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Landscape features of rice fields as drivers of bat activity: a case study from Guinea-Bissau

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Esta dissertação foi desenvolvida no âmbito do Projeto EcoPestSupression: Conservar a biodiversidade, garantir a segurança alimentar: o papel de morcegos e aves como agentes de supressão de insetos-praga na cultura de arroz na África Ocidental, financiado exclusivamente por fundos portugueses pela Fundação para a Ciência e Tecnologia

Resumo Alargado

A expansão agrícola e subsequente destruição e conversão de habitats naturais para a agricultura é uma das maiores ameaças à conservação da biodiversidade, especialmente em zonas tropicais e subtropicais. Com o aumento populacional, aumenta também a procura por alimento, o que inevitavelmente promove a expansão de áreas de cultivo. Na Guiné-Bissau, o arroz é uma das mais importantes culturas e uma das principais fontes calóricas para a população local. O país encontra-se no 14º lugar globalmente em consumo de arroz per capita, sofrendo também um aumento da pressão antropogénica pela necessidade de produzir alimento em quantidade suficiente para colmatar as crescentes necessidades calóricas da população. É então, necessário procurar alternativas que conciliem a procura por alimento com a conservação da biodiversidade, como por exemplo utilizando diferentes designs paisagísticos ou a utilização de supressores ecológicos de pragas, tais como os morcegos insetívoros. Múltiplos estudos demostram que estes morcegos se podem alimentar de pragas nos mais diversos ecossistemas agrícolas, incluindo pragas de arroz.

Este projeto tem como objetivo identificar quais são as variáveis paisagísticas intrínsecas aos arrozais que influenciam a atividade de quirópteros. Pretende-se orientar o design paisagístico para que este habitat possa ser atrativo para morcegos. Isto dado que aumentando a sua densidade e consequentemente o consumo de potenciais pragas de arroz poderemos contribuir para um aumento da produtividade dos arrozais. Neste contexto, propomos a seguinte hipótese: áreas com maior pressão antropogénica quantificada pela presença de infraestruturas antropológicas irão influenciar negativamente a atividade de quirópteros. Por exemplo, devido ao aumento da mortalidade por causa de atropelamentos e distúrbios no padrão de voo causados pela incidência de luzes do tráfego rodoviário, a presença de estradas irá influenciar negativamente a atividade de quirópteros. Considerando cada sonótipo identificado, foram também propostas as seguintes hipóteses: Variáveis ambientais como a hora do nascer da lua, ocaso da lua, percentagem de lua iluminada e temperatura irão influenciar cada sonótipo de forma distinta. É esperado que a largura do arrozal influencie positivamente morcegos que se alimentam em espaço aberto, como os Molossídeos; também para este sonótipo prevemos que o habitat predominante tenha uma influência significativa, e espera-se que habitats mais abertos como arrozais ou campos de pousio sejam mais atraentes para morcegos deste sonótipo. Pelo contrário, prevê-se que espécies com adaptações para caçar em espaços fechados, como as espécies do género *Rhinolophus*, sejam positivamente influenciadas pela presença de áreas de mato próximo dos pontos de amostragem. Por fim, prevê-se que uma maior disponibilidade de alimento influencie positivamente todos os sonótipos.

Foram utilizados gravadores de ultrassons para avaliar a atividade dos morcegos em 25 pontos de amostragem em cinco arrozais localizados numa área rural no setor de Oio, Guiné-Bissau. A área de estudo caracteriza-se por ser uma região relativamente plana, numa área rural com predominância de áreas agrícolas maioritariamente de cultivo de arroz e caju, incluindo também áreas de floresta secundária dispersas e pequenas localidades rurais. Os gravadores foram colocados nos pontos de amostragem e registaram a atividade de quirópteros durante três noites consecutivas. A amostragem repetiu-se em cada ponto de amostragem após um intervalo nove dias, iniciando assim um novo ciclo de gravação. Os programas informáticos kaleidoscope e batsound foram utilizados para analisar as gravações e para classificar os registos com morcegos até ao nível taxonómico mais baixo possível. Foram também recolhidos valores ambientais referentes às características paisagísticas de cada ponto de amostragem: Densidade de cobertura vegetal num raio de 250 metros, distância à zona de mato mais próxima, distância à estrada mais próxima, distância à aldeia mais próxima, largura do arrozal, habitat predominante num raio de 250 metros, percentagem de cobertura da lua iluminada, nascer da lua, ocaso da lua, temperatura, disponibilidade de alimento, semana e aldeia mais próxima. Foi utilizado o

programa Rstudio para realizar a análise numérica dos dados recolhidos. Esta incluiu numa primeira fase, uma análise exploratória gráfica e testes de correlações de Spearmann. Foram também ajustados modelos lineares generalizados mistos (GLMM) binomiais negativos com função log link ou modelos lineares generalizados (GLMs) binomiais negativos quando os efeitos das variáveis aleatórias não justificaram o uso de um GLMM. Estes modelos foram utilizados para analisar os efeitos das variáveis ambientais e de paisagem sobre a atividade de quirópteros. Posteriormente foi utilizado o package DHARMa para confirmação da qualidade dos modelos ajustados.

Os resultados mostram que, ao contrário do que era esperado, as variáveis ambientais: temperatura, percentagem da lua iluminada, nascer e ocaso da lua, não influenciaram nenhum dos sonótipos estudados. A disponibilidade de alimentos influenciou positivamente a atividade dos morcegos para dois sonótipos e para a atividade total de quirópteros e, portanto, é um fator chave para determinar a atividade dos morcegos. Este foi, de facto, a única variável significativa a influenciar a atividade de *Scotophilus sp.*, influenciando positivamente também *Afronycteris nana*. *Hiposideros sp* apresentou maior atividade nos arrozais do que nos demais habitats, sendo que a variável habitat predominante foi a única que mostrou influenciar significativamente membros deste sonótipo. A distância à área florestal mais próxima, a distância até a aldeia mais próxima e a disponibilidade de alimento mostraram uma influência esperada na atividade de *A.nana*. A atividade dessa espécie diminuiu em locais de amostragem mais distantes de áreas arborizadas, mas aumentou com distâncias maiores às estradas e com o aumento da disponibilidade de alimento. Ao contrário do que esperávamos, a atividade de *Rhinolophus sp* aumentou à medida que o local de amostragem se afastava das áreas arborizadas. A atividade de *Pipistrellus sp* foi significativamente maior em pomares de caju. A atividade total dos morcegos também foi maior nos pomares de caju do que nos restantes habitats. A atividade total de quirópteros foi também influenciada positivamente pela disponibilidade de alimento. De acordo com os modelos, nenhuma das variáveis consideradas na análise mostrou qualquer influência na atividade dos Molossídeos. Os testes DHARMa realizados para avaliar a qualidade do modelo mostraram que todos os modelos cumprem os pressupostos exigidos, com exceção do GLM realizado para *Rhinolophus sp.*, provavelmente devido ao baixo número de passagens de morcegos detetadas para este género.

Relacionando os resultados obtidos com as hipóteses previamente propostas, concluímos que as hipóteses referentes as variáveis ambientais, as hipóteses referentes ao sonótipo dos molossideos e a hipótese referente ao sonótipo dos *Rhinolophus sp* não foram confirmadas por este projeto. Podemos, no entanto, afirmar que as restantes hipóteses foram confirmadas ou parcialmente confirmadas. A influencia negativa prevista pela presença de estradas foi apenas detetada para *A.nana*, no entanto tal se deve provavelmente ao facto de que as estradas apresentem pouco tráfego rodoviário especialmente durante o período de maior atividade de quirópteros, reduzindo assim o seu impacto negativo neste sonótipo. A disponibilidade de alimentos mostrou ser uma variável significativa para dois sonótipos, *A.nana* e *Scotophilus sp*, para além de influenciar positivamente o total de atividade de morcegos, sendo por isso o principal fator de influência na atividade de quirópteros detetado neste projeto. Para finalizar, a hipótese central proposta não foi totalmente confirmada, no entanto os resultados indicam que a alteração de paisagem, consequência direta do aumento da pressão antropogénica, nomeadamente a conversão de habitats naturais em campos de cultivo de arroz ou de caju mostrou influenciar significativamente a atividade de quirópteros ainda que, ao contrário do esperado, os pomares de caju mostrem influenciar positivamente a atividade total de morcegos.

Concluindo, este estudo demonstra como é importante considerar designs ecológicos que promovam um equilíbrio entre a necessidade do aumento da produção agrícola com a conservação da biodiversidade, com o objetivo de manter um equilíbrio nos ecossistemas envolventes. Em específico, é necessário procurar compreender quais os fatores que influenciam a disponibilidade de alimento com o objetivo de procurar aplicar os conhecimentos adquiridos para criar ecossistemas agrícolas que promovam a

presença de supressores ecológicos de pestes como os morcegos nestes habitats, de forma a promover o aumento da produção agrícola sem a necessidade de converter áreas naturais.

Palavras-chave: Controlo de pragas, Serviços de ecossistema, Acústica, Chiroptera, Arroz

Summary

Agricultural expansion and natural habitat conversion are some of the biggest threats to biodiversity conservation, especially in underdeveloped economies dependent on primary sector activities. In Guinea-Bissau, rice is one of the primary sources of caloric intake for its population. It ranks 14th globally in rice consumption per capita. It is also one of the most essential crops produced in the country. However, as food demands rise, so does the need to expand agricultural areas, increasing the pressure on natural habitats that may be converted into agricultural fields. It is vital to search for eco-friendly alternatives, such as the usage of eco-pest suppressors and better agricultural landscape design. As many studies have shown, insectivorous bats provide an essential ecosystem service by feeding on different rice pests, acting as biological pest suppressors. This project aims to assess what rice fields' landscape characteristics influence bat activity and gather information on how to better design rice field landscapes to attract pest predators that may increase crop yield without expanding agricultural areas and converting natural habitats. We used autonomous acoustic recording devices in 25 different sampling locations in five rice fields. Bat calls were manually identified to the lowest possible taxonomic level ending with six sonotypes. We performed an exploratory analysis and generalised linear mixed models (GLMMs) to explain which landscape and environmental variables influence bat activity. Our results showed that different variables influence distinct sonotypes: predominant habitat affected *Hipposideros sp.*, *Pipistrellus sp.*, and total bat activity, the distance to the nearest road and food availability positively influenced *A. nana*. In contrast, the distance to the nearest wooded area negatively affected this sonotype. Food availability also positively influenced *Scotophilus sp*, while no variable was detected influencing *Molossids*.

Keywords: Pest control, Ecosystem services, Acoustics, Chiroptera, Rice

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1. Introduction

Rice (*Oryza* spp.) is one of the most important staple foods worldwide, with approximately 480 million metric tons of milled rice produced annually (Muthayya *et al.*, 2014). Guinea-Bissau ranked 14th globally in rice consumption per capita. This country's rice production averaged 177 tons between 2015 and 2019(FAO, 2021), indicating that this crop is critical economically and nutritionally for Guinean people, especially in rural areas. However, as food demands rise, so does the need to clear forests and woodlands to give place to new agricultural areas. Guinea-Bissau lost about 77 percent of its forests between 1975 and 2013 (USGS, 2022). The rate of deforestation has increased from about 2 percent per year between 1975 and 2000 to 3.9 percent over the 2000 to 2013 period (USGS, 2022). An alternative to deforestation is necessary to improve crop output by designing eco-friendly agricultural landscapes (Landis, 2017).

Multiple studies show that bats can act as pest suppressors in tropical and temperate ecosystems. They feed on agricultural pests and are used as a biological control for integrated pest management practices (Puig-Montserrat *et al.*, 2015; Aizpurua *et al.*, 2018; Ali *et al.*, 2019; Baroja *et al.*, 2019; Rodríguez-San Pedro *et al.*, 2020). Some studies have also shown that the presence of bats in rice fields can improve crop yield as they feed on pests such as *Spodoptera mauritia* and *Herpetogramma licarsisalis* (Srilopan *et al.*, 2018; Kemp *et al.*, 2019). However, few studies focused on assessing the tropical agricultural landscape variables influencing bat activity and foraging activity. This is important so that agricultural landscapes can be shaped to attract bats that forage on rice pests to improve crop quality and yield.

The currently available evidence suggests that bat activity is heavily influenced by human activity and infrastructure (Stone *et al.*, 2009; López-Baucells *et al.*, 2017; Claireau *et al.*, 2019; de Figueiredo Ramalho *et al.*, 2021). Some studies show that the presence of roads can induce higher rates of bat mortality (Claireau *et al.*, 2019; de Figueiredo Ramalho *et al.*, 2021). Although houses and other human infrastructure can be used as roosting sites for many species, artificial lighting in such humanized landscapes can disturb echolocation activity (López-Baucells *et al.*, 2017; Stone *et al.*, 2009). Other studies show that distinct species have different preferences regarding foraging habitat, so it is expected that the predominant habitat, woody vegetation cover, and rice field size also influence foraging activity (Russo *et al.*, 2003; Ober and Hayes, 2008).

In this work, we used autonomous acoustic recording devices to assess what specific landscape characteristics drive bat activity and foraging over rice fields, improving our understanding of how to design agricultural landscapes to maximize the ecosystem services bats provide.

We hypothesize that rice fields with more humanized landscapes, such as broader rice fields, less vegetation cover, or smaller distances to human infrastructure, will have a lower bat activity. We predict that the distance to the nearest road would negatively influence bat activity for all sonotypes because traffic lights can disturb bats flying patterns and especially due to an increase in bat mortality rate due to road kills (Claireau *et al.*, 2019; de Figueiredo Ramalho *et al.*, 2021). Rice field width should also positively influence open-space foragers from the *Molossidae* family since these bats' wing morphology is less suited for maneuvering in more confined spaces, such as between tree-tops or in forest gaps (Voigt and Holderied, 2012). Bats from this family are thus expected to show more activity in wide and open habitats such as rice fields.

For the same reason, we predicted that the predominant habitat would influence bat activity. Thus, bat activity was expected to be higher in rice and fallow fields than in cashew orchards and wooded areas (Fenton and Rautenbach, 1986; Voigt and Holderied, 2012). Landcover and habitat variables may influence different sonotypes differently (Jantzen and Fenton, 2012). Unlike open-foragers, cluster-tolerant species have wing morphology and echolocation adaptions to forage in dense habitats like woodlands (Aldridge and Rautenbach, 1987; Neuweiler, 1989). Thus, we expect more natural wooded habitats to benefit cluster-tolerant forest bats from the *Rhinolophus* genera (Neuweiler *et al.*, 1987; Pavey, 1998).

Environmental variables such as temperature and moon phase also affect bat activity (Richards, 1989; Appel *et al.*, 2019a). Previous studies regarding the moon's effect suggest that bat activity negatively correlates with moonlight intensity. This effect is more evident in forest species. It is also more apparent in secondary forests and open habitats when compared to continuous forests (Saldaña-Vázquez and Munguía-Rosas, 2013; Appel *et al.*, 2021). However, the currently available evidence is contradictory because some other studies have shown that moonlight can have a positive influence on some species and a negative influence on others in the same habitat (Appel *et al.*, 2017, 2019a), or show no influence at all (Musila *et al.*, 2019). We hypothesize that changes in weather and moon phase will affect bat activity. We predict that environmental variables such as temperature, lunar phase, moonrise, and moonset will have a species-specific effect, with the lunar phase having a negative effect on open space foragers like Molossids. In some tropical areas, the observed decrease in bat activity is correlated to changes and declines in the abundance of insect communities due to weather changes, specifically cold temperatures (Richards, 1989). Evidence also suggests that bat communities adapt their diet according to the composition of prey communities (Fenton *et al.*, 1977; Fenton and Thomas, 1980). We considered the hypothesis that food availability will positively influence bat activity across all sonotypes in this study.

Since the response to the variables is often guild or species-specific, we hypothesized that species composition in the rice fields and surrounding habitats is affected by landscape and environmental variables. To assess the sonotypes composition in each sampling point in the study area, we performed a non-metric multidimensional scaling (NMDS) weighted by bat activity based on Bray-Curtis dissimilarity. We predict that habitat type will be the major driver of species composition changes in this landscape.

2. Methods

2.1 Study area

Fieldwork was carried out between the beginning of October and mid-December in a rural area of northern Guinea-Bissau, West Africa. It was located in the Oio sector, approximately 10 kilometres north of Mansaba and 10 kilometres south of Farim. This tropical region has two pronounced seasons: a dry season from November to April and a wet season from April to November. The average annual precipitation in Guinea-Bissau is 1,500 to 3,000 mm per year. The relative humidity in inland Guinea-Bissau varies between 58 and 68%. The average minimum temperature during the fieldwork was 22.47 ºC, and the average maximum temperature was 32.96 ºC (The World Bank Group, 2020).

The fieldwork was conducted in a relatively flat sector of Guinea-Bissau with a predominance of agricultural fields (cashew orchards and rice fields) and dispersed secondary forest areas. The landscape was relatively humanized, with some small, scattered villages and a poorly maintained dirt road network connected to a main tarred road between Farim and Mansaba. Five areas with rice fields (locally known as *bolanhas*) and their adjacent habitats were selected to conduct the fieldwork. These were named after the villages (locally known as *tabancas*) of Djalicunda, Bironqui, Lenquebato, Bereco, and Demba Só (Figure 1). The local communities were previously consulted, informed and agreed upon all the sampling methods used in this project.

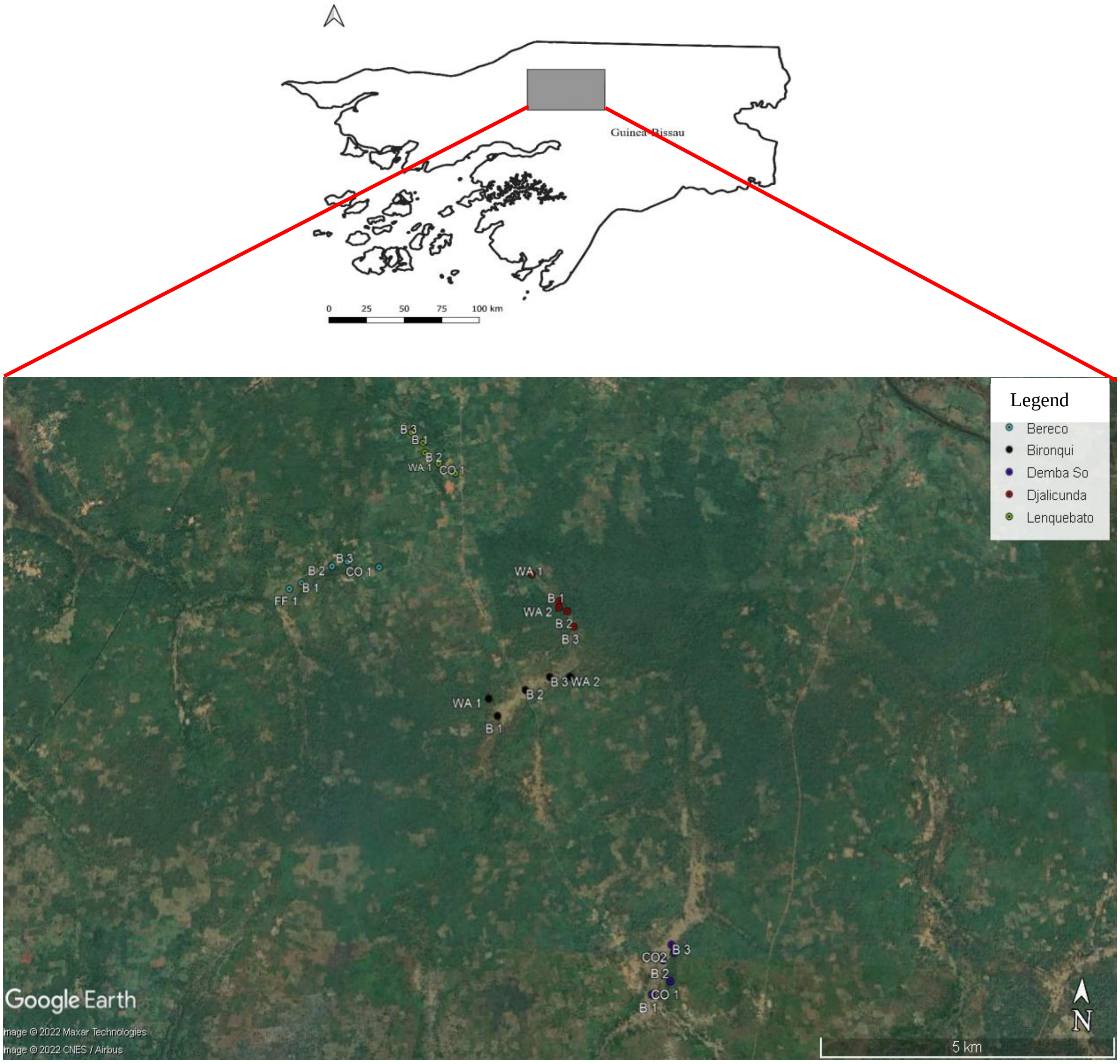


Figure 1: Map of the study area and sampling sites, B- Rice field; WA- wooded area; CO- cashew orchards; FF- Fallow fields

2.2 Acoustic sampling

Bat calls were recorded using ten autonomous acoustic recording devices (AudioMoth 1.0.0 full spectrum recorders, Open Acoustic Devices, United Kingdom) distributed over the five studied areas. Each area included five sampling sites that were classified into four landcover categories: rice field *bolanha* (n=15), wooded areas (n=5), cashew orchards (n=4), and fallow fields (n=1). The recorders were secured to a tree at approximately 2 meters high. They were set to record from 18:26 to 23:56 and from 04:20 to 06:50 with a sample rate of 250 kHz, medium gain, and cycled recordings of 5 seconds separated by 55 seconds intervals. Detectors were deployed at each sampling site for three consecutive nights, with a nine-night gap between detector deployments.

2.3 Insect sampling

Two yellow sticky traps were used for each sampling site to calculate insect relative abundance. Each trap pair was stationed at each sampling site for twelve consecutive nights before being replaced when bat recorders were deployed for a new sampling cycle. Insects were counted on both sides of each trap. Due to different sampling effort amongst sampling sites, the average number of insects per sticky trap side for twelve consecutive nights was used to calculate insect relative abundance. The average value was used as a metric of food availability.

2.4 Bioacoustic analysis

All files were first subject to an automatic filtering process to remove noise files (i.e., files with no bat calls recorded). This process was performed using the Kaleidoscope software version 5.4.2 (Wildlife Acoustics, Concord, MA, USA). Bat passes were defined as a recording of five seconds maximum with at least two echolocation pulses, a frequency range between 8 and 125 kHz, length of pulses between 2 and 20 ms and 250 ms maximum inter-syllable gap. The call sequences found in the selected files were further analyzed using BatSound vs. 4.2 (Pettersson Elektronik, Uppsala, Sweden). These were manually identified to the lowest taxonomic level possible – species, genus, species pairs or most often sonotypes, as the lack of knowledge on bat calls of the regions often made it impossible to assign a call to a particular taxon (Table 1). The frequency of maximum energy (kHz), the start and end frequencies (kHz), the duration (ms), and the call shape were used to identify or group species. Identification was based on data collected from the existing literature (Taylor, 1999; Monadjem *et al.*, 2017), previous works in Guinea-Bissau (Rainho & Palmeirim 2017 and references therein), and bat calls recorded during hand releasing of animals mist-netted in the study area.

Table 1. Identified sonotypes according to sonotypes and possible species included in each sonotypes and their call characteristics. Call shape: CF = constant frequency, QCF =quasiconstant frequency, IUCN category: LC = Least Concern; NT = Near threatened, EN = Endangered. In bold are the species already confirmed in the study area by morphological and/or molecular methods (Rainho et al. in prep).

Sonotype	frequency of maximum energy (kHz)	Call shape	Genus	Species possible	IUCN category (IUCN 2022)
Rhinolophus.sp	79 - 89	CF	*Rhinolophus*	*R. alcyone*	LC
				R. fumigatus	LC
				R. guineensis	EN
A.nana	60 - 90	QCF	*Afronycteris*	***A. nana***	LC
Hipposideros.sp	50 - 70	CF	*Macronycteris*	***M. gigas***	LC
				M. vittatus	NT
			Doryrhina	***D. cyclops***	LC
Pipistrellus.sp	<55	QCF	*Pseudoromicia*	***P. rendalli***	LC
				P. tenuipinnis	LC
			Neoromicia	***N. somalica***	LC
			Laephotis	*L. capensis*	LC
Scotophilus.sp	28-50	QCF	*Scotophilus*	***S. dinganii***	LC
				S. leucogaster	LC
Molossids	<28	QCF	*Chaerephon*	***C. pumilus***	LC
			Mops	***M. condilurus***	LC

2.5 Habitat and landscape descriptors

Habitat was characterized at each sampling site, and changes observed during the sampling period were recorded. Other potential drivers of bat activity were recorded for each sampling site using QGIS 3.28.23 (Open Source Geospatial Foundation, 2022) data and satellite images in Google Earth (vs 7.3.6.9345 (64-bit)). For each sampling site, the rice field width, distance to the nearest wooded area, distance to the nearest village, distance to the nearest road, percentage of woody vegetation cover and predominant habitat within a radius of 250 meters (maximum sampling distance by audiomoths considering species present in the study area), temperature, lunar phase, moonset, moonrise, and relative abundance of insects were recorded (Table 2).

Table 2: Variables used in the project as environmental, habitat and landscape descriptors.

Name	Acronym	Description	Type, range, and unit	Source (data)
Landscape variables				
Rice field width	RiceW	Rice field width	Continuous. 0.045 to 0.360 km	QGIS data and satellite images in Google Earth (09/02/2020)
Distance to the nearest wooded area	DWood	Distance to the nearest wooded area	Continuous. 0.005 to 0.350 km	Ditto
Percentage of woody vegetation cover	Cover	Percentage of woody vegetation cover in a radius of 250 meters	Continuous. 21 to 87 %	Ditto
Distance to the nearest road	DRoad	Distance to the nearest road	Continuous. 0.035 to 1.370 km	Ditto
Distance to the nearest village	DVillage	Distance to the nearest village	Continuous. 0.065 to 1.580 km	Ditto
Predominant habitat	Habitat	Predominant habitat in a radius of 250 meters	Categorical. Rice Field, Cashew, Wooded, fallow	Ditto
Food availability	Food	Average number of insects per sticky trap	Continuous. [range] ind/trap	Fields data: Sticky traps
Environmental variables				
Temperature	Temp	Temperature measured at 22 pm	Continuous. 20.1 to 30.7 ºC	Field data: Audiomoth data reading
Lunar Phase	Moon	Percentage of the Moon illuminated	Continuous. 0 to 100 %	The World Bank Group 2020
Moonrise	Rise	Hour of moonrise	Continuous. 0 to 24 Hour	Ditto
Moonset	Set	Hour of moonset	Continuous. 0 to 24 Hour	Ditto
Random variables				
Week	Week	Sampling week	Categorical. 1 to 12	
Village	Tabanca	Village that managed the area	Categorical. Djalicunda,Bironqui, Bereco, Demba So, Lenquebato	Field data

2.6 Numerical analysis

Bat activity was defined as the number of bat passes recorded per night for all species and sonotypes. Exploratory analyses included bar plots, Spearman correlation tests, plots, histograms, and statistical analysis. The graphical analysis showed that the sampling effort (total number of sampled nights) was unequal amongst each sampling site and that the data followed a Gaussian distribution. There were also differences in bat passes between sampling sites, rice fields, and within each rice field. A non-metric multidimensional scaling (NMDS, with 999 permutations, R-package vegan) based on Bray-Curtis dissimilarity was performed to analyze potential differences in bat composition, weighted by bat activity, in the study area. Spearman correlation tests showed that the pairs of variables distance to the nearest road and percentage of woody vegetation cover, and distance to the nearest wooded area and rice field width, and distance to nearest road and distance to the nearest village were correlated. Thus, they were never used together in any model.

Negative binomial generalised linear mixed models (GLMMs) with a log link function or negative binomial generalised linear models (GLMs) when the effects of the random variables did not justify the use of a GLMM were used to model the relationship between bat activity and habitat descriptors. Univariable GLMMs were performed in a variable reduction process to select the most significant variables. Final model selection was based on the significant variables and lowest AIC. GLMMs were performed for every sonotype. However, when the random variable effect variance was small GLMs were performed instead. Due to a low sampling effort in fallow fields, this habitat was not considered in some models when the assumptions were not met because of the low number of bat passes detected for some sonotypes in this habitat. The R software package DHARMa was used to confirm that the adjusted models met the general modelling assumptions. The data was analyzed and presented using R statistical software 3.4.1 (R Development Core Team, 2020) with the packages: lme4 (Bates *et al.*, 2015), lmerTest (Kuznetsova *et al.*, 2017), pROC (Robin *et al.*, 2011), ggplot2 (Wickham, 2016), DHARMa (Hartig, 2018), and effects (Fox and Weisberg 2018).

3. Results

A total of 6221 bat passes were recorded, of which 1292 were identified to species level (*Afronycteris nana*) while the remaining were grouped according to sonotypes of two or more species (*Hipposideros.sp* - 188, *Pipistrellus.sp* - 1585, *Rhinolophus.sp* - 61, *Scotophilus.sp* - 384 and *Molossids* - 2711, see Table 3)

The analyse of the performed NMDS indicates that cashew orchards sampling points distribute alongside the two axes of the NMDS, clutched at the center of the 1 axis. Rice fields and wooded areas overlap and are scattered around the plot. Food availability was the only variable that showed significance in explaining the species composition differences in each sampling point (Pr 0.032). *Hipposideros sp.* and *Rhinolophus sp.* are associated with wooded areas and rice fields due to their positions in the far left and far right of 1 axis of NMDS, respectively. *Scotophilus sp* is associated with a non-overlapped wooded area patch. All other sonotypes overlap with the distribution of all habitats in the center of 1 axis and alongside the 2 axis (Figure 2).

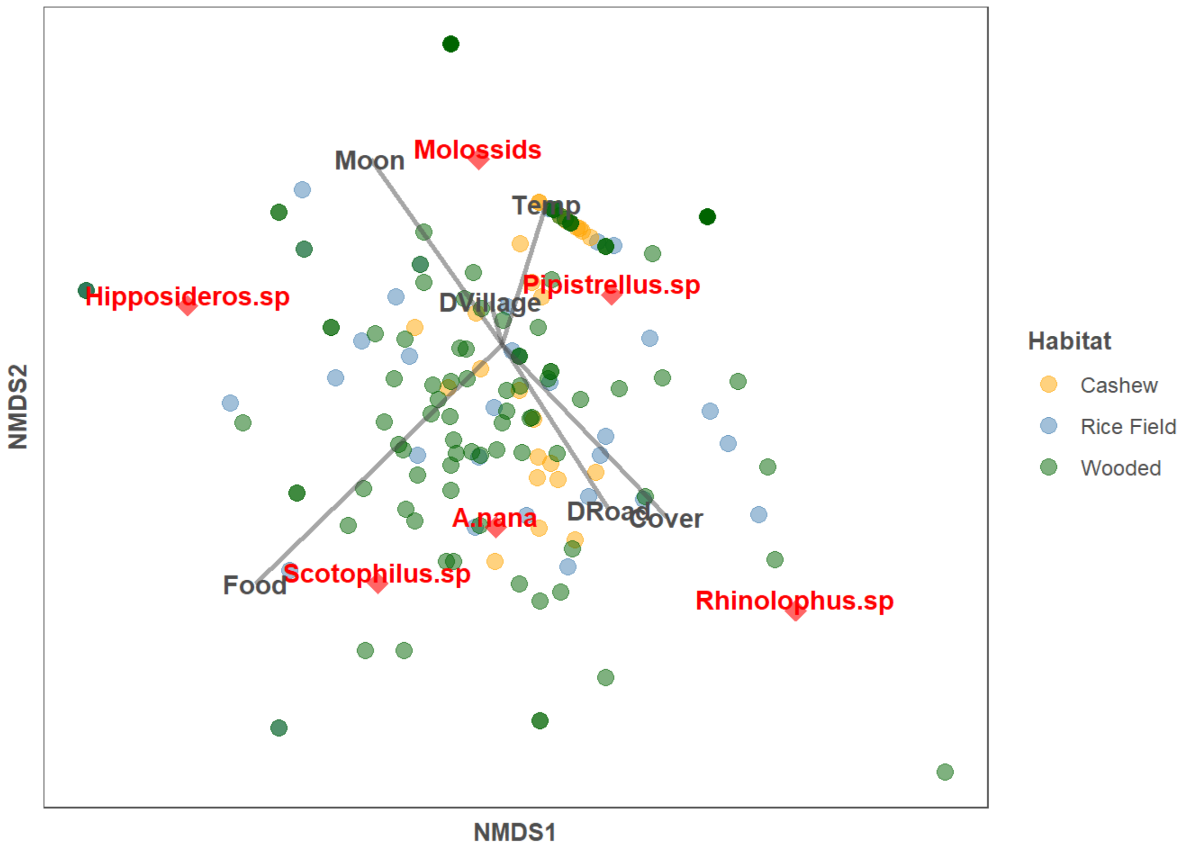


Figure 2: Weekly ordination of the different sampling points in an NMDS space based on Bray-Curtis dissimilarity of bat sonotypes composition. The circles represent the placement of sampling points, and the diamonds represent the placement of sonotypes within a multidimensional space. The landscape variables explaining differences in species composition between plots are represented as vectors and were fitted using the function envfit (R-package vegan).

The models showed that the lunar phase, moonrise, moonset, and temperature didn't influence bat activity, contrary to what was expected. Food availability positively influenced bat activity for almost all sonotypes and thus is a key factor determining bat activity (Figure 3). This was, in fact, the only significant driver of *Scotophilus sp.* activity. *Hipposideros sp.* showed higher activity over rice fields than in the other habitats. Distance to the nearest wooded area, distance to the nearest village, and food availability showed an expected influence on *A. nana* activity. The activity of this species decreased in sampling sites further away from wooded areas. Still, it increased with higher distances to the nearest roads and food availability.

Contrary to what we expected, *Rhinolophus sp.* activity increased the further away the sampling site was from wooded areas. However, the DHARMa analysis of the GLM assumptions showed that this model is not well-fitted, probably due to the low number of bat passes classified in this sonotype. *Pipistrellus sp.* activity was significantly higher in cashew orchards than in all other habitats. Total bat activity also showed higher activity in cashew orchards than in other habitats while being positively influenced by food availability. According to the models, none of the variables considered in the analysis affected *Molossids'* activity.

The DHARMa tests used to assess model quality showed that all models meet the required assumptions except for the GLM performed for *Rhinolophus sp*. This was probably due to the low number of bat passes detected for this genus (Figure 4).

Table 3: GLMM and GLM model output for each sonotype. No random variables and effects are presented for the *Rhinolophus*.sp model because this was fitted using a GLM. Habitat variables use Rice fields as reference. Variable acronyms and descriptions are summarized in Table 2.

Sonotype	**Random Variable**	**Random effect**	**Fixed Variable**	**Estimate**	**Std error**	**Pr**
Intercept				-0.603	0.356	0.089
Hipposideros.sp	Tabanca	0.092	Cashew	-1.005	0.491	0.040
			Wooded	-0.879	0.415	0.034
	Week	0.214	Fallow	-0.407	0.924	0.659
Intercept				-4.314	1.636	0.008
A.nana	Week	0.142	Food	1.200	0.466	0.010
			Dwood	-0.339	0.156	0.030
			DRoad	0.852	0.191	8.31e-06
Intercept				0.730	0.376	0.052
Pipistrellus.sp	Week	0.199	Cashew	1.364	0.334	4.41e-05
	Tabanca	0.365	Wooded	-0.092	0.306	0.764
Intercept				0.185	0.055	9.79e-04
Rhinolophus.sp	NA	NA	Dwood	0.046	0.020	0.023
Intercept				-4.458	0.995	7.49e-06
Scotophilus.sp	Week	0,276	Food	1,032	0,261	7.63e-05
	Tabanca	0,405				
Intercept				-0.052	0.964	0.956
Total	Week	1.293	Cashew	1.060	0.469	0.023
			Wooded	0.166	0.306	0.588
	Tabanca	0.471	Food	0.456	0.228	0.046

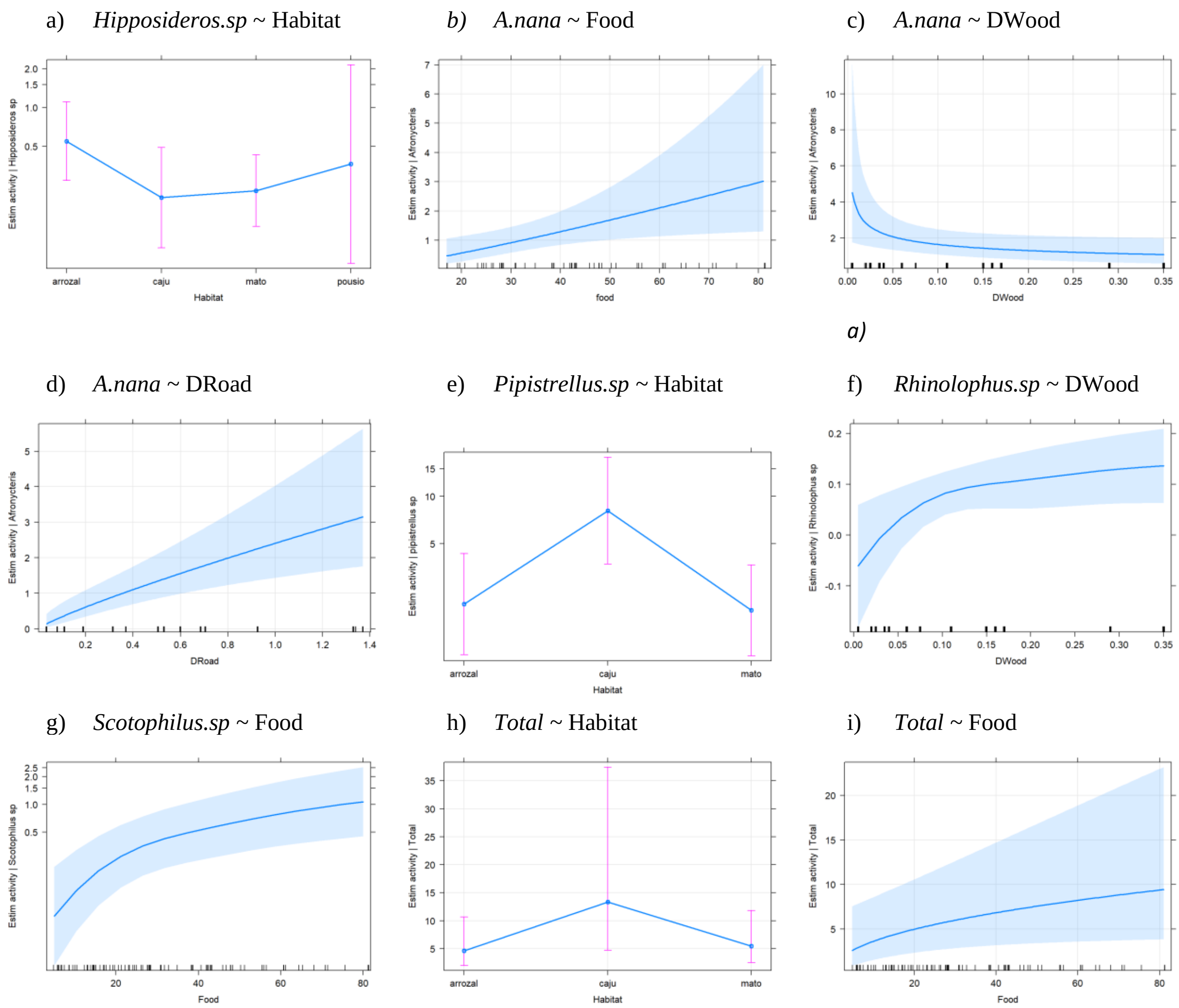
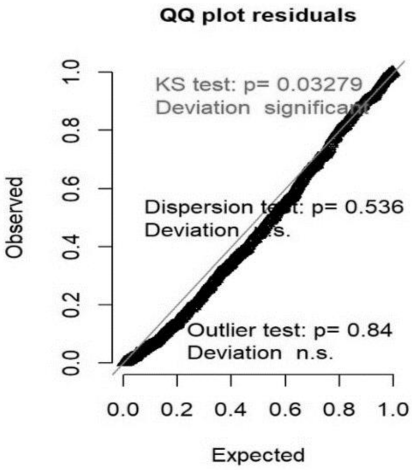
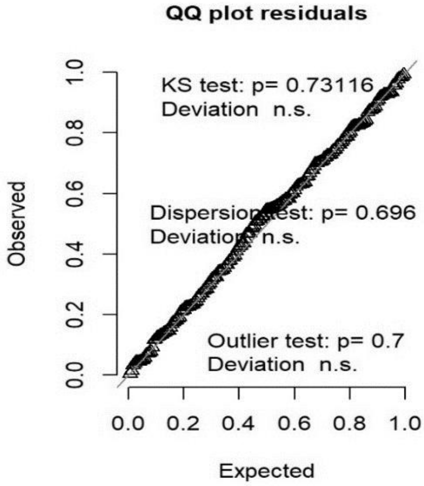


Figure 3: Model partial effects of significant variables for all sonotypes. The effect of continuous variables is positive except for the distance to the nearest wooded area for *A.nana*. Cashew orchards were the preferred dominant habitat for all sonotypes except for *Hipposideros* sp., which was rice fields.

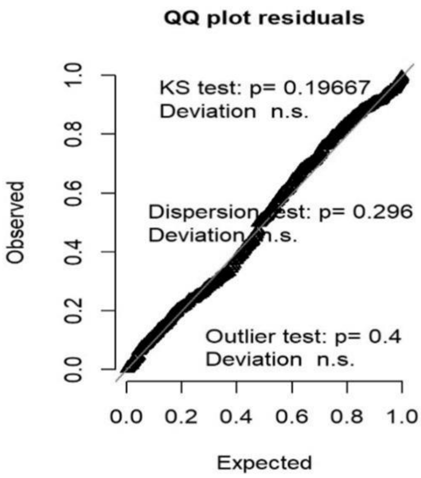
a) *Hipposideros.sp*



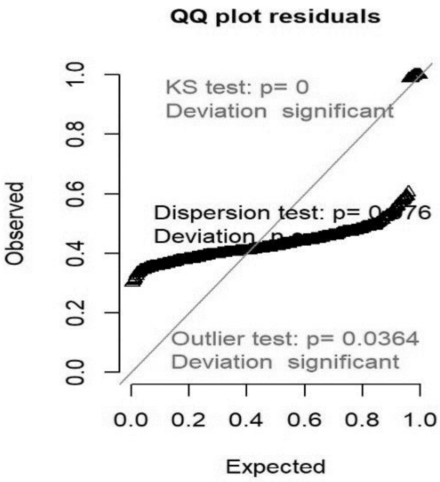
b) *A.nana*



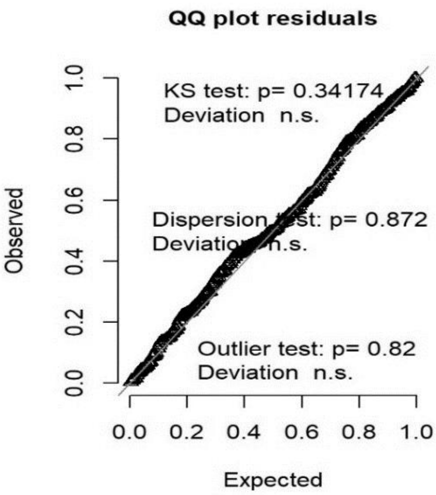
c) *Pipistrellus.sp*



d) *Rhinolophus.sp*



e) *Scotophilus.sp*



f) Total

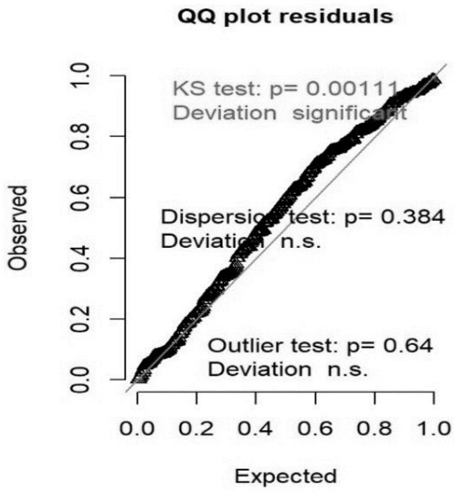


Figure 4: Model residual diagnostics - QQ plot residuals with KS test, dispersion test and outlier test, within group deviation from uniformity and test for homogeneity of variance for all performed models. All executed DHARMa tests corroborate the model's validity except for *Rhinolophus*.sp.

4. Discussion

The thorough analyses of the results indicate that although some proposed hypotheses were not confirmed, there is enough evidence showing that agricultural landscape characteristics influence overall bat activity. The predominant habitat surrounding sampling points, the distance to the nearest wooded area and the distance to the nearest road showed an influence on bat activity for some sonotypes, indicating that landscape characteristics can be adapted and changed to attract this group of natural pest suppressors. The results also show that, as expected, food availability significantly influences overall bat activity. Even though the composition of prey communities was not analyzed, variations in said composition could also have a differential influence on bat activity for different sonotypes. It is important to note that due to the lack of information on the bat calls of the region a more accurate bat pulse identification wasn't possible, with only one sonotype being identified to a species level. This information gap influenced some of the results since it is possible that some variables in study exercise a species-specific effect that may be concealed by grouping different species into sonotypes. Different species within the same sonotype may also have small differences in ecology that may influence the results.

4.1. Human structures in the landscape

Human infrastructure, such as roads or houses, can affect bat activity. Roads may increase bat mortality rates due to roadkill, and traffic lights can also disturb commuting bats (Stone *et al.*, 2015; Secco *et al.*, 2017). Roads can also reduce landscape permeability, leading to habitat loss and increasing habitat fragmentation (Bennett, 2017). In fact, although not the object of this study, roadkill mortality was reported and confirmed in the study area. Villages and roads are also a source of anthropogenic noise which may alter bat activity and echolocation calls (Bunkley *et al.*, 2015). Some houses and other buildings in villages can be used as roosting sites, benefiting some bat species in sub-tropical environments (López-Baucells *et al.*, 2017). Artificial light has the opposite effect, as it can negatively influence bat activity patterns (Stone *et al.*, 2009). However, this may not be the case since the assessed villages were poorly lit at night. These two variables, distance to the nearest road and distance to the nearest village, are highly correlated, as shown in the performed spearman correlation test. This correlation was somewhat predictable since all villages also have at least one road, so the effect of villages and houses may be disguised under the effect of the presence of roads. The hypothesis concerning the distance to the nearest road was confirmed in this study, although not equally amongst all sonotypes. In fact, the only sonotypes that showed an influence regarding this variable was *A.nana*, visibly increasing its activity with the distance to the nearest road. This influence was not detected for other sonotypes, possibly because a few sampling points were close enough to the roads for them to have an actual impact on bat activity. Another reason that may explain this result is that those roads, although tarred, do not have much traffic, especially during bat peak activity hours and thus reducing the expected negative impacts of disturbance due to traffic lights and higher mortality due to roadkill in the study area (Claireau *et al.*, 2019; de Figueiredo Ramalho *et al.*, 2021).

4.2. Landcover characteristics

Specific agricultural landscape characteristics may influence bat activity. Agricultural landscapes with dense networks of connecting elements, like wooded areas, may benefit overall bat activity (Heim *et al.*, 2015). Another proposed hypothesis regarding Molossids was that since bats from this family present long and narrow wings more adapted to fast straight flights (Voigt and Holderied, 2012), open-space habitats like broad rice fields and fallow fields would be a better suit for Molossids. Rice field width would thus show a positive influence on bat activity. However, this was not the case. In fact, this study did not detect any variable influencing *Molossidae* activity. This may be because this sonotype was the most detected in this study, with 2711 bat passes recorded, roughly 43 percent of all bat passes detected. Being the most common sonotype, they were represented in all sampling locations. Even though they showed a preference to forage in open spaces, bats from the *Molossidae* family also foraged above the canopies(Fenton & Rautenbach 1986; Denzinger & Schnitzler 2013), meaning that audiomoths located in the dense lower layers of wooded areas and cashew orchards detected Molossids foraging above the canopies of these habitats.

According to the proposed hypothesis, we expected that cluster-tolerant species from the *Rhinolophus* genus would be positively influenced by the presence of more natural wooded habitats since these species' wing morphology and echolocation makes them well adapted to forage in closed habitats like woodlands(Aldridge & Rautenbach 1987; Neuweiler 1989). However, this was not the case. In fact, the distance to the nearest wooded areas was the only variable showing any influence on *Rhinolophus* activity. Still, it was a positive influence, meaning that the furthest away from a wooded area the sampling point is, the more likely it was to detect a bat pass from this sonotype. Nevertheless, the DHARMa test performed to examine if the models follow the modelling assumptions showed that GLM for *Rhinolophus* did not meet such assumptions, failing the performed KS test and outlier test. Thus, this model's result should be considered with care. This is because there was a low number of bat passes detected from this sonotype (61), making it impossible to reach a good fit. The high frequencies used by the species of these genus makes them detectable only at a very close range (Stoffberg *et al.*, 2007). Its presence is thus often undersampled, particularly in wooded habitats where sound is quickly attenuated (Jacobs *et al.*, 2017). However, it must also be noted that another likely reason why this sonotype was not commonly found in this study may be related to the fact that clutter-tolerant species are more vulnerable to deforestation and habitat fragmentation since they lose preferable foraging habitats (Pavey, 1998). Since this study was performed in a highly fragmented landscape with a predominance of agricultural fields and dispersed secondary forest areas, it is possible that bats from *Rhinolophus* were not common in the study area due to sub-optimal habitat conditions and, thus, a conservation concern in the area.

This study also showed an unexpected preference in habitat selection, especially for *Pipistrellus.sp* sonotype and total bat activity. Both groups showed significantly more activity in cashew orchards than the other sampled habitats, while *Hipposideros.sp* showed a preference for rice fields. Habitat fragmentation and deforestation have a negative impact on biodiversity. Although highly vagile, bats are also negatively affected, showing less diversity and activity in agricultural landscapes than in natural habitats (Estrada *et al.*, 1993; Webala *et al.*, 2019; Weier *et al.*, 2021). *Hipposideros.sp* sonotype may be using all habitats as flight paths for commuting to foraging areas while showing a preference for open space habitats such as fallow fields or rice fields (Nkrumah *et al.*, 2016). Although there is little information regarding bat activity in cashew orchards, bats also act as ecological pest suppressors in similar habitats, such as macadamia orchards (Taylor *et al.*, 2018; Weier *et al.*, 2019). Such agro-ecosystems may be used by insectivorous bats as roosting sites (Musila *et al.*, 2022). A seasonal correlation between bat activity and prey abundance and composition (Taylor *et al.*, 2013; Weier *et al.*, 2018) may also explain the higher bat activity in cashew orchards compared to other considered habitats in the study area.

4.3. Food availability

Our hypothesis based on the available bibliography states that food availability would influence bat activity, flying patterns and diet composition (Ciechanowski *et al.*, 2007; Müller *et al.*, 2012). Bat communities adapt their diet to the composition of prey communities, which can change according to weather conditions (Fenton *et al.*, 1977; Fenton and Thomas, 1980). In some tropical areas, the observed decrease in bat activity is a consequence of insect community changes and a decline in abundance due to weather changes, specifically cold temperatures (Richards, 1989). As we predicted, the relative abundance of insects in the study area was a significant driver of bat activity. Our results indicate that food availability positively influenced the bat activity of *A.nana* and *Scotophilus sp*. In fact, it was the only detected variable influencing the activity of *Scotophilus sp.* Not only that, but food availability also positively influenced the total bat activity, with all species considered. Even though the composition of the prey community was not analyzed in this study, such composition likely influenced the studied sonotypes diet and flight patterns differently. It is clear that, as expected, the relative abundance of prey affects bat activity. Although not evident for all sonotypes, it is still likely that a more thorough analysis of prey community composition and variations through time would have shown an influence on bat activity and a diet adaptation for all sonotypes.

4.4. Environmental factors

Concerning the environmental variables, the models showed that temperature, lunar phase, moonrise, and moonset did not significantly influence bat activity for all sonotypes. Although it was expected that temperature would affect bat activity for some sonotypes (Appel et al. 2019a), the temperature variation in the study area may not be enough to show any influence on bat activity throughout the three months sampling period. However, temperature variations during the night can influence prey activity patterns and, thus, bat activity (Nkrumah *et al.*, 2017). However, we did not assess changes in bat activity during the night in this study. It was expected that the lunar phase would have a species-specific influence on bat activity of some sonotypes due to the adaptative behaviour of bats, reducing activity during bright moonlights to reduce predation risk, and because of the lower visibility of prey (Lang *et al.*, 2006; Appel *et al.*, 2017). However, this effect was not observed in this study. This may be due to the existing contradictory evidence regarding the effect of the lunar phase and lunar illumination on bat activity (Saldaña-Vázquez and Munguía-Rosas, 2013; Musila *et al.*, 2019). This supports the idea that there is no lunar influence on bat activity in the study area, or because a species-specific effect may be disguised in grouping bat species into sonotypes. Other environmental weather descriptors not considered in this study may directly or indirectly influence bat activity and thus may obscure the influence of the considered variables. High nebulosity may counter the effect of moonlight on bat activity. At the same time, rainfall is expected to negatively influence bat activity and change bat activity patterns (Erickson and West, 2002; Appel *et al.*, 2019b). Although most of the study was performed during the dry season, rainy nights were not uncommon, especially in October, which may help explain the lack of detectability of any influence of lunar phase, moonrise, and moonset in bat activity for all sonotypes.

4.5. Relevance to biodiversity conservation and human welfare

The primary objective of this study was to investigate the impact of agricultural landscape characteristics on the activity patterns of a group of natural pest suppressors to gather information that could aid in managing the farm landscape around rice fields. This research aimed to increase the attractiveness of the landscape for bats, which can potentially prey on rice pests, thereby increasing the yield of the rice fields. This study showed that landscape characteristics influence bat activity more than environmental variables such as temperature, lunar phases, and illumination over the last three months of rice production. Our study found that the predominant habitat surrounding sampling points, the distance to the nearest wooded area, and the distance to the nearest road significantly impacted bat activity for specific sonotypes. These findings suggest that when planning expansions or construction of new rice fields, it is crucial to consider the influence of adjacent habitats and human infrastructure on bat activity, specifically roads, to maximize their potential as natural pest suppressors in agricultural areas. Doing so may reduce the need for additional rice production through crop intensification or field expansions while potentially increasing overall crop yields.

The results of this study have also highlighted the importance of food availability in determining bat activity. The use of pesticides in these areas should thus be deterred. These agrochemicals can potentially reduce prey abundance and richness (Brittain *et al.*, 2010) while increasing bat mortality by intoxication and bio-accumulation (Torquetti *et al.*, 2021). It may be argued that pesticides have a similar action to bats – both controlling insect populations. However, most bats are opportunistic and prey on the most abundant insects (usually pests), controlling their populations (Kahnonitch *et al.*, 2018). Pesticides have an indiscriminate impact on all insects. Abundant insect species may benefit from pesticides as they quickly become resistant to their influence (Nighswander *et al.*, 2021). Future studies should consider the relative abundance of prey, the composition of insect communities, and their role in the diet and flying patterns of different bat sonotypes. Investigating the impact landscape characteristics and potential changes over time have on these insect communities and their composition is also essential. This will allow a more comprehensive understanding of the relationships between bats, insects, and the environment.

Not only indiscriminate pesticide use has a possible negative impact on insect and consequently bat communities, it also carries risk for human health (Chagnon *et al.*, 2015). Economically underdeveloped societies such as small farming communities in rural Africa are more at risk of suffering healthcare problems derived from pesticide use by being under-trained and using unsafe and unregulated pesticides, causing health problems in most farmers that regularly apply pesticides in their crops (Ngowi *et al.*, 2007; Oluwole and Cheke, 2009). Thus, the application of integrated pest management using ecological pest suppressors such as bats as an alternative to insecticides can also benefit health and overall wellbeing of rural farming communities. Bats also predate mosquitos that can cause direct harm to human populations transmitting several infectious diseases (Puig-Montserrat *et al.,* 2020).

It is also essential to consider the integration of local communities when planning the construction or expansion of new agricultural landscapes while having conservation goals in mind (Perfecto and Vandermeer, 2008). Changes in planning and execution of agricultural landscape expansion and construction that incorporate a conservation objective have many constraints, including funding, scientific support, policy coordination, and cooperation by local communities (Scherr and McNeely, 2008; Trimble and van Aarde, 2014). To effectively implement conservation measures that target human-made landscapes like rice fields is vital to consider the needs of the local communities, including cooperative decision-making and clear and open science communication. This type of agricultural landscape change is more easily implemented when the local communities are well informed of the benefits of such conservations actions regarding a potential increase in food availability and crop output (Fifanou *et al.*, 2011; Agula *et al.*, 2018) to implement any proposed conservation measures is necessary a strict cooperation and communication policy with the local farming community.

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