

Small mammals in the uppermost Congo-Guinean forests of West Africa: inventoring and understanding responses to cashew expansion

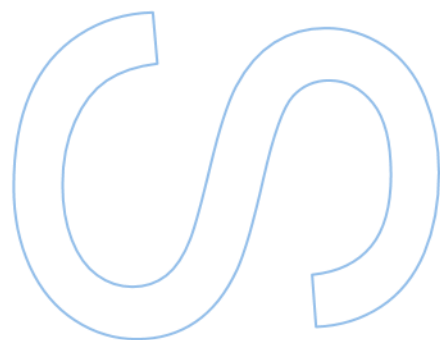
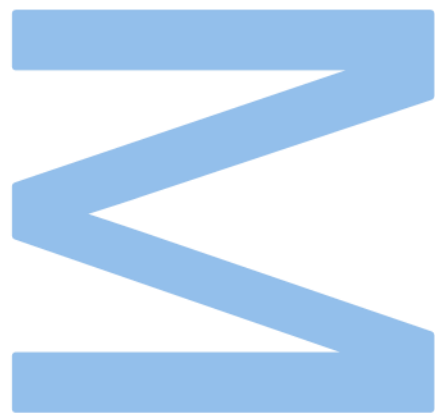
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Dedicado a ti,

Benny

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Resumo

A recente intensificação agrícola representa uma ameaça séria à biodiversidade nos trópicos. A África Ocidental, um hotspot globalmente reconhecido, não é exceção, apesar de existirem ainda lacunas no conhecimento no que se refere à distribuição geográfica de muitas espécies. No Parque Nacional de Cantanhez (PNC) na Guiné-Bissau, a diversidade de pequenos mamíferos é pouco conhecida, assim como os efeitos que a conversão de florestas em hortas de caju nesta diversidade de espécies. No capítulo 2, amostrámos pequenos mamíferos (pertencentes às ordens Rodentia e Eulipotyphla) no PNC utilizando armadilhas tipo Sherman e de queda em quatro tipos de habitat - florestas cobertas, florestas dominadas por palmeiras, “lalas” e hortas de caju, para um levantamento das espécies. Um total de 183 indivíduos de 11 espécies (oito roedores e três musaranhos) foram registados, sendo *Praomys rostratus* (48,1%) a espécie mais capturada, seguida por *Mastomys huberti* (18,0%) e *Mastomys erythroleucus* (7,7%). Os nossos levantamentos expandiram a distribuição geográfica de *Mus mattheyi* em 250 km para a Guiné-Bissau. No capítulo 3, amostrámos mamíferos em 24 “sites” específicos (12 em hortas de caju e 12 em florestas) para avaliar o impacto da conversão do habitat. As hortas de caju apresentaram uma maior riqueza de espécies em relação às áreas florestais, com a obstrução do sub-bosque destacando-se como um fator preditivo relevante. No entanto, áreas com maior área de hortas de caju apresentaram uma redução significativa na abundância de espécies, favorecendo espécies generalistas. *Praomys rostratus*, uma espécie especialista de floresta, foi mais comum em locais com maior cobertura de floresta nativa. Os resultados confirmam a elevada diversidade de pequenos mamíferos no PNC, com variações significativas entre os diferentes tipos de habitat. A hiperdominância de *P. rostratus* na região, restrita principalmente às florestas cobertas, e o impacto negativo da expansão das hortas de caju na abundância de pequenos mamíferos reforçam a necessidade de preservar os fragmentos de floresta nativa. Adicionalmente, recomendamos a criação de zonas de amortecimento como uma estratégia para mitigar os efeitos adversos da expansão agrícola sobre a biodiversidade.

Palavras-chave: Pequenos mamíferos, Guiné-Bissau, caju, biodiversidade, conversão de habitat, especialistas, generalistas, riqueza, abundância, composição, *Praomys rostratus*, *Mastomys erythroleucus*, florestas nativas

Abstract

The recent intensification of agriculture represents a serious threat to biodiversity in the tropics. West Africa, a globally recognized hotspot, is no exception, despite existing gaps in knowledge regarding the geographic distribution of many species. In Cantanhez National Park (CNP) in Guinea-Bissau, the diversity of small mammals is poorly understood, as are the effects of converting forests into cashew orchards on the species diversity. In Chapter 2, we sampled small mammals (from the orders Rodentia and Eulipotyphla) in the CNP using Sherman and pitfall traps across four habitat types—closed-canopy forests, palm-dominated forests, wet grasslands, and cashew orchards—to survey species. A total of 183 individuals from 11 species (eight rodents and three shrews) were recorded, with *Praomys rostratus* (48.1%) being the most captured, followed by *Mastomys huberti* (18.0%) and *Mastomys erythroleucus* (7.7%). Our surveys extended the known distribution of *Mus mattheyi* by 250 km into Guinea-Bissau. In Chapter 3, we sampled mammals at 24 specific sites (12 in cashew orchards and 12 in forests) to assess the impact of habitat conversion. Cashew orchards exhibited higher species richness compared to forested areas, with understory obstruction emerging as a significant predictive factor. However, areas with a greater proportion of cashew orchards showed a significant reduction in species abundance, favoring generalist species. *Praomys rostratus*, a forest specialist, was more common in sites with higher native forest cover. Our results highlighted the high diversity of small mammals in the CNP, with clear variations across different habitat types. The hyperdominance of *P. rostratus* in the region, restricted primarily to closed-canopy forests, and the negative impact of cashew orchard expansion on small mammal abundance underscore the need to preserve native forest fragments. Additionally, we recommend the establishment of buffer zones around native forests as a strategy to mitigate the adverse effects of agricultural expansion on biodiversity.

Keywords: Small mammals, Guinea-Bissau, cashew, biodiversity, habitat conversion, specialists, generalists, richness, abundance, composition, *Praomys rostratus*, *Mastomys erythroleucus*, native forests

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List of Abbreviations

µL	MICROLITER
µM	MICROMOLAR
AICC	CORRECTED AKAIKE INFORMATION CRITERION
ANOVA	ANALYSIS OF VARIANCE
BLAST	BASIC LOCAL ALIGNMENT SEARCH TOOL
CAM	CAMBEQUE
CAP	CANOPY OPENNESS
CIBIO	RESEARCH CENTRE IN BIODIVERSITY AND GENETIC RESOURCES
CM	CENTIMETER(S)
CNP	CANTANHEZ NATIONAL PARK
CSH	CASHEW
CTM	CENTRE FOR MOLECULAR ANALYSIS
CYTB	CYTOCHROME B
DBH	DIAMETER AT BREAST HEIGHT
DNA	DEOXYRIBONUCLEIC ACID
E.G.	FOR EXAMPLE (EXEMPLI GRATIA)
ED	EDGE DENSITY
FAO	FOOD AND AGRICULTURE ORGANIZATION (OF THE UNITED NATIONS)
FCUP	FACULTY OF SCIENCES OF THE UNIVERSITY OF PORTO
FIG	FIGURE
FMI	INTERNATIONAL MONETARY FUND
FOR	FOREST
GDP	GROSS DOMESTIC PRODUCT
GIS	GEOGRAPHIC INFORMATION SYSTEM
GLA	GAP LIGHT ANALYSER
GLMM	GENERALIZED LINEAR MIXED MODEL
GOOGLE LLC	GOOGLE LIMITED LIABILITY COMPANY
GRD	GROUND OBSTRUCTION
I.E.	THAT IS (ID EST)
IBAP	INSTITUTE OF BIODIVERSITY AND PROTECTED AREAS
IUCN	INTERNATIONAL UNION FOR CONSERVATION OF NATURE

JLG	JOINT LIAISON GROUP
KM	KILOMETER(S)
L	LITER(S)
LAU	LAUTCHANDE
LMM	LINEAR MIXED MODEL
M	METER(S)
MAD	MADINA
MM	MILIMETER(S)
MXH	MAXIMUM TREE HEIGHT
N	NORTH / SAMPLE SIZE
NCBI	NATIONAL CENTER FOR BIOTECHNOLOGY INFORMATION
NE	NORTHEAST
NMDS	NON-METRIC MULTIDIMENSIONAL SCALING
NRP	NUMBER OF OIL OR COCONUT PALM TREES/M ²
NRT	NUMBER OF TREES/M ²
°C	DEGREES CELSIUS
PCR	POLYMERASE CHAIN REACTION
PERMANOVA	PERMUTATIONAL MULTIVARIATE ANALYSIS OF VARIANCE
PERMDISP	PERMUTATIONAL ANALYSIS OF MULTIVARIATE DISPERSION
PNC	PARQUE NACIONAL DE CANTANHEZ
R ² C	CONDITIONAL R-SQUARED
R ² M	MARGINAL R-SQUARED
S	SECOND(S)
SCBD	SECRETARIAT OF THE CONVENTION ON BIOLOGICAL DIVERSITY
SD	STANDARD DEVIATION
SH	SHERMAN TRAP
SP.	SPECIES (SINGULAR)
SW	SOUTHWEST
TSR	TREE SPECIES RICHNESS
UN	UNITED NATIONS

UN-FCCC	UNITED NATIONS FRAMEWORK CONVENTION ON CLIMATE CHANGE
UST	UNDERSTORY OBSTRUCTION
UP	UNIVERSITY OF PORTO
VD	VINE DENSITY
W	WEST

1. Introduction

Knowledge about global biodiversity still remains critically incomplete, being hampered by the Wallacean and Linnean shortfalls (Lomolino, 2004; Whittaker et al., 2005). The Linnean shortfall refers to the vast number of species yet to be formally described, while the Wallacean shortfall highlights the gaps in our understanding of species' geographical distributions. These knowledge gaps still persist, and our ability to forecast species diversity considering complex environmental and historical factors is still limited (Bini et al., 2006). The lack of detailed knowledge about species richness, abundance, and distribution has long been recognized as a significant obstacle in designing conservation plans (Bini et al., 2006). This issue has driven extensive research efforts in ecology and systematics aimed at mapping species distributions, as emphasized by various studies and conservation frameworks (Brooks et al., 2004; Meir et al., 2004; Polasky et al., 2000). The implications of these shortfalls are especially acute in poorly studied, developing regions, which are also often characterized by high biodiversity levels and changes in land-use, due to an increasingly rapid demographic expansion (IUCN, 2022). In these areas, the lack of comprehensive biodiversity data can severely undermine conservation planning and efforts. Significant investment in biodiversity inventories is crucial to address these shortfalls, providing the foundation for effective conservation in biodiversity hotspots (Balmford & Gaston, 1999).

Forests are indispensable ecosystems for human life, providing essential ecosystem services and playing a crucial role in global climate regulation (Lawrence & Vandecar, 2015). They also serve as critical habitats for global biodiversity, supporting many of the world's terrestrial species (Arroyo-Rodríguez et al., 2020). Despite the global recognition of forests' importance for biodiversity and the prioritization of their preservation through various international processes (JLG, 2008; SCBD, 2006), global forest area has continued to decline over recent decades (Keenan et al., 2015; Morales-Hidalgo et al., 2015). Tropical forests (Fig.1.1.), which cover less than one-fifth of the Earth's terrestrial area (Dinerstein et al., 2017), are particularly significant due to their extraordinary species diversity (Hillebrand, 2004), hosting more than half of the world's terrestrial and vertebrate species (Pillay et al., 2022). Despite of that, tropical forests are experiencing the highest rates of deforestation globally, leading to significant declines in forest-dwelling species populations (Green et al., 2020). Approximately a third of all endangered species in terrestrial ecosystems are forest species, with land-use changes posing a great threat to biodiversity (Caro et al., 2022; Dirzo & Raven, 2003; Foley et al., 2005; Sala et al., 2000). The remaining forests worldwide are increasingly fragmented

due to human activity. Agricultural expansion, logging, and other land uses have rapidly transformed native tropical forests into human-dominated ecosystems (Foley et al., 2005; Gardner et al., 2009; Sala et al., 2000), leaving few areas of truly undisturbed tropical forest (Gibson et al., 2011). Consequently, the prevalence of secondary and plantation forests is rising rapidly (Chazdon, 2008; Wright, 2005). The African continent, which contains the world's second-largest contiguous tropical forest (Gardner et al., 2009), still suffers from limited data regarding the impact of human activities on its biodiversity. Given that human well-being is critically dependent on the ecosystem services forests provided (Cardinale et al., 2012; Isbell et al., 2017), understanding how land-use change is impacting biodiversity and overall ecosystem services is of major importance (Betts et al., 2017; Hansen et al., 2020a; Watson et al., 2018).



Fig. 1.1 – Native forest area in the "Madina" zone of Cantanhez National Park

Agricultural practices play a vital role in the economic development of numerous Sub-Saharan African countries (Jellason et al., 2021). The rapid intensification of cropland, driven by factors such as population growth, increasing global demand, and rising commodity prices, seeks to alleviate poverty and supply essential resources (Alexander et al., 2015; Alexandratos & Bruinsma, 2012). Nevertheless, this intensification frequently results in deforestation, as monoculture agriculture replaces native tropical landscapes to enhance food production (Laurance et al., 2014; Monteiro et al., 2017). The environmental consequences of this shift include habitat fragmentation (Hansen et al., 2020a) and landscape homogenization (Jeliazkov et al., 2016), as well as adverse effects on soil resources and water quality (Laurance et al., 2014). These alterations contribute to species loss (Hurst et al., 2013), changes in species composition (Newbold

et al., 2014), and reductions in functional diversity (Flynn et al., 2009; Hurst et al., 2013), thereby exacerbating the ongoing biodiversity crisis (Robertson & Swinton, 2005; Tscharrntke et al., 2012). In Sub-Saharan Africa, agriculture is largely carried out by smallholder farmers. Nonetheless, decisions related to resettlement and commercial expansion are generally made at higher governmental levels, often influenced by political or financial motivations (Lambin et al., 2001). Historically, agricultural expansion has been driven by subsistence farming and local market cultivation rather than export crops (Gibbs et al., 2010; Kissinger et al., 2012). While traditional crops such as rice and maize have been the mainstay of agricultural production in West Africa (Doggart et al., 2020), there is a growing shift towards cash crops, which is increasingly impacting local economies (FAO, 2016). Although research into land-use change, including agricultural expansion, is expanding (Geist & Lambin, 2002; Lambin & Meyfroidt, 2010), focused studies on Sub-Saharan Africa are still limited (Piquer-Rodríguez et al., 2018). The impacts of these changes on native species diversity vary by region, and the limited comprehensive knowledge of West African taxa further complicates our understanding of these effects (Hortal et al., 2015; Amori & Luiselli, 2011; Barnett & Prangley, 1997).

Located in West Africa, Guinea-Bissau is a small country with a remarkable natural capital. Its native landscapes are comprised by a mosaic of savannas and forests, featuring an incredibly diverse array of ecosystems, from dense tropical forests to expansive mangrove swamps. Although approximately 70% of Guinea-Bissau's land remains forested, with nearly 45% of these forests classified as primary formations (UN-FCCC, 2019), the country has faced severe forest degradation. Between 2001 and 2018 alone, Guinea-Bissau lost 77% of its closed-canopy forests, indicating significant pressure on its most densely vegetated areas (UN-FCCC, 2019). The southern regions are particularly rich in biodiversity, home to some of the best-preserved forest patches in West Africa, and the densest northern forest areas in Western Africa. Compared to neighboring countries like Senegal and the Republic of Guinea, Guinea-Bissau stands out for its exceptional biodiversity (UN-FCCC, 2019). However, this natural wealth is increasingly under threat due to human activities. Rapid population growth, extensive livestock farming, the expansion of cashew orchards, and widespread wood exploitation have led to alarming rates of deforestation. The deforestation rate surged from about 2% per year between 1975 and 2000 to 3.9% between 2000 and 2013 (UN-FCCC, 2019). In response to these challenges, Guinea-Bissau has established Protected National Parks, safeguarding 26% of its land and sea territory (The World Bank, 2015). Despite the fact that approximately one quarter of Guinea-Bissau's territory has been designated as

protected areas, there is increasing concern about the consequences of changing land use inside these areas (Pereira et al., 2022). These changes are expected to accelerate in the future decades, potentially affecting habitat availability for various kinds of organisms (Catarino et al., 2015; Temudo & Abrantes, 2014).

Cashew trees (*Anacardium occidentale*) were introduced to Guinea-Bissau during the 19th century. Due to the tree's natural resilience and minimal soil requirements, cashew orchards (Fig.1.2.) gradually expanded into fallow lands within semi-natural or savanna woodlands, primarily to prevent erosion and restore soil fertility (Catarino et al., 2015; Temudo & Abrantes, 2014). Following the country's independence in 1974, the cultivation of cashew trees accelerated rapidly, driven by increasing demand and the crop's emerging status as a valuable tropical cash crop (Monteiro et al., 2017). By the mid-1980s, government policies aimed at increasing agricultural output led to the granting of large land concessions to commercial farmers, and cashew quickly emerged as a favored crop due to its rapid growth and hardiness, leading to its extensive expansion. By 2015, West Africa produced 45% of the world's cashews, with Guinea-Bissau responsible for 15% of global raw cashew exports (Catarino et al., 2015). Despite its economic significance for Guinea-Bissau, cashew production faces challenges due to the lack of high-yield varieties and inadequate land-use management. The conversion of native forests into cashew monocultures results in reduced structural complexity and eventually in lower levels of biodiversity as noticed for mammals (Rege et al., 2020) and anurans in India (Komanduri et al., 2023). In Guinea-Bissau, the expansion of cashew orchards has been demonstrated to negatively affect the critically endangered western chimpanzee (*Pan troglodytes verus*) (Carvalho et al., 2013) and disrupt the functional structure of mammal communities, particularly impacting carnivores (Fernández, 2023). In northern Guinea-Bissau, Oliveira (2023) noted that nearly all small mammal species found in cashew orchards were also present in other habitats, indicating that these species are generalists and that cashew orchards might function as recipient habitats. Specialist butterfly species have also suffered due to the expansion of cashew cultivation (Vasconcelos et al., 2015a). Conversely, Dos Reis Silva (2023) reported that the expansion of cashew orchards did not significantly affect reptile richness, amphibian richness, or amphibian abundance and composition, which were comparable to those in forest remnants. As the area of cashew plantations grows, it is crucial to understand their effects on biodiversity, though current insights are still limited (Guedes et al., 2024; Rege & Lee, 2023).



Fig. 1.2 – Cashew orchard (CSH 2) in the Lautchande zone of Cantanhez National Park

Small non-volant mammals are crucial to forest ecosystems, enhancing both biological and functional diversity through their roles as consumers, predators, seed dispersers, burrowers, and prey for higher trophic levels (Adjapong et al., 2022; Decher et al., 2021; Ofori et al., 2018; Osman et al., 2022). Their brief lifespans and fluctuating populations allow them to quickly adapt to environmental changes and habitat fragmentation (Avenant & Cavallini, 2007; Hoffmann & Zeller, 2005; Hurst et al., 2013; Singleton, 2010). In West Africa, small non-flying mammals, primarily from the Rodentia and Eulipotyphla orders, are a diverse group that respond differently to habitat changes (Decher et al., 2021; Ofori et al., 2018; Oliveira, 2023). While forest-dependent specialist species may decline under habitat conversion, some small mammals thrive in disturbed or edge habitats with dense understory and abundant resources (Brown et al., 2017; Byrom et al., 2014; Hilty et al., 2006; Lambert et al., 2006; Niang et al., 2022). Vertical stratification of ecosystems also affects small mammal diversity, with some species preferring higher vegetation layers for foraging and nesting (Bakker & Kelt, 2000; Malcolm & Lowman, 2004). Increased habitat complexity can reduce interspecies competition and support co-existence (Carey et al., 1980; Carey et al., 1999; Grant, 1972). As a result, changes in habitat structure and complexity frequently cause shifts in small mammal community composition and species richness, demonstrating their effectiveness as indicators of ecosystem disturbance (Avenant & Cavallini, 2007; Decher et al., 2021). Nevertheless, small mammals, especially rodents, can also act as reservoirs for zoonotic diseases and have the potential to become destructive agricultural pests (Abdel Rahman Ahmed et al.,

2008; Andreazzi et al., 2023; Htwe et al., 2021; Singleton, 2010). To date, research on this understudied mammal group in Guinea-Bissau has been limited to two studies (Oliveira, 2023; Westra et al., 2022). Oliveira (2023) investigated small mammal communities in the Oio region, located in northern Guinea-Bissau, across forests, “*bolanhas*” (traditional rice paddies), and cashew orchards. Conversely, Westra et al. (2022) conducted their study in the Boé region of southeastern Guinea-Bissau, focusing on savannah biotopes, forest corridors, and abandoned, overgrown rice fields.

The Cantanhez National Park (CNP), located in the Tombali region of southwestern Guinea-Bissau (10°55'–12°45' N, 13°37'–16°43' W), is a protected area encompassing 1,067 km². It is bordered to the west by the Cacine River and to the east by the Cumbijã River Estuary (Cantanhez National Park Management Plan, 2017). As the largest remaining expanse of subtropical forest in Guinea-Bissau, CNP is among the largest forested areas in West Africa (Sousa et al., 2017). The park encompasses a wide range of habitats, including coastal sub-humid forests, mangroves, wet grasslands, and agricultural fields dominated by cashew orchards, alongside small human settlements (Sousa et al., 2017; Vieira et al., 2019). CNP is particularly renowned for its exceptional patches of primary sub-humid forests, regarded as some of the best-preserved in Guinea-Bissau. Additionally, the park features diverse ecosystems such as savannahs, evergreen forests, semi-deciduous forests, and mangroves (Gippoliti & Dell'Omo, 2003; Oom et al., 2009; Temudo, 2009). The Cantanhez region was first settled by the Nalu ethnic group, who are believed to have arrived before the 15th century and continue to hold traditional ownership of the land. The Nalu predominantly engaged in rainfed agriculture, palm oil extraction, and fishing for subsistence (Bout & Ghiurghi, 2017). By the late 19th century, the Fula people settled in CNP, leading a sedentary lifestyle and practicing a more intensive form of agriculture. They also played a key role in introducing Islam to the region. Concurrently, the Sosso ethnic group arrived in Cantanhez, bringing with them expertise in fruit cultivation and a focus on commercial trade activities (Bout & Ghiurghi, 2017). The Balanta ethnic group followed in 1924, contributing to the agricultural landscape by introducing rice cultivation (Bout & Ghiurghi, 2017). Human activities have significantly altered these landscapes, with anthropogenic pressures including slash-and-burn agriculture and expansion of cashew plantations leading to deforestation and habitat fragmentation (Temudo & Abrantes, 2014). The park supports significant biodiversity, including endangered species such as the Western chimpanzee (*Pan troglodytes*), the king colobus (*Colobus polykomos*), and the Temminck's red colobus (*Piliocolobus badius temminckii*) (Gonedelé Bi et al., 2020; Humle et al., 2016;

Minhós et al., 2020). CNP is among the few locations in Guinea-Bissau that has garnered substantial scientific attention (Hockings & Sousa, 2013; Pereira et al., 2022; Sousa et al., 2017; Vieira et al., 2019). However, no research has yet focused on small non-volant mammals, leaving a gap in species information.

In this thesis, we aimed to enhance the understanding of small mammal assemblages in Guinea-Bissau by examining their diversity and variation across both natural and anthropogenically altered habitats within CNP. In Chapter 2, we aimed to compile a comprehensive species list of rodents and shrews across the main habitat types within the CNP, thereby contributing novel data to the understanding of small mammal diversity in this region of West Africa. This work has been peer-reviewed and published in the *African Journal of Ecology* (Palmeirim et al., 2024). In Chapter 3, we investigated the effects of habitat conversion on small mammal communities, specifically examining the impact of transforming native forests into cashew orchards. We conducted systematic and opportunistic surveys across various habitats within CNP, comparing small mammal communities in native forest areas with those in areas converted to cashew orchards. This chapter focused on evaluating differences in species richness, abundance, and community composition between these habitat types. Through this analysis, the study aimed to shed light on the ecological consequences of habitat conversion, offering insights into how changes in land use affect small mammal diversity and community structure within the park.

2. Small mammal diversity across different habitat types in an Upper Guinean Forest National Park

This chapter, titled "*Small mammal diversity across different habitat types in an Upper Guinean Forest National Park*", has undergone peer review and has been published in the African Journal of Ecology.

For further details, please check: Palmeirim, A. F., Soares, J., Oliveira, R., Nhassé, I., Mone, D. N., Martins, F., Palma, L., & Lima, M. (2024). Small mammal diversity across different habitat types in an Upper Guinean Forest National Park. *African Journal of Ecology*, 62(3), e13314, <http://dx.doi.org/10.1111/aje.13314>.

2.1. Abstract

Baseline information on species diversity is lacking in many parts of the world. To address this gap, we conducted the first assessment of small mammal diversity in the Cantanhez National Park, Guinea-Bissau, West Africa. We used live- and pitfalltrapping to sample small mammals and identified them molecularly. We recorded 183 individuals from 11 species (eight rodents and three shrews). Half of the captures were made up of the forest soft-furred mouse *Praomys rostratus* (48.1%), followed by the multimammate mice *Mastomys huberti* (18.0%) and *Mastomys erythroleucus* (7.7%). Our surveys extended the geographic distribution of Matthey's mouse, *Mus mattheyi*, by 250 km into Guinea-Bissau.

2.2. Introduction

While land-use change continues to threaten biodiversity (Caro et al., 2022; Sala et al., 2000), baseline information on existing species diversity is lacking in many parts of the world (Hortal et al., 2015). The Wallacean shortfall, defined by the inadequate knowledge we have on the taxa geographic distributions (Lomolino, 2004), is particularly acute across the West African tropics (Amori & Luiselli, 2011; Barnett & Prangley, 1997), where it prevents the quantification of the impacts of land-use change (Gibson et al., 2011). Meanwhile, the highly species-rich tropical environments are also the current targets for global agricultural expansion (Hoang & Kanemoto, 2021).

In West Africa, although with only 36,126 km², Guinea-Bissau is home to a great biological diversity (Temudo & Abrantes, 2014). The country was typically covered by forest-savannah mosaics, which, particularly since the country's independence in 1974, have been succumbing to the accelerated expansion of introduced cashew monocultures, the main crop being grown in the country (Monteiro et al., 2017). Between 2001 and 2018 alone, Guinea-Bissau lost 77% of its closed-canopy forests (UN-FCCC, 2019). Moreover, although protected areas cover nearly 25% of the country, land-use changes within them are also worrying (Pereira et al., 2022) and are expected to worsen in the coming decades (Catarino et al., 2015). Such land-use changes are likely to affect habitat availability for biodiversity (Temudo & Abrantes, 2014), but little is known about their impacts (but see Vasconcelos et al., 2015b). Understanding the impacts of land-use change is further precluded by the so far limited knowledge of the country's biodiversity, especially when it comes to cryptic species that are not commonly recorded by direct observation. For instance, only two studies were conducted on small non-volant mammals on the country's mainland (i.e. Oliveira, 2023; Westra et al., 2022).

The African non-volant small mammals, including rodents and shrews, comprise a species-rich group characterised by a wide range of habitat preferences and feeding habits. As such, small mammals play important roles in the ecosystem functioning, acting as seed dispersers (Terborgh et al., 2001), pollinators (Goldingay et al., 1991), arthropod predators (Posa et al., 2007) and prey for higher trophic levels (Hughes et al., 1994). Small mammals can also be regarded in terms of their potential ecosystem disservices, such as crop pests (Abdel Rahman Ahmed et al., 2008) and reservoirs of zoonotic diseases (Andreazzi et al., 2023).

In southern Guinea-Bissau, the Cantanhez National Park (CNP) extends over 1067 km², harboring the uppermost tip of Guinean dense forests. Despite being one of the few places in the country receiving considerable research attention (e.g. (Pereira et al., 2022; Sousa et al., 2017), no study to date focused on small non-volant mammals, and no information is available on the species present. Here, we addressed this gap by conducting systematic and opportunistic small mammal surveys across the different habitat types available in the western part of the park, providing the first list of rodent and shrew species for this area in West Africa.

2.3. Methods

2.3.1 Study Area

This study was developed in the Cantanhez National Park, a protected area in the Tombali region (10°55'–12°45' N, 13°37'– 16°43' W; Fig. 2.1.), in the south of Guinea-Bissau. The CNP contains coastal sub-humid forests, mangroves, wet grasslands, agricultural fields, mostly cashew orchards, and small human settlements (Sousa et al., 2017). Like many other places in the country, it is home to a significant amount of biodiversity, including the following endangered species: the Western chimpanzee (*Pan troglodytes*; (Humble et al., 2016), the king colobus (*Colobus polykomos*; (Gonedelé Bi et al., 2020) and the Temminck's red colobus (*Piliocolobus badius temminckii*; Minhós et al., 2020). The climate is classified as humid, with markedly dry (November–May) and rainy seasons (June–October) (Catarino et al., 2001). The Mean annual temperature varies between 28 and 31°C and rainfall reaches 2400 mm/year (Catarino et al., 2001).

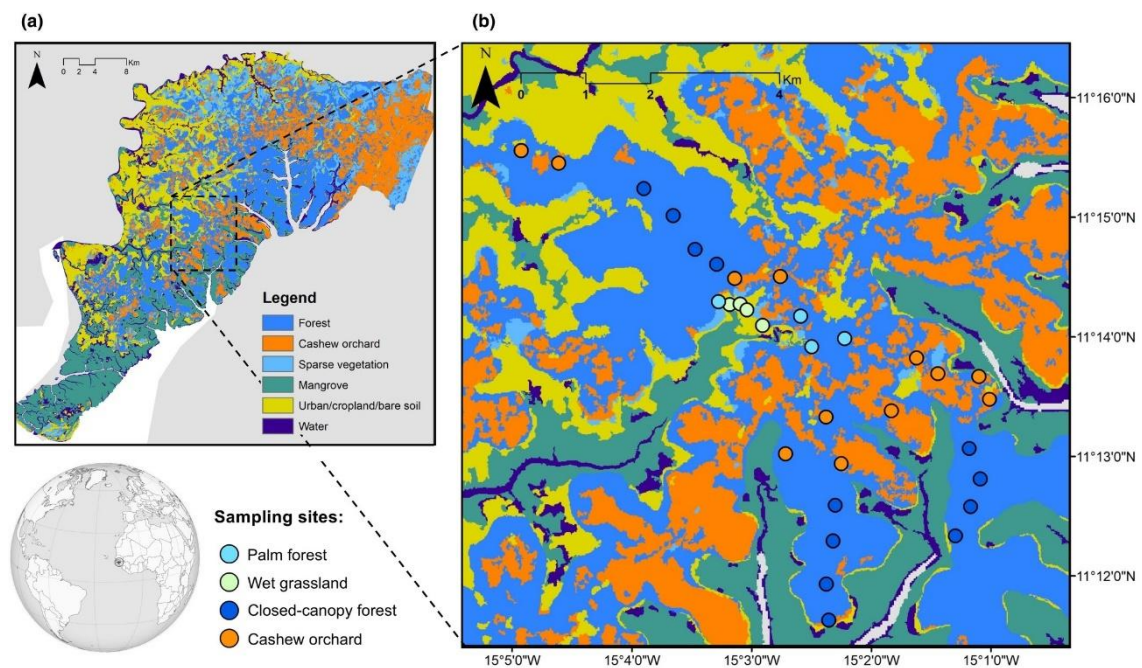


Fig. 2.1. - (a) Location of the study area within the Cantanhez National Park, in Guinea-Bissau, and (b) location of each sampling site as denoted by each circle colour-coded according to the habitat type where that was located. The area of the Cantanhez National Park is colour-coded according to the land-use following the mapping of Pereira et al. (2022).

2.3.2 Small Mammal Surveys

Small mammals were surveyed in four habitat types: closed-canopy forests, palm-dominated forests (*Elaeis guineensis*), wet grasslands (locally named as 'lalas') and cashew orchards, which correspond to the main cover types in the CNP (Fig. S2.1.). As an exception, due to logistical constraints, we did not survey mangroves, although this

is also an important habitat type in the CNP. Small mammals were sampled both systematically and opportunistically.

Systematic surveys were undertaken at 32 sampling sites (i.e. 12 in closed-canopy forests, 12 in cashew orchards, four in palm-dominated forests and four in wet grasslands), each one sampled using a single linear live-trap transect. Each transect consisted of 15 stations, with each station containing a single Sherman trap (23 × 9 × 8 cm, H. B. Sherman Traps Inc., Tallahassee, Florida). Transects were surveyed in eight-night trapping sessions. Three trapping sessions were conducted in sites located in closed-canopy forests and cashew orchards, whereas only two trapping sessions were done in palm-dominated forests and in wet grasslands (with the second trapping session in the latter lasting only five nights). The first trapping session was carried out for 15 days (9th–23rd of May 2023), the second during 35 days (9th of October–12th of November 2023) and the third during 27 days (13rd of November–9th of December 2023). Also, four of the 12 closed-canopy forest sites and four of the 12 cashew orchard sites were only sampled in the second and third trapping sessions. During the first trapping session, all sampling sites consisted of only 10 stations and were sampled for eight nights. In the forest transects, traps were placed alternately on the floor and the understory (~2 m height) (Fig. S2.2.a), whereas in other habitat types, all traps were placed on the forest floor.

Pitfall trapping is known to be more effective in recording fossorial and semi-fossorial species, such as shrews, and even species that are not attracted to enter live traps (Palmeirim et al., 2019). As such, we deployed four pitfall-trapping transects opportunistically in the four western most closed-canopy forest sites. Each transect consisted of three pitfall traps (plastic buckets of 30 L) spaced 10 m apart and connected by a plastic drift fence 50 cm high and 10 cm buried underground, with 5 m of fence extending beyond the two terminal pitfalls (Fig. S2.2.b). Pitfall trapping sessions were repeated twice, lasting 10 and 8 nights in the first and second sessions, respectively. Sampling effort amounted to a total of 10,360 trap-nights of systematic surveys (44% in closedcanopy forests, 44% in cashew orchards, 6% in palm-dominated forests in 6% in wet grasslands), in addition to 216 pitfall trap-nights (Table S2.1.).

Both live and pitfall traps were checked early every morning. The live traps were baited with a mixture of peanut butter, banana, sardines and oat flakes. All small mammal individuals were weighed, measured and had a tissue sample (ear tip) collected. Rodents (but not shrews) were also tagged by placing one numbered metal tag (Fish and Small Animal Tag, size 1; National Band and Tag Co., Newport, Kentucky) in one of the ears

(typically in the ear that did not receive a cut), so that any subsequent recaptures could be distinguished. Tissue samples from all recorded individuals were analysed using molecular techniques to confirm the taxonomic identification to the lowest possible level. The molecular approach was employed due to the challenges in identifying small mammals in the field.

2.3.3. Molecular Analysis

Molecular analyses were conducted at the Centre for Molecular Analysis (CTM) of the Research Centre in Biodiversity and Genetic Resources (CIBIO) in Portugal. The mitochondrial cytochrome b (Cytb) gene was selected because of its extensive use in other studies (e.g. Lecompte et al., 2002; Mamba et al., 2021; Pagès et al., 2010), ensuring adequate haplotype coverage for families and genera under study. This study was approved by Guinea-Bissau's Institute of Biodiversity and Protected Areas (IBAP) and followed the Guidelines of the American Society of Mammalogists (Sikes et al., 2016).

2.3.4. Data Analysis

To evaluate the effectiveness of our live-trapping surveys, we used the “iNEXT” R package (Hsieh et al., 2016) to generate a sample-based rarefaction curve using the order $q = 0$ of the Hill numbers. This analysis was conducted using R version 4.1.2 (Team, 2020).

2.4. Results

A total of 183 small mammals representing 12 species, including eight rodents and three shrews, were recorded across the surveyed sites (Table 2.1.). The overall capture success rate was 1.68% in the live traps and 3.70% in the pitfall traps. The most frequently observed species was the forest soft-furred mouse *Praomys rostratus* (N = 88 individuals; 48.08%), followed by the multimammate mice *Mastomys huberti* (N = 33; 18.03%) and *Mastomys erythroleucus* (N = 14; 7.65%). The least commonly recorded species was the house rat, *Rattus rattus*, recorded only once (Table 2.1.; Fig. S2.3).

Table 2.1 - Number of individuals recorded per habitat type, including closed-canopy forests, palm-dominated forests, wet grasslands, and cashew orchards, and trapping method, including Sherman (Sh) and pitfall traps used to survey small mammal assemblages in the Cantanhez National Park, in Guinea-Bissau

Order/family/species	Closed-canopy forests		Palm-dominated forests	Wet grasslands	Cashew orchards
	Sh	Pitfall			
Rodentia					
Muridae					
<i>Dasymys rufulus</i>				6	
<i>Gerbilliscus guineae</i>					5
<i>Mastomys erythroleucus</i>	1			1	12
<i>Mastomys huberti</i>				33	
<i>Mus mattheyi</i>	1				9
<i>Praomys rostratus</i>	83	1	2		2
<i>Uranomys ruddi</i>				8	
<i>Rattus rattus</i>					1
Eulipotyphla					
Soricidae					
<i>Crocidura olivieri</i>		1		1	1
<i>Crocidura</i> sp. 1		7			4
<i>Crocidura</i> sp. 2				4	

Small mammals were mostly recorded in closed-canopy forests (N = 94), followed by wet grasslands (N = 53) and cashew orchards (N = 34). Only two individuals of one species were recorded in palm-dominated forests. Seven species were recorded in the cashew orchards, followed by six in wet grasslands and five in closed-canopy forests (Table 2.1.). Shrew species were recorded in the forest using pitfall traps and in the Sherman traps deployed in both wet grasslands and cashew orchards (Table 2.1.). According to the rarefaction curve of the number of records across all sites and sampling methods, our sampling of the mammal assemblages in Cantanhez Nacional Park was deemed satisfactory (Fig. 2.2.).

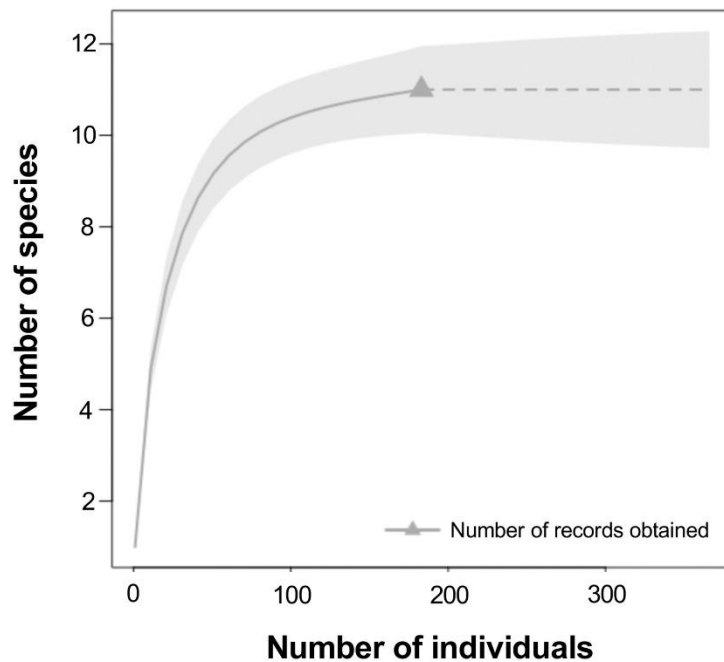


Fig. 2.2 - Rarefaction curve of the small mammal diversity recorded in the Cantanhez National Park, Guinea-Bissau

2.5. Discussion

Cantanhez National Park is home to a diverse range of habitats, which collectively support a rich biodiversity (Bersacola et al., 2022). However, most of the studies conducted in the CNP have focused on chimpanzee populations (e.g. Bessa et al., 2015; Sousa et al., 2014; Vieira et al., 2019). Overall mammal communities (Barnett & Prangley, 1997), particularly those of rodents and shrews (Amori & Luiselli, 2011), are virtually unknown in Guinea-Bissau. In these initial small, non-volant mammal surveys, we were able to distinguish 11 species, including eight rodents and possibly three shrews. One new species record has been added to the country for the Matthey's mouse, *Mus mattheyi*, extending its geographic distribution southwestwards by 250 km into Guinea-Bissau. Although this small rodent is geographically limited to West Africa, our results confirm its ecological adaptability (Granjon, 2016). As for the two shrew species that could not be identified to the species level, no genetic reference was available for *Crocidura* sp. 1, while we failed to obtain the molecular information for what we called *Crocidura* sp. 2 because the optimized protocol for obtaining genetic information for *Crocidura* sp. 1 did not work for samples of *Crocidura* sp. 2. These individuals were recorded in wet grasslands and consistently showed distinct body mass (16.3 ± 3.3 g; $N=4$ individuals) in comparison to *C. olivieri* (31.3 ± 6.1 g; $N=3$) or *Crocidura* sp. 1 (4.7 ± 1.5 g; $N=11$). Therefore, we believe that this represents a distinct species that has yet to be identified.

Small mammal assemblages in CNP were composed of species with diverse habitat affinities, resulting in different sets of species for each habitat type. Closed-canopy forests were primarily occupied by one forest-dependent species, *P. rostratus*, which was virtually absent from any other habitat type except the palm-dominated forests. In fact, the two individuals of this species recorded in cashew orchards were relatively close to the forest nearby. The hyperdominance of *P. rostratus* in the forests resulted in a substantial biomass of small mammals in this habitat. In the Boé region in the country's southeast, this was also one of the most frequently observed species, particularly in abandoned fields characterized by low shrubs and tall bunches of grass (Westra et al., 2022). However, this species was not recorded in northern Guinea-Bissau (Oliveira, 2023). Wet grasslands in the CNP are likely to have the highest small mammal abundance and are widely characterized by open-areas' small mammals. This habitat may provide small mammals with greater food availability due to the presence of grass and insects, which are more abundant during the seasonal presence of water (Oyediran et al., 1999). Unexpectedly, cashew orchards harbored as many species as closed-canopy forests or wet grasslands. As an exception, two typical open-area species, the *Uranomys ruddi* and the *Dasymys rufulus*, were not present in the cashew orchards, while the forest species *P. rostratus* was only observed twice. Despite the reasonable small mammal species richness of the cashew orchards, these habitats seem to better suit a set of generalist species as observed for other groups (Vasconcelos et al., 2015b).

The number of recorded small mammal species in the CNP is lower than the 21 small species reported for the Boé region, where the same sampling methods were used (Westra et al., 2022). In that study, sites surveyed included a savannah biotope, a forest corridor and an abandoned overgrown rice field. In comparison to our study, Westra et al. (2022) recorded two additional shrew species (*Crocidura crosseii* and *Crocidura lamottei*), the arboreal rodent *Grammomys macmillani*, the multimammate rat *Mastomys natalensis*, three savannah-dwelling *Lemniscomys* sp. and the arboreal dormouse *Graphiurus kelleni*. While the higher number of species in the Boé may be attributed to the more contrasting habitat types (Westra et al., 2022), it is possible that our study may have missed some shrew species in habitats where they are less common. This is highlighted by the absence of shrews in the Sherman traps, except for the Shermans deployed in the wet grassland habitat. In fact, Westra et al. (2022) conducted more extensive pitfall trapping, using five buckets in each of the five pitfall transects that operated for 96 survey days. In another study conducted in the rural landscape of the Oio region in northern Guinea-Bissau, Oliveira (2023) identified 11 species using

Sherman traps deployed in open forests, rice paddies and cashew orchards. Eight of these species matched those we recorded in the CNP. In comparison to Northern Guinea-Bissau, we did not detect the open-area rodent *Arvicanthis* sp., the habitat generalist *Praomys daltoni* and the dormice *Graphiurus* sp. On the contrary, we did record the forest dwelling *P. rostratus*, the grassland dwelling *Dasimys rufulus* and the house mouse *Rattus rattus* (but which has also been opportunistically recorded in the study area of Oliveira 2023; A.F. Palmeirim, pers. obs.). Other studies in West Africa suggest a higher species diversity of small mammals, which may be due to higher sampling efforts in those studies. For instance, 13 genera have been recorded in coastal Guinea (Denys et al., 2009), 25 species in Ghana (Decher, 1997), 24 species in Mali (Granjon & Duplantier, 2011) and 25 in the cross-border area between Liberia and Guinea (Mamba et al., 2021). Other studies also recorded higher small mammal diversity in West Africa (e.g. Granjon & Duplantier, 2011; Westra et al., 2022), although they had a higher sampling effort than ours. Overall, our rarefaction curve suggests a satisfactory performance of our small mammal surveys, which in part might be due to the relatively low species diversity within closed-canopy forests, largely dominated by a single species. While further surveys are strongly recommended to continue documenting biodiversity in West Africa, this study contributes to filling an important knowledge gap by unveiling the small mammal species present in a major protected area and further adding a new species to the country.

3. Small mammal responses to cashew expansion in the uppermost Congo-Guinean forests of West Africa

3.1. Abstract

The conversion of native habitats into anthropogenic land-use types is one of the main drivers of biodiversity loss in the tropics. While Guinea-Bissau, in West Africa, is facing high rates of native habitat conversion into cashew orchards, little is known about such impacts on biodiversity. To address this gap, we investigated the local and landscape-scale drivers of small mammal diversity within forests and cashew orchards in Guinea-Bissau. To do so, we examined species richness, abundance, and composition across 12 sites in cashew orchards and 12 in closed-canopy forests in the Cantanhez National Park (CNP). For each site, we conducted a detailed characterization of local-scale habitat variables, including obstruction at the canopy, understory, and ground level; the number of trees with a diameter at breast height (DBH) >10 cm; the number of palm trees; vine density; and tree species richness. At the landscape scale, we assessed the percentage of forest and cashew orchards surrounding each site, as well as edge density, using multiple buffer sizes. Using Sherman live traps, we recorded 105 individuals from 7 species (5 rodents and 2 shrews). Our results revealed that understory obstruction was the main predictor of species richness, having a positive impact. Additionally, areas with a higher proportion of cashew orchards experienced significantly reduced species abundance. The extent of cashew orchards also influenced species composition. Although cashew orchards presented a higher variety of species, this is mainly due to the presence of generalist species. The forest specialist *Praomys rostratus* was largely confined to forests. We recommend prioritizing the conservation of remaining native forest fragments within the CNP, as they are crucial for supporting specialist species like *Praomys rostratus*. Therefore, it is crucial to balance the benefits of cashew orchards for generalist species with the need to safeguard native forest habitats that are critical for specialized small mammal species. Additionally, park management should enhance strategies by defining buffer zones around forested areas to mitigate the broader impacts of agricultural expansion.

3.2. Introduction

Tropical forests hold the highest species diversity globally (Hillebrand, 2004). Yet, they are succumbing to the highest deforestation rates worldwide, causing populations of forest-dwelling species to decline (Green et al., 2020). Around 30% of all endangered species in terrestrial ecosystems are forest species (IUCN 2019), with land-use changes representing one of the most serious threats to biodiversity presently (Caro et al., 2022; Sala et al., 2000). The remaining forests worldwide are increasingly more fragmented due to human activity, and the tropics are prime targets for agricultural expansion and intensification (IUCN, 2022).

Conventional agricultural practices in West Africa, such as the cultivation of rice and maize, have traditionally dominated the region's food production. However, recent decades have seen a sharp increase in the cultivation of cash crops like cocoa, coffee, and palm oil, which now play a critical role in the economies of these countries (FAO 2016). These shifts in agricultural priorities often lead to the fragmentation of native habitats (Hansen et al., 2020b) and the homogenization of landscapes, reducing the variety of ecosystems (Jeliazkov et al., 2016). Such changes in habitat structure contribute to species loss (Hurst et al., 2013; Scales & Marsden, 2008), shifts in species composition (Newbold et al., 2020; Oliveira, 2023), and declines in functional diversity (Flynn et al., 2009; Hurst et al., 2013), exacerbating the biodiversity crisis (Robertson & Swinton, 2005; Tscharntke et al., 2012). Many autochthonous forests are being converted into agricultural land, particularly for cash crop production, further impacting native species diversity (Myers et al., 2000). Despite these challenges, the extent to which these habitat changes affect species in West Africa remains unclear due to a lack of comprehensive data on species distributions in the region (Amori & Luiselli, 2011; Barnett & Prangle, 1997; Hortal et al., 2015).

In West Africa, although it only has 36,126 km², Guinea-Bissau presents great biodiversity (Temudo & Abrantes, 2014), with some Upper-Guinean forest blocks being identified as priority areas for global biodiversity conservation (Küper et al., 2004; Myers et al., 2000). Other than the capital (Bissau), Guinea-Bissau's population is mainly rural. Its native landscapes are comprised of a mosaic of open forests and wooded savannas (Catarino et al., 2008; Happold & Lock, 2013), and can be divided into three distinct zones. The litoral area can be characterized by the presence of mangrove forests, palm groves, woodlands, and canopy-covered forests. The interior regions present mosaics of woodlands, savanna, and shrubby and herbaceous steppes. The transitional zone is comprised of mosaics of woodland and savanna woodland, as well as tall grass

savannas in the inner valleys. Due to human activity, most formations present in Guinea-Bissau are secondary formations (Catarino et al., 2008). Standing amongst the top five largest producers of raw cashew nuts (Catarino et al., 2015), Guinea-Bissau's native forests are being converted into cashew (*Anacardium occidentale*) tree monocultures at unprecedented rates (Monteiro et al., 2017; Pereira et al., 2022; Temudo & Abrantes, 2014).

The Portuguese introduced cashew from Brazil to Guinea-Bissau (Catarino et al., 2015), during the 19th century, being used mainly in local farmers' gardens. Due to their high tolerance to external conditions and moderate demand on soil characteristics, cashew plantations started being implemented in fallow lands within semi-natural or savanna woodlands, to prevent erosion and recover soil (Catarino et al., 2015; Monteiro et al., 2017; Temudo & Abrantes, 2014). Following the country's independence in 1974, there has been an accelerated expansion of introduced cashew monocultures (Monteiro et al., 2017), due to high demand with them being regarded as an emerging tropical cash crop (Rege & Lee, 2023). Cashew is primarily cultivated for its nuts, which are highly valued both nutritionally and commercially, although its leaves and trunk bark are also used medicinally throughout the country (Catarino et al., 2013). By the mid-1980s, government policies aimed at boosting agricultural output resulted in large land concessions being granted to commercial farmers, sparking a rush among villagers to occupy land. Cashew became a popular choice for cultivation because of its fast growth and resilience (Catarino et al., 2015). According to FAO (2016), the yearly growth rates for the area under cultivation and production of cashews between 1978 and 2012 were 8% and 12%, respectively. West Africa is regarded as one of the most recent and active cashew production regions in the world (FAO 2016), contributing to 45% of the international cashew production in 2015 (Rabany et al., 2015), with Guinea-Bissau contributing to 15% of the raw exports worldwide. Between 2001 and 2018 alone, Guinea-Bissau lost over 77% of its closed canopy forests to cashew plantations (UN-FCCC, 2019). This country strongly relies on the export of cashew nut shells (FMI, 2015; Monteiro et al., 2017) for its economy and global cashew production is increasing exponentially due to the high demand driven by its recognized health advantages and use in various market-derived products (Dendena & Corsi, 2014; Oliveira et al., 2020). Besides its importance to Guinea-Bissau's GDP, cashew also stands as an important resource to the livelihood of smallholder farmers, which represent most of its producers (Dendena & Corsi, 2014). Appropriate management of the cashew sector is thus indispensable for inclusive growth

and poverty alleviation in Guinea-Bissau, involving around 85% of the rural population (Cont & Porto, 2014; Doré, 2006; Kyle, 2009).

The potential of cashew plantations to sustain biodiversity is widely unknown, so the consequences for biodiversity are not yet fully understood (Guedes et al., 2024; Rege & Lee, 2023). However, as the area occupied by cashew plantations increases, natural landscapes become increasingly more fragmented. Cashews are small trees cultivated in monospecific orchards with a closed and monolayered vegetation structure (Catarino et al., 2015). Orchards are often portrayed as a single-crop agroecosystem, with 98% of them being only cashews as adult trees (Monteiro, 2017). Native forest conversion into cashew monocultures thus entails a loss of structural horizontal and vertical multilayer complexity, besides the periodic removal of understory vegetation, supporting the notion that these plantations feature either a lower species diversity or a different species composition than nearby forests (Komanduri et al., 2023; Rege et al., 2020; Temudo & Abrantes, 2014), with generalist species being favored (Hurst et al., 2013; Mamba et al., 2019; Scales & Marsden, 2008; S. Vasconcelos et al., 2015b) whereas specialist species that rely on our shorter spectrum of resources are more likely to be negatively affected by these conversions (Andrade-Núñez & Aide, 2010; Palmeirim et al., 2023; Vasconcelos et al., 2015b).

Alterations in habitat structure and complexity are often associated with small mammal community structure changes and species richness (Avenant, 2000; Boahene et al., 2024), making small mammals a good indicator of the degree of disturbance in an ecosystem (Decher et al., 2001). Their reduced longevity, combined with their r-strategy traits—such as high reproductive rates, short generation times, and rapid population growth—enables them to respond quickly to shifts in environmental conditions and habitat fragmentation (Blaise & Violaine, 2018; Hurst et al., 2013; Singleton, 2010). This adaptability provides valuable insight into the consequences of land-use alterations (Avenant & Cavallini, 2007; Hoffmann & Zeller, 2005). In West Africa, non-flying small mammals typically belong to the Rodentia and Eulipotyphla orders (Oliveira, 2023; Palmeirim et al., 2024). They typically play important roles in forest ecosystems, contributing to their biological and functional diversity (Boahene et al., 2024; Decher et al., 2001; Ofori et al., 2018) as consumers, predators, dispersers of seeds, burrowers and as prey for carnivores higher on the trophic chain (Adjapong et al., 2022; Boahene et al., 2024; Osman et al., 2022). However small mammals, particularly rodents, often can also be regarded as crop pests (Abdel Rahman Ahmed et al., 2008; Htwe et al., 2021; Singleton, 2010) and reservoirs of zoonotic diseases (Andreazzi et al., 2023). In

complex and heterogeneous ecosystems, small mammal diversity is likely influenced by the degree of ecological simplification associated with specific landscape management practices (Panzacchi et al., 2010), with both local and landscape-scale characteristics playing a significant role in shaping small mammal assemblages (Lambert et al., 2006). Small mammals constitute a diverse group of species with varying habitat preferences and eating patterns, and therefore, they respond differently to changes in their habitat (Hurst et al., 2013). While forest-dependent and specialist species tend to vanish under habitat change (Henle et al., 2004), some small mammals species often flourish in disturbed or edge habitats characterized by a dense understory layer, abundant downed wood, and thick vine tangles, due to reduced predation pressure and increased resource availability (Brown et al., 2017; Byrom et al., 2014; Hilty et al., 2006; Lambert et al., 2006; Niang et al., 2022). Additionally, the vertical stratification of an ecosystem also impacts small mammal diversity (Bakker & Kelt, 2000; Malcolm & Lowman, 2004). Some species may favor higher vegetation layers for foraging and nesting (August, 1983; Malcolm, 1995), leading to variations in their abundance relative to the structure of the canopy layer. Increased habitat complexity also leads to a larger multidimensional space (Carey et al., 1999), which reduces the likelihood and intensity of interspecies interactions (Carey et al., 1980; Grant, 1972). Ultimately, this allows potentially competing species to coexist within the same community (Carey & Harrington, 2001; Carey & Johnson, 1995). Forest interior specialists that depend greatly on this habitat complexity tend to be more strongly and negatively impacted by habitat conversion (Galán-Acedo et al., 2019), whilst generalists have higher adaptability and can therefore make use of the resources from different land cover types. An effective management approach should take into account these differing responses, in order to simultaneously benefit the maximum number of species in human modified forest landscapes (Arroyo-Rodríguez et al., 2020).

In this study, we investigated the responses of small mammal communities to the conversion of forests into cashew orchards within Cantanhez National Park, located in southern Guinea-Bissau. To examine these impacts, we surveyed small mammal assemblages across 24 sampling sites, evenly distributed between native forests and areas where forests have been converted into cashew orchards. Specifically, we analyzed species richness, abundance, and composition. We accounted for local scale metrics of the habitat structure further reflecting degree of human disturbance (i.e., ground, understory and canopy obstruction; presence of palm trees and density of vines; number, species richness and maximum height of trees). At the landscape scale, we considered the percentage of native forest and cashew orchard area, as well as the

density of the edge between habitats within multiple buffer sizes. We expected overall higher small mammal diversity at higher proportions of forest cover and conversely lower proportions of cashew orchards cover. Yet, we also expected edge density to contribute to boost species diversity by increasing habitat heterogeneity at the landscape scale (Henle et al., 2004). At the local scale, species richness is expected to be positively influenced by the complexity of the understory and ground layers, while higher levels of canopy openness and increased palm tree density, indicative of ecosystem simplification, are predicted to have a negative impact. Furthermore, we hypothesize that species abundance is intrinsically linked to ecosystem complexity. Habitat features that reflect higher structural complexity, such as maximum tree height, ground, and understory obstruction, are anticipated to positively affect abundance, whereas increased canopy openness is expected to have a negative effect.

3.3. Methods

3.3.1. Study Area

Cantanhez National Park (CNP) comprises 1067 km² and is located southwest in the Tombali region in Guinea-Bissau (NE limit: 11°22'58", 14°46'12"W; SW limit: 11°02'18"N, 15°15'58"W), alongside the border with Guinea-Conacri. It is bordered on the west by the Cacine River and on the east by the Cumbijã River Estuary and stands as the largest remaining area of subtropical forest in Guinea-Bissau, which are amongst the biggest forests in West Africa (Cantanhez Management Plan, 2017). Guinea-Bissau features a predominantly flat topography, characterized by extensive coastal plains (Temudo & Abrantes, 2014). The highest point, located in the interior, reaches an elevation of 260 meters above sea level (Gippoliti & Dell'Omo, 2003). The country is characterized by two seasons: a dry season, from November to May, and a wet season, from June to October country (Catarino et al., 2015; Vasconcelos et al., 2015a). With average annual rainfall in coastal sections ranging from 2200 to 2500 mm and in the park's most central portions from 1400 to 1900 mm, CNP is the region with the most precipitation in the country. Average temperatures range from 24.7°C in January to 28°C in July (Gippoliti & Dell'Omo, 2003).

The CNP hosts a wide diversity of habitats, such as patches of forest, mangrove, savanna woodland and agricultural fields (Sousa et al., 2017). Currently, Cantanhez National Park has an estimated population of 24,000 people (Cantanhez National Park Management Plan, 2017; (Hockings & Sousa, 2013). Human settlements can be found

next to prominent natural formations, resulting in highly anthropized landscapes including reconstitution scrublands, rice, cashew, and palm plantations, as well as ruderal vegetation. These varied habitats support a high level of biodiversity by offering distinct ecological niches, allowing for the coexistence of numerous species in the park, including both endemic and endangered species (Pereira, 2022). However, slash-and-burn agriculture and the clearing of land for cashew plantations have led to significant deforestation and habitat fragmentation, threatening some of the most well-preserved patches of primary sub-humid forests in the country (Pereira, 2022). This deforestation also complicates the effective monitoring and management of these species, particularly due to the interspersed agricultural areas with forest patches, further exacerbating conservation challenges (Sousa et al., 2017). The coexistence of both natural and anthropogenic landscapes within Cantanhez National Park plays a pivotal role in shaping species composition and ecosystem processes. This intricate mosaic of habitats underscores the challenges of conservation in the region and emphasizes the park's importance as a critical area for ecological research and biodiversity preservation.

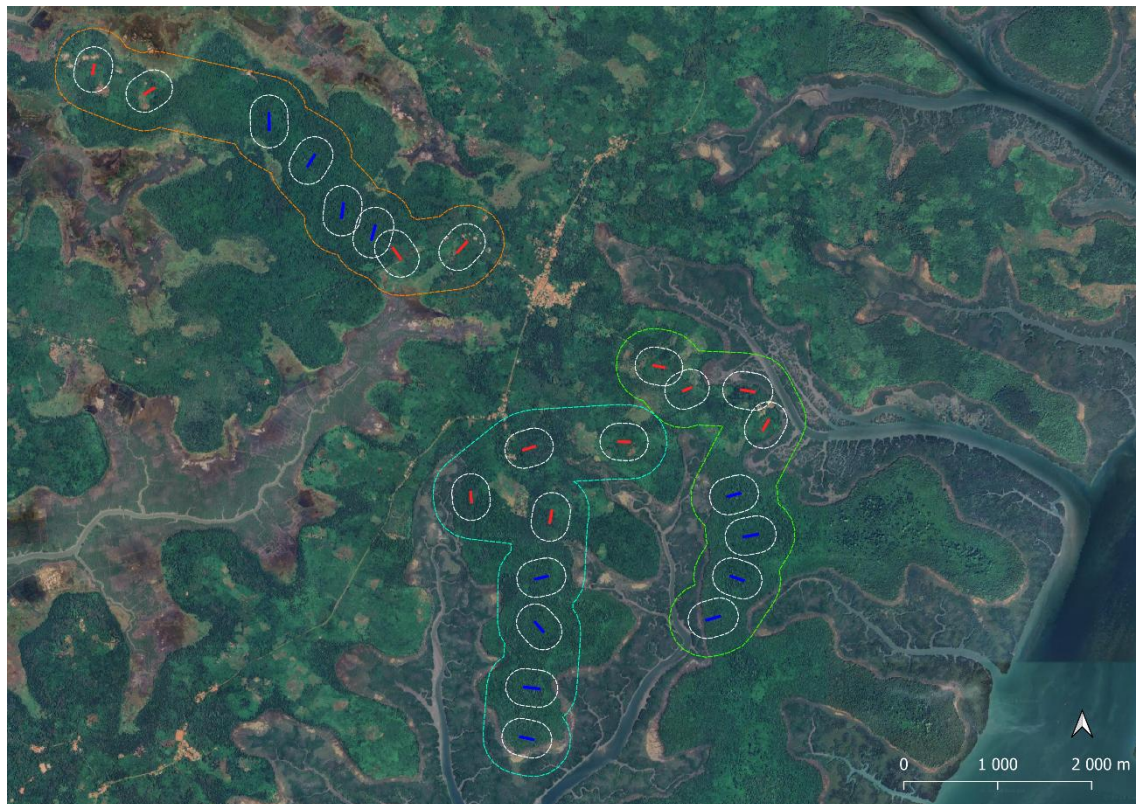


Fig. 3.1 . Google satellite image of the study area in Cantanhez National Park, showing three distinct sampling zones: Lautchande (orange), Cambeque (green), and Madina (blue). Red lines represent cashew transects, while blue lines represent forest transects. White lines represent a 200m buffer around the transects.

3.3.2. Small mammal surveys

Small mammals were sampled at 24 sites, evenly distributed between two habitat types: 12 in closed-canopy forests and 12 in cashew orchards. To ensure spatial independence, all sites were separated by a minimum distance of 200 meters. All cashew orchards sampled were previously forested areas that were converted into cashew plantations. The sampling sites were grouped into three distinct “zones”: the “Lautchande” zone (LAU), the “Madina” zone (MAD), and the “Cambeque” zone (CAM). Each zone included four forest sites and four cashew orchards (see Fig. 3.1.). Sampling within these “zones” was conducted simultaneously across all sites. Each site was sampled using a single linear live-trapping transect, including 15 stations distanced 10 meters from each other. Each station comprised a single Sherman trap (23 × 9 × 8 cm, H. B. Sherman Traps Inc., Tallahassee, Florida). In cashew orchards, traps were set exclusively on the ground, whereas in forest transects, traps were alternately deployed on the ground and in the understory (~2 m height). We undertook two trapping sessions of 8 nights in each sampling site. To sample all the 24 sampling sites, the first trapping session lasted 35 days, from 9th of October to 12th of November of 2023. The second trapping session lasted 27 days, from 13th of November to 9th of December of 2023. The sampling effort amounted to a total of 5,760 trap-nights.

The Sherman traps were baited using a mixture of sardines, banana, peanut butter and oat flakes. Every morning, the traps were checked, and all individuals captured were weighed, measured, photographed and had a tissue sample (ear tip) collected. Rodents were also tagged with a numbered metal tag in one of their ears (Fish and Small Animal Tag, size 1; National Band and Tag Co., Newport, Kentucky), to identify future recaptures. Shrews were not tagged due to their small size, and shrew recaptures were recognized based on the mark left by the ear cut. Tissue samples were subsequently analyzed using molecular techniques for later taxonomic identification. The molecular approach was chosen due to challenges in the identification of small mammals on the field. Biological material collection was collected and transported with the authorization from Guinea Bissau’s Institute of Biodiversity and Protected Areas (IBAP).

3.3.3. Genetic analysis

The tissue samples recovered from each individual's ear tips were stored in Eppendorf tubes containing 96% ethanol and subsequently examined at the Research Centre in Biodiversity and Genetic Resources (CIBIO), Portugal. Genomic DNA was extracted

from tissue samples using the ®BioBasic DNA Extraction Kit procedure. To assess the quality and rough quantity of DNA, a 0.8% agarose gel electrophoresis analysis stained with GelRed™ (Biotium) was carried out.

The mitochondrial cytochrome b (Cytb) gene was used for molecular taxonomic identification, as has been done in previous research (e.g., Mamba et al., 2021; Lecompte et al., 2002; Pagès et al., 2010), and to guarantee adequate haplotype coverage for the investigated families and taxa. The Cytb gene was amplified using the primer set H15915/L14723 (Irwin et al., 1991). For genera in which this primer pair was unsuccessful in amplifying or providing high-quality sequences, a new primer set was designed based on full Cytb gene sequences of Guinea-Bissau's small mammals retrieved from GenBank - Cytb_RodF1 (forward, 5'- GAC ATG AAA AAT CAY CGT TG -3') and Cytb_RodR1 (reverse, 5'- CAT TTY TGG TTT ACA AGA CC -3').

PCRs (Polymerase Chain Reactions) were carried out in a final volume of 10 µL, containing 5 µL of MyTaq™ Mix (Bioline), 0.4 µM of each primer, 3.2 µL of ultra-pure water, and 1 µL of DNA. For the H15915/L14723 set, the PCRs were run under the following thermal conditions: 15 minutes of initial denaturation at 95 °C; 7 cycles at 95 °C for 30 s, 59 °C decreasing by 0.5 °C per cycle for 30 s and 1 minute at 72 °C; then 33 cycles at 95 °C for 30 s, 56 °C for 30 s and 1 minute at 72 °C; and a final elongation step at 60 °C for 10 min. For the new primer pair (Cytb_RodF1/R1), the PCRs were run under the following thermal conditions: 15 minutes of initial denaturation at 95 °C; 40 cycles at 95 °C for 30 s, 53 °C for 30 s, and 1 minute at 72 °C; and a 10-minute final elongation step at 60 °C. ExoSap (USB® ExoSAP-IT® PCR Product Cleanup, Affymetrix) was used to purify the PCR products. A 10-µL sequencing reaction was prepared using BigDye® Terminator v3.1 Sequencing Kits (AB Applied Biosystems) according to the manufacturer's protocol. Lastly, Sephadex was used to purify the sequencing products, which were then sequenced using capillary electrophoresis on an ABI 3500XL Genetic Analyzer (Applied Biosystems).

The chromatograms were examined using Geneious 8 v.8.1.9 (Kearse et al., 2012), and resulting sequences were identified to the lowest possible taxonomic level using the NCBI database's Basic Local Alignment Search Tool (BLAST) (Sayers et al., 2022).

3.3.4. Local and Landscape Scale Variables

To understand the drivers of small mammal diversity across sampling sites, a set of local and landscape scale variables was predicted to affect the trophic and structural habitat availability for small mammals. In each sampling site, four stations matching the small mammal transect (corresponding to distances of 0m, 40m, 90m, and 140m from the start of the transect) were targeted for measuring the set of local scale variables. These variables included obstruction at the canopy, understory and ground level, number of trees with a diameter at breast height (DBH) >10 cm, number of palm trees, vine density and tree species richness. Each variable was selected based on its ecological relevance to small mammal habitat use and distribution. Canopy, understory, and ground-level obstruction reflect habitat complexity, influencing movement, shelter availability, and predation risk. The number of trees with DBH >10 cm was included to account for the role of larger trees in providing critical resources such as nesting sites and food. The number of palm trees was measured as an indicator of anthropogenic disturbance, as palm cultivation often correlates with human-modified landscapes. Vine density was included due to its potential to enhance connectivity and provide shelter, while tree species richness was considered a proxy for resource diversity.

At the landscape scale, we measured the proportion of forest and cashew orchards, as well as the edge density, using multiple buffer sizes. To do so, we used the GIS made available by Pereira et al (2022), who mapped the different land-use types across the Cantanhez National Park, including cashew orchards, urban area, forest, mangrove, sparse vegetation/savanna and water. To calculate the proportions of each habitat type, the coordinates of stations were overlapped with the map produced from this study using QGIS v.3.24.1 (QGIS Development Team, 2022). Different buffer polygons for each transect were produced with the following radius: 100, 150, 200, 250 and 300 meters. Buffer sizes were chosen to capture habitat features at different spatial scales, reflecting potential home-range sizes and broader landscape-level influences on small mammal populations. Mangrove areas represented a minor habitat type within the buffers considered (Fig S3.1.). Yet, for simplicity's sake, we considered forest and mangrove within the same category of land-use. Using the line tool in QGIS (QGIS Development Team, 2022), the edges of each habitat within each buffer were also delineated, to calculate the total edge length of each sampling site. We then used the following formula for each transect to calculate the edge density: $ED = \frac{E}{A} * 10000$; where **ED** represents edge density, **E** is the length of the edge (in meters) at each sampling site, and **A** is the area within the buffer (in square meters). Four of the cashew plantations (CSH 9 to 12, located in the MAD zone) were more recent when compared to the others and thus the

Table 3.1 - Environmental variables measured in cashew Orchards and canopy-covered forests at local and landscape scales. Local scale variables include canopy openness, maximum tree height, ground and understory level obstruction, density of trees and vines within a 5-meter radius and density of palm trees and tree species richness within a 10-meter radius. Landscape variables, such as the percentage of native forest area, cashew area, and edge density, were calculated using QGIS for 100m and 250m buffers, which were determined to be the most suitable spatial scales for the landscape-scale predictors.

Name - Code Name	Variable Description	Range (Mean±SD)
Cashew Orchards		
Local Scale		
In a 5-meter radius:		
Canopy openness (%) - CAP	Photos were taken at the center of each station using a smartphone's wide-angle (0.5x) camera and later analyzed with the Gap Light Analyzer software (Frazer, 1999) to measure the percentage of canopy openness.	5.28-99.89 (21.88±18.57)
Maximum tree height (m) - MXH	Using the same person for scale, the heights of the three tallest trees were estimated, and then averaged out	2.50-14.17 (7.15±2.75)
Ground level obstruction (%) - GRD	The ground-level obstruction (0 to 50 cm height) was estimated on a scale from 0 to 100%.	60.00-97.00 (87.12±10.39)
Understory level obstruction (%) - UST	The understory-level obstruction (50 cm to 2m height) was estimated on a scale from 0 to 100%.	0.00-95.00 (42.00±27.18)
Number of trees/m ² - NRT	The number of trees with a diameter over 10 cm at breast height was counted and then divided by the area of the 5-meter radius.	0.000-0.114 (0.032±0.021)
Vine density - VD	Vine density was classified on a scale from 0 (no vines) to 5 (maximum density)	0-1 (0.021±0.144)
In a 10 meter radius:		
Number of oil or coconut palm trees/m ² - NRP	With a local guide's help, the number of palm trees was counted and divided by the area of the radius	0.000-0.029 (0.004±0.007)
Tree species richness - TSR	With a local guide's help, the number of tree species in the radius was estimated.	1-8 (2.128±1.424)
Landscape Scale		
In a 100m buffer:		
Proportion of native forest area (%) - FOR	The percentage of native forest within this buffer was determined using QGIS, based on the shapefile created by Pereira (2022)	18.40-71.11 (43.94±18.02)
Proportion of cashew area (%) - CSH	The percentage of cashew orchards within this buffer was determined using QGIS, based on the shapefile created by Pereira (2022)	21.53-76.06 (53.83±17.87)
Edge density - ED	The length of habitat edge within this buffer was determined using QGIS, based on the shapefile created by Pereira (2022), and was subsequently divided by the area of the buffer	86.079-282.927 (188.820±71.425)
In a 250m buffer:		
Proportion of native forest area (%) - FOR	The percentage of native forest within this buffer was determined using QGIS, based on the shapefile created by Pereira (2022)	26.02-85.94 (54.85±17.68)
Proportion of cashew area (%) - CSH	The percentage of cashew orchards within this buffer was determined using QGIS, based on the shapefile created by Pereira (2022)	7.30-57.94 (34.35±15.63)
Edge density - ED	The length of habitat edge within this buffer was determined using QGIS, based on the shapefile created by Pereira (2022), and was subsequently divided by the area of the buffer	86.411-244.333 (158.006±54.270)
Canopy-Covered Forests		
Local Scale		
In a 5-meter radius:		
Canopy openness (%) - CAP	Photos were taken at the center of each station using a smartphone's wide-angle (0.5x) camera and later analyzed with the Gap Light Analyzer software (Frazer, 1999) to measure the percentage of canopy openness.	2.06-23.94 (9.164±4.078)
Maximum tree height (m) - MXH	Using the same person for scale, the heights of the three tallest trees were estimated, and then averaged out	6.833-24.667 (14.765±4.366)
Ground level obstruction (%) - GRD	The ground-level obstruction (0 to 50 cm height) was estimated on a scale from 0 to 100%.	30.00-97.00 (71.812±15.417)
Understory level obstruction (%) - UST	The understory-level obstruction (50 cm to 2m height) was estimated on a scale from 0 to 100%.	15.00-85.00 (52.083±18.184)
Number of trees/m ² - NRT	The number of trees with a diameter over 10 cm at breast height was counted and then divided by the area of the 5-meter radius.	0.012-0.114 (0.052±0.022)
Vine density - VD	Vine density was classified on a scale from 0 (no vines) to 5 (maximum density)	0-3 (1.896±1.077)
In a 10 meter radius:		
Number of oil or coconut palm trees/m ² - NRP	With a local guide's help, the number of palm trees was counted and divided by the area of the radius	0.000-0.025 (0.001±0.001)
Tree species richness - TSR	With a local guide's help, the number of tree species in the radius was estimated.	2-7 (4.362±1.131)
Landscape Scale		
In a 100m buffer:		
Proportion of native forest area (%) - FOR	The percentage of native forest within this buffer was determined using QGIS, based on the shapefile created by Pereira (2022)	82.98-100.00 (97.61±5.70)
Proportion of cashew area (%) - CSH	The percentage of cashew orchards within this buffer was determined using QGIS, based on the shapefile created by Pereira (2022)	0.00-12.14 (1.01±3.50)
Edge density - ED	The length of habitat edge within this buffer was determined using QGIS, based on the shapefile created by Pereira (2022), and was subsequently divided by the area of the buffer	0.000-135.029 (16.564±41.563)
In a 250m buffer:		
Proportion of native forest area (%) - FOR	The percentage of native forest within this buffer was determined using QGIS, based on the shapefile created by Pereira (2022)	71.05-100.00 (95.83±8.34)
Proportion of cashew area (%) - CSH	The percentage of cashew orchards within this buffer was determined using QGIS, based on the shapefile created by Pereira (2022)	0.00-7.43 (1.00±2.22)
Edge density - ED	The length of habitat edge within this buffer was determined using QGIS, based on the shapefile created by Pereira (2022), and was subsequently divided by the area of the buffer	0.000-139.564 (23.123±41.607)

previous map was not accurate to their current proportions. As such, satellite imagery obtained from Google Earth v.9.180.0.1 (Google LLC, 2023) was used to better characterize these sites. All local and landscape scale variables are detailed in the respective table (see Table 3.1.).

3.3.4. Data Analysis

Small mammal diversity was evaluated considering species richness, species abundance, and species composition. Species richness corresponds to the number of species recorded; species abundance to the number of individuals recorded (excluding recaptures); species composition refers to the identity and relative abundances of species in a given area. In this study, species composition was assessed using Non-Metric Multidimensional Scaling (NMDS), with the first axis of the analysis capturing the variation in species composition across sites. The NMDS analysis used the Bray-Curtis dissimilarity index and was conducted in two dimensions ($k = 2$) using the “metaMDS” function from the “vegan” package in R (Oksanen et al., 2013). Four sampling sites (i.e. CSH3, CSH4, CSH7, and CSH12) were excluded from the NMDS analysis due to the absence of any small mammal record. The resultant NMDS ordination presented a stress value of 0.033, suggesting a highly faithful representation of the dissimilarities in the dataset (Clarke, 1993).

To examine how the local habitat variables vary between each sampling site, a Principal Component Analysis was conducted using the base R function “prcomp”. The “ggbiplot” function from the “ggbiplot” package (Vu, 2011) was used to create enhanced and customizable biplots for visualizing the results. The first two components of the Principal Component Analysis (PCA) accounted for 70.04% of the total variability in habitat characteristics across sites (PC1 explains about 51.63% of the data; PC2 explains an additional 18.41%). The PCA biplot revealed a clear separation between forested areas and cashew orchards along the x-axis (PC1), with cashew orchards displaying greater variability within their group (Fig.S3.3.).

3.3.4.1. Sampling Sufficiency

To evaluate sampling sufficiency at each site, rarefaction curves were analyzed using the “iNEXT” function from the “iNEXT” package in R (Hsieh et al., 2016). These curves illustrate the relationship between the number of observed species and the number of sampled individuals, indicating whether further sampling might uncover additional

species (indicated by a positive slope) or if the current sampling effort has captured most species present (suggested by a leveling off of the curve). Sites with no captures, i.e., CSH3, CSH4, CSH7, and CSH12, were excluded from this analysis.

3.3.4.2. Scale of Effect Analysis

The scale of effect was evaluated for each of the three landscape scale variables (i.e., % of cashew area; % of native forest area and edge density) to determine the spatial extent at which landscape variables most strongly influence observed species richness, abundance, and composition (Jackson & Fahrig, 2015). Prior to model fitting, the distribution of each response variable was assessed using the “descdist” function from the “fitdistrplus” package (Delignette-Muller & Dutang, 2015). Generalized Linear Mixed Models (GLMMs) were applied to analyze observed species richness, as well as species abundance, using the “glmer” function from the “lme4” package (Bates, 2016). Linear Mixed Models (LMMs) were employed for species composition analysis using the “lmer” function from the “lme4” package (Bates, 2016). For each response variable, a total of 10 models were fitted, with each model corresponding to a different buffer size (100, 150, 200, 250, and 300 m-radii) across two habitat types (forest and cashew orchards). The “zone” in which each sampling site was located was included as a random effect in all models to account for spatial nestedness. Model selection was conducted using the Akaike Information Criterion corrected for small sample sizes (AICc) (Burnham & Anderson, 2004). Models were ranked from lowest to highest AICc values, with the most plausible models identified based on a difference lower than 2 between the lowest AICc and the corresponding AICc. In cases where the AICc difference between top-ranked models was less than 2, conditional R^2 values (R^2c) were used to select the buffer size for subsequent analyses (e.g., Oliveira, 2023 and Palmeirim et al., 2018). Given the high correlation between all landscape-scale habitat variables values (Table S3.1.), we selected the one that provided the best model fit for each response variable variable. Specifically, we used the proportion of forests for analyzing species composition, whilst the proportion of cashews was used for analyzing observed species richness and abundance, as it yielded lower AICc values and higher R^2c values, ensuring a consistent approach across our analyses. The best buffer scales for evaluating different ecological metrics were determined as follows: for observed species richness and abundance, the 250 m buffer scale proved most effective (AICc = 67.465, R^2c = 0.040 for observed species richness; AICc = 133.701, R^2c = 0.711 for species abundance). In contrast, the 100 m buffer scale was most suitable for assessing species composition (AICc = 71.306, R^2c = 0.494) (Table S3.2.).

3.3.4.3. Patterns and Predictors of Small Mammal Diversity

Initially, the variation in species composition between forests and cashew plantations was assessed by examining the ordination diagram generated through Non-Metric Multidimensional Scaling (NMDS) (Kruskal, 1978). To statistically compare species composition across habitat types, a Permutational Multivariate Analysis of Variance (PERMANOVA) was performed using the “adonis2” function, and the homogeneity of group dispersions was evaluated with a Permutational Analysis of Multivariate Dispersions (PERMDISP) using the “betadisper” function, both from the “vegan” R package (Oksanen et al., 2013).

To investigate the predictors of small mammal diversity at both local and landscape scales, Generalized Linear Mixed Models (GLMMs) were applied to analyze observed species richness and abundance, while a Linear Mixed Model (LMM) was used to examine species composition, represented by the scores of NMDS axis 1. For species richness, a Poisson distribution was used, and we utilized the “glm” function from the “stats” package (Team, 2020). To account for overdispersion in species abundance, the “glm.nb” function from the “MASS” package (Venables & Ripley, 2013) was employed to fit a negative binomial distribution. The sampling unit ‘zone’ was initially included as a random effect in all the models. However, it was not retained in the models for any of the response variables, as it did not significantly improve the model fit, as indicated R^2_c and R^2_m values being equal ($R^2_m/R^2_c = 0.512$ for observed species richness; $R^2_m/R^2_c = 0.607$ for species abundance; $R^2_m/R^2_c = 0.745$ for species composition). When high correlation between two variables (i.e., $> |70\%|$) was detected, the variable deemed less ecologically relevant or less directly related to the response variable was removed to avoid multicollinearity. The variables retained included: % of forest/cashew orchards (depending on the response variable), ground level obstruction, understory level obstruction, canopy openness, number of palm trees, and maximum tree height.

The “dredge” function from the “MuMIn” package (Barton, 2009) was utilized to create a set of candidate models by varying predictors and ranking them based on their AICc values. This methodology was used to identify the models that best represent the data while accounting for both model complexity and sample size. Following this, the “model.avg” function from the “MuMIn” package (Barton, 2009) was applied to average results from best models (i.e., $\Delta AICc < 2$). The model assumptions were evaluated using the “simulateResiduals” function, from the “DHARMA” package (Hartig, 2020). The

residuals were subsequently plotted to analyze the model fit. The results of this assessment confirmed that the model assumptions were met and that the model fit the data appropriately, without significant issues related to residuals, dispersion, or outliers, ensuring the reliability and accuracy of the model results for both species abundance and composition. For species richness, however, the model revealed significant quantile deviations, yet only at higher quantiles. This likely resulted from the data distribution which included 13 sites (54.16%) where only one species has been recorded, posing difficulty in adjusting a fitting distribution to the model.

3.4. Results

A total of 105 individuals were recorded, yielding a trapping success rate of 1.82% (excluding recaptures). We identified seven species, comprising two shrew species (Eulipotyphla) and five rodent species (Rodentia). The most frequently recorded species was the forest soft-furred mouse (*Praomys rostratus*), which constituted 68.57% of all captures (N = 72 records) across 13 (54.17%) sampling sites. The second most common species was the Guinea multimammate mouse (*Mastomys erythroleucus*), representing 11.42% of the records (N = 12) (Fig. S3.2.). All recorded species were native to West Africa except for the black rat (*Rattus rattus*) which was recorded only once at a cashew orchard. Although *Praomys rostratus* was the most prevalent species, it was predominantly found in forested areas, with only two individuals captured in cashew orchards. In contrast, the remaining species – the Guinea multimammate mouse (*Mastomys erythroleucus*), the Guinean gerbil (*Gerbilliscus guineae*), Matthey's mouse (*Mus mattheyi*), the African giant shrew (*Crocidura olivieri*), an unidentified shrew (*Crocidura* sp.), and the black rat (*Rattus rattus*) — were primarily associated with cashew orchards, except for one individual of *Mus mattheyi* recorded in CAM3 and one *Mastomys erythroleucus* observed in LAU3 (Table 3.2.).

Table 2.2. – Number of small mammal records across closed-canopy forests and cashew orchards in Cantanhez National Park

Order	Family	Species	Closed-Canopy Forests	Cashew Orchards
Rodentia				
	<u>Muridae</u>			
		<i>Gerbilliscus guinea</i>		5
		<i>Mastomys erythroleucus</i>	1	11
		<i>Mus mattheyi</i>	1	9
		<i>Praomys rostratus</i>	70	2
		<i>Rattus rattus</i>		1
Eulipotyphla				
	<u>Soricidae</u>			
		<i>Crocidura olivieri</i>		1
		<i>Crocidura sp.</i>		4

Three species were recorded in the sampling sites located in the forests (mean $\pm$ SD: 1.17 ± 0.39 species) and seven species were recorded in sites located in the cashew orchards (1.25 ± 1.14). Most small mammals captured were found in forests, with 68.57% of all individuals being recorded within forest sites. The number of individuals captured in forest habitats ranged from 1 in MAD1 and MAD3 to 16 in CAM1 (6.00 ± 4.16). In contrast, the number of individuals captured in cashew orchards varied from 0 in CSH 3, 4, 7, and 12 to 13 in CSH 6 (2.75 ± 3.96). The rarefaction curves suggest that the sampling effort for forested areas represented by CAM, LAU, and some MAD sites (MAD1, MAD2) is largely adequate (Fig. 3.2.). In contrast, some - but not all - MAD sites (MAD3, MAD4) show signs of incomplete sampling. Given the reduced number of records in the sites located in the cashew orchards, the corresponding rarefaction curves did not reach an asymptote and show wider confidence intervals.

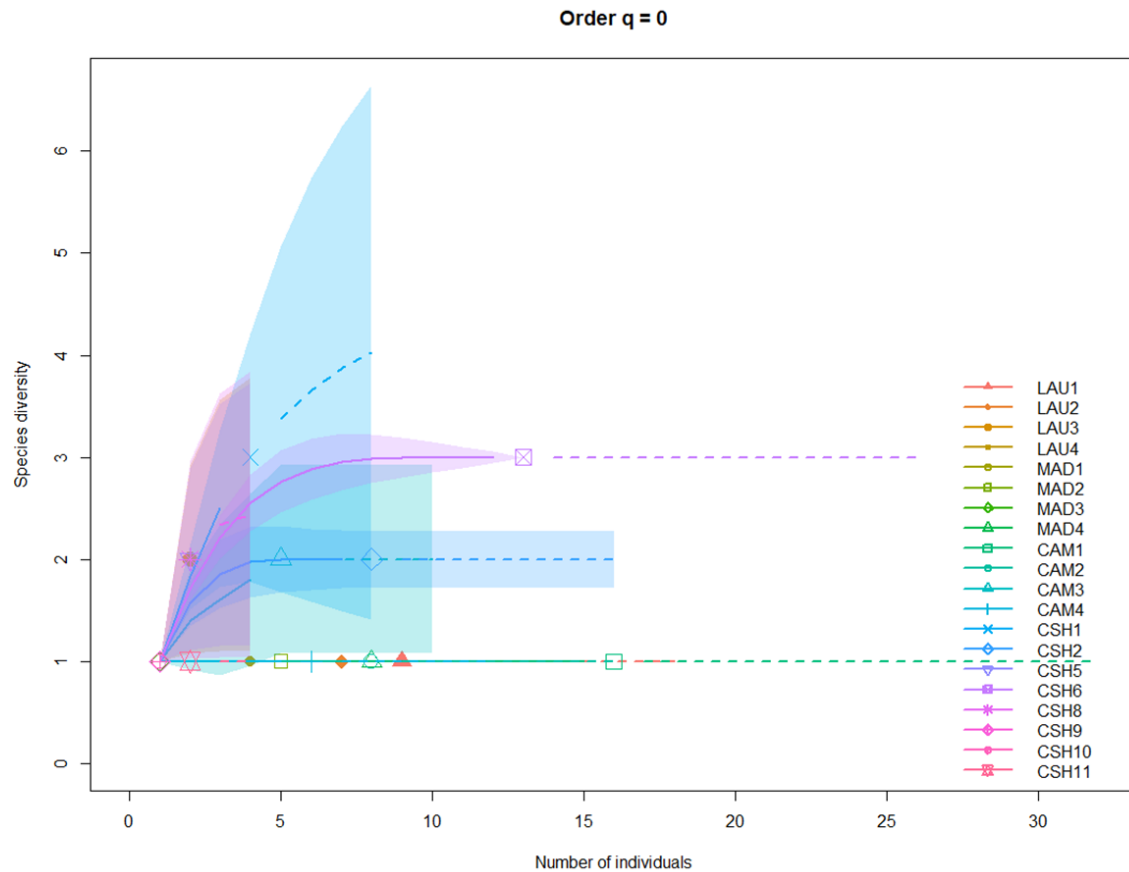


Fig. 3.2 - Rarefaction curves representing species diversity (y-axis) as a function of the number of individuals (x-axis) across different sampling sites in Parque Nacional de Cantanhez. Each curve corresponds to a specific transect, identified by different colors and markers (listed in the legend on the right).

3.4.1. Patterns and predictors of small mammal diversity

3.4.1.1. Species Richness

The best-fitting model included “understory obstruction” and “canopy openness” (Table S3.3.). According to this model, understory obstruction had a positive effect on species richness ($\beta_{UST} = 0.444$, $p = 0.044$). (Table 3.3.).

Table 3.3 - Best model for analysing species richness. Model considered "Understory Obstruction" (UST) and "Canopy Openness" (CAP) as coefficients. Significant values at the conventional p-value threshold of 0.05 are marked in green

	Estimate	Std. Error	z value	Pr(> z)
Intercept	0.064	0.209	0.306	0.760
Understory (UST)	0.444	0.220	2.014	0.044
Canopy (CAP)	0.221	0.147	1.502	0.133

3.4.1.2. Species Abundance

The average of all best-fitting models included canopy openness, understory obstruction and ground obstruction; and by the % of cashew orchards, on a landscape scale (Table S3.4.). The results from these models indicated that the % of area covered by cashew orchards had a negative effect on species abundance ($\beta_{\text{CSH}} = -0.813$, $p = 0.002$) (Table 3.4.).

Table 3.4. – Averaged model for analysing species abundance. Model considered "% of Area Covered by Cashew Orchards" (CSH), "Understory Obstruction" (UST), "Canopy Openness" (CAP) and "Ground Obstruction" (GRD) as coefficients. Significant values at the conventional p-value threshold of 0.05 are marked in green

	Estimate	Std. Error	Adjusted SE	z value	Pr(> z)
Intercept	1.242	0.188	0.199	6.230	< 2e-16
%Cashew Orchards (CSH)	-0.813	0.253	0.266	3.057	0.002
Understory (UST)	0.309	0.224	0.237	1.303	0.193
Canopy (CAP)	0.208	0.162	0.172	1.208	0.227
Ground (GRD)	0.258	0.227	0.241	1.074	0.283

3.4.1.3. Species Composition

The NMDS plot illustrated a significant difference in species composition between the cashew and forest sites (Fig.3.3.). Each habitat supports a distinct assemblage of species, as evidenced by the minimal overlap in species distributions between the two habitats. Furthermore, cashew orchards exhibited greater heterogeneity in species

composition compared to the forests. Specifically, *Praomys rostratus* was closely associated with forest habitats, whereas *Crocidura olivieri*, *Crocidura* sp., *Gerbilliscus guineae*, *Mastomys erythroleucus*, *Mus mattheyi*, and *Rattus rattus* were more strongly related with cashew habitats.

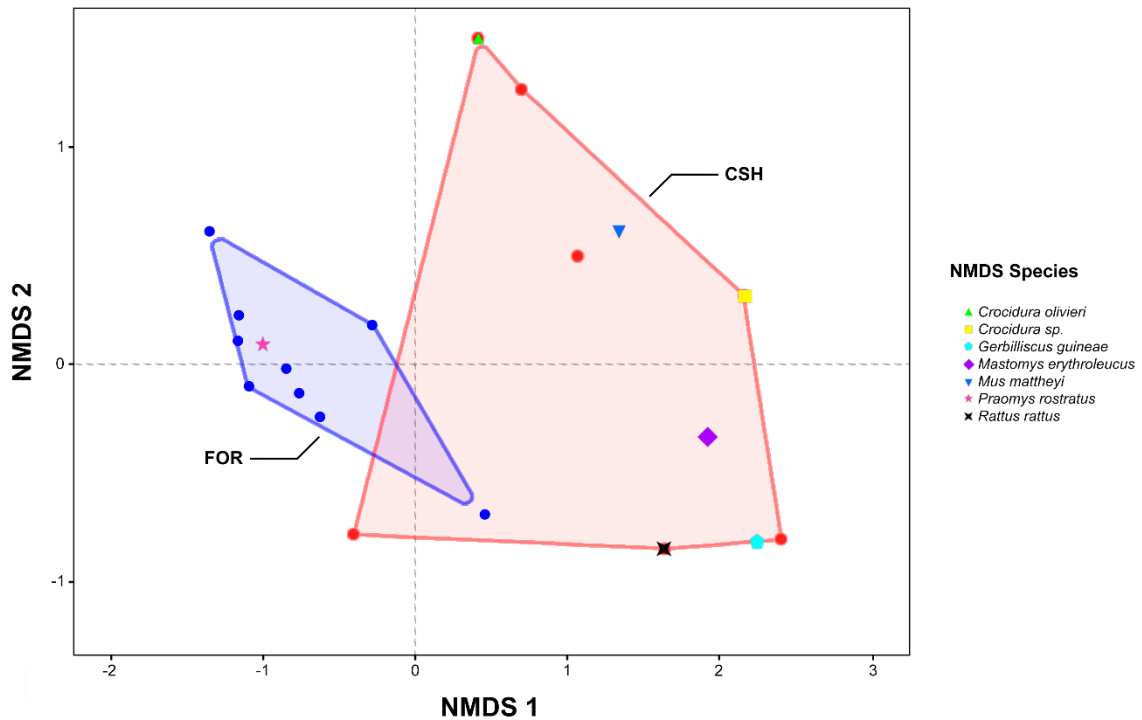


Fig. 3.3 - NMDS plot showing small mammal species composition across forest (FOR) and cashew orchard (CSH) habitats. The X-axis (NMDS 1) and Y-axis (NMDS 2) represent ordination axes derived from non-metric multidimensional scaling (NMDS), summarizing species composition differences between habitats. Points represent individual sample sites, with blue circles for forest (FOR) and red circles for cashew orchards (CSH). The shaded areas enclose samples within each habitat type. Different species are represented by symbols and colors: **Green triangle:** *Crocidura olivieri*; **Yellow square:** *Crocidura* sp.; **Cyan pentagon:** *Gerbilliscus guineae*; **Purple diamond:** *Mastomys erythroleucus*; **Blue downward triangle:** *Mus mattheyi*; **Pink star:** *Praomys rostratus*; **Black X:** *Rattus rattus*

The PERMANOVA analysis revealed a highly significant difference in species composition between cashew plantations and forest sites ($p = 0.001$), with habitat type explaining a substantial proportion of the variation in composition ($R^2 = 0.352$) (Table 3.5.). The PERMDISP analysis suggested a marginal difference in species dispersion between cashew plantations and forests; however, this difference was not statistically significant at the conventional 0.05 level (ANOVA: $p = 0.076$; Permutation Test: $p = 0.081$) (Tables 3.6. and 3.7.).

Table 3.5 - PERMANOVA results showing the effect of habitat on small mammal species composition. Habitat type explains 35.2% of the variation in species composition ($p = 0.001$), marked in green, indicating a statistically significant effect of habitat on species composition. Residual variation accounts for the remaining 64.8%

	Df	Sum Sq	R2	F	Pr(>F)
Habitat	1.000	2.120	0.352	9.773	0.001
Residual	18.000	3.905	0.648		
Total	19.000	6.025	1.000		

Table 3.6 - ANOVA results showing the effect of groups on dispersion. The group effect explains 16.4% of the variation in dispersion, with an ANOVA result of $p = 0.076$, which is not statistically significant (p -value threshold = 0.05). Residual variation accounts for 83.6%.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Groups	1.000	0.208	0.208	3.533	0.076
Residuals	18.000	1.060	0.059		

Table 3.7. - PERMDISP results showing the effect of groups on dispersion. The PERMDISP result of $Pr(>F) = 0.081$ is not statistically significant (p -value threshold = 0.05).

	Df	Sum Sq	Mean Sq	F	N.Perm	Pr(>F)
Groups	1.000	0.208	0.208	3.533	999.000	0.081
Residuals	18.000	1.060	0.059			

The average of all best-fitting models included canopy openness, maximum tree height, and understory obstruction, along with the % of area covered by native forests at the landscape scale (Table S3.5.). This model revealed that canopy openness significantly influences species composition ($\beta_{CAP} = 0.624$, $p = 0.004$). In addition, the extent of native forest cover and maximum tree height were also identified as significant predictors of species composition ($\beta_{FOR} = -0.418$, $p = 0.014$; $\beta_{MXH} = -0.540$, $p = 0.011$). It is noteworthy that the effect of canopy openness on species composition was in the opposite direction compared to the other variables ($\beta_{CAP} = 0.624$, $p = 0.004$) (Table 3.8.).

Table 3.8. - Averaged model for analysing species composition. Model considered “Canopy Openness” (CAP), “Maximum Tree Height” (MXH), “Understory Obstruction” (UST) and “% of Area Covered by Native Forests” (FOR) as coefficients. Significant values at the conventional p-value threshold of 0.05 are marked in green

	Estimate	Std. Error	Adjusted SE	z value	Pr(> z)
Intercept	0.000	0.141	0.152	0.000	1.000
Canopy (CAP)	0.624	0.207	0.219	2.849	0.004
Tree Height (MXH)	-0.540	0.198	0.214	2.528	0.011
Understory (UST)	-0.271	0.150	0.161	1.681	0.093
%Forest (FOR)	-0.418	0.159	0.171	2.445	0.014

3.5. Discussion

As hypothesized, we found that areas with a higher % of cashew orchards exhibited lower small mammal abundance, primarily due to the absence of *Praomys rostratus*, a forest-specialist species that constituted a substantial portion of the captured biomass in the Cantanhez National Park. At the local scale, species richness was positively associated with understory complexity, affirming our hypothesis that more complex vegetation supports greater diversity. At the local scale, species richness exhibited a positive association with understory complexity, supporting our hypothesis that increased vegetation complexity enhances biodiversity.

Our results showed that species composition varied significantly between cashew orchards and canopy-covered forest sites, illustrating the role of habitat type in determining species presence. Canopy-covered forests exhibited a more homogeneous species composition, predominantly characterized by the forest-specialist *Praomys rostratus*. This species, native to Western Africa, was observed almost exclusively within forest habitats. *P. rostratus* is known for its ground foraging behavior, climbing abilities, and mixed diet, which includes seeds, fruits, and insects (Hanney, 1965; Genest-Villard, 1980; Happold, 2013). *Praomys rostratus* constituted a significant portion of the small mammal biomass in CNP, with over half of the captured individuals belonging to this species. Previous research in the Boé region of southeastern Guinea-Bissau also identified *P. rostratus* as a dominant species. However, in that study, *P. rostratus* was observed occupying a broader range of habitats, including abandoned agricultural fields (Westra et al., 2021). In contrast, *P. rostratus* was notably absent from surveys conducted in the Oio region of northern Guinea-Bissau (Oliveira, 2023). In contrast, cashew orchards supported a more diverse assemblage of generalist species, including

Crocidura olivieri, *Crocidura sp.*, *Gerbilliscus guineae*, *Mastomys erythroleucus*, *Mus mattheyi*, and *Rattus rattus*. *Praomys rostratus* was notably absent from cashew orchards. These small mammals are terrestrial species typically associated with open-area habitats such as grasslands, savannas, and agricultural fields across Sub-Saharan Africa (Monadjem et al., 2015). Additionally, a specimen of *Rattus rattus* was found within the cashew orchards. This introduced species, now widespread in Sub-Saharan Africa, often thrives in human settlements, where it benefits from human food and waste (Konečný et al., 2013). *Rattus rattus* is known for its prolific breeding and potential as a significant pest (Monadjem et al., 2015), and reservoir of diseases (Kamani et al., 2013). Beyond rodents, two shrew species were also documented. *Crocidura olivieri*, a generalist species inhabiting various anthropized landscapes, savannas, and forest habitats across Sub-Saharan Africa, was captured in cashew orchards (Churchfield et al., 2013). The second shrew could not be identified taxonomically down to the species level, but it is likely another generalist terrestrial species, as it was found exclusively in cashew orchards. These findings highlight the crucial role of native canopy-covered forests in preserving the diversity of forest specialist species, such as *Praomys rostratus*, which rely on the complex vegetation structures of forest environments (Monadjem et al., 2015). In contrast, cashew orchards primarily supported assemblages of small mammal generalist species that are adapted to and thrive under disturbed conditions.

3.5.1. Species Richness

As observed in previous studies (Bowman et al., 2001; Carrilho et al., 2017; Rhim et al., 2015), understory obstruction emerged as the primary significant predictor of species richness among small mammals. This positive correlation between understory obstruction and species richness suggests that areas with denser understory vegetation support a more diverse assemblage of small mammals. A well-developed understory layer provides essential resources such as shelter and protection from predators (Choi & Choi, 2007; Rosalino et al., 2009; Torre et al., 2014) and a greater variety of food resources (Blaum et al., 2009). Additionally, increased understory density contributes to greater vegetation complexity, which, in turn, supports a higher diversity of ecological niches (Bowman et al., 2001; Carey & Harrington, 2001; Carey et al., 1999; Panzacchi et al., 2010), thereby facilitating the presence of a more varied assemblage of small mammal species.

Contrary to our expectations, however, landscape-scale variables did not appear to significantly influence species richness of small mammals in this study. Although larger-scale habitat features, including patch size, connectivity, and landscape composition are

often cited as influential factors in affecting small mammal diversity (Palmeirim et al., 2020), our results suggest that these factors were not strong determinants of species richness in the study area. Given that small mammals typically have more limited home range sizes (Swihart et al., 1988), it is plausible that local-scale habitat characteristics, such as understory obstruction, exerted a more substantial influence on species richness at the site level, thereby overshadowing the effects of broader landscape factors (Delciellos et al., 2016).

3.5.2. Species Abundance

As anticipated, the proportion of area covered by cashew orchards exhibited a pronounced negative impact on species abundance. The monoculture practices inherent to these non-native plantations lead to a marked reduction in plant diversity and a simplification of the vegetation structure (Catarino et al., 2015). This homogenization of the habitat likely limits the availability of resources for small mammal species, ultimately resulting in a decrease in their population density. Furthermore, our analysis revealed a strong positive relationship between the extent of cashew orchard coverage and increased edge density (see Table S3.1.). Edge effects, which arise from the juxtaposition of different habitat types, are closely linked to the quality of the local habitat. These effects can significantly influence the spectrum of ecological niches available, thereby shaping local species diversity (August, 1983). Forest-dependent species are particularly at risk in such altered landscapes, as they often struggle to navigate the fragmented habitat and are less capable of crossing the open areas between isolated forest patches. This increased isolation can lead to higher extinction risks for these species, as they become confined to diminishing and disconnected habitats (Henle et al., 2004; Palmeirim et al., 2018).

3.5.3. Species Composition

At the landscape scale, the amount of native forest significantly influenced species composition. Landscapes with higher forest cover feature more complex vegetation structures and greater fruit availability, which together create suitable habitats for arboreal species (Arroyo-Rodríguez et al., 2020). The higher the percentage of native forest, the more viable populations of forest-specialist species are likely to persist, as the increased habitat area supports more species, as predicted by species-area relationships (Fahrig, 2013). Consistent with previous studies (Estavillo et al., 2013; Palmeirim et al., 2018; Santos-Filho et al., 2016), forest-specialist small mammal species were less frequently encountered in areas with lower proportions of native forest. This

shift is associated with a replacement of forest specialists by more habitat-generalist species, which can persist in smaller, more fragmented landscapes due to their greater trophic plasticity and fewer habitat-specific requirements (Pardini et al., 2005; Santos-Filho et al., 2012; Umetsu & Pardini, 2007). Thus, our results suggest that the quantity of suitable habitat plays a critical role in supporting forest-dependent species like *Praomys rostratus*.

Similarly, on a local scale, maximum tree height was found to affect composition of small mammal assemblages. This observation aligns with previous research indicating that in tropical forests, the structural attributes of the forest play a crucial role in influencing species occurrence and shaping animal communities (Avenant & Cavallini, 2007; Palmeirim et al., 2018; Pardini et al., 2005; Tews et al., 2004). Increased maximum tree height contributes to greater vertical heterogeneity, thereby expanding the multidimensional habitat space available (Carey et al., 1999). This enhanced vertical complexity provides arboreal species with more opportunities for foraging and shelter. Additionally, the increased structural complexity reduces the likelihood of interspecies interactions, which facilitates the coexistence of potentially competing species within the same area (Carey & Harrington, 2001; Carey & Johnson, 1995).

Canopy openness also had an effect on species composition. Increased canopy openness, which is often linked to reduced tree cover, leads to a simplification of the vegetation structure. This simplified structure creates habitat conditions that are unsuitable for forest-dependent species (Devictor et al., 2008; Newbold et al., 2014), thereby favoring species adapted to more open environments (Palmeirim et al., 2020). Consequently, we found that small mammal communities in areas with higher canopy openness were predominantly composed of open-area generalist species.

3.5.4. Implications for Conservation Strategies

The rapid expansion of cashew cultivation in tropical regions has recently garnered significant attention from conservation scientists (Powell et al., 2023). Despite this growing concern, there remains a notable lack of published research addressing the impacts of this land-use change on biodiversity, particularly in Western Africa (Rege & Lee, 2023). In Guinea-Bissau, specifically, there is limited knowledge about small mammal diversity, which hampers the development of effective conservation strategies. This study thus provided a foundational understanding of how habitat conversion driven by the expanding cashew industry in Guinea-Bissau affects local biodiversity in Cantanhez National Park. Our analysis revealed that landscape-scale variables,

particularly the proportion of cashew orchards, significantly influenced small mammal diversity in CNP. An increased amount of cashew orchard area was associated with a reduction in small mammal abundance and a shift in species composition towards generalist species. The presence of generalist species in these habitats may lead to the displacement or even extinction of forest-dependent species (Henle et al., 2004; Rege et al., 2020), as they are better adapted to inhabiting disturbed environments. Notably, *Rattus rattus*, an invasive species known for its potential as a pest and its role in zoonotic disease transmission (Kamani et al., 2013; Monadjem et al., 2015), was observed in these cashew orchards. Our findings align with previous research on avian and anuran communities, which similarly observed that communities associated with cashew orchards predominantly consist of generalist species (Komanduri et al., 2023; Munje & Kumar, 2022; Ranganathan et al., 2008). Additionally, medium-sized mammals have been shown to be less abundant in cashew orchards located near forested areas (Rege et al., 2020). However, cashew orchards are noted for sustaining a high diversity of invertebrates (Bhat et al., 2013; Mahata et al., 2019; Vanitha et al., 2017) and reptiles (Jayakumar & Nameer, 2018).

By establishing a baseline of small mammal diversity in the context of land-use changes, our research opens the door for formulating targeted and effective management strategies for preserving biodiversity in CNP. To effectively conserve biodiversity amidst the pressures of the expansion of cashew orchards, it is essential to focus on preserving native forest areas. These forests proved to be indispensable habitats for the main small mammal species captured during our sampling effort – the forest specialist *Praomys rostratus* - which rely on their complex habitat structure to obtain the resources necessary for its survival (Monadjem et al., 2015). Strengthening the management and enforcement capacities within CNP is crucial to prevent further encroachment by cashew cultivation (Guedes et al., 2024). This includes clearly demarcating buffer zones around forested areas to mitigate the impact of agricultural expansion (Guedes et al., 2024). In addition, improving habitat connectivity between fragmented forest patches is vital for supporting small mammal communities. Forest-dependent species often face difficulties traversing between isolated forest fragments, which can lead to reduced genetic diversity and population viability (Henle et al., 2004; Palmeirim et al., 2018). Establishing ecological corridors to connect fragmented habitats can facilitate movement and migration, thereby enhancing the resilience of small mammal populations (Palmeirim et al., 2020).

However, the role of cashew orchards in providing income for local populations cannot be overlooked. Cashew cultivation contributes significantly to the livelihoods of people living within and around CNP. Therefore, conservation efforts must balance the protection of natural habitats with the economic needs of local populations. Integrating specific regulations for cashew cultivation into the management plans of protected areas is essential. Maintaining habitat complexity is further crucial for supporting biodiversity. Our results, along with previous studies (Bowman et al., 2001; Carrilho et al., 2017; Rhim et al., 2015), has shown that increased understory cover contributes to higher small mammal richness. Therefore, on a local scale, agricultural practices should aim to preserve and enhance habitat complexity within cashew orchards. This can be achieved by maintaining some level of natural vegetation and structural diversity, which provides essential resources and shelter for wildlife. Furthermore, integrating regenerative agricultural principles can help reconcile agricultural practices with conservation goals. By incorporating these principles, cashew crops can be managed in a way that enhances their compatibility with surrounding natural habitats. Agroecological mosaics, which involve a combination of agricultural and natural landscapes, can be developed through collaborations among agroecologists, biodiversity experts, and traditional farmers (Tittonell, 2023). This approach fosters a more harmonious coexistence between agriculture and conservation. Additionally, supporting local communities in developing alternative revenue sources that also contribute to ecosystem conservation is important. For instance, in Guinea-Bissau, communities have successfully utilized non-timber forest products for urban markets, demonstrating that it is possible to sustain livelihoods while valuing forest (Palmeirim et al., 2023). Moreover, preserving native forests can also attract investment in ecotourism (UN-FCCC, 2019), providing an additional economic incentive for conservation.

In sum, the expansion of cashew cultivation presents significant challenges for biodiversity conservation in Cantanhez National Park. The conversion of native forests to cashew orchards adversely affects small mammal diversity, favoring generalist species over forest specialists. To mitigate these impacts, it is essential to implement strategic conservation measures, including enhancing the management and enforcement of protected areas, improving habitat connectivity, and integrating sustainable agricultural practices. Promoting agroecological approaches and supporting alternative livelihoods can help balance ecological preservation with local economic needs, fostering a resilient and biodiverse landscape in Guinea-Bissau.

3.5.5. Limitations and Future Research

Future research should address several limitations identified in this study. A significant concern was the low number of animals captured per sampling site, resulting in relatively low sampling adequacy. This limitation can be attributed to multiple factors, including the consumption of bait by invertebrates, particularly ants, which compromised the effectiveness of the traps. Additionally, during several sampling nights, some traps had to remain inactive due to the presence of carnivorous ants in the area, in an effort to minimize small mammal mortality. These low capture rates suggest that the dataset may not accurately represent the small mammal assemblages within CNP, potentially leading to an underestimation of species diversity metrics. Consequently, the reduced sampling adequacy impacts the reliability of the findings and may obscure significant patterns and trends within the small mammal population. Another limitation was the difference in trap placement between forests and cashew orchards, with traps set both on the ground and in the understory (~2 m height) in forests, but exclusively on the ground in cashew orchards. Although this reflects the structural contrast between forests and cashews, this variation in sampling effort may have influenced the comparability of results by targeting different subsets of species in each habitat. Furthermore, the clearance of understory vegetation from cashew orchards during the sampling period also influenced the characterization of these areas.

To mitigate these limitations, future research should incorporate alternative trapping methods, such as pitfall traps, to specifically target shrew species that may not be as attracted to baited Sherman traps. Additionally, the use of camera traps could provide valuable insights into the impact of habitat conversion on species diversity, circumventing issues related to bait. Increasing the number of captures would also enhance the fit of the species richness model, as a greater diversity of species would likely be detected at each site.

Further studies should focus on mapping and monitoring cashew orchards across various regions of Guinea-Bissau to evaluate temporal changes in biodiversity patterns (Pereira et al., 2022). Expanding research on small mammal communities throughout Guinea-Bissau will help address existing knowledge gaps. Additionally, conducting studies across different seasons may offer insights into temporal variations in biodiversity and species behavior, potentially influenced by seasonal changes in habitat and resource availability.

4. Conclusion

Cantanhez National Park (CNP) is of paramount importance to Guinea-Bissau's biodiversity, encompassing the largest remaining expanse of subtropical forest in the country. Its diverse habitats collectively support a rich array of species (Bersacola et al., 2022). Despite its status as a protected area, the encroachment of cashew orchards has resulted in significant fragmentation of native forests (Pereira et al., 2022). This study provides essential baseline data on small mammal diversity within CNP, elucidating how habitat conversion influences species richness, abundance, and composition, while reinforcing the ecological significance of preserving native forests in landscapes altered by human activity.

Through systematic and opportunistic surveys, we identified 11 small mammal species, comprising eight rodents and three potential shrew species. The geographic range of *Mus mattheyi* was extended by 250 km, adding this species to Guinea-Bissau's documented fauna. This finding highlights the ecological adaptability of this rodent and emphasizes the importance of continued research in understudied regions. The small mammal assemblages in Cantanhez National Park (CNP) displayed a variety of habitat preferences, leading to distinct species compositions in each habitat type. Closed-canopy forests were mainly inhabited by *Praomys rostratus*, a species dependent on forest environments, who was almost entirely absent from other habitats except palm-dominated forests. Wet grasslands in CNP potentially harbored the highest abundance of small mammals, with a predominance of species adapted to open-area environments. Cashew orchards exhibited notable species richness, which was predominantly comprised of generalist species, consistent with patterns observed in other taxa (Vasconcelos et al., 2015b).

Our findings indicated that the extent of cashew orchards had a pronounced effect on small mammal abundance and species composition, leading to a reduction in the number of individuals and an increased prevalence of generalist species adapted to open-area habitats. The proliferation of common or invasive generalist species in disturbed environments poses a significant threat to forest-dependent species. Specifically, *Praomys rostratus*, which constitutes a substantial portion of the small mammal biomass in the park, is particularly vulnerable to such changes. Although this species is classified as one of least concern (Cassola, 2016), it plays a pivotal ecological role in forest ecosystems through its contributions to ecosystem functioning and species interactions.

The absence of *P. rostratus* from cashew orchards emphasizes the importance of intact forest habitats for species with specific ecological requirements. Moreover, the protection of native forests is vital not only for this species but also for maintaining broader biodiversity, as forest habitats support a variety of species adapted to complex, undisturbed environments. While native forests provide crucial habitats for specialists, cashew orchards, despite hosting a greater number of species, fail to support forest-dependent taxa effectively. These patterns reflect a fundamental trade-off: the economic benefits of cashew cultivation versus the ecological costs of habitat simplification and biodiversity loss.

The conversion of native forests into cashew monocultures presents significant challenges for biodiversity conservation. Forest-dependent species, which rely on the structural complexity of native habitats, experience severe declines as landscapes become homogenized. The dominance of *Praomys rostratus* in forested areas highlights the irreplaceable role of native habitats in supporting specialist species. Observed reductions in small mammal abundance in regions with greater cashew coverage further emphasize the detrimental effects of agricultural expansion. To mitigate these impacts, conservation strategies should prioritize preserving native forest fragments. Establishing buffer zones around these fragments could reduce edge effects and create transitional habitats that accommodate both generalist and specialist species. Furthermore, promoting agroforestry systems that integrate cashew cultivation with native vegetation could enhance landscape heterogeneity, benefiting biodiversity while maintaining agricultural productivity.

The insights gained from this study have broader implications for biodiversity conservation in other tropical regions undergoing rapid agricultural expansion. As global demand for cash crops rises, understanding the ecological trade-offs of land-use changes is increasingly critical. This study underscores the importance of integrated land-use planning that balances economic development with ecological sustainability.

Several avenues for future research emerge from this work. Longitudinal studies could elucidate temporal changes in small mammal communities as cashew orchards mature and their structural complexity evolves. Expanding surveys to include other taxa—such as birds, reptiles, and insects—would provide a more holistic understanding of biodiversity dynamics in these landscapes. Genetic analyses should also be further utilized to explore population connectivity and gene flow among fragmented habitats, informing conservation strategies such as habitat corridors to enhance landscape connectivity. Finally, incorporating socioeconomic factors into future studies could

identify strategies that align biodiversity conservation with local livelihoods, fostering more sustainable land-use practices.

Cantanhez National Park exemplifies the challenges and opportunities inherent in balancing conservation and development in tropical landscapes. Our findings reaffirm the vital role of native forests in maintaining biodiversity and the need for innovative conservation strategies to mitigate the ecological impacts of agricultural expansion. By integrating ecological research with community engagement and sustainable practices, it is possible to chart a path forward that supports both biodiversity and human well-being.

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Attachments

Attachment 1

Table S2.1 - Detailed information on the sampling effort (number of trap-nights) per habitat type and trapping method used to survey small mammal assemblages in the Cantanhez National Park, in Guinea-Bissau

Habitat type	Sherman traps	Pitfall traps
Closed-canopy forest	4560	216
Palm-dominated forest	620	-
Wet grasslands	620	-
Cashew orchards	4560	-

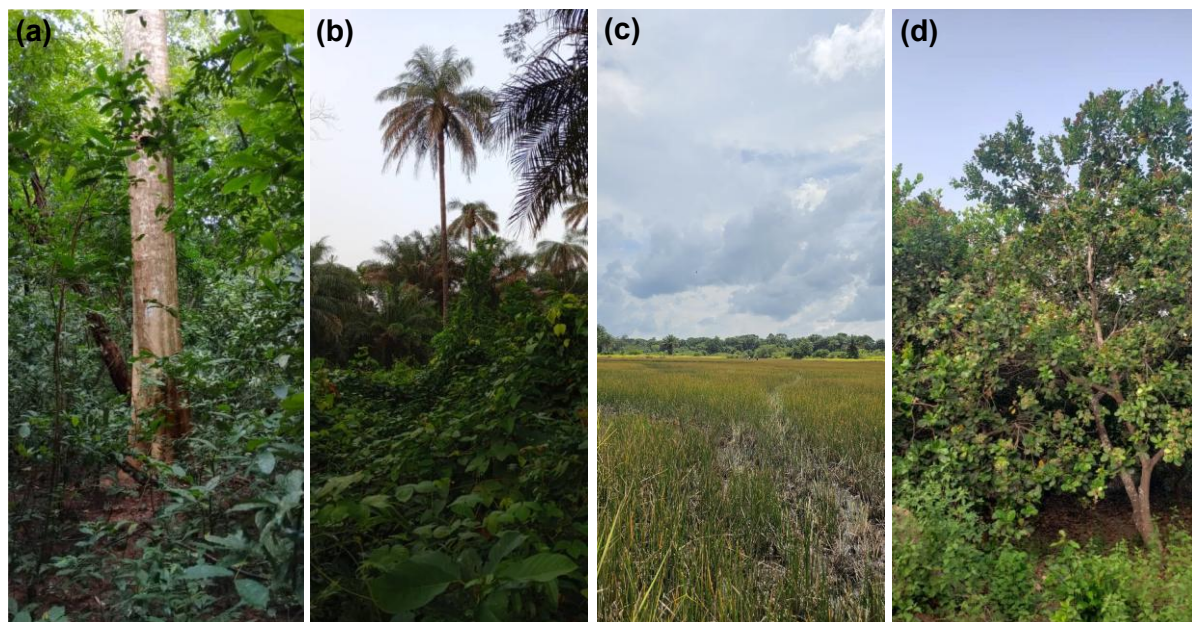


Fig. S2.1 - Main habitat types in the Cantanhez National Park, in Guinea-Bissau, where small mammals were surveyed: (a) closed-canopy forest, (b) palm-dominated forest, (c) wet grassland and (d) cashew orchard.

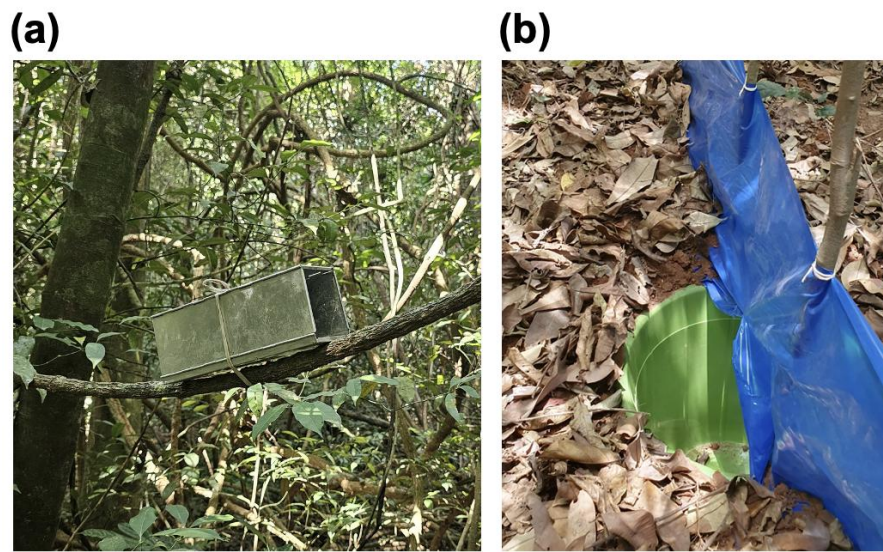


Fig. S1.2. - Illustration of each of the trapping methods used to survey small mammal assemblages in the Cantanhez National Park, in Guinea-Bissau, including a: (a) Sherman trap, and (b) Pitfall trap

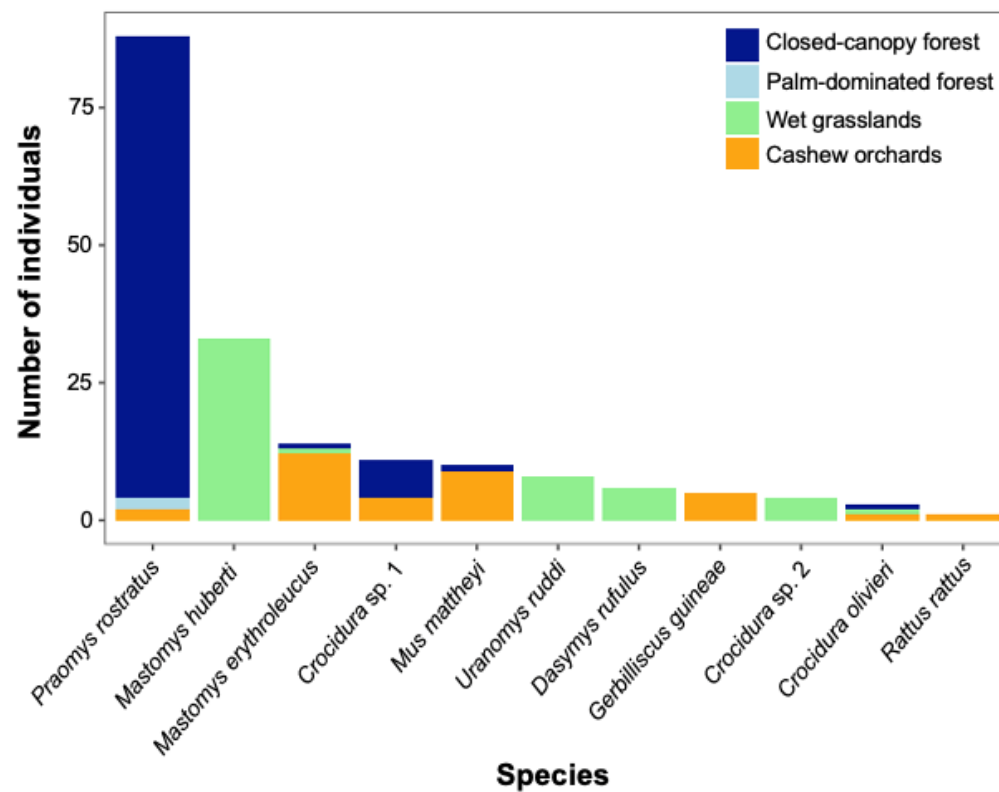


Fig. S2.2 - Small mammals recorded in the Cantanhez National Park, Guinea-Bissau, including the number of individuals recorded per species. The bars are colour-coded according to the habitat type where each individual has been recorded.

Attachment 2

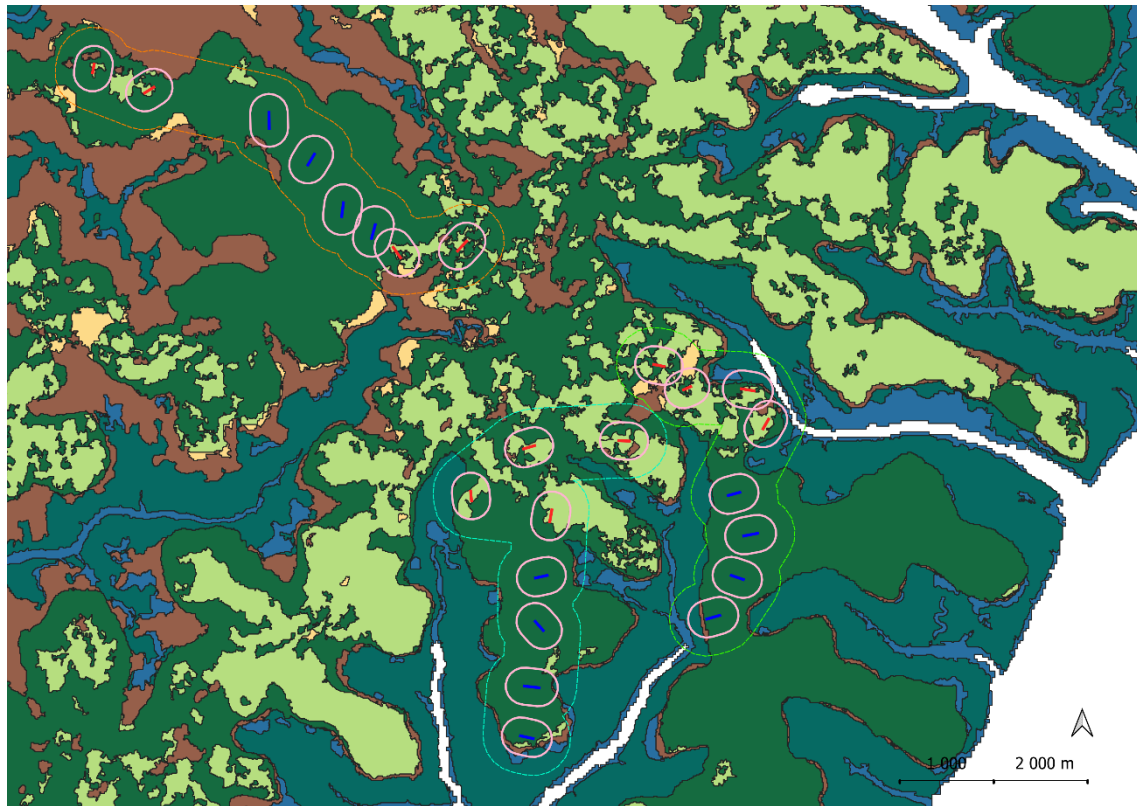


Fig. S3.1 - GIS map of the study area provided by Pereira et al. (2022), displaying key habitat types and survey zones. Dark green areas represent closed canopy forests, dark sea green indicates mangroves, lime green signifies cashew orchards, yellow corresponds to savannas/grasslands, brown highlights urban settlements, and blue represents water bodies. The study covered multiple transects, showing three distinct sampling zones: Lautchande (orange), Cambeque (green), and Madina (blue). Red lines represent cashew transects, while blue lines represent forest transects. White lines represent a 200m buffer around the transects. Cashew orchards in the Madina zone were updated based on Google Satellite imagery.

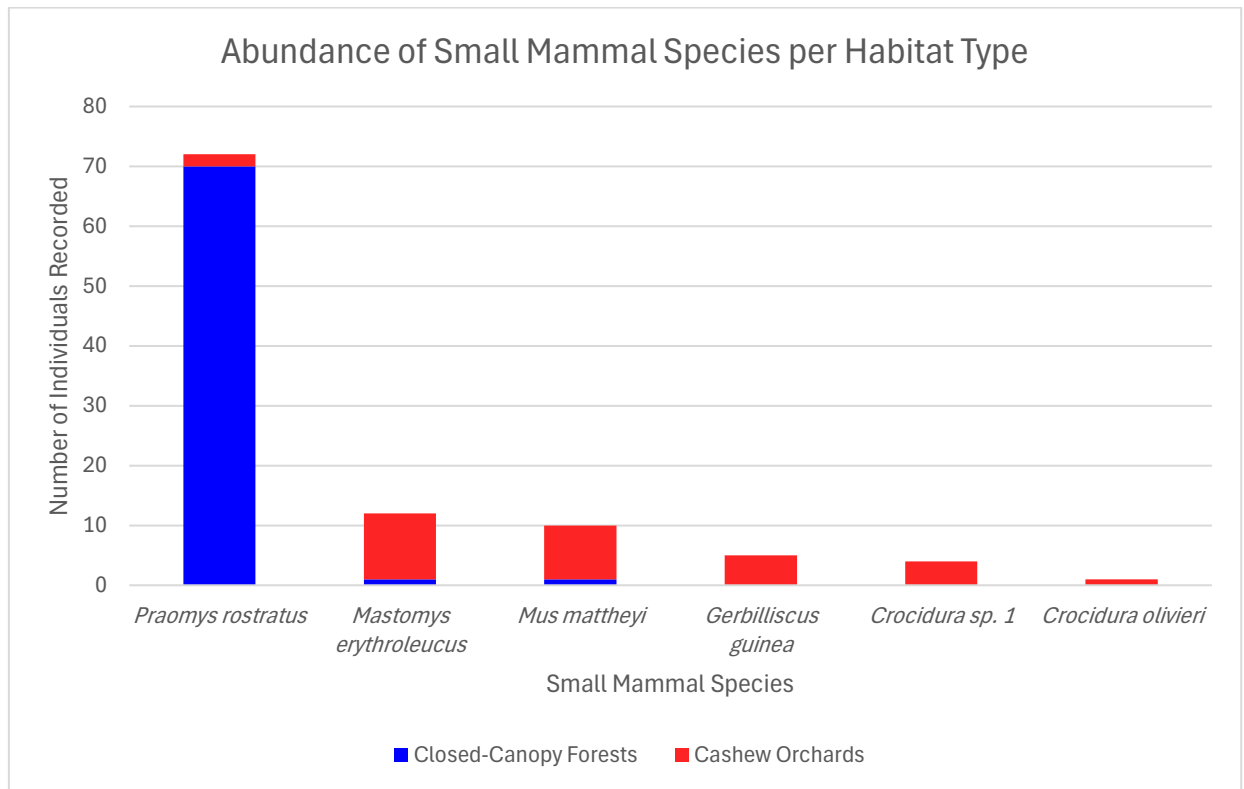


Fig. S3.2 - Small mammal species abundance across closed-canopy forests and cashew orchards in CNP. The X-axis shows six small mammal species, while the Y-axis represents the number of individuals recorded for each species. The two habitat types are differentiated by color: blue for closed-canopy forests and red for cashew orchards.

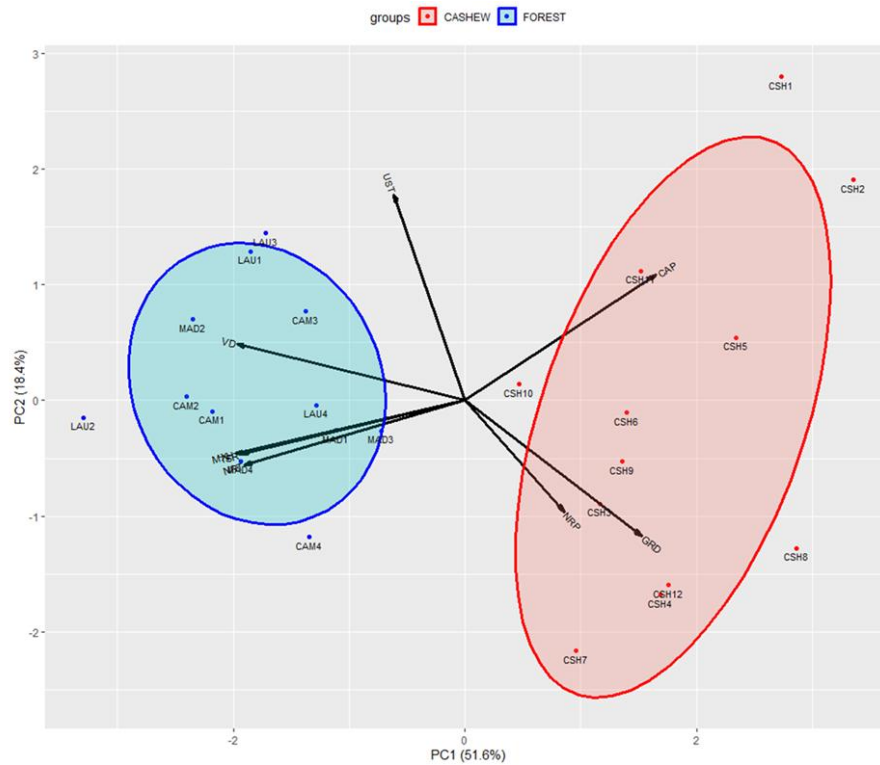


Fig. S3.3. - Principal Component Analysis (PCA) biplot representing two distinct sampling groups: Forest (blue) and Cashew (red). The x-axis (PC1) explains 51.6% of the variation, while the y-axis (PC2) explains 18.4% of the variation in the dataset. Each point represents a sampling site, with blue circles for forest sites and red circles for cashew sites. The ellipses around the points illustrate the clustering of forest and cashew sites based on similarities in the data. The black vectors represent various environmental or site-level variables, with their length and direction indicating their influence on the ordination. Cashew orchards were generally characterized by higher levels of ground obstruction and more open canopies compared to forested areas. Additionally, although to a lesser extent, cashew orchards tended to have a greater density of oil or coconut palm trees. In contrast, forest sites were associated with a denser vine presence, a greater number of trees per square meter, and higher tree species richness. The understory obstruction variable, although not as strong as other factors, still showed a slight association with forested areas, indicating a somewhat more developed understory layer in these habitats.

Table S3.1. - Correlation matrix amongst local and landscape-scale habitat variables. Variables include forest cover (FOR), cashew cover (CSH), edge density (ED), ground obstruction (GRD), understory obstruction (UST), canopy openness (CAP), vine density (VD), number of palm trees (NRP), number of trees (NRT), tree species richness (TSR), and maximum tree height (MXH). Strong correlations ($>|0.70|$) are highlighted in red.

	FOR_100m	CSH_100m	ED_100m	CSH_150m	FOR_200m	CSH_250m	ED_300m	GRD	UST	CAP	VD	NRP	NRT	TSR	MXH
FOR_100m		-0.994	-0.753	-0.976	0.966	-0.942	-0.809	-0.704	0.439	-0.305	0.792	-0.375	0.545	0.668	0.653
CSH_100m	-0.994		0.736	0.987	-0.966	0.951	0.809	0.681	-0.402	0.282	-0.791	0.391	-0.541	-0.668	-0.655
ED_100m	-0.753	0.736		0.754	-0.791	0.707	0.927	0.711	-0.611	0.431	-0.748	0.479	-0.508	-0.587	-0.639
CSH_150m	-0.976	0.987	0.754		-0.985	0.974	0.835	0.677	-0.449	0.219	-0.771	0.469	-0.474	-0.601	-0.617
FOR_200m	0.966	-0.966	-0.791	-0.985		-0.970	-0.856	-0.697	0.514	-0.229	0.763	-0.475	0.451	0.578	0.594
CSH_250m	-0.942	0.951	0.707	0.974	-0.970		0.774	0.628	-0.513	0.199	-0.744	0.384	-0.391	-0.582	-0.562
ED_300m	-0.809	0.809	0.927	0.835	-0.856	0.774		0.761	-0.572	0.294	-0.763	0.532	-0.559	-0.502	-0.596
GRD	-0.704	0.681	0.711	0.677	-0.697	0.628	0.761		-0.434	0.240	-0.589	0.430	-0.481	-0.446	-0.404
UST	0.439	-0.402	-0.611	-0.449	0.514	-0.513	-0.572	-0.434		0.079	0.457	-0.120	-0.019	0.128	0.089
CAP	-0.305	0.282	0.431	0.219	-0.229	0.199	0.294	0.240	0.079		-0.514	0.059	-0.623	-0.669	-0.655
VD	0.792	-0.791	-0.748	-0.771	0.763	-0.744	-0.763	-0.589	0.457	-0.514		-0.279	0.604	0.740	0.662
NRP	-0.375	0.391	0.479	0.469	-0.475	0.384	0.532	0.430	-0.120	0.059	-0.279		-0.263	-0.093	-0.316
NRT	0.545	-0.541	-0.508	-0.474	0.451	-0.391	-0.559	-0.481	-0.019	-0.623	0.604	-0.263		0.656	0.776
TSR	0.668	-0.668	-0.587	-0.601	0.578	-0.582	-0.502	-0.446	0.128	-0.669	0.740	-0.093	0.656		0.717
MXH	0.653	-0.655	-0.639	-0.617	0.594	-0.562	-0.596	-0.404	0.089	-0.655	0.662	-0.316	0.776	0.717	

Table S1.2. - Model selection results for identifying the best spatial scale (buffer distances) in relation to species richness, abundance, and composition across different landscape variables. Models are ranked by AICc values, with the best scales indicated by lower AICc values and higher R²c

Response Variable	Landscape Variable	Buffer (m)	AICc	delta AIC	R ² c
Richness	% of Native Forests	100	68.207	0.358	0.005
Richness	% of Native Forests	150	67.974	0.381	0.015
Richness	% of Native Forests	200	67.849	0.000	0.021
Richness	% of Native Forests	250	68.011	0.163	0.014
Richness	% of Native Forests	300	67.912	0.063	0.019
Richness	% of Cashews	100	68.230	0.765	0.004
Richness	% of Cashews	150	68.000	0.535	0.014
Richness	% of Cashews	200	67.832	0.368	0.022
Richness	% of Cashews	250	67.465	0.000	0.040
Richness	% of Cashews	300	67.772	0.307	0.025
Richness	Edge Density	100	68.033	0.000	0.013
Richness	Edge Density	150	68.211	0.178	0.005
Richness	Edge Density	200	68.239	0.205	0.004
Richness	Edge Density	250	68.063	0.030	0.011
Richness	Edge Density	300	68.263	0.229	0.003
Abundance	% of Native Forests	100	141.338	4.380	
Abundance	% of Native Forests	150	139.482	2.524	
Abundance	% of Native Forests	200	136.958	0.000	0.668
Abundance	% of Native Forests	250	140.544	3.586	
Abundance	% of Native Forests	300	138.089	1.131	0.659
Abundance	% of Cashews	100	140.639	6.939	
Abundance	% of Cashews	150	136.849	3.148	
Abundance	% of Cashews	200	134.372	0.671	0.696
Abundance	% of Cashews	250	133.701	0.000	0.711
Abundance	% of Cashews	300	137.054	3.353	
Abundance	Edge Density	100	147.941	0.415	0.588
Abundance	Edge Density	150	151.250	3.723	
Abundance	Edge Density	200	148.571	1.044	0.569
Abundance	Edge Density	250	147.526	0.000	0.570
Abundance	Edge Density	300	147.807	0.280	0.576
Composition	% of Native Forests	100	71.306	0.231	0.494
Composition	% of Native Forests	150	72.406	1.331	0.459
Composition	% of Native Forests	200	73.438	2.362	
Composition	% of Native Forests	250	73.407	2.332	
Composition	% of Native Forests	300	71.075	0.000	0.433
Composition	% of Cashews	100	71.899	0.000	0.470
Composition	% of Cashews	150	73.423	1.524	0.409
Composition	% of Cashews	200	73.993	2.094	
Composition	% of Cashews	250	72.970	1.072	0.408
Composition	% of Cashews	300	72.105	0.206	0.430
Composition	Edge Density	100	71.565	0.000	0.436
Composition	Edge Density	150	72.923	1.358	0.397
Composition	Edge Density	200	73.818	2.253	
Composition	Edge Density	250	73.041	1.476	0.464
Composition	Edge Density	300	73.309	1.744	0.467

Table S3.3. - Model selection results for species richness in relation to environmental variables, ranked by AICc. Models are ranked by AICc values, where the top models indicate the best fit, with lower AICc values and higher model weights representing better model performance. Variables with higher explanatory power, such as canopy openness and understory obstruction, are shown across different models, highlighting their influence on small mammal species richness in the study area.

	(Int)	scl(c)	scl(cnp)	scl(grn)	scl(mxh)	scl(plm)	scl(und)	df	logLik	AICc	delta	weight
35	1.208		0.3843				0.4711	4	-18.915	47.9	0	0.43
36	1.208	-0.0618	0.3992				0.4382	5	-18.809	51	3.02	0.095
51	1.208		0.3825			0.02563	0.4743	5	-18.888	51.1	3.18	0.088
43	1.208		0.3651		-0.0288		0.4752	5	-18.896	51.1	3.19	0.087
39	1.208		0.3804	0.01415			0.4776	5	-18.909	51.2	3.22	0.086
41	1.208				-0.2725		0.5258	4	-21.567	53.2	5.3	0.03
44	1.208	-0.1167	0.3428		-0.1045		0.4238	6	-18.645	54.2	6.3	0.018
52	1.208	-0.0853	0.4012			0.05218	0.4323	6	-18.714	54.4	6.44	0.017
40	1.208	-0.0894	0.3905	0.05537			0.4488	6	-18.738	54.4	6.48	0.017
59	1.208		0.3701		-0.0191	0.02056	0.4764	6	-18.881	54.7	6.77	0.015
33	1.208						0.5016	3	-23.753	54.7	6.77	0.015
55	1.208		0.382	0.002		0.0249	0.4752	6	-18.888	54.7	6.78	0.014
47	1.208		0.3646	0.00761	-0.0263		0.4783	6	-18.894	54.7	6.8	0.014
42	1.208	-0.1939			-0.3734		0.4352	5	-20.98	55.3	7.36	0.011
57	1.208				-0.2834	-0.0356	0.5224	5	-21.53	56.4	8.46	0.006
45	1.208			0.02396	-0.2636		0.5354	5	-21.554	56.4	8.51	0.006
37	1.208			0.1428			0.5636	4	-23.295	56.7	8.76	0.005
4	1.208	-0.3031	0.4819					4	-23.354	56.8	8.88	0.005
34	1.208	0.06794					0.5365	4	-23.66	57.4	9.49	0.004
49	1.208					0.05233	0.5079	4	-23.679	57.5	9.53	0.004
48	1.208	-0.1436	0.3347	0.05449	-0.1037		0.4342	7	-18.575	58.2	10.22	0.003
60	1.208	-0.1293	0.3505		-0.0932	0.04119	0.4206	7	-18.588	58.2	10.24	0.003
56	1.208	-0.1008	0.3946	0.0399		0.0424	0.441	7	-18.681	58.4	10.43	0.002
3	1.208		0.4216					3	-25.605	58.4	10.48	0.002
46	1.208	-0.2398		0.1	-0.3604		0.4539	6	-20.781	58.5	10.57	0.002
63	1.208		0.3702	-0.0008	-0.0193	0.02081	0.4761	7	-18.881	58.8	10.83	0.002
58	1.208	-0.1938			-0.3734	-0.0002	0.4352	6	-20.98	58.9	10.97	0.002
12	1.208	-0.3993	0.3609		-0.2138			5	-22.861	59.1	11.12	0.002
7	1.208		0.4734	-0.2156				4	-24.541	59.2	11.25	0.002
10	1.208	-0.4887			-0.5005			4	-24.723	59.6	11.62	0.001
20	1.208	-0.339	0.4835			0.09267		5	-23.147	59.6	11.69	0.001
38	1.208	-0.0146		0.1501			0.5593	5	-23.292	59.9	11.98	0.001
53	1.208			0.1442		-0.003	0.5639	5	-23.295	59.9	11.99	0.001
61	1.208			0.04294	-0.2716	-0.0484	0.5385	6	-21.494	59.9	11.99	0.001
8	1.208	-0.2754	0.4874	-0.046				5	-23.319	60	12.04	0.001
50	1.208	0.05258				0.03515	0.5328	5	-23.632	60.6	12.66	0.001
11	1.208		0.4794		0.08823			4	-25.501	61.1	13.17	0.001
19	1.208		0.4237			-0.0339		4	-25.579	61.3	13.33	0.001
23	1.208		0.4766	-0.2459		0.06883		5	-24.443	62.2	14.28	0
15	1.208		0.47	-0.2171	-0.0057			5	-24.541	62.4	14.48	0
28	1.208	-0.4165	0.3733		-0.194	0.06754		6	-22.751	62.4	14.51	0
62	1.208	-0.2349		0.1083	-0.3625	-0.025	0.4572	7	-20.764	62.5	14.59	0
16	1.208	-0.3738	0.3667	-0.0411	-0.2123			6	-22.832	62.6	14.67	0
64	1.208	-0.1474	0.342	0.04353	-0.0956	0.03025	0.4298	8	-18.547	62.7	14.76	0
26	1.208	-0.496			-0.4969	0.02428		5	-24.71	62.8	14.82	0
14	1.208	-0.4912		0.00427	-0.5002			5	-24.722	62.8	14.84	0
1	1.208							2	-29.158	62.9	14.95	0
24	1.208	-0.2967	0.4937	-0.0819		0.1111		6	-23.041	63	15.09	0
54	1.208	-0.0145		0.1504		-0.0006	0.5594	6	-23.292	63.5	15.59	0
9	1.208				-0.2259			3	-28.241	63.7	15.75	0
2	1.208	-0.2074						3	-28.39	64	16.04	0
27	1.208		0.4767		0.08301	-0.0107		5	-25.499	64.3	16.4	0
13	1.208			-0.231	-0.3193			4	-27.378	64.9	16.93	0
5	1.208			-0.1019				3	-28.977	65.2	17.22	0
17	1.208					-0.0087		3	-29.156	65.5	17.58	0
31	1.208		0.4877	-0.2428	0.01846	0.07266		6	-24.439	65.8	17.88	0
25	1.208				-0.2541	-0.0892		4	-28.107	66.3	18.38	0
32	1.208	-0.378	0.386	-0.0688	-0.1867	0.08393		7	-22.675	66.3	18.42	0
30	1.208	-0.4943		-0.0033	-0.497	0.02499		6	-24.71	66.4	18.43	0
18	1.208	-0.2393				0.08304		4	-28.281	66.7	18.73	0
6	1.208	-0.2368		0.04679				4	-28.365	66.8	18.9	0
21	1.208			-0.1204		0.04306		4	-28.95	68	20.07	0
29	1.208			-0.2263	-0.3215	-0.0132		5	-27.375	68.1	20.15	0
22	1.208	-0.2514		0.02239		0.07807		5	-28.276	69.9	21.95	0

Models ranked by AICc(x)

Table S3.4. - Model selection results for species abundance in relation to environmental variables, ranked by AICc. Models are ranked by AICc values, where the top models indicate the best fit, with lower AICc values and higher model weights representing better model performance. Variables with higher explanatory power, such as “% of Area Covered by Cashew Orchards” (CSH), “Understory Obstruction” (UST), “Canopy Openness” (CAP) and “Ground Obstruction” (GRD), are shown across different models, highlighting their influence on small mammal species abundance in the study area.

	(Int)	scl(c)	scl(cnp)	scl(grn)	scl(mxh)	scl(plm)	scl(und)	df	logLik	AICc	delta	weight
2	1.259	-0.794						3.000	-56.444	120.100	0.000	0.189
34	1.227	-0.669					0.309	4.000	-55.636	121.400	1.290	0.099
4	1.231	-0.867	0.208					4.000	-55.717	121.500	1.450	0.091
6	1.234	-0.969		0.258				4.000	-55.803	121.700	1.620	0.084
38	1.197	-0.858		0.294			0.341	5.000	-54.762	122.900	2.770	0.047
18	1.258	-0.782				-0.033		4.000	-56.431	123.000	2.880	0.045
10	1.258	-0.800			-0.007			4.000	-56.443	123.000	2.900	0.044
12	1.222	-0.656	0.399		0.343			5.000	-54.962	123.300	3.170	0.039
36	1.204	-0.744	0.181				0.281	5.000	-55.040	123.400	3.320	0.036
8	1.211	-1.016	0.184	0.227				5.000	-55.204	123.700	3.650	0.030
43	1.251		0.482		0.662		0.477	5.000	-55.523	124.400	4.290	0.022
50	1.226	-0.642				-0.063	0.317	5.000	-55.591	124.500	4.430	0.021
42	1.229	-0.640			0.033		0.314	5.000	-55.623	124.600	4.490	0.020
22	1.231	-0.948		0.284		-0.099		5.000	-55.699	124.700	4.640	0.019
20	1.231	-0.864	0.207			-0.007		5.000	-55.717	124.800	4.680	0.018
14	1.234	-0.977		0.259	-0.009			5.000	-55.802	124.900	4.850	0.017
44	1.195	-0.491	0.392		0.387		0.308	6.000	-54.056	125.100	4.960	0.016
33	1.358						0.622	3.000	-59.095	125.400	5.300	0.013
40	1.180	-0.904	0.149	0.262			0.311	6.000	-54.333	125.600	5.520	0.012
41	1.321				0.281		0.540	4.000	-57.942	126.000	5.900	0.010
54	1.191	-0.819		0.332		-0.144	0.362	6.000	-54.535	126.000	5.920	0.010
11	1.327		0.528		0.742			4.000	-57.981	126.100	5.980	0.009
16	1.210	-0.797	0.357	0.182	0.304			6.000	-54.605	126.200	6.060	0.009
26	1.258	-0.787			-0.006	-0.033		5.000	-56.431	126.200	6.110	0.009
46	1.200	-0.820		0.295	0.043		0.349	6.000	-54.739	126.400	6.330	0.008
28	1.222	-0.660	0.400		0.344	0.013		6.000	-54.960	126.900	6.770	0.006
49	1.332					-0.251	0.609	4.000	-58.431	127.000	6.880	0.006
52	1.204	-0.726	0.178			-0.037	0.286	6.000	-55.024	127.000	6.900	0.006
24	1.210	-1.000	0.177	0.245		-0.067		6.000	-55.154	127.300	7.160	0.005
59	1.245		0.461		0.627	-0.107	0.475	6.000	-55.382	127.700	7.620	0.004
47	1.252		0.480	0.027	0.668		0.487	6.000	-55.514	128.000	7.880	0.004
48	1.180	-0.646	0.342	0.221	0.349		0.337	7.000	-53.505	128.000	7.920	0.004
58	1.228	-0.611			0.035	-0.064	0.322	6.000	-55.577	128.100	8.010	0.003
9	1.414				0.332			3.000	-60.448	128.100	8.010	0.003
35	1.356		0.059				0.627	4.000	-59.039	128.200	8.100	0.003
37	1.357			-0.055			0.600	4.000	-59.065	128.200	8.150	0.003
30	1.230	-0.955		0.284	-0.008	-0.098		6.000	-55.698	128.300	8.250	0.003
57	1.303				0.253	-0.197	0.534	5.000	-57.504	128.300	8.250	0.003
1	1.476							2.000	-61.906	128.400	8.300	0.003
15	1.319		0.539	-0.127	0.710			5.000	-57.779	128.900	8.800	0.002
27	1.319		0.506		0.706	-0.118		5.000	-57.825	129.000	8.900	0.002
60	1.195	-0.486	0.390		0.386	-0.014	0.310	7.000	-54.053	129.100	9.020	0.002
45	1.320			0.055	0.297		0.560	5.000	-57.911	129.200	9.070	0.002
56	1.177	-0.869	0.135	0.295		-0.114	0.330	7.000	-54.189	129.400	9.290	0.002
17	1.447					-0.259		3.000	-61.308	129.800	9.730	0.001
62	1.194	-0.776		0.334	0.049	-0.146	0.371	7.000	-54.504	130.000	9.920	0.001
51	1.330		0.057			-0.251	0.615	5.000	-58.378	130.100	10.000	0.001
53	1.332			0.056		-0.274	0.631	5.000	-58.403	130.100	10.050	0.001
5	1.457			-0.223				3.000	-61.477	130.200	10.070	0.001
25	1.394				0.308	-0.204		4.000	-60.033	130.200	10.080	0.001
32	1.210	-0.793	0.349	0.194	0.297	-0.038		7.000	-54.589	130.200	10.090	0.001
13	1.409			-0.113	0.304			4.000	-60.329	130.800	10.680	0.001
3	1.475		0.032					3.000	-61.892	131.000	10.900	0.001
39	1.353		0.075	-0.080			0.597	5.000	-58.981	131.300	11.210	0.001
61	1.298			0.148	0.286	-0.249	0.585	6.000	-57.300	131.500	11.450	0.001
63	1.245		0.447	0.077	0.636	-0.137	0.503	7.000	-55.316	131.600	11.550	0.001
31	1.316		0.522	-0.099	0.694	-0.079		6.000	-57.719	132.400	12.290	0.000
21	1.441			-0.142		-0.204		4.000	-61.153	132.400	12.320	0.000
64	1.178	-0.631	0.326	0.247	0.337	-0.084	0.349	8.000	-53.426	132.500	12.360	0.000
19	1.446		0.031			-0.259		4.000	-61.294	132.700	12.610	0.000
7	1.453		0.084	-0.248				4.000	-61.387	132.900	12.790	0.000
29	1.393			-0.042	0.299	-0.189		5.000	-60.018	133.400	13.280	0.000
55	1.330		0.049	0.037		-0.266	0.628	6.000	-58.367	133.700	13.590	0.000
23	1.439		0.066	-0.166		-0.194		5.000	-61.097	135.500	15.440	0.000

Models ranked by AICc(x)

Table S3.5. - Model selection results for species composition in relation to environmental variables, ranked by AICc. Models are ranked by AICc values, where the top models indicate the best fit, with lower AICc values and higher model weights representing better model performance. Variables with higher explanatory power, such "Canopy Openness" (CAP), "Maximum Tree Height" (MXH), "Understory Obstruction" (UST) and "% of Area Covered by Native Forests" (FOR) are shown across different models, highlighting their influence on small mammal species composition in the study area.

	(Int)	scl(cnp)	scl(fm)	scl(grn)	scl(mxh)	scl(plm)	scl(und)	df	logLik	AICc	delta	weight
42	-1.50E-08	0.529			-0.556		-0.301	5.000	-15.999	46.300	0.000	0.173
4	-1.50E-08	0.724	-0.429					4.000	-17.949	46.600	0.280	0.150
10	-1.50E-08	0.532			-0.508			4.000	-18.546	47.800	1.470	0.083
36	-1.50E-08	0.755	-0.395				-0.194	5.000	-16.922	48.100	1.850	0.069
58	-1.50E-08	0.483			-0.643	-0.179	-0.320	6.000	-15.049	48.600	2.270	0.056
20	-1.50E-08	0.710	-0.503			-0.178		5.000	-17.202	48.700	2.410	0.052
12	-1.50E-08	0.586	-0.297		-0.272			5.000	-17.278	48.800	2.560	0.048
44	-1.50E-08	0.564	-0.191		-0.397		-0.259	6.000	-15.402	49.300	2.980	0.039
8	-1.50E-08	0.734	-0.522	-0.151				5.000	-17.584	49.500	3.170	0.035
46	-1.50E-08	0.528		0.012	-0.552		-0.299	6.000	-15.995	50.500	4.170	0.022
26	-1.50E-08	0.496			-0.575	-0.141		5.000	-18.096	50.500	4.190	0.021
2	-1.50E-08	0.879						3.000	-21.533	50.600	4.280	0.020
41	-1.50E-08				-0.918		-0.304	4.000	-19.963	50.600	4.310	0.020
52	-1.50E-08	0.741	-0.469			-0.178	-0.194	6.000	-16.086	50.600	4.350	0.020
28	-1.50E-08	0.544	-0.359		-0.320	-0.207		6.000	-16.204	50.900	4.590	0.017
9	-1.50E-08				-0.872			3.000	-21.775	51.100	4.770	0.016
60	-1.50E-08	0.519	-0.253		-0.453	-0.219	-0.268	7.000	-13.917	51.200	4.880	0.015
34	-1.50E-08	0.904					-0.254	4.000	-20.252	51.200	4.890	0.015
14	-1.50E-08	0.526		0.068	-0.487			5.000	-18.444	51.200	4.890	0.015
40	-1.50E-08	0.767	-0.496	-0.165			-0.201	6.000	-16.435	51.300	5.050	0.014
57	-1.50E-08				-0.997	-0.252	-0.330	5.000	-18.620	51.500	5.240	0.013
24	-1.50E-08	0.718	-0.554	-0.099		-0.155		6.000	-17.048	52.600	6.270	0.008
25	-1.50E-08				-0.936	-0.214		4.000	-20.975	52.600	6.330	0.007
16	-1.50E-08	0.610	-0.381	-0.111	-0.239			6.000	-17.079	52.600	6.330	0.007
6	-1.50E-08	0.835		0.154				4.000	-21.113	52.900	6.610	0.006
62	-1.50E-08	0.466		0.095	-0.629	-0.215	-0.308	7.000	-14.811	53.000	6.670	0.006
11	-1.50E-08		-0.193		-0.742			4.000	-21.389	53.400	7.160	0.005
48	-1.50E-08	0.588	-0.274	-0.109	-0.364		-0.258	7.000	-15.171	53.700	7.390	0.004
18	-1.50E-08	0.879				0.005		4.000	-21.532	53.700	7.450	0.004
30	-1.50E-08	0.470		0.146	-0.557	-0.198		6.000	-17.673	53.800	7.520	0.004
13	-1.50E-08			0.093	-0.838			4.000	-21.635	53.900	7.650	0.004
43	-1.50E-08		-0.081		-0.861		-0.286	5.000	-19.890	54.100	7.780	0.004
45	-1.50E-08			0.038	-0.903		-0.297	5.000	-19.936	54.200	7.870	0.003
38	-1.50E-08	0.868		0.119			-0.238	5.000	-19.976	54.200	7.950	0.003
27	-1.50E-08		-0.285		-0.762	-0.273		5.000	-20.108	54.500	8.220	0.003
50	-1.50E-08	0.905				-0.012	-0.255	5.000	-20.249	54.800	8.500	0.002
61	-1.50E-08			0.152	-0.956	-0.305	-0.311	6.000	-18.185	54.800	8.550	0.002
29	-1.50E-08			0.203	-0.885	-0.288		5.000	-20.340	55.000	8.680	0.002
59	-1.50E-08		-0.173		-0.886	-0.283	-0.295	6.000	-18.258	55.000	8.690	0.002
56	-1.50E-08	0.751	-0.528	-0.114		-0.152	-0.199	7.000	-15.856	55.000	8.760	0.002
32	-1.50E-08	0.553	-0.381	-0.033	-0.308	-0.198		7.000	-16.187	55.700	9.420	0.002
22	-1.50E-08	0.830		0.188		-0.075		5.000	-21.025	56.300	10.050	0.001
64	-1.50E-08	0.526	-0.271	-0.025	-0.443	-0.213	-0.268	8.000	-13.905	56.900	10.620	0.001
15	-1.50E-08		-0.188	0.007	-0.743			5.000	-21.389	57.100	10.780	0.001
54	-1.50E-08	0.864		0.154		-0.075	-0.238	6.000	-19.874	58.200	11.930	0.000
47	-1.50E-08		-0.078	0.005	-0.861		-0.286	6.000	-19.890	58.200	11.960	0.000
31	-1.50E-08		-0.216	0.108	-0.777	-0.298		6.000	-19.971	58.400	12.120	0.000
3	-1.50E-08		-0.691					3.000	-25.958	59.400	13.130	0.000
63	-1.50E-08		-0.102	0.109	-0.901	-0.308	-0.296	7.000	-18.090	59.500	13.230	0.000
19	-1.50E-08		-0.782			-0.236		4.000	-25.366	61.400	15.110	0.000
35	-1.50E-08		-0.681				-0.086	4.000	-25.869	62.400	16.120	0.000
7	-1.50E-08		-0.742	-0.079				4.000	-25.913	62.500	16.210	0.000
51	-1.50E-08		-0.773			-0.238	-0.090	5.000	-25.264	64.800	18.530	0.000
23	-1.50E-08		-0.784	-0.002		-0.236		5.000	-25.366	65.000	18.730	0.000
1	-1.50E-08							2.000	-30.519	65.700	19.460	0.000
39	-1.50E-08		-0.735	-0.084			-0.089	5.000	-25.818	65.900	19.640	0.000
5	-1.50E-08			0.396				3.000	-29.240	66.000	19.700	0.000
33	-1.50E-08						-0.164	3.000	-30.309	68.100	21.830	0.000
17	-1.50E-08					0.066		3.000	-30.485	68.500	22.190	0.000
37	-1.50E-08			0.382			-0.124	4.000	-29.107	68.900	22.600	0.000
21	-1.50E-08			0.454		-0.134		4.000	-29.113	68.900	22.610	0.000
55	-1.50E-08		-0.777	-0.007		-0.236	-0.090	6.000	-25.264	69.000	22.710	0.000
49	-1.50E-08				0.057	-0.161		4.000	-30.284	71.200	24.950	0.000
53	-1.50E-08			0.442		-0.135	-0.125	5.000	-28.976	72.200	25.950	0.000

Models ranked by AICc(x)