩 0.38	⬜ 0.21	🟥 0.07	⬜ 0.19	🟩 0.36	🟩 0.32	🟩 0.51	⬜ 0.20	🟥 0.04	🟥 0.00	🟥 0.12	🟥 0.01	🟥 0.09	🟥 0.01	🟥 0.00
Nyc cf his			🟥 0.02	🟥 0.13	🟥 0.07	🟥 0.03	⬜ 0.17	🟥 0.02	🟥 0.02	🟥 0.04	🟥 0.00	🟥 0.03	🟥 0.06	🟥 0.02	🟥 0.00	🟥 0.02	🟥 0.01	🟥 0.01	🟥 0.05	⬜ 0.24
Mop con				🟩 0.31	⬜ 0.19	🟩 0.58	🟩 0.35	⬜ 0.14	⬜ 0.13	🟩 0.55	🟩 0.29	🟩 0.48	🟥 0.17	🟥 0.05	🟥 0.00	⬜ 0.18	🟥 0.00	⬜ 0.08	🟥 0.04	🟥 0.00
Neo som					⬜ 0.26	🟩 0.55	🟩 0.66	🟥 0.12	🟥 0.10	🟩 0.48	🟥 0.07	🟩 0.25	🟥 0.02	🟥 0.02	🟥 0.01	🟥 0.16	🟥 0.00	🟥 0.03	🟥 0.10	🟥 0.02
Neo sp						🟥 0.28	⬜ 0.22	⬜ 0.35	🟩 0.47	🟥 0.15	🟥 0.04	🟩 0.35	🟥 0.02	🟥 0.07	🟥 0.01	🟥 0.16	🟥 0.20	🟥 0.02	🟥 0.01	🟥 0.01
Pse ren							🟩 0.56	🟥 0.10	🟥 0.07	🟩 0.84	🟥 0.01	🟩 0.42	🟥 0.01	🟥 0.01	🟥 0.00	🟥 0.26	🟥 0.00	🟥 0.03	🟥 0.02	🟥 0.00
Afr nan								🟥 0.07	🟥 0.04	🟩 0.50	🟥 0.04	🟩 0.19	🟥 0.02	🟥 0.01	🟥 0.00	🟥 0.20	🟥 0.01	🟥 0.02	🟥 0.02	🟥 0.02
Scoe alb									⬜ 0.33	🟥 0.01	🟥 0.05	🟥 0.18	🟥 0.02	🟥 0.10	🟥 0.03	🟥 0.05	🟥 0.00	🟥 0.02	⬜ 0.15	🟥 0.01
Scoe sp										🟥 0.00	🟥 0.10	🟩 0.37	🟥 0.06	🟥 0.09	🟥 0.01	🟥 0.05	🟥 0.00	🟥 0.01	🟥 0.03	🟥 0.03
Gla var											🟥 0.02	🟩 0.36	🟥 0.01	🟥 0.01	🟥 0.00	⬜ 0.25	🟥 0.00	🟥 0.02	🟥 0.00	🟥 0.00
Scop leu												🟩 0.27	🟥 0.10	🟥 0.01	🟥 0.00	🟥 0.01	🟥 0.00	🟥 0.05	🟥 0.04	🟥 0.00
Scop sp													🟥 0.14	🟥 0.03	🟥 0.00	⬜ 0.14	🟥 0.00	⬜ 0.09	🟥 0.07	🟥 0.11
Isp pic														🟥 0.04	🟥 0.01	🟥 0.07	🟥 0.09	🟥 0.08	🟥 0.06	🟥 0.01
Pri sub															🟥 0.00	🟥 0.07	🟥 0.03	🟥 0.01	🟥 0.02	🟥 0.03
Hir luc																🟥 0.07	🟥 0.03	🟥 0.00	🟥 0.00	🟥 0.01
Lag sen																	🟥 0.16	🟥 0.03	🟥 0.03	🟥 0.00
Ura ben																		🟥 0.01	🟥 0.01	🟥 0.00
Eup fra																			🟥 0.05	🟥 0.07
Plo cuc																				⬜ 0.12

🟩 Significant overlap
🟥 Significant segregation
⬜ Non-significant

Figure 3.4 – 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 3.1.

Piaka's index also revealed a high dietary overlap between a group of morphological and phylogenetic similar Pipistrelloid species (*Neoromicia somalica*, *Pseudoromicia rendalli*, and *A. nanus*) (Figure 3.4). However, we also found that highly consumed termites (*M. bellicosus* and *Microtermes* sp.) displayed a great influence in the diet overlap of some bat species. Given the temporal pattern in the consumption of these prey, we recalculated the Pianka's overlaps in this Pipistrelloid group, without these two insect species, to ensure their dietary similarity was not a reflection of temporal correlation. Despite a general decrease, the overlaps between the three predator species remained significant ($O_{\text{Neo som – Afr nan}} = 0.36$, $p_{\text{Neo som – Afr nan}} = 0.047$; $O_{\text{Neo som – Pse ren}} = 0.39$, $p_{\text{Neo som – Pse ren}} = 0.041$; $O_{\text{Pse ren – Afr nan}} = 0.40$, $p_{\text{Pse ren – Afr nan}} = 0.012$).

Despite the high overlap among some closely related species, no significant correlation was found between phylogenetic distance and diet overlap at either the OTU prey level (Spearman's rank correlation: $\rho_{\text{bats}} = -0.14$, $p_{\text{bats}} = 0.29$; $\rho_{\text{birds}} = 0.08$, $p_{\text{birds}} = 0.69$) or the family prey level ($\rho_{\text{bats}} = -0.13$, $p_{\text{bats}} = 0.34$; $\rho_{\text{birds}} = -0.15$, $p_{\text{birds}} = 0.49$).

3.3. Traits driving diet differences

GLM models revealed that when considering both predator groups, habitat density, tail length, and trophic niche appeared to influence the dietary breath at OTU level (Table 3.2). Trophic niche also emerged as the most significant trait explaining diet composition of bats and birds together, at OTU level ($r^2 = 0.1679$; $p = 0.043$; Figure 3.5A). However, when accounting for the difference between the two predator groups these traits ceased to significantly explain dietary variation among predators. GLM analyses showed that invertivores have lower consumption of Araneae and Tettigoniidae (Figure S8, available in Supplementary Information section).

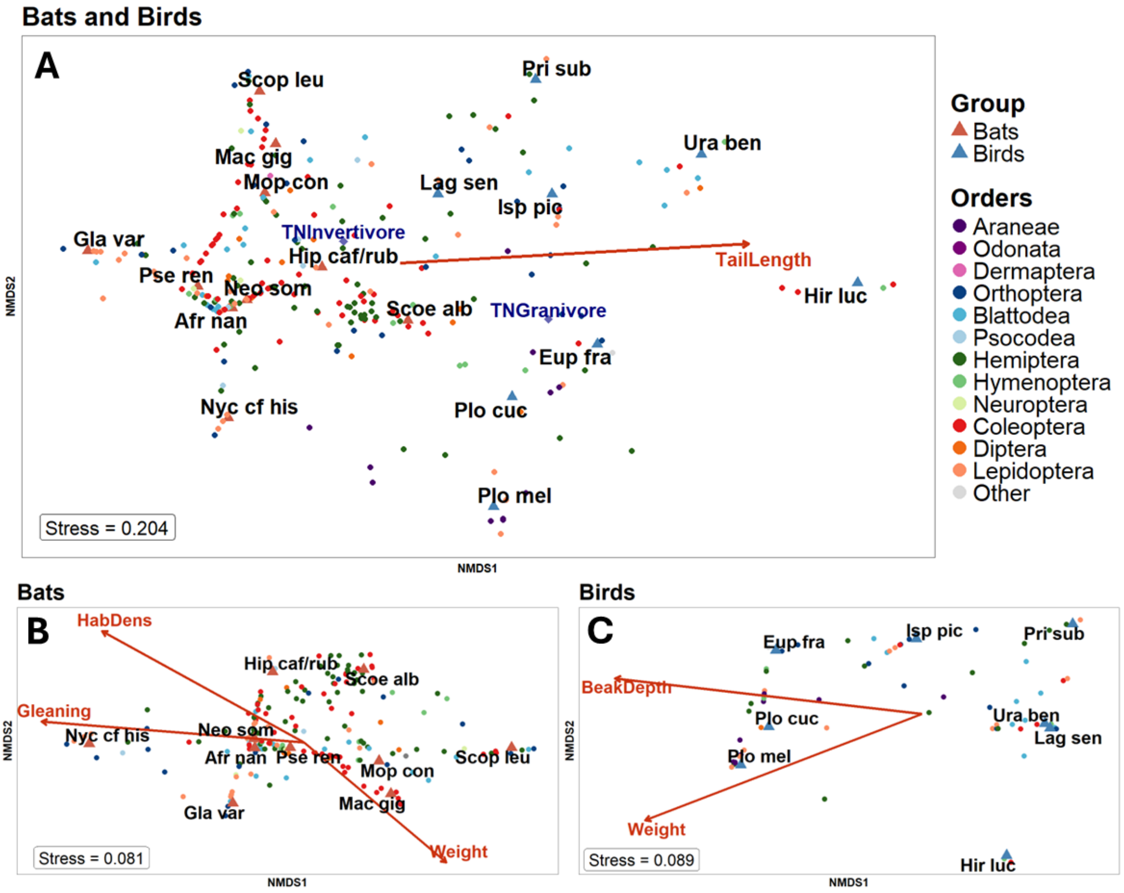


Figure 3.5 – NMDS ordination of molecular bat and bird diets (at the OTU prey level) from lowland rainfed rice fields of Guinea Bissau. Triangles represent predator species (bats in red and birds in blue), and dots represent prey OTUs coloured by their respective order. Vectors represent continuous functional traits, and rhombuses represent categorical functional traits. A: NMDS ordination of bat and bird diets. B: NMDS ordination of bat diets. C: NMDS ordination of birds' diets. The ordination stress level is indicated in the respective panel. Predators who were not identified to the species level were not included in the ordination. Predator species acronyms are listed in Table 3.1. Trait description is available in Table S1 in the Supplementary Information section.

No trait strongly explained the ordination of dietary composition when considering bats alone. Habitat density approached significance ($r^2 = 0.46$, $p = 0.084$; Figure 3.5B) while gleaning and weight showed no clear influence. Despite, not achieving the level for remotion (> 0.75) habitat density and gleaning showed some level of correlation (Spearman's correlation = 0.75, p = 0.01). GLM analyses revealed that bats foraging in denser habitats consumed more Araneae and Psocodea, and less Blattodea. At the family level, these bats also showed a trend toward higher consumption of Erebidae and lower consumption of Limoniidae (Figure 3.6).

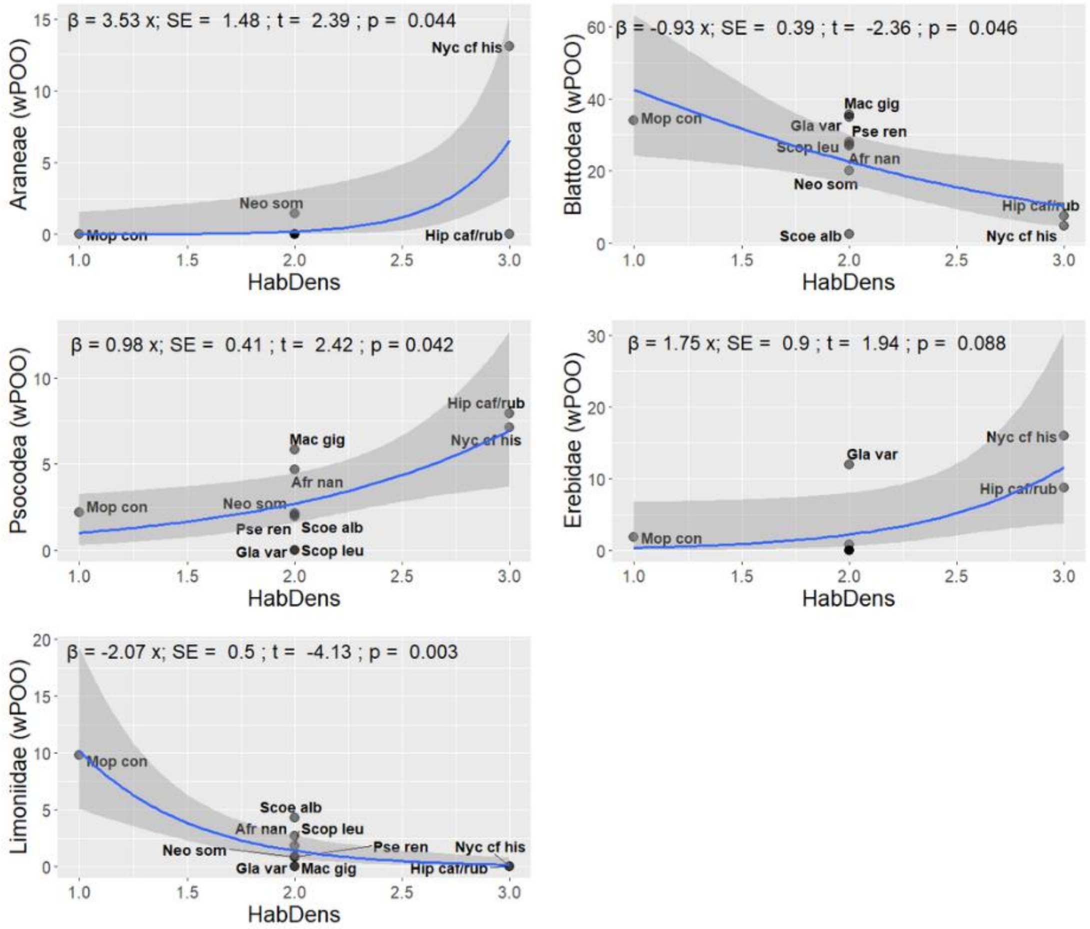


Figure 3.6 – Graphical representation of GLM predictions for bats from lowland rainfed rice fields of Guinea Bissau. The weighted percentages of occurrence (wPOO) of the diet components are modelled by birds' habitat density preferences. GLMs were built with distribution family Gaussian and "log" as the link function. Model predictions are represented by the blue line and the 95% confidence intervals are presented by the shadow area. Dots represent the observed values for each species. The model parameters are indicated in the respective panel. Predator species acronyms are listed in Table 3.1. Trait descriptions and characteristics are summarized in Table S1 in the Supplementary Information section.

Weight (r^2 = 0.66, p = 0.040) and beak depth (r^2 = 65, p = 0.053) were the traits most strongly associated with the ordination of bird diet composition (Figure 3.5C). Despite, not achieving the level for remotion (> 0.75) these traits showed some level of correlation (Spearman's correlation = 0.65, p = 0.05). Weight was mostly related to the diet preferences of the heaviest species P. cucullatus and *P. melanocephalus*. GLM analyses revealed that these heavier birds preyed mainly on Hymenoptera, Mantodea, and Neuroptera, and tended to prey more on Araneae. At the family level, they preyed more on Formicidae (Figure 3.7). Beak depth was mostly correlated not only with these granivores (*P. cucullatus, P. melanocephalus*, and *E. franciscanus*), but also with the insectivore *Ispidina picta*. GLM revealed that species with larger beak depth consumed more Mantodea and Neuroptera, and less Dermaptera. They also tended to consume more Araneae. At the family level, birds with larger beak depth tended to consume more Salticidae, and less Ephydridae (Figure 3.8).

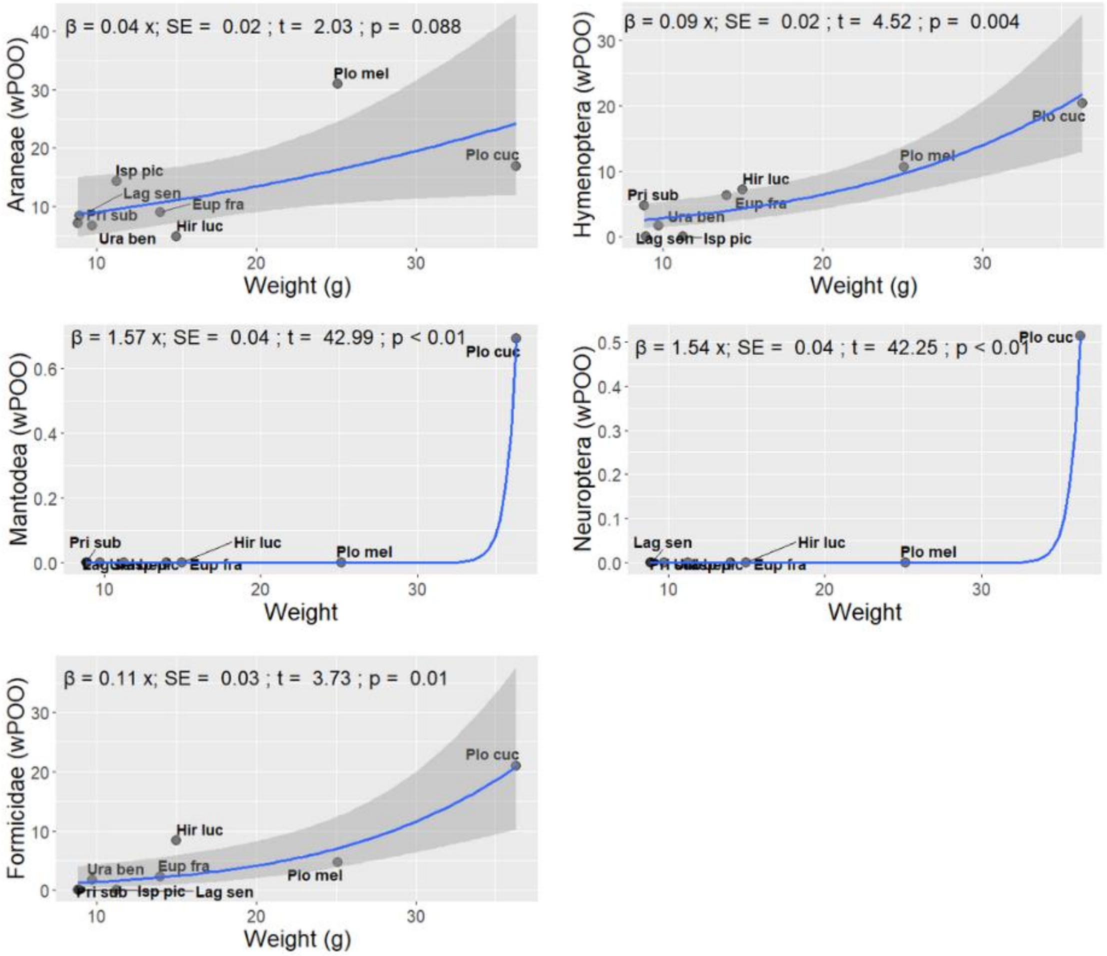


Figure 3.7 – Graphical representation of GLM predictions for birds from lowland rainfed rice fields of Guinea Bissau. The weighted percentages of occurrence (wPOO) of the diet components are modelled by birds' weight. GLMs were built with distribution family Gaussian and "log" as the link function. Model predictions are represented by the blue line and the 95% confidence intervals are presented by the shadow area. Dots represent the observed values for each species. The model parameters are indicated in the respective panel. Trait descriptions and characteristics are summarized in Table S1 in the Supplementary Information section.

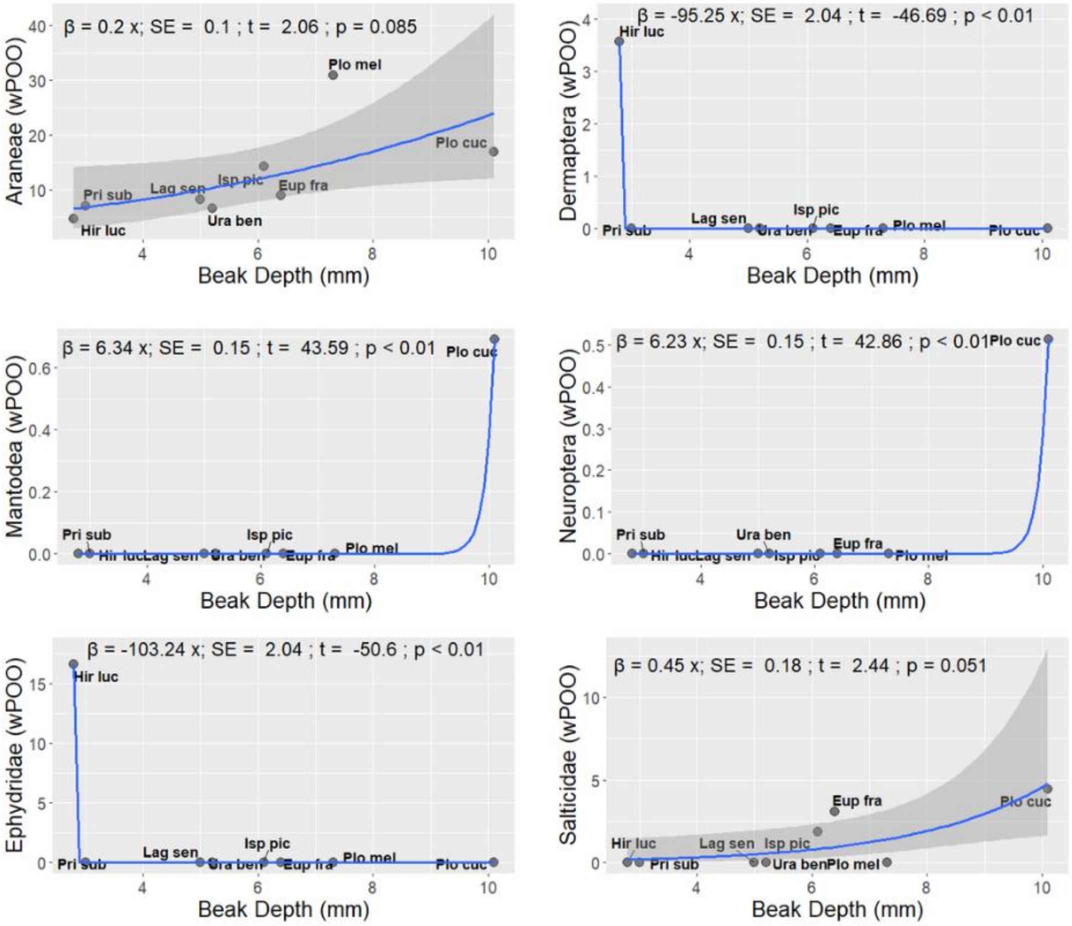


Figure 3.8 – Graphical representation of GLM predictions for birds from lowland rainfed rice fields of Guinea Bissau. The weighted percentages of occurrence (wPOO) of the diet components are modelled by birds' beak depth. GLMs were built with distribution family Gaussian and "log" as the link function. Model predictions are represented by the blue line and the 95% confidence intervals are presented by the shadow area. Dots represent the observed values for each species. The model parameters are indicated in the respective panel. Predator species acronyms are listed in Table 3.1. Trait descriptions and characteristics are summarized in Table S1 in the Supplementary Information section.

4. Discussion

In this study, we applied metabarcoding for the first time to analyse the diet of a community of invertebrate-eating flying vertebrates foraging in smallholder rice fields in West Africa. Our results offer the first detailed invertivore dietary description for several species, including *N. somalica*, *H. lucida*, *E. franciscanus*, *P. melanocephalus*, *U. bengalus*, *L. senegala*. The observed overall dietary patterns agreed with our expectations, and foraging time – nocturnal and diurnal - appeared as a major mechanism of niche segregation, clearly separating the diets of bats and birds. All predators revealed broad diets including a high number of rare prey OTUs, with bats generally exhibiting broader diets than birds. Some predators heavily exploited prey species with peaks of abundance, and almost all predator species consumed at least one potential agricultural pest or disease vector invertebrate. Several bat species showed significant dietary overlap, particularly Pipistrelloid species, whereas birds revealed no significant dietary overlap at the OTU level. While some overlap occurred among closely related species, we found no correlation between dietary overlap and phylogenetic distance in either group. Habitat density preferences appeared to influence dietary differences in bats, whereas beak depth and body weight significantly shaped the diet of birds.

4.1. Diet breadth and composition

Both bats and birds displayed broad diets, reflecting the high diversity of invertebrates (1252 OTUs) and their generalist foraging strategies. Bats tend to exhibit a broader invertivorous diet than birds, potentially due to differences in foraging periods and strategies. Invertebrates often have higher nocturnal activity, especially in warmer environments (Wong and Didham 2024), aligning with the bats' nocturnal feeding habits. Granivorous birds also prey on a diversity of invertebrate species similar to the other birds, further supporting the idea of broad dietary diversity across predator groups.

The most consumed invertebrate orders across all predators, and specifically among bats, were Hemiptera, Blattodea, Coleoptera, Lepidoptera, and Orthoptera. This aligns with the general patterns of bat diets (Kunz et al. 2011), though Blattodea consumption was notably higher than expected. When focusing on birds, Araneae also emerged as a highly consumed order, consistent with known bird dietary patterns (Nyffeler et al. 2018).

Among the most significant prey items, termites (Blattodea), emerged as a major component. 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 (Korb and Salewski 2000). For example, *U. bengalus* showed the highest termite consumption, with one termite OTU, *Odontotermes* sp., comprising 26.7% of its diet and consumed exclusively by *U. bengalus*. Hamed and Evans' (1983) reported that termites are vital to the diet of nestlings of this species, however, *U. bengalus* consumed termites consistently throughout the sampling period, suggesting a preference for specific prey rather than seasonal availability or phenological variation. In contrast, species such as *G. variegata*, and *P. rendalli*, which consumed termites seasonally (e.g. *M. bellicosus* and *Microtermes* sp.), exhibited dietary shifts corresponding with termite reproductive cycles, typically peaking between late June and early July when alate termites emerge shortly after the first heavy rains (Mitchell 2008; Manzoor and Mir 2010). These patterns highlight the role of seasonal prey availability in shaping predator diets.

The proportion of rare OTUs was high in both bat and bird diets. Our findings challenge the notion that gleaning invertivorous birds are more specialized predators and reinforces the generalist character of bats (Maas et al. 2016). Although consistent with previous studies (Garfinkel et al. 2022; Bookwalter et al. 2023), the high number of rare OTUs could also be partially due to the low sample coverage, which may have skewed the relative abundance of prey, particularly in birds. Nevertheless, the prevalence of rare OTUs, alongside the consumption of prey during peaks of abundance, highlights the opportunistic feeding behaviour of these predators (Mwansat et al. 2015; Andriollo et al. 2021).

This opportunistic behaviour highlights the potential role of these predators as pest suppressors, particularly in agricultural ecosystems. Almost all predator species consumed invertebrate pests, and about half individuals sampled consumed at least one potential pest or disease vector. These findings align with studies suggesting that bats and birds could be effective agents in the suppression of harmful invertebrates in agricultural fields (Cohen et al. 2020; Liu et al. 2023), including rice pests, which often exhibit periodic peaks of abundance similar to termites (Heinrichs 1994). The consumption of pests and vectors of human, cattle, and crop diseases in these predators' diets underscores their potential contribution to pest management and disease control in West Africa, as already documented for other regions and other crops (Díaz-Siefer et al. 2022; Tuneu-Corral et al. 2023).

However, the number of potential pests and disease vectors in the diet of these predators could be underestimated due to limitations in our sampling, *COI* databases and invertebrate knowledge in the region. These include the broader diets of predators than sampled here, incomplete barcoding, which resulted in a low proportion of OTUs identified to the species level, and a limited knowledge of the ecological role of many invertebrate species and their potentially harmful impact on agricultural crops. Despite these challenges, both bats and birds seem to play an essential role in maintaining the health of rice fields by controlling pest populations.

Overall, the broad and opportunistic diets of flying vertebrates in West African rice fields seem to be a product of both the diverse invertebrate prey available and the generalist foraging strategies of these predators (MacArthur and Pianka 1966; Pyke 2019). Although both groups exhibited broad dietary patterns, some species demonstrate specialization in specific prey, suggesting trophic niche segregation. These dietary differences likely stem from a combination of seasonal prey availability, morphological traits, and foraging behaviours.

4.2. Diet overlap and phylogenetic relationships

As discussed in the previous section, both bats and birds exhibit broad, generalist diets, largely due to the abundance of diverse prey in their environment. However, we observed significant dietary segregation between the two groups, which reflects their distinct foraging times. Bats primarily forage during the night and thus consume more nocturnal prey, such as Dermaptera, Coleoptera, and Blattodea (Rankin and Palmer 2009; Wong and Didham 2024). In contrast, sampled birds, which forage diurnally, consumed more species of typical diurnal orders, such as, Odonata and Hymenoptera (Corbet 1980; Wong and Didham 2024).

Despite this separation, overlap was observed within the bat group, particularly among closely related species, such as those in the Pipistrelloid group. This overlap was strongly 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 that specialize in swarming termites, or other peaking species, thus inflating the perceived importance of these prey across the bat community. Although these termites were a significant component of the bat diet, the high dietary overlap observed between bats, particularly between closely related species challenges traditional niche theory, which suggests that similar species should avoid competing for the same resources (Macarthur and Levins 1967). This overlap likely reflects a lower degree of competition for food resources among bats, a pattern consistent with previous studies (Findley and Black 1983; Schoeman and Jacobs 2011; Dammhahn and Goodman 2014; Blanch et al. 2023). Several factors may explain this low competition, including the high mobility and extensive home ranges of bats, the lack of food scarcity (Fenton 1990), and the variability in habitat and food resources that prevent bats from reaching equilibrium densities (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).

In contrast, birds showed no significant dietary overlap at OTU level. This lack of overlap, which has also been reported in previous studies (Orłowski and Karg 2013; Bookwalter et al. 2023), may partly stem from limited sample sizes for some birds, which can affect the detection of dietary patterns, especially when the prey spectrum is broad (Deagle et al. 2019; Mata et al. 2019).

However, the low overlap may also reflect a greater diversity in foraging strategies, among bird species, as this study included exclusively invertivorous, primarily granivorous, and granivorous-invertivorous bird species (Owiunji and Plumptre 1998; Billerman et al. 2022; Tobias et al. 2022). Even among exclusively invertivores, we examined highly aerial foragers, as is the case of *H. lucida* (Turner and Rose 1989; Tobias et al. 2022), and ground-foraging species such as *P. subflava* and *I. picta* (Ryan and Dean 2020; Woodall 2021). Notably, we observed a trend of smaller overlaps between *H. lucida* and other bird species, likely due to its unique foraging behaviour and habitat preferences (Turner and Rose 1989; Tobias et al. 2022).

The significant dietary overlap observed between closely related bat species was not correlated with phylogeny, suggesting that dietary overlap does not always reflect evolutionary relatedness. This lack of correlation may reflect the limited number of species compared or the influence of complex evolutionary processes, such as convergence and divergence (López-Aguirre et al. 2023), as evidenced by the high overlap between *M. gigas* and *M. condylurus*, two species from distinct suborders, that is not driven by termite consumption.

Overall, while temporal foraging behaviour plays a key role in dietary segregation 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.

4.3. Traits driving diet differences

When considering birds and bats together, dietary breadth appeared to be explained by habitat density preference, tail length, and trophic niche. However, these traits primarily reflected broader differences between bats and birds. Most bats included in the study preferred cluttered and edge habitats, whereas birds were species of open habitat. Birds also had longer tails, and included granivorous species, contrasting with the strictly invertivorous bats. The influence of trophic niche on diet composition further underscores these inter-group distinctions. For example, birds showed higher consumption of Araneae, which accounted for 96.2% of all detections, and Tettigoniidae, largely consumed by the granivorous *L. senegala* and *E. franciscanus*.

Contrarily to what we expected, no single trait strongly explained the diet composition of bats, although habitat density preferences showed moderate influence. This relationship appeared linked to gleaning behaviour, particularly in species like *N.* cf. *hispida* and *H. caffer/ruber*, which generally forage in cluttered environments by gleaning. *Nycteris* cf. *hispida* was nearly the sole consumer of Araneae, and more specifically Araneidae spiders known to construct webs in vegetation (Nogueira and Pinto-da-Rocha 2016), thus more abundant in clutter environments and in ground vegetation. This aspect might explain their higher consumption by species that prefer cluttered environments and forage by gleaning. *Hipposideros caffer/ruber*, which shares similar foraging behaviours and habitat preferences, did not consume Araneae, suggesting that traits such as other echolocation characteristics may influence prey selection. Other prey associations, such as the consumption of the litter-dwellers Psocoptera (New 1987) by clutter-specialist bats and Limoniidae by open habitat foragers like *M. condylurus*, reflect habitat-specific prey availability (Happold and Happold 2013; Podenas and Byun 2013; Olsen and Andersen 2021). The consumption of Blattodea, especially alate termites during dispersal flights, by open- and edge-foragers also highlights the influence of habitat density and prey behaviour on dietary composition.

For birds, weight and beak depth emerged as important factors in shaping their diet. Larger-bodied birds with large beaks, such as *P. melanocephalus* and *P. cucullatus* consumed more Araneae, likely due to their ability to handle prey with complex anti-predator strategies (Eisner 1985; Cloudsley-Thompson 1995). The association between these traits and predation on rare prey orders, like Mantodea and Neuroptera, likely reflects sampling biases, as these orders were only detected in *P. cucullatus* a species highly sampled. Similarly, the relation between Hymenoptera and weight is mostly driven by the high consumption of Formicidae by *P. cucullatus* and by the estimate of wPOO, as the number of occurrences of these insects doesn´t vary much in the diet of the remaining bird species. The consumption of Dermaptera and Ephydridae by *H. lucida* likely relates to its aerial foraging behaviour rather than to its low beak depth, given its unique hawking strategy (Turner and Rose 1989).

While several morphological, behavioural, and habitat traits appear to influence the diets of invertebrate-eating flying vertebrates, a more nuanced understanding may require larger sample sizes and additional predator species to test these patterns more robustly. Additionally, the influence of these traits might become more evident when examining diets at a finer taxonomic resolution. However, the high prey diversity and low individual OTU consumption observed in this study limit the feasibility of such analysis. In addition, invertebrate taxonomy may not properly reflect the functional traits driving predator-prey interactions. Future analysis based on prey functional traits, such as size, behaviour, or habitat use may provide deeper insights into niche partitioning among these predators. Such efforts would require substantial improvements in barcoding databases and a better understanding of African invertebrate traits.

5. Conclusion

As predicted, our findings highlight the importance of diet breadth, overlap, and functional traits in resource partitioning among invertebrate-eating flying vertebrates foraging on lowland rainfed rice fields. These species displayed a remarkably diverse diet, encompassing a wide range of invertebrate species, including potential crop pests and disease vectors. Their generalist and opportunistic feeding behaviour suggest that bats and birds play a significant role in arthropod population control, which likely contributes to pest suppression in rice production systems. This pest control service is likely underestimated, due to the broader diets of predators and limited knowledge about invertebrate species in Africa and their effect on crops.

Rice is critical for global food security, particularly in Africa, and Guinea-Bissau (Maclean et al. 2002; Djata et al. 2003). Arthropod pests, however, pose a major threat to rice production (Oerke 2006; Waddington et al. 2010), prompting farmers to resort to chemical pesticides, which can harm human health and wildlife (Ansari et al. 2014). It is therefore essential to find sustainable alternatives to manage agricultural pests. Globally, invertebrate-eating bats and birds have proven to be effective natural pest suppressors, providing important ecological and economic benefits (Díaz-Siefer et al. 2022; Tuneu-Corral et al. 2023). Their complementary ecological roles, shaped by dietary specialization and foraging strategies, underscore the importance of preserving diverse communities of birds and bats for effective arthropod management. Moreover, dietary overlap among some bat species may enhance ecosystem resilience by mitigating fluctuations in prey availability.

Some of the granivorous bird species prey on rice pests but can also act as rice pests (de Mey et al. 2012; Downs and Hart 2020). Additionally, both predator groups prey on spiders, thereby regulating the populations of this important insect mesopredator. Therefore, further studies are needed to evaluate the trade-offs between pest suppression, rice predation, and consumption of beneficial invertebrate predators by bats and birds (Sottomayor et al. 2024). Such studies could provide a deeper understanding of their ecological roles and reinforce their importance for rural communities.

To enhance and sustain the pest control services provided by bats and birds, management strategies must be developed in collaboration with farmers and rural communities (Temudo and Abrantes 2014). Key measures include maintaining patches of native vegetation (Horgan et al. 2017) and isolated trees within the rice fields (Fernandes 2024), which support higher diversity of bat and bird species by catering to their varied habitat and dietary needs. Maintaining access to drinking water sources during the dry season, ensuring adequate roosting sites, and reducing agrochemical usage (Tuneu-Corral et al. 2023) are also crucial. These practices not only promote biodiversity but also align with sustainable agricultural practices, fostering coexistence between wildlife and farming systems.

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Supplementary material

Table S1 – Compilation of bat and bird functional traits.

Trait	Trait description	Variable type	Possible values	Source
Bats				
ActivityDawn	Activity during dawn.	Categorical	Yes; No	Afrobat[1]
ActivityDusk	Activity during dusk.	Categorical	Yes; No	Afrobat[1]
EchoType	Type of echolocation signal.	Categorical	LD-FM; LD-QCF and LD-CF; HD-CF;	Monadjem[2]
Flycatching	Hunting by flycatching.	Discrete	0 – Never; 1 – Occasionally; 2 – Typically	Afrobat[1]
FMaxE	Frequency of maximum energy in echolocation call (kHz)	Continuous	-	Afrobat [1]
ForearmLength	Length of the forearm (mm)	Continuous	-	Capture data
Gleaning	Hunting by gleaning.	Discrete	0 – Never; 1 – Occasionally; 2 – Typically	Afrobat[1]
HabDens	Vegetation density of foraging habitat.	Discrete	1 – Open; 2 – Clutter-edge; 3 - Clutter	Afrobat[1]
HeadBodyLength	Length from the tip of the nose to anus, base of tail, or vent (mm).	Continuous	-	Afrobat[1]
TailLength	Length of the tail in (mm).	Continuous	-	Afrobat[1]
TotalLength	Length from the tip of the nose to the tip of tail. When not available, it was calculated as HeadBodyLength + TailLength (mm).	Continuous	-	Afrobat[1]
TrophicNiche	Classification of the trophic niche based on most consumed food resource.	Categorical	Insectivorous	Afrobat[1]
Weight	Body mass (g).	Continuous	-	Capture data
Wingspan	Distance between wingtips (mm).	Continuous	-	Afrobat[1]
Birds				
BeakDepth	Depth of the beak at the anterior edge of the nostrils (mm).	Continuous	-	Avonet[3]
BeakLengthCulmen	Length from the tip of the beak to the base of the skull (mm).	Continuous	-	Avonet[3]
BeakLengthNares	Length from the tip of the beak to the anterior edge of the nostrils (mm).	Continuous	-	Avonet[3]
BeakWidth	Width of the beak at the anterior edge of the nostrils (mm).	Continuous	-	Avonet[3]
HabDens	Vegetation density of foraging habitat.	Discrete	1 – Open; 2 – Semi-open; 3 - Dense	Avonet[3]
HWIndex	Index calculated as KippsDistance /WingLength x 100	Continuous	-	Avonet[3]
KippsDistance	Length between the tip of the first secondary to the tip of the longest primary (mm).	Continuous	-	Avonet[3]
TailLength	Distance between the tip of the longest rectrix and the point at which the two central	Continuous	-	Avonet[3]

	rectrices protrude from the skin (mm).			
RelativeSize	Length (cm).	Continuous	-	Borrow & Demey[4]
Trophic niche	Classification of the trophic niche based on most consumed food resource.	Categorical	Granivore; Invertivore	Avonet[3]
Weight	Body mass (g).	Continuous	-	Capture data
WingLength	Length from the carpal joint to the tip of the longest primary.	Continuous	-	Capture data

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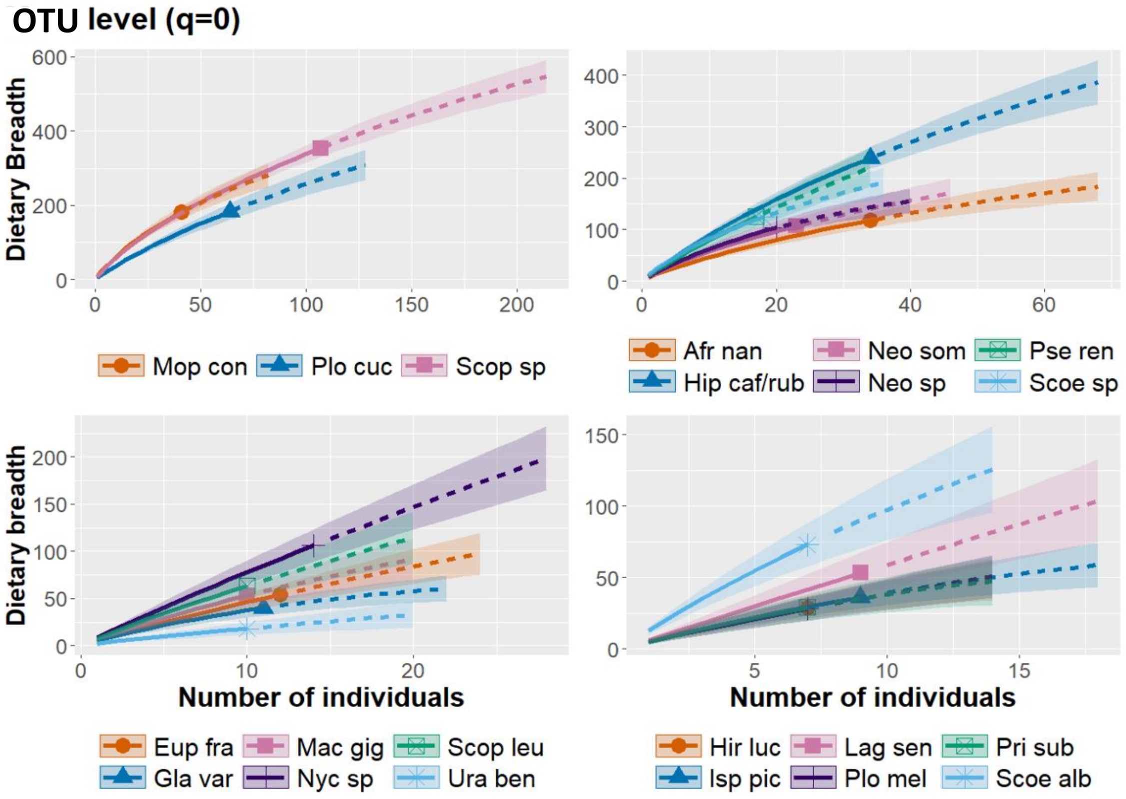

Figure S1 – Dietary niche breadth of bats and birds from lowland rainfed rice fields of Guinea Bissau, at the OTU level. Dietary breadth rarefaction is represented by the solid line and extrapolation by the dashed line. 95% confidence intervals are represented by the shaded area. Curves were built with Hill number species richness (q=0) and with 1000 bootstraps.

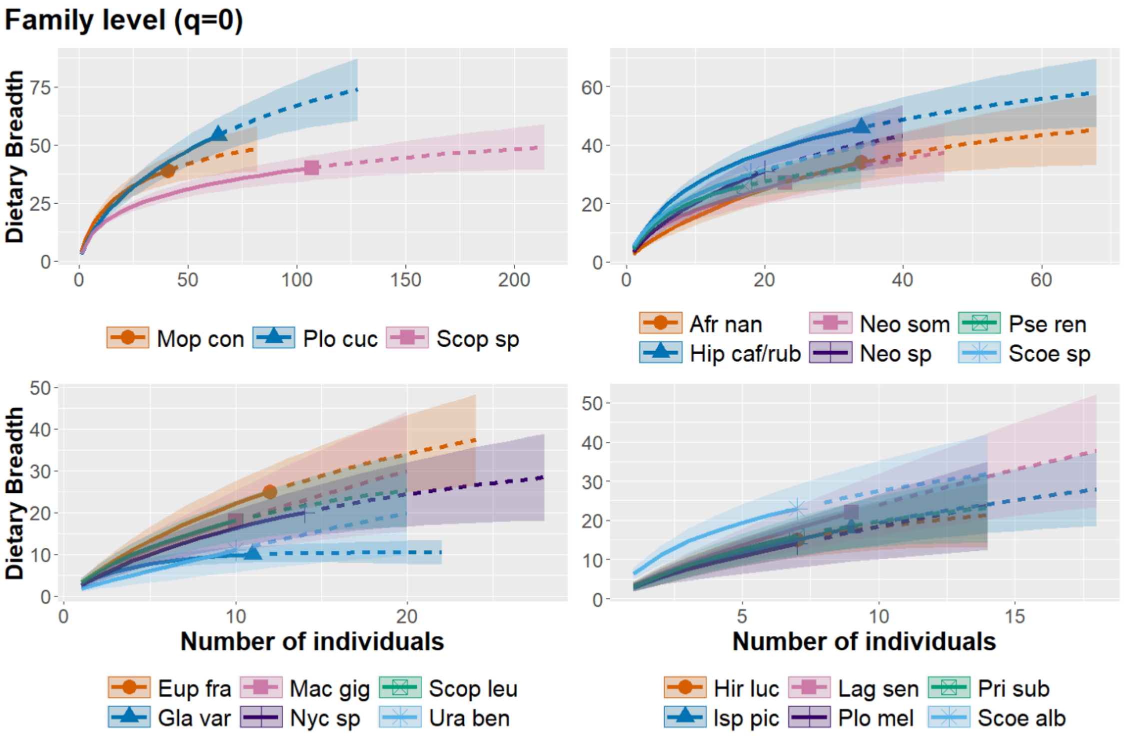

Figure S2 – Dietary niche breadth of bats and birds from lowland rainfed rice fields of Guinea Bissau, at the family level. Dietary breadth rarefaction is represented by the solid line and extrapolation by the dashed line. 95% confidence intervals are represented by the shaded area. Curves were built with Hill number species richness (q=0) and with 1000 bootstraps.

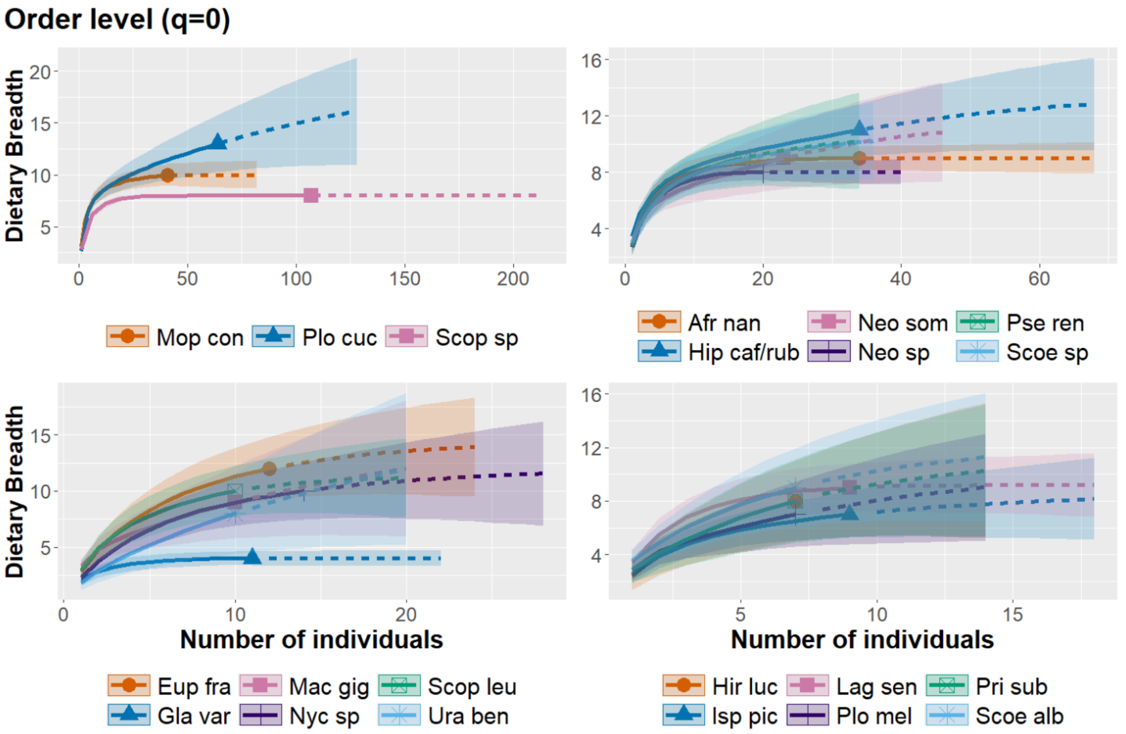

Figure S3 – Dietary niche breadth of bats and birds from lowland rainfed rice fields of Guinea Bissau, at the order level. Dietary breadth rarefaction is represented by the solid line and extrapolation by the dashed line. 95% confidence intervals are represented by the shaded area. Curves were built with Hill number species richness (q=0) and with 1000 bootstraps.

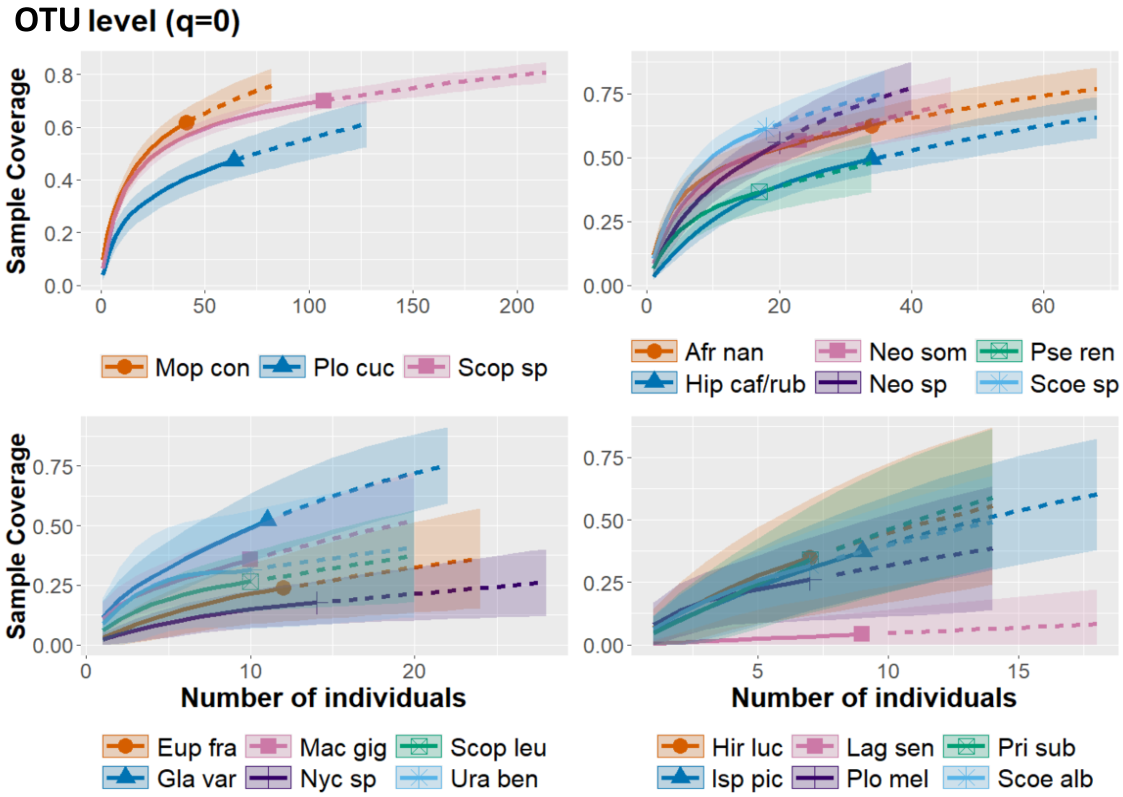

Figure S4 – Dietary niche breadth of bats and birds from lowland rainfed rice fields of Guinea Bissau, at the OTU level. Sample coverage rarefaction is represented by the solid line and extrapolation by the dashed line. 95% confidence intervals are represented by the shaded area. Curves were built with Hill number species richness (q=0) and with 1000 bootstraps.

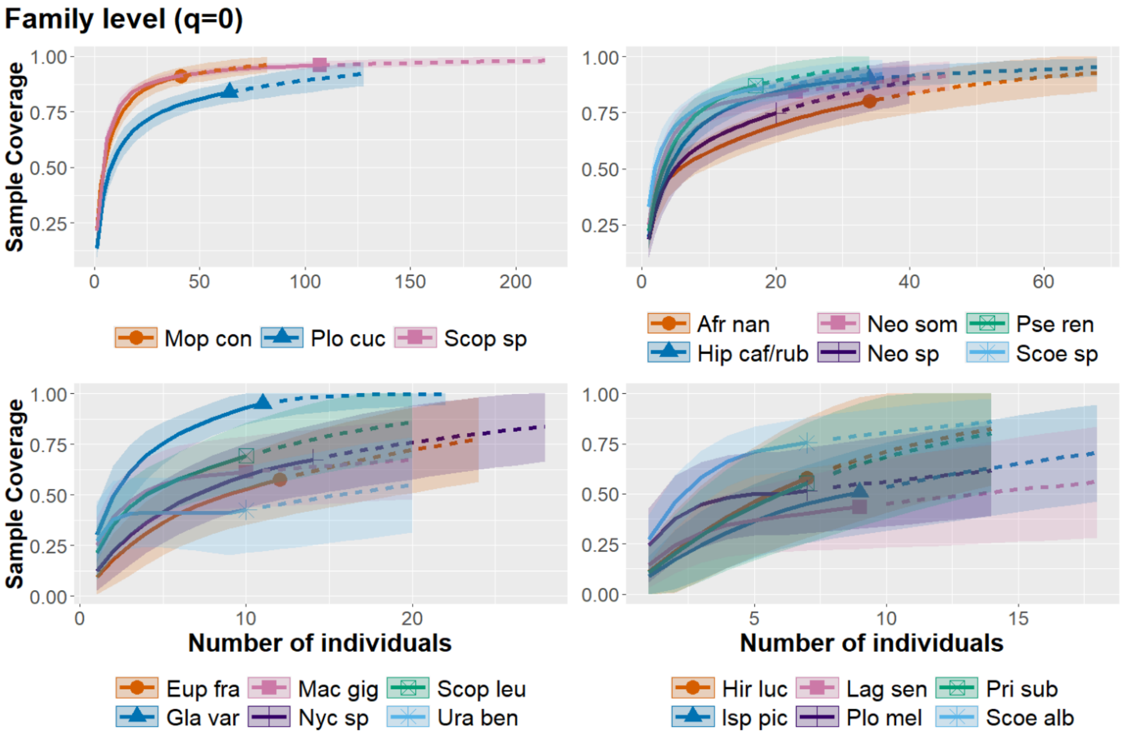

Figure S5 – Dietary niche breadth of bats and birds from lowland rainfed rice fields of Guinea Bissau, at the family level. Sample coverage rarefaction is represented by the solid line and extrapolation by the dashed line. 95% confidence intervals are represented by the shaded area. Curves were built with Hill number species richness (q=0) and with 1000 bootstraps.

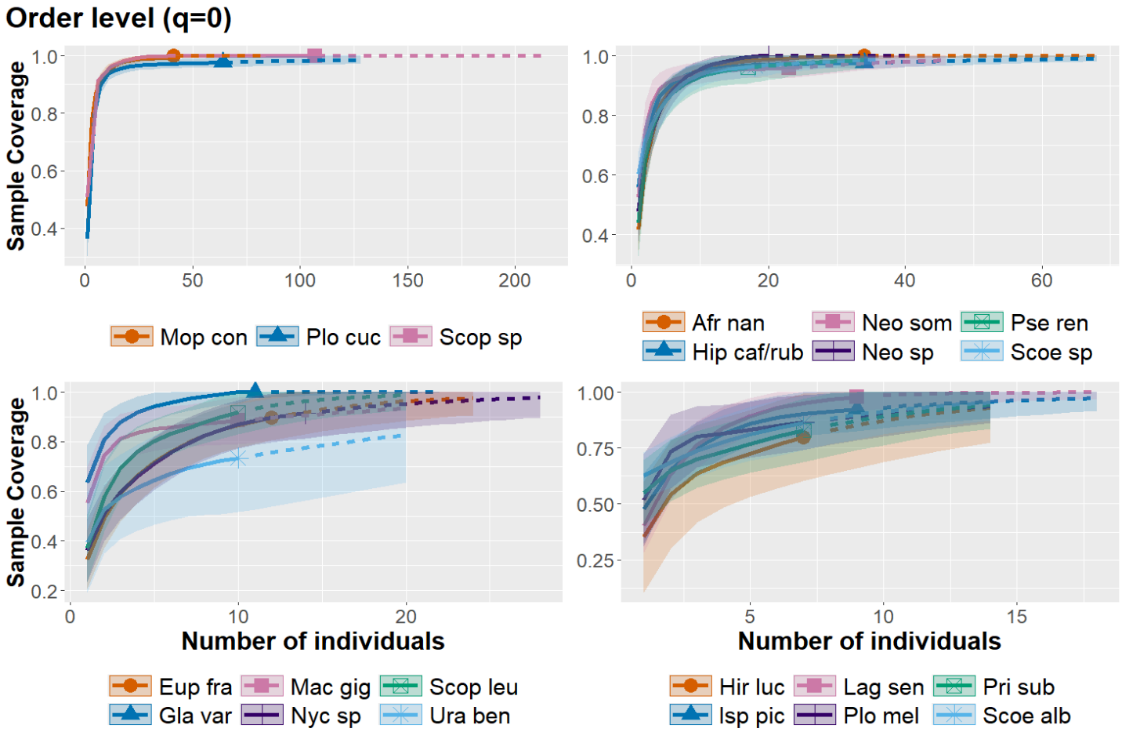

Figure S6 – Dietary niche breadth of bats and birds from lowland rainfed rice fields of Guinea Bissau, at the order level. Sample coverage rarefaction is represented by the solid line and extrapolation by the dashed line. 95% confidence intervals are represented by the shaded area. Curves were built with Hill number species richness (q=0) and with 1000 bootstraps.

Table S2 – Summary table of potential pests and disease vectors found in the diet of each predator species. For prey species eaten by multiple individuals, the number of predator individuals is indicated next to the prey species.

Predator	% of ind. eating ≥ one potential harmful prey	Prey (No invividuas)	Ecology	References
Afronycteris nana	41.2	*Ancistrotermes cavithorax*	Crop pest	(Akpesse et al. 2008; Rouland-Lefèvre 2011; Ano et al. 2018; Loko et al. 2021)
		Macrotermes bellicosus (13)	Rice pest; Crop pest	(Hill 2008; Rouland-Lefèvre 2011; Freitas 2017)
		Orseolia oryzae	Rice pest	(Pathak and Khan 1994; Hill 2008)
		Xyleborus affinis	Crop pest	(Merkl and Tusnádi 1992; Singh Rathore 1995; Zanuncio et al. 2002; Hill 2008; Castrejón-Antonio et al. 2020)
		Clogmia albipunctata	Disease vector	(Faulde and Spiesberger 2013; Kirk-Sprigs and Sinclair 2017a)
Euplectes franciscanus	75.0	*Aiolopus thalassinus (2)*	Rice pest; Crop pest	(Gentry 1965; Usmani et al. 2012; Pawar Prabhakar et al. 2021)

		Chrysodeixis chalcites	Crop pest	(Gentry 1965; Hill 2008; Riccucci and Lanza 2014; Mishra et al. 2017)
		Hysteroneura setariae	Rice pest; Crop pest	(Heinrichs and Barrion 2004; Jahn et al. 2005; Hundessa et al. 2015; Freitas 2017)
		Leptoglossus gonagra	Crop pest	(Duarte et al. 2008; Lee et al. 2020)
		Macrotermes bellicosus	Rice pest; Crop pest	(Hill 2008; Rouland-Lefèvre 2011; Freitas 2017)
		Mythimna phaea	Crop pest	(Carnegie and Leslie 1991; Ganeshan 2007)
		Odontotermes nilensis	Crop pest	(Appiah and Aisagbonhi 2000; Delgarde and Rouland-Lefèvre 2001; Rouland-Lefèvre 2011)
		Orseolia oryzae	Rice pest	(Pathak and Khan 1994; Hill 2008)
		Bulinus forskalii	Disease vector	(Gaye et al. 2023)
		Bulinus senegalensis	Disease vector	(Gaye et al. 2021)
Glauconycteris variegata	90.9	*Conocephalus maculatus (2)*	Rice pest	(Baccetti and Abukar 1987; Chitra et al. 2000; Heinrichs and Barrion 2004; Sadou 2017)
		Herpetogramma licarsisalis	Rice pest; Crop pest	(Grant 1982; Barrion and Litsinger 1987; Lewis 2003; Kemp et al. 2019)
		Macrotermes bellicosus (7)	Rice pest; Crop pest	(Hill 2008; Rouland-Lefèvre 2011; Freitas 2017)
		Scopula minorata (2)	Crop pest	(Sannino et al. 1984; Carrai and Loi 1988)
		Trigonidium cicindeloides (2)	Crop pest	(Garg and Tandon 1982; Ranjith et al. 2022)
Hipposideros caffer/ruber	61.8	*Aiolopus thalassinus*	Rice pest; Crop pest	(Gentry 1965; Usmani et al. 2012; Pawar Prabhakar et al. 2021)
		Antigastra catalaunalis	Crop pest	(Hill 2008; Anandh et al. 2010)
		Cofana unimaculata	Rice pest	(Heinrichs et al. 1997; Oyediran and Heinrichs 2001; Heinrichs and Barrion 2004; Igbinosa et al. 2007; Patra et al. 2013)
		Conocephalus maculatus	Rice pest	(Baccetti and Abukar 1987; Chitra et al. 2000; Heinrichs and Barrion 2004; Sadou 2017)

		Duponchelia fovealis	Crop pest	Journal of Biopesticides 3(1 Special Issue) 152 - 154 (2010)
		Glyphodes bicolor	Crop pest	(Mathew et al. 2005)
		Lobesia vanillana	Crop pest	(Brown et al. 2014; Preez et al. 2021)
		Macrotermes bellicosus	Rice pest; Crop pest	(Hill 2008; Rouland-Lefèvre 2011; Freitas 2017)
		Mythimna curvula	Crop pest	(Ganeshan 2007)
		Orseolia oryzae (2)	Rice pest	(Pathak and Khan 1994; Hill 2008)
		Parapoynx fluctuosalis	Rice pest	(Chantaraprapha and Litsinger 1986; Litsinger and Chantaraprapha 1995)
		Piezodorus guildinii (3)	Crop pest	(Panizzi et al. 2022)
		Poophilus costalis	Rice pest; Crop pest	(Ajayi and Oboite 2000; Saini et al. 2011; Bhat 2017)
		Pyrausta phoenicealis	Crop pest	(Yamada 1979; Chikkarugi et al. 2023)
		Scopula minorata (2)	Crop pest	(Sannino et al. 1984; Carrai and Loi 1988)
		Tenebrio molitor	Storage pest	(Hagstrum and Subramanyam 2006; Hill 2008; Martynov et al. 2019)
		Trigonidium cicindeloides (6)	Crop pest	(Garg and Tandon 1982; Ranjith et al. 2022)
		Trigonodes hyppasia (2)	Crop pest	(Khan et al. 1988; Ngampongsai et al. 2005)
		Udea ferrugalis (3)	Crop pest	(Shigehara and Shigehara 1937; Loginova 1992)
		Clogmia albipunctata	Disease vector	(Faulde and Spiesberger 2013; Kirk-Sprigs and Sinclair 2017a)
		Mansonia uniformis	Disease vector	(Ughasi et al. 2012; Kirk-Sprigs and Sinclair 2017a)
Hirundo lucida	14.3	*Locris rubra*	Rice pest; Disease vector	(Heinrichs et al. 1997; Heinrichs and Barrion 2004)
Ispidina picta	66.7	*Aiolopus thalassinus*	Rice pest; Crop pest	(Gentry 1965; Usmani et al. 2012; Pawar Prabhakar et al. 2021)
		Ancistrotermes cavithorax (2)	Crop pest	(Akpesse et al. 2008; Rouland-Lefèvre 2011; Ano et al. 2018; Loko et al. 2021)
		Chrysodeixis acuta	Crop pest	(Ahirwar et al. 2015; Soumia et al. 2022)
		Conocephalus maculatus (2)	Rice pest	(Baccetti and Abukar 1987; Chitra et al. 2000;

				Heinrichs and Barrion 2004; Sadou 2017)
		Holotrichia parallela	Crop pest	(Guo et al. 2009; Liu et al. 2012; Qin et al. 2019; Pan et al. 2022)
		Odontotermes nilensis	Crop pest	(Appiah and Aisagbonhi 2000; Delgarde and Rouland-Lefèvre 2001; Rouland-Lefèvre 2011)
Lagonosticta senegala	55.6	*Ancistrotermes cavithorax*	Crop pest	(Akpesse et al. 2008; Rouland-Lefèvre 2011; Ano et al. 2018; Loko et al. 2021)
		Ericeia inangulata	Crop pest	(Kemp et al. 2019; Swafvan and Sureshan 2022)
		Macrotermes bellicosus (2)	Rice pest; Crop pest	(Hill 2008; Rouland-Lefèvre 2011; Freitas 2017)
		Odontotermes nilensis	Crop pest	(Appiah and Aisagbonhi 2000; Delgarde and Rouland-Lefèvre 2001; Rouland-Lefèvre 2011)
		Spodoptera littoralis	Crop pest	(Hill 2008)
Macronycteris gigas	30.0	*Macrotermes bellicosus*	Rice pest; Crop pest	(Hill 2008; Rouland-Lefèvre 2011; Freitas 2017)
		Piezodorus guildinii (2)	Crop pest	(Panizzi et al. 2022)
		Poophilus costalis	Rice pest; Crop pest	(Ajayi and Oboite 2000; Saini et al. 2011; Bhat 2017)
Mops condylurus	36.6	*Balclutha incisa*	Crop pest	(Brohi et al. 2019)
		Diaperasticus erythrocephalus (2)	Rice pest	(Heinrichs and Barrion 2004; Koji et al. 2007; Régis Ahissou et al. 2021)
		Exitianus capicola (2)	Disease Vector	(Salehi et al. 2009; Nesmi and Mathew 2018; Jones and Medina 2020)
		Macrotermes bellicosus (7)	Rice pest; Crop pest	(Hill 2008; Rouland-Lefèvre 2011; Freitas 2017)
		Ptyelus grossus (2)	Crop pest	(Singh Rathore 1995; Hill 2008)
		Trigonidium cicindeloides	Crop pest	(Garg and Tandon 1982; Ranjith et al. 2022)
		Mansonia uniformis	Disease vector	(Ughasi et al. 2012; Kirk-Sprigs and Sinclair 2017a)
Neoromicia somalica	39.1	*Macrotermes bellicosus (9)*	Rice pest; Crop pest	(Hill 2008; Rouland-Lefèvre 2011; Freitas 2017)
Neoromicia sp.	53.8	*Dieuches armatipes*	Crop pest	(Hodges and Morse 2009)

		Macrotermes bellicosus (3)	Rice pest; Crop pest	(Hill 2008; Rouland-Lefèvre 2011; Freitas 2017)
		Piezodorus guildinii	Crop pest	(Panizzi et al. 2022)
		Poophilus costalis	Rice pest; Crop pest	(Ajayi and Oboite 2000; Saini et al. 2011; Bhat 2017)
		Trigonidium cicindeloides	Crop pest	(Garg and Tandon 1982; Ranjith et al. 2022)
Ploceus cucullatus	26.2	*Bactrocera invadens (2)*	Crop pest	(Khamis et al. 2009; Calvert and Gucker 2014; Kirk-Sprigs and Sinclair 2017b)
		Chrysodeixis chalcites (3)	Crop pest	(Gentry 1965; Hill 2008; Riccucci and Lanza 2014; Mishra et al. 2017)
		Colocleora divisaria	Crop pest	(Wagner et al. 2008)
		Ericeia inangulata	Crop pest	(Kemp et al. 2019; Swafvan and Sureshan 2022)
		Hippotion eson	Crop pest	(Rubinstein and Polson 1977)
		Holotrichia parallela	Crop pest	(Guo et al. 2009; Liu et al. 2012; Qin et al. 2019; Pan et al. 2022)
		Macrotermes subhyalinus	Crop pest	(Rouland-Lefèvre 2011)
		Ophiusa tirhaca	Crop pest	(Berlinger et al. 2001; Hill 2008)
		Polydesma umbricola	Crop pest	(Kamran 1968; Singh Rathore 1995)
		Poophilus costalis	Rice pest; Crop pest	(Ajayi and Oboite 2000; Saini et al. 2011; Bhat 2017)
		Zaprionus indianus (3)	Crop pest	(Renkema et al. 2013; Raspi et al. 2014)
		Zaprionus tuberculatus (2)	Crop pest	(Renkema et al. 2013; Raspi et al. 2014)
		Zophopetes cerymica	Crop pest	(Howard et al. 2001)
		Culicoides similis	Disease vector	(Kar et al. 2022)
Ploceus melanocephalus	57.1	*Bruchidius securiger*	Crop pest	(Ernst et al. 1990; Marohasy 1995; Delobel and Anton 2003)
		Marasmia poeyalis	Rice pest; Crop pest	(Hinckley 1963; Fraenkel et al. 1981)
		Marasmia trapezalis	Rice pest; Crop pest	(Leuschner et al. 1985; Pathak and Khan 1994; Mathew et al. 2005; Patra et al. 2013)
		Rhesala moestalis (2)	Crop pest	(Mathew 1995)
		Zophopetes cerymica	Crop pest	(Howard et al. 2001)
		Locris rubra	Rice pest; Disease vector	(Heinrichs et al. 1997; Heinrichs and Barrion 2004)
Prinia subflava	57.1	*Conocephalus maculatus*	Rice pest	(Baccetti and Abukar 1987; Chitra et al. 2000;

				Heinrichs and Barrion 2004; Sadou 2017)
		Odontotermes nilensis	Crop pest	(Appiah and Aisagbonhi 2000; Delgarde and Rouland-Lefèvre 2001; Rouland-Lefèvre 2011)
		Poophilus costalis (2)	Rice pest; Crop pest	(Ajayi and Oboite 2000; Saini et al. 2011; Bhat 2017)
		Spodoptera littoralis	Crop pest	(Hill 2008)
Pseudoromicia rendalli	58.8	*Macrotermes bellicosus (8)*	Rice pest; Crop pest	(Hill 2008; Rouland-Lefèvre 2011; Freitas 2017)
		Poophilus costalis	Rice pest; Crop pest	(Ajayi and Oboite 2000; Saini et al. 2011; Bhat 2017)
		Mansonia uniformis	Disease vector	(Ughasi et al. 2012; Kirk-Sprigs and Sinclair 2017a)
Scotoecus albofuscus	28.6	*Liposcelis bostrychophila*	Storage pest	(Wang et al. 2001; Green and Turner 2005; Pascual-Villalobos et al. 2005; Hagstrum and Subramanyam 2006)
		Poophilus costalis	Rice pest; Crop pest	(Ajayi and Oboite 2000; Saini et al. 2011; Bhat 2017)
Scotoecus sp.	44.4	*Cofana unimaculata*	Rice pest	(Heinrichs et al. 1997; Oyediran and Heinrichs 2001; Heinrichs and Barrion 2004; Igbinosa et al. 2007; Patra et al. 2013)
		Dieuches armatipes	Crop pest	(Hodges and Morse 2009)
		Elasmolomus pallens	Crop pest	(Nimanthika et al. 2019; Umaru and Simarani 2020; Bihal et al. 2023)
		Liorhyssus hyalinus	Crop pest	(Gentry 1965; Wheeler 2016; Cruces et al. 2022; Cruces et al. 2023)
		Piezodorus guildinii (4)	Crop pest	(Panizzi et al. 2022)
		Poophilus costalis (2)	Rice pest; Crop pest	(Ajayi and Oboite 2000; Saini et al. 2011; Bhat 2017)
		Trigonidium cicindeloides (3)	Crop pest	(Garg and Tandon 1982; Ranjith et al. 2022)
		Exitianus capicola	Disease vector	(Salehi et al. 2009; Nesmi and Mathew 2018; Jones and Medina 2020)
Scotophilus leucogaster	10.0	*Piezodorus guildinii*	Crop pest	(Panizzi et al. 2022)
Scotophilus sp.	41.7	*Aiolopus thalassinus (3)*	Rice pest; Crop pest	(Gentry 1965; Usmani et al. 2012; Pawar Prabhakar et al. 2021)

		Chirista compta (7)	Crop pest	(Fouelifack-Nintidem et al. 2021; Ngoute et al. 2021)
		Conocephalus maculatus (2)	Rice pest	(Baccetti and Abukar 1987; Chitra et al. 2000; Heinrichs and Barrion 2004; Sadou 2017)
		Diaperasticus erythrocephalus	Rice pest	(Heinrichs and Barrion 2004; Koji et al. 2007; Régis Ahissou et al. 2021)
		Dieuches armatipes (11)	Crop pest	(Hodges and Morse 2009)
		Elasmolomus pallens (9)	Crop pest	(Nimanthika et al. 2019; Umaru and Simarani 2020; Bihal et al. 2023)
		Macrotermes bellicosus (5)	Rice pest; Crop pest	(Hill 2008; Rouland-Lefèvre 2011; Freitas 2017)
		Piezodorus guildinii (8)	Crop pest	(Panizzi et al. 2022)
		Polydesma umbricola	Crop pest	(Kamran 1968; Singh Rathore 1995)
		Poophilus costalis	Rice pest; Crop pest	(Ajayi and Oboite 2000; Saini et al. 2011; Bhat 2017)
		Ruspolia nitidula	Crop pest	(Marina et al. 2018)
		Trigonidium cicindeloides (2)	Crop pest	(Garg and Tandon 1982; Ranjith et al. 2022)
		Culicoides miombo	Disease vector	(Rawlings et al. 1998; Ciss et al. 2019)
Uraeginthus bengalus	40.0	*Ancistrotermes cavithorax (3)*	Crop pest	(Akpesse et al. 2008; Rouland-Lefèvre 2011; Ano et al. 2018; Loko et al. 2021)
		Odontotermes nilensis	Crop pest	(Appiah and Aisagbonhi 2000; Delgarde and Rouland-Lefèvre 2001; Rouland-Lefèvre 2011)
		Polydesma umbricola	Crop pest	(Kamran 1968; Singh Rathore 1995)

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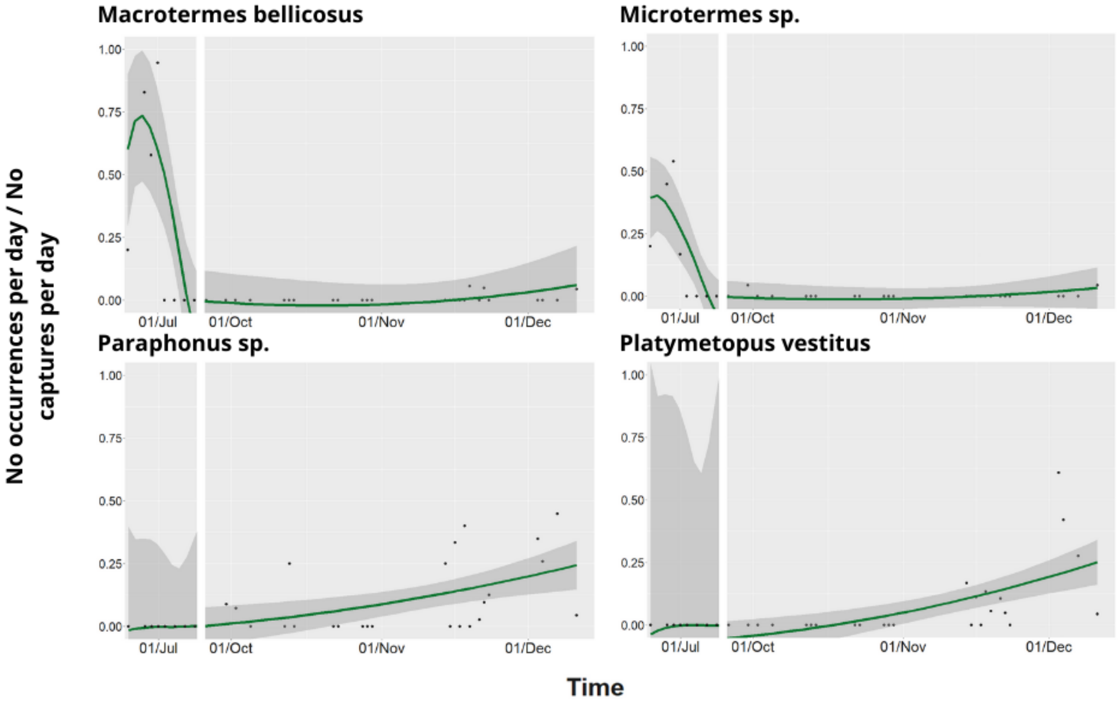

Figure S7 – Seasonal variation of consumption of four different prey species by bats and birds from lowland rainfed rice fields of Guinea Bissau. Dots represent de frequency of detection of each prey in the diet of bats and birds. Green lines represent the trend built with LOESS smoother. Shadow areas represent the 95% intervals.

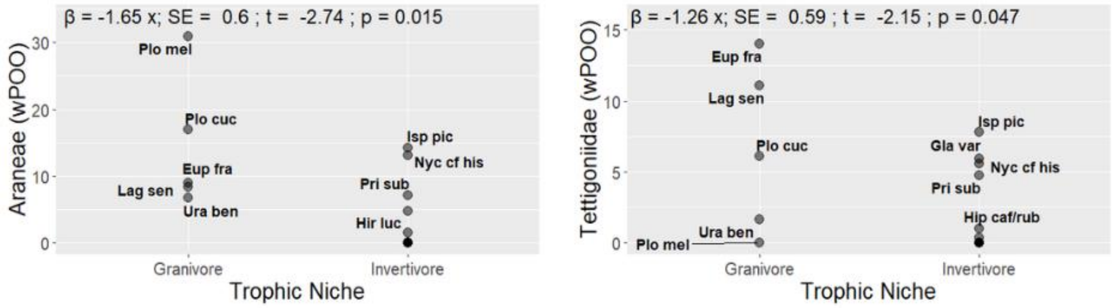

Figure S8 – Graphical representation of GLM predictions for bats and birds from lowland rainfed rice fields of Guinea Bissau. The weighted percentages of occurrence (wPOO) of the diet components are modelled by trophic niche. GLMs were built with distribution family quasibinomial and “logit” as link function. Dots represent the observed values for each species. The model parameters are indicated in the respective panel. Predator species acronyms are listed in Table 3.1. Trait descriptions and characteristics are summarized in Table S1 in the Supplementary Information section.