THE DRIVERS OF INSECTIVOROUS BAT COMMUNITY STRUCTURE IN A SOUTHERN AFRICAN SAVANNA

by

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Declaration

Declaration I, Lindokuhle Sherlyn Gumede, declare that this dissertation is my own original work and has not been submitted for any degree or examination at any other institution. All the sources that I have used or quoted have been indicated and acknowledged by means of complete references. I further declare that this work has been carried out by me during the period of study at the University of Mpumalanga, under the supervision of Prof. D.M. Parker and Prof. R.T.F. Bernard.

Signature: ____________________ Date: ________________________

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My sincere thanks go to the staff and management of MalaMala Game Reserve for granting access to the study area and for their logistical support during fieldwork. Special appreciation is extended to Keenan and Melissa for their assistance with field sampling, equipment setup, and data collection, often under challenging conditions.

This dissertation is lovingly dedicated to my late father, David Jeremia Gumede, whose wisdom, strength, and quiet encouragement have shaped the person I am today. Though you are no longer here to share this moment, I carry your lessons and love with me in every step. This achievement is as much yours as it is mine, and I hope I have made you proud.

Finally, I would like to thank me for believing in me.

Abstract

Insectivorous bats are critical components of savanna ecosystems, acting as natural pest controllers and sensitive bioindicators of environmental change. Their foraging ecology is closely linked to vegetation structure, water availability, and insect prey abundance, all of which are strongly shaped by the seasonal dynamics of savannas. However, despite their ecological importance, bat communities in African savannas remain understudied compared to other regions, leaving substantial gaps in our understanding of how key environmental drivers shape their diversity, activity, and species richness. My study was conducted in MalaMala Game Reserve, South Africa, during both the wet and dry seasons of 2021 and 2022, using acoustic monitoring of bats. The reserve, situated within the Greater Kruger National Park, provided an ideal natural landscape to examine how environmental variables may influence bat communities. Proximity to permanent water bodies, variation in vegetation structure, and seasonal changes in insect availability were found to significantly affect bat diversity and foraging activity. In addition, riparian corridors and structurally complex woodlands emerged as ecological hotspots, supporting higher bat richness, while areas further from permanent water displayed reduced diversity and activity. Seasonal differences further highlighted the role of rainfall driven insect emergence in shaping bat community dynamics. My findings highlight the ecological significance of landscape heterogeneity and water resources in maintaining bat biodiversity within African savannas. They further provide valuable baseline data for conservation and management in private reserves such as MalaMala, which are increasingly important for regional biodiversity persistence under changing climatic conditions.

Chapter 1: General introduction

Globally, subtropical savannas represent some of the most ecologically important and diverse terrestrial ecosystems, characterized by a combination of grasses, dispersed trees, and significant seasonal fluctuations (Scholes and Archer, 1997). These environments are influenced by the interaction of weather patterns, soil conditions, fire dynamics, and grazing, which all determine plant communities and overall ecological functionality (Scholes and Walker, 1993; Sankaran et al., 2005). Within savanna systems, insectivorous bats are essential animal components, providing important ecosystem services which include, but are not limited to, regulating insect populations and acting as bioindicators of environmental wellbeing (Jones et al., 2009).

The abundance, variety, and dynamics of bat communities in savannas are strongly shaped by environmental factors, especially natural vegetation structure, proximity to water sources, anthropogenic activities, seasonality, and insect prey availability (Monadjem and Reside, 2008; Jung et al., 2012; Korine et al., 2015). The structure of vegetation is crucial in influencing bat habitat suitability as it impacts roosting options, stability of the microclimate, and the geographic distribution of foraging resources (Taylor et al., 2012). In savanna ecosystems, the mosaic of open grasslands, various shrub layers, and woodland patches creates heterogeneous landscapes that support a diversity of bat species with varying ecological requirements (Monadjem and Reside, 2008). Structural complexity enhances edge effects promoting aerial insect abundance and enabling diverse bat foraging strategies that includes species that prefer cluttered habitats and those that prefer open space for feeding (Taylor et al., 2012). Thus, intact, heterogeneous vegetation is critical for sustaining and promoting bat activity and species richness (Jung et al., 2012).

Arthropods, which are the main food for insectivorous bats, are affected by various environmental factors like temperature, humidity, vegetation type, and proximity to water (Haddad et al., 2001). In savanna ecosystems, the diversity and numbers of insects usually peak in the wet season because the conditions support plant growth and reproduction (Shorrocks and Bates, 2015). However, temporary, or permanent water sources and proximal vegetation provide key habitat refuges for arthropods that help maintain arthropod populations during drier periods (Strayer, 2006; Samways et al., 2020). This complex relationship between bats and arthropods highlights the need to protect both land and water habitats in savanna ecosystems. Activities like dam building, draining wetlands, overusing water resources for livestock, and pollution can negatively affect aquatic arthropod populations and reduce the overall food supplies for bats (Vaughan et al., 1996; Bunn and Arthington, 2002; Korine et al., 2016, Mpanzeli et al., 2024).These reductions in food availability can negatively impact bat health, breeding success, and population stability (McCain, 2007). Therefore, changes in water levels or availability due to anthropogenic activities or seasonal shifts may create significant ripple effects throughout the food web (Korine et al., 2015).

Insectivorous bats are predators that rely on a wide arrangement of nocturnal arthropods, including Lepidoptera and Diptera (Clare et al., 2009). Seasonality plays a vital role in the distribution and abundance of these insect prey that are often strongly linked to vegetation type and productivity (Taylor et al., 2018). Arthropod communities are directly affected by changes in plant composition and structure, influencing prey diversity and biomass (Siemann et al., 1998; Haddad et al., 2001). Seasonal changes in rainfall and temperature have a significant impact on bat activity, mainly because they affect vegetation production is and how arthropods develop (Appel et al., 2019). Insectivorous bats are most active during the wet season, which aligns with a surge in insect populations and better foraging opportunities (Taylor et al., 2018, van der Meulen et al., 2025). Seasonal increases in precipitation enhance aquatic insect emergence and terrestrial arthropod abundance leading to elevated bat activity reproductive investment and foraging success (Haddaway and McGuire, 2022; Festa et al., 2023). In addition, fire (also routinely seasonal) plays a critical role in shaping savanna ecosystems (Bond and Keeley, 2005). Some bat species take advantage of areas that have recently burned, as these spots often have more insects available (Milne et al., 2005; Inkster-Draper et al., 2013). However, intense fires can harm roosting habitats and lessen the complexity of the environment (Fukui et al., 2008). As such, fire often interacts with seasonal changes and habitat structure to influence bat communities in both positive and negative ways (Fukui et al., 2008).

Water is another crucial ecological component which supports bats' hydration needs as well as those of their prey in arid and semi-arid savannas (Monadjem and Reside, 2008; Korine et al., 2015). Rivers, pans, and seasonal wetlands are examples of aquatic ecosystems that produce many aquatic arthropods, which are vital bat food sources (Vindigni et al., 2009). Many arthropods, like midges, mosquitoes, beetles, and moths either breed in or gather around water sources (Briers et al., 2002; Blaustein et al., 2004). Foraging near water is preferred by many bat species, especially during the dry season when terrestrial insects are scarce (Korine et al., 2015). Aquatic environments create structures and open airspace that help bats forage effectively in the air (Monadjem and Reside, 2008). Bat foraging activity and species richness are therefore often increased closer to water (Monadjem and Reside, 2008; Taylor et al., 2012; Korine et al., 2015).

Anthropogenic activities may also disturb savanna ecosystems, which poses direct and indirect threats to insectivorous bats (Mickleburgh et al., 2002, Mpandeli et al., 2024). Changes in habitat through agriculture, deforestation, and infrastructure development reduces roost and foraging habitat (Mickleburgh et al., 2002). Pesticide application diminishes arthropod prey abundance and introduces toxic substances into bat food webs (Bayat et al., 2014). Additionally, light and noise pollution may interfere with bat echolocation and navigation, indirectly affecting species that rely on clutter sensitive foraging strategies (Stone et al., 2015). These pressures contribute to declining bat populations and biodiversity loss across many regions (Mickleburgh et al., 2002).

Despite the crucial roles played by insectivorous bats in savannas (Kalka et al., 2008; Kunz et al., 2011), as a group they have not received adequate research attention in African subtropical savannas (Monadjem and Reside, 2008). Although previous studies have examined the impact of specific habitat features such as vegetation structure (Jung et al., 2012), water availability (Korine et al., 2015), and insect prey richness (Clare et al., 2009) on bat communities, there is a scarcity of integrated research that combines these variables to assess their collective influence on bats. My study seeks to fill this gap by examining how vegetation structure, water availability, prey abundance, fire regimes and anthropogenic factors influence bat species richness, diversity, and activity in an African subtropical savanna. I believe that the findings will enhance our understanding of the ecological needs of insectivorous bats and contribute to evidence-based conservation strategies and sustainable land management practices in these important ecosystems.

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Chapter 2: Study site

I conducted my study on MalaMala Game Reserve (MMGR) (133 km^2), South Africa, during the wet (January to March) and dry (June to August) seasons of 2021 and 2022. MalaMala Game Reserve is situated within the Sabi Sands Wildtuin-MalaMala-Sabi Game Reserve Complex and has an unfenced border with Kruger National Park (KNP) to the east, and is therefore part of the Greater Kruger National Park (>20 000 km^2) protected area. The Sabi Sand Game Reserve, which share the western boundary with the KNP and it is not fenced, is one of the oldest and most prestigious private conservation areas in South Africa. Established in 1948 by a group of pioneering landowners, the reserve represents a landmark in collaborative private conservation efforts in the country (Carruthers, 2008). Covering approximately 650 km^2, the reserve forms part of the Greater Limpopo Transfrontier Conservation Area, allowing for the free movement of wildlife between Sabi Sand and the adjacent KNP (Lindsey et al., 2017). The area is named after the Sand and Sabie Rivers, both of which traverse the reserve and provide critical water sources that sustain its diverse wildlife communities (Friedmann and Daly, 2004). Over the decades, the Sabi Sand has become renowned for its high densities of large predators, particularly leopards (*Panthera pardus*), and for its ecotourism model, which has contributed significantly to both conservation funding and local economies (Krüger, 2005). Annual rainfall in the area averages around 620 mm, with most rainfall occurring during the October-March wet season (Schulze, 2008). Wet season mean of monthly means approximately twenty-five degrees Celsius (temperature) and dry season mean of monthly means approximately twenty point three degrees Celsius (temperature)(MalaMala, n.d.).

MalaMala Game Reserve, established in 1929, is recognized as South Africa's oldest private Big Five game reserve and one of the earliest conservation areas managed under a photographic tourism model. Initially, the land was used for cattle grazing, and in 1926, following the National Parks Act, W.A. Campbell purchased the property and developed it for wildlife-based use, establishing a permanent camp in 1930 along the Sand River (MalaMala, n.d.). After Campbell's passing in 1962, his son Urban transitioned MalaMala into Africa's first dedicated photographic safari destination, marking a pioneering shift from consumptive to non-consumptive wildlife utilization (MalaMala, n.d.). In 1964, MalaMala Ranch (Pty) Ltd, under Michael Rattray, consolidated this conservation first ethos, introducing practices that continue today, including low visitor density and minimal ecological disturbance (MalaMala, n.d.)

An important turning point in MalaMala's history took a turn in 2013, when MalaMala's land was returned to the Nwandlamhari Communal Property Association (CPA) through South

Africa's land restitution programme, with a co-management agreement formalized in 2016 between the Rattray family and the CPA to ensure both conservation continuity and local community empowerment (MalaMala, n.d.). Today, MalaMala remains a cornerstone of the Greater Kruger ecosystem, sharing an unfenced 19 km boundary with KNP, which allows free wildlife movement and contributes significantly to the ecological integrity of the broader landscape (MalaMala, n.d.).

The vegetation of MalaMala (Figure 2.1) is classified as primarily a mixed *Combretum/Terminalia* woodland (granite lowveld), characterized by a mosaic of bushveld thickets, open savanna grassland, and riparian corridors along the Sand River, which bisects the reserve (Gertenbach, 1983). The geology of the MalaMala Game Reserve (Figure 2.2) is dominated by some of the oldest rocks on Earth, dating back over 3.5 billion years (Johnson et al., 2006). The basement rocks are primarily composed of granite and gneiss, with occasional gabbro intrusions, forming a stable and ancient foundation for the landscape (Schutte, 1986). Overlying these ancient rocks are Ecca Shales, formed approximately 200-300 million years ago during a period of wetter climatic conditions (Partridge and Maud, 1987). Subsequently, volcanic activity around 180 million years ago led to the deposition of basalt and rhyolite layers, adding further complexity to the area's geology (Johnson et al., 2006). The region's geological structure was later influenced by the break-up of the supercontinent Gondwanaland around 135 million years ago, which caused tilting and fracturing of the crust (Johnson et al., 2006).

The topography of the area reflects these ancient geological processes. Higher altitude regions, such as the nearby Malelane Mountains, consist of more erosion resistant rocks, standing prominently above the surrounding lowveld (Smith, 1993). This variation in terrain has shaped a mosaic of woodland savanna and dense riverine forests, with soils derived from the underlying rock types influencing vegetation patterns and habitat distribution (Cowling and Richardson, 1995).

A key feature shaped by the geology (Figure 2.2) is the Sand River, a perennial water source that flows through MalaMala, stretching over 20 km. The combination of ancient bedrock, sedimentary layers, volcanic deposits, and riverine processes has created fertile areas that support a diverse array of flora and fauna, making the reserve a biologically rich and ecologically important landscape (World Wildlife Fund, 2021).

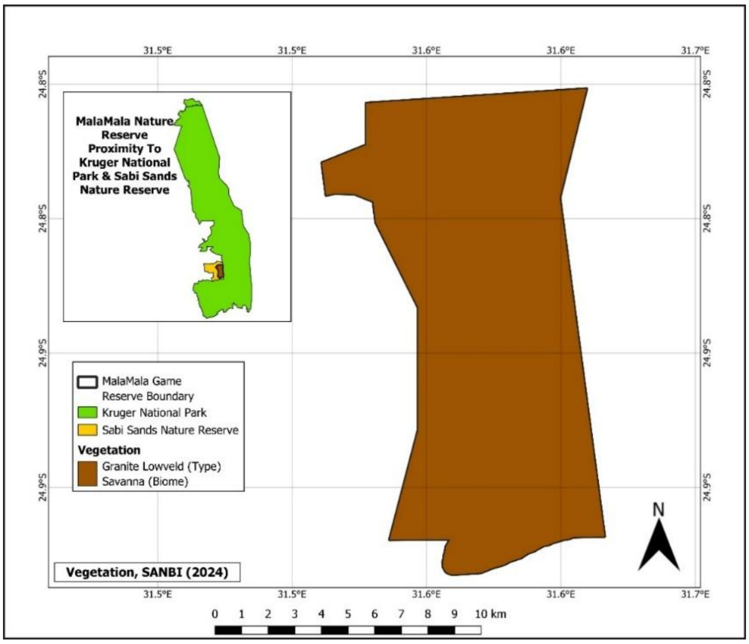

Figure 2.1: Location of MalaMala Game Reserve showing its boundary, dominant vegetation type (Granite Lowveld within the Savanna biome), and proximity to the Kruger National Park and Sabi Sands Nature Reserve. Vegetation data sourced from SANBI (2024).

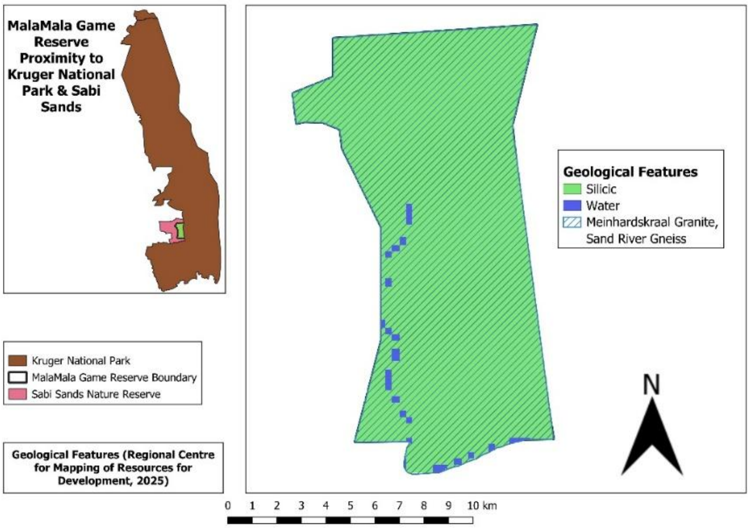

Figure 2.2: Location of MalaMala Game Reserve showing its boundary and geology type, and proximity to the Kruger National Park and Sabi Sands Nature Reserve. Vegetation data sourced from SANBI (2024).

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Chapter 3: Using acoustic monitoring to assess insectivorous bat richness and activity in a subtropical savanna

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Dissertation Author's contributions

My study contributes new bat species richness data from MalaMala Game Reserve, collected during the wet and dry season of 2021 and 2022, thereby filling temporal and ecological gaps in chiropteran research in the Lowveld. Furthermore, by contextualising these findings within the geology, conservation history, and ecological setting of MalaMala and the Sabi Sand Game Reserve, this research integrates biological and environmental perspectives, offering novel insights into how landscape history influences mammalian biodiversity.

I was responsible for part of the overall study design, including the formulation of research objectives and the selection of appropriate sampling protocols. I analysed all field data collected, which included the acoustic monitoring of bats, and the vegetation surveys. I carried out the data processing and statistical analyses, ensuring quality control and accuracy throughout. I interpreted the results within the ecological and conservation context of the study area, drawing links to broader scientific literature. Finally, I drafted the full manuscript and integrated feedback from my supervisors and co-authors, ensuring coherence in both the scientific argument and presentation.

Introduction

Bats, with over 1 500 species representing about 20 % of the world's extant mammals, play a crucial role in global ecosystems (Rocha et al., 2021; Bat Conservation International, 2025). Bats provide important ecosystem services by feeding on agricultural pests, mosquitoes, and other disease-carrying insects, while also contributing to pollination and the dispersal of seeds from numerous fruiting plants (Sieradzki and Mikkola, 2022). In some parts of the world, bats are a valuable food source, and their body parts are used in traditional medicine, while their guano is collected and used as agricultural fertilizer (Kunz et al., 2011). Insectivorous bats play essential roles in terrestrial food webs, serving as bioindicators of habitat change and providing ecosystem services such as regulating insect populations (Mtsetfwa et al., 2018; Roeleke et al., 2020). Almost all insect-eating bats are nocturnal, occupying various habitats where they feed on a diverse array of insects (Alviola et al., 2023). Their foraging behaviour is closely linked to insect activity, which is influenced by temperature, as arthropods are generally less active during colder conditions (Mellanby, 1939), leading bats to time their foraging to align with peak nocturnal insect activity (Alviola et al., 2023).

Even though 70 % of all bat species feed on arthropods and their interactions with arthropods populations are relatively well studied (Rydell, 2006), there remains a significant gap in understanding the conservation status of bats in Africa (Frick et al., 2020). This gap is concerning given the important ecosystem services provided by bats (Kunz et al., 2011). Additionally, basic information on many African bat species is lacking compared to their North American and European counterparts (Nelufule, 2019). The savanna biome, which dominates much of the African continent and comprises 54 % of South Africa's vegetation (Shapiro et al., 2020), is ecologically significant but often understudied and less protected compared to other vegetation types in the country. Savannas, with their diverse vegetative layers and river systems, are critical for promoting bat diversity, offering important foraging habitats, roosting sites, and abundant insect prey, especially in the warmer regions of southern Africa (Shapiro et al., 2020). For instance, the Pafuri region of the Kruger National Park, dominated by savanna vegetation, boasts the highest known bat diversity in South Africa (Rautenbach et al., 1985; Aldridge and Rautenbach, 1987 and Brinkley et al., 2021).

Bat foraging habitats, roost sites, and insect prey populations are highly sensitive to changes in land cover and land use (Shapiro et al., 2020). An east–west gradient in bat species richness is evident across southern Africa, with peak diversity recorded in northeastern South Africa, Namibia, and Zimbabwe, and reduced richness in the arid landscapes of South Africa and Botswana where environmental conditions limit prey resources and suitable habitats (Monadjem et al., 2018). Despite their relatively long lifespans and slow growth rates, anthropogenic habitat alterations continue to adversely affect bat community structures (Pierce, 2012). Threats such as habitat loss, fragmentation, and hunting for bushmeat are causing declines in bat populations across Africa (Pierce, 2012; Schoeman and Monadjem, 2018).

Cultural traditions and beliefs also significantly impact bat conservation. In Western cultures, bats are often seen as omens of ill luck, akin to owls and bush cats, and are frequently associated with vampires and evil spirits, contributing to negative perceptions and barriers to conservation (Sieradzki and Mikkola, 2022). Conversely, in the Asia-Pacific region, majority of people hold positive cultural values of bats, which supports efforts like ecotourism and bat cave visits (Tanalgo and Hughes, 2021). For example, the Montfort Bat Cave Sanctuary in the Philippines attracts tourists and supports local economies while prohibiting hunting (Carpenter et al., 2014). However, positive cultural values do not always align with conservation, as seen in China and India, where bats are both admired and hunted (Sieradzki and Mikkola, 2022). Addressing both positive and negative cultural associations and obtaining current ethnobiological data are essential for effective bat conservation efforts (Sieradzki and Mikkola, 2022).

Bats serve as an ideal model for investigating the impact of environmental changes on species distribution within habitats due to their high species diversity, well studied feeding habits, and sensitivity to environmental variations (Ngala et al., 2025). For instance, the availability, distribution, and quality of water significantly influence bat distributions, with water bodies acting as essential foraging and drinking sites (Korine et al., 2016; Laverty and Berger, 2020). Bat activity tends to be higher around water bodies, not only because these are critical drinking sources but also due to the abundance of insect prey in such areas (Taylor et al., 2020). On a global scale, climate warming, altered precipitation patterns, and disruptions in local stream hydrology are already impacting bat populations and species distributions (Adams and Hayes, 2008). Since most bat species need reliable water sources to compensate for daily water loss and many rely on water emergent insects for food (Vaughan et al., 1996; Grindal et al., 1999; Ciechanowski, 2002), increasing aridity is likely to lead to a decline in bat abundance and species richness as water sources dwindle.

Insectivorous bats can be classified into three major functional foraging groups: open-air, clutter-edge, and clutter foragers. Each group has distinct echolocation call patterns and wing morphology adapted to their specific foraging strategies (Barclay, 1985; Dezinger and Schnitzler, 2013). Open-air foragers hunt in open spaces and generally fly above any vegetation, possessing narrowband and low duty cycle echolocation calls (Dezinger and Schnitzler, 2013). They have long, narrow and pointed wings with high aspect ratios which allow them to reach high speeds (Dezinger and Schnitzler, 2013). Clutter-edge foragers on the other hand, hunt near and along vegetation edges. They navigate along the edges to avoid collisions and can distinguish insect echoes from vegetation echoes (Barclay, 1985Clutter-edge foraging bats produce mixed search-phase echolocation calls that consist of a shallow, narrowband modulated component followed by a broadband, steeply downward frequency-modulated signal (Dezinger and Schnitzler, 2013). Their wing morphology is characterised by moderate aspect ratios and wing loading, with rounded wing tips that facilitate slower flight in areas with surrounding vegetation or obstacles (Dezinger and Schnitzler, 2013). In contrast, clutter foraging bats typically hunt and capture insects within densely vegetated environments (Barclay, 1985). These species often emit constant frequency calls together with short, low duty-cycle frequency-modulated signals that assist with navigation and prey detection in complex habitats (Falk et al., 2014). Clutter specialists also possess short and broad wings, which improve manoeuvrability in such confined spaces (Barclay, 1985). Acoustic analysis of bat echolocation calls therefore provides an effective and non-invasive approach for surveying bat communities (Barclay, 1985).

In this study, I used seasonal acoustic monitoring to assess bat species richness and overall activity in a subtropical savanna. I hypothesized that bat activity would be highest in the warm, wet season when insect prey is most active and abundant (Pretorius et al., 2020). Additionally, I anticipated that bats from the open-air functional guild would be recorded most frequently due to their generally lower frequencies calls, which are more easily detected by acoustic recorders (Monadjem et al., 2017). I also expected bat activity to be higher near permanent water sources, given the important role of water as a resource for bats in arid and semi-arid environments (Taylor et al., 2020).

Methods

Data collection

Six song meter ultrasonic recorder (SM4BAT FS) (Wildlife Acoustics, Concord, MA, USA) were used to record insectivorous bat echolocation calls simultaneously for each season from the MalaMala Game Reserve (Figure 3.1) during my study. Each detector was powered by four D-cell batteries and stored data on two 64 GB SD cards. The detectors were housed in waterproof cases and equipped with Song Meter Ultrasonic Microphone (SMM-UI) highly sensitive, low-noise ultrasonic and weatherproof microphones. The detectors were configured to record ultrasonic sounds at a sampling rate of up to 384 kHz with a 16-bit resolution and were set to trigger recordings only for sounds exceeding 12 dB with a trigger frequency of 8 kHz (Parker, 2022). Detectors were mounted at 1.5 m above the ground with the microphones connected (Parker and Bernard, 2019) and programmed to record from sunset until dawn (Parker, 2022).

Sampling sites were selected based on their proximity to permanent water sources (Taylor et al., 2020), with three sites located within 500 m and three sites situated more than 3.5 km from such sources, as indicated on the MalaMala map (Figure 3.1). These sites were inspected on the ground before deploying the detectors (Figure 3.1). Each site was monitored for five consecutive nights in each season, specifically during periods of minimal lunar illumination (Mushabati et al., 2022), resulting in 30 sampling nights per treatment (near or far from water) per season.

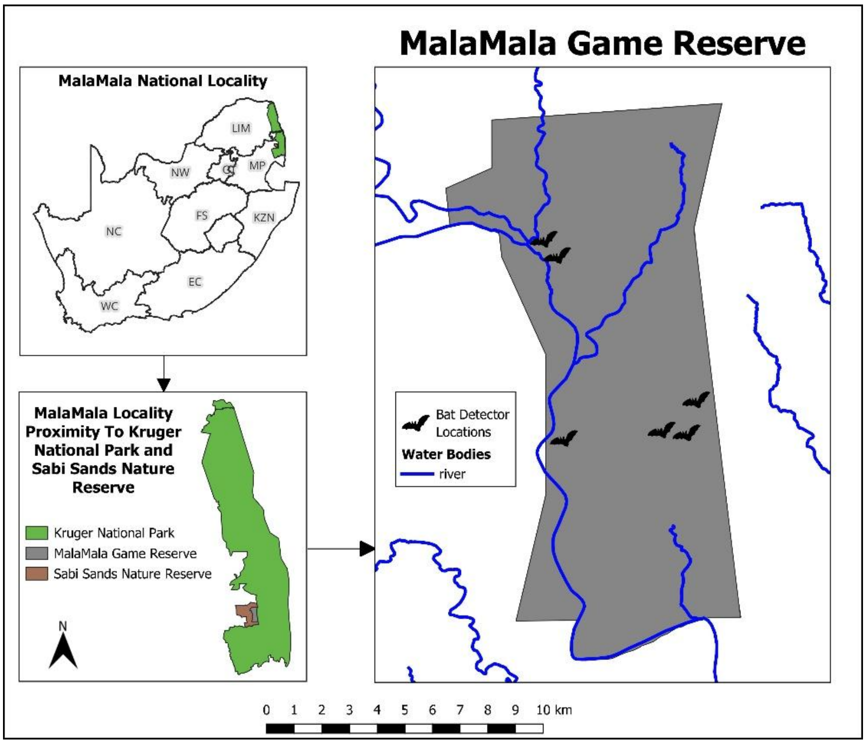

Figure 3.1: Study area map showing MalaMala Game Reserve within the Sabi Sand Nature Reserve and its position relative to Kruger National Park. The enlarged panel illustrates the Sand River and associated tributaries (blue) as well as the locations of acoustic detectors (black bat icons) used to monitor insectivorous bats.

For analysing and identifying bat calls, I used Kaleidoscope Pro Software version 5.4.9 (Wildlife Acoustics, Concord, MA, USA), which is designed for bat call identification (Parker and Bernard, 2019). The software utilizes built-in classifiers tailored to different global regions to automatically identify recordings. A KNP specific classifier developed by Brinkley et al. (2021), which was applicable to my study due to MalaMala's location within the same broad eco-region. Various aspects of the calls are considered by the classifier, such as duration (Dur), characteristic frequency (Fc), the minimum and maximum frequencies, and the call's frequency slope (Fk) (Parker and Bernard, 2018; Monadjem et al., 2020; Brinkley et al., 2021).

While Kaleidoscope efficiently filters and speeds up the identification process, it is not infallible (Rydell et al., 2017). Thus, I manually reviewed each bat call series post classification (Parker and Bernard, 2019; Brinkley et al., 2021). The classifier tool was primarily used to organize calls into clusters based on their characteristics, which were then further examined manually (Brinkley et al., 2021; Parker, 2022). Each bat call series within the resulting clusters was manually identified to species using a call reference library and existing published literature (Monadjem et al., 2020; Brinkley et al., 2021; Parker, 2022). Bat calls were identified to species level only if a sequence of at least three pulses was recorded to avoid errors due to noise, social calls, or insufficient data. Calls that could not be confidently identified were excluded. The manual identification process was conducted in three phases to minimize Type I errors (Parker and Bernard, 2019; Parker, 2022). In the first phase, calls were tentatively identified using known Fmin ranges for southern African bats. The second phase corroborated these identifications using known ranges of Fc or Fmax. Only calls that met the criteria of the first two phases proceeded to the final phase, where species assignments were confirmed with the known ranges of either Fmax or Fc (Parker and Bernard,2019; Parker, 2022).

Data analysis

To better interpret species richness at MalaMala, a rarefaction curve was constructed (Colwell et al., 2012). This approach models the relationship between the observed number of species (S(obs)) and sampling effort, represented by the number of survey nights (Gotelli and Colwell, 2001). The model presumes that as the number of sample nights increases, the number of newly observed species within the study area will decrease (Skalak et al., 2012). The *fossil* package in R version 4.4.1. (R Core Team, 2023), which stems from the EstimateS programme, was used to calculate species richness and various species richness estimators (Chao et al., 2000). Species richness is assessed by computing its mean and variance through repeated random sampling of the dataset, yielding the observed richness (S(obs)) along with ICE and ACE estimates (Gotelli and Colwell, 2001). S(obs) is the calculated species richness from the observed data, while ICE, derived from incidence data and ACE, derived from abundance data, estimate the sampling efficiency to infer species richness within the study area (Chao et al., 2000; Gotelli and Colwell, 2001). When an asymptote across the two estimators and the S(obs) is reached, sufficient sampling is achieved (Colwell et al., 2012).

To investigate the effects of season and distance from permanent water on bat species richness and activity (number of passes), I performed a two-way Analysis of Variance (ANOVA) using R. The ANOVA model included season (with levels "wet" and "dry") and distance (with levels "far" and "near") as fixed factors, and species richness as the dependent variable. The interaction between season and distance was also included in the model. Prior to conducting the ANOVA, data were checked for normality and homogeneity of variances using Shapiro-Wilk and Levene's tests, respectively. No significant deviations from these assumptions were detected for the species richness data. However, the number of passes had to be log transformed prior to analysis to satisfy the assumptions.

Results

Sampling completeness

The interpolated species richness, ACE and ICE values for my initial sampling during the wet season of 2021 are shown in Figure 3.2. Since the 95 % confidence intervals (error bars) of the observed species richness S(obs) and the two estimators overlapped after replicate two, and an asymptote was clearly reached between S(obs) and the two estimators after replicate four, sampling was deemed adequate after five nights (Figure 3.2) (Chao et al., 2000).

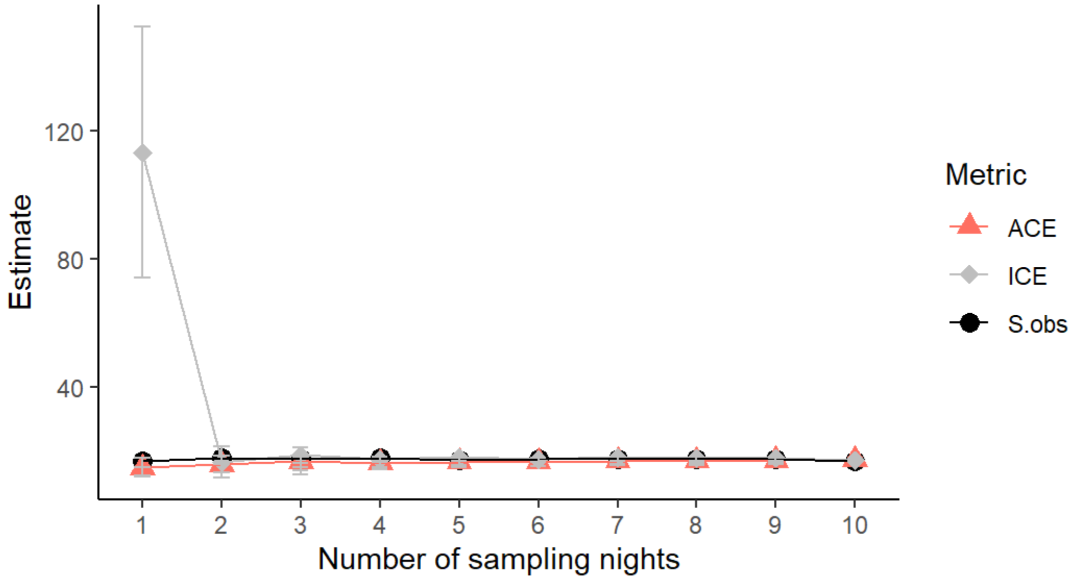

Figure 3.2: Species accumulation curve for the bat acoustic data collection in March 2021 from MalaMala Game Reserve, South Africa. S(obs) is the observed data and ACE (Abundance Coverage Estimator), and ICE (Incidence Coverage Estimator) are the two species richness estimators, error bars represent 95 % confidence intervals.

Bat species richness and activity

A total of 18 669 identifiable bat passes were recorded during wet and dry seasons in MalaMala Private Game Reserve in 2021 and 2022 (Table 1). A total of six families were recorded across the six sites which included Emballonuridae, Hipposideridae, Miniopteridae, Molossidae, Rhinolophidae and Vespertilionidae (Table 1). Within the six families identified, a total of sixteen putative bat species were identified (Table 1). Four species from the family Molossidae dominated the calls recorded (*Mops ansorgei, Mop condylurus, Mops midas* and *Tadarida aegyptiaca.*). In addition, the wet season had the greatest number of echolocation calls recorded (15 474). By comparison, far fewer calls were recorded in the dry season (3 195) (Table 1). *Hipposideros caffer, Rhinolophus acrotis, Rhinolophus simulator, Rhinolophus darlingi, Pipistrellus rusticus* and *Myotis tricolor* were only recorded during the wet season (Table 1).

Most echolocation calls were from open-air foraging bats (13 263 calls), primarily within the Molossidae and Emballonuridae families. Clutter-edge foraging bats were recorded 4 898 times (Vespertilionidae and Miniopteridae), while clutter foraging bats (Rhinolophidae and Hipposideridae) were the least frequently recorded (Table 1).

Table 1: Putative bat species, their associated family and foraging category (Ce = Clutter-edge; Cl = Clutter; Oa = Open-air) recorded during dry and wet seasons of 2021 and 2022 at MalaMala Private Game Reserve, South Africa. Detections = #echolocation call sequences/passes.

Family	**Species**	**Foraging category**	**Seasonal detections**		**Total detections**
			Dry	**Wet**	
Emballonuridae	*Taphozous mauritianus*	Oa	45	507	522
Hipposideridae	*Hipposideros caffer*	Cl	-	1	1
Miniopteridae	*Miniopterus natalensis*	Ce	73	391	464
Molossidae	*Mop condylurus*	Oa	371	4300	4671
	Mops midas	Oa	584	702	1286
	Mops ansorgei	Oa	696	782	1478
	Tadarida aegyptiaca	Oa	703	4573	5276
Rhinolophidae	*Rhinolophus simulator*	Cl	-	9	9
	Rhinolophus smithersi	Cl	131	361	492
	Rhinolophus darlingi	Cl	-	5	5
	Rhinolophus clivosus	Cl	-	1	1
Vespertilionidae	*Myotis tricolor*	Ce	-	2	2
	Laephotis capensis	Ce	260	2337	2597
	Neoromicia zuluensis	Ce	275	1275	1550
	Pipistrellus rusticus	Ce	-	2	2
	Scotophilus dinganii	Ce	57	226	283
	Total	**-**	**3 195**	**15 474**	**18 669**
	Number of species	**-**	**10**	**16**	**16**

The ANOVA results indicated significant main effects of both season ($F_{(1,56)} = 14.54$, $P < 0.01$) and distance to permanent water ($F_{(1,56)} = 18.50$, $P < 0.0001$) on bat species richness (Figure 3A). Bat species richness was significantly higher in the wet season compared to the dry season, and this effect tended to be more pronounced for sites nearer to permanent water (Figure 3.3A). The number of bat echolocation sequences (or passes) were also significantly affected by season ($F_{(1,56)} = 58.11$, $P < 0.0001$) and distance to permanent water ($F_{(1,56)} = 52.04$, $P < 0.0001$) (Figure 3B). Additionally, there was a significant interaction effect between season and distance to water ($F_{(1,56)} = 4.76$, $P < 0.05$). These results suggest that the influence of distance to water on the number of echolocation passes varies depending on the season, which means that distance to permanent water has an impact on echolocation activity and was season dependantThe number of passes was significantly higher in the wet season compared to the dry season, and this effect was most pronounced for sites closer to permanent water (Figure 3.3B).

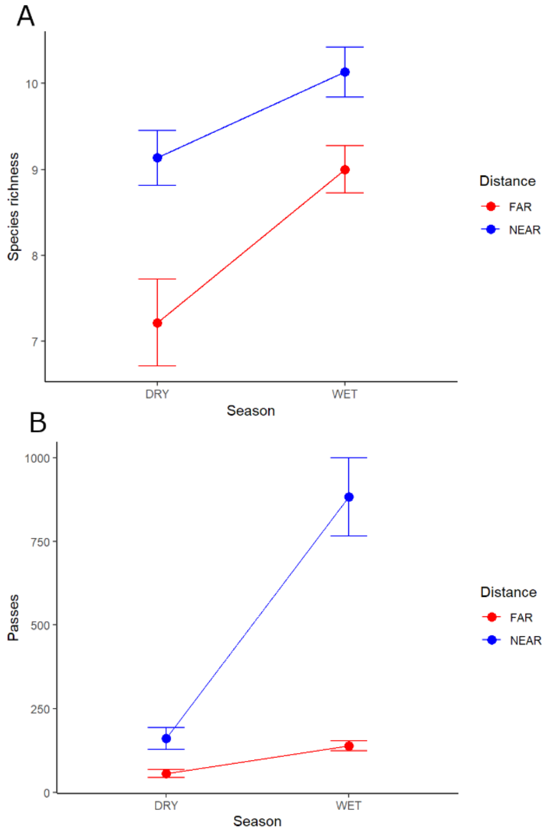

Figure 3.3: The effects of season (wet and dry) and distance to permanent water (near or far) on insectivorous bat species richness (A) and bat activity (# echolocation call sequences or passes) at MalaMala Game Reserve, South Africa. Data are means±se.

Discussion

Free-tailed bats (Molossidae), represented by 135 species in seven genera, dominate the southern African region (Ammerman et al., 2012) due to seasonal abundance of insect prey (Taylor et al., 2012). Historically, surveys conducted between 1960 and 1990 recorded 40 bat species in the northern regions of KNP (Rautenbach et al., 1985; Monadjem et al., 2020). However, more recent studies, such as Brinkley et al. (2021) have reported a much lower number of species, with only 27 identified. The southern region of KNP had not been previously studied for bats. Among these, the Vespertilionidae family was the second-most abundant, with 4 432 calls recorded. As the largest insectivorous bat family in southern Africa, Vespertilionidae includes approximately 19 species known to occur in KNP (Brinkley et al., 2021). Vespertilionids are characterized as clutter-edge foragers, navigating between open and dense vegetation (Ammerman et al., 2012). Given the generally heterogeneous nature of savanna habitats (i.e., a mosaic of trees, shrubs, and grasses) (Parker et al., 2023), the high abundance of Vespertilionids in my study is somewhat unsurprising (Sandor et al., 2019).

The Hipposideridae family recorded the fewest calls compared to the other families in my study. Among the families recorded in KNP, Hipposideridae is the smallest with only two species recorded, and species within this family typically forage within dense vegetation (Pavey et al., 2001). These bats emit very high frequency echolocation calls, ranging between 66 and 208 kHz, which attenuate rapidly over short distances (Thiagavel et al., 2017; Monadjem et al., 2017). Consequently, their calls can be challenging for acoustic detectors to capture (Monadjem et al., 2017). This difficulty may have contributed to the lower number of recorded calls for Hipposideridae in my study, which relied solely on acoustic methods to assess bat species richness and activity.

Bat activity differs between clutter-edge and open-air habitats due to differences in wing morphology, echolocating strategies, and flight behaviour (Jung and Threlfall, 2018). Clutter-edge foragers typically exploit structurally complex environments such as riparian corridors and savanna tree lines where insect prey accumulates. Clutter-edge species emit broadband frequency modulated calls that allow precise navigation and prey detection near vegetation (Schnitzler and Kalko, 2001). Whereas open-foragers are adapted to forage above canopy and typically have long, narrow wings and produce low frequency, narrowband echolocation calls that allow prey detection at greater distances in uncluttered airspace (Dezinger and Schnizler, 2013). As a result habitat structure influences bat activity patterns (Cory-Toussaint and Taylor, 2022). To minimize false positives, manual identifications of bat calls were required in addition to using the kaleidoscope cluster tool (Brinkley et al., 2021). Despite grouping calls based on their call characteristics (Brinkley et al., 2021), some species may have still been misidentified due to similarities in call traits (Brinkley et al, 2021). For example, *Laephotis capensis* and *Myotis tricolor* have similar call frequencies and durations (De Jong et al., 2024). *Taphozorous mauritianus*, *Mops pumilus* and *Rhinolophus darlingi* also exhibit overlapping frequency ranges, though *T. mauritianus* can be distinguished from *M. pumilus* by its broader call bandwidth and slightly longer duration (De Jong et al., 2024). Additionally, *Rhinolophus darlingi*, like all other Rhinolophid species, emits a distinct constant frequency call that is generally of longer duration than the other two species (Monadjem et al., 2020). Nevertheless, there is a possibility that some insectivorous bats were misidentified in my study (Nelufule, 2019). However, such misidentifications were likely minimized by using a call reference collection, published data and an overall conservative approach to the identifications (Reinhold et al., 2001).

Kaleidoscope software may also be limited to the species included in its original classifier tool, potentially leading to misidentifications or the classification of unlisted species as unknowns, further reinforcing the importance of manual identifications (Monadjem et al., 2020). Acoustic detections rely on ultrasonic bat detectors to monitor insectivorous bat echolocation calls (Brinkley et al., 2021). Acoustic detection has demonstrated significant advantages over traditional capture methods for identifying insectivorous bats (Monadjem et al., 2020). Specifically, detectors can be deployed across diverse locations and can record more species than traditional capture methods (Monadjem et al., 2020). Additionally, detectors minimize disturbances since they do not involve handling the species. However, a comprehensive library of authenticated calls is essential to accurately describe the echolocation call characteristics of each species in an area (Brinkley et al., 2021). Consequently, it may be more appropriate in certain scenarios to use a combination of live capture and acoustic sampling to ensure survey completeness (De Jong et al., 2024).

In my 2021 and 2022 survey at MalaMala, species abundance and activity increased significantly during the wet season (January to March) compared to the dry season (August). This seasonal pattern aligns with peak insectivorous bat activity during the wet season due to heightened insect abundance (Taylor et al., 2012). Additionally, reduced thermoregulatory costs during the warmer wet season may contribute to increased bat activity (Parker and Bernard, 2019). Such seasonal responses in bat activity are well documented across various regions (Monadjem and Reside, 2008; Mendes et al., 2017; Mtsetfwa et al., 2018; Nelufule, 2019; Parker and Bernard, 2019). The wet seasons abundance of insect prey and water (Fukui et al., 2006; Hagen and Sabo, 2012), likely alleviates constraints related to landscape composition and resource availability, highlighting the critical role of seasonal resource availability in shaping bat activity patterns.

Water availability supports bat survival and diversity by offering essential resources such as food and drinking water (Adams and Hayes, 2008; Monadjem and Reside, 2008; Adams, 2010). This is particularly important in savannas, where water availability may belower compared to other tropical biomes and may drive bat movement and activity across the landscape (Monadjem et al., 2017). Artificial water sources, such as dams and canals in human altered landscapes, can be crucial for supporting bat populations in these environments (Monadjem et al., 2017). Overall, my findings underscore the critical role of water and seasonal resource availability in shaping bat activity patterns, aligning with broader patterns observed in bat ecology across different regions and biomes.

The increasing interest in bat research has spurred public awareness and concern for their conservation (Fenton, 1997; Monadjem et al., 2018). However, bats are notoriously difficult to capture and survey, leading to limited knowledge about them, particularly in southern Africa (Howard et al., 2022). The advent of ultrasonic detectors has significantly improved the study of bat echolocation calls, greatly enhancing conservation efforts (Shoeman and Monadjem, 2018; Howard et al., 2022).

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Chapter 4: Riparian lifelines: How water and vegetation structure bat communities in a subtropical savanna

Introduction

Subtropical savannas, characterized by a mosaic of grasslands and scattered trees, represent ecologically complex biomes where bat diversity and activity are influenced by multiple interacting environmental factors such as climate and edaphic conditions (Zeng et al., 2014; Shapiro et al., 2020). In southern Africa, savannas are ecologically vital, supporting exceptional faunal and floral diversity, driving nutrient cycling, and sustaining a large and growing human population (Solbrig et al., 1996; Shackleton et al., 2007; Wang et al., 2009; Shorrocks and Bates, 2015).

Bats play a central role in maintaining ecosystem health and function through a range of ecological services, including pollination, seed dispersal, and insect pest suppression (Jones et al., 2009; Kunz et al., 2011; Ramírez-Fráncel et al., 2022). Their evolutionary and ecological diversity allows them to occupy nearly all trophic levels, from primary to tertiary consumers (Monadjem et al., 2018). In tropical and subtropical regions, bats contribute substantially to crop pollination and seed dispersal (Fleming and Geiselman, 2009), and in South Africa, insectivorous bats help suppress populations of crop pests, such as stink bugs (*Nevda viridula* and *Bathycoelia distincta*) in macadamia (*Macadamia integrifolia*) and litchi (*Litchi chinensis*) orchards, thereby enhancing yields (Taylor et al., 2018; Mphethe et al., 2025). In African savanna ecosystems, bats often form species-rich and abundant assemblages (Fenton, 1998; Herkt et al., 2016; Gumede et al., 2025) and serve as effective indicators of ecosystem health, reflecting the impacts of environmental stressors on broader ecological communities (Vaughan et al., 1996; Rocha et al., 2021).

Research from diverse ecosystems consistently shows that bat community composition, diversity, and functional traits are shaped by a combination of habitat structure, roost availability, resource distribution, and climatic gradients (Medellín et al., 2000; Estrada-Villegas et al., 2012; Raposeira et al., 2023; Russo et al., 2024). These factors interact across spatial and temporal scales, leading to dynamic and context-dependent bat assemblages. For example, in tropical rainforests, bat abundance and diversity are closely tied to forest structure, which determines both roost availability and foraging opportunities (Norberg and Rayner, 1987). In more arid regions, water availability exerts a stronger influence on community composition, with species showing behavioural and physiological adaptations to maximize use of ephemeral water sources (Kunz et al., 2011; Gumede et al., 2025).

Arthropods play a fundamental role in terrestrial ecosystems such as savannas by contributing to ecological processes including pollination and decomposition, while also serving as an important prey base for many bat species (Kunz and Fenton, 2005). Insect activity patterns, driven by temperature, humidity, and seasonality, fluctuate considerably among habitats and climatic zones (Johnson, 2008). Because bats are highly specialized insect predators (Kunz and Fenton, 2005) that rely on echolocation (Jones et al., 2009), their foraging behaviour, closely linked to morphology and echolocation ability (Gumede et al., 2025), is tightly coupled to insect abundance and temporal availability (Kalka and Kalko, 2006). However, prey abundance alone does not fully explain variation in bat assemblages. For instance, increased vegetation clutter negatively affected overall bat diversity in an Amazonian savanna (Carvalho et al., 2023), whereas in southern African savannas, diversity is often enhanced near perennial water sources and riparian vegetation (Monadjem and Reside, 2008; Nelufule et al., 2020; Gumede et al., 2025).

While prey abundance promotes bat occurrence, vegetation characteristics and clutter also influence occupancy and foraging success, though clutter alone rarely explains occupancy patterns (Bender et al., 2021). Vegetation structure affects foraging efficiency by shaping prey availability, flight space, and hunting opportunities suited to different species (Schnitzler and Kalko, 2001). Dense vegetation may hinder prey detection and capture, favouring manoeuvrable or clutter-tolerant species while excluding others (Denzinger and Schnitzler, 2013).

My study aimed to investigate how key environmental variables, namely natural vegetation cover and productivity, proximity to water, seasonality and insect availability and richness, affect bat species richness, activity, and diversity within a subtropical savanna ecosystem. I hypothesized that bat richness, activity, and diversity would increase with higher insect abundance and richness (Put et al., 2018) and closer proximity to water sources during the wet season (Nelufule et al., 2020; Puelles-Escobar and Muñoz-Sáez, 2024; Gumede et al., 2025), whereas increased woody cover would negatively influence these metrics (Carvalho et al., 2023).

Methods

Study site

This study was conducted at MalaMala Game Reserve (133 km^2) in northeastern South Africa during both the wet season (January–March) and dry season (June–August) of 2022 (Figure 4.1). MalaMala forms part of the Sabi Sands–MalaMala–Sabi Game Reserve Complex and shares an unfenced eastern boundary with Kruger National Park (KNP). As a component of the Greater Kruger National Park protected area (>20,000 km^2), the reserve contributes to a broader conservation landscape that enables free movement of wildlife between protected areas (Fisher et al., 2014). Furthermore, MalaMala lies within the Greater Limpopo Transfrontier Conservation Area, a large transboundary conservation initiative designed to enhance ecological connectivity across the region.

Vegetation within the reserve is primarily classified as mixed *Combretum-Terminalia* woodland characteristic of the granite lowveld, consisting of a heterogeneous mosaic of bushveld thickets, open savanna grasslands, and riparian habitats associated with the Sand River, which runs through the reserve (Gertenbach, 1983). The geology of the area is dominated by ancient granitic and gneissic formations, among the oldest rock systems on Earth, with occasional gabbro intrusions contributing to the area's varied landscape structure (Armstrong, 1982; Johnson et al., 2006). Climatically, the region receives an average annual rainfall of approximately 620 mm, with most precipitation occurring during the summer months between October and March. Twenty-five point three degrees Celsius during the wet season and twenty point three degrees Celsius in the dry season (Figure 4.2; MalaMala, n.d.).

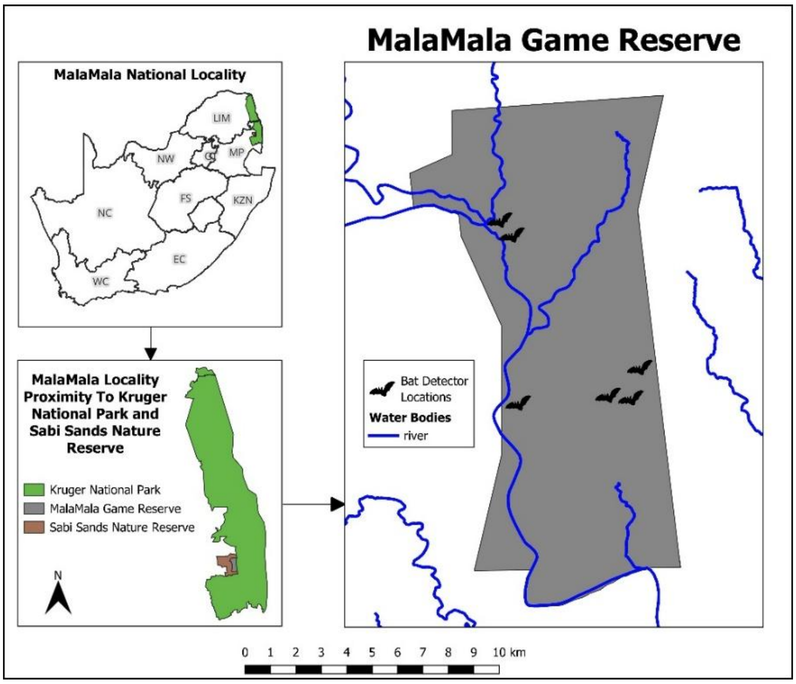

Figure 4.1: Study area map showing MalaMala Game Reserve within the Sabi Sand Nature Reserve and its position relative to Kruger National Park. The enlarged panel illustrates the Sand River and associated tributaries (blue) as well as the locations of acoustic detectors (black bat icons) used to monitor insectivorous bats.

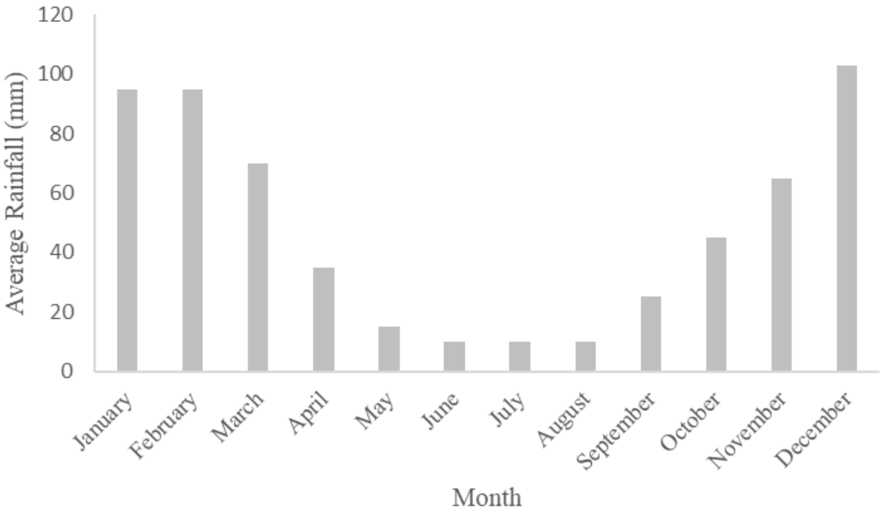

Figure 4.2: Average monthly rainfall (mm) recorded for MalaMala Game Reserve in 2022, illustrating the pronounced wet season with peak rainfall during January-February, and the dry season characterised by minimal precipitation

Data collection

Sample site selection

Sampling sites were selected based on their proximity to permanent water sources following methods of Taylor et al., (2020), with three sites located within 500 m and three sites situated more than 3.5 km from such sources (Figure 4.1). These sites were inspected on the ground before deploying the detectors and each site was monitored for five consecutive nights in each season (Gumede et al., 2025), specifically during periods of minimal lunar illumination (Mushabati et al., 2022), resulting in 30 sampling nights per treatment (close or far from water) per season.

Bat Acoustic Monitoring

Six song meter ultrasonic recorder (SM4BAT FS) song meter detectors (Wildlife Acoustics, Concord, MA, USA) were used to record insectivorous bat echolocation calls from the MalaMala Game Reserve during our study. Each detector was powered by four D-cell batteries and stored data on two 64 GB SD cards. Each detector was inspected on the final day of each sampling period throughout the study to ensure proper functioning and verify settings. No equipment malfunctions were encountered during the study period. However, in the event of a malfunction, the unit would have been reset at the next scheduled visit. Any incomplete recording nights would be excluded from the analysis to prevent potential bias. The detectors were housed in waterproof cases and equipped with Song Meter Ultrasonic Microphone (SMM-UI) highly sensitive, low-noise ultrasonic and weatherproof microphones. Recorders were programmed to capture ultrasound at sampling rates of up to 384 kHz with 16-bit sample resolution, and to initiate recording only when sounds above 12 dB with a trigger frequency of 8 kHz were detected (Parker, 2022). Detectors were mounted at 1,5 m above the ground with the microphones connected (Parker and Bernard, 2018) and programmed to record from sunset until dawn (Parker, 2022).

Bat Acoustic Analysis

For analysing and identifying bat calls, I used Kaleidoscope Pro Software version 5.4.9 (Wildlife Acoustics, Concord, MA, USA), which is designed for bat call identification (Parker and Bernard, 2018). The software utilizes built-in classifiers tailored to different global regions to automatically identify recordings. A KNP-specific classifier developed by Brinkley et al., (2021), which was applicable to our study due to MalaMala's location within the same broad eco-region. The classifier evaluates multiple features of bat calls, including call duration (Dur), characteristic frequency (Fc), minimum and maximum call frequencies (Fmin and Fmax), and the frequency slope (Fk) (Parker and Bernard, 2018; Monadjem et al., 2020; Brinkley et al., 2021).

While Kaleidoscope efficiently filters and speeds up the identification process, it is not infallible (Rydell et al., 2017). Thus, we manually reviewed each bat call series post-classification (Parker and Bernard, 2018; Brinkley et al., 2021). The classifier tool was primarily used to organize calls into clusters based on their characteristics, which were then further examined manually (Brinkley et al., 2021; Parker, 2022). Bat call series within the resulting clusters were manually identified to species level using a call reference library and relevant published literature (Monadjem et al., 2020; Brinkley et al., 2021; Parker, 2022). Bat calls were assigned to species only when a sequence containing at least three pulses was recorded, in order to minimise misidentification caused by background noise, social calls, or limited acoustic information. Recordings that could not be identified with confidence were excluded from the analysis. The manual identification process was conducted in three phases to minimize errors (Parker and Bernard, 2018; Parker, 2022). In the first phase, calls were tentatively identified using known Fmin ranges for southern African bats. The second phase corroborated these identifications using known ranges of Fc or Fmax. Only calls that met the criteria of the first two phases proceeded to the final phase, where species assignments were confirmed with the known ranges of either Fmax or Fc (Parker and Bernard, 2018; Parker, 2022).

Insect sampling

Insect sampling was done during both the wet and dry seasons at each of the six sites within MalaMala Game Reserve (Gumede et al., 2025). A standardized light-trapping technique was employed to estimate the abundance of winged arthropods by attracting nocturnal flying insects, especially members of the orders Lepidoptera and Diptera, known to form a major part of the diet of many African bats (Clare et al., 2009; Bohmann et al., 2011). Each sampling location was equipped with a battery-powered light trap (Figure 4.3) (Sheikh et al., 2016) in both the wet and dry seasons of 2021 and 2022. Light traps were operated for one night on or near the new moon and just after the bat acoustic sampling so that arthropods were not depleted for the bat sampling (Gumede et al., 2025). The darkest phase of the lunar cycle was selected to coincide with the bat acoustic sampling and when insects were most likely to be attracted to the light traps (Jones et al., 2009).

The light traps were deployed at dusk and collected at dawn the following day. All arthropods were preserved in 90 % ethanol and then identified to the family and morphospecies level (Altaf et al., 2022). The captured insects were sorted, identified, and quantified to provide data on their species composition and abundance. The insect data were analysed as total available prey (Ofori et al., 2015). Total number of arthropods was calculated, where the number of arthropods identified in each seasonal sample at each sampling site was recorded. We also recorded the total number of insect orders as a measure of insect richness at the sampling sites.

Figure 4.3: A picture of the battery-operated light traps placed at each site in 2022 in MalaMala Private Game Reserve.

Data analysis

Calculating Environmental Variables

In addition to season (categorical: wet and dry), the environmental variables used in the analyses were distance to water (categorical: close and far), normalized difference vegetation index (NDVI) at the 50 m scale for both seasons, and tree cover (tree/m^2) at the 50 m scale (Table 1). Three sites were located within 500 m and three sites situated more than 3.5 km from permanent water sources. The NDVI values were extracted for each bat detector location and various features presented in the 3-band satellite image in MalaMala. Using QGIS, the mean NDVI value within 50 m of each detector location were computed, based on the median value for each pixel on days with >5 % cloud coverage in each season. Vegetation indices allow for the definition of the distribution of vegetation based on the characteristic reflectance patterns of green vegetation (Bhandari et al., 2012). The NDVI was calculated as:

$$\text{RNDVI} = \frac{\text{NIR} - \text{RED}}{\text{NIR} + \text{RED}}$$

Similarly, tree cover data were also extracted for each bat detector location, using sentinel-1 time series and LiDAR data, and was the average percentage woody plant cover at the 50 m scale (Wessels et al., 2011). Using a 50 m scale for both tree cover and NDVI provides a fine resolution for identifying vegetation patterns, balancing computational efficiency and availability of data (Hansen et al., 2016). High resolution scales (50m included) have been used in studies for detailed vegetation dynamics (Hansen et al., 2016), particularly for areas with mixed vegetation types (Dahal et al., 2024). In addition, several studies have used similar scales for examining vegetation indices and monitor changes in vegetation cover ensuring accuracy to correlate ecological data (Noardo et al., 2020; Dahal et al., 2024). The scale used in our study aligns with detection abilities mostly used in remote sensing which has a resolution suitable for NDVI and tree cover assessments (Dahal et al., 2024). Moreover, bat detectors are typically able to detect echolocation calls at a minimum distance of 50 m and maximum of 100 m for very loud and low frequency bats, but within 10-30 m for high frequency bats due to rapid attenuation of the calls (Schuchmann and Siemers, 2010; Monadjem et al., 2017).

Calculating Diversity

Bat diversity as determined from Shannon and Simpson’s diversity indices were calculated using EstimateS (Colwell and Elsensohn, 2014) with the following equations:

$$Shannon\ Index\ = -\sum_{i=1}^{s} p_i\ \ln p_i$$

Where, the variable *p* represents the proportion of individuals of a single species (*i*) relative to the total number of individuals across all species (*N*). The formula uses the natural logarithm (*ln*), and the symbol *Σ* indicates that the calculation is summed across all species, with *s* denoting the total number of species (Shannon, 1948).

$$Simpson\ index = \frac{1}{\sum_{i=1}^{s} p_i 2}$$

Where, p also stands for the proportion of individuals of a specific species (i) compared to the total number of individuals (N). Like the Shannon Index, Σ is used to indicate summation, and s refers to the total species count (Simpson, 1949).

Shannon's index places more emphasis on richness by considering both the number of species and their relative abundances. It quantifies the uncertainty of predicting the species of a randomly chosen individual from the community (Shannon, 1948), making it sensitive to both the variety of species and how evenly they are distributed. In contrast, Simpson's index emphasizes evenness, focusing on the dominance of species within the community. It is particularly useful for identifying whether a few species dominate the community or if individuals are more evenly distributed across species (Simpson, 1949). By incorporating both indices, we aimed to capture a more holistic view of the bat community. While Shannon's index reflects overall biodiversity and the balance between richness and evenness, Simpson's index provides insights into how evenly the species are distributed. This approach is beneficial because both indices highlight different aspects of diversity (Nagendra, 2002), allowing for a more comprehensive analysis of the ecological dynamics in MalaMala.

Statistical Analyses

To investigate the potential drivers of bat community patterns, Generalised Linear Models (GLMs) were used to assess the relationships between a set of response variables (bat species richness, activity [number of bat calls], and diversity [Shannon and Simpson indices]) and our environmental predictors (Table 1). These analyses were conducted in R (R Core Team, 2024), using the MASS package for model fitting (Venables and Ripley, 2013), the CAR package for evaluating regression diagnostics (Fox and Weisberg, 2018), and the MuMIn package for estimating model coefficients and associated standard errors (Barton, 2020). Predictor variables in the models included insect abundance and the number of insect orders (as proxies for prey availability and richness), distance to permanent water (close or far), NDVI at the 50 m scale for both seasons (as a measure of vegetation productivity), and tree density (trees/m^2) within the same spatial scale (as a measure of habitat clutter) (Table 1). Prior to model interpretation, all response variables were checked for normality, non-constant variance, and overdispersion following best-practice guidelines for ecological regression modelling (Knief and Forstmeier, 2021). This approach enabled a robust evaluation of what we considered to be the key potential environmental drivers shaping bat assemblages across the landscape.

Table 1: An overview of the response and predictor variables used in the current study

Variable Type	Variable Name	Description
Response Variables (Dependent)	Bat Species Richness	The number of different bat species recorded at a site per season.
	Bat Abundance/Activity	Measured as the total number of bat calls recorded during sampling at a site per season.
	Shannon's Diversity Index	A diversity metric that accounts for both species' richness and the proportion of each species in the community, emphasizing species richness.
	Simpson's Diversity Index	A diversity metric that accounts for species dominance, emphasizing evenness by giving more weight to abundant species.
Predictor Variables (Independent)	Insect Abundance	The total abundance of all insects recorded at each site in each season, used as a measure of potential bat prey availability.
	Number of Insect Orders	The number of different insect orders recorded per site, indicating insect richness.
	Distance to Water	The distance from the sampling site to the nearest permanent water source, classified into two groups: within 500m or more than 3.5km from water (Taylor et al., 2020).
	Normalized Difference Vegetation Index (NDVI)	A remote sensing metric extracted at the 50m scale, representing vegetation density and productivity. NDVI values were obtained from 3-band satellite imagery at MalaMala (Bandari et al., 2012).
	Tree Cover (trees/m^2)	The density of trees per square meter at a 50m scale, used as an indicator of habitat structure.

Results

Bat Species Richness and Activity

Distance to permanent water had a significant negative effect on bat species richness at MalaMala, indicating that richness declined with increasing distance from water (Figure 4.4A; Table 2). The GLM examining bat activity (i.e., the number of passes) during the 2022 dry and wet seasons identified several significant ecological predictors (Figure 4.4B; Table 3). Seasonal effects were non-significant in predicting bat activity (Figure 4.4B; Table 3). However, insect order richness had a significant negative effect on bat activity (Figure 4.4B; Table 3), suggesting that sites with a greater variety of insect orders were associated with lower bat activity. Similarly, distance from rivers was a significant negative predictor (Figure 4.4B; Table 3), indicating that bat activity declined further away from permanent water. Tree cover was also negatively associated with bat activity (Figure 4.4B; Table 3).

Table 2: Estimates from generalized linear models for bat species richness during the dry and wet seasons of 2021 and 2022 at MalaMala Private Game Reserve. Significant or near-significant effects are highlighted in **bold**

Coefficients	**Estimate**	**Std. Error**	**t value**	**Pr(>|t|)**
(Intercept)	7.06	3.24	2.18	0.03
SEASONWET	-250	555.4	-0.45	0.65
INSECT_ORDERS	0.01	0.04	0.28	0.78
DIST_RIVERFAR	-1.77	0.81	-2.18	0.03
TREE_COVER_50m	0.009434	0.02	0.40	0.69
NDVI_50m	8.01	17.72	0.45	0.65

Table 3: Estimates from generalized linear models for bat activity (number of passes) during the dry and wet seasons of 2021 and 2022 at MalaMala Private Game Reserve, South Africa. Significant effects are highlighted in **bold**

Coefficients	**Estimate**	**Std. Error**	**t value**	**Pr(>|t|)**
(Intercept)	752.11	493.49	1.52	0.13
SEASONWET	2910.03	84657.22	0.03	0.97
INSECT_ORDERS	-37.81	7.40	-5.11	0.00000452
INSECT_ABUN	0.97	1.11	0.88	0.38
DIST_RIVERFAR	-289.34	124.05	-2.33	0.02
NDVI_50m	-57.11	2701.44	-0.02	0.98
TREE_COVER_50m	-10.92	3.63	-3.01	0.004

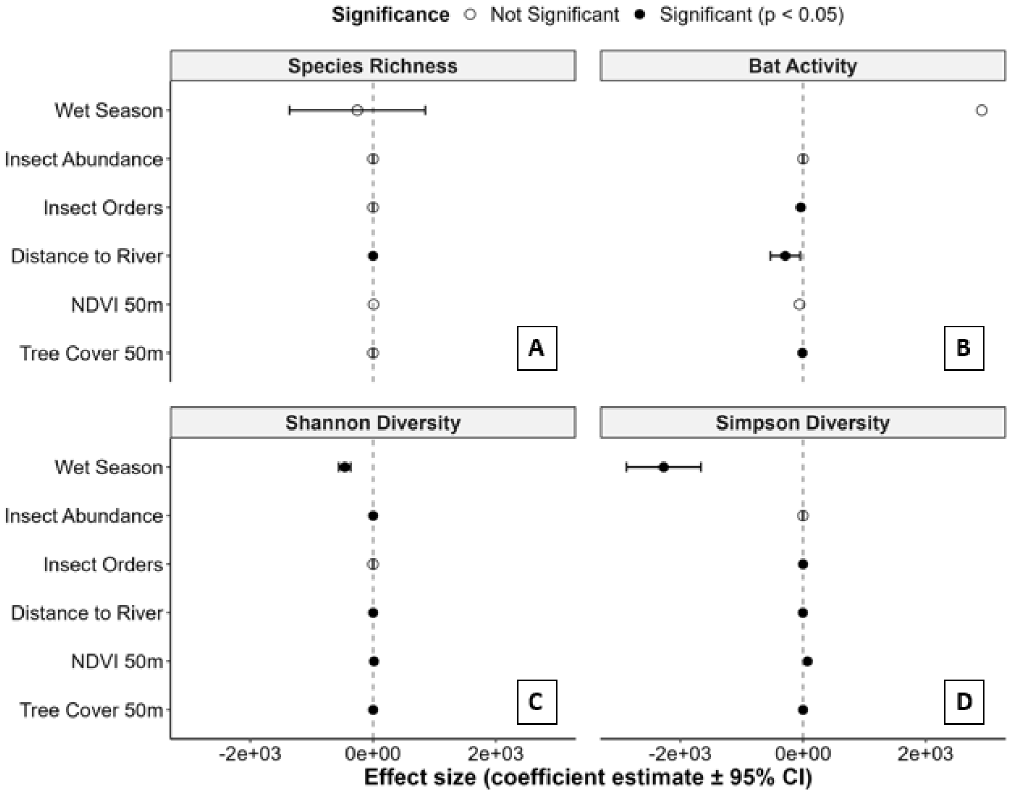

Figure 4.4: The influence of six environmental predictors of bat species richness, activity and diversity (Shannon and Simpson indices) in the MalaMala Game Reserve, South Africa. Error bars represent standard errors.

Bat Diversity

For Shannon diversity, season had a significant negative effect, with Shannon's index lower in the wet season compared to the dry season (Figure 4.4C; Table 4). This result indicates a pronounced seasonal shift in community composition or evenness. Among the other environmental variables, insect abundance was significantly negatively associated with Shannon diversity (Figure 4.4C; Table 4), suggesting that higher insect abundance did not necessarily correspond with more diverse bat communities. Although insect order richness had a positive effect, this relationship was not statistically significant (Figure 4.4C; Table 4). Distance from rivers had a significant negative effect (Figure 4.4C; Table 4), indicating that sites further from water supported less diverse bat communities. Vegetation productivity, as measured by NDVI at the 50 m scale, was a significant positive predictor (Figure 4.4C; Table 4), reinforcing the link between vegetative greenness and bat diversity. Conversely, tree cover was a significant negative predictor (Figure 4.4C; Table 4), suggesting that increased woody density may constrain species diversity or evenness within local bat communities.

For Simpson's diversity, there was a strong seasonal effect, with significantly lower diversity in the wet season (Figure 4.4D; Table 5). Among the environmental predictors, distance from rivers again emerged as a significant negative predictor (Figure 4.4D; Table 5), suggesting that sites located further from permanent water supported less even bat communities. In contrast, NDVI at the 50 m scale was positively associated with Simpson's diversity (Figure 4.4D; Table 5), indicating that areas with higher vegetation productivity supported more even bat assemblages. Tree cover also had a significant negative effect (Figure 4.4D; Table 5), implying that increasing woody cover reduced evenness, potentially favouring a subset of species better adapted to cluttered habitats. In addition, insect order richness was positively associated with Simpson's diversity (Figure 4.4D; Table 5), albeit with a smaller effect size, suggesting a modest contribution of prey diversity to overall community structure.

Table 4: Estimates from generalized linear models for Shannon's diversity during the dry and wet seasons of 2021 and 2022 at MalaMala Private Game Reserve. Significant effects are highlighted in **bold**

Coefficients	**Estimate**	**Std. Error**	**t value**	**Pr(>|t|)**
(Intercept)	-0.94	0.28	-3.29	0.00178
SEASONWET	-460.7	49.17	-9.37	0.01
INSECT_ABUN	-0.002	0.0006438	-2.81	0.00693
DIST_RIVERFAR	-0.57	0.07205	-7.96	0.000000000132
NDVI_50m	14.69	1.569	9.36	0.000000000000795
TREE_COVER_50m	-0.01	0.002106	-5.41	0.00000153

Table 5: Estimates from generalized linear models for Simpson's diversity during the dry and wet seasons of 2021 and 2022 at MalaMala Private Game Reserve. Significant effects are highlighted in **bold**

Coefficients	**Estimate**	**Std. Error**	**t value**	**Pr(>|t|)**
(Intercept)	-8.58	1.80	-4.77	0.0000148
SEASONWET	-2270	308.7	-7.36	0.00000000121
INSECT_ORDERS	0.06	0.02	2.29	0.03
INSECT_ABUN	-0.006	0.004	-1.56	0.12
DIST_RIVERFAR	-3.07	0.45	-6.80	0.00000000956
NDVI_50m	72.37	9.85	7.35	0.00000000124
TREE_COVER_50m	-0.05	0.01	-4.14	0.000124

Discussion

My study found that bat community structure at MalaMala was strongly influenced by proximity to water, with sites closer to rivers supporting higher species richness, activity, and diversity, highlighting the ecological importance of riparian habitats. Vegetation structure also shaped bat activity, with dense tree cover negatively affecting activity and diversity, while vegetation productivity (NDVI) was positively associated with diversity, suggesting that moderate, productive habitats provide both prey and accessible foraging space. Insect diversity exhibited contrasting effects, positively influencing Simpson diversity but negatively affecting overall activity, indicating that prey availability and detectability may be decoupled. Finally, bat foraging guilds responded differently to habitat features: open- and edge-space species were more active in less cluttered areas, whereas clutter-adapted species, such as Rhinolophids, benefited from structurally complex habitats. Overall, riparian zones with moderate vegetation productivity and low clutter emerged as critical areas for maintaining diverse and active bat communities in the savanna ecosystem.

Insectivorous bats serve as valuable bioindicators due to their sensitivity to changes in habitat quality, water availability, and prey abundance (Jones et al., 2009). My study reinforces the important role of water and riparian vegetation in structuring bat communities, as evidenced by consistent negative effects of increased distance to rivers on bat species richness, activity, and both diversity indices used. These findings also support previous research highlighting the ecological significance of proximity to water bodies for foraging and roosting bats (Hackett, 2013; Straka et al., 2020; Gumede et al., 2025). For example, sites further from rivers consistently supported fewer bat species and exhibited lower overall activity and diversity, suggesting that water availability and associated habitat features, such as riparian vegetation, act as ecological attractors for bats.

Contrary to expectations and some previous studies (e.g., Amorim et al., 2018; Laverty and Berger, 2020), the observed bat species richness and activity did not increase significantly during the wet season. In fact, both Shannon and Simpson diversity were significantly lower during the wet season, indicating a potential reduction in community evenness and possibly greater dominance by a few generalist species (*Mops pumulis, Afronycteris nanus, Taphozous mauritianus*)These seasonal trends may reflect a dampened seasonal response due to the perennial availability of water at about half of the detector sites in MalaMala, which may buffer bats from typical dry-season constraints observed in more arid or ephemeral systems (Fjelldal et al., 2023).

Vegetation structure also emerged as a key driver of bat community composition at MalaMala. Tree cover at the 50 m scale was negatively associated with both bat activity and diversity, aligning with findings that denser vegetation can constrain bat foraging efficiency, especially for fast-flying or clutter-intolerant species (Mendes et al., 2017; Carvalho et al., 2023). In contrast, NDVI (a proxy for vegetation productivity) was positively associated with both Shannon and Simpson diversity, supporting the idea that greener, more productive habitats promote more even and potentially richer bat communities. This dual pattern suggests a nuanced effect of vegetation on bats with productive habitats providing greater resource availability, but habitats with excessive clutter potentially reducing access to insect prey.

Increased bat activity in areas with reduced vegetation has been documented across a range of forested landscapes and depends on the type of vegetation reduction, the bat foraging guild, and landscape features (Müller et al., 2013; Blakey et al., 2016; Mark et al., 2024). Vegetation structure and insect abundance interact to shape bat foraging activity; however, a bat's ability to exploit areas with both high insect availability and high structural complexity is constrained by its manoeuvrability and foraging strategy (Adams et al., 2009; Froidevaux et al., 2021). These contrasting effects highlight the functional diversity of bat species and their varied responses to habitat complexity. Species that specialize in open- or edge-space foraging, such as many Molossids and Vespertilionids, rely on high-speed, low manoeuvrability flight and are often excluded from habitats with dense understory or canopy cover due to increased collision risk and reduced acoustic detection range (Jung et al., 2012; Denzinger and Schnitzler, 2013).

Conversely, forest-adapted species, such as clutter foragers in Rhinolophidae family (e.g. *Rhinolophus simulator*), may be sensitive to habitat changes and, may benefit from dense vegetation, which provides both roosting opportunities and structurally complex foraging environments. However, high tree cover may also suppress insect abundance or alter community composition in ways that reduce the availability of energetically profitable prey (Dodd et al., 2012). Normalized Difference Vegetation Index (NDVI), in contrast, may better capture ecosystem productivity and prey biomass across multiple vertical strata, especially in heterogeneous landscapes. Unlike single metrics such as canopy cover, NDVI integrates information on green vegetation across spatial and vertical gradients, capturing complex ecological patterns relevant to bats and their prey (Pettorelli, 2013; Traba et al., 2022).

Interestingly, insect order richness had contrasting effects across response variables. It was positively associated with Simpson diversity but negatively associated with bat activity. This pattern may reflect a decoupling between prey diversity and prey abundance or accessibility. Sites with more insect orders may support a more even bat assemblage but not necessarily higher activity levels, possibly due to differences in prey detectability or nutritional value (De Oliveira et al., 2020). Additionally, this pattern could indicate behavioural or ecological trade-offs in bat foraging strategies. Some bat species may thrive in high prey diversity environments due to dietary flexibility, while others may reduce activity if their preferred prey becomes relatively scarce or harder to locate (Clare et al., 2009; Salinas-Ramos et al., 2015).

Furthermore, the structural complexity associated with diverse insect communities might impede bat hunting efficiency, particularly for species with fast, open-space flight patterns, contributing to lower activity despite higher diversity (Jung et al., 2012; Denzinger and Schnitzler, 2013). These dynamics underscore the complexity of trophic interactions and highlight that diversity metrics (such as Simpson's index) and measures of activity or abundance are not always directly linked. Predators' responses to changes in prey availability can involve either aggregation of individuals or increased foraging intensity (Fenton, 1990). When optimal prey sources are abundant, bats may compete to dominate access to these rich prey patches, enhancing their hunting efficiency (Racey and Entwistle, 2003). However, insect species richness remains crucial for ensuring prey continuity over time, which benefits bats with high site fidelity that rely on a consistent yet diverse prey base to maintain stable activity and occupancy patterns (Fukui et al., 2006; Salinas-Ramos et al., 2015).

Overall, our findings emphasize the complex interplay between water availability, vegetation structure and productivity, and prey characteristics in shaping insectivorous bat communities in African savannas. They highlight that riparian zones with moderate vegetation productivity and low clutter are particularly important for supporting diverse and active bat communities (Monadjem and Reside, 2008; Cistrone et al., 2024). Unlike in tropical systems where bat activity remains stable year-round due to consistently favourable conditions (Barros et al., 2014), seasonal shifts in savannas are evident in diversity metrics, albeit buffered by the availability of permanent water sources in protected areas such as MalaMala. These findings reinforce the concept that spatial and temporal resource heterogeneity is a critical determinant of bat community structure in semi-arid ecosystems such as African savannas. In these environments, permanent water sources may function as ecological refugia during dry seasons, sustaining both insect prey populations and the bats that rely on them (Korine et al., 2015).

Riparian corridors not only offer consistent water access but also provide habitat continuity, microclimatic stability, and increased insect biomass, particularly during seasonal droughts when upland areas become resource-poor (Fukui et al., 2006; Taylor et al., 2020). The observed association between moderate NDVI values and high bat diversity further suggests that intermediate levels of vegetation productivity may support a balance between prey availability and foraging accessibility (Fraser et al., 2015). These patterns underscore the importance of landscape-scale conservation strategies that protect riparian buffers and maintain year-round water availability in savanna biomes, particularly under increasing climate variability and anthropogenic pressure.

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Chapter 5: Summary and concluding remarks

My study investigated how key environmental variables, vegetation structure, proximity to water, and insect prey availability collectively shape bat species richness, activity, and diversity in a subtropical savanna. My findings emphasized that proximity to permanent water sources and structurally complex vegetation significantly enhanced bat activity and species richness likely due to increased arthropod abundance. Denser vegetation, while potentially offering more insect biomass, limited aerial space and echolocation efficiency for certain bat species, particularly open-air foragers Nevertheless, riparian zones often support more complex vegetation and sustained insect populations due to higher soil moisture, making them ecological hotspots for both bats and their prey.

Water bodies act as ecological hotspots by sustaining insect populations, especially during drier months when resources are scarce. Similarly, structurally complex vegetation promoted bat diversity by offering both roosting opportunities and diverse prey habitats, though dense vegetation also restricted aerial foragers with high flight demands. These patterns underscore the importance of environmental heterogeneity at multiple scales, where moderate vegetation productivity (as reflected by intermediate NDVI values) provided an optimal balance between foraging accessibility and prey availability. Seasonal shifts observed during the study highlight that conservation planning cannot rely solely on static habitat features, but must incorporate temporal variability in rainfall, insect emergence, and resource distribution (Sankaran et al., 2005).

My study also contributes to filling knowledge gaps on the ecology of insectivorous bats in African savannas. My results emphasize the need to conserve water bodies and maintain natural vegetation heterogeneity. Long-term monitoring approaches that combine ecological, climatic, and anthropogenic data are essential to ensure the sustainability of bat populations and the ecosystem services they provide (McCain, 2007; Brinkley et al., 2021).

Limitations

The spatial scope of this study was restricted to a single protected area, MalaMala Game Reserve, which, although ecologically significant, represents only a portion of the broader Greater Kruger landscape. As a result, the findings may not fully capture the ecological variability present across different habitats, soil types, and management systems within the region. Furthermore, the temporal coverage of the study was limited to selected months within the wet and dry seasons across two years. While this sampling design allowed for seasonal comparisons, it constrained the ability to detect longer term ecological or climatic patterns, such as inter annual variability, responses to extreme weather events, or gradual shifts linked to climate change. These limitations mean that while the results provide valuable insights into bat species richness and habitat use at MalaMala, caution should be exercised when extrapolating them to other reserves or to broader temporal scales without complementary long-term monitoring.

Opportunities for future research

Comparative studies across multiple reserves (e.g., communal rangelands and formally protected areas) would help unravel the relative effects of habitat heterogeneity, fire frequency, and human disturbance on bat community structure (Meyer et al., 2016; Clements et al., 2025). Long term monitoring extending across multiple years would also be valuable in assessing bat community responses to climate variability, particularly droughts and shifts in seasonal rainfall (McCain, 2007).

Beyond addressing these limitations, several opportunities arise from this work. Integrating acoustic monitoring with genetic tools, such as environmental DNA (eDNA) sampling, could improve species detection and resolve taxonomic uncertainties within cryptic bat assemblages (Clare et al., 2013). Expanding spatial coverage to include a mosaic of land uses, private reserves, communal lands, and national parks would allow for more robust testing of how landscape connectivity and management influence chiropteran diversity (Meyer et al., 2016). Furthermore, linking bat community dynamics with ecosystem services, such as insect suppression and pollination, could provide stronger arguments for their conservation within both protected and human-modified landscapes (Russo and Jones, 2015; Frick et al., 2020). Finally, collaborations with local communities and reserve managers present opportunities to embed bat monitoring into broader biodiversity management programmes, fostering both conservation outcomes and socio-ecological benefits (Frick et al., 2020).

Nevertheless, my study contributes significantly to long term ecological monitoring in savannas by providing a dataset that integrates acoustic bat data with prey sampling and environmental variables. Acoustic recordings, light trap insect sampling, NDVI measurements, and water proximity offer a scalable, repeatable framework for future monitoring efforts (Korine et al., 2016; Voigt et al., 2018). These methods enable tracking of bat activity, species richness, and community shifts in response to habitat modification, climatic fluctuations, and conservation interventions.

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