



Tree and landscape characteristics outweigh insect abundance in driving bat activity in West African rice fields



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ABSTRACT

The urgent need to sustainably feed a growing human population is particularly pressing in tropical regions where food security remains uncertain. Ecological intensification strategies, such as integrating nature-based solutions, can help achieve this goal by leveraging ecosystem services. Isolated trees in agricultural landscapes play a vital role in enhancing productivity and biodiversity, supporting organisms like insectivorous bats that provide pest control services. The implementation of measures to strengthen insectivorous bat populations holds significant potential to increase insect predation, suppress agricultural pests, and improve food security. Understanding how tree characteristics and surrounding landscapes influence bat foraging activity in staple tropical crops is thus essential. This study investigated how isolated trees influence the activity of bats and insects in smallholder rice fields in Guinea-Bissau. Specifically, we evaluated how tree characteristics and landscape features affect bat guild activity, insect abundance, and richness, as well as the indirect effects of insects on bats. Our findings indicate that larger, isolated trees of specific species located closer to other trees but further from wooded edges are associated with increased bat activity and richness, mediated partly by higher insect abundance. These results emphasise the ecological and agricultural importance of isolated trees in promoting biodiversity and enhancing pest suppression in agricultural landscapes.

1. Introduction

Feeding a rapidly growing human population sustainably is a major global challenge (Robertson and Swinton, 2005; Tscharntke et al., 2012), particularly in tropical regions where food security remains uncertain (Grote, 2014). Typical approaches to increasing food production and agricultural productivity have relied on intensification, characterised by landscape homogenisation and simplification (Gámez-Virués et al., 2015) alongside extensive use of agrochemicals such as fertilisers and pesticides to maximise provisioning services (Gámez-Virués et al., 2015; Matson et al., 1997). However, these practices are significant drivers of biodiversity loss (Emmerson et al., 2016; Kehoe et al., 2017), negatively impacting numerous taxonomic groups (Potts et al., 2010; Stanton et al., 2018) and imposing substantial environmental cost. These impacts ultimately degrade or even eliminate vital ecosystem services (Landis, 2017).

Ecological intensification offers a sustainable alternative by incorporating ecosystem services (Kremen, 2020) and employing

nature-based solutions in agricultural management (Keesstra et al., 2018). Isolated trees, a prominent feature of agricultural landscapes worldwide (Manning et al., 2006), play a vital role in this approach. By enhancing soil structure, reducing erosion, facilitating water infiltration, and supporting biodiversity, isolated trees provide ecosystem services that benefit both agriculture and the environment (Garrity et al., 2010; Hoosbeek et al., 2018; Manning et al., 2006). These trees also serve as “keystone ecological structures,” offering habitat, food resources, and connectivity for a wide range of species (Fischer et al., 2010; Prevedello et al., 2018). Notably, isolated trees can significantly support bat communities, particularly in agricultural matrices, by enhancing local habitat quality and increasing foraging opportunities (Froidevaux et al., 2022).

Insectivorous bats, key natural pest suppressors, exemplify the importance of biodiversity in agricultural systems (Tuney-Corral et al., 2024). Studies have shown that bats are voracious predators of agricultural pests worldwide (Boyles et al., 2011; Kemp et al., 2019), conclusion further supported by recent exclusion experiments in rice

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fields (Bhalla et al., 2023; Tuneu-Corral et al., 2024; Sierra-Durán et al., 2025). These findings position bats as integral to nature-based farming strategies (Maine and Boyles, 2015). In regions like West Africa, where rice (*Oryza sp.*) is a staple crop and a primary calorie source (Soullier et al., 2020), sustainable pest control methods are critical for long-term food security (Diaz and Wilby, 2005; Savary et al., 2012). However, the ongoing loss of landscape elements such as isolated trees, particularly in rice growing areas, threatens the biodiversity needed to sustain these ecosystem services (Gibbons et al., 2008; Monck-Whipp et al., 2018).

This study aims to bridge the gap between ecological research and practical implementation by examining how tree characteristics and landscape features influence bat and insect activity in rainfed rice fields in Guinea-Bissau. Specifically, we evaluated: 1) how tree characteristics and landscape features affect the activity of different bat guilds; 2) how these characteristics and features influence insect abundance and richness; and 3) how insect order abundance mediates the effects of tree

characteristics on bat activity. Considering the varied habitat preferences of bat guilds (Denzinger and Schnitzler, 2013; Shapiro et al., 2020), we hypothesise that larger trees and those near other trees or wooded areas will support higher activity of slow-flying and gleaning bats, whereas fast-flying open space foragers will be equally active across all trees. Additionally, we expect that tree size and proximity to wooded areas will enhance insect abundance and richness, and that insect abundance will mediate bat activity.

2. Methods

2.1. Study area and tree characteristics

This study was conducted in the Oio region, northern Guinea-Bissau, within the rural sector of Mansaba (12°19'45"N, 15°10'56"W; Fig. 1). Situated in West Africa, Guinea-Bissau experiences a tropical sub-humid

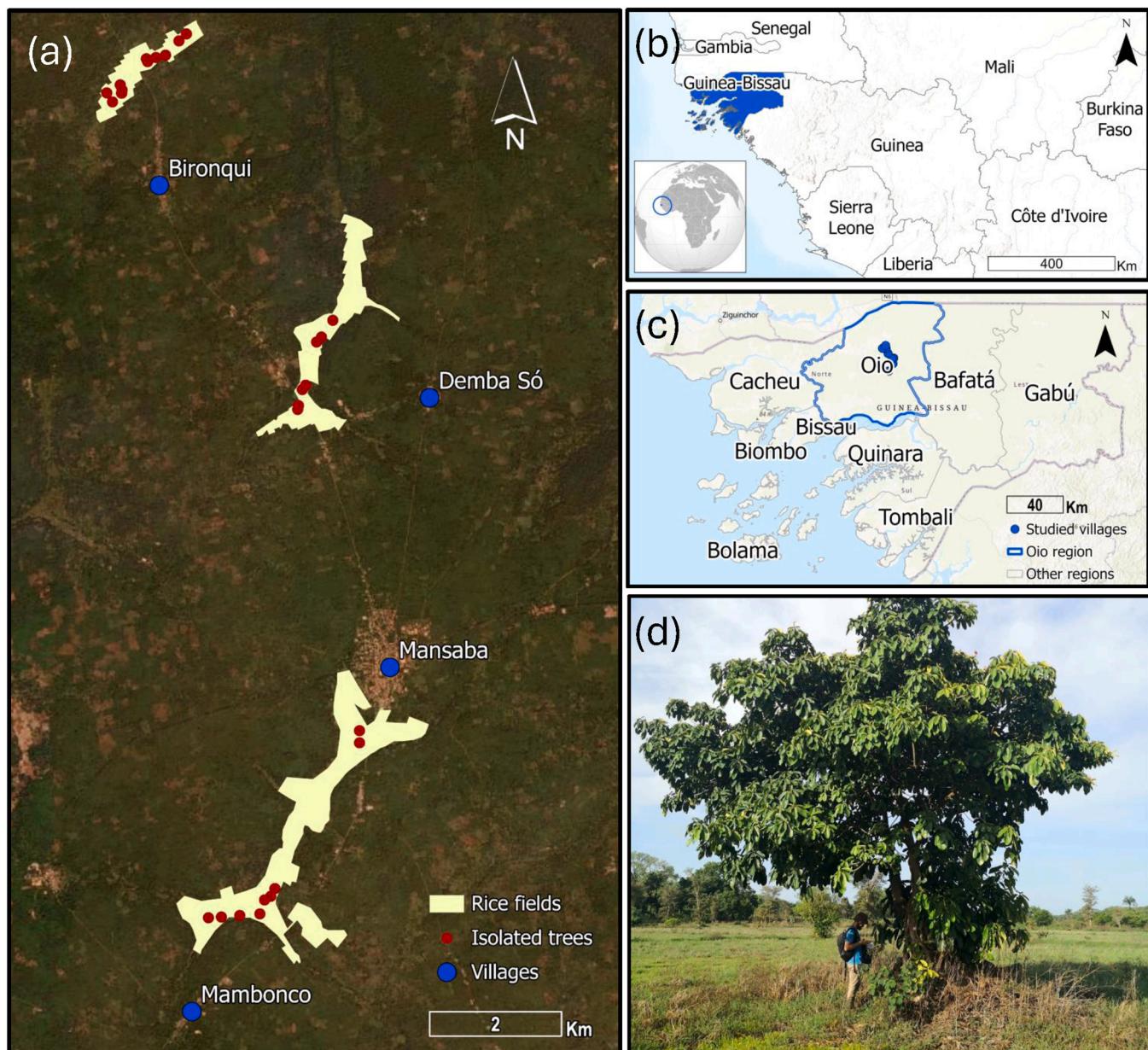


Fig. 1. Study area: (a) Satellite image showing the locations of the 28 isolated trees in the rice fields. Insets show (b) the location of Guinea-Bissau in West Africa, (c) the location of the Oio region within Guinea-Bissau and (d) an isolated *Ficus lutea* standing in the rice field at Bironqui (sources © Esri, Earthstar Geographics, USGS and GADM).

climate with two distinct seasons: a dry season typically lasting from November to May and a wet season from June to late October or early November (Catarino et al., 2001). The heaviest rainfall occurs between July and September, contributing to an annual precipitation of 1200–1400 mm in Oio (Catarino et al., 2001; Climate Change Knowledge Portal, 2023). The region's topography is gentle, with most areas lying below 50 m a.s.l. and none exceeding 100 m a.s.l. The landscape comprises smallholder rice fields interspersed with cashew orchards and forest patches.

Four areas of rainfed lowland rice fields were surveyed: Bironqui, Demba Só, Mansabá, and Mambonco, named after nearby villages (Fig. 1). Rice fields were first examined using satellite imagery from Google Earth (v7.3.6.9345, 2022) to identify isolated trees, which were subsequently mapped and validated through ground-truthing. Trees were considered isolated if no other trees or woody habitat patches were present within a 30 m radius, minimising the likelihood of recording bats from non-associated habitats (Froidevaux et al., 2022).

A total of 28 isolated trees, representing six species, met the isolation criteria and were selected for the study: African oil palm (*Elaeis guineensis*, n = 4), winter thorn (*Faidherbia albida*, n = 11), giant-leaved fig (*Ficus lutea*, n = 1), false abura (*Mitragyna inermis*, n = 8), African locust bean (*Parkia biglobosa*, n = 3), and black plum (*Vitex doniana*, n = 1). Tree species were identified using Catarino and Indjai (2019) and characteristics such as diameter at breast height (DBH), crown area, height, number of visible bird nests and presence of tree hollows within the lower three metres were recorded. Bird nests were recorded as some bat species (e.g., *Afronycteris nana* and *Kerivoula* spp.) use abandoned weaver (*Ploceus* sp.) nests as roosts (Happold et al., 1987; Page and Dechmann, 2022). To estimate tree crown areas, we used a measuring tape and compass to measure the distance from the tree trunk to the vertical projection of the crown edge in the four cardinal directions. The crown area was then calculated as the area of a circle with a radius equal to the average of these four measurements.

2.2. Bat sampling

Insectivorous bats were acoustically sampled between June and July and from September to December 2022. 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 in height. The devices were configured with a 384 kHz sampling rate and a gain of 30.6 dB (medium setting). Sampling followed a 5-second on / 55-second off cycle over two consecutive nights per month during peak bat activity periods (18:26–23:56 and 04:20–06:50; Meyer et al., 2004), totalling 12 bat-nights per tree. Bat activity was measured as the number of "bat passes", defined as at least two sequential recognisable echolocation pulses in a recording (López-Bosch et al., 2022).

All recordings were automatically filtered using sound analysis software (Kaleidoscope Pro version 5.4.2, Wildlife Acoustics), discarding files with no bat calls. Retained files were visually inspected, and call characteristics, including shape, frequency of maximum energy (kHz), start and end frequencies (kHz), inter-pulse interval (ms) and duration (ms), were extracted from spectrograms and oscillograms using the cursor. Bat calls were classified to the lowest possible taxonomic level based on the available literature (e.g., ACR, 2022; Kingdon, 2013; Monadjem et al., 2010, 2011, 2013, 2017; Taylor, 1999) and prior research in Guinea-Bissau (Rainho and Palmeirim, 2017 and references therein). Additionally, in a parallel mist-netting study, we recorded the calls of hand-released bats from the study area to build a reference call library and support acoustic identification (authors' data). When it was not possible to definitively assign a bat call to a species, calls were classified into mixed species groups or sonotypes (Rainho et al., 2023), a procedure largely stemming from the insufficient knowledge of bat calls in this region.

Recorded species and sonotypes were categorised into three foraging

guilds: Open space, Edge, and Clutter, based on their foraging ecology, echolocation, and morpho-ecological traits (Denzinger and Schnitzler, 2013; Monadjem et al., 2010; Schnitzler and Kalko, 2001; Shapiro et al., 2020) (Table 1). Open space foragers are adapted for fast but less manoeuvrable flight in open areas, while clutter foragers exhibit traits suited for slower, highly manoeuvrable flight within dense or cluttered vegetation. Edge foragers strike a balance between flight speed and manoeuvrability, exploiting the boundaries between open areas and more forested habitats (Denzinger and Schnitzler, 2013; Schnitzler and Kalko, 2001). Unidentified calls (2 %) and one sonotype group, which included Molossid open foragers and Vespertilionid edge foragers, were excluded from the guild analysis.

2.3. Insect sampling

The abundance and richness of flying insects at each isolated tree were estimated using 20 × 25 cm yellow sticky traps (ref. UIPFETA125, ECONEX; Böckmann et al., 2021; Pedigo and Buntin, 1993). A trap was hung on or near each tree, with both sides exposed, and deployed and retrieved in the same periods as the acoustic recording devices, except in July, when no insect sampling was possible. Insects captured on each trap were counted and identified to the order level using a magnifying lens. Insect abundance was the average number of insects per trap, and insect richness was the average number of orders per trap.

2.4. Landscape and environmental variables

The landscape surrounding each tree was characterised using QGIS (version 3.28.4; QGIS Development Team, 2022) to measure the distance from each isolated tree to the nearest tree, wooded edge (the closest border between a rice field and a forest or cashew orchard), and main road. Moonlight intensity, expressed as the percentage of the moon illuminated at midnight, was included due to its potential influence on bat activity (Appel et al., 2017, 2019; Bhalla et al., 2023; Meyer et al., 2004). Lowland rainfed rice fields in this region remain flooded during most of the rainy season. At each sampling period, water depth was measured at four locations around each tree using a measuring rod, and the average was used as the final value. All variables are detailed in Supplementary Table S1.

2.5. Data analysis

All statistical analyses were conducted using R statistical software version 4.3.1 (R Core Team, 2023) with the packages vegan (Oksanen et al., 2020), glmmTMB (Brooks et al., 2017), MuMIn (Barton, 2009), and others mentioned below. Statistical significance was set at p = 0.05.

Negative binomial Generalised Linear Mixed Models (GLMMs) with a log link function were used to identify the tree, landscape and environmental drivers of bat activity and insect abundance. For bats, response variables included total activity, guild-specific activity, and sonotype richness. For insects, models used total arthropod abundance, the abundance of individual orders, and insect richness at the order level as response variables. Due to limitations in the insect dataset, the effects of total insect abundance and insect order-level richness on bat activity were modelled separately, following a similar procedure. Month was included as a random effect to account for strong temporal structure in the data. We assessed spatial autocorrelation in insect abundance and richness (total and by major order) and bat activity and richness (total and by foraging guild) using Moran's I and Geary's C tests with the spdep package v. 1.3-10 (Bivand et al., 2025). Moran's I indicated some clustering in the Clutter guild data, due to the limited number of recordings for this guild (Supplementary Table S2). All tree characteristics, landscape, and environmental variables (Supplementary Table S1) were considered as predictors for both bat activity and insect abundance. Total insect abundance and insect order richness were used as predictors of bat activity and sonotype richness in separate models.

Table 1

Bat sonotypes and guilds. Sonotypes and corresponding call characteristics for potential species within each foraging guild. Echolocation call shape are categorised as follows: CF = constant frequency, QCF = quasi-constant frequency, FM = frequency modulation and MH = multi-harmonic. Frequencies in parentheses denote the characteristic frequency (or frequency range) of recorded individuals. Taxa listed in bold have been confirmed in the study area through morphological and/or molecular methods (authors' data).

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>Mops pumilus</i> <i>Mops condylurus</i>
Edge	Edges / gaps between open areas and dense vegetation	QCF-MH	(26)	TAPH_SP	<i>Taphozous</i> sp.
		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> <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)	PIPI_SP	<i>Scotophilus leucogaster</i> <i>Scotophilus</i> sp. <i>Scotoecus albofuscus</i> <i>Scotoecus</i> sp. <i>Glauconycteris variegata</i> <i>Rhinolophus alcyone</i> <i>Hipposideros caffer</i>
Clutter	Narrow spaces, dense/cluttered vegetation	FM-CF-FM	(40 – 50)	SCOT_SP	
		CF-FM	(32 – 39)	SCO/GLA	
			65 – 80 (78) 149 – 154 (153)	RHIALC HIPCAF	

Predictor collinearity was evaluated with Spearman's correlation, and issues among tree descriptors were resolved through PCA, creating a composite 'tree size' variable from the first component, which explained 85 % of the variance (Supplementary Fig. S1). Predictor linearity and interactions were tested but did not contribute significantly to the final models. Full models underwent variable reduction and selection and the best models were selected based on fit and parsimony using the lowest AICc and significance of predictors (Burnham and Anderson, 2002). Model fit was evaluated using the DHARMA package (Hartig, 2018). Partial effects plots, illustrating the estimated change in response variables for each unit of change in predictors, were generated using the package effects v. 4.2–2 (Fox, 2003; Fox and Weisberg, 2018).

To assess the relationships between non-categorical tree characteristics, insect order abundance, and bat guild activity, a structural equation model (SEM) was constructed and fitted using a piecewise approach. Categorical variables were excluded, as standardised path coefficients in SEM are not directly interpretable for categorical predictors (Grace et al., 2012; Lefcheck, 2016). GLMMs were first used to identify significant predictors of bat and insect responses, providing a robust framework to account for overdispersion and temporal random effects. These models also informed variable selection and model structure. SEM then complemented this analysis by clarifying the structure of relationships and revealing potential indirect effects, particularly how tree characteristics influence bats via insect abundance, thus offering a more integrated view of causal pathways (Grace et al., 2012; Lefcheck, 2016). Individual models for each path were fitted using negative binomial GLMMs with the glmmTMB package (Brooks et al., 2017). Indirect, direct, and total effects were computed manually by combining coefficients along the relevant paths, following Grace et al. (2010). Model evaluation and goodness-of-fit were assessed by examining residual diagnostics and marginal/conditional R² values for each component model (Nakagawa and Schielzeth, 2013).

3. Results

Over 328 recorder-nights (nights x recording devices), we recorded a total of 5382 bat passes representing 12 species or sonotypes (see Table 1) around 28 isolated trees within rice fields. Molossids dominated the acoustic sample, accounting for 2588 bat passes (48.1 % of total bat activity). In contrast, large Hipposiderids (1.77 %) and *Rhinolophus*

alcyone (Rhinolophidae, 0.22 %) were rarely detected, while *Taphozous* sp. (Emballonuridae) and *Hipposideros caffer* (Hipposideridae) were each recorded only once (Supplementary Fig. S2). From a guild perspective, open space foragers constituted the largest proportion (56 %) of the bat passes, followed by edge foragers (44 %), while clutter foragers represented less than 0.3 % of the recorded activity (Supplementary Fig. S2). During the sampling period (excluding July), over 41,000 insects were captured, representing more than 20 orders. Only 0.6 % of the specimens could not be identified to the order level. Diptera accounted for the largest proportion of captures (49.3 %), followed by Hemiptera (30.9 %) and Hymenoptera (12.5 %; Supplementary Fig. S2).

Larger isolated trees were associated with increased total bat activity and the activity of open space foragers (Fig. 2, Supplementary Table S3). Tree size exhibited a not-significant positive association with both sonotype richness and edge guild activity (Fig. 2, Supplementary Table S3). Tree species emerged as the only predictor to significantly and simultaneously influenced total bat activity, sonotype richness and guild-specific activity (open space and edge foragers) (Fig. 2, Supplementary Table S3). African oil palm (*E. guineensis*) and winter thorn (*F. albida*) were linked to higher bat activity and sonotype richness, while the false abura (*M. inermis*) and giant-leaved fig (*F. lutea*) were associated with lower values for both metrics. Neither the number of visible bird nests nor the presence of tree hollows had significant effects on bat activity or sonotype richness.

In terms of the trees' location within the landscape, greater distance to neighbouring trees reduced total bat activity, sonotype richness and the activity of open space foragers (Fig. 2, Supplementary Table S3). Conversely, greater distances to wooded edges increased total bat activity, as well as the activity of open space and edge foragers, and sonotype richness. The activity of clutter foragers showed a positive non-significant association with increasing water depth around the trees ($\beta = 0.105$, $p = 0.089$, Supplementary Table S3). Neither the percentage of the moon illuminated - sampled across its full range - nor the distance to main roads significantly influenced any of the bat or insect models.

Tree species and water depth emerged as the primary drivers of insect order and total abundance around isolated trees (Fig. 3, Supplementary Table S4). Additionally, none of the descriptors included in the models affected insect richness or Lepidoptera abundance. The white acacia (*F. albida*) and the oil palm (*E. guineensis*) supported higher abundance across most insect orders. Despite the higher abundance

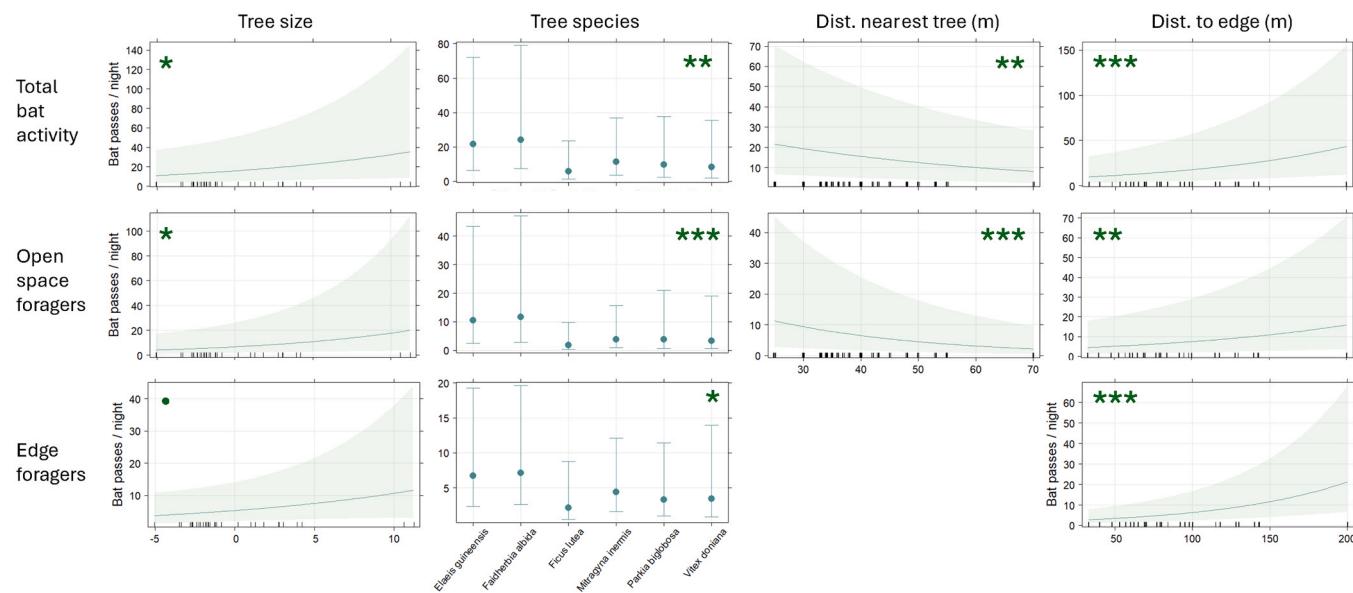


Fig. 2. Partial effects from GLMM models for total bat activity, sonotype richness, and the activity of open space and edge foragers. Error bars and shaded areas represent 95 % confidence intervals. Significance levels are indicated as follows: * ** < 0.001, * * < 0.01, * < 0.05, • < 0.1. The model statistics are summarised in Supplementary Table S3.

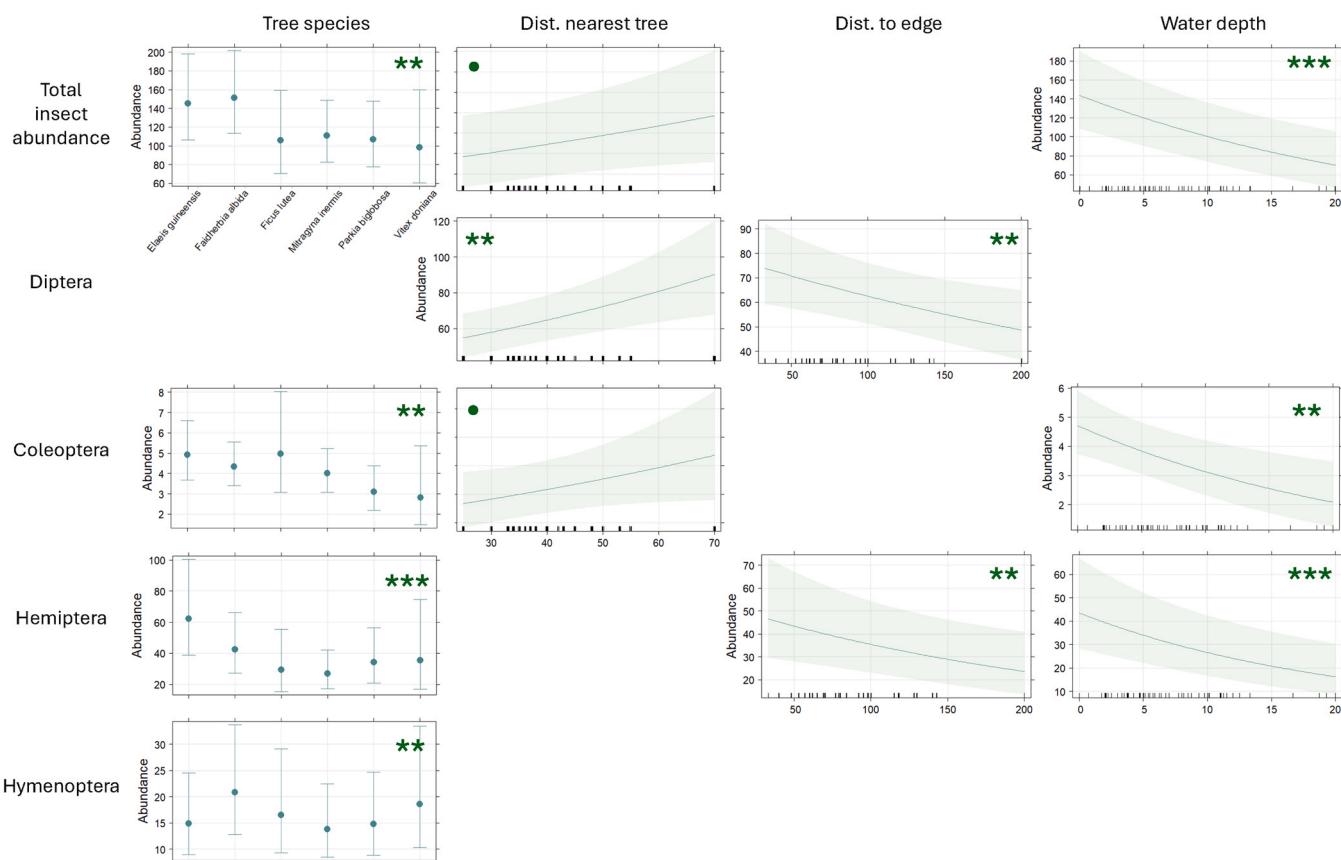


Fig. 3. Partial effects from GLMM models for the abundance of all insects and the orders Diptera, Coleoptera, Hemiptera, and Hymenoptera. Error bars and shaded areas represent 95 % confidence intervals. Significance levels are denoted as: * ** < 0.001, * * < 0.01, * < 0.05, • < 0.1. The negative effect of tree size on Diptera abundance ($\beta = -0.041$, $p < 0.001$) is not displayed. The model statistics are summarised in Supplementary Table S4.

during the wet season, insect abundance was generally higher in areas with lower water depth around the isolated trees ($\beta = -0.034$, $p < 0.001$), a trend also evident in Coleoptera ($\beta = -0.04$, $p = 0.002$) and Hemiptera ($\beta = -0.049$, $p = 0.0002$). Diptera showed a preference for smaller trees

($\beta = -0.04$, $p < 0.001$), located closer to the field edges ($\beta = -0.0025$, $p = 0.009$) and farther from other nearby trees ($\beta = 0.01$, $p = 0.002$, Supplementary Table S4).

Insect abundance significantly influenced the activity of

insectivorous bats, particularly edge foragers, with higher insect abundance associated with increased activity ($\beta = 0.003$, $p = 0.029$, Supplementary Table S5). In contrast, insect richness did not have a notable effect on bat activity or sonotype richness.

SEM results revealed that tree characteristics indirectly influenced edge forager activity through Diptera abundance (Fig. 4). However, these indirect effects were relatively small compared to the direct effects of tree and landscape features on bat activity. Diptera abundance decreased around larger trees ($\beta = -0.033$, $p = 0.005$), while open-space bat activity increased directly ($\beta = 0.055$, $p = 0.023$). Edge bat activity was indirectly influenced by Diptera abundance ($\beta = -0.0001$, $p = 0.043$) around larger trees. Conversely, greater distance to the nearest tree increased Diptera abundance ($\beta = 0.013$, $p = 0.005$) and indirectly enhanced edge bat activity ($\beta = 0.00004$, $p = 0.043$). Greater distance to wooded edges, however, reduced Hemiptera abundance ($\beta = -0.004$, $p = 0.04$) but directly supported higher open-space bat activity ($\beta = 0.005$, $p = 0.045$).

4. Discussion

Our findings demonstrate that the attractiveness of isolated trees in rice fields for insectivorous bats is influenced not only by the intrinsic characteristics of the trees but also by their location within the landscape. High insect abundance around isolated trees positively influenced the activity of edge foragers. However direct and indirect effects mediated by insects were generally small, highlighting that tree characteristics and landscape features are the primary drivers of bat guild activity. Although we advocate for retaining and integrating all isolated trees in agricultural landscapes, our findings emphasise that their ecological importance for bats, particularly open space and edge foragers, is determined by tree size, species, and proximity to neighbouring trees and wooded edges.

Open space foragers, dominated by Molossidae species, accounted for most of the bat activity. This family includes *M. pumilus* and *M. condylurus*, two species confirmed in our study area and that are abundant and widespread in Africa (Monadjem et al., 2010). Their long, narrow wings enable fast, straight flight over open landscapes such as

rice fields, which likely serve as suitable foraging grounds (Denzinger and Schnitzler, 2013; Voigt and Holderied, 2012). Additionally, their low-frequency, high-intensity calls make them more detectable over greater distances (Adams et al., 2012; Meyer et al., 2004), contributing to their dominance in acoustic surveys. Conversely, the low sample size of clutter foragers likely reflects both their lower abundance in predominantly open habitats and detectability issues, as these bats produce high-frequency, low-intensity calls that attenuate rapidly and are only detectable at close range (Adams et al., 2012; Fenton and Bell, 1981; Monadjem et al., 2017). Common species such as *Nycteris* spp. were not detected acoustically, likely due to their short FM pulses that are often excluded as noise by the sound analysis software. Some clutter species, such as *R. alcyone*, may also be locally rare or dependent on forested habitats, as evidenced by their low detection rates in our study (Monadjem et al., 2010; Wilson and Mittermeier, 2019). Additionally, acoustic surveys in this region are challenging due to the poorly known bat fauna, limiting species-level classification and potentially masking species-specific effects within sonotypes or guilds.

Tree size positively influenced total and open space bat activity, with non-significant positive trends observed for edge bat activity and sonotype richness. Larger trees likely serve as acoustic landmarks for orientation (Denzinger and Schnitzler, 2013) and provide better foraging conditions by sheltering prey from wind and creating a more suitable microclimate (Merckx et al., 2010; Polyakov et al., 2019). Although not observed in our study setting, these features have been shown to also benefit edge bats, which rely on manoeuvrable flight and proximity to vegetation for foraging (Polyakov et al., 2019; Toffoli, 2016). Larger isolated trees may also act as stepping-stones, increasing connectivity in agricultural landscapes (Frey-Ehrenbold et al., 2013; Saura et al., 2014). The absence of significant effects of tree hollows and bird nests on bat activity suggests that these structures are either not commonly used as roosts in this region or are not limiting, possibly due to the availability of alternative roosting sites.

Tree species emerged as a key driver of both bat activity and insect abundance. As a categorical variable, it could not be directly analysed in the SEM analysis integrating all effects (Grace et al., 2012; Lefcheck, 2016). However, the significant association of *E. guineensis* and *F. albida* with higher bat activity and insect abundance suggests that their influence on bats is likely mediated by the increased abundance of major insect orders around these trees. Another reason for the importance of these tree species may be that *E. guineensis* often hosts roosting bats, particularly Molossidae and other open space foragers, in its fronds due to its crown structure (Monadjem et al., 2010), potentially increasing local activity near roost sites. *F. albida*, a nitrogen-fixing species, enhances soil fertility and supports rich understorey invertebrate communities (Garrity et al., 2010), which may boost insect abundance and attract bats. Additionally, both tree species have open canopies that may facilitate bat flight (Froidevaux et al., 2022).

Landscape context also shaped bat activity and richness. Proximity to neighbouring trees increased total bat activity, sonotype richness, and open space forager activity, likely by enhancing connectivity (Polyakov et al., 2019). Interestingly, this descriptor had no effect on edge forager activity, suggesting complex, potentially opposing responses among bat species within this guild, likely mediated by reduced abundance of some insect orders, particularly Diptera (Gonçalves, 2025), when other trees were nearby. Additionally, total and guild-specific bat activity increased with distance from wooded edges, likely due to the preference of open space bats for less cluttered foraging areas. This trend for edge foragers might reflect increased edge habitat availability in open areas, as opposed to heavily wooded environments.

Environmental factors such as water availability and lunar illumination have been extensively documented to affect bat activity (Voigt and Kingston, 2016). Water availability was the only descriptor showing a near-significant effect on clutter forager activity, potentially linked to an increase in specific prey abundance (Kishimoto-Yamada and Itioka, 2015). However, the small sample size for this guild, limited knowledge

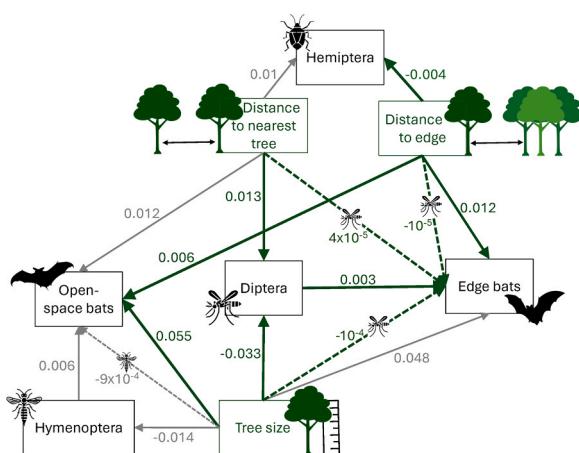


Fig. 4. Structural equation model (SEM) illustrating the relationships between non-categorical isolated tree and landscape characteristics, insect order abundance, and bat guild activity in rice fields of Oio region. Rectangles represent nodes – tree and landscape characteristics, insect mediators, and bat guild responses. Solid arrows indicate direct effects, while dashed arrows represent indirect effects mediated through other variables. Icons over dashed arrows indicate the insect order mediating the indirect effect. Green, thicker arrows highlight statistically significant paths ($p < 0.05$) while grey arrows represent non-significant relationships. Coefficients along the arrows denote the strength and direction of each effect, with positive values indicating an increase and negative values indicating a decrease in the response variable. The model statistics are summarised in Supplementary Table S6.

of bat diets in the region, and the low taxonomic resolution of sampled insect identification, constrain the ability to draw definitive conclusions. Similarly, lunar illumination had no significant impact on bat activity, contrasting with findings from some African studies (Meyer et al., 2004) but aligning with others (Musila et al., 2019; Taylor et al., 2013). This variability may reflect opposing responses within guilds, underscoring the need for further investigation into species-specific lunar effects (Rainho et al., 2023).

Higher insect abundance positively influenced edge forager activity, primarily through tree size and its mediation by Diptera, but had no effect on other guilds or total bat activity. Similarly, insect richness showed no discernible impact. These findings underscore the critical role of tree characteristics and landscape features as primary drivers of bat guild activity, suggesting that trees serve roles beyond merely providing prey resources for bats. While the region's low-impact farming likely prevents major insect outbreaks (Sotomayor et al., 2024), methodological limitations - such as the use of yellow sticky traps that capture diurnal insects less accessible to bats, and the low taxonomic resolution for insect richness - may have masked finer-scale patterns (Fenton et al., 1977; Lumsden and Bennett, 2005; Polyakov et al., 2019). Nevertheless, the strong influence of tree-related factors on bat activity remains evident, underscoring their importance in agricultural systems (Froidevaux et al., 2022; Heim et al., 2015). Future research should prioritise identifying the specific insect prey consumed by bats, ideally to the lowest taxonomic level, to better understand the ecological roles of isolated trees for different bat species and guilds.

5. Conclusions

Strengthening insectivorous bat populations offers significant potential for enhancing pest suppression, improving food security, and reducing dependence on harmful pesticides, particularly in tropical and economically vulnerable regions (Puig-Montserrat et al., 2015; Tuneu-Corral et al., 2023). Beyond agricultural pest control, bats also help regulate human disease vectors and plant pathogens (Kemp et al., 2019; Maslo et al., 2022; Puig-Montserrat et al., 2015, 2020) promoting sustainable and healthier farming practices (Ngowi et al., 2007; Oluwole and Cheke, 2009).

Preserving or encouraging the growth of large, isolated trees of diverse species, strategically placed closer to other trees but further from wooded edges, benefits the two most abundant bat guilds and maximises their pest suppression services. These results align with prior studies (Gibbons et al., 2008; Manning et al., 2006; Prevedello et al., 2018), underscoring the role of isolated trees as biodiversity hubs that enhance landscape connectivity and ecosystem services.

Beyond ecological benefits, the two most important tree species for bats in this region - *E. guineensis* and *F. albida*, provide vital cultural, provisioning, and supporting services for local communities. These include palm oil, palm wine, charcoal, soil enrichment through nitrogen fixation, as well as more general benefits such as shade and water retention (Garrity et al., 2010). Integrating these multifunctional values into farmland management can simultaneously meet ecological and community needs, fostering collaboration and long-term sustainability (Chaves et al., 2024).

Strategic conservation and restoration of isolated trees, particularly species that support both biodiversity and livelihoods, should be embedded within agroecological planning. Similar approaches in tropical agroecosystems have shown that retaining structural elements such as remnant trees or forest patches can boost pest control and pollination while supporting farmer wellbeing (Tscharntke et al., 2012; Ferreira et al., 2023). These measures may be implemented through community-based agroforestry, incentive-based conservation, or agri-environment schemes where appropriate. These strategies hold global significance for sustainable agriculture and resilient rural livelihoods, by promoting practices that reconcile biodiversity conservation with agricultural productivity.

CRediT authorship contribution statement

Gonçalo A. Fernandes: Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis, Data curation. **Chaves Patrícia A. P.:** Writing – review & editing, Investigation. **Mark Massaad:** Writing – review & editing, Methodology, Investigation. **Ana Rainho:** Writing – review & editing, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used ChatGPT-4o to improve the readability of parts of the text. After using this tool/service, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.agee.2025.109774](https://doi.org/10.1016/j.agee.2025.109774).

Data availability

Data will be made available on request.

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