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**Patterns and drivers of insectivorous bat activity around
isolated trees in rice fields of Guinea-Bissau (West Africa)**

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“It's surely our responsibility to do everything within our power to create a planet that provides a home
not just for us, but for all life on Earth.”
— **David Attenborough**

Resumo

Alimentar uma população humana em rápido crescimento de uma forma ambientalmente sustentável representa um grande desafio global. Este desafio é particularmente acentuado em algumas regiões tropicais, onde a segurança alimentar não é sequer garantida. Os métodos convencionais para aumentar a produtividade agrícola têm-se baseado na intensificação da agricultura, o que implica a homogeneização e simplificação da paisagem, bem como a utilização de agroquímicos, como fertilizantes e pesticidas, para alcançar a máxima eficiência dos serviços de aprovisionamento. Contudo, esta abordagem constitui um fator-chave na perda de biodiversidade e na deterioração ou mesmo perda total de serviços ecossistêmicos vitais. Uma forma de aumentar a produção agrícola, reduzir a dependência de agroquímicos e promover a biodiversidade é através da intensificação ecológica, incluindo os serviços dos ecossistemas e utilizando soluções baseadas na natureza na gestão agrícola. A integração de elementos da paisagem, como árvores isoladas, pode desempenhar um papel crucial nesta abordagem, sobretudo porque estas árvores podem suportar organismos como os morcegos insectívoros, que prestam valiosos serviços ecossistêmicos de controlo de pragas. Perceber o papel das árvores isoladas no suporte destes supressores naturais de pragas, particularmente em campos de culturas alimentares básicas, é essencial para fazer a ponte entre a investigação e a implementação da intensificação ecológica. Dada a importância do arroz como uma cultura alimentar básica a nível mundial, com particular importância na África Ocidental, onde constitui a principal fonte de calorías, o nosso trabalho centrou-se nesta cultura.

Utilizando dispositivos autónomos de gravação acústica, este estudo investigou como as árvores isoladas afetam a atividade dos morcegos em culturas de arroz de subsistência na Guiné-Bissau. Mais especificamente, pretendemos avaliar de que forma (a) as características das árvores, (b) a abundância e riqueza de insetos e (c) as características da paisagem em torno das árvores isoladas determinam a atividade de diferentes guildas de morcegos insectívoros. Tendo em conta as diferentes preferências de habitat entre as guildas de morcegos, prevemos que as árvores de maior dimensão, com outras árvores ou áreas arborizadas nas proximidades, terão uma maior atividade de espécies de morcegos florestais de voo lento, enquanto as espécies de voo rápido e que se alimentam em espaço aberto serão igualmente abundantes em todas as árvores estudadas. Prevemos também que as árvores com maior abundância e/ou riqueza de insetos terão maior atividade de morcegos.

Amostrámos vinte e oito árvores isoladas em quatro áreas de arrozais de água doce (localmente conhecidos como bolanhas). Cada árvore foi identificada ao nível da espécie e caracterizada quanto ao diâmetro à altura do peito, área da copa, altura, número de ninhos de aves e presença de cavidades. Os morcegos foram amostrados de junho a julho e de setembro a dezembro de 2022, com recurso a dispositivos autónomos de gravação acústica, em períodos de duas noites. O número de passagens de morcegos por noite foi utilizado para medir a sua atividade. As vocalizações registadas foram classificadas em espécies ou sonótipos (grupos de várias espécies), e agrupados em três guildas – Espaço aberto, Orla e Vegetação densa – com base na sua estratégia de procura de alimento, ecolocalização e características morfo-ecológicas. A paisagem em redor de cada árvore foi caracterizada para determinar a distância de cada árvore isolada à árvore mais próxima, à orla arborizada (fronteira entre o arrozal e a floresta ou o pomar de cajueiro) mais próxima e à estrada principal mais próxima. Fatores ambientais como a percentagem da lua iluminada e a profundidade de água ao redor de cada árvore isolada foram também obtidos. Para estimar a abundância e riqueza de potenciais presas em cada árvore isolada, amostrámos insetos voadores utilizando armadilhas adesivas amarelas em junho e de setembro a dezembro, com a mesma periodicidade que a colocação dos gravadores. Para compreender os principais fatores que determinam a atividade dos morcegos em

torno das árvores isoladas, utilizámos modelos lineares generalizados mistos (GLMM) binomiais negativos com uma função de ligação logarítmica. A atividade total dos morcegos, a atividade das guildas e a riqueza de sonótipos foram utilizadas como variáveis de resposta. Para ter em conta a estrutura temporal observada nos dados, utilizámos o mês como efeito aleatório. A modelação foi realizada separadamente para as características das árvores e da paisagem e para a abundância e riqueza de insetos.

Registámos um total de 5382 passagens de morcegos pertencentes a 12 espécies ou sonótipos. As espécies típicas de espaço aberto constituíram a maior proporção (56%) das passagens de morcegos, seguidas das espécies de orla (44%), enquanto as espécies que se alimentam entre vegetação mais densa constituíram menos de 0,3%. A atividade dos morcegos e a riqueza de sonótipos apresentaram um forte padrão sazonal, com um aumento pronunciado na estação húmida, consistente com o aumento de recursos cruciais como a água e insetos aquando da inundação sazonal dos campos de arroz. Os nossos resultados demonstram que a atividade total dos morcegos e das espécies de espaço aberto aumenta com o aumento do tamanho da árvore. Apesar do efeito não ser significativo a riqueza de sonótipos e a atividade de espécies de orla também apresentaram uma tendência positiva com este aumento. Árvores maiores funcionam melhor como marcos acústicos para orientação espacial e reconhecimento de biótopos, mas também podem providenciar melhores condições de alimentação, como maior proteção contra o vento ou disponibilidade de presas. Adicionalmente, as espécies *Elaeis guineensis* e *Faidherbia albida*, foram associadas a maior atividade de morcegos e riqueza de sonótipos.

Os nossos resultados evidenciam também que uma maior distância a árvores vizinhas diminuiu a atividade total dos morcegos e das espécies de espaço aberto, bem como a riqueza de sonótipos. Uma maior proximidade a outras árvores pode aumentar a conectividade local e as oportunidades de alimentação para os morcegos, sem a estrutura mais fechada de uma mancha de habitat mais arborizada. Por outro lado, uma maior distância a orlas arborizadas aumentou a atividade total dos morcegos, a atividade das espécies de espaço aberto e de orla, e a riqueza de sonótipos. Um aumento na atividade das espécies de espaço aberto e na atividade total era previsível, uma vez que árvores mais afastadas de zonas arborizadas são ideais para as espécies de espaço aberto, que constituem a maior proporção da atividade total dos morcegos. Complementarmente, a atividade das espécies de orla e a riqueza de sonótipos podem também beneficiar desta distância se esta atuar no sentido de aumentar o habitat de orla disponível. A atividade das espécies que se alimentam entre vegetação densa mostrou uma tendência não significativa, mas positiva, com a profundidade da água à volta da árvore. Apesar do pequeno tamanho da amostra, esta resposta pode ser particularmente importante, dado que estes morcegos preferem alimentar-se em habitats fechados, mas podem usar os arrozais devido à maior disponibilidade de água e presas. O número de ninhos de aves, a presença de cavidades, a distância a estradas principais e a percentagem da lua iluminada não tiveram qualquer efeito na atividade dos morcegos ou na riqueza de sonótipos. O aumento na abundância de insetos resultou num aumento da atividade das espécies de orla, enquanto a riqueza de insetos não teve qualquer efeito na atividade dos morcegos. Apesar do nosso método de amostragem e a resolução taxonómica na identificação dos insetos poder limitar a deteção de alguns padrões, é também possível que estes resultados se devam a uma baixa variação na abundância e riqueza de insetos em cada mês, sugerindo que a importância destas árvores vai para além de serem meramente uma fonte de presas para morcegos.

Este estudo providencia conhecimento de base sobre as dinâmicas dos morcegos insectívoros nas culturas de arroz da África Ocidental. Esta informação pode servir para orientar o desenvolvimento de

estratégias e diretrizes de gestão destinadas a aumentar a produtividade das culturas e a segurança alimentar através da supressão natural de pragas, preservando simultaneamente a biodiversidade.

Este estudo realça a importância das árvores isoladas como agentes de heterogeneidade nas paisagens agrícolas, enfatizando que os potenciais benefícios para as populações de morcegos resultam de processos ecológicos que operam tanto ao nível das árvores como da paisagem. Preservar ou permitir o crescimento de numerosas árvores de grande porte espalhadas pelos campos de arroz beneficiará as duas guildas de morcegos mais abundantes nesta cultura, reforçando os benefícios que estes predadores podem proporcionar ao suprimir as pragas de insetos.

Palavras-chave: Amostragem acústica, Heterogeneidade da paisagem, Paisagem agrícola, Serviços dos ecossistemas, Supressão de pragas.

Summary

The need to sustainably feed a rapidly growing human population has never been higher, especially in some tropical regions, where food security is presently not guaranteed. Ecological intensification strategies in agricultural management might help achieve this goal by including ecosystem services and using nature-based solutions. Integrating landscape elements such as isolated trees can play a crucial role in enhancing productivity while preserving biodiversity in agricultural landscapes, particularly since these trees may support organisms like insectivorous bats that provide valuable pest control ecosystem services. Therefore, there is a need to understand how isolated trees, based on their characteristics and the surrounding landscape, may drive the foraging activity of bats in staple tropical crop fields. We acoustically sampled bats at 28 isolated trees to evaluate how (a) tree characteristics, (b) insect abundance and richness, and (c) landscape features around isolated trees drive bat foraging activity within lowland rice crops in West Africa. Twelve bat species or sonotypes were recorded and classified into three foraging guilds. Our results show that bat activity increases with tree size and distance to the nearest wooded edge. Conversely, total bat activity, sonotype richness, and the activity of open space foragers declined with increasing distance to neighbouring trees. Higher insect abundance positively affected the activity of edge foragers, whereas insect richness showed no effect on bat activity. This study highlights the importance of isolated trees as agents of heterogeneity in agricultural landscapes, emphasising that the potential benefits for bat populations stem from ecological phenomena which occur at both tree and landscape levels. Preserving or allowing the growth of numerous large trees spread throughout the rice fields will benefit the two most abundant bat guilds within this crop, enhancing the benefits these predators may provide by suppressing insect pests.

Keywords: Acoustic sampling, Agricultural landscape, Ecosystem services, Landscape Heterogeneity, Pest suppression.

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List of Abbreviations

AICc – Akaike Information Criterion corrected for small sample sizes

ANOVA – Analysis of variance

DBH – Diameter at breast height

GIS – Geographic Information System

USNO – United States Naval Observatory

1. Introduction

Feeding a rapidly increasing human population in an environmentally sustainable way poses a major global challenge (Robertson and Swinton, 2005; Tschardt et al., 2012). This challenge is particularly pronounced in some tropical regions, where food security is not guaranteed (Grote, 2014). Typical means of increasing food production and agricultural productivity have relied on agricultural intensification, which entails homogenising and simplifying the landscape (Gómez-Virués et al., 2015) as well as the use of agrochemical inputs, such as fertilisers and pesticides, to achieve maximum efficiency of provisioning services (Gómez-Virués et al., 2015; Matson et al., 1997). This course of action constitutes a key driver of biodiversity loss (Emmerson et al., 2016; Kehoe et al., 2017), negatively impacting several taxonomic groups (Emmerson et al., 2016; Potts et al., 2010; Stanton et al., 2018), and comes at a tremendous environmental cost that culminates in the deterioration or even total loss of vital ecosystem services (Landis, 2017).

One way to increase agricultural production, reduce dependency on agrochemical inputs and promote biodiversity is through ecological intensification by including ecosystem services (Kremen, 2020) and using nature-based solutions in agricultural management (Keesstra et al., 2018). Some elements of the landscape, such as isolated trees, can play an integral role in this respect. Isolated trees, also referred to as remnant, scattered or paddock trees, are a conspicuous element of agricultural landscapes globally (Manning et al., 2006). Integrating them into agricultural practice has the potential to improve soil structure, facilitating water infiltration and reducing soil erosion, and enhance the provision of ecosystem services such as water purification, pollination, carbon sequestration, regulation of nutrient dynamics (e.g., nitrogen and phosphorus) and pest suppression (Garrity et al., 2010; Hoosbeek et al., 2018; Manning et al., 2006). These natural ecosystem processes benefit farmers through enhanced productivity and reduced expenses in agrochemical inputs (Garrity et al., 2010).

Isolated trees are increasingly acknowledged as essential in supporting biodiversity in agricultural landscapes (Manning et al., 2006; Prevedello et al., 2018), providing habitat and food resources for many vertebrates, arthropods, and plants (Prevedello et al., 2018). Isolated trees also increase spatial heterogeneity and connectivity, promoting species dispersal within cultivated areas (Fischer and Lindenmayer, 2002; Manning et al., 2006; Prevedello et al., 2018). Moreover, for humanised landscapes such as farmlands, it is consensual that increasing landscape heterogeneity leads to increased biodiversity at the landscape scale (Benton et al., 2003). On the basis that they can have this disproportionately high ecological significance relative to the tiny fraction of the landscape they occupy, isolated trees are considered “keystone ecological structures” (Fischer et al., 2010; Manning et al., 2006).

In the context of ecological intensification, isolated trees may be particularly important in supporting organisms that assist crop growth. Insectivorous bats stand out as a prime example of such organisms, as several studies have shown that they are voracious predators and consume many relevant agricultural pests worldwide (Boyles et al., 2011; Kemp et al., 2019; Puig-Montserrat et al., 2015, 2020; Tuneu-Corral et al., 2024; Williams-Guillén et al., 2008). Thus, bats may be a crucial element of nature-based agricultural ecosystems by providing effective pest suppression services (Boyles et al., 2011; Maine and Boyles, 2015). This is especially relevant in many regions of the world where sustainable pest control methods are imperative to guarantee long-term food security (Diaz and Wilby, 2005; Savary et al., 2012).

The ongoing loss of landscape elements, such as isolated trees and hedgerows, frequently regarded as incompatible with current agricultural practices and agricultural intensification (Gibbons et al., 2008), imperils biodiversity at large. Agricultural management actions focused on retaining these elements and improving heterogeneity can be paramount to bolster bat populations and potentiate their associated ecosystem services (Monck-Whipp et al., 2018; Tuneu-Corral et al., 2023).

Solid scientific knowledge should ease bridging the gap between ecological intensification research and implementation (Kleijn et al., 2019). Therefore, understanding the importance of isolated trees in supporting these potential natural pest suppressors, particularly in staple crop fields, is imperative. Rice (*Oryza* spp.) plays a pivotal role as a staple food crop globally, meeting the dietary needs of more than half of the world's population (IRRI, 2020; Muthayya et al., 2014). Constituting the most important calorie source in West Africa, its significance is accentuated in Guinea-Bissau, where it accounts for a substantial portion of the daily caloric intake (Soullier et al., 2020). Such a heavy reliance on rice becomes problematic whenever yields are compromised by climatic events or pest infestations (Harvey et al., 2014). Given the importance of rice on a global scale but also in West Africa, our study focused on this crop.

We used autonomous acoustic recording devices to evaluate how isolated trees affect insectivorous bat activity within smallholder rice crops in Guinea-Bissau. More specifically, we aimed to assess how (a) tree characteristics, (b) insect abundance and richness, and (c) landscape features around isolated trees drive the activity of different insectivorous bat guilds. Taking into account the varying habitat preferences among bat guilds (Denzinger and Schnitzler, 2013; Shapiro et al., 2020), we hypothesise that larger trees having other trees or wooded areas nearby, will have higher activity of slow-flying and gleaning forest species, while fast-flying open space foragers will be equally abundant in all studied trees. We also hypothesise that trees with higher insect abundance and/or richness will have higher bat activity.

2. Methods

2.1. Study area and tree selection

This study was conducted in the Oio region, northern Guinea-Bissau, in a rural area within the sector of Mansaba (12°19'45"N, 15°10'56"W; Figure 2.1). Located in West Africa, Guinea-Bissau has a tropical sub-humid climate with two pronounced seasons: a dry season that normally runs from November to May, and a wet season beginning in June and ending in late October or early November (Catarino et al., 2001). The highest precipitation occurs between July and September, contributing to a regional annual rainfall of 1200 to 1400 mm in Oio (Catarino et al., 2001; Climate Change Knowledge Portal, 2023). Nonetheless, the climate and precipitation regime – which are mainly defined by the seasonal migration of the intertropical convergence zone (ITCZ) (Catarino et al., 2001) – have been affected by climate change, increasing the irregularity of rainfalls (Temudo et al., 2020). The region features a smooth topography, with most of its terrain situated at an altitude of 50 m or less, never exceeding 100 m (Catarino et al., 2008). In the study area, the landscape is very uniform and consists of a mosaic of agricultural land, mostly cashew orchards and rice fields, and forested areas.

Four areas of rainfed lowland rice fields (locally known as *bolanhas*) were surveyed. These areas were named after the villages (locally known as *tabancas*) where they were situated: Bironqui, Demba Só, Mansabá and Mambonco. The areas were surveyed using satellite imagery from Google Earth (v7.3.6.9345, 2022), and all isolated trees present were mapped. Trees were considered isolated if there were no other trees or woody habitat patches within at least 30 m. This criterion was applied as it reduces the probability of recording bats from other habitats not associated with the trees (Froidevaux et al., 2022). All mapped trees were validated recurring to ground-truthing. In total, 28 trees were selected for the study, as the rice farming in the area is extensive and maintains many trees amongst the crops, making it challenging to select trees that could be classified as isolated. Since sampling was done in *bolanhas* managed by communities from the aforementioned villages, their consent was obtained before conducting this study.

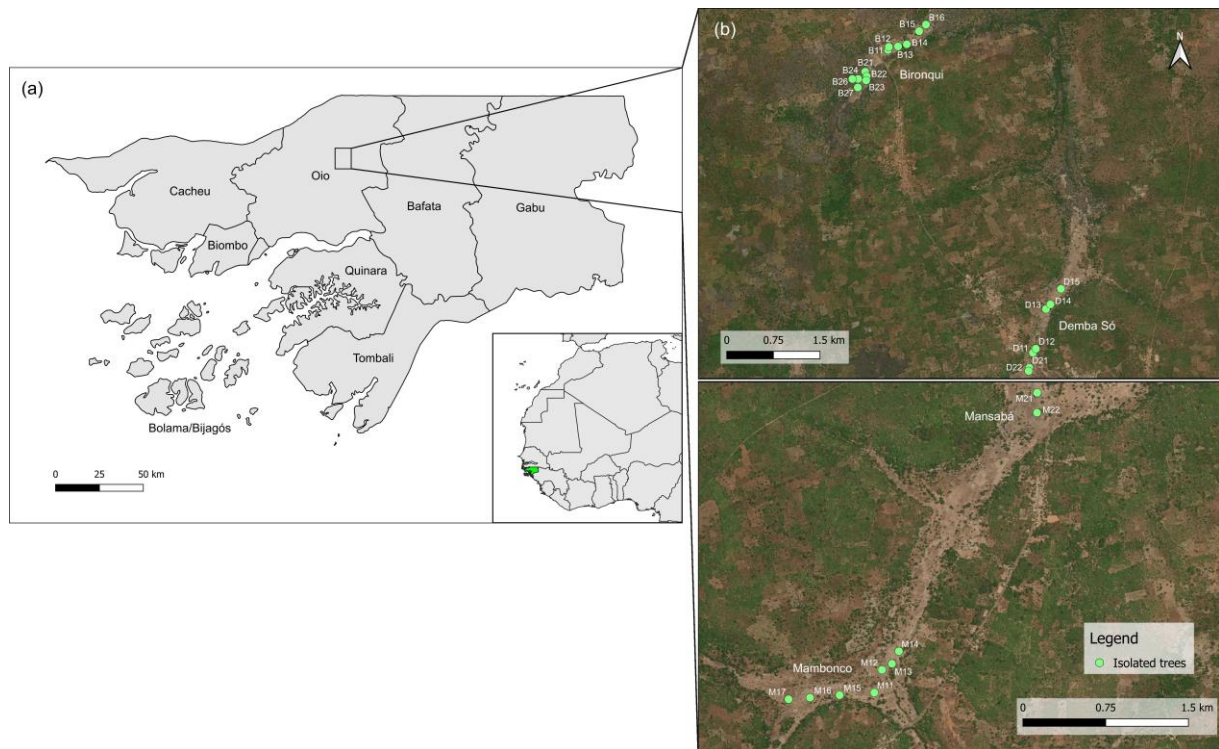


Figure 2.1. Study area and sampling sites; (a) Location of Guinea-Bissau and the study area; (b) Maps of the study area highlighting the locations of the twenty-eight sampled trees (notice that the two maps are in different scales).

2.2. Tree characterisation

Each tree was identified to species level (using Catarino and Indjai, 2019) and characterised regarding diameter at breast height (measured at 1.3 m from the ground, hereinafter referred to as DBH), crown area, height, number of visible bird nests and presence of tree hollows within the first three metres. Bird nests were counted as it has been reported that some species of bats present in the region (*Afronycteris nana* and *Kerivoula* spp.) roost in deserted *Ploceus* spp. nests (Happold et al., 1987; Page and Dechmann, 2022), but also because bird presence can disturb roosting sites (Fenton and Fleming, 1976). To calculate tree crown areas, the distance from the tree trunk to the vertical projection of the edge of the crown was measured at the four cardinal directions. Crown areas were then estimated as the area of a circle with a radius equal to the average of those four measurements.

2.3. Bat acoustic sampling and classification

Insectivorous bats were acoustically sampled from June to July and September to December 2022. Bat echolocation calls were recorded using autonomous acoustic recording devices (Audiomoth v1.1.0, Open Acoustic Devices) attached to the trunk of each isolated tree at approximately 1.8 m height, pointing in the direction with the least vegetation in front of it. We simultaneously sampled all trees within a single rice field, rotating the recording devices between rice fields. Recording devices were set with a 384 kHz sample rate and gain set to 30.6 dB (medium setting). Sampling was cyclical, recording for 5 seconds followed by a 55-second pause, and encompassed two consecutive nights. In each night, we sampled bat activity during two periods, from 18:26 to 23:56 and 04:20 to 06:50, as these correspond to peaks of insectivorous bat activity (Meyer et al., 2004). Our sample unit for bat activity was a “bat pass”, defined as at least two sequential recognisable echolocation pulses in a recording (López-Bosch et al., 2022). The number of bat passes per night was used to measure bat foraging activity (Torrent et al., 2018).

All recordings were automatically filtered using a sound analysis software (Kaleidoscope Pro version 5.4.2, Wildlife Acoustics) that detects and preliminarily classifies bat calls, discarding files with no calls. Bat calls were visually inspected, and classification was performed to the lowest taxonomic level possible. When it was not possible to undoubtedly attribute a bat call to a species, calls were classified as mixed species groups, or sonotypes (Torrent et al., 2018). This was most often the case due to the lack of knowledge on bat calls in this region. The call's shape, frequency of maximum energy (kHz), start and end frequencies (kHz), inter-pulse interval (ms) and duration (ms) were taken from the spectrogram and oscillogram using the cursor and used for identification and grouping of bat species into sonotypes (Table 2.1). Bat call classification was based on the available literature (ACR, 2022; Bakwo Fils et al., 2018; Fawcett et al., 2015; Fenton and Bell, 1981; Jones et al., 1993; Monadjem et al., 2010, 2011, 2013, 2017; Obrist et al., 1989; Taylor, 1999; Kingdon, 2013) and information collected during previous work in Guinea-Bissau (Rainho and Palmeirim, 2017 and references therein). Furthermore, calls of hand-released bats captured in the study area using mist nets were recorded to contribute towards a bat call library and facilitate acoustic identification.

Table 2.1. Bat sonotypes and guilds. Sonotypes and corresponding call characteristics of potential species encompassed within each foraging guild. Echolocation call shape: CF = constant frequency, QCF = quasiconstant frequency, FM = frequency modulation, MH = multi-harmonic. Frequencies in parentheses denote the characteristic frequency (or frequency interval) of recorded individuals. The occurrence of taxa in bold was already confirmed in the study area by morphological and/or molecular methods (Rainho et al. in prep).

Foraging guild	Foraging ecology	Echolocation call shape	Frequency of maximum energy (kHz)	Sonotype	Possible taxa
Open space	Open areas, high altitudes	QCF	(<28)	MOLO_SP	<i>Chaerephon pumilus</i> <i>Mops condylurus</i>
		QCF-MH	(26)	TAPH_SP	<i>Taphozous</i> sp.
Edge	Edges / gaps between open areas and dense vegetation	FM-CF	(60 – 75) (89 – 96)	AFRNAN73 AFRNAN93	<i>Afronycteris nana</i>
		CF-FM	50 – 70 (58)	HIP<70	<i>Doryrhina cyclops</i> <i>Macronycteris gigas</i>
			(40 – 50)	PIPI_SP	<i>Laephotis capensis</i> <i>Neoromicia guineensis</i> <i>Neoromicia somalica</i> <i>Neoromicia</i> sp. <i>Pseudoromicia rendali</i> <i>Pseudoromicia tenuipinnis</i>
		FM-CF	(40 – 50)	SCOT_SP	<i>Scotophilus leucogaster</i> <i>Scotophilus</i> sp.
			(32 – 39)	SCO/GLA	<i>Scotoecus albofuscus</i> <i>Scotoecus</i> sp. <i>Glauconycteris variegata</i>
Clutter	Narrow spaces, dense/cluttered vegetation	FM-CF-FM	65 – 80 (78)	RHIALC	<i>Rhinolophus alcyone</i>
		CF-FM	149 – 154 (153)	HIPCAF	<i>Hipposideros caffer</i>

Pipistrelle-like calls recorded within and above the *A. nana* known frequency range (FMaxE between 60 and 96 kHz) showed a bimodal peak frequency distribution (peaking at 73kHz and 93kHz) and were thus classified into two distinct sonotypes (AFRNAN73 and AFRNAN93). Whenever there was uncertainty in the classification between sonotypes, both were considered (e.g. MOLO_SP/SCO_GLA and PIPI_SP/SCOT_SP).

Recorded species and sonotypes were grouped into three foraging guilds – Open space, Edge, and Clutter – based on their foraging ecology, echolocation, and morpho-ecological traits (Denzinger and Schnitzler, 2013; Meyer et al., 2004; Monadjem et al., 2010; Schnitzler and Kalko, 2001; Shapiro et al., 2020) (Table 2.1). Open space foragers have evolved to excel in fast, less manoeuvrable flight in open areas, contrasting with clutter foragers, which exhibit adaptations for slower, highly manoeuvrable flight within dense/cluttered vegetation environments; edge foragers balance flight speed and manoeuvrability, leveraging the boundary between open areas and more vegetated areas (Denzinger and Schnitzler, 2013; Schnitzler and Kalko, 2001). One sonotype group – MOLO_SP/SCO_GLA – was excluded from the guild analysis as it may include both open space and edge foraging bat species.

2.4. Landscape and environmental variables

The landscape surrounding each tree was characterised using QGIS (version 3.28.4; QGIS Development Team, 2022) to determine the distance from each isolated tree to the nearest tree, wooded edge (nearest border between rice field and forest or cashew orchard) and main road. Considering that differences in moonlight intensity have been demonstrated to influence bat activity (Appel et al., 2017, 2019; Bhalla et al., 2023; Meyer et al., 2004), the percentage of the moon illuminated at midnight was also considered. At each 2-day sampling period, water depth was measured at four locations around each tree using a measuring rod with a scale and then averaged to obtain a final value. Water depth measurement served as a proxy for water availability, which can, in turn, influence insect prey availability, potentially affecting bat activity. All variables are described in Table 2.2.

2.5. Insect sampling

To estimate the abundance and richness of potential insect prey for bats at each isolated tree, we sampled flying insects using 20x25 cm yellow sticky traps. Each trap was hung on the tree or close to it so that both sides could capture insects, following the same schedule of deployment and retrieval as the acoustic recording devices. Insect sampling was performed in June and between September and December 2022.

The insects captured in each trap were counted and identified to the order level with the aid of a 6x to 20x magnifying lens. Insect abundance was defined as the average of the total number of insects on both sides of a trap, while insect richness was defined as the average of the number of insect orders on both sides of a trap. This averaging process was employed to accommodate data from traps which only captured insects on one side.

Table 2.2. Description of the predictor variables used in this study, with range, units, and source. Sample size of each tree species is given in parentheses after the species name.

Category	Variable	Range and Units	Source
	Tree species	6 classes: <i>Elaeis guineensis</i> (4), <i>Faidherbia albida</i> (11), <i>Ficus lutea</i> (1), <i>Mitragyna inermis</i> (8), <i>Parkia biglobosa</i> (3), <i>Vitex doniana</i> (1).	Field data
Tree characteristics	Tree diameter at breast height	7.80 - 188.50 cm	Field data
	Tree crown area	2 - 244 m ²	Field data
	Tree height	3.60 - 18.60 m	Field data
	Number of bird nests	0 – 300 nests	Field data
	Presence of tree hollows	Binary: 0 or 1	Field data
Landscape variables	Distance to the nearest tree	30 - 70 m	GIS
	Distance to the nearest edge	33 - 200 m	GIS
	Distance to the nearest main road	54 - 1055 m	GIS
Environmental variables	Percentage of the moon illuminated	0 - 100 %	USNO*
	Water depth around the tree	0 - 20 cm	Field data

* Astronomical Applications Department website

2.6. Data analysis

The data was tested for normality and homogeneity of variance (standard transformations were applied when required). Exploratory analyses, which included boxplots, Analysis of Variance (ANOVA) and post hoc Tukey’s HSD tests, were undertaken to investigate the presence of patterns in bat activity and sonotype richness (a surrogate of bat richness). Specifically, we aimed to assess variations in bat activity and sonotype richness across sampled sites and months.

Collinearity among predictor variables was assessed using Spearman’s correlation coefficient, and only DBH, tree crown area and tree height demonstrated collinearity issues (namely between DBH and tree crown area, $r = 0.68$, and between tree crown area and tree height, $r = 0.66$). To address this, we performed a Principal Component Analysis (PCA) on DBH, tree height, and tree crown area (Figure S1), and extracted the first principal component, which accounted for 85% of the variance. This newly derived variable, termed “tree size” was subsequently used as a predictor in our modelling analyses.

To understand the main drivers of bat activity around isolated trees, we fitted negative binomial Generalised Linear Mixed Models (GLMMs) with a log link function. Total bat activity, the activity of the different guilds and sonotype richness were used as the response variables. To account for the observed temporal structure in the data, we used month as random effect. As part of a variable reduction process, we performed univariate models with all predictor variables. Due to constraints in the insect dataset, multivariate modelling was performed separately for tree and landscape variables,

and for insect abundance and richness. Predictor linearity and interactions were tested but demonstrated no significant contribution to the final models. We considered statistical significance at an alpha value of 0.05. Model selection followed a parsimonious approach, considering both the significance of included variables and the attainment of the lowest AICc value (Burnham and Anderson 2002). Model goodness-of-fit was assessed using the DHARMA package (Hartig, 2022).

To visually illustrate the impact of significant variables on total bat activity, sonotype richness and guild-specific activity, we employed the R package “effects” v. 4.2-2 (Fox, 2003); Fox and Weisberg, 2018). This package generated graphical representations of the estimated change in the response variable for each unit change in the predictor variables.

All statistical analyses were conducted using R statistical software 4.3.1 (R Core Team, 2023) with the packages: vegan (Oksanen et al., 2020), glmmTMB (Brooks et al., 2017), MuMIn (Bartoń, 2009), and all aforementioned packages.

3. Results

During 328 detector-nights, we recorded a total of 5382 bat passes from 12 species or sonotypes (see Table 2.1) around the 28 isolated trees in rice fields. The Molossidae sonotype (MOLO_SP) dominated the acoustic sample, with 2588 bat passes (48.1% of the total bat activity), succeeded by MOLO_SP/SCO_GLA (13.15%), AFRNAN73 (8.08%), SCO/GLA (7.41%), PIPI_SP/SCOT_SP (7.23%), AFRNAN93 (6.09%), PIPI_SP (3.31%), SCOT_SP (2.73%), HIP<70 (1.77%), and RHIALC (0.22%). *Taphozous* sp. and *Hipposideros caffer* were recorded only once. Around 2% of the bat passes could not be attributed to a species or sonotype and were thus only considered in the total bat activity. From a guild perspective, open space foragers comprised the largest proportion (56%) of the bat passes, followed by edge foragers (44%), while clutter foragers constituted less than 0.3% of the recorded bat passes.

Bat activity and sonotype richness presented a strong seasonal pattern, with significant variation observed across sampled months (ANOVA, $p < 0.001$) (Figure 3.1). However, no such differences in bat activity and sonotype richness were identified across sampled sites (ANOVA, $p = 0.605$ and $p = 0.131$, respectively).

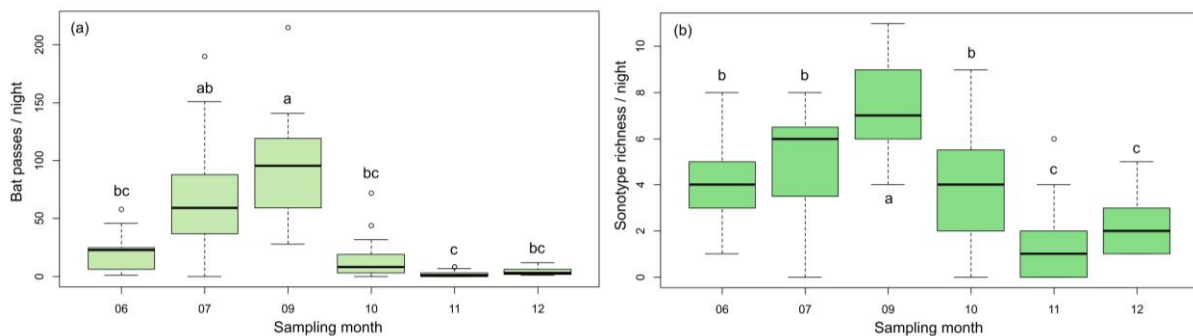


Figure 3.1. Boxplots displaying (a) total bat activity and (b) sonotype richness in relation to sampling month. Different letters indicate significant differences in pairwise comparisons using Tukey’s HSD test.

3.1. Tree characteristics and landscape features

An increase in the size of isolated trees positively influenced both total bat activity and the activity of open space foragers (Figure 3.2, Table S1). Although the effect was not significant, there was also a positive trend between tree size and both sonotype richness and edge guild activity (Figure 3.2, Table S1). Tree species was the sole predictor that significantly and concurrently impacted total bat activity, sonotype richness and guild-specific (open space and edge) activity (Figure 3.2, Table

S1). The Oil palm (*Elaeis guineensis*) and Winter thorn (*Faidherbia albida*) trees were associated with higher bat activity and sonotype richness, while the False abura (*Mitragyna inermis*) and Giant-leaved Fig (*Ficus lutea*) trees were associated with lower bat activity and sonotype richness. Neither the number of visible bird nests nor the presence of tree hollows had significant effects on bat activity or sonotype richness.

As for the trees' location in the landscape, a greater distance to neighbouring trees decreased total bat activity, sonotype richness and the activity of open space foragers (Figure 3.2, Table S1). On the other hand, a greater distance to a wooded edge led to an increase in total bat activity, open space and edge foragers' activity, and sonotype richness. The distance to main roads did not have a significant effect on bat activity or sonotype richness.

The activity of clutter foragers showed a non-significant but positive trend with the increase in water depth around the tree (estimate = 0.105, $p = 0.089$, Table S1). The percentage of the moon illuminated did not arise as a significant predictor in any model.

3.2. Insects

Only insect abundance significantly impacted the activity of insectivorous bats, specifically that of edge foragers, with higher insect abundance increasing their activity (estimate = 0.003, $p = 0.029$, Table S2). On the other hand, insect richness had no notable effect on either bat activity or sonotype richness.

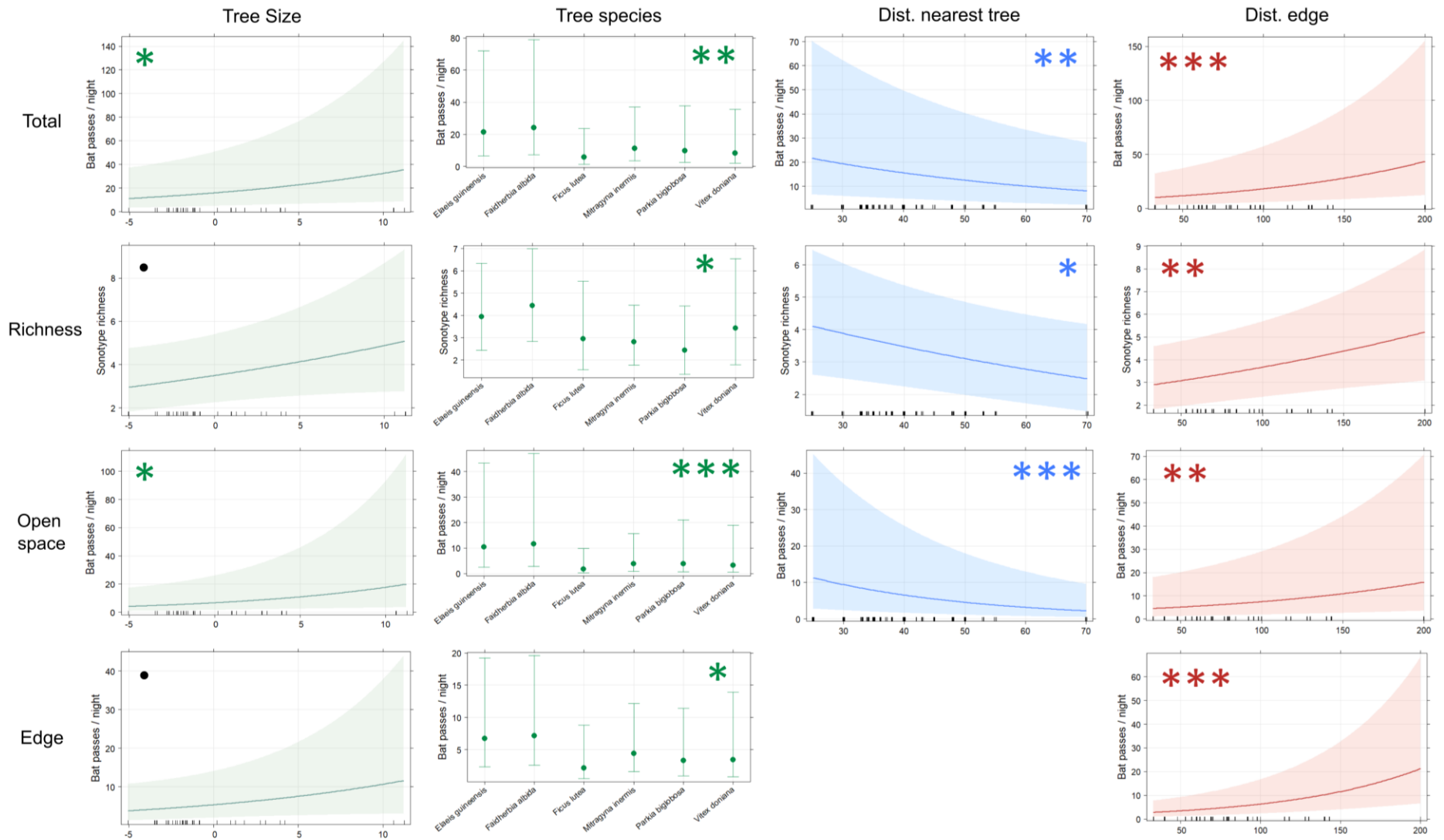


Figure 3.2. GLMMs partial effects for total bat activity, sonotype richness, and the activity of open space and edge foragers. Error bars and shaded areas represent 95% confidence intervals. The significance of the results is presented as: *** < 0.001; ** < 0.01; * < 0.05; • < 0.1. The tick marks on the x-axis are the observed data points.

4. Discussion

Our study demonstrates that the attractiveness of isolated trees in rice fields for insectivorous bats is not only determined by trees' intrinsic characteristics but also by their location in the landscape. Contrary to our expectations and existing studies (Lumsden and Bennett, 2005), high insect abundance around isolated trees only positively influenced the activity of edge foragers. In addition, insect richness had no significant impact on bat activity or sonotype richness. Although we advocate for the retention and inclusion of all isolated trees in agricultural landscapes, our findings highlight that the ecological importance of isolated trees for bats, especially the two most abundant bat guilds within this crop, is determined by tree size, tree species and the distance to neighbouring trees and edges.

4.1. Overall patterns

Unsurprisingly, open space foragers – almost solely composed of bats from the Molossidae family – constituted the majority of the bat assemblage. This family includes the two most abundant and ubiquitous bat species in Africa – *C. pumilus* and *M. condylurus* (Monadjem et al 2010), both confirmed in our study area (Rainho et al. in prep). These species are characterized by their long and narrow wings, designed for fast, straight flight (Denzinger and Schnitzler, 2013; Voigt and Holderied, 2012) and may find in the rice fields highly suitable foraging grounds. Moreover, several studies confirm higher activity of open space foragers over open agricultural landscapes (Freudmann et al., 2015; Heim et al., 2016; Mtsetfwa et al., 2018). Besides, these species emit low frequency calls with high intensity (Meyer et al., 2004), making them significantly more detectable (and at larger distances) than other species, thus increasing the number of records in the acoustic sample (Adams et al., 2012; Meyer et al., 2004; Monadjem et al., 2017).

The low sample size of clutter foragers in this study was anticipated and may simply be a problem of detectability, as bats producing high frequency, low-intensity echolocation calls are poorly detectable or only at close distances (Fenton and Bell, 1981; Monadjem et al., 2017). Since sound attenuation increases acutely with frequency (Lawrence and Simmons, 1982), these bats are often undersampled in acoustic surveys (Adams et al., 2012). Some of the bat species composing this guild may also not be very abundant in the area and thus be of conservation concern locally. This may be true, for instance, for *R. alcyone*, a species that was only detected twelve times in the study area. This species typically inhabits closed tropical moist forests but can also be found in savannas where pockets of suitable habitat are available (Grubb et al. 1998). Clutter bats are expected to be less abundant within such open areas as rice fields, since their echolocation and foraging behaviour are adapted to narrow spaces with cluttered vegetation, capturing prey which are positioned on or near background vegetation (Denzinger and Schnitzler, 2013; Shapiro et al., 2020).

Our findings revealed a strong seasonal pattern, with a pronounced increase in bat activity and sonotype richness in the wet season, particularly in months associated with highest rainfall. This seasonal variation in bat activity is consistent with other studies (Shapiro et al., 2020; Weier et al., 2021), but our observations specifically parallel those of Mtsetfwa et al. (2018) in another agricultural landscape in Africa, where changes in both bat activity and bat richness were documented. During the wet season, when rice fields experience flooding, there is an abundant availability of crucial resources, such as water and insect prey (Kishimoto-Yamada and Itioka, 2015; Rautenbach et al., 1988), which positively impacts bat populations (Fukui et al., 2006).

The absence of differences in bat activity and sonotype richness observed among sampled sites may be attributed to the proximity and landscape similarity of the rice fields under study. Furthermore, the maximum distance between sampling points is close to 13 km, and many bat species

in the region might forage in areas over 15 km from their day roosts, as exemplified by similar species (Marques et al., 2004; Rainho and Palmeirim, 2011).

The bimodal distribution of the peak frequency of pipistrelle-like echolocation calls within and a little beyond the range emitted by *A. nana* suggests the presence of two phonic types, and possibly distinct species. This was the case with *Pipistrellus pipistrellus* and *Pipistrellus pygmaeus* – two widely occurring species in Europe (Mayer and Von Helversen, 2001) – formerly known as the 45kHz and 55kHz phonic types of *P. pipistrellus* until genetic analyses allowed for the differentiation of these species (Barratt et al., 1997; Jones and Van Parij, 1993). Furthermore, similar instances have been observed in other species (Thabah et al., 2006). African pipistrelle-like or pipistrelloid bats (subfamily Vespertilioninae, tribes Pipistrellini and Vespertilionini, *sensu* Amador et al., 2016) are still understudied, partly as a consequence of difficulties in species identification due to their similar external morphology and high diversity, resulting in many cryptic species (Monadjem et al., 2010, 2013, 2021).

4.2. Influence of tree characteristics

Tree size had a positive effect on total and open space bat activity, with edge bat activity and sonotype richness also showing a positive but non-significant relationship. Although our results differ from those of Polyakov et al. (2019) and Froidevaux et al. (2022), who found that larger isolated trees increase total and edge bat activity, but not that of open space foragers, it is noteworthy that these findings originated from two agricultural landscapes in temperate regions. While we initially anticipated results akin to those observed by these studies, differences in guild species composition and particularly in our studies' landscape – a smallholder farmland surrounded by wooded areas with frequent single trees within the rice fields – may account for the observed differences. The significance of isolated trees for bats may in fact increase with the intensification and extensiveness of the farmed area.

The positive effects of tree size on bat activity may be explained by a variety of reasons, several of which have already been identified by Polyakov et al. (2019) and Froidevaux et al. (2022). Tall trees with wide canopies may serve as better acoustic landmarks for spatial orientation and biotope recognition (Denzinger and Schnitzler, 2013) than smaller trees. This is particularly true for bat species which predominantly depend on woody features for commuting (Frey-Ehrenbold et al., 2013). Additionally, bats may also benefit from better foraging conditions around larger trees, as they offer greater protection from wind and are expected to support a higher number of insect prey than smaller ones (Merckx et al., 2010; Polyakov et al., 2019). Nevertheless, improved foraging conditions around larger trees may disproportionately benefit edge-specialist and clutter-adapted bats, that have a less powerful but more manoeuvrable flight (Denzinger and Schnitzler, 2013). For all the abovementioned reasons, larger isolated trees may function as stepping stones within the agricultural matrix, facilitating the use of different areas and important resources (e.g., water, food, roosts) by increasing landscape connectivity (Frey-Ehrenbold et al., 2013; Saura et al., 2014). Moreover, larger, older trees usually provide more roosting opportunities for tree-dwelling bat species than smaller trees (Tillon et al., 2016). On this account, it was expected that the presence of tree hollows would enhance bat activity by providing roosting sites for tree-dwelling bat species. Bird nests could also affect bat activity, either positively or negatively, depending on whether the presence of birds interfered with bats roosting inside unoccupied nests. The absence of impact of tree hollows and bird nests in isolated trees on bat activity and sonotype richness suggests that these structures are not drivers of bat activity around these trees in this region. A possible explanation for the lack of impact from bird nests is that only vacant nests could be used by bats as roosting sites; however, as it was not possible to distinguish

between occupied and vacant nests, all nests were counted. Furthermore, there may not be a lack of roosting sites (in trees or other structures) in the wider landscape.

Tree species was an important driver of bat activity, impacting total, open space, and edge bat activity, as well as sonotype richness. Although *E. guineensis* and *F. albida* exhibited significantly higher bat activity than other tree species (specially *F. lutea* and *M. inermis*) we could not find an explanation for this based on functional and phenological tree traits. The only apparent difference is in tree morphology, with *E. guineensis* and *F. albida* having smaller tree sizes than some of the other species (Figure S2). Nevertheless, palm trees like *E. guineensis* are known to harbour bat roosts in their fronds (Monadjem, et al. 2010). Moreover, while *F. lutea* exhibited the lowest bat activity (total and guild-specific) among all tree species, it is important to note that our observations are based on a single sampled tree of this species.

4.3. Influence of the surrounding environment and trees' location in the landscape

The tree's location in the landscape was also an important factor driving bat foraging activity and sonotype richness. As observed by Polyakov et al. (2019), we found that total bat activity increased with the proximity to neighbouring trees. Additionally, we also found increased activity of open space foragers and sonotype richness with neighbouring tree proximity. Interestingly, the same was not observed for the activity of edge foragers, as our knowledge of their foraging ecology would suggest. However, the fact that sonotype richness (a metric mostly composed by edge sonotypes) increased with neighbouring tree proximity, may suggest that there were opposing responses within the edge guild. The closer proximity to neighbouring trees might enhance local connectivity (Polyakov et al., 2019) and increase foraging opportunities for bats, without the narrow/cluttered structure of a more wooded habitat patch.

Our results also demonstrated a positive influence of the distance to wooded edges on total and guild-specific (open space and edge) bat activity, in addition to sonotype richness. An increase in open space and even total bat activity was expected, as trees further away from wooded areas are ideal for open space foraging bats, which comprise the largest proportion of the total bat activity. Edge bat activity and sonotype richness might also benefit from the increased distance to wooded areas/edges if this distance acts to increase the edge habitat available for these species to forage in an otherwise somewhat open landscape.

Although roads are associated with increased mortality due to roadkill incidents (Lesiński, 2007; Voigt and Kingston, 2016), and bats have been documented exhibiting road avoidance behaviour (Zurcher et al., 2010), the distance to main roads was not a significant driver of bat activity in our study. Despite occasional accounts of roadkill in the study area, it is important to note that these roads experience minimal traffic during the night (pers. obs.), when bats are most active. Furthermore, since road verges are often cleared of vegetation, roads might not constitute a barrier to the movement of bats between rice fields on either side of the road.

Environmental factors such as water availability and lunar illumination have been extensively documented to affect bat activity (Voigt and Kingston, 2016). In this regard, since these rice fields are rain-fed, the water level in the rice field may be an important factor influencing bat activity. The activity of clutter foragers showed a positive yet non-significant correlation with the increase in the water depth, that may be related to an increased prey abundance due to the higher water availability (Kishimoto-Yamada and Itioka, 2015; Oyediran et al., 1999). The response of clutter foragers to water depth may be particularly important (compared to other guilds), as these bats prefer to forage in cluttered environments, such as forests or cashew orchards, but may forage in the rice fields due to the increased availability of water and prey. Notwithstanding, due to the small sample size, it is not

possible to draw definitive conclusions about the activity patterns of bats belonging to the clutter guild.

The percentage of the moon illuminated did not exhibit a significant influence on bat activity, indicating that moonlight may not be a relevant driver of bat activity in our specific context. This effect was tested to see whether bats restricted their activity during nights with more moonlight, a strategy known as lunar phobia, presumably used by bats to reduce the risk of predation (Saldaña-Vázquez and Munguía-Rosas, 2013). Nevertheless, the effect of moonlight on the activity of insectivorous bats is complex, varying depending on the species of bat, ecological setting, and time of year. While Meyer et al. (2004) recorded an impact on open and edge foragers from West Africa, other studies conducted in Africa found no effect of moonlight on bat activity (Musila et al., 2019; Taylor et al., 2013). Alternatively, the absence of a discernible effect may result from opposing responses within species belonging to the same guild, with some species exhibiting increased activity while others reducing it. This variability in behavioural responses highlights the intricate nature of bat interactions with moonlight, emphasising the need for further research to elucidate the mechanisms behind these differential effects. Moreover, the influence of confounding factors such as rain-induced changes in bat activity or the effect of cloud cover on moonlight intensity may have also contributed to the complexity of understanding bat behaviour in response to lunar illumination. Adverse weather conditions, specifically heavy rainfall or fog are known to suppress bat activity (Fenton et al., 1977; Meyer et al., 2004), potentially overshadowing any discernible impact of moonlight on their foraging behaviour.

4.4. Impact of insect prey

Contrary to our predictions, higher insect abundance around isolated trees only positively influenced the activity of edge foragers. Additionally, insect richness had no discernible impact on total bat activity, guild-specific activity or sonotype richness. These findings suggest that trees have a broader resource value than merely being a source of prey for bats.

The literature on this topic presents conflicting results; while some studies report positive correlations between bat activity and insect abundance around isolated trees (Lumsden and Bennett, 2005), others find no such associations (Polyakov et al., 2019). Although different ecological contexts or bat species may have different responses, it is also worth noting that these studies employed different trapping methods – Polyakov et al. (2019) used sticky traps, while Lumsden and Bennett (2005) used light traps – which could contribute to the observed differences.

However, since we used the sampling month as a random effect, it is possible that our results are due to a low variation in insect abundance and richness within each month.

4.5. Limitations and further studies

Identifying bats using their echolocation calls is often challenging, particularly in regions where even the identity of the occurring bat species is poorly known. This limited our ability to classify bat calls to species level and prevented us from evaluating possible species-specific effects of studied variables that may be masked by grouping different species into sonotypes or guilds. Moreover, bats may adjust their echolocation calls in response to vegetation clutter (Kalko and Schnitzler, 1993; Obrist, 1995; Schnitzler et al., 2003), water (Rydell et al., 1999), insect noise (Gillam and McCracken, 2007) or the presence of other bats while in flight (Obrist, 1995), making their identification more complex.

Additionally, any similar study using acoustic monitoring to assess bat activity is confronted with the problem of varying detectability among species. This problem emerges from differences in

the intensity and frequency (through attenuation, as discussed) of their echolocation calls (Hayes, 2000) and is one researchers must be cognizant of when interpreting results and deriving conclusions. Our acoustic recorders might have also been unable to record all echolocating bat species; for instance, *Nycteris* and *Kerivoula* spp. are present in the study area (pers. observ.) but emit low intensity calls that are typically not captured unless emitted remarkably close to the microphone (Monadjem et al., 2017). Our filtering process might have additionally contributed to the exclusion of *Nycteris* spp. from our analyses, since their echolocation calls are characteristically sharp/pure FM (Frequency Modulated) pulses of very short duration that are often interpreted as noise by the sound analysis software.

Operating day and night, sticky traps introduced a confounding factor by capturing diurnal insects, which are not often accessible to bats while foraging at night, dusk, and dawn. Additionally, existing research indicates that the attractiveness of these traps is influenced by colour preferences of different insects (Böckmann and Meyhöfer, 2017; Carrillo-Arámbula et al., 2022). As we did not assess bat diet or identify insects to a lower taxonomic level, it was impossible to determine which of the trapped insects were included in the bats' diet. There is still much to learn about the diet composition of individual species and variations existing within foraging guilds, such as edge foragers of the Hipposideridae and Vespertilionidae families. Therefore, the identification of the specific insects consumed by bats (ideally to the lowest taxonomic level) should be the focus of further studies, considering the diverse preferences of different bat species for insect prey (Fenton et al., 1977; Lumsden and Bennett, 2005). The low taxonomic resolution used to quantify insect richness may have also limited our ability to detect differences between sampled trees. Subsequent studies should delve deeper into the relationship between tree characteristics and surrounding insect abundance and diversity.

The close proximity of sampled isolated trees introduced significant spatial correlation within variables measuring landscape composition (e.g. percentage of forest/woody cover, edge density, etc.). This limitation impeded our ability to characterise the landscape around isolated trees at different spatial scales. Moreover, the distance to the nearest edge did not differentiate between type of edge – native forest or cashew orchard – and bats may be differently attracted to these habitats.

Future research should increase the number of sampled trees and investigate season-specific responses of bats to tree and landscape variables, as, for example, the higher resource abundance during the wet season might alleviate the constraints or influences of landscape composition and configuration on bats.

4.6. Conclusions

The implementation of measures to strengthen insectivorous bat populations holds considerable potential to increase insect predation, thereby suppressing rice pests (Puig-Montserrat et al., 2015; Tuneu-Corral et al., 2023) and improving food security. However, in order to maximise the potential ecosystem services provided by insectivorous bats, it is necessary to have a comprehensive understanding of the drivers of their activity and distribution. Therefore, the primary objective of this study was understanding how isolated trees drive the activity of bats in rice fields, so that we could aid rice producers in managing this landscape. Our study provides essential baseline knowledge on the dynamics of insectivorous bats in rice crops. This information may serve to guide the development of management strategies and guidelines aimed at enhancing crop productivity and food security through natural pest suppression, all while concurrently preserving biodiversity. Our findings indicate that preserving or allowing the growth of large isolated trees of different species, closer to other trees but further from wooded edges, will benefit the two most abundant bat guilds within this crop, enhancing the benefits these predators may bring by suppressing insect pests. In accordance with other studies

(Gibbons et al., 2008; Manning et al., 2006; Prevedello et al., 2018), our research highlights the importance of isolated trees as agents of heterogeneity in agricultural landscapes, emphasising that the potential benefits for bat populations stem from ecological phenomena occurring at both tree and landscape levels.

In addition to their diverse ecological functions (Manning et al., 2006) and pest suppression services they may enable, isolated trees provide other ecosystem services that benefit farmers and local communities. This is particularly evident with the Oil Palm (*E. guineensis*) and Winter thorn (*F. albida*) trees. In addition to their significance for bat activity, these trees are extremely important for local human communities by providing essential cultural, provisioning, and supporting ecosystem services. These services include the supply of food such as palm oil or palm wine, commodities like charcoal (from burnt palm kernels), and soil fertilisation through nitrogen fixing by *F. albida* – an aspect used in African agroforestry systems to enhance productivity and reduce reliance on inorganic fertilisers (Garrity et al., 2010). Importantly, we believe that conservation efforts and management strategies can be more effective and long lasting, by actively involving and collaborating with local communities. Furthermore, incorporating the social, cultural, and economic dimensions of conservation ensures a holistic approach that addresses the diverse needs of these communities.

Regulating services provided by bats include agricultural pest suppression but may importantly also include the suppression of human disease vectors and vectors of plant pathogens (Kemp et al., 2019; Maslo et al., 2022; Puig-Montserrat et al., 2015, 2020), which has significant implications for human health and livelihoods. Furthermore, increased crop yields via the suppression of insect pests by insectivorous bats (Kemp et al., 2019; Maas et al., 2015), presents a viable alternative to agrochemical inputs such as fertilisers and pesticides (Puig-Montserrat et al., 2015). Economically vulnerable communities, like small farming communities in rural Africa, are particularly susceptible to health complications associated with pesticide usage due to inexistence or insufficient training and the use of unsafe and unregulated chemicals (Ngowi et al., 2007; Oluwole and Cheke, 2009). For these reasons, implementing integrated pest management (IPM), using natural pest controllers like bats, offers a sustainable alternative to insecticides that also promotes the health and well-being of rural farming communities.

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Supplementary material

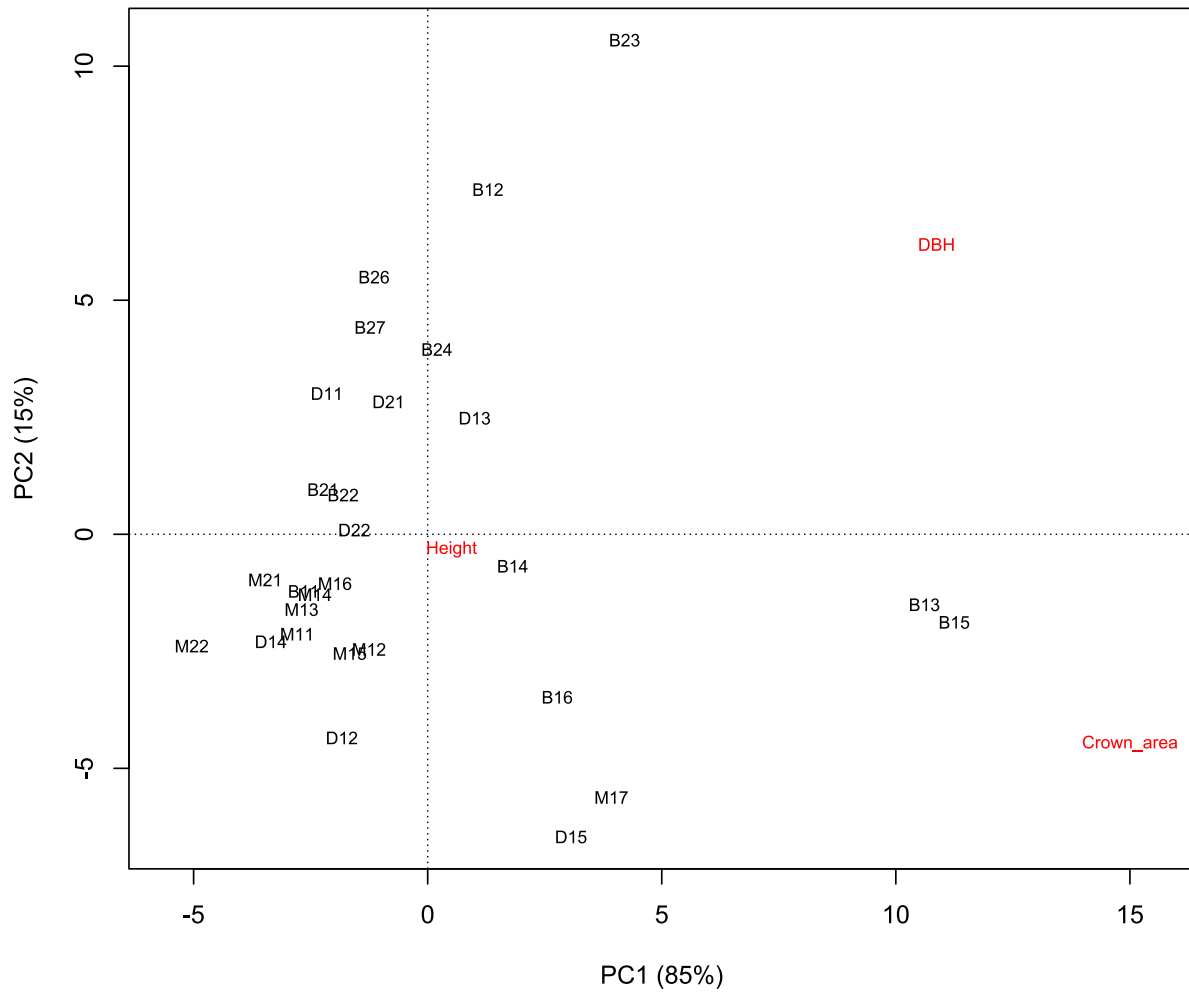


Figure S1. PCA of tree diameter at breast height (DBH), crown area and height. The proportion of variance explained by each principal component is given in parentheses.

Table S1. Outputs of the Generalized Linear Mixed Models (GLMMs) investigating total bat activity, sonotype richness, and the activity of the different guilds, according to tree and landscape variables. Tree species was a categorical variable, with *Elaeis guineensis* as the reference. The significance of the results is presented as: *** < 0.001; ** < 0.01; * < 0.05; • < 0.1. For random effects, the values given are variance estimates and their standard deviations.

Model	Predictors	Estimate	Std. error	z-value	P-value
Total bat activity	Random: Month	Var: 2.049	SD: 1.431		
	(Intercept)	3.543	0.964	3.676	<0.001***
	Tree Size (PC1)	0.072	0.036	2.010	0.044*
	Tree Species				
	<i>Faidherbia albida</i>	0.113	0.218	0.517	0.605
	<i>Ficus lutea</i>	-1.332	0.465	-2.866	0.004**
	<i>Mitragyna inermis</i>	-0.648	0.225	-2.877	0.004**
	<i>Parkia biglobosa</i>	-0.800	0.445	-1.798	0.072•
	<i>Vitex doniana</i>	-0.948	0.493	-1.922	0.055•
	Distance to tree	-0.297	0.100	-2.978	0.003**
Distance to edge	0.153	0.043	3.532	<0.001***	
Sonotype richness	Random: Month	Var: 0.280	SD: 0.529		
	(Intercept)	2.015	0.455	4.427	<0.001***
	Tree Size (PC1)	0.033	0.019	1.708	0.088•
	Tree Species				
	<i>Faidherbia albida</i>	0.118	0.121	0.970	0.331
	<i>Ficus lutea</i>	-0.283	0.259	-1.094	0.274
	<i>Mitragyna inermis</i>	-0.341	0.134	-2.553	0.011*
	<i>Parkia biglobosa</i>	-0.479	0.250	-1.912	0.056•
	<i>Vitex doniana</i>	-0.133	0.275	-0.484	0.628
	Distance to tree	-0.150	0.059	-2.539	0.011*
Distance to edge	0.004	0.001	2.634	0.008**	
Open space activity	Random: Month	Var: 2.816	SD: 1.678		
	(Intercept)	3.143	0.847	3.712	<0.001***
	Tree Size (PC1)	0.098	0.048	2.041	0.041*
	Tree Species				
	<i>Faidherbia albida</i>	0.102	0.256	0.398	0.691
	<i>Ficus lutea</i>	-1.738	0.564	-3.083	0.002**
	<i>Mitragyna inermis</i>	-0.994	0.277	-3.592	<0.001***
	<i>Parkia biglobosa</i>	-0.988	0.605	-1.634	0.102
	<i>Vitex doniana</i>	-1.141	0.609	-1.872	0.061•
	Distance to tree	-0.036	0.009	-3.908	<0.001***
Distance to edge	0.008	0.003	2.798	0.005**	
Edge activity	Random: Month	Var: 1.413	SD: 1.189		
	(Intercept)	1.353	0.684	1.977	0.048*
	Tree Size (PC1)	0.070	0.041	1.694	0.090•
	Tree Species				
	<i>Faidherbia albida</i>	0.059	0.259	0.228	0.820
	<i>Ficus lutea</i>	-1.139	0.567	-2.009	0.045*
	<i>Mitragyna inermis</i>	-0.427	0.266	-1.605	0.109
	<i>Parkia biglobosa</i>	-0.706	0.485	-1.456	0.146
	<i>Vitex doniana</i>	-0.674	0.581	-1.161	0.246
	Distance to tree	-0.012	0.009	-1.338	0.181
Distance to edge	0.012	0.003	4.231	<0.001***	
Clutter activity	Random: Month	Var: <0.001	SD: <0.001		
	(Intercept)	-2.941	0.434	-6.773	<0.001***
	Water depth	0.105	0.062	1.700	0.089•

Table S2. Outputs of the Generalized Linear Mixed Models (GLMMs) investigating total bat activity, sonotype richness, and the activity of the different guilds, according to insect abundance and richness. Due to the very low sample size, the clutter guild analysis was done recurring to two univariate models. The significance of the results is presented as: *** < 0.001; ** < 0.01; * < 0.05; • < 0.1. For random effects, the values given are variance estimates and their standard deviations.

Model	Predictors	Estimate	Std. error	z-value	P-value
Total bat activity	Random: Month	Var: 1.807	SD: 1.344		
	(Intercept)	2.349	0.811	2.897	0.004**
	Insect abundance	0.002	0.001	1.435	0.151
	Insect richness	-0.011	0.102	-0.108	0.914
Sonotype richness	Random: Month	Var: 0.289	SD: 0.538		
	(Intercept)	0.985	0.363	2.713	0.007**
	Insect abundance	0.001	0.001	1.058	0.290
	Insect richness	0.021	0.050	0.411	0.680
Open space activity	Random: Month	Var: 2.099	SD: 1.449		
	(Intercept)	1.785	0.953	1.873	0.061•
	Insect abundance	<0.001	0.001	-0.126	0.899
	Insect richness	-0.030	0.129	-0.236	0.813
Edge activity	Random: Month	Var: 1.871	SD: 1.368		
	(Intercept)	1.253	0.872	1.437	0.151
	Insect abundance	0.003	0.001	2.180	0.029*
	Insect richness	-0.006	0.116	-0.050	0.960
Clutter activity	Random: Month	Var: <0.001	SD: <0.001		
	(Intercept)	-1.328	1.056	-1.257	0.209
	Insect abundance	-0.012	0.009	-1.300	0.194
	Random: Month	Var: <0.001	SD: <0.001		
	(Intercept)	2.229	2.616	0.852	0.394
	Insect richness	-0.991	0.539	-1.839	0.066•

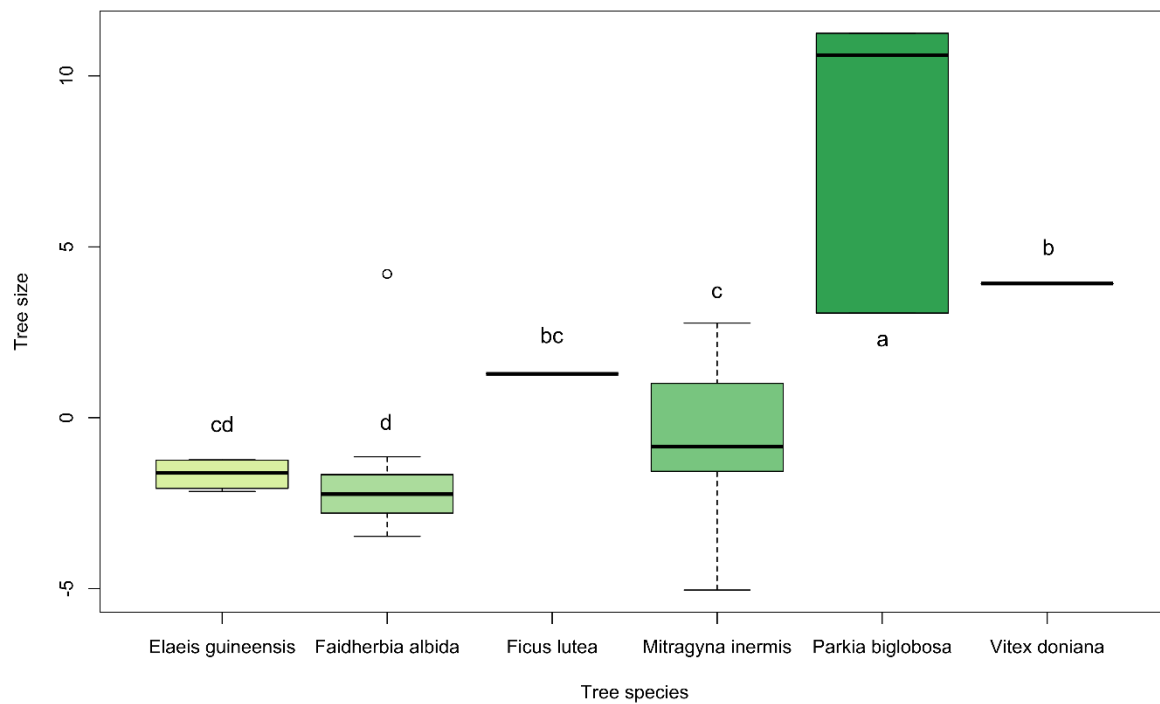


Figure S2. Boxplot displaying tree size (PC1) in relation to tree species. Different letters indicate significant differences in pairwise comparisons using Tukey's HSD test.