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PhD Thesis

Population Ecology of Small Mammals in Mount Rungwe Nature Forest Reserve

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POPULATION ECOLOGY OF SMALL MAMMALS IN MOUNT RUNGWE NATURE FOREST RESERVE

Thesis Submitted to Sokoine University of Agriculture in Fulfillment of the Requirements for the Degree of Doctor of Philosophy.

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EXTENDED ABSTRACT

Small mammals play significant ecological and economical role among many societies. Therefore, conducting ecological assessment of small mammals is crucial for maintaining functioning ecosystems and societal well being. The tropical mountains are characterised by diverse habitats, favourable environmental conditions, as well as abundant flora and fauna, including numerous endemic species. Among tropical mountains, Mount Rungwe Nature Forest Reserve (MRNFR) in southwestern Tanzania stands out as the second-highest mountain in the region, boasting its high diversity of flora and fauna, including several important IUCN endemic species such as *Rungwecerbus kipunji, Cephalophus spadix* and *Galagoides sp.* While there have been various studies on small mammals in Tanzania, the studies on mountainous small mammals remain limited, with most of them conducted in the northern part of the country and Eastern Arc mountains. This study aimed to understanding the ecology of small mammals in MRNFR which is situated at the intersection of the western, eastern and southern East Africa rift valleys. The study was conducted between 2020 and 2022 and involved data collection along an altitudinal gradient encompassing low-elevation, mid-elevation, and high-elevation with habitats low and mid montane forests, montane bamboo forests, montane bushland and montane grassland. Different methodologies were employed based on the stated specific objectives. The total of 300 Shearman traps, 60 pitfall traps, 132 snap traps and 18 Havahart traps were used. To determine the species composition, a combination of Sherman traps, pitfalls and Havahart traps was used along transects whereby five trapping nights were conducted at each elevation. Grids measuring 70 m X 70 m were established at each elevation to examine the influence of microhabitat parameters on small mammal abundance. Each grid contained 49 Sherman traps which were set over three consecutive nights. Microhabitat parameters, including vegetation and soil characteristics were collected using nested quadrant approach and soil core method. The data on population dynamics were obtained from permanent grids established over three consecutive days within a 24-month period at each elevation. For the purpose of diet analysis, the snap traps were placed in four transect lines at each elevation for six nights during both wet and dry periods and food categories were determined through macro-histological analysis of stomach contents. All collected species were identified using relevant keys and confirmed by sequencing the mitochondrial cytochrome b gene. A total of 3,183 individual small mammals comprised four families, eleven genera and twelve species were collected. Identified small mammals were *Montemys delectorum, Crocidura luna, Lophuromys machangui, Grammomys cometes, Cricetomy ansorgei, Dendromus nyassae, Mysorex kihaulei, Crocidura olivieri, Hylomyscus arcimontensis, Beamys hindei, Graphiurus sp. nov. and Mus triton*. A total of nine species were recorded during the wet season whereas ten species were recorded during the dry season. The results revealed that habitat characteristics and season significantly influenced small mammal richness, composition and diversity. The mid-montane forest exhibited the highest diversity compared to low-montane forests. Small mammal composition varied across habitats (Est ± SE = 3.36 ± 0.032, Z= 103.8, $p < 0.001$) with montane bushland showing significantly lower composition. Season and habitat significantly influenced species composition with montane bushland habitats having lower species composition and diversity during the dry season. The study further found out that small mammal abundance was influenced by elevation and season with mid-elevation and short rain period depicting the highest abundance. Elevation affected some species differently with *P. delectorum* decreasing and *Lophuromys machangui* increasing with an increase in elevation. On the contrary, *Crocidura luna* was not affected. Moreover, the results revealed that microhabitat parameters influenced abundance of individual species differently, thus indicating that altering the microhabitat could impact small mammal assemblage and abundance.

Therefore, microhabitat, elevation and season are important factors that influence small mammal abundance and they can be used to evaluate the biodiversity of montane tropical small mammal communities. Additionally, diet analysis was carried out on four rodent species, namely *Beamys hindei, Praomys delectorum, Lophuromys machangui* and *Grammomys dolichurus*. The food categories consumed varied among those rodent species. While *B. hindei.* consumed a significantly high number of seeds/grains, *G. dolichulus* and *L. machangui* consumed a significantly high number of invertebrates. The study further revealed that *G. dolichurus* had narrow niche breadth <0.3, thus indicating that it might be experiencing competition. On the other hand, *P. delectorum, L. machangui,* and *B. hindei* had higher niche breadth >0.5 with high overlap, thus suggesting that these species can coexist without competition. Furthermore, the population structure, breeding pattern and sex ratio analysis were carried out on *Montemys delectorum* which was the dominant and abundant species in the area. Abundant species can influences species diversity and area productivity due to their high density. The study revealed high population of *M. delectorum* in low (Est.± SE = 1.37 ± 0.077, Z = 17.85, p = <0.0001) and mid-elevations (Est.± SE = 1.408 ± 0.076, Z = 178.435, p = <0.0001) compared to high-elevation. High population was observed during wet season compared to dry season. The aspect of elevation influenced both juvenile and adult populations while the season influenced juvenile populations only. The mid-elevation sex ratio of 0.58 indicates significant imbalance with a higher proportion of females compared to males (χ2 = 51.84, df = 2, p = 0.0005). The study suggests that rainfall and elevation gradient are responsible for varying population abundance, breeding activities pattern and sex ratio of *M. delectorum* at the MRNFR. As the rainfall increases, food availability increases leading to an increase in the population of *M. delectorum* due to increased reproduction. Overall, the study provides significant ecological information about the current distribution of small mammals in the Rungwe Forest.

Molecular information has revealed the presence of small mammal species such as *Graphiurus sp.* which was reported for the first time in this area. The study also demonstrated that habitat and microhabitat types, elevation gradient and seasonal variations strongly influence small mammal species abundance, diversity, richness and distribution at both the population level and individual species like *P. delectorum* and *L. machangui*. Some species such as *L. machangui* and *P. delectorum* are distributed in Northern and Southern Highlands, thus showing less influence from the boundaries between these two regions. However, the distribution of other species such as *Graphiurus sp*. and *M. kihaulei* is impacted by these boundaries. In particular, the study revealed the presence of endangered *Myosorex kihaulei* in MRNFR, which was previously believed to be endemic to Udzungwa Mountain only. Based on genomic analysis, the study documented novel *Graphiurus sp.* Such findings suggest the need to incorporate the observed species in the management plans of Southern Highland landscapes, particularly Rungwe Mountain, and consider the conservation of the noted endangered species. The findings also suggest that monitoring of species along the elevation gradient is crucial due to a greater diversity of species in Rungwe Mountains.

Keyword: Ecology, Small mammals, Population, Mount Rungwe.

IKISIRI KUU

Mamalia wadogo wana umuhimu katika ikolojia na uchumi kwani wanachangia bioanuwai na pia wana athari za kiuchumi. Kwa hivyo, tathmini yao ya kiikolojia ni muhimu kwa utendaji wa mfumo wa ikolojia na kupunguza athari za kiuchumi. Milima inayopatikana maeneo ya kitropiki ni nyumbani mwa mimea na wanyama mbalimbali ambao baadhi yao wanapatikana katika maeneo hayo tu kwa sababu ya kuwa na aina mbalimbali za makazi na hali nzuri ya hewa na mazingira kwa ujumla hivyo kuhitaji utafiti wa kina. Hifadhi ya Asili ya Msitu wa Mlima Rungwe, Mount Rungwe Nature Forest Reserve (MRNFR) ni mlima wa pili kwa urefu kusini mwa Tanzania wenye aina nyingi za mimea na wanyama. MRNFR ina spishi kadhaa za asili zenye umuhimu kwa IUCN kama *Rungwecerbus kipunji, Cephalophus spadix* na *Galagoides sp.* Ingawa nchini Tanzania kumefanyika tafiti kadhaa zinazohusu mamalia wadogo, tafiti za mamalia wadogo wa milimani bado ni chache; na kwa baadhi ya tafiti zilizofanywa nyingi ni kwa upande wa kaskazini mwa nchi na milima ya Tao la Mashariki. Utafiti wa sasa unakusudia kuelezea ikolojia ya mamalia wadogo wanaopatikana nyanda za juu kusini mwa Tanzania katika MRNFR ambayo unapatikana kwenye makutano ya mabonde ya ufa la Africa Mashariki kati ya magharibi, mashariki na kusini. Utafiti huu ulifanyika tangia mwaka 2020 hadi 2022. Takwimu za mamalia wadogo zilikusanywa katika miinuko tofauti ya mlima (chini, kati, na juu) unaojumuisha misitu ya chini na ya kati ya milima, misitu ya mianzi na maeneo ya milima ya nyasi na vichaka. Mbinu mbalimbali zilitumika kulingana na malengo mahususi. Jumla ya mitego 300 ya Sherman, 60 ya mashimo, 132 ya snap na 18 ya Havahart ilitumika. Kwa kujua aina ya spishi wanaopatikana, mistari ya mkato na mchanganyiko wa mitego aina ya Sherman, mitego ya shimo na mitego ya Havahart ilitumika. Mitego iliwekwa kwa siku tano katika kila mwinuko wa mlima kwa misimu miwili. Kufikia lengo la pili la kuangalia jinsi makazi mahsusi kama vile sifa za udongo na mimea zinavyoathiri wingi wa mamalia wadogo; maeneo madogomadogo (gridi) yenye vipimo vya mita 70 kwa 70 yaliwekwa katika kila mwinuko na mitego 49 ya Sherman katika kila gridi ilitumika. Mitego iliwekwa kwa siku 3 mfululizo na hali mahsusi (microhabitat) ya mimea na udongo ilikusanywa kwenye kila gridi. Kwenye lengo la kuangalia idadi na jinsi miendendo ya idadi ya mamalia wadogo wanavyobadilika, gridi za kudumu ziliwekwa na takwimu zilikusanywa kwa siku tatu kwa mwezi kwa kipindi cha miezi 24. Kwa upande wa takwimu juu ya mamalia wadogo wanakula nini, mitego ya kuuwa ilitumika ambayo kila mwinuko ilikuwa na jumla ya mistari ya mitego minne iliyowekwa kwa siku 6 katika kipindi cha mvua na ukame. Uchunguzi wa chakula kilichopo kwenye tumbo ulifanyika na kuangalia makundi ya vyakula ambavyo wanyama hao wanakula. Mamalia wote waliokamatwa walitambuliwa na kuhakikiwa kwa njia ya jeni. Jumla ya mamalia wadogo 3,184 walikusanywa wakijumuisha spishi 12, familia nne na genera 11. Aina zilizokusanywa zilikuwa *Montemys delectorum, Crocidura luna, Lophuromys machangui, Grammomys cometes, Cricetomy ansorgei, Dendromus nyassae, Mysorex kihaulei, Crocidura olivieri, Hylomyscus arcimontensis, Beamys hindei, Graphiurus sp. nov.* na *Mus triton*. Jumla ya spishi tisa zilikusanywa kipindi cha mvua na kipindi cha ukame zilikusanywa spishi kumi. Matokeo yalionyesha hali ya mazingira pamoja na utofauti wa hali ya hewa uliathiri uwepo, idadi na anuwai ya mamalia wadogo. Msitu wa kati wa mlima ulikuwa na anuai kubwa kulinganisha na msitu wa chini ya mlima. Uwepo wa spishi ulitofautiana katika makazi tofauti (Est ± SE = 3.36 ± 0.032, Z= 103.8, $p < 0.001$), maeneo ya vichaka yalikuwa na idadi ndogo ya wanyama wadogo. Misimu ya hali ya hewa na aina za makazi zilionekana kuathiri uwepo wa spishi kwa kuwa na uwepo mdogo wa spishi katika maeneo ya vichaka. Ilionekana pia kuwa wingi wa wanyama wadogo uliathiriwa na mwinuko wa mlima na hali ya hewa ambapo mwinuko wa kati ya mlima kulikuwa na idadi kubwa ya wanyama wadogo katika kipind cha mvua. Mwinuko pia uliathiri spindi mmoja mmoja tofauto ambapo idadi ya *P. delectorum* ilikuwa inapungua jinsi mwinuko ulivyoongezeka, wakati idadi ya *L. machangui* ilikuwa inaongezeka jinsi mwinuko unavyoongezeka na *Crocidura luna* hawakuathiriwa na mabadiliko ya

mwinuko. Kutokana na haya, vigezo vya makazi vikibadilika husababisha mabadiliko kwa wingi wa mamalia wadogo. Katika uchambuzi wa chakula, spishi nne za panya; *B. hindei, P. delectorum, L. machangui* na *G. dolichurus* zilifanyiwa utafiti wa chakula. Ilibainika aina za vyakula vilivyoliwa vilitofautiana baina ya spishi za panya. Kwa mfano, *B, hindei* alikuwa na idadi kubwa ya mbegu/nafaka huku *G. dolichurus* na *L. machangui* wakiwa na idadi kubwa zaidi ya wadudu. Nafasi bora za kuishi (niche) zilionekana kuwa ndogo kwa *G. dolichurus* wakati *P. delectorum, L. machngui*, na *B. hindei* walikuwa na niche ya wastani lakini, mwingiliano wa chakula ulikuwa wa juu katika aina zote nne za panya. *L. machangui, P. delectorum* na *B. hindei* walikuwa na niche ya >0.5 na mwingiliano wa juu na hivyo wanaweza kuishi pamoja bila ushindani wakati *G. dolichurus* anaweza kupata ushindani kwa sababu ya niche yake kuwa chini <0.3. Uwiano wa jinsia, kuzaliana na muundo wa idadi ulifanywa kwa *M. delectorum* ambaye ndio spishi iliyopatikana kwa wingi zaidi. Idadi kubwa ya *M*. *delectorum* ilirekodiwa katika mwinuko wa chini (Est.± SE = 1.37 ± 0.077, Z = 17.85, p = <2e-16) na mwinuko ya kati (Est.± SE = 1.408 ± 0.076, Z = 178.435, p = <2e- 16) ikilinganishwa na mwinuko ya juu. Vilevile msimu wa mvua ulikuwa na idadi kubwa ya *M. delectorum* kulinganisha na msimu wa kiangazi. Mwinuko ulionekana kuathiri idadi ya panya wadogo na wakubwa lakini msimu wa hali ya hewa uliathiri panya wadogo pekee. Uwiano wa jinsia ulikuwa 0.51. kwa upande wa mwinuko wa kati uwiano ulikuwa 0.58 kukiwa na uwiano mkubwa wa majike kuliko madume ($\chi 2$ = 51.84, df = 2, p = 0.0005). Kwa hiyo hali ya hewa na mwinuko vilionekana ndio sababu ya tofauti ya idadi ya panya, kuzaliana na uwiano wa jinsia katika msitu wa Mlima Rungwe. Kipindi cha mvua, chakula huongezeka na hii hupelekea kuingezeka kwa idadi ya *M. delectorum* kwa sababu ya kuongezeka kuzaliana. Kwa ujumla, utafiti huu umefafanua ikolojia ya mamalia wadogo katika msitu wa mlima Rungwe na hivyo kuongeza uelewa wa ikolojia ya mamalia wadogo wa milimani. Ingawa ueneaji wa spishi kama *L. machangui* na *M. delectorum* unaonyesha ukaribu wa muunganiko wa kijiografia kati ya

milima ya Nyanda za Juu Kaskazini na Kusini, uwepo wa spishi kama *Graphiurus sp.* na *Mysorex kihaulei* katika MRNFR inaonyesha vinginevyo. *Mysorex kihaulei* ni spishi iliyo hatarini kutoweka iliyokuwa ikipatikana Udzungwa, pia imepatikana katika misitu ya Mlima Rungwe. Matokeo mengine ya kuvutia katika utafiti huu ni kupatikana kwa spishi ya *Graphiurus sp*. nov (Rungwe) ambayo ni spishi mpya kulingana na takwimu za maumbile. Utafiti huu umefichua bioanuai kubwa katika milima ya Kusini na kwa hivyo inapendekeza juhudi zaidi za uhifadhi.

Maneno muhimu: Ikoloji, Mlima Rungwe, mamalia wadogo, hali ya idadi ya mamalia wadogo

DECLARATION

I, UPENDO RICHARD, declare to the Senate of the Sokoine University of Agriculture that this thesis is my original work done within the period of registration, and that it has neither been submitted nor being concurrently submitted in any other institution.

_______________ ___________

UPENDO RICHARD Date

(PhD Candidate)

The above declaration is confirmed by

_______________ ___________

DR. R. M. BYAMUNGU Date

(Supervisor)

06 May

_______________ ___________

PROF. F. J. MAGIGE Date

(Supervisor)

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DEDICATION

This work is dedicated to my parents, the late Dr. Richard Ngoda and Mrs. Idda Ngoda.

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LIST OF PUBLISHED PAPERS AND MANUSCRIPT

PAPER I: Influence of environmental factors on small mammal communities along altitudinal gradient of mount Rungwe in South Western Tanzania Published by *Journal of Global Ecology and Conservation* 35 (2022)

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PAPER II: Microhabitat, altitude and seasonal influence on the abundance of non-volant small mammals in Mount Rungwe Forest Nature Reserve Published by *Global Ecology and Conservation* 35 (2022) e02069https://doi.org/10.1016/j.gecco.2022.e02069..41

PAPER III: Diet composition and niche overlap of four sympatric rodent species inhabiting Mount Rungwe Forest Nature Reserve, Tanzania Published by *Tanzania Journal of Forestry and Nature Conservation*, vol 91, No. 2 (2022) 178-192..51

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LIST OF ABBREVIATIONS AND SYMBOLS

CMR	Capture mark-recapture
df	Degree of freedom

EABH	Eastern Afromontane Biodiversity Hotspot
EAM	Eastern Arc Mountains
GLM	Generalised linear model
H'	Shannon diversity index
IUCN	International Union for conserving nature
m	Meter
m a.s. l	Meters above sea level
MRNFR	Mount Rungwe Nature Forest Reserve
P	Probability value
PCA	Principal Component Analysis
SE	Standard error
t	t-test
χ^2	Chi-squared

CHAPTER ONE

1.0 GENERAL INTRODUCTION

1.1 Eastern Afromontane Regions in Tanzania and their Diversity

Eastern and Western rift valley mountains constitute part of the Eastern Afromontane Biodiversity Hotspot (EABH) in Tanzania, which is distributed along the eastern edge of Africa (Cuypers *et al*., 2022). The EABH comprises the elevated regions of the East African rift valley which is characterised by afromontane vegetation. Although the Eastern Afromontane is fragmented, its patches exhibit similar flora. It is worth noting that EABH ranks as one of the biodiversity hotspots with the second highest number of endemic higher vertebrate genera, following Madagascar and the Indian Ocean islands (Mittermeier *et al*., 2011). The Eastern Afromontane is estimated to be the home to at least 7,598 species (including 2 356 endemics), along with 1 325 bird species (including 157 endemics), 490 mammal species (including 104 endemics), 347 reptile species (including 93 endemics) and 323 amphibian species (including 100 endemics) (Mittermeier *et al*., 2004; *Birdlife International*, 2011). Such statistics are not final since the ongoing studies continue to discover new species (Rovero *et al*., 2008; Konečný *et al*., 2020).

The Afro-montane region in Tanzania encompasses various high mountain areas, including Kilimanjaro, Meru, Hanang, Ngorongoro, Rungwe, Livingstone, Mporoto, Mahale and Mbizi among others. Additionally, Afro-montane vegetation can also be found in the Eastern Arc mountains such as Pare, Usambara, Nguu, Nguru, Uluguru, Ukaguru, Rubeho, Malundwe, Udzungwa and Mahenge (Cuypers *et al*., 2022; Davenport *et al*., 2004). Tropical Afro-montane regions boast a higher diversity of plants and animals due to their favorable climate and environmental stability. Moreover, these regions exhibit a significant degree of endemism (Dimitrov *et al*., 2012).

Mount Rungwe which is located in Tanzania's southern region is a volcanic mountain which is situated at the triplet junction of the eastern, western and southern arms of the East Africa Rift Valley, which is part of the EABH (Figure 1.1). This junction area is known as the Livingstone Mountains encompassing a range of mountains, including the Livingstone Mountains themselves, Mbeya Range, Uporoto Mountain, Mt. Ngozi, Mt. Rungwe, Kitulo Plateau and Kipengere Range (Cuypers *et al*., 2022). The rainforest montane habitat in southern Tanzania holds a significant value due to its high flora and fauna species diversity, local or regional endemism and its role as water catchment area. Mount Rungwe, in particular, exhibits the remarkable diversity and endemism. It acts as home to approximately 390 fauna and 500 floras species, with 400 flora species used for traditional medicines (URT, 2017). The mountain hosts 38 endemic faunas, including the critically endangered *Rungwecerbus kipunji*, near threatened *Serinus melanochrous*, *Cephalophus spadix, Galagoides sp. Nov., Colobus angolensis sharpei, Rhynchocyon cimei hendersoni, Paraxerus lucifer lucifer* and others (URT, 2017).

The dominant habitats on Mount Rungwe encompass the evergreen lower montane forest at the elevation of 1700-2100 meters above sea level (m a.s.l.), upper montane forest at the elevation of 2100-2600 m a.s.l., line of bamboo forest at 2500-2600 m a.s.l and montane bushland at the highest elevation of 2600-2900 m a.s.l. However, the human activities in the surrounding area of the mountains pose increased pressure on natural forests and their vertebrate fauna. The major threats facing Mount Rungwe Nature Forest Reserve include forest fires, illegal hunting, illegal collection of medicinal plants, and the invasion of pine trees (URT, 2017). For instance, according to Davenport (2004), pine trees have invaded and colonized a significant portion of the reserve, even at higher elevations, causing damage to the reserve's ecology and posing threats to indigenous flora and fauna.

1.2 Non-Volant Small Mammals Ecology

Non-volant small mammals are groups of mammals weighing less than 500g including orders such as Rodentia, Soricomorpha, Macroscelidea and Afrosoricidea. Rodentia and Soricomorpha are widely distributed in Africa with Rodentia being most successful in terms of distribution, richness and abundance. Being one of the most successful small mammal groups, the rodent group is distinguished by having constantly growing pairs of incisors in their upper and lower jaws. The rodents account for over 42% of all mammals and exhibit high diversity and abundance in tropical Africa (Wilson & Reeder, 2005; Dontas *et al*., 2010). In the sub-Sahara Africa, an estimated 463 rodent species are adapted to heterogeneous environments and are found in all types of habitats (Ara *et al*., 2015). Soricomorpha is characterised by long, pointed snouts, numerous sharp teeth, tiny ears and small eyes and it is expected that there are approximately 150 species in Africa (Happold, 2013; Kingdon, 2015). Small mammals are found in a wide range of natural habitats, agricultural landscapes as well as rural and urban areas (Ken *et al*., 2003). Their ecological success can be attributed to their adaptability in a diverse habitats, food sources, and short reproductive cycles (Emily & Hoekstra, 2008; Makundi *et al*., 2009; Yihune & Bekele, 2012). Due to their environmental adaptability and diverse morphology, physiology, feeding behaviors and life strategies, they have colonized large part of the world, making them a highly successful group of mammals (Corbet & Hill, 1994; Musila *et al*., 2019; Paniccia *et al*., 2022). The distribution of small mammals in different geographical areas is influenced by environmental factors such as temperature, humidity, altitude, food availability, and habitat characteristics (Baker *et al*., 2003; Heroldová *et al*., 2007).

Nevertheless, small mammals play a significant role as an integral part of the food web and functioning of ecosystems. For instance, the study on leopard food habits at Mount Rungwe-Kitulo landscape reveals that small mammals, including rodents accounted for more than 59.57% of the leopard's diet (de Luca & Mpunga, 2018). Further, small mammals contribute to seed dispersal through their feeding behaviors, regulate the population of other animals such as invertebrates through predation, and aid in soil modification and aeration through burrowing activities. Given their high richness, abundance and diversity across various environments, small mammals have been utilized as ecological indicators for assessing habitat disturbance, species diversity, energy flow, and climate change within an ecological area (Mason-Romo et al., 2018; López-García et al., 2021). While the small mammals offer numerous benefits to ecosystem, they also pose challenges to human beings and their assets. The referred challenges include the spread of zoonotic diseases and as pest that affect human belongings. However, it is estimated that around 7% of small mammals, primarily rodents, are considered pest impacting agriculture, stored products and as diseases transmission agent (Capizzi *et al.,* 2014). Therefore, the study of small mammals constitutes a crucial component for the sustainable conservation of terrestrial ecosystem.

The population ecology which is a sub field of ecology focuses on understanding population dynamics and species interactions within their surrounding environment (Tuljapurkar, 2013). It involves studying the species occurrence, distribution, abundance, population density, dispersion, age structure, breeding pattern and sex ratio of organisms (Lacey *et al.,* 2000). Such interactions between species and their environment play a crucial role in understanding species biology and how environmental conditions influence population size (Lacey, 2001). Having knowledge of species populations is fundamental to biology as it provides insights into population growth and the impact of environmental factors such as seasonality, soil properties and vegetation characteristics and altitude (Ellis *et al*., 1997; Lacey *et al*., 2000; Eccard *et al*., 2000).

1.3 Factors Affecting Small Mammals

Small mammal composition and diversity are influenced by a range of abiotic variables, including the resource availability, disturbance and physical conditions as well as biotic factors like competition, predation and genetic diversity. Geographical factors such as species dispersal also play a role (McCain', 2005; Márquez *et al*., 2011; Galiano *et al*., 2014; Charney *et al*., 2021). Vegetation parameters have shown strongly association with the occurrence and dynamics of small mammals as vegetations serve as food, cover, and habitat for these species (Andrews & O'Brien, 2000; Tews *et al.,* 2004). Habitat characteristics have been found to be the primary drivers of variations in small mammals' composition, abundance and diversity (Karasov-Olson & Kelt, 2020; Ademola *et al.*, 2022; Carmignotto *et al.,* 2022). Additionally, variations in altitude have been shown to impact small mammal composition, abundance, distribution and diversity as changes in climatic characteristics and vegetation occur along altitudinal gradients (Ferreguetti *et al.,* 2021; Chirichella *et al*., 2022).

The responses of small mammals to environmental changes along gradients have been studied worldwide and the observed patterns of response vary. Altitude is one such gradient where small mammals have exhibited strong responses (Author & Sanchez-Cordero, 2001; Kasangaki *et al.,* 2003; Rica & McCain, 2004). The diversity of small mammals along altitudinal gradients has been found to be higher at lower altitudes (Kasangaki *et al.*, 2003) and middle altitudes (McCain, 2004). Such response patterns may be influenced by several factors, including climate, habitat heterogeneity, species-area effect and mid-domain effect (McCain', 2005; Körner, 2007). The distribution patterns and structures of these mammals do not always adhere to a uniform pattern across different geographical areas such as altitudinal ranges of small mammals (Heaney, 2001; McCain', 2005; Magige, 2013).

Some studies have reported the positive correlation between small mammal species richness and abundance with an increase altitudinal range (Magige, 2013; Kohlmann *et al.*, 2022) while other studies have shown diversity peaks at mid-elevation (Brown, 2001; McCain', 2005).

Vegetation parameters play a crucial role in the interaction between small mammals and their habitat. The abundance and diversity of small mammals have been strongly associated with habitat heterogeneity (Clausnitzer & Kityo, 2001; Mulungu *et al.*, 2008; Yihune & Bekele, 2012). However, the habitat selection among small mammals is not uniform and varies among species and the available resources (Galiano *et al*., 2014) as well as other environmental attributes (Meliyo *et al.,* 2015). For instance, Galiano *et al.* (2016) found out that the distribution of subterranean rodents was influenced by factors such as soil moisture content and hardness. Similarly, Meliyo *et al*. (2015) examined the impact of physical properties and microclimate of soil on burrowing rodents and found out that the soil properties affected the abundance of rodent burrows. On the other hand, the species like *Praomys delectorum* have demonstrated the preference for intact forests, thus exhibiting higher composition and abundance in comparison to other vegetation types (Ademola *et al.,* 2022). Although small mammals are widely spread, their populations have geographical ranges that are limited by physical factors such as humidity, temperature or interactions with other species (Baselga *et al.*, 2012). These changes are influenced by both independent and dependent factors, including nutrient limitations, climate extremes, predation and competition.

1.4 Species Coexistence and Dietary Composition

The ecological perspective suggests that species coexist by exploiting their differences. When the species share similar resources, they must either share those resources or partition them in order to reduce competition. The coexistence mechanisms such as abundant resources, resource sharing, dietary differences, and foraging strategies, aid in the coexistence of species within an area (Perrin & Kotler, 2005; Mulungu *et al.*, 2011; Saar *et al.,* 2018). Dietary variations play the crucial role in facilitating resource partitioning and reduce competition among species living in the same environment (Meliyo *et al*., 2015). Sympatric species rely on their utilization and partitioning of available resources for coexistence. The theories of niche partitioning and niche overlap underlie species coexistence (Pianka,1974). Resources partitioning can involve shared resource among ecologically similar species, thus resulting in resource or niche overlap. Ecosystem with greater niche overlap is likely to support more species compared to those ecosystems with narrow niche overlap (Porter & Dueser, 1982).

Assessing diet of coexisting species provides the insights into the mechanism of their coexistence. Small mammals have diverse diets since they consume various plant and animal materials. The differences in food resources among small mammals reduce competition, thus allowing for their coexistence within a small area. Understanding the dietary composition of small mammals help in setting conservation initiatives for their food resources, thus contributing to their sustainable conservation. Therefore, the studies on the diets of coexisting small mammals are essential for the forest conservation management. The research on small mammal diets in sub-Sahara Africa has primarily focused on economically importance species such as the pestiferous rodent *Mastomys natalensis* (Odhiambo *et al.,* 2008; Mulungu *et al.,* 2011; Ademola *et al.,* 2022). Despite their ecological significance, there are few studies on small mammal diets in natural habitats and forests (Clausnitzer *et al.,* 2003; Ademola *et al.,* 2022). The knowledge of diet partitioning and overlapping in mountainous forest small mammals of MRNFR lacks, and hence their coexistence patterns remain unknown. Generally, the rodents are opportunistic feeders that consume a variety of food types, including both plant and animal materials depending on availability, habitat and season (Verde Arregoitia & D’Elía, 2021).

On the other hand, the shrews are carnivores, predominantly feeding on invertebrates (Rychlik, 2002). Various studies have shown different rodent species that exhibit preference for certain food types over others. For example, *G. dolichurus* was found to prefer fruits and plant materials over invertebrates in a temperate forest study in South Africa (Wirminghaus & Perrin, 1992) while *Beamys* sp. is known to store more seeds than other food items (Hanney & Morris, 1962). The rodents tend to adapt to food scarcity through food partitioning, specialization, or altered foraging behavior to reduce competition but when the food is abundant, they prefer their favored food sources (Verde Arregoitia & D'Elía, 2021).

1.5 Demographic Characteristics of Small Mammals and Associated Factors

Rodent population demography is subjected to fluctuations over time and these changes are driven by environmental factors like climatic condition which comprises temperature, humidity and rainfall (Lin & Batzli, 2001; Getz *et al.,* 2007). In tropical regions, the rainfall plays a crucial role in regulating demographic processes and population dynamics of small mammals (Massawe *et al.,* 2012; Mason-Romo *et al.,* 2018). The population demography reflects individual performances in terms of reproduction, growth, movement, and survival, which are influenced by behavioral and physiological responses to changing environmental conditions (Lin & Batzli, 2001)**.** The rainfall has a particular strong association with population dynamics in tropical forests due to the high-water availability and resulting abundance of food resources under the suitable climatic conditions. The altitudinal gradient can also impact the sex ratios, breeding patterns and population dynamics of small mammals (Makundi *et al.,* 2007) since each altitude range is characterised by distinct environmental factors. The previous studies have shown that species in low and mid-montane forests with extensive canopy covers experienced fewer predation pressures and have greater access to food resources which can positively affect their population size and demographics (Grether *et al.,* 2001). In contrast, the higher altitudes often have low canopy cover, harsher environmental conditions and limited food abundance and diversity, which may negatively impact population density of small mammals (Wegge *et al.,* 2012).

The sex ratios of small mammals also vary across different habitats along the elevation gradient and seasons due to their differences in behavior, activities between sexes, and sex-specific mortalities (Delany, 1972; Avenant & Smith, 2004; Mlyashimbi *et al.,* 2020). Similarly, the age structure of population changes over time and it is influenced by the breeding patterns (Happold & Happold, 1989; Delany, 1972). The environment influences population dynamics through its effects on demographic parameters (Dobson & Oli, 2001). Therefore, understanding the link between the population oscillations and underlying demographic parameters is essential for the comprehensive understanding of species population dynamics (Lima *et al.,* 2003; van Benthem *et al.,* 2017).

1.6 Problem Statement and Justification

The conservation of landscape requires knowledge of available resources and their status. Surveying and documenting flora and fauna are crucial for ecological preservation of tropical mountainous areas. The tropical mountainous regions particularly the Mount Rungwe Nature Forest Reserve in Tanzania are of significant importance due to their high concentration of endemic plant and animal species as recognized by the International Union for Conservation of Nature (IUCN). The IUCN has identified several endangered or threatened tropical forest species in Tanzania. The referred tropical forest species include *Myosorex kihaulei, Otomys uzungwensis* (Udzungwa Mountain), *Crocidura desperate* (Rungwe Mountain) and *Crocidura tansaniana* (Usambara forest). Among those species, the small mammals are of particular concern among the conservationists due to their high diversity, reproductive rate and spatial-temporal distribution, and ecological-economic significance (Verde Arregoitia & D’Elía, 2021). However, the research on non-pestiferous small mammals in the region is inadequate, thus hampering the implementation of effective conservation measures.

The climate change further amplifies the urgency to prioritize conservation efforts in altitudinal landscapes as it affects biodiversity by influencing factors such as humidity, rainfall, water supply, temperature, and distribution range (Muluneh, 2021). This is especially relevant in highland areas where climate change can drive species to shift to higher altitude zones, thus posing risks to ecosystem like Mount Rungwe forest (Foster, 2001; Engler *et al.*, 2011).

While small mammal ecology has been studied in various geographical locations worldwide (Jorgensen, 2004; Novillo & Ojeda, 2012, 2014; Batsuuri & Lkhagvasuren, 2021), including East Africa (Magige, 2013; Michael et al., 2016; Lema & Magige, 2018 Ssuuna *et al.,* 2020), the research efforts in the highlands such as Kilimanjaro, Meru, Elgon, and Eastern Arc Mountains (Clausnitzer & Kityo, 2001; Makundi et al., 2007; Mulungu *et al.*, 2008; Stanley *et al.,* 2014; Stanley & Kihaule, 2016) have overshadowed the lesser-known mountains like Mount Rungwe. Consequently, there is a research gap in understanding the composition, diversity, coexistence and distribution of small mammals species in MRNFR which is the nature reserve and water catchment forest with limited information available.

Moreover, the previous studies which were conducted in MRNFR have predominantly focused on vegetation, large mammals, and other species, leaving small mammals less studied (Gravlund, 2002; Enghoff, 2017; Mwakisunga, 2017; de Luca & Mpunga, 2018). The studies on small mammals in the area include the study by Hutterer *et al.* (1991)

which revealed an endemic and endangered *Crocidura desperate*. Another study focused on the biogeography importance of Livingstone Mountain with inclusion of the data collected from MRNFR in 1987. The referred study compared genetic structure of small mammals in the area (Cuypers *et al.,* 2022). The above studies on small mammals at Mount Rungwe were short-term studies and they, in total, managed to document the following small mammals in Mount Rungwe Nature Forest Reserve: *Crocidura desperate* (shrews), *Fukomys whyte, Dendromus nyassae, Hylomyscus arcimontensis, Lophuromys machangui, Mastomys natalensis, Montemys delectorum, Mus minutoides, Mus triton, Pelomys falax, Otomys lacustris, Rattus rattus, Rhabdomys dilectus, Graphiurus* sp. and *Paraxerus lucifer* (Rodents) (Hutterer *et al.,* 1991; Cuypers *et al.*, 2022).

The threats that face Mount Rungwe include the forest fires, pine invasion, illegal hunting, and illegal traditional medicine collections (Mittermeier *et al.*, 2007; Bracebridge *et al.,* 2012; Ojija, 2022). Additionally, there is scarcity information regarding the diet of most forest small mammals despite its significant contribution to the ecosystem. Understanding the dietary habits of these species is essential for comprehending the mechanisms of coexistence among sympatric species such as niche partitioning. Therefore, this study aimed to address the research gap by conducting a comprehensive investigation of small mammal ecology in MRNFR which is found in Southern part of Tanzania. This research will contribute valuable insights to effective management and conservation of the Livingstone Forest ecosystem in Mount Rungwe by studying the composition, diversity, diet, coexistence and population dynamics of small mammals.

1.7 Objectives

1.7.1 Main Objective

The general objective of this study was to investigate the habitat attributes associated with the small mammal population in Mount Rungwe Nature Forest Reserve.

1.7.2 Specific Objectives

The specific objectives of this study were:

i. To determine small mammal species diversity, composition and richness in different habitats along an altitude gradient;
ii. To assess the influence of soil properties and vegetation characteristics on small mammal abundance along the altitudinal gradient;
iii. To examine dietary composition as a mechanism of the coexistence of rodent species along altitudinal gradients and
iv. To determine the sex ratio, breeding pattern and population dynamics of dominant rodent species along the altitudinal gradient.

1.7.3 Research Hypotheses

i. The small mammals diversity, composition and richness in different habitats along the elevation gradient are significantly higher in the mid-elevations following mid-domain effect.
ii. The small mammals abundance will be significantly higher in areas with optimal microhabitat characteristics.
iii. The coexistence of small mammals is influenced by resource partitioning.
iv. The population dynamics and breeding patterns of rodents are influenced by seasonal changes along the elevation gradient.

1.8 Methodology

1.8.1 Study area

The study was conducted in Mount Rungwe Nature Forest Reserve which is a high category of protected in Tanzania. It is found in the southern highland of Mbeya Region. The reserve encompasses 13 652 hectors and it is situated at the junction of the eastern and western arms of East African Rift Valley. Forest elevation ranges from 1700 to 2960 meters above sea level. Climate of the area is characterised by tropical climate with rainfall ranges from 900 - 2700 mm with temperature ranges from - 6^0 C in cold season at higher elevations to 29^0 C (Williamson *et al*., 2014). The reserve has two major seasons including wet season starting from November to May and dry season starting from June to August (Williamson *et al*., 2014). According to the management plan of the reserve, MRNFR has three major elevation; low elevation which lies from 1700 - 2000 m a.s.l characterised by Low montane forest habitats, mid elevation from 2000 - 2400 m a.s.l characterised by mid montane forest habitat and a line of montane bamboo forest at higher elevation which is characterised by Montane bushland, montane grassland and bare land at the top and stretches from 2400 to 2960 m a.s.l. (URT, 2017).

1.8.2 Trapping of small mammals

Small mammals were trapped in different habitats along elevation from 2020 to 2022. The trapping sites of small mammals were chosen based on the elevation and habitat found within. Several traps were used including 300 Sherman traps, 60 pitfall traps, 132 snap traps and 18 Havahart traps (Nicolous & Colyn, 2003: Mulungu *et al.*, 2008; Stanley *et al*., 2007; Stanley *et al.,* 2014; Cuypers *et al.*, 2022) Traps were evenly distributed along the sampling localities. Depending on specific objectives, each objective had its specific traps and sampling effort. Minimum abundance thresholds of 10 individuals per species for microhabitat influence analysis and five individuals for diet analysis were established, ensuring statistical robustness (Balčiauskas *et al.*, 2021).

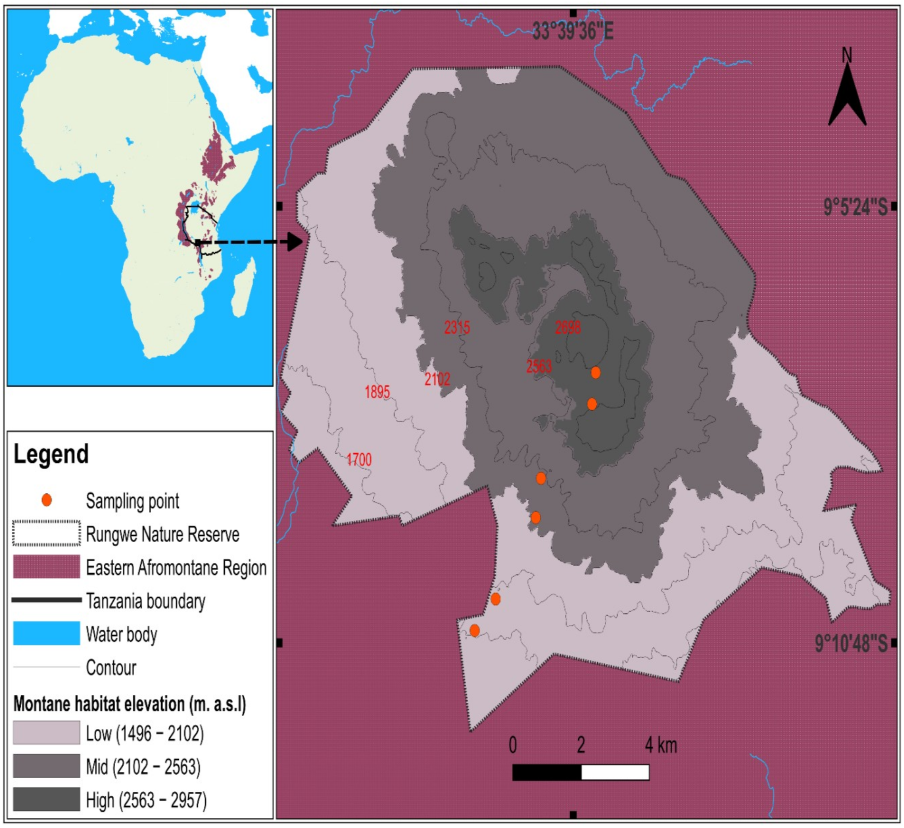

Figure 1.1: Map of Mount Rungwe Nature Forest Reserve (Richard, 2024)

1.9 Thesis Structure

The thesis comprises six chapters which are briefly described as follows: Chapter One presents the introduction, background information on the small mammal ecology and introduction of the Eastern Afro-montane biodiversity Hotspot. Chapter Two investigates the composition of small mammal community and explores the influence of environmental factors along the altitudinal gradient of Mount Rungwe. Chapter Three examines how the microhabitat, altitude and season impact the abundance of non-volant small mammals in the Mount Rungwe nature forest reserve. An assessment of the diet composition and niche overlap of four sympatric rodent species on Mount Rungwe nature forest reserve is presented in Chapter Four. Chapter Five investigates the population dynamics, breeding pattern and sex ratio of the dominant species *Montemys delectorum* on the Mount Rungwe nature forest reserve. Chapter Six comprises the conclusion chapter which presents the summary of the major findings, practical implications and recommendations for further research and conservation efforts.

1.10 Study Limitations

i. The broader altitudinal gradient was considered with 200 m intervals along one altitude and other altitudinal grids.
ii. Due to the limited resources, accessibility constrains and limited size and number of trapping grids at each trapping altitude, not all potential habitats of small mammals were sampled.

References

Ademola, O. J., Massawe, A. W., Mulungu, L. S., Hieronimo, P., Makonda, F. B. S., & Makundi, R. H. (2022). Habitat type impacts small mammal diversity in the Ukaguru Mountains, Tanzania. *Mammalia*, *86*(2), 123–133. https://doi.org/10.1515/ mammalia-2020-0158

Ademola, O. J., Massawe, A. W., Mulungu, L. S., & Makundi, R. H. (2022). Dietary composition of rodents across different habitats in the Ukaguru Mountains, Tanzania. *African Journal of Ecology*. https://doi.org/10.1111/aje.13042

Andrews, P., & O'Brien, E. M. (2000). Climate, vegetation, and predictable gradients in mammal species richness in southern Africa. *Journal of Zoology*, *251*(2), 205–231. https://doi.org/10.1111/j.1469-7998.2000.tb00605.x

Ara, M., Taylor, P. J., Denys, C., & Cotterill, F. P. (2015). *Rodents of sub-Saharan Africa: a biogeographic and taxonomic synthesis*. Walter de Gruyter GmbH & Co KG.

Author, M., & Sanchez-Cordero, V. (2001). Elevation Gradients of Diversity for Rodents and Bats in Oaxaca. In *Source: Global Ecology and Biogeography* (Vol. 10, Issue 1).

Avenant, N. L., & Smith, V. R. (2004). Seasonal changes in age class structure and reproductive status of house mice on Marion Island (sub-Antarctic). *Polar Biology*, *27*(2), 99–111. https://doi.org/10.1007/s00300-003-0569-x

Baker, P. J., Ansell, R. J., Dodds, P. A. A., Webber, C. E., & Harris, S. (2003). Factors affecting the distribution of small mammals in an urban area. *Mammal Review*, *33*(1), 95–100. https://doi.org/10.1046/j.1365-2907.2003.00003.x

Balčiauskas, L., Balčiauskienė, L., Garbaras, A., & Stirkė, V. (2021). Diversity and Diet Differences of Small Mammals in Commensal Habitats. *Diversity*, *13*(8), 346. https://doi.org/10.3390/d13080346

Baselga, A., Lobo, J. M., Svenning, J.-C., & Araújo, M. B. (2012). Global patterns in the shape of species geographical ranges reveal range determinants. *Journal of Biogeography*, *39*(4), 760–771. https://doi.org/10.1111/j.1365-2699.2011.02612.x

Batsuuri, D., & Lkhagvasuren, M. (2021). *Species composition of small mammal and abundance in natural and rehabilitated saxaul forest at the Gunii khooloi, Khanbogd soum*. 353–366. https://doi.org/10.36487/ACG_repo/2152_42

BirdLife International. (2011). State of the World's Birds. http://www.birdlife.org/datazone/sowb/introduction/INTRO3

Bracebridge, C. E., Davenport, T. R., & Marsden, S. J. (2012). The Impact of Forest Disturbance on the Seasonal Foraging Ecology of a Critically Endangered African Primate. *Biotropica*, *44*(4), 560–568. https://doi.org/10.1111/j.1744-7429.2012.00854.x

Brown, J. H. (2001). Mammals on mountainsides: elevational patterns of diversity. *Global Ecology and Biogeography*, *10*(1), 101–109. https://doi.org/10.1046/j.1466-822x.2001.00228.x

Capizzi, D., Bertolino, S., & Mortelliti, A. (2014). Rating the rat: global patterns and research priorities in impacts and management of rodent pests. *Mammal Review*, *44*(2), 148–162. https://doi.org/10.1111/mam.12019

Carmignotto, A. P., Pardini, R., & de Vivo, M. (2022). Habitat Heterogeneity and Geographic Location as Major Drivers of Cerrado Small Mammal Diversity Across Multiple Spatial Scales. *Frontiers in Ecology and Evolution*, *9*. https://doi.org/10.3389/fevo.2021.739919

Charney, N. D., Record, S., Gerstner, B. E., Merow, C., Zarnetske, P. L., & Enquist, B. J. (2021). A Test of Species Distribution Model Transferability Across Environmental and Geographic Space for 108 Western North American Tree Species. *Frontiers in Ecology and Evolution*, *9*. https://doi.org/10.3389/fevo.2021.689295

Chirichella, R., Ricci, E., Armanini, M., Gobbi, M., Mustoni, A., & Apollonio, M. (2022). Small mammals in a mountain ecosystem: the effect of topographic, micrometeorological, and biological correlates on their community structure. *Community Ecology*, *23*(3), 289–299. https://doi.org/10.1007/s42974-022-00104-8

Clausnitzer, V., Churchfield, S., & Hutterer, R. (2003). Habitat occurrence and feeding ecology of Crocidura montis and Lophuromys flavopunctatus on Mt. Elgon, Uganda. *African Journal of Ecology*, *41*(1), 1–8. https://doi.org/10.1046/j.1365-2028.2003.00386.x

Clausnitzer, V., & Kityo, R. (2001). Altitudinal distribution of rodents (muridae and gliridae) on mt elgon, uganda. *Tropical Zoology*, *14*(1), 95–118. https://doi.org/10.1080/03946975.2001.10531145

Corbet, G. B., & Hill, J. E. (1994). Wilson, D. E., and D. M. Reeder (eds.). 1993. MAMMAL SPECIES OF THE WORLD: A TAXONOMIC AND GEOGRAPHIC REFERENCE, 2nd Edition. Smithsonian Institution Press, Washington, D.C., xviii + 1206 pp. ISBN 1-56098-217-9. Price (hardcover), $75.00 ($60.00 to member. *Journal of Mammalogy*, *75*(1), 239–243. https://doi.org/10.2307/1382263

Cuypers, L. N., Sabuni, C., Šumbera, R., Aghová, T., Lišková, E., Leirs, H., Baird, S. J. E., Goüy de Bellocq, J., & Bryja, J. (2022). Biogeographical Importance of the Livingstone Mountains in Southern Tanzania: Comparative Genetic Structure of Small Non-volant Mammals. *Frontiers in Ecology and Evolution*, *9*. https://doi.org/10.3389/fevo.2021.742851

Davenport, T. (2004). *Invasive Pine Trees on Mt Rungwe, Problems and Solutions.* Wildlife Conservation Society.

de Luca, D. W., & Mpunga, N. E. (2018). Leopard abundance, distribution and food habits in the Mt. Rungwe-Kitulo landscape, Southern Tanzania. *African Journal of Ecology*, *56*(2), 358–367. https://doi.org/10.1111/aje.12464

Delany, M. J. (1972). The ecology of small rodents in tropical Africa. *Mammal Review*, *2*(1), 1–42. https://doi.org/10.1111/j.1365-2907.1972.tb00155.x

Dimitrov, D., Nogués-Bravo, D., & Scharff, N. (2012). Why Do Tropical Mountains Support Exceptionally High Biodiversity? The Eastern Arc Mountains and the Drivers of Saintpaulia Diversity. *PLoS ONE*, *7*(11), e48908. https://doi.org/10.1371/journal.pone.0048908

Dobson, F. S., & Oli, M. K. (2001). The Demographic Basis of Population Regulation in Columbian Ground Squirrels. *The American Naturalist*, *158*(3), 236–247. https://doi.org/10.1086/321322

Dontas, I. A., Tsolaki, A. I., Khaldi, L., Patra, E., & Lyritis, G. P. (2010). Malocclusion in Aging Wistar Rats. *Journal of the American Association for Laboratory Animal Science*, *49*, 22–29.

Eccard, J. A., Walther, R. B., & Milton, S. J. (2000). How livestock grazing affects vegetation structures and small mammal distribution in the semi-arid Karoo. *Journal of Arid Environments*, *46*(2), 103–106. https://doi.org/10.1006/JARE.2000.0659

Ellis, B. A., Mills, J. N., Childs, J. E., Muzzini, M. C., McKee, K. T. Jr., Enria, D. A., & Glass, G. A. (1997). Structue and floristics of habitats associated with five rodent species in an agroecosystem in Central Argentina. *Journal of Zoology*, *243*, 437–460.

Emily, K. H., & Hoekstra, H. (2008). Rodents. *Current Biology*, *18*(10), R406–R410.

Enghoff, H. (2017). A new East African genus of spirostreptid millipedes (Diplopoda, Spirostreptida, Spirostreptidae), with notes on their fungal ectoparasite Rickia gigas. *Zootaxa*, *4273*(4), 501. https://doi.org/10.11646/zootaxa.4273.4.3

Engler, R., Randin, C. F., Thuiller, W., Dullinger, S., Zimmermann, N. E., Araujo, M. B., Pearman, P. B., le Lay, G., Piedallu, C., Albert, C. H., Choler, P., Coldea, G., de Lamo, X., Dirnböck, T., Gégout, J.-C., Gómez-García, D., Grytnes, J.-A., Heegaard, E., Høistad, F., & Guisan, A. (2011). 21st century climate change threatens mountain flora unequally across Europe. *Global Change Biology*, *17*(7), 2330–2341. https://doi.org/10.1111/j.1365-2486.2010.02393.x

Ferreguetti, Á. C., Bezerra de Menezes, M., Pereira-Ribeiro, J., Rocha, C. F. D., & Bergallo, H. G. (2021). Influence of altitude and climate on species richness and endemism: A study case with non-volant small mammals in the Atlantic Forest, Brazil. *Austral Ecology*, *46*(4), 603–612. https://doi.org/10.1111/aec.13010

Foster, P. (2001). The potential negative impacts of global climate change on tropical montane cloud forests. *Earth-Science Reviews*, *55*(1–2), 73–106. https://doi.org/10.1016/S0012-8252(01)00056-3

Galiano, D., Kubiak, B. B., Menezes, L. S., Overbeck, G. E., & de Freitas, T. R. O. (2016). Wet soils affect habitat selection of a solitary subterranean rodent (Ctenomys minutus) in a Neotropical region. *Journal of Mammalogy*, *97*(4), 1095–1101. https://doi.org/10.1093/jmammal/gyw062

Galiano, D., Kubiak, B. B., Overbeck, G. E., & de Freitas, T. R. O. (2014). Effects of rodents on plant cover, soil hardness, and soil nutrient content: a case study on tuco-tucos (Ctenomys minutus). *Acta Theriologica*, *59*(4), 583–587. https://doi.org/10.1007/s13364-014-0193-x

Getz, L. L., Oli, M. K., Hofmann, J. E., & McGuire, B. (2007). Vole population dynamics: factors affecting peak densities and amplitudes of annual population fluctuations ofMicrotus pennsylvanicus. *Acta Theriologica*, *52*(2), 159–170. https://doi.org/10.1007/BF03194211

Gravlund, P. (2002). Molecular phylogeny of Tornier's cat snake (Crotaphopeltis tornieri), endemic to East African mountain forests: biogeography, vicariance events and problematic species boundaries. *Journal of Zoological Systematics and Evolutionary Research*, *40*(1), 46–56. https://doi.org/10.1046 /j.439-0469. 2002.00175.x

Grether, G. F., Millie, D. F., Bryant, M. J., Reznick, D. N., & Mayea, W. (2001). Rain Forest Canopy Cover, Resource Availability, and Life History Evolution in Guppies. *Ecology*, *82*(6), 1546. https://doi.org/10.2307/2679799

Hanney, P., & Morris, B. (1962). Some Observations upon the Pouched Rat in Nyasaland. *Journal of Mammalogy*, *43*(2), 238–248. https://doi.org/10.2307/1377095

Happold, D. C. D. (2013). Mammals of Africa : Rodents, Hares and Rabbits. In *Mammals of Africa : Rodents, Hares and Rabbits: Vol. III*. Bloomsbury Publishing. https://doi.org/10.5040/9781472926937

Happold, D. C. D., & Happold, M. (1989). Demography and habitat selection of small mammals on Zomba Plateau, Malawi. *Journal of Zoology*, *219*(4), 581–605. https://doi.org/10.1111/j.1469-7998.1989.tb02602.x

Heaney, L. R. (2001). Small mammal diversity along elevational gradients in the Philippines: an assessment of patterns and hypotheses. *Global Ecology and Biogeography*, *10*(1), 15–39. https://doi.org/10.1046/j.1466-822x.2001.00227.x

Heroldová, M., Bryja, J., Zejda, J., & Tkadlec, E. (2007). Structure and diversity of small mammal communities in agriculture landscape. *Agriculture, Ecosystems & Environment*, *120*(2–4), 206–210. https://doi.org/10.1016/j.agee.2006.09.007

Hutterer, R., Jenkins, P. D., & Verheyen, W. N. (1991). A new forest shrew from southern Tanzania. *Oryx*, *25*(3), 165–168. https://doi.org/10.1017/S0030605300034190

IUCN. (2022). The IUCN Red List of Threatened Species. Version 2022-2.

Jorgensen, E. E. (2004). SMALL MAMMAL USE OF MICROHABITAT REVIEWED. *Journal of Mammalogy*, *85*(3), 531–539. https://doi.org/10.1644/BER-019

Karasov-Olson, A., & Kelt, D. A. (2020). Small mammal assemblage composition and habitat associations across an elevational gradient in southern California. *Journal of Mammalogy*, *101*(1), 92–106. https://doi.org/10.1093/jmammal/gyz178

Kasangaki, A., Kityo, R., & Kerbis, J. (2003). Diversity of rodents and shrews along an elevational gradient in Bwindi Impenetrable National Park, south-western Uganda. *African Journal of Ecology*, *41*(2), 115–123. https://doi.org/10.1046/j.1365-2028.2003.00383.x

Ken, A. P., Brown, P. R., Jacob, J., Krebs, C. J., & Singleton, G. R. (2003). *Field methods for rodent studies in Asia and the Indo-Pacific.*

Kingdon, J. (2015). *The Kingdon field guide to Africa Mammals* (Second edi). Bloomsbury Publishing Plc.

Kohlmann, B., Arriaga-Jiménez, A., & Portela Salomão, R. (2022). Rapoport's Rule and the effect of the last glaciation upon elevational range size: An analysis using a dung beetle model (Coleoptera: Scarabaeidae: Onthophagus) in Mexican tropical mountains. *The Holocene*, *32*(3), 208–219. https://doi.org/10.1177/09596836211060488

Konečný, A., Hutterer, R., Meheretu, Y., & Bryja, J. (2020). Two new species of Crocidura (Mammalia: Soricidae) from Ethiopia and updates on the Ethiopian shrew fauna. *Journal of Vertebrate Biology*, *69*(2). https://doi.org/10.25225/jvb.20064

Körner, C. (2007). The use of 'altitude' in ecological research. *Trends in Ecology & Evolution*, *22*(11), 569–574. https://doi.org/10.1016/j.tree.2007.09.006

Lacey, E. A. (2001). Microsatellite variation in solitary and social tuco-tucos: molecular properties and population dynamics. *Heredity*, *86*(5), 628–637. https://doi.org/10.1046/j.1365-2540.2001.00881.x

Lacey, E. A., Patton, J. L., & Cameron, G. N. (2000). *Life underground : the biology of subterranean rodents* (1st Editio). University of Chicago Press.

Lema, R., & Magige, F. J. (2018). The influence of agricultural activities on the diversity of rodents in Kindoroko forest reserve and surrounding areas, North Pare Mountains, Tanzania. *Tanzania Journal of Science*, *44*(1), 97–106.

Lima, M., Stenseth, N. Chr., Leirs, H., & Jaksic, F. M. (2003). Population dynamics of small mammals in semi-arid regions: a comparative study of demographic variability in two rodent species. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *270*(1528), 1997–2007. https://doi.org/10.1098/rspb.2003.2448

Lin, Y.-T. K., & Batzli, G. O. (2001). The Influence of Habitat Quality on Dispersal, Demography, and Population Dynamics of Voles. *Ecological Monographs*, *71*(2), 245. https://doi.org/10.2307/2657218

López-García, J. M., Cuenca-Bescós, G., Galindo-Pellicena, M. Á., Luzi, E., Berto, C., Lebreton, L., & Desclaux, E. (2021). Rodents as indicators of the climatic conditions during the Middle Pleistocene in the southwestern Mediterranean region: implications for the environment in which hominins lived. *Journal of Human Evolution*, *150*, 102911. https://doi.org/10.1016/j.jhevol.2020.102911

Magige, F. J. (2013). Rodent species diversity in relation to altitudinal gradient in Northern Serengeti, Tanzania. *African Journal of Ecology*, *51*(4), 618–624. https://doi.org/10.1111/aje.12075

Makundi, R. H., Massawe, A. W., & Mulungu, L. S. (2007). Breeding seasonality and population dynamics of three rodent species in the Magamba Forest Reserve, Western Usambara Mountains, north-east Tanzania. *African Journal of Ecology*, *45*(1), 17–21. https://doi.org/10.1111/j.1365-2028.2006.00667.x

Makundi, R. H., Massawe, A. W., Mulungu, L. S., & Katakweba, A. (2009). Species diversity and population dynamics of rodents in a farm-fallow field mosaic system in Central Tanzania. *African Journal of Ecology*, *48*(2), 313–320. https://doi.org/10.1111/j.1365-2028.2009.01109.x

Márquez, A. L., Real, R., Olivero, J., & Estrada, A. (2011). Combining climate with other influential factors for modelling the impact of climate change on species distribution. *Climatic Change*, *108*(1–2), 135–157. https://doi.org/10.1007/s10584-010-0010-8

Mason-Romo, E. D., Ceballos, G., Lima, M., Martínez-Yrízar, A., Jaramillo, V. J., & Maass, M. (2018). Long-term population dynamics of small mammals in tropical dry forests, effects of unusual climate events, and implications for management and conservation. *Forest Ecology and Management*, *426*, 123–133. https://doi.org/10.1016/j.foreco.2018.05.058

Massawe, A. W., Makundi, R. H., Mulungu, L. S., Katakweba, A., & Shayo, T. N. (2012). Breeding Dynamics of Rodent Species Inhabiting Farm—Fallow Mosaic Fields in Central Tanzania †. *African Zoology*, *47*(1), 128–137. https://doi.org/10.3377/004.047.0117

McCain, C. M. (2004). The mid-domain effect applied to elevational gradients: species richness of small mammals in Costa Rica. *Journal of Biogeography*, *31*(1), 19–31. https://doi.org/10.1046/j.0305-0270.2003.00992.x

Mccain', C. M. (2005). Elevational gradients in diversity of small mammals. In *Source: Ecology* (Vol. 86, Issue 2).

Meliyo, J., Brabers, L., Massawe, B., Msanya, B., Kimaro, D., Mulungu, L., Kihupi, N., Deckers, J., Gulinck, H., & Leirs, H. (2015). The Effect of Soil Physical Properties and Soil Microclimate on Rodent Burrows' Abundance and their Characteristics in Western Usambara Mountains, Tanzania. *Journal of Agriculture and Ecology Research International*, *2*(2), 105–119. https://doi.org/10.9734/JAERI/2015/13695

Michael, N., Japhet, R., & Shyamala, R. (2016). Diversity, Composition and Richness of Small Mammals in Natural and Agricultural Areas in Mbeya Region, Tanzania. *International Journal of Modern Plant & Animal Sciences*, *4*(1), 35–46.

Mittermeier, R. A., Patricio, R. G., Hoffman, M., Pilgrim, J., Brooks, T., Mittermeier, C. G., Lamoreux, J., & da Fonseca, G. A. (2004). *Hotspots revisited CEMEX*.

Mittermeier, R. A., Ratsimbazafy, J., Rylands, A. B., Williamson, L., Oates, J. F., Mbora, D., Ganzhorn, J. U., Rodríguez-Luna, E., Palacios, E., Heymann, E. W., Kierulff, M. C. M., Yongcheng, L., Supriatna, J., Roos, C., Walker, S., & Aguiar, J. M. (2007). Primates in Peril: The World's 25 Most Endangered Primates, 2006–2008. *Primate Conservation*, *22*(1), 1–40. https://doi.org/10.1896/052.022.0101

Mittermeier, R. A., Turner, W. R., Larsen, F. W., Brooks, T. M., & Gascon, C. (2011). Global Biodiversity Conservation: The Critical Role of Hotspots. In *Biodiversity Hotspots* (pp. 3–22). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-642-20992-5_1

Mlyashimbi, E. C. M., Mariën, J., Kimaro, D. N., Tarimo, A. J. P., Machang'u, R. S., Makundi, R. H., Isabirye, M., Massawe, A. W., Leirs, H., Mdangi, M. E., Belmain, S. R., & Mulungu, L. S. (2020). Home ranges, sex ratio and recruitment of the multimammate rat (Mastomys natalensis) in semi-arid areas in Tanzania. *Mammalia*, *84*(4), 336–343. https://doi.org/10.1515/mammalia-2019-0048

Muluneh, M. G. (2021). Impact of climate change on biodiversity and food security: a global perspective—a review article. *Agriculture & Food Security*, *10*(1), 36. https://doi.org/10.1186/s40066-021-00318-5

Mulungu, L. S., Mahlaba, T. A., Massawe, A. W., Kennis, J., Crauwels, D., Eiseb, S., Monadjem, A., Makundi, R. H., Katakweba, A. A. S., Leirs, H., & Belmain, S. R. (2011). Dietary differences of the multimammate mouse, Mastomys natalensis (Smith, 1834), across different habitats and seasons in Tanzania and Swaziland. *Wildlife Research*, *38*(7), 640. https://doi.org/10.1071/WR11028

Mulungu, L. S., Makundi, R. H., Massawe, A. W., Machang'u, R. S., & Mbije, N. E. (2008). Diversity and distribution of rodent and shrew species associated with variations in altitude on Mount Kilimanjaro, Tanzania. *Mammalia*, *72*(3), 178–185. https://doi.org/10.1515/MAMM.2008.021

Musila, S., Yego, R., Onditi, K., Muthoni, I., Omondi, S., Mathenge, J., N. Kioko, E., Musila, S., Chen, Z.-Z., Li, Q., Yego, R., Zhang, B., Onditi, K., Muthoni, I., He, S.-W., Omondi, S., Mathenge, J., N. Kioko, E., & Jiang, X.-L. (2019). Diversity and distribution patterns of non-volant small mammals along different elevation gradients on Mt. Kenya, Kenya. *Zoological Research*, *40*(1), 53–60. https://doi.org/10.24272/j.issn.2095-8137.2019.004

Mwakisunga, B. (2017). Forest Biomass Management challenges in Commercially Exotic Tree Plantations Areas. A case study from the Rungwe Volcanic Province (Southern Highlands of Tanzania). *Journal of Geoscience and Environment Protection*, *05*(03), 67–75. https://doi.org/10.4236/gep.2017.53006

Novillo, A., & Ojeda, R. A. (2012). Diversity and distribution of small mammals in the South American Dry Andes. *Austral Ecology*, *37*(7), 758–766. https://doi.org/10.1111/j.1442-9993.2011.02336.x

Novillo, A., & Ojeda, R. A. (2014). Elevation patterns in rodent diversity in the dry Andes: disentangling the role of environmental factors. *Journal of Mammalogy*, *95*(1), 99–107. https://doi.org/10.1644/13-MAMM-A-086.1

Odhiambo, R. O., Makundi, R. H., Leirs, H., & Verhagen, R. (2008). Demography, reproductive biology and diet of the bushveld gerbil Tatera leucogaster (Rodentia: Gerbillinae) in the Lake Rukwa valley, south-western Tanzania. *Integrative Zoology*, *3*(1), 31–37. https://doi.org/10.1111/j.1749-4877.2008.00073.x

Ojija, F. (2022). Awareness, Habitats and Population Status of the Endangered Rungwecebus kipunji in Mt. Rungwe Nature Reserve, Tanzania. *MUST Journal of Research and Development*, *1*(7), 14–21.

Paniccia, C., Laura Carranza, M., Frate, L., di Febbraro, M., Rocchini, D., & Loy, A. (2022). Distribution and functional traits of small mammals across the Mediterranean area: landscape composition and structure definitively matter. *Ecological Indicators*, *135*, 108550. https://doi.org/10.1016/j.ecolind.2022.108550

Perrin, M. R., & Kotler, B. P. (2005). A test of five mechanisms of species coexistence between rodents in a southern African savanna. *African Zoology*, *40*(1), 55–61. https://doi.org/10.1080/15627020.2005.11407309

Pianka, E. R. (1974). Niche Overlap and Diffuse Competition. *Proceedings of the National Academy of Sciences*, *71*(5), 2141–2145. https://doi.org/10.1073/pnas.71.5.2141

Porter, J. H., & Dueser, R. D. (1982). Niche Overlap and Competition in an Insular Small Mammal Fauna: A Test of the Niche Overlap Hypothesis. *Oikos*, *39*(2), 228. https://doi.org/10.2307/3544489

Rica, C., & Mccain, C. M. (2004). The Mid-Domain Effect Applied to Elevational Gradients: Species Richness of Small

Mammals in. In *Source: Journal of Biogeography* (Vol. 31, Issue 1).

Richard U. (2024). Population Ecology of Small Mammals in Mount Rungwe Nature Forest Reserve. Sokoine University of Agriculture.pg. 1-20.

Rovero, F., Rathbun, G. B., Perkin, A., Jones, T., Ribble, D. O., Leonard, C., Mwakisoma, R. R., & Doggart, N. (2008). A new species of giant sengi or elephant-shrew (genus Rhynchocyon) highlights the exceptional biodiversity of the Udzungwa Mountains of Tanzania. *Journal of Zoology*, *274*(2), 126–133. https://doi.org/10.1111/j.1469-7998.2007.00363.x

Saar, M., Subach, A., Reato, I., Liber, T., Pruitt, J. N., & Scharf, I. (2018). Consistent differences in foraging behavior in 2 sympatric harvester ant species may facilitate coexistence. *Current Zoology*, *64*(5), 653–661. https://doi.org/10.1093/cz/zox054

Ssuuna, J., Makundi, R. H., Isabirye, M., Sabuni, C. A., Babyesiza, W. S., & Mulungu, L. S. (2020). Rodent species composition, relative abundance, and habitat association in the Mabira Central Forest Reserve, Uganda. *Journal of Vertebrate Biology*, *69*(2). https://doi.org/10.25225/jvb.20021

Stanley, W. T., & Kihaule, P. M. (2016). Elevational Distribution and Ecology of Small Mammals on Tanzania's Second Highest Mountain. *PLOS ONE*, *11*(9), e0162009. https://doi.org/10.1371/journal.pone.0162009

Stanley, W. T., Rogers, M. A., Kihaule, P. M., & Munissi, M. J. (2014). Elevational Distribution and Ecology of Small Mammals on Africa's Highest Mountain. *PLoS ONE*, *9*(11), e109904. https://doi.org/10.1371/journal.pone.0109904

Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M. C., Schwager, M., & Jeltsch, F. (2004). Animal species diversity driven by habitat heterogeneity/diversity: the

importance of keystone structures. *Journal of Biogeography*, *31*(1), 79–92. https://doi.org/10.1046/j.0305-0270.2003.00994.x
Tuljapurkar, Shripad. (2013). *Population dynamics in variable environments.* Springer Science & Business Media.
URT. (2017). *Management Plan For Mount Rungwe Nature Forest Reserve*.
van Benthem, K. J., Froy, H., Coulson, T., Getz, L. L., Oli, M. K., & Ozgul, A. (2017). Trait-demography relationships underlying small mammal population fluctuations. *Journal of Animal Ecology*, *86*(2), 348–358. https://doi.org/10.1111/1365-2656.12627
Verde Arregoitia, L. D., & D’Elía, G. (2021). Classifying rodent diets for comparative research. *Mammal Review*, *51*(1), 51–65. https://doi.org/10.1111/mam.12214
Wegge, P., Ingul, H., Pollen, O. V., Halvorsrud, E., Sivkov, A. v., & Hjeljord, O. (2012). Comparing predation on forest grouse nestsby avian and mammalian predators in two contrastingboreal forest landscapes by the use of artificial nests. *Ornis Fennica*, *89*(3), 145–156.
Wilson, D. E., & Reeder, D. M. (2005). *Mammal species of the world: a taxonomic and geographic reference* (Eds.). JHU press.
Wirminghaus, J. O., & Perrin, M. R. (1992). Diet of small mammals in the southern African temperate forest. *Israel Journal of Zoology*, *38*, 353–361. https://doi.org/10.1080/00212210.1992.10688682
Yihune, M., & Bekele, A. (2012). Diversity, Distribution and Abundance of Rodent Community in the Afro-alpine Habitats of the Simien Mountains National Park, Ethiopia. *International Journal of Zoological Research*, *8*(4), 137–149. https://doi.org/10.3923/ijzr.2012.137.149

CHAPTER TWO
PAPER I

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RESEARCH ARTICLE

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Influence of environmental factors on small mammal communities along an altitudinal gradient of Mount Rungwe in South Western Tanzania

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Abstract

The study aimed to investigate the effects of environmental factors on the small mammal community in Mount Rungwe, Tanzania. To achieve this, three habitats low-, mid-mountainous forests at 1700–2000 and 2000–2400 m a.s.l., respectively, and bushland habitats at 2400–2800 m a.s.l. were sampled. Animal samples were collected during the wet and dry seasons in year 2020 and 2021 using live traps. A total of 12 species of small mammals were collected, comprising of nine rodents and three shrews. During the wet season, nine species were recorded, while 10 species were recorded during the dry season. Small mammals were more diverse and richer in the mid-montane forests than in the low-montane and bushland habitats. Furthermore, bushland habitats had significantly lower species composition than low- and mid-mountain forests. In addition, low-mountain forest exhibited high degrees of dominance and low level of evenness. The observed spatio-temporal patterns of small mammals in terms of composition, richness, diversity, evenness and dominance are related to differences in habitat structure and seasonal variations. Based on the findings of this study, it is recommended to monitor forest communities to ensuring sustainable biodiversity conservation, with a particular focus on protecting habitats to increase small mammal diversity under changing environmental conditions.

KEYWORDS
altitude, Mount Rungwe, species composition, species richness

Résumé

L'étude visait à analyser les conséquences des facteurs environnementaux sur la communauté de petits mammifères du Mont Rungwe, en Tanzanie. Pour ce faire, trois habitats ont été échantillonnés : les forêts de basse altitude, les forêts de moyenne altitude situées respectivement à 1700-2000 et 2000-2400 m d'altitude, et les habitats de brousse situés à 2400-2800 m d'altitude. Des échantillons d'animaux ont été collectés pendant les saisons humides et sèches des années 2020 et 2021 à l'aide de pièges en direct. Au total, 12 espèces de petits mammifères ont été collectées, dont neuf rongeurs et trois musaraignes. Pendant la saison humide, neuf espèces ont été recensées, tandis que dix espèces ont été recensées pendant la saison sèche. Les petits mammifères étaient plus diversifiés et plus riches dans les forêts de moyenne altitude que dans les habitats de basse altitude et de brousse. En outre, les habitats de brousse présentaient une composition d'espèces considérablement inférieure à celle des forêts de basse et de moyenne altitude. En outre, les forêts de basse altitude présentaient des degrés élevés de dominance et un faible niveau d'uniformité. Les structures spatio-temporelles observées chez les petits mammifères en termes de composition, de richesse, de diversité, d'uniformité et de dominance sont liées aux différences dans la structure de l'habitat et aux variations saisonnières. Sur la base des résultats de cette étude, il est recommandé de surveiller les communautés forestières afin de garantir une conservation durable de la biodiversité, en mettant particulièrement l'accent sur la protection des habitats dans le but d'accroître la diversité des petits mammifères dans des conditions environnementales changeantes.

1 | INTRODUCTION

Mount Rungwe is a volcanic mountain located in East Africa and is part of the East African Rift Valley, which include several other isolated volcanic mountains, such as Mt. Kilimanjaro, Meru, Usambara, Uluguru, Udzungwa and Rungwe. The flora and fauna of these montane islands differ from the surrounding lowlands, with high endemism of species and highly disjunct distributions, making them Galapagos of Africa (Mairal et al., 2017). The elevation gradient in these mountain ranges provides a potential candidate for understanding the influences underlying local and global diversity (Kameništák et al., 2020).

Species community composition variations can be associated with many variables (Rahbek & Graves, 2001). The frequently mentioned primary drivers that determine species composition are the attributes of the area where the species occur. These include the environment (climate and habitat) and its physical features (topography and landscape heterogeneity). On the other hand, species composition in different habitats along elevation gradients replicates among mountain ranges, making it possible to test for generality in patterns (Sanders & Rahbek, 2012). Evaluation of species diversity and composition along elevational gradients has become popular in recent years. In the most recently reviewed studies, mid-elevation peak in diversity and richness is the most common pattern documented across taxa and regions Rahbek (2004) including non-flying small mammal community assemblages (McCain, 2005).

Changes in biotic and abiotic parameters such as temperature, rainfall, topography, vegetation composition and habitat variables in a relatively small area are associated with a change in altitudinal gradient (Körner, 2007). These changes can directly impact the composition, richness (Ferro & Barquez, 2009) and diversity of small mammal community (Mulungu et al., 2008). Furthermore, although traditional views suggest a negative relationship between elevation and species richness, with a decline in species richness and composition from low to high altitude, recent literature reviews have shown that this pattern is not universal in small mammal communities (Amori et al., 2019; Begon, 1990; Rahbek, 1995). Example, pattern in small mammal richness (Andrade & Monjeau, 2014; Clausnitzer & Kityo, 2001; Ferro & Barquez, 2009), composition and diversity (Clausnitzer & Kityo, 2001; Mulungu et al., 2008) along the altitudinal gradient are not uniform though peaks at middle elevation are common (Heaney, 2001; Rica & McCain, 2004).

Small mammal richness peaks in mid-elevational gradients have been documented in several parts of the world, including the Philippines (Rickart et al., 2011), Costa Rica (Rica & McCain, 2004) and Tanzania (Mulungu et al., 2008; Stanley et al., 2014; Stanley & Kihaule, 2016). Some of the proposed processes that account for richness and diversity patterns along gradients are the species-area relationship (Rosenzweig, 1995), species-energy relationship (Wright, 1983), climatic condition (Krömer et al., 2013) and the mid-domain effect (Colwell & Hurtt, 1994). Though from recent studies of non-volant small mammals, a unimodal diversity pattern seems to be common (Mulungu et al., 2008; Stanley & Kihaule, 2016). Mid-domain refers to the tendency for species richness to be highest in the middle of a geographical range, rather than at its edges. This effect can be explained by several factors. For example, the middle of the range may provide more stable environmental conditions than the edges, which can experience more extreme and variable conditions. Additionally, the middle of a range may have more available habitat or resources, which can support greater species diversity (Colwell & Lees, 2000). According to the mid-domain null model, species richness is predicted to be highest at the elevational mid-point and decline symmetrically towards sea level and the mountaintop irrespective of mountain height or latitude (McCain, 2005).

We conducted a study to examine the influence of environmental factors on small mammal communities along altitudinal gradient of Mount Rungwe Forest Nature Reserve in southwestern Tanzania. Mount Rungwe is home to a range of different habitats, and variations in habitats along elevation gradients have been shown to influence small mammal composition and diversity (Glišić et al., 2021). The reserve contains several habitats at different elevations, each with distinct vegetation composition that is thought to affect small mammals species composition. The habitats in Mount Rungwe montane forest, which cover a large part of the mountain and is comprised of low-montane and mid-montane forest. In addition, there is a line of bamboo forest above the mid-range, and at higher elevations, there is bushland habitat. These different elevational ranges differ in environmental resources spatially and seasonally. Therefore, species composition and diversity are expected to vary seasonally according to the productivity-diversity theory, which predicts that environments with higher productivity to sustain a larger number of individuals and higher species richness (Brown, 2001; Hawkins et al., 2003).

Several studies on mountainsides conducted in Tanzania (Stanley & Kihaule, 2016; Stanley et al., 2007, 2014) have shown that the distribution pattern of small mammals is significantly affected by elevation and vegetation cover. While previous research on Rungwe Mountain has reported about eighteen small mammal species including seventeen rodents and one shrew, no studies have examined the general pattern of small mammals composition, and diversity along Mount Rungwe's elevational gradient. Therefore, this study aimed to investigate how environmental factors influence small mammals species richness, composition and diversity in the Mount Rungwe Forest Reserve (MRFNR). Specifically, the study aimed to determined richness, composition and diversity on small mammals and assess the effect of habitats and seasonality on the same. The study hypothesised that species diversity is highest in the mid-elevation forests and decreasing with increasing altitude or decrease vegetation cover. Additionally, the study hypothesised that species diversity would be highest during the wet seasons.

2 | METHODOLOGY

2.1 | Study area

The project was conducted in Mount Rungwe forest, a protected natural area in the southern highlands of Tanzania's Mbeya Region. The forest encompasses 13,652 hectares and is situated at the junction of the Eastern and Western arms of the East African Rift Valley. The elevation of the forest ranges from 1700 to 2960 m above sea level, with a tropical climate characterised by wet and dry seasons. The temperature varies from −6 to 29°C, and rainfall fluctuate between 900 and 2700 mm, depending on altitude and season (Williamson et al., 2014).

Mount Rungwe forest comprises several habitat types, including low-elevation mountainous forest (LMF) occurring at of 1700–2000 m a.s.l. and dominated by species such as *Afrocrania volkensii*, *Ficus capensis*, *Cyathea deckenii Tabernaemontana stapfiana*, *Albizia gummifera* and *Macaranga capensis var. kilimandscharica*. The mid-elevation montane forest (MMF) ranging from 2000 to 2400 m altitude, is home to *T. stapfiana*, *Cassipourea gummiflua* and *Prunus Africana*. The bamboo forest, located at 2600 m a.s.l. is dominated by *Bamboo nutans*, while the mountain top is a bushland at an elevation above 2500 m a.s.l. and dominated by *Embelia schimperi*, *Pteridium* sp., *A. volkensii and Cyperus*, *Hagenia abyssinica*, *B. nutans* and *Maesa lanceolata* (Table 1; URT, 2017).

2.2 | Trapping of small mammals

Small mammals were trapped along 36 transects at six locations in the western part of Mount Rungwe from 2020 to 2021. Transects covered an altitudinal gradient ranging from 1700 to 2800 m a.s.l. and were chosen based on elevation, habitat type and accessibility covering low-montane forest, mid-montane forest and bushland habitats. Animals were captured using Sherman traps, pitfalls and Havahart traps with a total of 50 Sherman traps were placed on five lines of 100 m with 10 stations spaced 10 m apart. Additionally, a line of 10 buckets was used for pitfall traps, while six Havahart traps were arranged randomly at trapping sites. The bait used for trapping was peanut butter, maize flour and banana. The study conducted trapping for five nights in each location and season. The collected species identified based on morphometric measurements, recent distribution data and cytochrome b gene sequence (Cuypers et al., 2022; Happold, 2013; Sabuni et al., 2015; Verheyen et al., 2007; Voelker et al., 2021).

2.3 | Data analysis

The data collected from transect lines at each elevation was combined to create a single data set per elevation. To assess species diversity, composition and richness were calculated from the pooled data from each elevation was used. In cases where variables were not normality distributed, the Shapiro–Wilk test was used to determine normality and the strongly skewed data were transformed before analysis to meet the assumption of homogeneity of variances and normality (Wilcoxon, 1945). To evaluate if the sampling effort was adequate to represent the species richness and estimate the

TABLE 1 Habitat types from which small mammals were trapped at Mount Rungwe Forest Reserve.

Altitude	Description	Topography	Habitat type
1700	Low elevation	Sloping	Montane forest in low elevation
1895	Low elevation	Gentle slope	Montane forest in low elevation
2102	Mid elevation	Gentle slope	Montane forest in mid elevation
2315	Mid elevation	Steep slope	Montane forest and bamboo in mid elevation
2563	High elevation	Gentle slope	Bushland in higher elevation
2698	High elevation	Steep slope	Bushland and montane grassland in higher elevations

species richness at each elevation, we used the species accumulation curve and Chao-1 Equation (1), respectively. Chao-1 was used to estimate the species richness at each elevation.

Chao-1:

$$S_1 = S_{obs} + \frac{F_1^2}{2F_2} \quad (1)$$

where F_1 and F_2 are the counts of singletons and doubletons, respectively, and S_{obs} is the number of observed species.

The species composition of small mammals was estimated as the relative contribution of each individual species in a sampling area. The composition of each species was expressed as a percentage so that all species components add up to 100% Equation (2).

$$\%\,\text{Composition Spp A} = \left(\frac{\#\,\text{Of Spp A}}{\text{Total}\,\#\,\text{individuals}}\right) \times 100 \quad (2)$$

Species richness was referred to as the number of species in a given elevation. When quantifying diversity in an elevation gradient, beta and alpha diversities are usually studied (McCain, 2005). Alpha diversity tracks diversity along the transect at local scale, usually on a single mountain slope, while beta diversity refers to differences in diversity and composition in different habitats (McCain, 2007). Species diversity was estimated using the Shannon–Wiener Index expresses by the following equation:

$$H = -\sum_{i=1}^{S} p_i \ln p_i \quad (3)$$

where H' is the Shannon–Wiener index for diversity, S is the total number of species, and p_i is proportional to the total sample belonging to ith species. A diversity t-test was performed to compute pairwise differences in diversity between the elevations. Evenness which is a degree of equitability in the distribution of individuals among a group of species was computed following (Pielou, 1975) as,

$$J' = H' / \ln(S) \quad (4)$$

where H' is the Shannon diversity index, S is the species richness and J' is species evenness, which ranges from 0 to 1. Evenness differences across elevations were computed by permutation tests. Species dominance was calculated from the formula:

$$D = \sum (n_i (n_i - 1)) / (N (N - 1)) \quad (5)$$

where n_i is the number of individuals in the ith species and N is the total number of individuals in the community. Dominance ranges from 0 meaning no dominant species to 1 meaning high dominance. Diversity t-tests and diversity permutation tests were used to test if there was a significant difference between diversity, dominance, richness and evenness among habitats along elevations.

Multivariate generalised linear models (GLM) were used to model changes in small mammal richness, composition and diversity across habitats and seasons assuming a poison distribution. Species (richness, composition and diversity) were the response variable and habitats and seasons were the determinant variables. Correlated variables with more than three Variance Inflation factors (VIF) were excluded from the models to reduce collinearity. The model used was:

$$\text{Richness; Composition; Diversity} \sim \text{HA} + \text{SE} + \text{HA} \times \text{SE}$$

whereby: HA, habitat; SE, season.

Then Non-Metric Multidimensional Scaling (NMDS) was performed to reveal the elevational composition structure and Bray–Curtis's dissimilarity index was used to test species similarities between elevation gradients. The statistical test was performed using R version 4.0.3 (R Core, 2020).

3 | RESULTS

3.1 | Species composition, richness and diversity

3.1.1 | Small mammal composition

The three techniques used to survey small mammals at Mount Rungwe were effective with different groups of small mammals. Most of the shrews were caught in pitfall buckets and most of the rodents were caught in Sherman traps while Havahart traps were effective in catching *Cricetomys ansorgei* exclusively. A total of 953 small mammals (rodents and shrews) from four families and 11 genera were recorded in 3960 trap nights (Table 2). Trap success was 26% and 22% in the wet and dry seasons, respectively. Wet season had a higher species composition of 54.7% compared to 45.3% during the dry season. Species richness was 9 in the wet and 10 in the dry seasons, respectively.

A total of 12 species, comprising nine rodents and three shrews, were recorded at MRFNR in the low montane forest, mid-montane forest and bushland habitats. Among them, six species (*Montemys delectorum, Lophuromys machangui, Beamys hindei, Dendromus nyassae, Crocidura luna* and *Graphiurus* sp.) were recorded across the habitats. The most caught species was *M. delectorum* with a composition of 74.29% in all habitats and the least captured were *Mus triton* and *Hylomyscus arcimontensis* (Table 2).

3.1.2 | Species richness

Mid-elevation montane forest had the highest species richness with 11 species, while low-elevation forest and high-elevation bushland had 9 and 7 species, respectively (Figure 1). Species richness increased from low to mid-montane forest elevation, peaking at 2103 m with 10 species, then decreased to six species at the highest

TABLE 2 Trap success and species composition in brackets in three habitats along an elevation gradient at Mount Rungwe Forest Reserve.

Species name	LMF	MMF	BL	Total
Rodents				
Nesomyidae				
Beamys hindei	0.25 (1.1)	0.80 (2.7)	0.12 (1.8)	0.39 (2.0)
Cricetomys ansorgei	0.1 (0.5)	0.12 (0.4)	0 (0)	0.08 (0.4)
Dendromus nyassae[a]	0.06 (0.3)	0.12 (0.4)	0.37 (5.4)	0.19 (0.9)
Gliridae				
Graphiurus sp.[c]	0.19 (0.8)	0.19 (0.6)	0.25 (3.6)	0.21 (1.1)
Muridae				
Grammomys cometes	0.31 (1.4)	0.31 (1.1)	0 (0)	0.21 (1.1)
Lophuromys machangui	0.25 (1.1)	1.98 (6.8)	0.49 (7.1)	0.91 (4.6)
Mus triton	0 (0)	0.06 (0.2)	0 (0)	0.02 (0.1)
Montemys delectorum[b]	18.52 (81.7)	19.88 (67.9)	5.31 (76.8)	14.57 (74.3)
Hylomyscus arcimontensis	0 (0)	0.06 (0.2)	0 (0)	0.02 (0.1)
Shrews				
Soricidae				
Crocidura olivieri	0.06 (0.3)	0.06 (0.2)	0 (0)	0.04 (0.2)
Crocidura luna	2.90 (12.8)	5.68 (19.4)	0.37 (3.57)	2.98 (11.9)
Myosorex kihaulei	0 (0)	0 (0)	0.12 (1.79)	0.04 (0.2)
Composition	38.5	49.7	11.8	100
Trap success	22.65	29.26	6.91	19.61
Trap effort	1320	1320	1320	3960
Richness	9	11	7	12

Abbreviations: BL, bushland in higher elevation; LMF, low-montane forest in low elevation; MMF, mid-montane forest in mid elevation.

[a]As *Dendromus nyassae* (but see Voelker et al., 2021).

[b]As *Montemys delectorum* in previous studies (but see Cuypers et al., 2022; Voelker et al., 2021).

[c]*Graphiurus* sp. Genomically very distinct from other taxa living in the Eastern Arc Mountains and Southern Rift Mountains.

elevation within bushland habitats. However, GLM results showed no significant differences in richness along the elevational habitats at MRFNR (Est. ± SE = −0.00089 ± 0.00083, $Z = -1.073$, $p = 0.28$).

The sapling effort for bushland at higher elevations was successful, reaching an asymptote after 50 samples. However, the accumulation curve for low and mid-montane forests continues to increase without reaching an asymptote by the end of trapping period (Figure 2). Chao-1 estimates were 9.5, 12 and 7 species for low, mid-montane forest and bushland habitats, respectively. Ten species (83%) were recorded in the initial survey after 2178 trap nights. Although the species accumulation curve showed a reasonable sampling effort with minimal new species encountered, it indicates that a few more species can be trapped with more sampling sessions in the low and mid-montane forests.

3.1.3 | Species diversity, evenness and dominance

Small mammal species diversity was measured in three habitats; low elevation, mid-elevation montane forest and high elevations bushland habitat. The diversity indices were $H' = 0.68$, $H' = 1.03$ and $H' = 0.9$, respectively. The highest species diversity was found in the mid-montane forest ($t = -4.28$, df = 783 $p < 0.001$). There were no significant different in species diversity between bushland and mid-montane forest ($t = 1.07$, df = 165, $p = 0.29$) or between low montane forest and bushland ($t = -1.67$, df = 183, $p = 0.1$). Species diversity was similar across seasons with $H' = 0.83$ and $H' = 0.96$ for dry and wet seasons on both sites, and no significant difference was found ($t = -1.799$, $p = 0.07$). The evenness value was low in all habitats due to the dominance of *M. delectorum* with the evenness of 0.22, 0.25 and 0.41 for low montane forest, mid-montane forest and bushland habitats, respectively (Figure 3b). Excluding *M. delectorum* from the analysis increased evenness to 0.4, 0.3 and 0.9 for low montane forest, mid-montane forest and bushland habitats, respectively. Dominance was highest in the low montane forest ($D = 0.69$), followed by bushland ($D = 0.60$) and mid-montane forest ($D = 0.50$; Figure 3a). Permutation tests showed significant differences in dominance, with low-montane forests having higher dominance than mid-montane forests. When excluding *M. delectorum* from the dominance tests, the

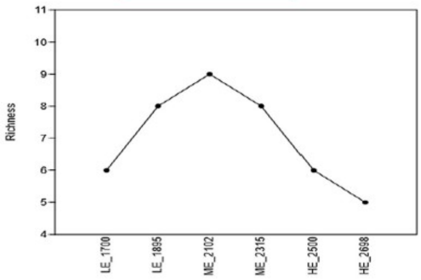

FIGURE 1 Species richness along the elevation gradient of the Mount Rungwe Forest Reserve. HE, high elevations; LE, low elevation; ME, mid elevation.

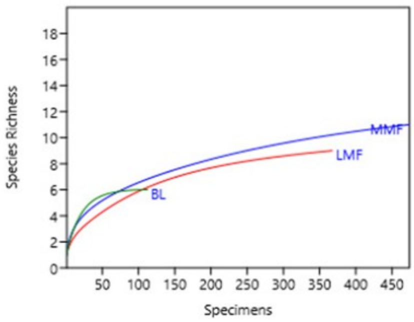

FIGURE 2 Species accumulation curve in sampled habitats. BL, bushland; LMF, low-montane forest; MMF, mid-montane forest at Mount Rungwe.

results were 0.5, 0.4 and 0.2 for low, mid-montane and bushland habitats, respectively.

3.2 | Association of small mammal communities with habitat and seasonality

At MRFNR small mammal richness was not affected by habitat or season as shown by the GLM (Table 3). Although the mid-elevation montane forest had the highest species richness, there was no significant difference in richness between low-, mid-montane and higher elevation bushland habitats. Moreover, there was no significant difference in species richness between the wet and dry seasons, except for the absence of two species (*M. triton* and *H. arcimontensis*) in wet season and one species (*Grammomys cometes*) in the dry season.

The small mammal diversity in MRFNR was found to be influenced by habitat types, as shown in Table 4. The mid- montane forest exhibited significantly higher diversity compared to the low-elevation montane forest and bushland habitats. Specifically, 11 species were recorded in the mid-montane forest, with a high percentage composition when compared to low montane forest and bushland habitats. However, no significant difference in small mammal diversity was observed for the habitat/season interaction factor.

The species composition varied across habitats ($Est \pm SE = -0.22 \pm 0.666$, $Z = -3.38$, $p = 0.001$) and between seasons ($Est \pm SE = 0.21057 \pm 0.0864$, $Z = 3.254$, $p = 0.004$). Habitat types and seasons independently affected the species composition of small mammal, and the interacted between these variables had an impact (Table 5). Furthermore, the interaction of habitat and season influenced species composition of small mammals, although to a lesser extent that when habitat and season acting independently. Notably, the interaction of habitat and season resulted in a significant difference in the composition of small mammals, with a higher composition found in the montane forest at low and mid elevation compared to the bushland (Table 5).

3.3 | Species similarity in the Mount Rungwe Forest Reserve

The non-metric Multidimensional Scaling (NMDS) analysis indicates a significant overlap of small mammal composition between low and mid-montane forest habitats compared to bushland habitats at higher elevations (Figure 4). In contrast, the Bray–Curtis similarity index revealed a high similarity (85%) between low and mid-montane forest habitats. The similarity index between mid-montane forest and bushland was 37% while for bushland and low-montane forest, the similarity index was 43%. A significant number of species were shared across habitats, including *M. delectorum*, *L. machangui*, *D. nyassae*, *Graphiurus* sp. and *C. luna*. However, *M. triton* and *H. arcimontensis* were exclusively captured in mid-montane forests, whereas *Myosorex kihaulei* was only found in bushland habitats. In forested area of low and mid-elevation montane forests, *C. ansorgei*, *C. olivieri* and *G. cometes* were captured.

4 | DISCUSSION

4.1 | Species richness, diversity and composition in different habitats and seasons

The study found no difference in small mammal richness between habitats or seasons in general, although the highest peak was observed in the mid-montane forest as shown in Figure 1. High richness in mid elevation is associated with habitat and climatic characteristics, which provides an opportunity for the emergence of distinct local biota and thus supports the mid-domain effect theory on species distribution. With the mid-domain effect, the joint

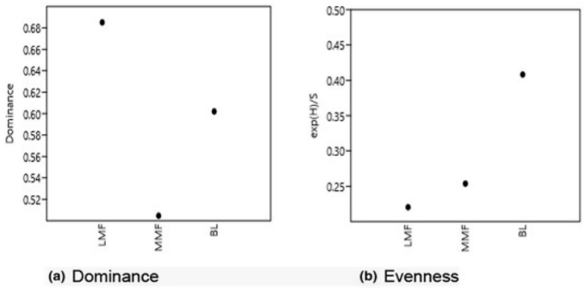

FIGURE 3 Species dominance (a) and evenness (b) in different habitats along the altitudinal gradient at Mount Rungwe. BL, bushland habitats; LMF, low-montane forest; MMF, mid-montane forest, respectively.

TABLE 3 Summary of the poison generalised linear models on species richness of small mammals in Mount Rungwe Forest Reserve.

	Estimate	Std. error z	Z value	Pr(>|z|)	Sign
(Intercept)	1.7198	0.1222	14.08	<0.001	***
HabitatBL	0.2877	0.3727	0.772	0.440	
HabitatMMF	0.2007	0.3957	0.507	0.612	
SeasonWET	0.2703	0.2466	1.096	0.273	
HabitatLMF:seasonWET	0.0223	0.0908	0.246	0.859	
HabitatMMF:seasonWET	0.1335	0.8172	−0.163	0.87	

Note: Signif. strength: ***0.001, **0.01, *0.05, 0.1, 1.

Abbreviations: BL, bush land; LMF, low-montane forest; MMF, mid-montane forest.

TABLE 4 Summary of the poison generalised linear models on species diversity of small mammals in Mount Rungwe Forest Reserve.

	Estimate	Std. error z	Z value	Pr(>|z|)	Sign
(Intercept)	−2.7420	0.9512	−2.883	0.00394	**
HabitatBL	0.1287	1.0427	0.172	0.754	
HabitatMMF	1.1594	0.90165	1.157	0.054	*
SeasonWET	0.1430	0.9331	0.153	0.8782	
HabitatLMF:seasonWET	−0.01682	2.35426	−0.007	0.994	
HabitatMMF:seasonWET	0.01717	2.23288	0.008	0.994	

Note: Signif. strength: ***0.001, **0.01, *0.05, 0.1, 1.

TABLE 5 Summary of the poison generalised linear models on species composition of small mammals in Mount Rungwe Forest Reserve.

	Estimate	Std. error z	Z value	Pr(>|z|)	Sign
(Intercept)	2.6741	0.03233	82.73	<0.001	***
HabitatBL	−0.2877	0.03727	−3.272	0.001	***
HabitatMMF	−0.2272	0.06641	−3.421	0.001	***
SeasonWET	0.19075	0.06495	2.937	0.003	**
HabitatLMF:seasonWET	0.4585	0.2242	−2.045	0.041	*
HabitatMMF:seasonWET	0.5175	0.2186	−2.368	0.0179	*

Note: Signif. strength: ***0.001, **0.01, *0.05, 0.1, 1.

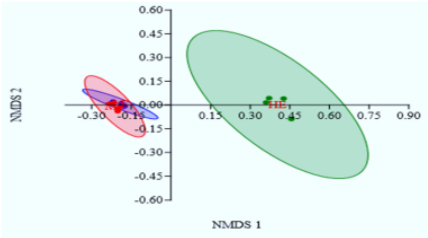

FIGURE 4 Non-metric multidimensional scaling of small mammal community composition in response to the habitats along elevations in Mount Rungwe (Blue-LMF, low-montane forest; Red-MMF, mid-montane forest; and Green-BL, bushland habitats, respectively; dots represents the sampling). An axis defines a 2D space that allows a best spatial representation of sample distance, based on Bray–Curtis distance with stress = 0.0552.

effect of climate and topography seems to be a better predictor of the mammal species richness patterns (McCain, 2007). Elevation changes can affect atmospheric and climatic conditions as well as the connectivity among habitats and habitat areas. As a result, the mid elevations have more species than the ones found in the lower or higher elevations (Grytnes & Vetaas, 2002; McCain, 2007). In the current study, the mid elevation had two more species than low and higher elevations. For example, *H. arcimontensis* was only recorded in the mid-montane forest, possibly due to habitat preference as it occurs mostly in undisturbed or slightly disturbed forest. This is supported by the study by Stanley et al. (2011) in East Usambara where *H. arcimontensis* was found more frequently in a protected forest suggesting preferences for certain microhabitat with specific vegetation composition. Studies show that habitats possessing multidominant vegetation communities create suitable habitats for fauna species (Sa et al., 2012; Williams et al., 2002). Species richness peaks in the mid-montane forest found at the intermediate elevation of the mountain have been described in the elevational gradient of other mountains around the globe see for example Kameništák et al. (2020), and this trend is consistent with the mid-elevational domain effect (McCain, 2004). Mid-elevation habitats in montane forests tend to have greater diversity of small mammals compared to other types of habitats due to conducive environmental conditions. The mid-domain effect is frequently observed in mountainous regions in the tropics within Africa (Mulungu et al., 2008; Stanley & Kihaule, 2016), the Americas (Andrade & Monjeau, 2014; Novillo & Ojeda, 2014) and Asia (Li et al., 2003; Nor, 2001). In the mountainous forests at mid elevation, there is a high degree of diversity, possibly due to the mid-domain effect, because it is situated between montane forests at low elevations and bushland habitats at the top of the mountains. Steinbauer et al. (2018) found that intermediate habitats have warmer temperatures than higher elevations. Due to the warm temperatures, vegetation richness increases in various habitats throughout the mountain range, resulting in an increased density of small mammals. As one moves up a mountain, the vegetation structure changes, resulting in different habitats. The mid-montane forest is known for its high diversity and abundance of vegetation, thus contributing to the high species diversity (Richard, Byamungu, Magige, & Makonda, 2022).

The high diversity and richness of vegetation in mid-elevation montane forest leads to high primary productivity, which, in turn, supports more primary consumers such as small mammals. The Mount Rungwe Forest Reserve (MRFNR) is characterised by a tropical mountainous cold climate with a drop in air temperature and increasing rainfall and humidity at higher elevations where bushland habitat exists (Mwakisunga & Majule, 2012). Climate limit the number of species that can survive in a certain location and habitat, while physiology also influences their occurrence (McCain & Grytnes, 2010). Biotic conditions are closely linked to changes in the composition and diversity of the habitat and environmental productivity, resulting in changes in the richness, composition and diversity of the species in the area. The bushland habitat located at higher elevations had low diversity, richness and composition compared to low and mid-elevation montane forests. This may be due to unfavourable climatic conditions that lead to lower productivity, thereby supporting fewer small mammals. For example, a small mammal altitudinal study in Australia showed that at higher elevations, the richness and diversity were lower compared to lower elevations due to harsh climatic condition at the mountain top that affect the richness and diversity of small mammals. (Bateman et al., 2010). The habitat complexity and vertical strata of the three sampled habitats changed from one habitat to another, which affected the small mammal assemblage. The bushland habitat of MRFNR had low vegetation diversity, affecting the productivity of other trophic levels and resulting in lower small mammal richness compared to low and mid-elevation montane forest habitats (Richard, Byamungu, Magige, & Makonda, 2022). In addition, the open ground and canopy cover in the bushland habitat exposed small mammals to predation, which further affected their adaptability and richness. Although diversity differed among habitats, there were no significant differences between the seasons. This can be explained by the fact that MRFNR is a tropical evergreen forest with heavy rains (3000 mm) that make it almost moist throughout the year, ensuring consistent food supply and cover for species during the wet and dry seasons. Previous studies showed that relatively low rainfall in the dry season between June and October contributes to maintaining relatively wet conditions in the montane, mid-montane and bamboo forests above 1500 m a.s.l. at Mount Rungwe (Williamson et al., 2014).

The small mammal community in the study area is dominated by *M. delectorum*, comprising 75% of all small mammals caught. This results in a low evenness index across all habitats, indicating that other species are not evenly distributed. The evenness index increases when the dominant species are more evenly distributed (Sa et al., 2012). However, when *M. delectorum* was excluded from the analysis, the bushland habitat had a high evenness index, implying species were evenly distributed. The dominance of *M. delectorum* could be due to its adaptability to a wider environmental variable and ability to tolerate harsh climatic conditions at higher elevations.

A study in Slovakia by Kamenišťák et al. (2020) noted environmental conditions influencing the dominance of mountain species, whereby species with wider tolerance capabilities to prevailing environmental conditions were more abundant.

4.2 | Association of small mammals species composition with habitat and seasonality

Small mammal composition varied across habitats and seasons at MRFNR. Bushland habitats had fewer species than low and mid-elevation montane forests, with only one unique species (*M. kihaulei*) recorded in the bushland habitat. At a mid-montane forest ecotone layer, ten species were collected, including all those from low elevation and six from bushland habitats. Studies have shown that differences in small mammal composition in different habitats are influenced by the biotic and abiotic characteristics of the area and sampling intensity. However, differences in sampling intensity between habitats may result in missing rare species or under sampling in some habitats (McCain & Grytnes, 2010). The sampling intensity was equal across all habitats, indicating that differences in biotic and abiotic characteristics likely caused the observed differences in species composition.

Small mammal species composition is influenced by seasons, with higher species composition during the wet season. This may be due to increased vegetation complexity, food abundance and better survival and reproduction. Studies have shown similar findings, with rainfall patterns and food availability affecting small mammal populations (Merritt et al., 2001; Nicolas & Colyn, 2003; Rabinowitz & Nottingham, 1989).

4.3 | Species similarities in Mount Rungwe Forest Reserve habitats

Small mammal communities in bushland and forest habitats at low and mid elevations exhibit significant differences, likely due to varying climatic and topographical conditions. Landscape structures, such as topography and climatic factors such as rainfall, solar radiation, humidity and temperature effects, also impact species composition. At higher elevations, environmental productivity is limited and there is a high predation risk due to low canopy cover, which restricts the species composition and abundance (McCain & Grytnes, 2010; Richard, Byamungu, & Magige, 2022). Ecotones between habitats tend to have more species due to overlapping range limits (McCain & Grytnes, 2010). Landscape structures also have a large impact on small mammal species composition as they influence the intensity of solar radiation and wind effects (Liu et al., 2009). High-altitude mountain tops without forests cover may act as a barrier for forest-dwelling small mammals, and the harsh climate and rough terrain in bushland habitats may explain their low species richness, diversity and composition in the MRFNR. Seasonal effects on richness and diversity were not significantly different, indicating that small mammals at MRFNR were not influenced by seasons as the area is receiving enough rainfall.

Based on the findings of the study, it can be concluded that small mammal diversity and composition at the Western MRFNR are significantly influenced by habitat types and seasons. For example, the climbing habitat of *D. nyassae* indicate a reliance on a healthy alpine zone, as well as dense grasses and twigs (Grimshaw et al., 1995; Stanley et al., 2014). The peak in richness, composition and diversity at MRFNR occurred in intermediate habitats following the mid-domain effect. The study emphasises the importance of monitoring forest communities to ensure sustainable biodiversity conservation, with particular focus on habitat protection to increase complexity of small mammal populations under changing environmental conditions.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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REFERENCES

Amori, G., Boitani, L., Milana, G., Maiorano, L., & Luiselli, L. (2019). Endemism and diversity of European montane mammals: Macro-ecological patterns. *Biological Journal Linnean Society*, *128*, 225–237. https://doi.org/10.1093/biolinnean/blz081

Andrade, A., & Monjeau, A. (2014). Patterns in community assemblage and species richness of small mammals across an altitudinal gradient in semi-arid Patagonia, Argentina. *Journal of Arid Environments*, *106*, 18–26. https://doi.org/10.1016/j.jaridenv.2014.02.004

Bateman, B. L., Kutt, A. S., Vanderduys, E. P., & Kemp, J. E. (2010). Small-mammal species richness and abundance along a tropical altitudinal gradient: An Australian example. *Journal of Tropical Ecology*, *26*(2), 139–149. https://doi.org/10.1017/S0266467409990460

Begon, M. (1990). *Ecology: Individual, population and community*. Blackwell Scientific Publication.

Brown, J. H. (2001). Mammals on mountainsides: Elevational patterns of diversity. *Global Ecology and Biogeography*, *10*(1), 101–109.

Clausnitzer, V., & Kityo, R. (2001). Altitudinal distribution of rodents (Muridae and Gliridae) on Mt Elgon, Uganda. *Tropical Zoology*, *14*(1), 95–118. https://doi.org/10.1080/03946975.2001.10531145

Colwell, R. K., & Hurtt, G. C. (1994). Nonbiological gradients in species richness and a spurious Rapoport effect. *American Naturalist*, *144*(4), 570–595. https://doi.org/10.1086/285695

Colwell, R. K., & Lees, D. C. (2000). The mid-domain effect: Geometric constraints on the geography of species richness. *Trends in Ecology & Evolution*, *15*(2), 70–76.

Cuypers, L. N., Sabuni, C., Šumbera, R., Aghová, T., Lišková, E., Leirs, H., Baird, S. J. E., Goüy de Bellocq, J., & Bryja, J. (2022). Biogeographical importance of the Livingstone Mountains in Southern Tanzania: Comparative genetic structure of small non-volant mammals. *Frontiers in Ecology and Evolution*, *9*, 742851. https://doi.org/10.3389/fevo.2021.742851

Ferro, L. I., & Barquez, R. M. (2009). Species richness of non-volant small mammals along elevational gradients in Northwestern Argentina. *Biotropica*, *41*(6), 759–767. https://doi.org/10.1111/j.1744-7429.2009.00522.x

Glišić, M., Jakovljević, K., Lakušić, D., Šinžar-Sekulić, J., Vukojičić, S., Tabašević, M., & Jovanović, S. (2021). Influence of habitat types on diversity and species composition of urban Flora—A case study in Serbia. *Plants*, *10*(12), 2572. https://doi.org/10.3390/plants10122572

Grimshaw, J. M., Cordeiro, N. J., & Foley, C. A. H. (1995). The mammals of Kilimanjaro. *Journal of East African Natural History*, *84*(2), 105–139. https://doi.org/10.2982/0012-8317(1995)84[105:tmok]2.0.co;2

Grytnes, J.-A., & Vetaas, O. R. (2002). Distribution of vascular plant species richness and endemic richness along the Himalayan elevation gradient in Nepal. *Global Ecology and Biogeography*, *11*(4), 291–301. https://doi.org/10.1046/j.1466-822X.2002.00297.x

Happold, D. C. D. (2013). Mammals of Africa: Rodents, hares and rabbits. In *Mammals of Africa: Rodents, hares and rabbits* (Vol. *III*). Bloomsbury Publishing. https://doi.org/10.5040/9781472926937

Hawkins, B. A., Field, R., Cornell, H. V., Currie, D. J., Guégan, J. F., Kaufman, D. M., Kerr, J. T., Mittelbach, G. G., Oberdorff, T., O'Brien, E. M., Porter, E. E., & Turner, J. R. G. (2003). Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, *84*(12), 3105–3117. https://doi.org/10.1890/03-8006

Heaney, L. R. (2001). Small mammal diversity along elevational gradients in the Philippines: An assessment of patterns and hypotheses. *Global Ecology and Biogeography*, *10*(1), 15–39. https://doi.org/10.1046/j.1466-822x.2001.00227.x

Kameništák, J., Baláž, I., Tulis, F., Jakab, I., Ševčík, M., Poláčiková, Z., Klimant, P., Ambros, M., & Rychlik, L. (2020). Changes of small mammal communities with the altitude gradient. *Biologia*, *75*(5), 713–722. https://doi.org/10.2478/s11756-019-00339-3

Körner, C. (2007). The use of 'altitude' in ecological research. *Trends in Ecology & Evolution*, *22*(11), 569–574. https://doi.org/10.1016/j.tree.2007.09.006

Krömer, T., Acebey, A., Kluge, J., & Kessler, M. (2013). Effects of altitude and climate in determining elevational plant species richness patterns: A case study from Los Tuxtlas, Mexico. *Flora-Morphology, Distribution, Functional Ecology of Plants*, *208*(3), 197–210. https://doi.org/10.1016/j.flora.2013.03.003

Li, J. S., Song, Y. L., & Zeng, Z. G. (2003). Elevational gradients of small mammal diversity on the northern slopes of Mt. Qilian, China. *Global Ecology and Biogeography*, *12*(6), 449–460. https://doi.org/10.1046/j.1466-822X.2003.00052.x

Liu, J., Du, H., Tian, G., Yu, P., Wang, S., & Peng, H. (2009). Community structure and diversity distributions of small mammals in different sample plots in the eastern part of Wuling Mountains. *Zoological Research*, *29*(6), 637–645. https://doi.org/10.3724/SP.J.1141.2008.06637

Mairal, M., Sanmartín, I., Herrero, A., Pokorny, L., Vargas, P., Aldasoro, J. J., & Alarcón, M. (2017). Geographic barriers and Pleistocene climate change shaped patterns of genetic variation in the Eastern Afromontane biodiversity hotspot. *Nature Publishing Group*, *7*, 45749. https://doi.org/10.1038/srep45749

McCain, C. M. (2004). The mid-domain effect applied to elevational gradients: Species richness of small mammals in Costa Rica. *Journal of Biogeography*, *31*(1), 19–31. https://doi.org/10.1046/j.0305-0270.2003.00992.x

McCain, C. M. (2005). Elevation gradients in diversity of small mammals. *Ecology*, *86*(2), 366–372. https://doi.org/10.1890/03-3147

McCain, C. M. (2007). Area and mammalian elevational diversity. *Ecology*, *88*(1), 76–86.

McCain, C. M., & Grytnes, J. (2010). Elevational gradients in species richness. In *eLS*. John Willey & Sons, Ltd. https://doi.org/10.1002/9780470015902.a0022548

Merritt, J. F., Lima, M., & Bozinovic, F. (2001). Seasonal regulation in fluctuating small mammal populations: Feedback structure and climate. *Oikos*, *94*(3), 505–514. https://doi.org/10.1034/j.1600-0706.2001.940312.x

Mulungu, L. S., Makundi, R. H., Massawe, A. W., Machang'u, R. S., & Mbije, N. E. (2008). Diversity and distribution of rodent and shrew species associated with variations in altitude on Mount Kilimanjaro Tanzania. *Mammalia*, *72*(3), 178–185. https://doi.org/10.1515/MAMM.2008.021

Mwakisunga, B., & Majule, A. E. (2012). The influence of altitude and management on carbon stock quantities in rungwe forest, southern highland of Tanzania. *Open Journal of Ecology*, *2*(4), 214–221. https://doi.org/10.4236/oje.2012.24025

Nicolas, V., & Colyn, M. (2003). Seasonal variations in population and community structure of small rodents in a tropical forest of Gabon. *Canadian Journal of Zoology*, *81*(6), 1034–1046. https://doi.org/10.1139/z03-092

Nor, S. M. D. (2001). Elevational diversity patterns of small mammals on Mount Kinabalu, Sabah, Malaysia. *Global Ecology and Biogeography*, *10*(1), 41–62. https://doi.org/10.1046/j.1466-822x.2001.00231.x

Novillo, A., & Ojeda, R. A. (2014). Elevation patterns in rodent diversity in the dry Andes: Disentangling the role of environmental factors. *Journal of Mammalogy*, *95*(1), 99–107. https://doi.org/10.1644/13-MAMM-A-086.1

Pielou, E. C. (1975). *Ecological diversity*. Wiley.

R Core, Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Rabinowitz, A., & Nottingham, B. G. J. R. (1989). Mammal species richness and relative abundance of small mammals in a subtropical wet forest of Central America. *Mammalia*, *53*(2), 217–220. https://doi.org/10.1515/mamm.1989.53.2.217

Rahbek, C. (1995). The elevation gradient of species richness: A uniform pattern? *Ecography*, *18*(2), 200–205.

Rahbek, C. (2004). The role of spatial scale and the perception of large-scale species-richness patterns. *Ecology Letters*, *8*(2), 224–239. https://doi.org/10.1111/j.1461-0248.2004.00701.x

Rahbek, C., & Graves, G. R. (2001). Multiscale assessment of patterns of avian species richness. *Proceedings of the National Academy of Sciences*, *98*(8), 4534–4539. https://doi.org/10.1073/pnas.071034898

Rica, C., & McCain, C. M. (2004). The mid-domain effect applied to elevational gradients: Species richness of small mammals in Costa Rica. *Journal of Biogeography*, *31*(1), 19–31.

Richard, U., Byamungu, R. M., & Magige, F. (2022). Diet composition and niche overlap of four sympatric rodent species inhabiting Mount Rungwe Forest Nature Reserve, Tanzania. *Tanzania Journal of Forest and Nature Conservation*, *91*(2), 178–192.

Richard, U., Byamungu, R. M., Magige, F., & Makonda, F. B. S. (2022). Microhabitat, altitude and seasonal influence on the abundance of non-volant small mammals in Mount Rungwe Forest Nature Reserve. *Global Ecology and Conservation*, *35*, e02069. https://doi.org/10.1016/J.GECCO.2022.E02069

Rickart, E. A., Heaney, L. R., Balete, D. S., & Tabaranza, B. R. (2011). Small mammal diversity along an elevational gradient in northern Luzon, Philippines. *Mammalian Biology*, *76*(1), 12–21. https://doi.org/10.1016/j.mambio.2010.01.006

Rosenzweig, M. L. (1995). *Species diversity in space and time*.

Sa, W., An, L., & Sa, W. (2012). Changes in plant community diversity and aboveground biomass along with altitude within an alpine meadow on the three-river source region. *Chinese Science Bulletin*, *57*(27), 3573–3577. https://doi.org/10.1007/s11434-012-5287-8

Sabuni, C. A., Sluydts, V., Mulungu, L. S., Maganga, S. L. S., Makundi, R. H., & Leirs, H. (2015). Distribution and ecology of lesser pouched rat, *Beamys hindei*, in Tanzanian coastal forests. *Integrative Zoology*, *10*(6), 531–542. https://doi.org/10.1111/1749-4877.12159

Sanders, N. J., & Rahbek, C. (2012). The patterns and causes of elevational diversity gradients. *Ecography*, *35*(1), 1–3. https://doi.org/10.1111/j.1600-0587.2011.07338.x

Stanley, W. T., Goodman, S. M., & Newmark, W. D. (2011). Small mammal inventories in the east and west Usambara Mountains, Tanzania. *Fieldiana Life and Earth Sciences*, *4*, 1–17. https://doi.org/10.3158/2158-5520-4.1.1

Stanley, W. T., & Kihaule, P. M. (2016). Elevational distribution and ecology of small mammals on Tanzania's second highest mountain. *PLoS One*, *11*(9), e0162009. https://doi.org/10.1371/journal.pone.0162009

Stanley, W. T., Kihaule, P. M., & Munissi, M. J. (2007). Small mammals of two forest reserves in the North Pare Mountains, Tanzania. *Journal of East African Natural History*, *96*(2), 215–226. https://doi.org/10.2982/0012-8317(2007)96[215:smotfr]2.0.co;2

Stanley, W. T., Rogers, M. A., Kihaule, P. M., & Munissi, M. J. (2014). Elevational distribution and ecology of small mammals on Africa's highest mountain. *PLoS One*, *9*(11), e109904. https://doi.org/10.1371/journal.pone.0109904

Steinbauer, M. J., Grytnes, J. A., Jurasinski, G., Kulonen, A., Lenoir, J., Pauli, H., & Winkler, M. (2018). Accelerated increase in plant species richness on mountain summits is linked to warming. *Nature*, *556*(7700), 231–234.

URT. (2017). *Management plan for Mount Rungwe nature forest reserve*.

Verheyen, W. N., Hulselmans, J., Dierckx, T., Mulungu, L. S., Leirs, H., Corti, M., & Verheyen, E. (2007). The characterization of the Kilimanjaro Lophuromys Aquilus True 1892 population and the description of five new Lophuromys species (Rodentia, Muridae). *Biologie*, *77*, 23–75.

Voelker, G., Huntley, J. W., Bryja, J., Denys, C., Šumbera, R., Demos, T. C., Lavrenchenko, L., Nicolas, V., Gnoske, T. P., & Kerbis Peterhans, J. C. (2021). Molecular systematics and biogeographic history of the African climbing-mouse complex (Dendromus). *Molecular Phylogenetics and Evolution*, *161*, 107166. https://doi.org/10.1016/j.ympev.2021.107166

Wilcoxon, F. (1945). Individual comparisons by ranking methods. *Biometrics Bulletin*, *1*(6), 80. https://doi.org/10.2307/3001968

Williams, S. E., Marsh, H., & Winter, J. (2002). Spatial scale, species diversity, and habitat structure: Small mammals in Australian tropical rain forest. *Ecological Society of America*, *83*(5), 1317–1329. https://doi.org/10.1890/0012-9658

Williamson, D., Majule, A., Delalande, M., Mwakisunga, B., Mathé, P. E., Gwambene, B., & Bergonzini, L. (2014). A potential feedback between landuse and climate in the Rungwe tropical highland stresses a critical environmental research challenge. *Current Opinion in Environmental Sustainability*, *6*(1), 116–122. https://doi.org/10.1016/J.COSUST.2013.11.014

Wright, D. H. (1983). Species-energy theory: An extension of species-area theory. *Oikos*, *41*(3), 496. https://doi.org/10.2307/3544109

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CHAPTER THREE
PAPER II

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Microhabitat, altitude and seasonal influence on the abundance of non-volant small mammals in Mount Rungwe forest nature reserve

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A R T I C L E I N F O

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A B S T R A C T

A study on microhabitat, altitudinal and seasonal influences on small mammal abundance in Mount Rungwe Nature Forest Reserve, Tanzania was carried out from March 2020 to February 2021 during the wet and dry seasons. Live traps were used in six grids and six transect lines for capturing small mammals at the low, mid, and high elevations (1700–2600 m.a.s.l.). Generalized linear models were used to examine the effects of microhabitat characteristics, altitude, and seasons on the relative abundance of small mammals. A total of 444 rodents and shrews were recorded on 4320 trap nights. Rodent species recorded included *Beamys hindei, Cricetomys ansorgei, Dendromus insignis, Grammomys cometes, Graphiurus murinus, Lophuromys machangui, Praomys delectorum,* and one shrew, *Crocidura* sp. Overall, *P. delectorum* was the most dominant species in all elevations, with 68.9% of all captures. Mid elevation had a higher abundance of small mammals (Estimate ± SE = 1.17 ± 0.49, Z = 2.37, p = 0.0176). Species abundance was influenced differently by elevation. While *P. delectorum* decreases with increasing elevation, *L. machangui* increases with an increase in elevation. Although overall small mammal abundance was not affected by microhabitat variables (Estimate ± SE = —0.08 ± 0.13, Z = —0.67, p = 0.5050), individual species (*P. delectorum* and *L. machangui*; Estimate ± SE = 0.13 ± 0.06, Z = 1.95, p = 0.05 and —0.31 ± 0.09, Z = 3.34, p = 0.0008 respectively) were affected differently. While *P. delectorum* abundance showed a positive correlation and increased with an increase in PCA1 in GLM, *L. machangui* had a negative trend that shows they were affected differently. Small mammal abundance, on the other hand, was affected by season and, in particular, rain, with low abundance during heavy rains and dry cold periods (Estimate ± SE = 0.51 ± 0.14, Z = 3.6, p = 0.0003 and 0.3 ± 0.15, Z = 2.08 p = 0.04 respectively). In general, the results show that microhabitat parameters, elevation, and season influenced small mammals' abundance in MRFNR. This outcome indicates that altering the microhabitat could have an impact on the small mammal assemblage and particularly their abundance. Thus, microhabitat, elevation, and season influence small mammal abundance and can be used as a proxy for evaluating the biodiversity of montane tropical small mammal communities.

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1. Introduction

Small mammal communities, like any other animal community, can be affected by several landscape features such as elevation, topography, forest patches, and forest edges (Michael and Jeffrey, 2012). In the tropical forest, small mammal communities are largely influenced by habitat structure and composition on a large scale and microhabitat characteristics on a small scale. Habitat and microhabitat selection provides a useful way of determining how species respond to environmental heterogeneity, and it is an adaptive basis in reproductive strategy (Nowak, 1999). Moreover, seasonal variations affect microhabitat characteristics, hence influencing the abundance and habitat of small mammals (Bantihun and Bekele, 2015).

Small mammals have a relatively small home range and rapid population growth, which can quickly respond to microhabitat change (Bagne and Finch, 2010). Some studies have shown that different species of small mammals cohabit because of basic mechanisms of distinct microhabitat requirements (Dalmagro and Vieira, 2005). Microhabitats such as landscape characteristics (topography and soil), climatic conditions, vegetation characteristics, diseases, predation, and habitat utilization by humans help in the creation of a diverse ecosystem (Lim et al., 2018; Xingyuan et al., 2015). Such variation in microhabitat influences population parameters such as the presence and abundance of different species in a particular habitat (Sponchiado et al., 2012). Abundance and diversity of food and microhabitat conditions such as vegetation characteristics, leaf litter depth, ground cover, canopy cover, and soil properties determine the presence and abundance of small mammals on a local scale (Leis et al., 2007). This is because small mammals select their microhabitat and acclimatize to different microhabitat conditions. Moreover, they can be used to understand the influence of elevation and seasons on population abundance as they have a direct influence on the microhabitat of the area (e.g., a small change in microclimate results in a relatively large change in behavior and population dynamics). Studying small mammals based on morphological and ecological characteristics has great value in determining the microhabitat requirements of different species, including both large and medium-sized species.

The current study focused on non-volant members of the Rodentia and Eulipotyphla. Non-volant terrestrial mammals are land-based mammals that cannot fly or all land-based mammals, excluding bats. Rodentia is the largest order in the Mammalia group and occupies a large percentage of the nonvolant small mammals. Rodents, being one of the non-volant mammals, are the most successful order with great diversity in ecology, morphology, physiology, behavior, distribution, and life history strategies (Admas and Yihune, 2016). They occupy a diverse terrestrial habitat from low elevations on the coasts to high elevations in the mountains with different vegetation characteristics, climatic conditions, soil types, and topography. This is due to their diverse diet, adaptability to many ecosystems, and most of them are small in size with a short breeding cycle (Fitzherbert et al., 2016). In the current study, we expect the non-volant abundance of small mammals to increase with elevation and decrease at the higher elevations to form a hump

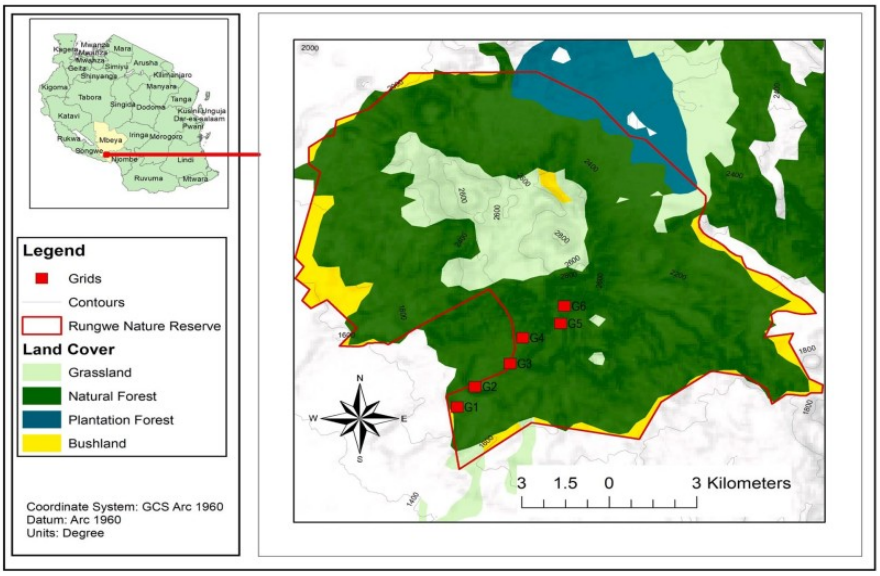

Fig. 1. Study area showing sampling points in the Mount Rungwe Forest Nature Reserve.

shape due to different microhabitat characteristics and climatic conditions in different elevations (Heaney, 2001; Rickart et al., 2011).

Mount Rungwe Nature Forest Reserve (MRNFR) in Tanzania is one of the protected forests that have been demarcated as a catchment forest. The reserve is a tropical montane forest that has important conservation status in the southern part of Tanzania. It hosts two flagship species: Abbot's duiker (*Cephalophus spadix*) and the Kipunji monkey (*Rungwecebus kipunji*). The reserve has been impacted by various threats such as pine plantation, illegal hunting of mammals including endemic and endangered *R. kipunji,* and illegal timber logging. This study aimed at investigating the influence of microhabitat characteristics on rodents and shrews along the elevation gradient of MRFNR. Thus, the study will add ecological information of small mammals of MRFNR that will help in formulating their conservation plan.

Altitudinal study of rodents in Tanzania has been conducted mostly in the northern side of the country including Mt Kilimanjaro and Mt Meru as well as within the Eastern arc mountains (Mulungu et al., 2008; Stanley et al., 2007; Stanley and Goodman, 2011). However, the southern mountains have received little attention with few studies on *R. kipunji* (Bracebridge et al., 2012; Davenport et al., 2008). How small non-volant mammal abundance is influenced by their surrounding microhabitat and altitude in MRFNR is not known.

2. Materials and methods

2.1. Study area

The study was conducted in MRNFR, Rungwe District, Mbeya in Southern Tanzania. The reserve is situated between 9°03' - 9°12' S and 33°35' - 33°45' E, at an elevation of 2981 m a.s.l. (Fig. 1). It has a total area of 13,652 ha with a boundary length of 69.3 km. The reserve experiences different weather patterns; heavy rain from March-May, cold and dry from June-Aug, hot and dry from September to October, and short rain from November to February. The rainfall ranges from 700 mm to 2700 mm in low and higher elevations, respectively (URT-MRNRMP 2017). Exceptionally, the southeastern part of the mountain receives rainfall of up to 3000 mm per year, which is the highest in Tanzania. The temperature varies between — 6° C in the highlands and 29° C in the lowlands (Williamson et al., 2014).

To the east, MRNFR is bordered by Livingstone Forest, which is part of Kitulo National Park. The reserve is bordered and surrounded by 16 villages. In the north, the reserve is bordered by Kiwira Forest Plantation, which is primarily a pine plantation. Bordering the reserve in the west are Rungwe Avocado Farm and the Moravian Mission, which owns a small section of the Rungwe forest.

2.2. Sampling design

The area was divided into three main elevations and sampling points were selected based on elevation and vegetation composition. There was low elevation (LE) (1700–2000 m a.s.l), mid-elevation (ME) (2000–2300 m a.s.l) and higher elevation (HE) (2400–2981 m a.s.l). In each elevation, there were two sampling grids and two transect lines, for a total of six sampling grids and six transect lines as shown in Table 1.

2.3. Trapping procedures

A capture, mark, and release method (Williams et al., 2002) were employed in all selected plots. A total of six grids, each measuring 70 m x 70 m and consisting of two grids in each elevation, were established. Sampling was done from March 2020 to February 2021, covering both the wet and dry seasons. Live traps used include Sherman live traps, Havahart Traps, and pitfall traps. A total of 49 Sherman live traps (H.B. Sherman Traps, Inc., Tallahassee, FL, USA) were set in each grid, containing seven parallel lines spaced 10 m apart and 10 m between traps (Stanley et al., 2014; Mulungu et al., 2008; Magige, 2013). The trapping stations were marked using a flag marker tied to a nearby pole for easy identification and were identified using lines 1–7 and coordinates labeled A–G in each line. The distance between the grids at each elevation was at least 150 m. There were also two transect lines of 10-liter bucket pitfall traps spaced 5 m apart in each elevation. Each line of pitfall contains 10 pitfall traps. Pitfall lines were placed at least 50 m from the CMR

Table 1
Sampling grids and vegetation description at MRFNR (LE - Low elevation, ME - Mid elevation, HE - High elevation).

Sampling Grid & transect No.	Altitude	Description	General vegetation type	Dominant plants
1	1748	Low Elevation	Sub Montane Forest	*Tabernaemontana stapfiana, Albizia gummifera, Macaranga capensis* var. *kilimandscharica*
2	1892	Low Elevation	Sub Montane Forest	*Ficus capensis, Cyathea deckenii,* and *C. capensis*
3	2010	Mid Elevation	Montane forest	*Coffea mufindiensi, Tabernaemontana stapfiana*
4	2178	Mid Elevation	Montane forest	*Tabernaemontana stapfiana, Cassipourea gummiflua* and *Prunus africana*
5	2500	High Elevation	Montane Forest	*Hagenia abyssinica, Bamboo nutans* and *Maesa lanceolata*
6	2650	High Elevation	Montane forest	*Embelia schimperi, Pteridium sp., Afrocrania volkensii,* and *Cyperus*

grids. Moreover, there were six Havahart traps placed randomly in the grid at each elevation. The pitfall and Havahart traps were designed to increase trap success for very light mammals that cannot trigger Sherman traps and large mammals that cannot fit into Sherman traps, respectively. Traps were baited with peanut butter mixed with maize flour, ripe bananas, and roasted coconut. The traps were set for 3 consecutive nights and were checked early in the morning between 06:00 and 9:00 am. Trap nights here refer to the number of traps set in 24 h. Species identification is based on morphometric measurements and recent distributional data based on Happold (2013); Bryja et al. (2014); Sabuni et al. (2015); Fitzgibb et al. (1995) and Verheyen et al. (2007).

2.4. Microhabitat sampling

We sampled microhabitat parameters (vegetation and soil characteristics) in all selected elevations to determine whether small mammal presence and abundance were affected by microhabitat along the elevation. As described by Stohlgren and Falkner (1995), a nested quadrat approach, which is a modified Whittaker method, was employed. Each small mammal quadrant of 70 m x 70 m provided 2 nested quadrats of 50 m x 20 m for trees, 2 nested plots of 5 m x 2 m for shrubs, and 4 nested plots of 1 m x 1 m for grass and herb sampling (Stohlgren and Falkner, 1995). All trees, shrubs, herbs, and grasses in the nested plots were counted and identified to species level. According to Avsar and Ayyildiz (2010), canopy and ground cover was estimated as the percent of a forest area occupied by the vertical projections of tree crowns and the percent of ground cover. The soil core method was used to collect the soil according to B´elanger and Van Rees (2006), whereby soil was collected in each rodent sampling grid at a depth of 0–30 cm. In each grid, there were 10 soil samples; 5 samples at 0 cm and 5 samples at 30 cm for organic matter, pH, and texture measures. Samples were taken at four angles of the grid and the center. For bulk density, we collected two samples from each grid. Collected soil was put in sealed plastic bags for further laboratory analysis.

2.5. Data analysis

The relative abundance of small mammals was used as a measure of abundance for small mammals. Results from vegetation and soil parameters were used in the Principal Component Analysis (PCA). To remove the effects of multicollinearity among microhabitat structure variables, PCA analysis was performed before constructing the models. A cut-off point of 0.5 was applied to choose the PCA axis that combines variables to factors. All microhabitat variables (tree density, shrub density, herb density, diversity, cover, richness, bulk density, texture, organic matter, pH, and moisture) measured from each grid were placed independently in PCA. The Kaiser-Guttman criterion (eigenvalue > 1; Kaiser (1991), Peres-Neto et al. (2005) were used to select the number of components to retain, which resulted in two important principal components. A generalized linear model (GLM) with negative binomial distribution was employed to analyze the effect of microhabitat variables (principal component selected) as the explanatory variable on the relative abundance of each small mammal as a response variable in MRNFR. Statistical analysis was performed using R version 4.0.3 (Core, 2020).

3. Results

In 4680 trap nights, 444 individuals of small mammals from 8 species belonging to 3 families of Rodentia and one family of Soricomorpha (Soricidae) were recorded as per Table 2 below.

Praomys delectorum was the most captured small mammal in all three elevations with a relative abundance of 68.9% and the least captured species was *C. ansorgei* with a 0.5% relative abundance. Mid elevation had eight captured, while lower and higher elevations had seven and six respectively. (Table 3).

3.1. Microhabitat structure

The influence of microhabitat variables focused on the three most captured species; *P. delectorum*, *L. machangui,* and *Crocidura* sp. Less than 10 individuals per species trapped were excluded for further microhabitat effect analysis as their abundance was not enough to analyze their microhabitat influence.

Principal component analysis (PCA) can distinguish small mammal species primarily associated with certain gross habitats, e.g., wooded habitats (e.g., *Acomys* sp.) and even microhabitats by focusing on the chosen parameters as in Table 4 below. From our data,

Table 2
Species collected during the study period at MNFNR.

Family	Scientific name	Common name
Gliridae	*Graphiurus murinus* (Desmarest 1822)	Forest African Dormouse
Muridae	*Praomys delectorum* (Thomas 1910)	Delicate Soft-furred mouse
Muridae	*Lophuromys machangui* (Walter et al., 2007)	Machangu's Brush-furred rat
Muridae	*Grammomys cometes* (Thomas & Wroughton, 1908)	East African Thicket rat
Nesomiydae	*Beamys hindei* (Thomas 1909)	Hindes's Long-tailed pouched rat
Nesomiydae	*Dendromus insignis* (Thomas 1903)	Montane African climbing mouse
Nesomiydae	*Cricetomys ansorgei* (Thomas, 1904)	Southern Giant Pouched rat
Soricidae	*Crocidura* sp.	White-toothed Shrew

Table 3
Small mammals captured during the study period and their relative abundance (%) in the low, mid, and higher altitudes of MRFNR.

Species	No. of SM in LE (%)	No. of SM in ME (%)	No. of SM in HE (%)	Overall SM (%)
Praomys delectorum	149(82.3)	115(60.8)	42(56.8)	306 (68.9)
Lophuromys machangui	3(1.7)	10(5.3)	12(16.2)	25(5.6)
Cricetomys ansorgei	0	1(0.5)	0	1(0.2)
Graphiurus murinus	1(0.6)	1(0.5)	3(4.1)	5(1.1)
Grammomys cometes	2(1.1)	1(0.5)	0	3(0.8)
Dendromus insignis	1(0.6)	2(1.1)	2(2.7)	5(1.1)
Beamys hindei	3(1.7)	5(2.6)	1(1.4)	9(2.0)
Crocidura sp.	22(12.2)	54(28.6)	14(18.9)	90(20.3)
Total capture (TS)	181(40.8)	189(42.6)	74(16.7)	444(100)
Trap Night	1560	1560	1560	4680
Trap success	11.6%	12.12%	4.7%	28.5%
Richness	7	8	6	8

(LE - Lower elevation, ME - Mid elevation, HE - Higher elevation, and SM – Small mammal)

PCA describes the number of microhabitat variables by reducing them to two principal components (PCA1 and PCA2) that explain 86.19% of the total variances. PCA1 was positively correlated with vegetation diversity, vegetation richness, tree abundance, canopy cover, organic matter, and soil moisture and negatively correlated with herb abundance and soil bulk density (Table 4). This outcome suggests that grids with high PCA1 scores are predominantly comprised of the forested areas, while grids with low PCA1 scores are dominated by herbs. The second principal component was positively correlated with shrub abundance and soil moisture and negatively correlated with soil pH.

3.2. *The abundance of small mammals at MRFNR*

GLM results reveal that the overall (all species abundance) abundance of small mammals was not influenced by microhabitat variables along the PCA1 and PCA2 axis, but the individual (single) species abundance was influenced differently. GLM results (Fig. 2a) show microhabitat characteristics affect *P. delectorum* and *L. machangui* (rodents) abundance but not *Crocidura* sp. (white-toothed shrew) abundance in MRFNR. Our model shows that PCA1 was a significant abundance predictor of *P. delectorum* (Estimation ± SE = 0.13 ± 0.06, Z = 1.95, p = 0.05) and *L. machangui* (Estimation ± SE = —0.31 ± 0.09, Z = —3.34, p = 0.0008) (Table 4; Fig. 2a). *Praomys delectorum* was more often captured in LE and ME with high vegetation diversity, vegetation richness, trees abundance, canopy cover, organic matter, and soil moisture. *Praomys delectorum* abundance was decreasing with increasing elevation, while *L. machangui* abundance was increasing with increasing elevation and was mostly captured in areas with a high abundance of herbs and high soil bulk density. Areas with high vegetation diversity, vegetation richness, trees abundance, canopy cover, organic matter, and soil moisture had a negative effect on *L. machangui.* PCA1 could not explain the effect of microhabitat variables on *Crocidura* sp. abundance. On the other hand, PCA2 shows no correlation with abundance of small mammals (Estimation ± SE = 0.004 ± 0.06, Z = 0.07 p = 0.9) (Table 4; Fig. 2b).

The abundance of small mammals was significantly influenced by elevation, with higher abundance in ME (Estimation ± SE = 1.17 ± 0.49, Z = 2.37, p = 0.02) when compared with HE. Nevertheless, comparing small mammals' abundance in LE and HE had no significant effect. (Table 5).

GLM results also reveal the influence of season on the abundance of small mammals. There was a significant difference in abundance whereby hot dry (Estimation ± SE = 0.303 ± 0.145, Z = 2.08, p = 0.04) and short rain (Estimation ± SE = 0.51 ± 0.14, Z = 3.62, p = 0.0003) had significantly higher abundance (Table 5) while abundance in heavy rain period was not statistically significant with that of cold dry (Estimation. ± SE = 0.09 ± 0.15, Z = 0.61, p = 0.5). Significantly more small mammals were collected

Table 4
Principal component analysis showing the correlation of eleven different microhabitat variables in PCA1 and PCA2.

Axis:	Princ1	Princ2
Vegdiversity	0.998	-0.005
Vegrichness	0.898	-0.254
Ph	0.418	-0.553
Moisture	0.587	0.631
Organic Matter	0.853	0.445
Bulk density	-0.767	-0.043
canopy cover	0.907	-0.131
ground cover	-0.426	-0.042
Trees abundance	0.879	0.292
Shrub's abundance	-0.03	0.628
Herb abundance	-0.969	0.034
Proportion of variance (%)	59.104	27.083
Eigenvalue	1.773	0.812

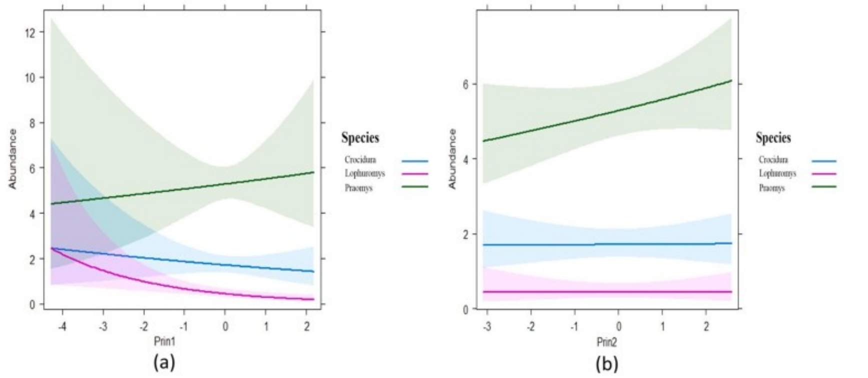

Fig. 2. a-b. Predicted effect (line) and the standard error (shades) of the habitat variables (PCA1 and PCA2) on the abundance of *Praomys delectorum* (green line), *Lophuromys machangui* (pink line), and *Crocidura* sp. (blue line). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

during the start of the rain period (shot rain) which had a relative abundance of 34% than during the hot dry period with a relative abundance of 26%.

4. Discussion

As observed in other studies (Stanley and Goodman, 2011; Stanley and Kihaule, 2016), the combination of Sherman, pitfall, and Havahart traps were effective in the sampling of the non-volant small mammals at different elevations in MRNFR. The composition of MRFNR small mammals somehow differed from the composition of small mammals in other montane areas of Tanzania. The noticeable difference was the collection of some species like *Beamys hindei* and *Cricetomys ansorgei* which had not been collected from Mt. Kilimanjaro and Mt. Meru (Mulungu et al., 2008; Stanley and Kihaule, 2016; Stanley et al., 2014). *Beamys hindei* was only collected from the Eastern Arc Mountains (Stanley and Hutterer, 2007) (Stanley and Goodman, 2011). Some species, like *Rhabdomys* sp. and *Otomys* sp., were collected from Mt. Kilimanjaro and Mt. Meru (Stanley et al., 2014), but have not been collected in MRNFR. The remaining species were collected in both areas.

4.1. The impact of microhabitat and altitude on small mammal abundance

The results demonstrate that, while variations in microhabitat structure did not influence the overall abundance of small mammals, they did impact individual species abundances. According to the model, microhabitat variables in PCA 1 (vegetation diversity,

Table 5
Estimated regression parameter, standard error, z value, and p-value for the negative binomial distribution GLM.

	Estimate	Std. Error z	Z value	Pr (>|z|)	
(Intercept)	-0.3793	0.423187	-0.896	0.370096	
SiteLE	1.050187	0.667552	1.573	0.115674	
SiteME	1.173378	0.494215	2.374	0.017586	*
SiteHE	Ref				
Seasonhotdry	0.302811	0.145616	2.08	0.03757	*
Seasonheavyrain	0.09309	0.152664	0.61	0.542011	
Seasonshotrain	0.505936	0.139814	3.619	0.000296	* **
Seasoncolddry	Ref				
Prin1	-0.083927	0.125972	-0.666	0.505262	
Prin2	0.004219	0.063252	0.067	0.946818	
SpeciesLophuromys	-1.35134	0.247131	-5.468	4.55E-08	* **
SpeciesPraomys	1.127128	0.129001	8.737	< 2e-16	* **
Prin1:speciesLophuromys	-0.314629	0.094148	-3.342	0.000832	* **
Prin1:speciesPraomys	0.1258	0.064421	1.953	0.050846	*
Prin2:speciesLophuromys	-0.00847	0.138772	-0.061	0.951329	
Prin2:speciesPraomys	0.049856	0.061884	0.806	0.420445	

ref- referred variable; * - * ** shows significance strength vegetation richness, tree abundance, shrub abundance, herb abundance, canopy cover, ground cover, pH, soil bulk density, soil moisture, and organic matter) influence small mammal assemblages, potentially shaping the presence and abundance of *P. delectorum* and *L. machangui* in MRFNR. *Praomys delectorum* was positively correlated with vegetation diversity, vegetation richness, tree abundance, and canopy cover, as also reported in other findings (Bryja et al., 2014), as well as organic matter and soil moisture, which are typically found in the mountainous forested area. On the other hand, *L. machangui* was frequently caught in areas of herb abundance, bulk density, and low canopy cover (Table 4, Fig. 2a), which is characteristically a grassland area. From the model, the abundance of *P. delectorum* decreased with increasing elevation, as seen also in another study (Stanley and Kihaule, 2016), where they were most abundant in the lower elevation and least in the higher elevation. This might be explained by the changing weather conditions along elevation, species adaptability, and the amount of primary productivity in different elevations (Peng et al., 2020; Wang et al., 2021; Kaleme et al., 2008). *Praomys delectorum* is a forest-dwelling species (Happold, 2013). In MRNFR, the number of trees, shrubs, vegetation richness, and canopy cover are reduced following an increase in altitude, and this might explain the low number of *P. delectorum* caught at higher elevations. Similar findings were found on Mt. Kilimanjaro (Mulungu et al., 2008) and Mt. Meru (Stanley and Kihaule, 2016), where *P. delectorum* was abundant at lower elevations and scarce at higher elevations.

Since *P. delectorum is* a tropical moist montane forest rodent, its abundance is expected to be high in a forested area with high canopy cover. Canopy cover helps to maintain the humidity and moisture of the area, which has been shown to affect the *P. delectorum* abundance in our study. This is supported by the results of Bantihun and Bekele (2015) in Aridtsy forest, Ethiopia, where their study showed a positive correlation between small mammals' abundance and canopy cover. High canopy cover results in dense litter, which provides abundant shelter for small mammals. This helps the animal movement in a large area rather than on bare land where they face a risk of being exposed (Ferdriani and Boulay, 2006).

A significant difference in overall abundance was observed in mid-elevation. Small mammal abundance results support the general pattern of abundance and distribution proposed by Betz et al. (2020) and Brown (1984). The pattern explains that species abundances are intense at the centers of their distributions and gradually diminish toward their boundaries. The mid-elevation has optimal environmental conditions with conducive climate conditions, high vegetation abundance, vegetation richness, canopy cover, and vegetation diversity, thus creating a better microhabitat for small mammals (Yihune and Bekele, 2012; Manhou and Jing, 2018). Our results are consistent with other previous studies that found that species abundance and richness in altitudinal gradients were confined to the mid-elevation (Ssuuna et al., 2020; Betz et al., 2020). It has been reported that rainfall and humidity usually peak at mid-elevation, hence creating a conducive environment for small mammal survival (Li et al., 2003). At low elevations, where there is an MRFNR border, it is impacted by edge effects resulting from human activities, thus creating less complexity in vegetation. On the other hand, high elevations had harsh environmental conditions that included low temperatures below 0 °C, compact soil, and high humidity that limited primary productivity. Ground cover in Rungwe HE is high as a result of a large percent of herbs and grass cover and less tree cover, thus less canopy cover compared to mid and low elevations. Canopy cover helps increase microhabitat diversity and reduces predation risk (Carey and Wilson, 2001). Low capture of small mammals in higher elevations might be because of weather and topography (Novillo and Ojeda, 2014). Mount Rungwe Forest Nature Reserve's higher elevations have a small area, steep rocks, and harsh weather conditions that make the habitat less suitable for most of the species. At MRNFR's higher elevation, temperatures may drop up to — 6 °C during the cold period which reduces primary production, thus limiting food production, vegetation diversity, and canopy cover. Another reason for low abundance at high elevations could be the species-area relationship and topography theory (Li et al., 2003). The species-area relationship suggests that the number of species is positively correlated with area size, so a small area will have a few species compared to large areas (Connor and McCoy, 2017). MRFNR high elevation topography has a small area of steep and rough terrain with high bulk density soil compared to low and mid-elevation. The arrangement of surface forms and features in the higher elevations limits the growth of primary producers, thus affecting consumers. Interestingly, in this study, the area with the highest vegetation abundance also has the lowest small mammal abundance. Higher elevations were dominated by shrubs, herbs, and grasses, resulting in higher vegetation abundance but with low vegetation diversity and richness compared to the mid and lower elevations. This indicates that microhabitat selection for small mammals largely relies on the vegetation characteristics (Madden et al., 2019) of the area. Further, Ramírez-Bautista and Williams, (2019); Kameniˇsťa´k et al., (2020) suggest a positive productivity-diversity relationship between producers and consumers. Low elevation had no significant effect on abundance because of the high abundance variation and dominance of *P. delectorum* compared to other species captured, thus creating a large error bar. *Praomys delectorum* which is a generalist was the most abundant species in the LE.

Although in our study, small mammals were higher in the mid-elevation, it was not the case for individual mammals. Individual mammals showed a different trend of abundance along the elevation. *Lophuromys machangui,* abundance increased with increasing elevation thus was more frequently recorded at 2650 m a.s.l compared to 1750 m a.s.l. In contrast, the abundance of *P. delectorum* decreased with increasing elevation, their abundance was high at the low elevation of 1750 m a.s.l and lower at higher elevations of 2650 m asl. For *Crocidura* sp., abundance formed a hump shape and they were abundant at the mid-elevation. This confirms that different groups have different needs and tolerance capacities. Although the altitude itself is not the ultimate determination of small mammals' abundance and distribution, the most important factors are vegetation structure and types (Clausnitzer and Kityo, 2001). Variations in individual trends along elevation have been observed in other altitudinal gradients. A similar observation was made in another mountainous setting like Mount Meru (Stanley and Kihaule, 2016), where the most recorded *Lophuromys* sp. was at 3000 m a.s. l and the least recorded at 1950 m a.s.l. This might be because of the high herb density (Bantihun and Bekele, 2015) at the higher altitude than at the low and mid-elevation. According to LGM results (Fig. 2a), *L. machangui* abundance decreased with increasing PCA1 value and was more abundant in areas with more shrubs and herbs and less tree abundance, canopy cover, vegetation richness, and diversity (Table 4). This suggests that *Lophuromys* sp. is found more in vegetation dominated by herbs and grasses (Bantihun and Bekele, 2015), while *P. delectorum*, *L. machangui,* and *Crocidura* sp. were dominant small mammals in all altitudes as they were present in high numbers in all elevations, low abundance with narrow distribution small mammals at MRFNR included *C. ansorgei*, *D. insignis*, *G. cometes*, *B. hindei*, and *G. murinus* with a relative abundance of 5.2% of the total abundance.

4.2. Seasonal effect on small mammal abundance

Seasonal species abundance showed that there was a significantly high abundance of small mammals during the periods of short rain and hot dry weather ($p < 0.05$), while heavy rain and cold dry periods had low abundance. This means that small mammal abundance was also influenced by the season and much of the rainfall. Hot dry weather was hypothesized to have a lower abundance because of the dry weather, hence limiting food, but the abundance was significantly higher (Table 5) compared to the cold dry season. This is because during the study period there was an unusual rainfall pattern compared to previous years, and the study area experienced rainfall of approximately 137 mm, (https://www.hobolink.com/Tanzania_mount_Rungwe) during the dry period. This unexpected rainfall during the dry season triggered the abundance of small mammals to be high as it stimulated the primary productivity and cover. The start of the rain follows the rapid growth of vegetation (Ofori et al., 2015) that provides cover and food (Bantihun and Bekele, 2015). In areas with continued rainfall, rodents reproduce almost throughout the year (Gebresilassie et al., 2006; Ofori et al., 2013), and this leads to small mammal populations being highly dynamic following changes in environmental conditions like weather on a local scale (Mulungu et al., 2013). The higher abundance of small mammals in short rain and hot dry weather might be explained by the high amounts of food, foliage, and cover. The abundance was low during the cold dry and heavy rain periods; this might be because of the harsh weather that probably forces most of the small mammals to restrict movements and hide due to extreme cold weather. Similar results have been observed at Kogyae nature reserves (Ofori et al., 2015), where the higher species abundance and diversity were in the early wet season rather than in the cold dry period.

5. Conclusion

Overall, the results of our study indicate that variations in small mammal abundance depend not only on microhabitat but also in terms of elevation and season. The nature of the microhabitat and the altitude of the area influence small mammal abundance and composition. Understanding these characteristics of small mammal species in a given ecosystem is key information for the conservation and management of small mammals. Composition and relative abundance reflect the requirements of individual species and can be used as proxies for evaluating the biodiversity of highland tropical forests.

Ethical clearance

This study was approved by Tanzania Wildlife Research Institute (TAWIRI) Ref. No. TWRI/RS-342/2019/255, Tanzania Commission for Science and Technology (COSTECH) Permit No. 2021–021-NA-2020–282, Tanzania Forest Service Agency (TFS) Ref. No. AC.198/303/01/46, and Sokoine University of Agriculture: Ref. No: SUA/ADM/R.1/8/575.

Declaration of Competing Interest

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

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References

Admas, A., Yihune, M., 2016. Species composition, relative abundance and habitat association of rodents in Yekoche Forest, East Gojjam, Ethiopia. Int. J. Biodivers. Conserv. 8, 216–223. https://doi.org/10.5897/IJBC2016.0956.

Avsar, M., Ayyildiz, V., 2010. Estimation of stand canopy cover by different methods on crown projections: sample of Lebanon Cedar Stands of the Yavsan Mountain, Kahramanmaras, Turkey. J. Appl. Sci. 10, 1326–1330. https://doi.org/10.3923/jas.2010.1326.1330.

Bagne, K.E., Finch, D.M., 2010. Response of small mammals population to fuel treatment and precipitation in a Ponderosa Pine Forest, New Mexico. Restor. Ecol. 18, 409–417. https://doi.org/10.1111/j.1526-100X.2009.00601.x.

Bantihun, G., Bekele, A., 2015. Diversity and habitat association of small mammals in Aridtsy forest, Awi Zone, Ethiopia. Zool. Res 36, 88–94. https://doi.org/10.13918/j.issn.2095-8137.2015.2.88.

B´elanger, N., Van Rees, K.C., 2006. Soil Sampling and Methods of Analysis. CRC Press.

Betz, O., Srisuka, W., Puthz, V., 2020. Elevational gradients of species richness, community structure, and niche occupation of tropical rove beetles (Coleoptera: Staphylinidae: Steninae) across mountain slopes in Northern Thailand. Evol. Ecol. 34, 193–216. https://doi.org/10.1007/s10682-020-10036-2.

Bracebridge E, Claire, Davenport R, Tim, Marsden J, Stuart, 2012. The Impact of Forest Disturbance on the Seasonal Foraging Ecology of a Critically Endangered African Primate. BioTROPICA 44 (4), 560–568. https://doi.org/10.1111/j.1744-7429.2012.00854.x.

Brown, J.H., 1984. On the relationship between abundance and distribution of species. Am. Nat. 124, 255–279. ⟨http://www.jstor.org/stable/2461494⟩ .

Bryja, J., Mikula, O., Patzenhauerova´, H., 2014. The role of dispersal and vicariance in the Pleistocene history of an East African mountain rodent, Praomys delectorum. J. Biogeogr. 41, 196–208.

Bryja, J., Mikula, O., S ˇumbera, R., Meheretu, Y., Aghova´, T., Lavrenchenko, L.A., Mazoch, V., Oguge, N., Mbau, J.S., Welegerima, K., Amundala, N., Colyn, M., Leirs, H., Verheyen, E., 2014. Pan-African phylogeny of *Mus* (subgenus *Nannomys*) reveals one of the most successful mammal radiations in Africa. BMC Evol. Biol. 14, 256. https://doi.org/10.1186/s12862-014-0256-2.

Carey, A.B., Wilson, S.M., 2001. Induced spatial heterogeneity in forest canopies: responses of small mammals. J. Wildl. Manag. 64, 1014–1027. https://doi.org/10.2307/3803050.

Clausnitzer, V., Kityo, R., 2001. Altitudinal distribution of rodents (Muridae and Gliridae on Mount Elgon, Uganda. Trop. Zool. 14, 95–118. https://doi.org/10.1080/03946975.2001.10531145.

Connor, E.F., McCoy, E.D., 2017. Species–Area Relationships. Reference Module in Life Science. Elsevier, pp. 1–17. https://doi.org/10.1016/B978-0-12-809633-8.02354-2.

Dalmagro, A., Vieira, E., 2005. Pattern of habitat utilization of small rodents in an area of *Araucaria* forest in Southern Brazil. Austral Ecol. 30, 353–362. https://doi.org/10.1111/j.1442-9993.2005.01447.x.

Davenport, T., De Luka, D., Jones, T., Mpunga, N., Machaga, S., Kitegile, A., Phillipps, G., 2008. The Critically Endangered kipunji Rungwecebus kipunji of southern Tanzania: First census and conservation status assessment. Oryx 42 (3), 352–359. https://doi.org/10.1017/S0030605308000422.

Ferdriani, J.M., Boulay, R., 2006. Foraging by fearful frugivores: combined effect of fruit ripening and predation risk. Funct. Ecol. 20, 1070–1079. https://doi.org/10.1111/j.1365-2435.2006.01199.x.

Fitzgibb, C.D., Leir, H., Verhryen, W., 1995. Distribution, population dynamics and habitat use of the lesser pouched rat, Beamys hindei. Zool. Soc. Lond. 236, 499–512. https://doi.org/10.1111/J.1469-7998.1995.TB02727.X.

Fitzherbert, E., Gardner, T.A., Caro, T., Jenkins, P., 2016. Habitat preferences of small mammals in the Katavi ecosystem of Western Tanzania. Afr. J. Ecol. 45, 249–257.

Gebresilassie, W., Bekele, A., Belay, G., Balakrishnan, M., 2006. Home range and reproduction of rodents in Maynugus. Ethiop. J. Sci. 29, 57–62. https://doi.org/10.4314/sinet.v29i1.18259.

Happold, D.C., 2013. Mammals of Africa Volume III - Rodents, Hares and Rabbits. Bloomsbury Publishers, London.

Heaney, L.R., 2001. Small mammal diversity along elevational gradients in the Philippines: an assessment of patterns and. Glob. Ecol. Biogeogr. 10, 15–39. https://doi.org/10.1046/j.1466-822x.2001.00227.x.

Kaiser, H.F., 1991. Coefficient alpha for a principal component and the kaiser-guttman rule. J. Index. Matrix 68, 855–858. https://doi.org/10.2466/pr0.1991.68.3.855.

Kaleme, P.K., Bates, J., Peterans, J.K., Jacques, M.M., Ndara, B.R., 2008. Small mammal diversity and habitat requirements in the Kahuzi-Biega National Park and surrounding areas, eastern Democratic Republic of Congo. Integr. Zool. 2, 239–246. https://doi.org/10.1111/j.1749-4877.2007.00066.x.

Kameniˇst´ak, J., Bal´aˇz, I., Tulis, F., Jakab, I., S ˇevˇcík, M., Pol´aˇcikova´, Z., Klimant, P., Ambros, M., Rychlik, L., 2020. Changes of small mammal communities with the altitude gradient. Biologia 75, 713–722.

Leis, S.A., Leslie Jr, D.M., Engle, D.M., Fehmi, J.S., 2007. Small mammals as indicators of short-term and long-term disturbance in mixed prairie. Environ. Monit. Assess. 137, 75–84. https://doi.org/10.1007/s10661-007-9730-2.

Li, J.S., Song, Y.L., Zeng, Z.G., 2003. Elevational gradients of small mammal diversity on the northern slopes of Mt. Qilian. China A J. macroecology 12, 449–460. https://doi.org/10.1046/j.1466-822X.2003.00052.x.

Lim, C.H., Yoo, S., Choi, Y., Jeon, S.W., Son, Y., Lee, W.-K., 2018. Assessing climate change impact on forest habitatsuitability and diversity in the Korean peninsula. Forests 5, 259–272. https://doi.org/10.3390/f9050259.

Madden, H., Andel, T.V., Miller, J., Stech, M., Verdel, K., Eggermont, E., 2019. Vegetation association and relative abundance of rodents on St. Eustatius, Caribbean Netherland. e00743–e00743 Glob. Ecol. Conserv. 20. https://doi.org/10.1016/j.gecco.2019.e00743.

Magige, F., 2013. Rodent species diversity in relation to altitudinal gradient in northern Serengeti, Tanzania. Afr. J. Ecol. 51, 618–624. https://doi.org/10.1111/AJE.12075.

Manhou, X., Jing, W., 2018. The mid-domain effect of species diversity of mountainous plants is determined by community life form and family flora in a temperate semi-arid region of China. PeerJ Prepr. 6, e27386v1 https://doi.org/10.7287/peerj.preprints.27386v1.

Michael, P., Jeffrey, H.A., 2012. Associations between multiscale landscape characteristics and breeding bird abundance and diversity across urban-rural gradients in Northeastern Georgia, USA. Urban Ecosyst. 15, 1–22. https://doi.org/10.1007/s11252-011-0191-6.

Mulungu, L.S., Makundi, R.H., Massawe, A.W., Machangu, S.R., Mbije, N.E., 2008. Diversity and distribution of rodents and shrew species associated with variations in altitude on Mount Kilimanjaro, Tanzania. Mammalia 72, 178–185. https://doi.org/10.1515/MAMM.2008.021.

Mulungu S, Loth, Ngowo, Victoria, Mdangi, Mashaka, Katakweba S, Abdul, Tesha, Protas, Mrosso P, Furaha, Mchomvu, Mary, Sheyo M, Paul, Kilonzo S, Bukhet, 2013. Population dynamics and breeding patterns of multimammate mouse, Mastomys natalensis (Smith 1834), in irrigated rice fields in Eastern Tanzania. Pest Manag Sci 69, 371–377. https://doi.org/10.1002/ps.3346.

Novillo, A., Ojeda, R.A., 2014. Elevation pattern in rodents diversity in the dry Andes: disentangling the role of environmental factors. J. Mammal. 95, 99–107. https://doi.org/10.1644/13-MAMM-A-086.1.

Nowak, R.M., 1999. Walker's Mammals of the World, 6th edn.,. The Johns Hopkins University Press,, London.

Ofori, B.Y., Attuquayefio, D.K., Owusu, E.H., 2013. Aspects of the Ecology of the Tullberg's soft-furred mouse (*Praomys tullbergi*: Thomas 1894) in Mount Afadjato, Ghana. J. Exp. Biol. Agric. Sci. 1, 398–404.

Ofori, B.Y., Daniel, A.K., Owusu, E.H., Musah, R.K., Quartey, J.K., Ntiamoa-Baidu, Y., 2015. Seasonal changes in small mammals assemblage in Kogyae Strict Nature Reserve, Ghana. Int. J. Biodivers. Conserv 7, 238–244. https://doi.org/10.5897/IJBC2015.0835.

Peng, Y., Bloomfield, K.J., Colin Prentice, I., 2020. A theory of plant function helps to explain leaf-trait and productivity responses to elevation. N. Phytol. 226, 1274–1284. https://doi.org/10.1111/nph.1644.

Peres-Neto, P.R., Jackson, D.A., Somers, K.M., 2005. How many principal components? stopping rules for determining the number of non-trivial axes revisited. Comput. Stat. Data Anal. 49, 974–997. https://doi.org/10.1016/j.csda.2004.06.015.

Ramírez-Bautista, A., Williams, J.N., 2019. The importance of productivity and seasonality for structuring small rodent diversity across a tropical elevation gradient. Oecologia 190, 275–286. https://doi.org/10.1007/s00442-018-4287-z.

Rickart, E.A., Heaney, L.R., Balete, D.S., Tabaranza Jr., B.R., 2011. Small mammal diversity along an elevational gradient in northern Luzon, Philippines. Mamm. Biol. 76, 12–21. https://doi.org/10.1016/j.mambio.2010.01.006.

Sabuni, C., Sluydts, V., Mulungu, L., Maganga, S., Makundi, R., Leirs, H., 2015. Distribution and ecology of lesser pouched rat, *Beamys hindei*, in Tanzania coastal forests. Integr. Zool. 10, 531–542. https://doi.org/10.1111/1749-4877.12159.

Sponchiado, J., Melo, G.L., Ca´ceres, N.C., 2012. Habitat selection by small mammals in Brazilian Pampas biome. J. Nat. Hist. 46, 1321–1335. https://doi.org/10.1080/00222933.2012.655796.

Ssuuna, J., MakundiA, R.H., Isabirye, M., Sabuni, C.A., Babyesiza, W.S., Mulungu, L.S., 2020. Rodent species composition, relative abundance, and habitat association in the Mabira Central Forest Reserve, Uganda. J. Vertebr. Biol. 69, 1–15. https://doi.org/10.25225/jvb.20021.

Stanley, W.D., Kihaule, P.M., Munissi, M.J., 2007. Small mammals of two forest reserves in the north pare mountains, Tanzania (https://doi.org/doi:). J. East Afr. Nat. Hist. 96, 215–226. https://doi.org/10.2982/0012-8317(2007)96[215:SMOTFR]2.0.CO;2.

Stanley, W.T., Hutterer, R., 2007. Differences in abundance and species richness between shrews and rodents along an elevational gradient in the Udzungwa Mountains, Tanzania. *Acta* Theriol. 52, 261–275. https://doi.org/10.1007/BF03194222.

Stanley, W.T., Marry Anne, R., Kihaule, P.M., Munissi, M.J., 2014. Elevational distribution and ecology of small mammals on Africa's highest mountain. PLoS ONE 9 (11), e109904. https://doi.org/10.1371/journal.pone.0109904.

Stanley, W., Goodman, S., 2011. Small Mammal Inventories in the East and West Usambara Mountains, Tanzania. Rodentia. Fieldiana Life Earth Sci. 4, 53–73. https://doi.org/10.3158/2158-5520-4.1.1.

Stanley, W., Kihaule, P., 2016. Elevational distribution and ecology of small mammals on Tanzania's second highest mountain. PLOS ONE 9 (11), e0162009.

Stohlgren, T.J., Falkner, M., 1995. A Modified-Whittaker nested vegetation sampling method. Plant Ecol. 117, 113–121. https://doi.org/10.1007/BF00045503.

Verheyen, W.N., Hulselmans, J.L., Dierckks, T., Mulungu, L., Leirs, H., Corti, M., Verheyen, E., 2007. The characterization of the Kilimanjaro *Lophuromys aquilus* TRUE 1892 population and the description of five new *Lophuromys* species (Rodentia, Muridae). Bull. Van. het K. Belg. Inst. voor Nat. Biol. 77, 23–75.

Wang, J., Yu, C., Fu, G., 2021. Warming reconstructs the elevation distributions of aboveground net primary production, plant species and phylogenetic diversity in alpine grasslands. Ecol. Indic. 133, 108355 https://doi.org/10.1016/j.ecolind.2021.108355.

Williams, B.K., Nichols, J.D., Conroy, M.J., 2002. Analysis and Management of Animal Populations. Academic Press, Califonia.

Williamson, D., Majule, A., Delalande, M., Mwakisunga, B., Mathe, P.-E., Gwambene, B., Bergonzini, L., 2014. A potential feedback between landuse and climate in the Rungwe tropical highland stresses a critical environmental research challenge. Curr. Opin. Environ. Sustain. 6, 116–122. https://doi.org/10.1016/j.cosust.2013.11.014.

Xingyuan, M., Xianguo, G., Wenge, D., Nan, D., Tijun, Q., 2015. Influence of human disturbance to the small mammal communities in the forests. Open J. 5, 1–9. https://doi.org/10.4236/ojf.2015.51001.

Yihune, M., Bekele, A., 2012. Diversity, distribution and abundance of rodent community in the afro-alpine habitats of the simien mountains national park, Ethiopia. Int. J. Zool. Res. 8, 137–149. https://doi.org/10.3923/ijzr.2012.137.149.

R Core, Team. 2020. *R: A language and environment for statistical computing. R Foundation for Statistical Computing*. Vienna, Austria.

CHAPTER FOUR
PAPER III

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Diet Composition and Niche Overlap of Four Sympatric Rodent Species Inhabiting Mount Rungwe Forest Nature Reserve, Tanzania

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ABSTRACT

Understanding animal feeding behaviour is key in determining coexistence mechanisms which are vital for conservation and management. The coexistence mechanisms of sympatric species in mount Rungwe are unknown. From 2020 to 2021 a study on the dietary contribution, overlap and niche breadth of four rodents in Mount Rungwe Forest Nature Reserve was conducted. Random sampling was employed with the removal method, whereby captured rodents' stomachs were removed and their contents analyzed. Dietary contribution, overlap and niche breadth were calculated. All species consume diverse food resources and categories where *Beamys hindei* had a significantly high number of seeds/grains while *Grammomys dolichurus* and *Lophuromys machangui* contained a significantly higher number of invertebrates. Narrow niche breadth was observed for *G. dolichurus* while *Praomys delectorum, L. machangui,* and *B. hindei* had a moderate niche breadth but the dietary overlap was high in all four species. Our results conclude that *L. machangui, P. delectorum,* and *B. hindei* can coexist without competition as they have >0.5 niche breadth and high overlap, while *G. dolichurus* might experience competition because of low niche breadth and food diversity. Further investigation regarding seasonal diet partitioning and micro identification of food items is recommended.

Keywords: diet partitioning - dietary niche breadth - coexistence.

INTRODUCTION

Species coexistence depends largely on how species utilize their environment, and how they utilized resources are distributed to serve different species in an area. Several theories are involved in understanding the determinant of species coexistence in a particular community, which have been suggested in several ecological studies (Dakota *et al.* 2020, Espinelli *et al.* 2017, Kotler and Brown 1999, Pinotti, *et al.* 2011). Ecologists have proposed some theories underlying species coexistence, such as the Niche partitioning and Niche Overlap theory (Pianka 1974). The niche partitioning theory suggests that the coexistence of ecologically similar species in the same area requires some forms of resource partitioning to reduce or avoid interspecific competition (Villanueva-Bonilla *et al.* 2019). In resource partitioning, some of the resources are shared by ecologically similar species resulting in resource overlap or niche overlap. The niche overlap theory states that 'within an ecological community species partition available resource among themselves (Pianka 1974). Thus, a community with

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greater niche overlap is more likely to support more species than a community with less niche overlap or with less resource sharing. Resource partitioning and niche overlap help related species to coexist in an area and develop a specialization in resource utilization thus reducing interspecific competition (Delaval and Henry 2005). Thus, this might be the case for small mammals, with high metabolic rates and low energy storage capacity, hence required to consume large amounts of food relative to their body weight (Hudson and White 1985). Studying resource use and factors underlying co-existence highly depends on the organisms under study as different organisms utilize different resources differently. Coexisting species generally compete for resources e.g food, space, etc (Nie *et al.* 2019). Thus, understanding the factors behind species co-existence is fundamental, especially for communities occupying harsh environments such as mountainous areas.

On the other hand, coexistence results when each species by itself lives sufficiently in a profitable condition. Community structure can then be studied by testing for the existence of necessary conditions under various alternative scenarios of coexistence (Brown 1989, Leibold and McPeek 2006, Siepielski and McPeek 2010). Here we follow the niche partitioning and niche overlap theories to evaluate the co-existence of rodent species at Mount Rungwe Forest Nature Reserve (MRFNR). According to the competitive exclusion principle, more than one species occupying the same habitat with limited resources would exclude each other unless there are niche partitioning mechanisms among them (Hardin 1960). Thus, niche partitioning is virtual in achieving greater biodiversity and adequate resource use (Finke and Snyder 2008). However, competition occurs when the resource is limited but it is less important when resources are not a limiting factor (Mwasi *et al*. 2013).

In East Africa, few studies have analyzed the diet composition of forest rodents (Clausnitzer *et al.* 2013, Schuchmann 2003). Most of the knowledge about rodent diets is based on crop fields and pestiferous rodents (Mlyashimbi *et al.* 2018, Mulungu *et al.* 2011, Odhiambo *et al.* 2008). Diet partitioning and overlap in mountainous forest rodents of MRFNR is lacking and thus their coexistence knowledge is not known. This study will help to understand if the coexistence of these rodent species in MRFNR is aided by diet partitioning and niche overlap, thus adding knowledge of the ecological requirement for the studied species in the area. Commonly, rodents are opportunistic feeders consuming a variety of food types including seeds, fruits, grains, vegetative plant materials, invertebrates, and small animals depending on the availability, habitat, and season (Arregoitia and D'eli 2021). In areas of abundant resources, they will adopt preferable food but if food is scarce, they have to adapt by either food partitioning and specialization (Arregoitia and D'eli 2021) or having different forage behavior to reduce competition. At MRFNR the vegetation is typically a montane afro-alpine that supports a thriving community of small mammals including rodents. Vertical stratification of the forest is considered an important factor allowing resource partition (Sushma and Singh 2006) among forested small mammals.

The objective of this study was to determine dietary composition as a mechanism for the coexistence of sympatric rodent species at MRFNR. Specifically, (i) to determine the percentage occurrence, percentage contribution, and relative importance of the dietary items between the sympatric species; (ii) to determine diet diversity and niche breadth of the sympatric species; (iii) to determine niche overlap among the species; and (iv) to assess the relationship between percentage food categories, percentage food categories and rodent species at MRFNR. The results will have conservation management implications as they will serve

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in understanding species' relationships in their sympatric existence.

MATERIALS AND METHODS

Study area

The study was carried out at Mount Rungwe Forest Nature Reserve in Rungwe District, Mbeya Region in Southern Tanzania (Fig 1). The study site lies between 9^0 03′ - 9^0 12′S and 33^0 35′ - 33^0 45′E with an elevation peak of 2981m a.s.l. The reserve experience two major seasons; a Wet season from November to May with short and heavy rains and a dry season from June to October). The mean annual rainfall ranges from 700 mm to 2,700 mm in low and higher elevations respectively Exceptionally, the southeastern part of the mountain receives rainfall of up to 3000 mm per year. The temperature varies between − 6^0 C in the highlands and 29^0 C in the lowlands (Williamson *et al.* 2014). The area is dominated by sub-mountainous and mountainous forests with some shrubs and grasses in the higher elevation.

The study was conducted in three elevations; low-elevation, mid-elevation and higher-elevation as previously described in the MRFNR management plan (URT-MRNRMP 2017). The three elevations vary in habitats, climate and vegetation composition. Lower elevation ranges from 1700-2000 m a.s.l with low montane forests habitat; mid-elevation ranges from 2000-2400 m a.s.l with montane forest habitat, and high-elevation ranges from 2400-2900 m a.s.l with bushland habitat.

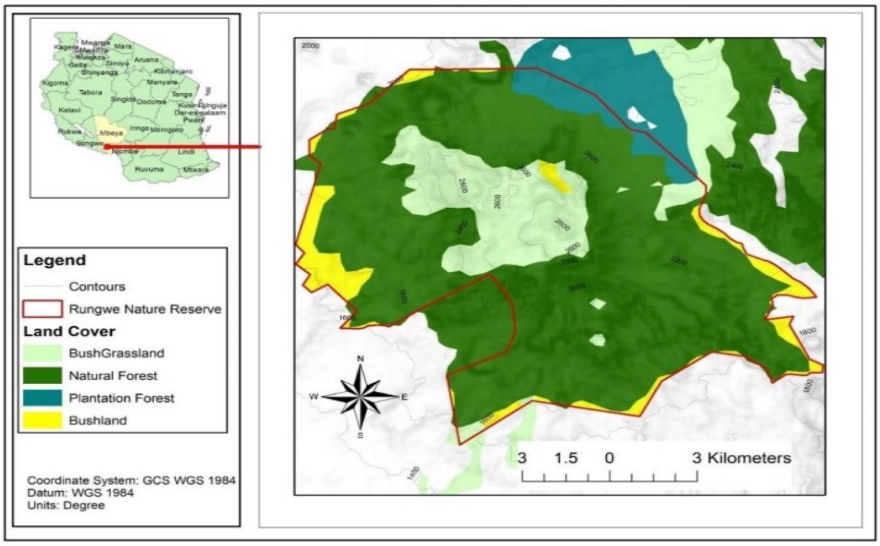

Figure 1: Map of Rungwe Forest Nature Reserve. ***Source:*** Richard *et al.* (2022)

Sampling design, rodent trapping and data collection

Sampling points were selected along the elevational gradient between 1700 to 2900 m a.s.l. covering low (1700-2000m a.s.l), mid (2000-2400m a.s.l), and high (2400-2900m a.s.l) elevations (URT-MRNRMP 2017). Data were collected between March 2020 and September 2021. The removal method

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using snap traps (1.0 × 8.5 × 16.5 cm), was employed with 4 transect lines of 100 m in each sampling point making a total of 12 transect lines. One hundred and thirty-two traps were set for six nights, during wet and dry seasons, with 11 traps in each transect at a 10 m distance. Snap traps were used as they kill the animal instantly before ingesting the bait and the digestion process ceases instantly. The traps were baited with a mixture of roasted coconut and peanut butter and they were checked early in the morning between 0600-0900 hrs. Trapped animals were collected and identified based on morphometric measurements and recent distribution (Bryja *et al.* 2014; Fitzgibb *et al.* 1995, Happold 2013, Walter *et al.* 2007). Collected individuals were dissected, stomach (Pylorus and Cardium) removed and fixed in 70% ethanol for food analysis based on micro-histological examination of undigested fragments.

The collected stomachs were opened and the contents were spread out in a Petri dish and sorted under X25 or X50 magnifications using a binocular microscope CX41RF, Olympus. All fragments in the stomach were examined viz. seed/grain, roots, stem, leaves, invertebrates, hairs, and other unidentified materials. When needed, a Lugol solution was used to determine the presence of starch to indicate the presence of seeds/grain in a diet.

Data analysis

Diet composition

Diet was statistically compared among the captured species of which five or more stomach samples were collected (Balˇciauskas *et al.* 2021) as these were considered the most abundant rodent species in the study area. The diet partitioning was analyzed for four species *Beamys hindei*, *Lophuromys machangui*, *Praomys delectorum* and *Grammomys dolichurus*. Analysis for seasonal and elevation differences in diet also depends on the number of stomachs collected in each season and elevation. Species whose stomachs were not analyzed due to a small number of captured individuals were *Graphiurus murinus* (n=1), *Mus spp* (n=1), *Dendromus insignis* (n=1), and *Crocidura* sp. (n=2). Percentage contribution of each diet category to the volume of the particular stomach contents (PV) was estimated to be the nearest 10% (crude), with an additional category of 5% where an item was present but contributed <10% to stomach content by volume (Smith *et al.* 2002). Percentage occurrence (PC) of a particular food item in a sampling period was calculated from the number of stomachs it was found, divided by the number of stomachs examined.

Niche breadth and dietary overlap

Niche Breadth was calculated using diet diversity which is the number of dietary items recorded per individual per species during the sampling period. Diet diversity was calculated following Ebersole and Wilson (1980) using Levins' index (Levins 1968) as:

Diet diversity(B) = $1/\sum Pi^2$ .... *Eq. 1*

Where P = (PV/100) i.e., the mean proportion in the volume of each of the dietary items. Levins' index ranges from 1 to n (n = total number of food item categories).

Diversity was standardized to scale 0.0 to 1.0 by using Hurlbert's method (Krebs 1989) to obtain niche breadth:

$B_s = (B-1)/(n-1)$ .... *Eq. 2*

Where B_s = Levins' standardized niche breadth, B = Levins' measure of niche breadth, and n = the number of possible resource states.

Niche breadth here means diversity of food items used by an animal and it ranges from 0 meaning the species has limited food choices, narrow niche (<0.4) and is more specialist taxa and favour specific environment and 0.75-1 indicates broad niche, generalist taxa that are equally abundant across the environment, while 0.4-0.75 indicate the species had a moderate niche breadth.

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Importance value (IV) is the values of resources understudy when compared with other resources in which if resources contribute a high percentage and had a high frequency then their importance is high than the resource which contributes less percentage with low frequency. Thus, important food value (IV) is the food item with a high contribution and frequency percentage in the diet compared to other food items consumed. An importance value for each diet item from each species was calculated following Cooper and Skinner (1978):

$IV = PV \times PC/100$ .... *Eq. 3*

Where IV = Important value, PV= % contribution to volume of a stomach content and PC = percentage occurrence/frequency.

The relative importance (RI) value of a particular food item was then taken as the importance value of that item expressed as the average percentage of the importance values for all food items

$RI = 100 \times IV/\sum IV$ .... *Eq. 4*

Niche overlap measure was computed using the following symmetric formula (Pianka 1974):

$$O_{jk} = \frac{\sum_{i}^{n} p_{ij} p_{ik}}{\sqrt{\sum_{i}^{n} p_{ij}^2 \sum_{i}^{n} p_{ik}^2}}$$ .... *Eq. 5*

Where, O_{jk} = Pianka's measure of niche overlap between species $_j$ and $_k$, P_{ij} and P_{ik} = are proportions of the *i*th resource used by the *j*th and *k*th species, respectively. Overlap values vary from zero (no overlap) to one (total overlap).

Moreover, a general linear model was performed to determine the relationship in percent food categories consumed by rodents at MRFNR and to see if there was variation in the percentage contribution of food categories within and between rodent species.

Percent ~ FG + RS + FG*RS .... *Eq. 6*

Where; Percent = percent in food categories, FG = food categories, RS = rodent species, FG*RS = interaction between food categories and rodent species

Finally, pairwise comparison was done by Tukey Honest Significant Difference (Tukey HSD) with 95% confidence limits and results presented in Compact Letter Display (CLD) whereby groups with the same letters are not detectably different and groups that are detectably different get a different letter. Groups can have more than one letter to reflect overlap between sets of groups. Statistical analysis was performed using R version 4.0.3 (R Core Team 2020).

RESULTS

A total of 171 individual stomachs belonging to Muridae (*Praomys delectorum; Lophuromys machangui; Grammomys dolichurus; Mus* sp), Gliridae (*Graphiurus murinus*), Nesomyidae (*Beamys hindei; Dendromus insignis*) and Soricidae (*Crocidura* sp) were collected. However, 166 stomach contents from *Grammomys dolichurus* n=12, *Lophuromys machangui* n=22, Praomys *delectorum* n=119, and *Beamys hindei* n=13 was analyzed for diet composition. This was due to the fact that, gut contents were analyzed for species with more than five collected stomachs.

Food items and fragments identified in stomach analysis included seeds/grains, stems, leaves, roots, invertebrates and hairs. (Plate 1).

Variation of food categories contributing to the diet of rodents

Invertebrates contributed high in the mean percent of diet categories (19%) followed by seeds/grain (10%) which was not different from leaves and stems. The least mean percentage contribution in the diet of rodents at MNFRN was roots (5%). A significant difference was observed in percent diet contribution among diet categories ($F_{5,966}$ =

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34.25, $p < 0.001$) in the diet of rodents (Fig. 2). Invertebrates (a) shows significant different with seeds/grains (b), leaves (bc), stem (bc), roots (c) and hairs (c). Seeds/grains (b) were insignificant when compared to leaves (bc) and stem (bc) b significant when compared with roots (c) a hairs (c). While leaves (bc), stems (bc), roo (c), and hairs (c) contributions to the di were insignificant

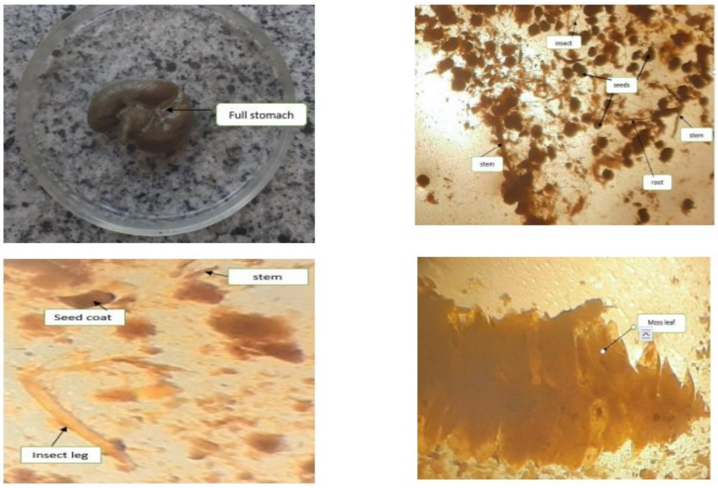

Plate 1: **Some of the food items and fragments found in MRFNR rodent stomachs.**

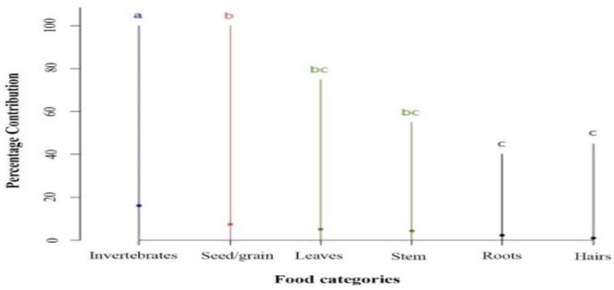

Figure. 2: Food items contribution and their difference in the diet of rodents at MRFN
[*Same letters indicate insignificant contribution; different letters mean significant differen between the food categories' contribution*.]

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Percentage of diet categories contribution to the diet, within and among rodents

The diets of all four rodent species comprised fragments of seeds/grain, stems, leaves, roots, invertebrates and hairs (Fig. 3). There was a significant difference in the percentage contribution of diet categories among rodent species ($F_{20,966}$=19.59, p<0.001). Invertebrates were highly consumed by *L. machangui* (33.9), followed by *G. dolichurus* (16.3) and *B. hindei* (15.4), but were least consumed by *P. delectorum* (13.2). Meanwhile, *B. hindei* and *L. machangui* were recorded to mostly consume seed/grain (Table 1).

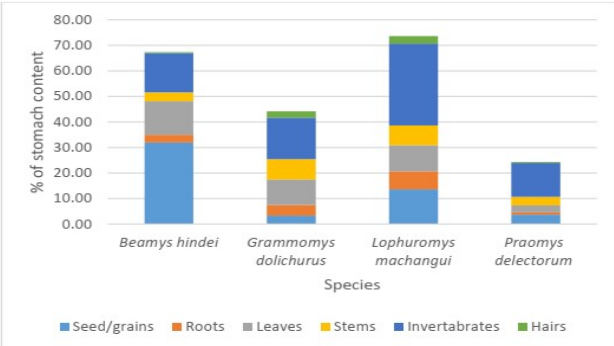

Figure 3: Mean Relative Abundance (%) diet contribution of major food categories found in stomachs of *B. hindei, G. dolichurus, L. machangui,* and *P. delectorum*.

Table 1: Variation in Percentage of diet categories contribution within and between rodent species in MRFNR

Food categories	Species	Percent Contribution
Seed/grains	*B. hindei*	31.9[ab]
Roots	*B. hindei*	3.1[c]
Leaves	*B. hindei*	13.1[c]
Stems	*B. hindei*	3.5[c]
Invertebrates	*B. hindei*	15.4[bc]
Hairs	*B. hindei*	0.4[c]
Seed/grains	*G. dolichurus*	3.3[c]
Roots	*G. dolichurus*	4.2[c]
Leaves	*G. dolichurus*	10[c]
Stems	*G. dolichurus*	7.9[c]
Invertebrates	*G. dolichurus*	16.3[abc]
Hairs	*G. dolichurus*	2.5[c]
Seed/grains	*L. machangui*	15.56[bc]
Roots	*L. machangui*	8.6[c]
Leaves	*L. machangui*	11.9[c]
Stems	*L. machangui*	9.4[c]
Invertebrates	*L. machangui*	33.9[a]
Hairs	*L. machangui*	5[c]
Seed/grains	*P. delectorum*	3.7[c]
Roots	*P. delectorum*	0.9[c]
Leaves	*P. delectorum*	2.7[c]

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Food categories	Species	Percent Contribution
Stems	*P. delectorum*	3.3^c
Invertebrates	*P. delectorum*	13.2^c
Hairs	*P. delectorum*	0.4^c

(Superscript letters indicate significance level by CLD using Tukey HSD method; the same letter means the percent of food categories contribution was insignificant and different letters mean the percent of food categories contribution was significant within and/or between the rodent).

Relative food importance, niche breadth, and overlap

Important food items in the diet of *Lophuromys machangui, P. delectorum,* and *G. dolichurus* were invertebrates while *B. hindei* the important foods item in the diet were seeds/grains. Standardized diet diversity (niche breadth) for rodents at MRFNR ranged from 0.28 for *G. dolichurus* to 0.59 for *L. machangui* (Table 2).

The niche overlap of rodents in MRFNR ranged from 0.75 to 0.99. *Praomys delectorum* and *G. dolichurus* had the highest overlap of 0.99 which means they share almost all of the available resources and the least were *P. delectorum* and *B. hindei* (Table 3). Overlap ranges from 0 means the species do not share any resource to 1 when more than one species shares all the resources.

Table 2: Relative importance of food types in the diet and niche breadth of rodents in MRFNR (n=sampled stomach).

	B. hindei (n=13) %	*G. dolichurus* (n=12) %	*L. machangui* (n=22) %	*P. delectorum* (n=119) %
Seed/grains	33.43	1.05	7.05	1.00
Roots	1.29	1.74	5.72	0.18
Leaves	10.95	6.27	10.57	1.52
Stems	2.17	4.97	6.27	2.00
Invertebrates	11.28	13.59	33.12	17.94
Hairs	0.04	0.26	0.44	0.03
Others	40.84	72.13	36.84	77.33
Niche Breadth	0.54	0.28	0.59	0.53

Table 3: Niche overlap for dietary partitioning between four rodent species in MRFNR.

	B. hindei	*G. dolichurus*	*L. machangui*	*P. delectorum*
B. hindei	1	0.76	0.85	0.75
G. dolichurus		1	0.82	0.99
L. machangui			1	0.8
P. delectorum				1

DISCUSSION

In general, it is seemingly that MRFNR rodent species consume a greater proportion of available resources in their environment. *Beamys hindei, L. machangui, G. dolichurus,* and *P. delectorum* each consume a variety of plants (stem, seeds, leaves, roots) and animals (invertebrates, hairs) where they coexist in this tropical mountainous forest. The consumed food categories vary in their diet with a significant-high percentage contribution of invertebrates followed by seeds/grain, leaves, stem, and least roots and hairs (Fig. 2). Although most rodents are generalist and have opportunistic feeding habits, there are some differences in their diet that are determined by food availability and rodent species as also reported in other studies (Monadjem 1996, Samaniego-Herrera *et al.* 2017). As predicted, all four rodent species were omnivorous; however, the percentage contribution of food items (fruit, seed, leaves, stem, roots, and invertebrates) in the diet differed among rodents.

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Relative food contribution and relative food importance

The results showed variations in food categories contributing to the diet (Table 1) and differences in relative importance (Table 2) within individual species. For example, for *Beamys hindei* seeds were relatively important and contributed highly to the diet. Members of the Genus Beamys are pouched rats and thus make use of their pouches to carry food and store them for future use. Unlike other food items such as invertebrates, leaves, roots, etc seeds and grains can be stored for a long period and used during the food scarce period. *Beamys* spp are reported to store more seeds than other food items (Hanney and Morris 1962), and this suggests that seed is an important food value in the diet of *B. hindei*. To our knowledge, this is the first study describing the diet of *B. hindei, L. machangui,* and *G. dolichurus* at MRFNR however available information on related species to *Beamys* shows that they eat more seeds (Happold 2013). However, there are variations in the Genus Lophuromys depending on species, but they consume more invertebrates and vegetative materials (Clausnitzer *et al*. 2013; Happold 2013).

For *G. dolichurus* invertebrates scored high as an important food item (Table 2) and this can suggest that *G. dolichurus* prefers invertebrates to other food items. However, invertebrates' contribution to the stomach of *G. dolichurus* was insignificant to other food items (Table 1). This might be because, either the sample size was small to detect the differences, or the species utilized all food items in the area.

A similar study in South Africa in a temperate forest showed *G. dolichurus* preferred more fruits and plant materials than invertebrates (Wirminghaus and Perrin 1992). Another study conducted along the Riverine forest in Somalia showed that seeds were the major food item and had a high volume in the diet of *G. dolichurus* (Varty 1990). This shows that even for the same species the important food item can be different depending on geographical location and seasonality (Lunghi *et al.* 2020). *Lophuromys machangui* diet varied and had a significantly high percentage contribution of invertebrates in its diet compared to other food items (Table 1). Likewise, we found no other study on the diet of *L. machangui* but a similar study in Mount Elgon reported *L. flavopuncatus* which is a close relative of *L. machangui* to eat a diversity of invertebrates (Clausnitzer *et al.* 2013). Another study by Ademola (2022) on *Lophuromys kilonzoi,* which share the Genus with *Lophuromys machangui* found out that the species consume more plant materials 37% than invertebrates 8%.

Praomys delectorum although showed a higher amount of invertebrates in its diet but this food items contribution was not significantly different from other food categories. Also, the number of invertebrates in *P. delectorum* species was significantly less when compared with invertebrates in the diet of *L. machangui*. The contribution of seeds/grain was also insignificant compared with that of *B. hindei*. The important food for *P. delectorum* was also invertebrates. Members of the genus *Praomys* forage on the ground on leaf litter (Happold 2013) this means that they are expected to feed more on underground materials such as ground invertebrates, dropped seeds, and short leaves. Hanney (1965), in his study, found that invertebrates contributed 82% and vegetables 78% in the diet of *P. delectorum* respectively. This supports our study that *Praomys spp* is omnivorous with invertebrates contributing a higher percentage to their diet. In all four studied species, hairs had a low percent contribution to the diet (1.56 mean) and also less important food categories for all rodents species. Hairs found in the stomach are not a precise indication of the use of mammals as food since some hairs maybe probably as a result of grooming (Samaniego-Herrera *et al.* 2017).

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Niche breadth

Niche breadth for the studied species ranged from narrowest niche breadth which was 0.28 for *G. dolichurus* to moderate niche breadth of 0.53, 0.54, and 0.56 for *P. delectorum, B. hindei,* and *L. machangui* respectively. The narrow niche breadth for *G. dolichurus* indicates that it uses relatively few food items resources and might be a specialist. A similar study by (Pereira *et al.* 2012) on carnivores reports that the niche breadth with high specialization was a result of low population density which diminishes the need of the species to exploit the unfavourable habitats and makes the species more specialized in the suitable one. This might also be true for *G. dolichurus* as it was the least in density among the captured species. Other species *P. delectorum, B. hindei,* and *L. machangui* had moderate niche breadth and this indicated that they considerably proportionally consume several food items. For example, in the case of *L. machangui* invertebrates contributed significantly high to the diet (33.9%) but also other food items substantially contributed such as seeds (15.6%) and leaves (11.9%). This indicates that diet diversity consumed by *P. delectorum, B. hindei,* and *L. machangui* is higher than that of *G. dolichurus* which had a narrow niche breadth.

Niche overlap

The diet overlap between all four species was considerably high. High overlap might probably be a result of sharing the abundant common food items in the area. The extensive niche overlap does not necessarily signify competition as two or more organisms can share abundant resources without impacting the welfare of the other (Pianka 1974). When resources are abundant, interspecific competition declines, and high trophic niche overlap is permitted (Reid *et al.* 2013). Therefore, the overlap may be directly attributed to environmental heterogeneity and resource abundance (Mulungu *et al.* 2011). Though diet overlap can also be detected when the demand for resources exceeds supply and this will lead to interspecific competition as species need to expand their trophic niche to make up for their nutritional demands (Reid *et al.* 2013). Mwakisunga (2017), Bracebridge *et al.* 2012, and Richard *et al.* 2022 report the abundance and diverse resources at MRFNR and this might be the reason for high niche overlap between rodents as the resources are abundant hence they can be shared with minimal competition.

Grammomys dolichurus

Invertebrates in the diet of *G. dolichurus* ranked high among other food items (Table 2). This is true also when comparing food resource overlap. *G. dolichurus* had a very strong overlap with *P. delectorum* (0.99), and *L. machangui* (0.82) which also feed primarily on invertebrates. The very strong overlap between *P. delectorum, G. Dolichurus,* and *L. machangui* may not be due to indicative of competition but rather reflective of the heterogeneous nature of their habitat and high resource abundance in the area (Mulungu *et al.* 2011). MRNFR is a tropical forest and presents a heterogeneous environment with an abundance and variety of food for rodents (Richard *et al.* 2022).

Beamys hindei

The overlap of *B. hindei* was very strong with *L. machangui (0.85)* and strong with *P. delectorum (0.75)* and *G. dolichurus (0.76)*. This is because apart from seeds which were the major contributor and important food category in the diet for *B. hindei*, invertebrates were the second major contributor in its diet, so higher overlaps with *L. machangui* whose important food was also the invertebrates.

Lophuromys machangui

The niche overlap between *L. machangui* and *P. delectorum, B. hindei,* and *G. dolichurus* was very strong. Relatively *L. machangui* consumes a variety of food items in a considerable proportion and also it shows a moderate degree of diet specialization hence overlapping with other

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species in the area. Although the diet of *L. machangui* was significantly high in invertebrates also other food items like seeds (15.6%) and leaves (11.9%) contributed a considerable amount to the diet.

Praomys delectorum

Praomys delectorum had a strong overlap (0.99) with G. dolichurus and *L. machangui* (0.80) than the *B. hindei* (0.76) (Table 4). Our results suggest that *P. delectorum, L. machangui, G. dolichurus,* and *B. hindei* can coexist through high food availability and diet partitioning. A similar study attributed the coexistence of *P. californicus* and *P. boylii* which has similar diets to *P. delectorum* to feeding primarily on invertebrates but of different species (Reid et al. 2013). The coexistence of these rodents at MRFNR might be a result of food abundance or the consumed food materials e.g., invertebrates might be of different species for different rodents hence the difference in proportion and preference. The coexistence due to the abundant foods can be supported by our findings as during the rain period all four species were recorded contrary to the dry season where only *P. delectorum* and *L. machangui* were recorded. During the rainy season dietary partitioning breaks down and the diet converges due to high food abundance. Thus, the availability of food resources largely determines the niche breadth and overlap between species (Sushma and Singh 2006).

CONCLUSIONS AND RECOMMENDATIONS

From the current study, it is concluded that if more than one coexisting species has high diet overlap but also high niche breadth it means that those species have a variety of food choices. These coexisting species may reduce competition by feeding on those wide varieties of food categories and this was a case for *L. machangui* but also for *P. delectorum* and *B. hindei.* Moreover, if coexisting species have high niche overlap but narrow niche breadth then their coexistence is less likely and they will have competition for resources and this was the case for *G. dolichurus.* This might also explain their low abundance in terms of numbers compared to other species in the area (Richard *et al.* 2022). This implies that *L. machangui, B. hindei,* and *P. delectorum* can coexist in MRFNR without competition for food resources while *G. dolichurus* might face competition with other rodent species. The study has provided baseline data on dietary habit, niche breadth, and overlap for four sympatric rodents but further studies are required for microanalysis of those diet items contributed in each species. In this study, invertebrates have been shown as one of the food items that small mammals mostly depend on, and this gives an alert for the importance of these invertebrates in the ecology of MRFNR. Enhancing conservation of the area will increase food items in terms of abundance and diversity and this will contribute to the increase of small mammals' density and diversity and thus enhance the functionality of the Rungwe ecosystem. It is essential to preserve habitats such as isolated mountains e.g. the Rungwe forest that maintains rodent assemblage with diverse diets in a natural habitat. This may have important implications for the ecological functioning of the area.

REFERENCES

Ademola, O.J. 2021. Ecology of rodent species in the Ukaguru Mountains within Eastern Arc Mountains, Tanzania. PhD Thesis. Morogoro: Sokoine University of Agriculture.

Arregoitia, L.D. & D'eli, G. 2021. Classifying rodent diets for comparative research. Mammalia review, 51: 51-65. https://doi.org/10.1111/mam.12214

Balˇciauskas, L., Balˇciauskiene, L., Garbaras, A. & Stirke, V. 2021. Diversity and Diet Differences of Small Mammals in Commensal

Habitats. Diversity, 13(8): 346-359. https://doi:10.3390/d13080346

Bracebridge, C.E., Davenport, T.R. & Marsden, S.J. 2012. The Impact of Forest Disturbance on the Season Endangered African Primate. Biotropica, 44(4): 560-568. https://doi:10.1111/j.1744-7429.2012.00854.x

Brown, J.S. 1989. Desert Rodent Community Structure: A Test of Four Mechanisms of Coexistence. Ecological Monographs, 59: 1-20. https://doi.org/10.2307/2937289

Bryja, J., Mikula, O. & Patzenhauerová, H. 2014. The role of dispersal and vicariance in the Pleistocene history of an East African mountain rodent, *Praomysdelectorum*. Journal of Biogeography, 41: 196–208. https://doi.org/10.1111/jbi.12195

Clausnitzer, V., Churchfield, S. & Hutterer, R. 2013. Habitat occurrence and feeding ecology of Crocidura montis and Lophuromys flavopunctatus on Mt. Elgon, Uganda. African Journal of Ecology, 41(1): 1-8. http://dx.doi.org/10.1046/j.1365-2028.2003.00386.x

Cooper, R.L. & Skinner, J.D. 1978. Importance of termites in the diet of the aardwolf Proteles cristatus in South Africa. South Africa Journal of Zoology, 14: 5-8. https://doi.org/10.1080/02541858.1979.11447640

Dakota, R.M., Ryan, K.M. & Sharon, J.A. 2020. The dietary morphology of two island-endemic murid rodent clades is consistent with persistent, incumbent-imposed competitive interactions. Proceedings Royal Society. B. 287: 20192746. https://doi.org/10.1098/rspb.2019.2746.

Delaval, M. & Henry, M. 2005. Interspecific competition and niche partitioning: Example of a Neotropical rainforest Bat Community. Revue d'Ecologie, 60 (2): 149-165.

Ebersole, J.P. & Wilson, J.C. 1980. Optimal foraging: the responses of Peromyscus leucopus to experimental changes in processing time and hunger. Oecologia, 46: 80-85. https://doi.org/10.1007/bf00346970

Espinelli, F.P., Correa, F., Colares, E.P. & Colares, I.G. 2017. The partitioning of food resources between two rodents in the subtropical region of southern Brazil. Anais da Academia Brasileira de Ciências, 89(1): 191-202. https://doi.org/10.1590/0001-3765201720160445

Finke, D.L. & Snyder, W.E. 2008. Niche Partitioning Increases Resource Exploitation by Diverse Communities. Science, 321(5895): 1488-1490. https://doi.org/10.1126/science.1160854

Fitzgibb, C.D., Leir, H. & Verhryen, W. 1995. Distribution, population dynamics and habitat use of the lesser pouched rat, Beamys hindei. Journal of Zoological Society of London, 236: 499-512. https://doi:10.1111/J.1469-7998.1995.TB02727.X

Hanney, P. 1965. The Muridae of Malawi (Africa: Nyasaland). Journal of Zoology, 146: 577-633. https://doi.org/10.1111/j.1469-7998.1965.tb05224.x.

Hanney, P. & Morris, B. 1962. Some Observations upon the Pouched Rat in Nyasaland. Journal of Mammalogy, 43(2): 238-248. https://doi.org/10.2307/1377095.

Happold, D.C. 2013. Mammals of Africa Volume III- Rodents, Hares and Rabbits. London: Bloomsbury Publishing. http://dx.doi.org/10.5040/9781472926937.

Hardin, G. 1960. The Competitive Exclusion Principle. Science, 131(3409): 1292-1297.

Hudson, R.J. & White, R.G. 1985. Bioenergetics of Wild Herbivores. Florida: CRC Press Inc. https://doi.org/10.1201/9781351070218.

Kotler, B.P. & Brown, J.S. 1999. Mechanisms of coexistence of optimal forages as determinant of local abundances and distribution of desert granivores. Journal of Mammalogy, 80(2): 361-374. https://doi.org/10.2307/1383285.

Krebs, C.J. 1989. Niche overlaps and diet analysis. Krebs C. (Editor). Ecological Methodology. New York: Harper & Row.

Leibold, M.A. & McPeek, M.A. 2006. Coexistence of the Niche and Neutral Perspectives in Community Ecology. Ecology, 87(6): 1399-1410. https://www.jstor.org/stable/20069089

Levins, R. 1968. Evolution in Changing Environment. Princeton: Princeton University Press.

Lunghi, E., Mamenti, R., Cianferoni, F., Ceccolini, F., Veith, M., Corti, C., Ficetola, G. F. & Mancinelli, G. 2020. Interspecific and interpopulation variation in individual diet specialization: Do environmental factors have a role? Ecology, 101 (8): e03088 https://doi.org/10.1002/ecy.3088.

Mlyashimbi, E.C., Mariën, J., Kimaro, D.N., Tarimo, A.J., Isabirye, M., Makundi, R.H., Mulungu, L.S. 2018. Relationships between seasonal changes in diet of Multimammate rat (*Mastomys natalensis)* and its breeding patterns in semi-arid areas in Tanzania. Cogent Food & Agriculture, 4(1): e1507509. https://doi:10.1080/23311932.2018.1507509.

Monadjem, A. 1996. Stomach contents of 19 species of small mammals from Swaziland. South African Journal of Zoology, 23-26. https://doi.org/10.1080/02541858.1997.11448423.

Mulungu, L.S., Massawe, A.W., Kennis, J., Crauwels, D., Eiseb, S., Mahlaba, T. A., Belmain, S.R. 2011. Differences in diet between two rodent species, *Mastomys natalensis* and *Gerbilliscus vicinus*, in fallow land habitats in central Tanzania. African Zoology, 46(2): 387-392. https://doi.org/10.3377/004.046.0218.

Mulungu, L.S., Themb'alilahlwa, M.A., Massawe, A.W., Kennis, J., Crauwels, D., Eiseb, S., Belmain, S. R. 2011. Dietary differences of the multimammate mouse, *Mastomys natalensis* (Smith, 1834), across different habitats and seasons in Tanzania and Swaziland. Wildlife Research, 38(7): 640-646. http://dx.doi.org/10.1071/WR11028.

Mwakisunga, B. 2017. Forest Biomass Management Challenges in Commercially Exotic Tree Plantation Areas: A Case Study from the Rungwe Volcanic Province (Southern Highlands of Tanzania. Journal of Geoscience and Environment Protection, *5*: 67-75. https://doi:10.4236/gep.2017.53006.

Mwasi, S.M., Van Wieren, S.E., Heitkönig, I.M. & Prins, H.H. 2013. Seasonal resource use and niche breadth in an assemblage of coexisting grazers in a fenced Park. Open journal of ecology, 3(6): 383-388. http://dx.doi.org/10.4236/oje.2013.36043.

Nie, Y., Zhou, W., Gao, K., Swaisgood, R.R. & Wei, F. 2019. Seasonal competition between sympatric species for a key resource: Implications for conservation management. Biological

Conservation, 234: 1-6. http://dx.doi.org/10.1016/j.biocon.2019.03.013.

Odhiambo, R.O., Makundi, R.H., Leirs, H. & Verhagen, R. 2008. Demography, reproductive biology and diet of the bushveld gerbil *Tatera leucogaster* (Rodentia: Gerbillinae) in the Lake Rukwa valley, south-western Tanzania. Integrative Zoology, 3: 31-37. https://doi.org/10.1111/j.1749-4877.2008.00073.x.

Pereira, P., Alves da Silva, A., Alves, J., Matos, M. & Carlos, F. 2012. Coexistence of carnivores in a heterogeneous landscape: habitat selection and ecological niches. Ecological Research, 27: 745–753 https://10.1007/s11284-012-0949-1

Pianka, E.R. 1974. Niche Overlap and Diffuse Competition. Proceedings of the National Academy of Sciences of the United States of America, 71(5): 2141-2145. https://doi:10.1073/pnas.71.5.2141.

Pinotti, B.T., Naxara, L. & Pardini, R. 2011. Diet and food selection by small mammals in an old-growth Atlantic forest of south-eastern Brazil. Studies on Neotropical Fauna and Environment, 20(1): 1-9. http://dx.doi.org/10.1080/01650521.2010.535250

R Core, T. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. http://www.r-project.org/index.html.

Reid, R.E., Greenwald, E.N., Wang, Y. & Wilmers, C.C. 2013. Dietary niche partitioning by sympatric Peromyscus boylii and P. californicus in a mixed evergreen forest. Journal of Mammalogy, 94(6): 1248–1257. https://10.1644/13-MAMM-A-104.1

Richard, U., Byamungu, R.M., Magige, F. & Makonda, F. B. 2022. Microhabitat, altitude and seasonal influence on the abundance of non-volant small mammals in Mount Rungwe forest nature reserve. Global Ecology and Conservation, 35: e02069. https://doi:10.1016/j.gecco.2022.e02069.

Samaniego-Herrera, A., Clout, M.N., Aguirre-Muñoz, A. & Russell, J.C. 2017. Rodent eradications as ecosystem experiments: a case study from the Mexican tropics. Biological Invasion, 19: 1761–1779.

Schuchmann, K.L. 2003. Rodents of Mt. Elgon, Uganda: Ecology, Biogeography, and the Significance of Fire (3 ed.). Bonn, German: The German Society for Tropical Ecology.

Siepielski, A.M. & McPeek, M.A. 2010. On the evidence for species coexistence: a critique of the coexistence program. Ecology, 91(11): 3153-3164. https://www.jstor.org/stable/20788149

Smith, V.R., Avenant, N.L. & Chown, S.L. 2002. The diet and impact of house mice on a sub-Antarctic island. Polar Biology, 25: 703–715. http://dx.doi.org/10.1007/s00300-002-0405-8.

Sushma, H.S. & Singh, M. 2006. Resource partitioning and interspecific interactions among sympatric rain forest arboreal mammals of the Western Ghats, India. Behavioral Ecology, 17(3): 479–490. https://doi.org/10.1093/beheco/arj058.

URT. 2017. Mount Rungwe Nature Forest Reserve Management Plan. United Republic of Tanzania. 133 pp.

Varty, N. 1990. Ecology of the small mammals in the riverine forests of the Jubba Valley, Southern Somalia. Journal of Tropical Ecology, 6(2): 179-189. https://doi:10.1017/S0266467400004272.

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Villanueva-Bonilla, A.G., Safuan-Naide, S., Pires, M.M., & Vasconcellos-Neto, J. 2019. Niche partitioning and coexistence of two spiders of the genus Peucetia (Araneae, Oxyopidae) inhabiting Trichogoniopsis adenantha plants (Asterales, Asteraceae). PLoS ONE, 14(10): e0213887. https://doi:10.1371/journal.pone.0213887

Walter, V.N., Jan, H.L., Dierckx, T., Mulung, L., Leirs, H., Corti, M. & Verheyen, E. 2007. The characterization of the Kilimanjaro *Lophuromys aquilus* TRUE 1892 population and the description of five new Lophuromys species (Rodentia, Muridae). BIOLOGIE, 77: 23-75.

Williamson, D., Majule, A., Delalande, M., Mwakisunga, B., Mathe, P.E., Gwambene, B., & Bergonzini, L. 2014. Potential feedback between land use and climate in the Rungwe tropical highland stresses a critical environmental research challenge. Current Opinion on Environmental Sustainability. 6: 116–122. https://doi.org/10.1016/j.cosust.2013.11.014

CHAPTER FIVE
PAPER IV

POPULATION DYNAMICS, BREEDING PATTERN AND SEX RATIO OF RODENT SOFT-FURRED RESIDING MOUNT RUNGWE NATURE FOREST RESERVE, TANZANIA

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"The material contained in this chapter is in preparation for submission to the Journal "

Abstract

The fluctuation in population of small mammals can be attributed to changes in reproduction and survival caused by environmental factors. Elevation is a significant natural gradient which shape animal community in small areas. Rodents in natural mountainous tropical forest areas have abundant food resources and face less predation pressure which potentially impact their population and demographic parameters positively. However, there is limited information on rodent demographics and population dynamics in elevational gradient areas. This study aimed to generate information on demographic structure and population dynamics of soft-furred mouse *Montemys delectorum* which is the dominant rodent species on Mount Rungwe Nature Forest Reserve (MRNFR). A Capture–Mark–Recapture study was conducted along the elevation gradient (low, mid- and high elevations) using two plots measuring 70 m by 70 m with 49 evenly spaced Sherman traps. Monthly trapping took place for three consecutive nights from March 2020 to February 2022. Generalised Linear Model analysis revealed significantly higher population density estimates in low (Est.± SE = 1.37 ± 0.077, Z = 17.85, p = <2e-16) and mid-elevations (Est.± SE = 1.408 ± 0.076, Z = 178.435, p = <2e-16) compared to higher elevations. Additionally, population density during the wet season was significantly higher (Est.± SE = 0.167 ± 0.04707, Z = 3.55, p = 0.00038) compared to dry season. Furthermore, incorporation of season effect on elevation model showed significantly higher population density in low elevation during wet season (Est ± SE = -0.359 ±0.16, Z = -2.189, p = 0.0286). On the contrary, there was no significant difference in mid-elevation during the same season (Est ± SE = -0.3065 ± 0.1638, Z = -1.87, p = 0.0614).

The model indicated that juveniles were influenced by seasons with significantly higher density during wet season (Est ± SE = 0.3851 ± 0.078, Z = 4.929, p = 8.4e-07) while adult population density was not influenced by seasonal changes (Est ± SE = 0.015 ± 0.059, Z = 0.25, p = 0.02795). Overall, juveniles were strongly affected by both elevation and season while adults were only affected by elevation gradient. Results also showed significantly higher population density of females than males in mid-elevation ($\chi2 = 51.84$, $p = 0.0005$) with sex ratio 0.58 while low and high elevation sex ratio was 1:1. Additionally, wet season recorded significantly higher female density ($\chi2 = 225.65$, $p = 2.37$ e-27) than dry season. Breeding females were present throughout trapping seasons but they demonstrated significantly higher density during wet season (Est ± SE = 1.0498 ± 0.1863, Z = 5.634, p = 1.76e-8). Moreover, low- and mid-elevations recorded significantly higher numbers of breeding females than higher elevations. The results suggest rainfall and elevation gradient to be factors that influence varying population abundance, sexual activities and sex ratio of *M. delectorum* at MRNFR.

Keywords: Rodents, elevation gradient, rainfall, reproduction, population

5.1 Introduction

Rodents exhibit significant population fluctuations in various spatial-temporal situations. Such population dynamics are influenced by underlying demographic parameters such as population size, density, age structure, fecundity, mortality, and sex ratio (Dobson & Oli, 2001). The variations in the community structure of these small mammals can be attributed to the changes in environmental variables due to their sensitivity to even slight alteration in environmental conditions (Avenant & Smith, 2004; Ofori *et al*., 2016). The population dynamics of small rodents are driven by changes in their reproductive and/or survival rates which are assumed to be crucial variables in explaining temporal and spatial differences in rodent population fluctuation (Getz *et al*., 2007). The litter size, male/female proportion, proportion of pregnant females, age at sexual maturity, length of reproductive period and survival rate are among the variables associated with differences in density peak and amplitude fluctuations. The environmental factors, both biotic and abiotic, have a significant influence on the dynamics of small rodent populations. Such factors include the habitat quality (cover and food), predation and climatic factors such as rainfall, humidity and temperature (Lin & Batzli, 2001; Getz *et al*., 2007).

The impactful changes in any of the habitat quality (cover and food), predation and climatic factors during the cycle can lead to fluctuations in the reproductive rates. This mechanism can be significant in explaining the changes in rodent population fluctuation (Norrdahl & Korpimäki, 2002). However, the rainfall emerges as the fundamental factor driving the population dynamics of small rodents in tropic climates. The rainfall triggers the primary productivity (food availability), thus leading to high reproductive rates. Additionally, the rainfall increases the canopy cover, thus providing rodents with protection against predators (Joneidi *et al*., 2020). Therefore, establishing a connection between the population fluctuations and underlying environmental factors such as rainfall which affects the demographic parameters is crucial for gaining an understanding of population dynamics.

In an environment with distinct seasons, the seasonally structured population model offers a better understanding of the interplay between the demography and population dynamics. The seasonality reveals that the small rodent population undergoes significant changes between two distinct seasons. The wet season is characterised by high population of reproductive individuals while the dry season sees the high population of non-reproductive individuals. The population growth and density-dependent factors such as diseases, predation and competition also vary between the two seasons. This variation may be attributed to the occurrence of reproduction peaks in one season and differing survival rates influenced by variables available during each season (Merritt *et al*., 2001).

The demographic changes in small mammals have been extensively studied by scholars worldwide (Krebs & Myers, 1974; Dobson & Oli, 2001; Oli & Dobson, 2001; Ecke *et al*., 2002; Norrdahl & Korpimäki, 2002). In East Africa, for instance, there have been studies on small mammal demography with a particular focus on economically important pestiferous rodents (Makundi *et al*., 2009; Massawe *et al*., 2011; Mulungu S & Lopa, 2016; Mayamba *et al*., 2021). However, there have been only a few studies on demographic characteristics of forest rodents (Makundi *et al*., 2007a; Mayamba *et al*., 2021). Therefore, the population dynamics and demography of rodent species inhabiting most Tanzanian forests, especially protected highland areas, remain undocumented. Furthermore, the community structure of these species is less understood.

This study aimed to investigate the population structure, breeding pattern and sex ratio of *Montemys delectorum* in the MRNFR in relation to elevation and seasonal changes. There is limited information regarding the basic ecology of *M. delectorum* which is the most abundant and dominant species in the area (Richard *et al*., 2022). Understanding the relationship between the rainfall patterns (seasons), elevations, rodent population abundance and breeding cycle in MRNFR will provide the baseline data on the community structure of the species. Additionally, it will assist in making informed management decisions and guiding future research on small mammal in the study area.

5.2 Methodology

5.2.1 Study Site

The study was conducted at Mount Rungwe Nature Forest Reserve which is located at the junction of the Eastern and Western Arms of the East African Rift Valley. The reserve covers approximately 13,652 ha and it is situated in the Southern highlands of Tanzania, specifically in Mbeya Region between 9^0 03′ - 9^0 12′S and 33^0 35′ - 33^0 45′E. The altitudinal gradient in the area ranges from 1700 to 2960 m a.s.l. The tropical climate is characterised by wet and dry season. During the cold season, the lowest temperature recorded is -6^0 C while the highest temperature recorded during the hot season reaches 29^0 C. The annual rainfall varies between 900 mm and 2700 mm (Williamson *et al*., 2014). The area encompasses several habitats along the elevation gradient. The Low Mountainous Forest (LMF) is found between 1700 to 2000 m a.s.l and it is dominated by the *Afrocrania volkensii (Harms) Hutch, Ficus capensis, Cyathea deckenii Tabernaemontana stapfiana, Albizia gummifera* and *Macaranga capensis var kilimandscharica.* The mid- montane forest occupies elevation range from 2000 to 2400 m a.s.l. and it is characterised by the dominant species such as *Tabernaemontana stapfiana*, *Cassipourea gummiflua* and *Prunus Africana*. There is a montane bushland habitat dominated by *Embelia schimperi*, *Pteridium sp*., *Afrocrania volkensii, Cyperus, Hagenia abyssinica, Bamboo nutans* and *Maesa lanceolata* at the mountain top above 2500 m a.s.l. Some areas at 2600m a.s.l. exihibit a line of bamboo forest which is primarily dominated by *Bamboo mutans*. The elevation gradient is defined in the Mount Rungwe Nature Forest Reserve Management Plan (URT, 2017). Trapping of small mammals was conducted at three distinct elevations, namely low elevation (LE), mid-elevation (ME) and high elevation (HE).

5.2.2 Trapping of Small Mammals

The Capture Mark Recapture technique was employed to capture the rodents from March 2020 to February 2022. Sherman traps were utilized within 70 m X 70 m permanent grids positioned along each elevation gradient. A total of 49 Sherman LFA live trap (H.B. Sherman Traps Inc., Tallahassee, FL) were set up in each grid. These traps were deployed for three consecutive nights per month over a period of twenty-four months. They were baited with a mixture of peanut butter and maize flour and were checked every morning. The collected data included the information on trapping station, species, sex, weight, reproductive status, and age class determined by weight measurement (Stanley *et al*., 1998; Makundi *et al*., 2007b). Each grid consisted seven parallel lines spaced 10 m apart with seven trapping stations per line which were also separated by 10 m.

The classification of age structures distinguished between juveniles and adults was based on the body weight. The presence of juveniles indicates the recent reproduction with individuals weighing less than 20g, which are classified as juveniles. It also indicates individuals weighing more than 20g, which are categorized as adults. The sub-adults were included in the adult categories.

The sex ratio represented the proportion of males to females within the overall population and it was found to favour females due to ability of single males to impregnate multiple females within a breeding season and maintain reproductive activity throughout the seasons (Mulungu *et al*., 2013). In determining the breeding conditions for males, an observation was made regarding scrotal and abdominal structure visibility, thus assessing whether they were visible, not visible, large, or small. The examination for females focused on the presence of the perforated vagina and signs of lactating or pregnancy (Makundi *et al*., 2007b). The breeding pattern of sexually active female rodents was determined by establishing the proportion of active versus non-active females in each month and at each elevation. The breeding patterns in females were determined following Leirs (1995) based on the observation of physiological conditions rather than typical behaviour. The female rodents were considered sexually active if they had a perforated vagina, pregnancy or exhibited swollen nipples. The identification of the species was conducted using relevant keys and recent data (Happold, 2013; Ara *et al*., 2015) and mitochondrial DNA from toe tissue sample which was sequenced to confirm the species. The rainfall data were measured and recorded from the weather station within the reserve.

5.2.3 Data Analysis

The population was estimated using the Minimum Number Alive (MNA) method which takes into account the actual number of individuals caught at a time (t) (*Nu*) and those present but not caught at a time (t) and subsequently caught. The MNA is calculated as MN*A* = *Nu* + *Ns* (Krebs, 1966). The sex ratio (SR) was calculated as SR = $(N_f/(N_f + N_m))$
Where: SR = Sex ratio, N_f and N_m = the number of females and males collected from within a population.

To assess the significance of differences in *M. delectorum* abundance across the elevations and seasons, a Generalised Linear Model (GLM) with Poisson distribution was applied. The "me4" package (Karim & Zeger, 1992) in R software (R Core, 2020) was used for this analysis. The influence of season (wet and dry season), elevation (low, mid- and high elevations) as well as their combination and interaction on *M. delectorum* population abundance was examined. Chi-square test was employed to compare the abundance of males and females across the elevation gradients and seasons. The descriptive bar graphs were created in order to illustrate the variation in population abundance along the elevation gradient and over the months in the different trapping years.

5.3 Results

5.3.1 Population Structure, Dynamics and Sex Ratio

5.3.1.1 Population Structure and Dynamics

Total individual collected for a period of 24 month was 1,922 *M. delectorum.* The population abundance of *M. delectorum* exhibits the temporal and spatially variation across the seasons and elevations within MRNFR. The GLM model indicates that both the elevation and season significantly influence the abundance of *M. delectorum.* During the wet season, the abundance of *M. delectorum* was higher compared to dry season (Estimate ± SE = 0.16715 ± 0.04707, Z = 3.551 p = 0.000384). Furthermore, the population was higher at low elevation (Estimate ± SE = 1.36973 ± 0.07673, Z = 17.85 p = <2e-16) and mid- elevation (Estimate ± SE = 1.40835 ± 0.07644, Z = 178.43 p = <2e-16) compared to higher elevations. The highest number of individuals was captured during the wet season covering the period from November to March while the lowest number of individuals was observed during the dry season covering the period from July to October (Figure 5.1).

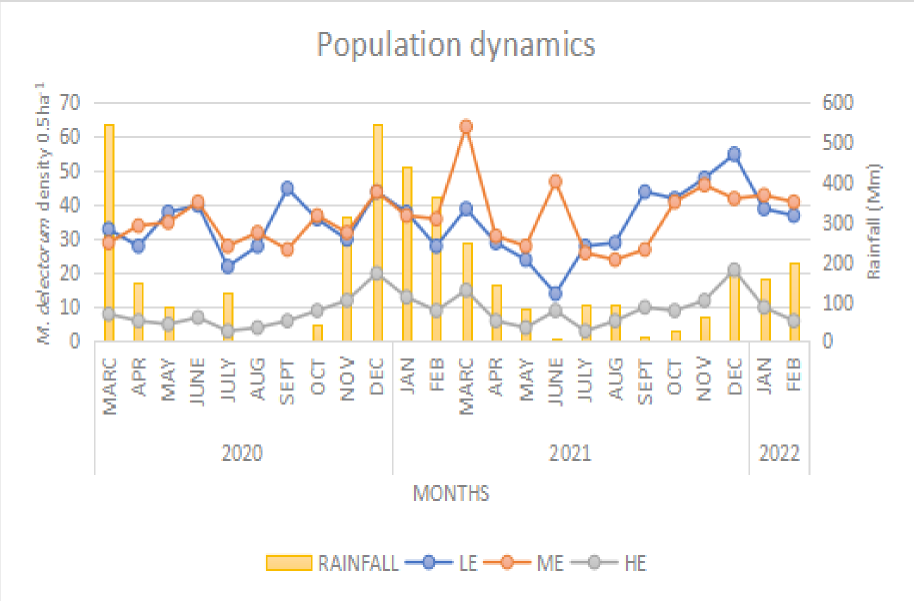


Figure 5.1: Population dynamics of *M. delectorum* in different months and elevations at Rungwe Mountain (LE- Low-elevation, ME- Mid-elevation and HE-high elevation)

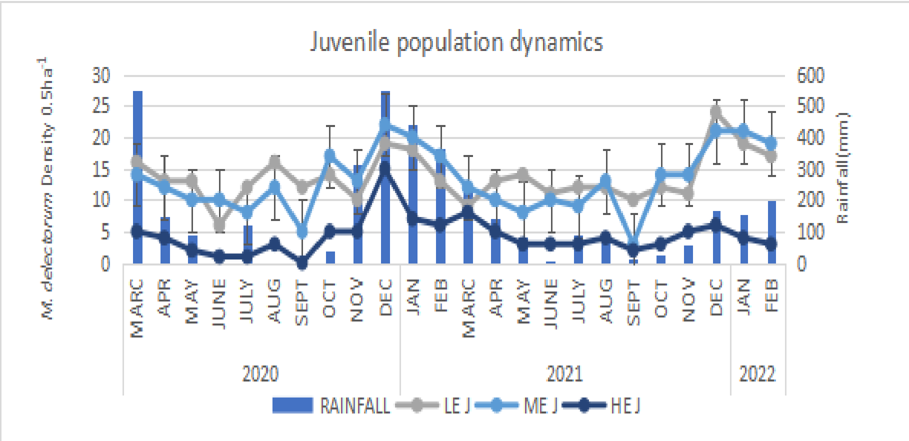
The population of *M. delectorum* is influenced by the season and elevation. The population shows positive correlation with the wet seasons of the year. Additionally, the elevation plays a role with low and mid- elevations exhibiting higher populations compared to higher elevations. The interaction between the season and elevation had a significant impact but it was weaker than the effect of individual variables (Table 5.1).

Table 5.1: Summary of Poisson GLM on season and elevation influence on M. delectorum abundance at MRNFR

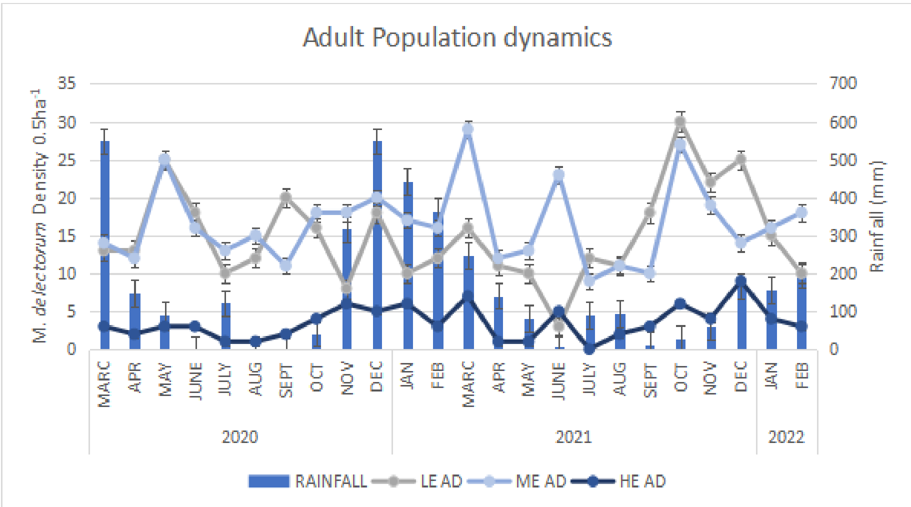
	Estimate	**std error z**	**Z value**	**Pr (>|z|)**
Intercept	2.18324	0.06852	31.86	<2e-16 ***
Seasonwet	0.4643	0.1482	3.134	0.0017 ***
ElevationLE	1.6034	0.1349	11.885	<2e-16 ***
ElevationME	1.6094	0.1348	11.936	<2e-16 ***
seasonwet:elevationLE	-0.3594	0.1642	-2.189	0.02863*
seasonwet:elevationME	-0.3065	0.1638	-1.871	0.006137

A high number of juveniles were observed between December (early wet season) and March (wet season) with peak abundance in December (Figure 5.2a). In contrast, the pattern for the adult population was less defined, thus showing several fluctuating peaks and declines (Figure 5.2b). The GLM model indicated that the juvenile population was significantly influenced by seasonal variation throughout the year (Estimates ± SE = 0.3851 ±0.0782, Z = 4.924, p = 8.47e-07) while the adult population was not significantly influenced by seasonal variation (Estimates ± SE = 0.01530 ±0.05890, Z = 0.26, p = 0.795).

The population of *M. delectorum* at MRNFR is also influenced by the elevation gradient with significantly higher population observed at low and mid- elevations compared to higher elevations (Table 5.1). The interaction between the season and elevation did not have the significant effect on the population of adult *M. delectorum* (p>0.05). However, there was a significant interaction (Est. ± SE = -0.5577 ± 0.2572, Z = -2.168, p = 0.030134) for the juvenile population, thus indicating that the notable number of juveniles were observed at lower elevations during the wet period. It is important to note that the influence resulting from variable interactions was weaker compared to when the variables independently influenced the population.



(a)



(b)

Figure 5.2 (a & b): Juvenile and adult population dynamics at MRNFR

5.3.1.2 Sex Ratio

The sex ratio of *Montemys delectorum* at MRNFR was calculated to be 0.5104. The significant deviation from equal proportional was observed along the elevation gradient, particularly at the mid-elevation where a sex ratio of 0.58:0.42 (female to male) was recorded (Figure 5.3). This indicates high number of females captured compared to males in mid-elevation. Conversely, the female to male proportion at both low and high elevations was insignificance with the sex ratio of 0.45 in low-elevation and 0.47 in high elevation observed. During July and August in the second year of capture at high elevation, there was no female *M. delectorum* individual which was notably captured (Table 5.2).

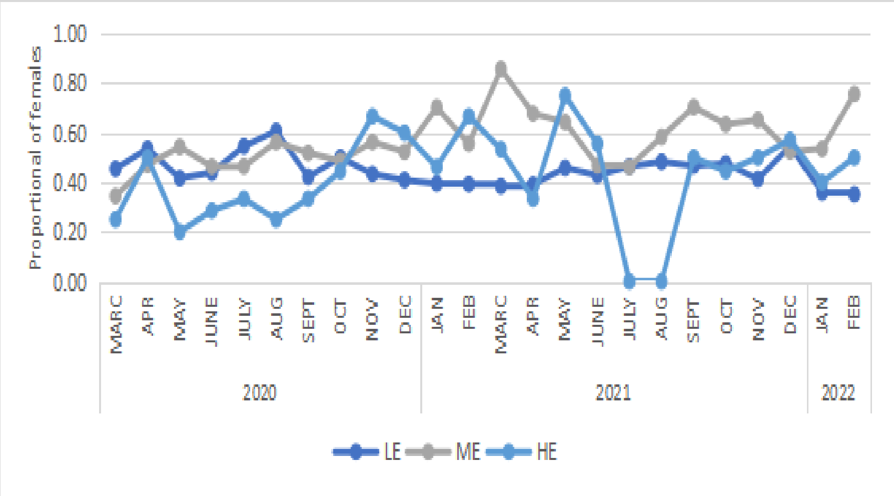


Figure 5.3: Sex ratio distribution of females *M. delectorum* at MRNFR (LE – Low - elevation, ME – Mid- elevation and HE- High elevations)

The sex ratio of 1:1 was observed in both wet and dry seasons in the low and higher elevations, thus indicating an equal proportion of females and males across the seasons.

However, in the mid elevation a sex ratio of 0.58:0.42 with a significant high number of females ($\chi2 = 51.84$, $p = 0.0005$) was observed. The wet season exhibited the notable difference in the number of females ($\chi2 = 225.65$, $p = 2.37$ e-27) and males (χ 2 = 111.55, $p = 1.912$ e-08) compared to the dry season. Specifically, the number of females was considerably higher than the number of males during the wet season in the mid-elevation. However, there were no significant differences observed in the number of individual *M. delectorum* females and males captured during the dry season (Table 5.2).

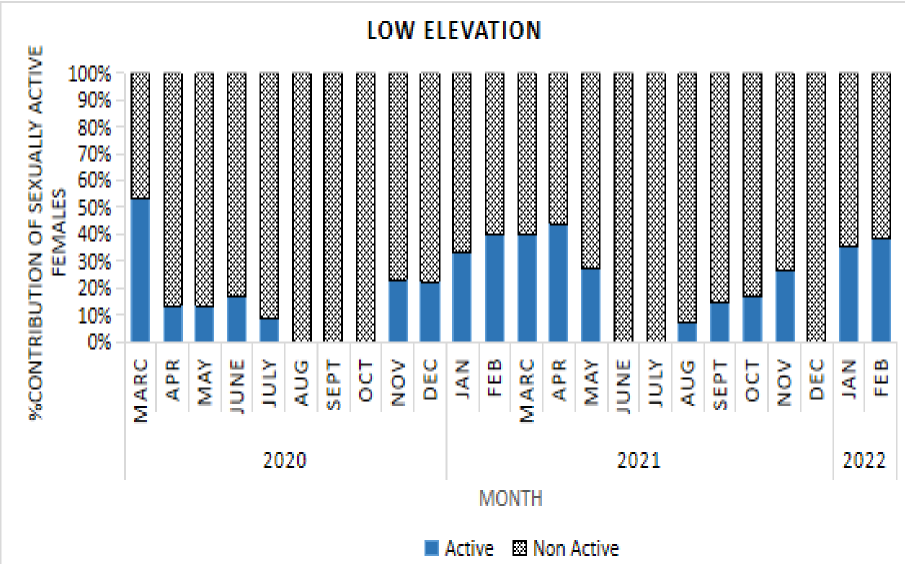
Table 5.2: Sex ratio of *M. delectorum* between wet and dry seasons along elevation (LE - Low elevation, ME - Mid- elevation and HE – Higher elevation)

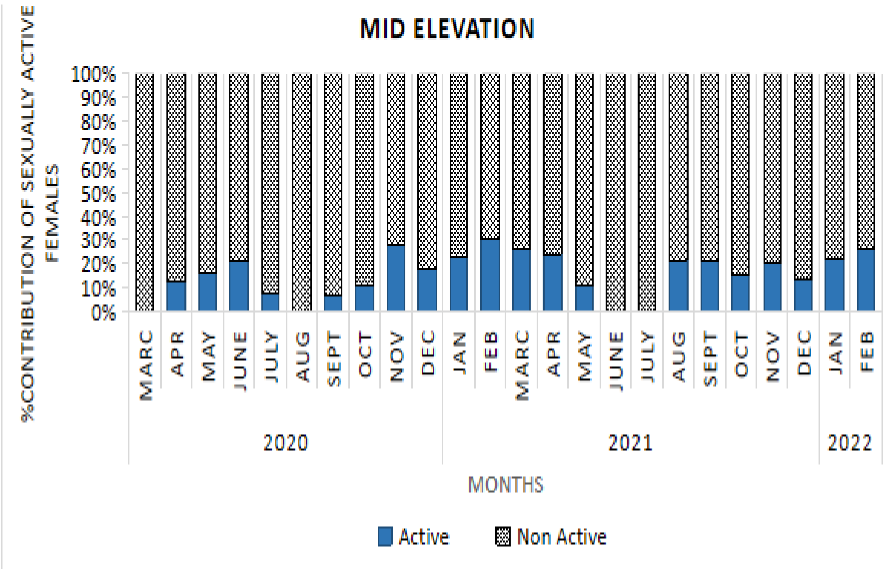
Elevation		**LE**		**ME**		**HE**
Season	**DRY**	**WET**	**DRY**	**WET**	**DRY**	**WET**
Female	158	213	175	331	24	76
Male	172	287	155	210	42	71
Sex ratio	0.48	0.43	0.53	0.61	0.36	0.52
χ^2	3.34	7.13	8.19	38.82	8.33	9.41
P VALUE	**0.9490**	**0.8955**	**0.5152**	**0.0002****	**0.5013**	**0.7410**

* It indicates that the female to male ratio significantly differs from 1:1 at **$p < 0.01$, *$p < 0.05$.

5.3.2 Breeding Pattern

The temporal variations in the proportions of reproductively active females were observed across all elevations (Figure 5.4) in attempt to show the prominent peaks between November and May in the low and mid-elevations and between September and March in the higher elevations. However, there were no sexually active females which were recorded across all elevation gradients during certain months such as August, 2020, June, 2021 and July, 2021). (Figure 5.4).


LOW ELEVATION
%CONTRIBUTION OF SEXUALLY ACTIVE FEMALES
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
MARC APR MAY JUNE JULY AUG SEPT OCT NOV DEC JAN FEB MARC APR MAY JUNE JULY AUG SEPT OCT NOV DEC JAN FEB
2020
2021
2022
MONTH
Active
Non Active


MID ELEVATION
%CONTRIBUTION OF SEXUALLY ACTIVE FEMALES
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
MARC APR MAY JUNE JULY AUG SEPT OCT NOV DEC JAN FEB MARC APR MAY JUNE JULY AUG SEPT OCT NOV DEC JAN FEB
2020
2021
2022
MONTHS
Active
Non Active

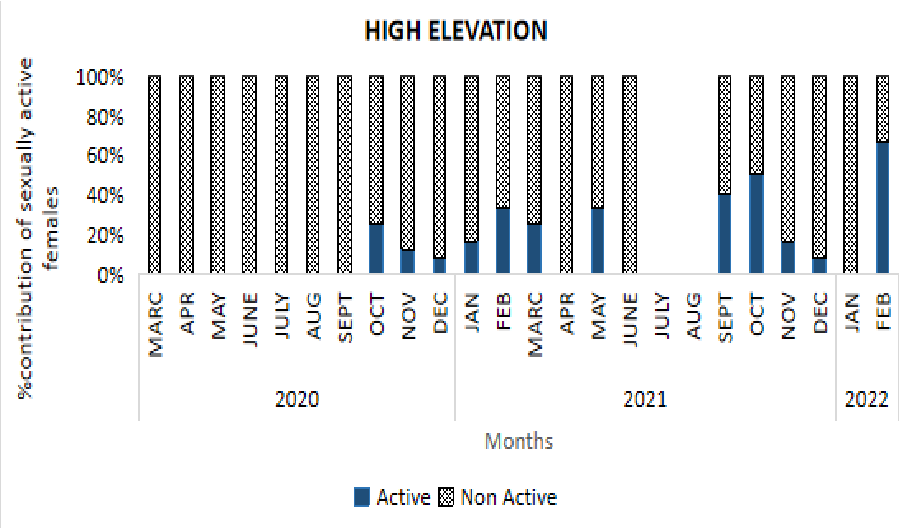


Figure 5.4: Variation of active reproductive abundance and non-active *M. delectorum* in MRNFR

The effect of season on reproductive females was found to be significant as high number of actively reproductive females were recorded during the wet seasons (Est ± SE = 1.0498 ± 0.1863, Z = 5.634, p = 1.76e-8). The elevation also had an influence on the breeding population with significantly higher number of reproductive females observed at low elevations (Est. ± SE = 1.4843 ± 0.2686, Z = 5.526, p = 3.28e-08) and mid-elevations (Est. ± SE = 1.6441 ± 0.2649, Z = 6.206, p = 5.44e-10) compared to high elevation. Variation between active and non active female was observed in mid-elevation.

5.4 Discussion

5.4.1 Population Structure, Dynamics and Sex Ratio of *M. delectorum*

5.4.1.1 Population Structure and Dynamics

In the current study, the significant differences in the population structure of *M. delectorum* in MRNFR were observed. The results of the study demonstrated that the population of *M. delectorum* varied along an elevation gradient with higher numbers observed in low and mid-elevations. Additionally, the study found out that the population of *M. delectorum* fluctuated throughout the year with significant peaks occurring during the wet seasons. This pattern may be attributed to high productivity of the area which is influenced by the substantial annual rainfall reaching up to 3000 mm (Williamson *et al*., 2014). The previous studies have indicated that rainfall plays a crucial role in triggering primary productivity and subsequently increasing the abundance of primary and secondary consumers such as rodents (Linger *et al*., 2020; Ritter *et al*., 2020). For instance, the study by Ernest *et al*. (2000) which was conducted in Mexico reported a correlation between the rodent populations, precipitation, vegetation cover and plant production. Similarly, Joneidi *et al*. (2020) found out a positive relationship between the canopy cover and population increase of small mammals, which is influenced by precipitation availability. The findings of the current align with the findings by Linger *et al*. (2020); Ritter *et al*. (2020): Joneidi *et al*. (2020) in that the population of *M. delectorum* increases during the wet season due to the availability of the food and cover resources associated with increased rainfall. Furthermore, the higher abundance of *M. delectorum* was observed in low and mid- elevations compared to higher elevations. This can be attributed to the greater resource availability in low and mid- elevations while harsh climatic condition in the higher elevations limits resource supply. Benedek & Sîrbu (2019) also reported lower populations of the small mammals in upper elevations due to environmental limiting factors when compared to low elevations.

Regarding the response of the juvenile and adult populations to changes in elevation and seasons, the study found out that they exhibited different patterns. Adult population showed significant changes in its abundance with response to elevation but not between seasons. In contrast, the juveniles showed significant changes in abundance in response to both the elevation and seasons. Specifically, the high population of juveniles was observed during the wet season. A peak of juvenile population in October, 2021, which is a dry month, was possibly influenced by the precipitation in July and August in the same year. The high primary productivity during the wet season is likely to promote the higher rate of reproduction, thus increasing the population of juveniles. Such findings are consistent with the study findings by Pucekz *et al*. (1993) which was conducted in Bialowieza National Park where they observed a significant proportion of juveniles during the spring time, which was attributed to favorable climatic condition and increased primary productivity. Similarly, the study by Omogbeme & Oko (2018) which was conducted in the lowland tropical rainforest ecosystem of Okomu National Park reported a high number of juveniles during the wet season, which corresponds to young recruitments in that season. In contrast, the number of juveniles decreased during the dry period, the practice which may be influenced by the changes in climatic condition. For instance, the months of June and July experience frigid dry periods with a drop in temperature up to - 06^0 C, thus potentially impacting on the juvenile survival. The GLM model revealed that the interaction between the season and elevation significantly affected the juvenile population, particularly with higher population in low elevations during the wet period. However, the effect of the interaction between the season and elevation on adults was not significant.

5.4.1.2 Sex Ratio of *M. delectorum*

The analysis of sex ratio in different elevation gradients revealed interesting patterns in the population of *M. delectorum*. The sex ratio in both low and upper elevations was not significantly different with an equal proportion of females and males. However, a notable difference in sex ratio with a higher number of females was observed in the mid-elevation compared to males (Table 5.2). The finding in question suggests a skewed sex ratio towards the females in the mid-elevation habitat. Additionally, the seasonality was found to influence the sex ratio, particularly in the mid-elevation. During the wet season, the number of females captured was significantly higher than the number of males, thus resulting in a sex ratio of 0.61. This observation aligns with previous studies that have reported increased females' activity and foraging behavior during breeding periods, thus leading to a higher likelihood of capturing females (Steinlechner & Puchalski, 2003).

5.4.2 Breeding Population of *M. delectorum*

The breeding populations were determined based on the presence of the active females exhibiting signs of breeding such as perforated vagina, swollen nipples and indications of lactation or pregnancy. The findings of the current study revealed that the breeding population of *M. delectorum* displayed the fluctuations throughout the year with the females exhibiting reproductive activity year-around. This continuous breeding activity can be attributed to the favourable environmental condition in the study area, which is characterised by ample rainfall and consistent primary productivity throughout the year (Williamson *et al*., 2014). However, at higher elevations which are characterised by harsh climatic conditions, including cold temperatures, the breeding populations of *M. delectorum* was lower. This is consistent with the previous studies which indicate that the rodents and mice generally prefer temperatures ranging from 21^{o}C to 24^{o}C (Robertson & Wilsterman, 2020; Dantas *et al*., 2021).

The integration of the season and elevation variables in the model demonstrated a significant difference in the breeding population of females, which was particularly observed at the mid-elevation. This suggests that the environmental conditions such as rainfall and temperatures, which are associated with different elevations, play a significant role in influencing the breeding dynamics of *M. delectorum.* The rainfall, for example, contributes to increased food availability and cover, which positively correlate with higher breeding activity. Conversely, the temperature influences the physiological processes of the species with moderate temperature which support the breeding activity while extreme hot or cold temperature can suppress or halt the breeding activity. During the cold periods, the small mammals face strong energy constraints due to the trade-off between energy needed for thermoregulation and reproduction (Steinlechner & Puchalski, 2003). Generally, the energy resources are primarily allocated to thermoregulation with any excess energy available for reproduction. This could explain the lower breeding population observed during the harsh climatic conditions such as cold periods.

5.5 Conclusion

In conclusion, the population dynamics and breeding patterns of *Montemys delectorum* in the MRNFR are influenced by the length of the breeding season, which is determined by the rainfall and elevation. The findings in question contribute to the researchers' understanding of the ecological factors shaping the population structure of *M. delectorum* and emphasize the importance of considering both the spatial and temporal variations in the population dynamics. The species is capable of occupying all the elevation gradients in the mountainous environment but with higher populations observed in the low and mid-elevations. The study highlights the seasonal population changes of *M. delectorum* with a positive correlation between the rainfall and population growth due to increased vegetation. This emphasizes the need for year-round management of the *M. delectorum* population in the MRNFR considering the continuous reproduction and population growth which are facilitated by the ample rainfall throughout the year. The findings can also serve as the model for managing the rodent pests in the surrounding areas with similar climate and rainfall patterns. Additionally, the study reveals the presence of the active breeding females throughout the year with peaks observed during the wet seasons, thus suggesting the significant role of food availability in the breeding cycle of *M. delectorum.* Such findings can inform the management about the plan for Rungwe Mountain and contribute to the understanding of the small mammal dynamics in the area.

References

Ara, M., Taylor, P. J., Denys, C., & Cotterill, F. P. (2015). *Rodents of sub-Saharan Africa: a biogeographic and taxonomic synthesis*. Walter de Gruyter GmbH & Co KG.

Avenant, N. L., & Smith, V. R. (2004). Seasonal changes in age class structure and reproductive status of house mice on Marion Island (sub-Antarctic). *Polar Biology*, *27*(2), 99–111. https://doi.org/10.1007/s00300-003-0569-x

Benedek, A. M., & Sîrbu, I. (2019). Dynamics of small-mammal communities along an elevational gradient. *Canadian Journal of Zoology*, *97*(4), 312–318. https://doi.org/10.1139/cjz-2018-0201

Dantas, M. R. T., Souza-Junior, J. B. F., Castelo, T. de S., Lago, A. E. de A., & Silva, A. R. (2021). Understanding how environmental factors influence reproductive aspects of wild myomorphic and hystricomorphic rodents. *Animal Reproduction*, *18*(1). https://doi.org/10.1590/1984-3143-ar2020-0213

Dobson, F. S., & Oli, M. K. (2001). The Demographic Basis of Population Regulation in Columbian Ground Squirrels. *The American Naturalist*, *158*(3), 236–247. https://doi.org/10.1086/321322

Ecke, F., Löfgren, O., & Sörlin, D. (2002). Population dynamics of small mammals in relation to forest age and structural habitat factors in northern Sweden. *Journal of Applied Ecology*, *39*(5), 781–792. https://doi.org/10.1046/j.1365-2664.2002.00759.x

Ernest, S. K. M., Brown, J. H., & Parmenter, R. R. (2000). Rodents, plants, and precipitation: spatial and temporal dynamics of consumers and resources. *Oikos*, *88*(3), 470–482. https://doi.org/10.1034/j.1600-0706.2000.880302.x

Getz, L. L., Oli, M. K., Hofmann, J. E., & McGuire, B. (2007). Vole population dynamics: factors affecting peak densities and amplitudes of annual population fluctuations ofMicrotus pennsylvanicus. *Acta Theriologica*, *52*(2), 159–170. https://doi.org/10.1007/BF03194211

Happold, D. C. D. (2013). Mammals of Africa: Rodents, Hares and Rabbits. In *Mammals of Africa: Rodents, Hares and Rabbits: Vol. III*. Bloomsbury Publishing. https://doi.org/10.5040/9781472926937

Joneidi, H., Azizi, N., Osati, K., & Bandak, I. (2020). The effects of precipitation variability on the canopy cover of forage species in arid rangelands, Iran. *Arabian Journal of Geosciences*, *13*(18), 931. https://doi.org/10.1007/s12517-020-05901-x

Karim, M. R., & Zeger, S. L. (1992). Generalised Linear Models with Random Effects; Salamander Mating Revisited. *Biometrics*, *48*(2), 631. https://doi.org/10.2307/2532317

Krebs, C. J., & Myers, J. H. (1974). *Population Cycles in Small Mammals* (pp. 267–399). https://doi.org/10.1016/S0065-2504(08)60280-9

Leirs H. (1995). *Population ecology of Mastomys natalensis (Smith 1834): implication for rodent control in East Africa.* Agricultural Edition No. 35, Belgian Administration for Development Cooperation.

Lin, Y.-T. K., & Batzli, G. O. (2001). The Influence of Habitat Quality on Dispersal, Demography, and Population Dynamics of Voles. *Ecological Monographs*, *71*(2), 245. https://doi.org/10.2307/2657218

Linger, E., Hogan, J. A., Cao, M., Zhang, W.-F., Yang, X.-F., & Hu, Y.-H. (2020). Precipitation influences on the net primary productivity of a tropical seasonal rainforest in Southwest China: A 9-year case study. *Forest Ecology and Management*, *467*, 118153. https://doi.org/10.1016/j.foreco.2020.118153

Makundi, R. H., Massawe, A. W., & Mulungu, L. S. (2007a). Breeding seasonality and population dynamics of three rodent species in the Magamba Forest Reserve, Western Usambara Mountains, north-east Tanzania. *African Journal of Ecology*, *45*(1), 17–21. https://doi.org/10.1111/j.1365-2028.2006.00667.x

Makundi, R. H., Massawe, A. W., & Mulungu, L. S. (2007b). Breeding seasonality and population dynamics of three rodent species in the Magamba Forest Reserve, Western Usambara Mountains, north-east Tanzania. *African Journal of Ecology*, *45*(1), 17–21. https://doi.org/10.1111/j.1365-2028.2006.00667.x

Makundi, R. H., Massawe, A. W., Mulungu, L. S., & Katakweba, A. (2009). Species diversity and population dynamics of rodents in a farm-fallow field mosaic system in Central Tanzania. *African Journal of Ecology*, *48*(2), 313–320. https://doi.org/10.1111/j.1365-2028.2009.01109.x

Massawe, A. W., Mulungu, L. S., Makundi, R. H., Dlamini, N., Eiseb, S. J., Kirsten, F., Mahlaba, T., Malebane, P., Von Maltitz, E., Monadjem, A., Taylor, P., Tutjavi, V., & Belmain, S. R. (2011). Spatial and temporal population dynamics of rodents in three geographically different regions in Africa: Implication for ecologically-based rodent management. *African Zoology*, *46*(2), 393–405. https://doi.org/10.1080/15627020.2011.11407513

Mayamba, A., Byamungu, R. M., Leirs, H., Moses, I., Makundi, R. H., Kimaro, D. N., Massawe, A. W., Kifumba, D., Nakiyemba, A., Mdangi, M. E., Isabirye, B. E., & Mulungu, L. S. (2021). Population and breeding patterns of the pest rodent: *Mastomys natalensis* in a maize dominated agroecosystem in Lake Victoria crescent zone, Eastern Uganda. *African Zoology*, *56*(1), 76–84. https://doi.org/10.1080/15627020.2021.1879675

Merritt, J. F., Lima, M., & Bozinovic, F. (2001). Seasonal Regulation in Fluctuating Small Mammal Populations: Feedback Structure and Climate. *Oikos*, *94*(3), 505–514.

Mulungu, L. S., Ngowo, V., Mdangi, M., Katakweba, A. S., Tesha, P., Mrosso, F. P., Mchomvu, M., Sheyo, P. M., & Kilonzo, B. S. (2013). Population dynamics and breeding patterns of multimammate mouse, *Mastomys natalensis* (Smith 1834), in irrigated rice fields in Eastern Tanzania. *Pest Management Science*, *69*(3), 371–377. https://doi.org/10.1002/ps.3346

Mulungu S, L., & Lopa, H. (2016). Comparative Study of Population Dynamics and Breeding Patterns of *Mastomys natalensis* in System Rice Intensification (SRI) and Conventional Rice Production in Irrigated Rice Ecosystems in Tanzania. *Rice Research: Open Access*, *4*(1). https://doi.org/10.4172/2375-4338.1000161

Norrdahl, K., & Korpimäki, E. (2002). Changes in population structure and reproduction during a 3-yr population cycle of voles. *Oikos*, *96*(2), 331–345. https://doi.org/10.1034/j.1600-0706.2002.960215.x

Ofori, B. Y., Attuquayefio, D. K., Owusu, E. H., Musah, Y., & Ntiamoa-Baidu, Y. (2016). Spatio-temporal variation in small mammal species richness, relative abundance and body mass reveal changes in a coastal wetland ecosystem in Ghana. *Environmental Monitoring and Assessment*, *188*(6). https://doi.org/10.1007/s10661-016-5320-5

Oli, M. K., & Dobson, F. S. (2001). Population cycles in small mammals: The α-Hypothesis. *Journal of Mammalogy*, *82*(2), 573–581. https://doi.org/10.1644/1545-1542(2001)082<0573:PCISMT>2.0.CO;2

Omogbeme, M., & Oko, C. (2018). Population dynamics of Rodents and Insectivores in lowland tropical rainforest ecosystem of Okomu National Park, Edo State, Nigeria. *Journal of Applied Sciences and Environmental Management*, *22*(3), 318. https://doi.org/10.4314/jasem.v22i3.5

Pucekz, Z., Jedrzejewski, W., Jedrzejewska, B., & Pucek, M. (1993). Rodent population dynamics in a primeval deciduous forest (Białowieża National Park) in relation to weather, seed crop, and predation. *Acta Theriologica*, *38*(2), 199–232.

R Core, Team. (2020). *R:A language and environment for statistical computing. R Foundation for Statistical Computing.* . Vienna, Austria.

Richard, U., Byamungu, R. M., Magige, F., & Makonda, F. B. S. (2022). Microhabitat, altitude and seasonal influence on the abundance of non-volant small mammals in Mount Rungwe forest nature reserve. *Global Ecology and Conservation*, *35*, e02069. https://doi.org/10.1016/j.gecco .2022.e02069

Ritter, F., Berkelhammer, M., & Garcia-Eidell, C. (2020). Distinct response of gross primary productivity in five terrestrial biomes to precipitation variability. *Communications Earth & Environment*, *1*(1), 34. https://doi.org/10.1038/s43247-020-00034-1

Robertson, C. E., & Wilsterman, K. (2020). Developmental and reproductive physiology of small mammals at high altitude: challenges and evolutionary innovations. *Journal of Experimental Biology*, *223*(24). https://doi.org/10.1242 /jeb.215350

Stanley, W. T., Kihaule, P. M., Howell, K. M., & Hutterer, R. (1998). Small mammals of the Eastern Arc Mountains, Tanzania. In *Journal of East African Natural History* (Vol. 87).

Steinlechner, S., & Puchalski, W. (2003). Mechanisms for Seasonal Control of Reproduction in Small Mammals. In *Environmental Signal Processing and Adaptation* (pp. 233–250). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-642-56096-5_11

URT. (2017). *Management Plan for Mount Rungwe Nature Forest Reserve*.

Williamson, D., Majule, A., Delalande, M., Mwakisunga, B., Mathé, P. E., Gwambene, B., & Bergonzini, L. (2014). A potential feedback between landuse and climate in the Rungwe tropical highland stresses a critical environmental research challenge. *Current Opinion in Environmental Sustainability*, *6*(1), 116–122. https://doi.org/10.1016/J.C OSUST.2013. 11.014

CHAPTER SIX

6.0 GENERAL DISCUSSION, CONCLUSION, IMPLICATION AND RECOMMENDATION

6.1 General Discussion

A total of 12 small mammal species were recorded in different habitats along the altitudinal gradient at MFRNR, which comprised nine species from Rodentia and three species from Soricomorpha orders. Total individuals collected for the entire study were 3 184 including 953 individuals for objective one, 444 individuals for objective two, 171 for objective three and 1 922 individuals for objective four. *Praomys delectorum* collected for objective two were also used for objective four. The majority of the rodents were trapped using Sherman, Snap and Havahart traps while most of the shrews were recorded in pitfall traps. The species collected in this study included *Beamys hindei, Cricetomys ansorgei, Montemys delectorum, Lophuromys machangui, Grammomys cometes, Mus triton, Dendromus nyassae, Graphiurus* sp*., Hylomyscus arcimontensis, Crocidura luna, Crocidura Olivier and Myosorex kihaulei.* However, some previously observed species such as *Otomys lacustris* and *Rhabdomys dilectus* from Mount Rungwe were not observed in this study. Additionally, the number of *Mus triton* observed in this study was lower than the previously recorded number in 1987 (Cuypers *et al*., 2022) which indicates the decline in population of the species. On the other hand, several species, including *Beamys hindei, Cricetomys ansorgei, Grammomys cometes, Crocidura olivier, Crocidura luna, Graphiurus* sp. and *Myosorex kihaulei* were recorded for the first time in the Rungwe mountain area. The *Myosorex kihaulei* was previously reported as endemic to Udzungwa Mountain and it is currently listed as the endangered species due to habitat loss.

The observed differences in the composition, abundance, richness and diversity along the elevation gradient in Mount Rungwe Nature Forest Reserve indicate that the changes are significantly influenced by the habitat characteristics, climate variations and altitudinal gradient. The observed differences in the small mammals species composition along the elevation gradient can be attributed to the changes in environmental variables, including abiotic and biotic factors such as the vegetation composition, cover and microclimate which vary along the gradient. The mid-elevation which is characterised by the forest montane vegetation exhibited the highest species abundance, composition and diversity. This finding can be explained by the mid-domain effect which suggests that mid-elevation tend to offer more favorable climatic conditions for species growth (McCain, 2004). Other studies such as that by Rahman *et al*. (2021) have also reported the variations in abiotic and biotic characteristics along the elevation gradient as factors contributing to differences in small mammal composition. However, the species richness did not show the likely significant differences across different habitats and seasons due to high rainfall in the area, thus ensuring sufficient food supply, shelter, and cover for small mammals. They will reduce the competition and allow for the greater number of species in all seasons.

The *Montemys delectorum* emerged as the most abundant and dominant species across the elevation gradients, habitats and seasons. Its high abundance can be attributed to its adaptability to the environment as adaptable species tend to dominate in a given area (Devi & Jain, 2020). The *Montemys* is a forest-dwelling species which exhibited particularly high abundance in the mid-elevation montane forest habitats. The dominance of *M. delectorum* over other species in the forested area has been documented by other scholars such as Lema & Magige (2018); Gebrezgiher *et al*. (2022); Mwasapi & Rija (2022).

The results have also showed that the different small mammals have different microhabitat requirements. For instance, being the forest-dwelling species, the *Montemys delectorum* was more frequently captured in grids with abundant trees and less frequently captured in open vegetation grids at higher elevations such as those placed on the herbs and grasses. Other studies by Ademola *et al*. (2022) and Gebrezgiher *et al*. (2022) have also demonstrated the *M. delectorum's* preference for forested areas with high number of trees. On the other hand, the species like *L. machangui* were collected in the grids with abundant herbs and grass vegetation and low canopy cover. The abundance *L. machangui* increased with elevation which was attributed to the specific habitat and microhabitats found in higher elevations which are characterised by the dominant herbs, shrubs and grass. Similar findings of *Lophuromys'* high abundance in herbs and grassland vegetation were reported by (Clausnitzer *et al*., 2003) who reported an abundant population of *Lophuromys* up to 4200m a.s.l. in Mount Elgon where the dominant shrubs and grassland were present. Ssuuna *et al*. (2020) also recorded a significant number of *Lophuromys* in the regenerated habitats with fewer trees and open canopy cover compared to intact forests.

In addition to differences in microhabitat requirements, the small mammals in MFRNR exhibited the niche diversification as the mechanism for coexistence. The variety and availability of food resources which are consumed by sympatric rodents reduce competition and facilitate the coexistence in the MRNFR ecosystem. The food categories consumed by sympatric rodents include the seeds/grains, leaves, stems, roots, invertebrates and hairs. Despite the fact that all species consume a diverse range of food resources, some species show a remarkable preference for certain food resources over others. For example, the *Beamys hindei* consume more seeds than other food resources. This is attributed to its behavious as pouched rats that use their pouches to carry and store seeds for extended period (Hanney & Morris, 1962; Happold, 2013).

The *Lophuromys machangui* and *Grammomys dolichurus* also had the higher proportion of invertebrates in their diet. The Lophuromys which is found in the areas with abundant herbs and grass and high ground cover encounters more invertebrates in its diet compared to other food types such as seeds and leaves. Other studies have also reported Lophuromys' feeding on invertebrates (Ademola *et al*., 2022; Clausnitzer *et al*., 2003). The *G. dolichurus* were predominantly caught in the tropical high-altitude bushland and tropical moist lowland forests which may have high invertebrate diversity compared to other food categories. However, *Grammomys dolichurus* in other locations have been reported to feed on the fruits, plant materials (Wirminghaus & Perrin, 1992) and seeds (Varty, 1990). This suggests that the rodent feeding behavior is heavily influenced by food availability (Lunghi *et al*., 2020). The observed low niche breadth and population density for *G. dolichurus* indicate that the species is a specialist and it has relatively few food resources that it can consume. In contrast, the moderate niche breadth for *Praomys delectorum, Lophuromys machangui* and *Beamys hindei* indicates that these species are generalist and have a wider range of food options. Several studies such as that by Harmáčková *et al*. (2019) have clearly shown that highly specialized species are characterised by low population density. As a result, the observed diet overlap is a result of the abundance and diversity of food resources consumed by these species. Reid *et al*. (2013) reported that high trophic niche overlap occurs when food is abundant, thus leading to a decline in interspecific competition and enabling species to feed without significant competition. Therefore, the food resource availability largely regulates the niche breadth and overlap of species and when the resources are abundant, the species coexistence with minimal competition.

Additionally, the population structure and dynamics of the dominant species which was the most abundant species in the area were analyzed. The dominant species have significant influence on the occurrence and distribution of other organisms by sharing the available resources. Highly abundant species within the communities are often expected to have strong effects on ecological processes such as food web structure and ecosystem function (Avolio *et al*., 2019). In the case of MRNFR, the dominant small mammal species was the soft-furred mice, *Montemys delectorum,* which exhibited high abundance throughout all seasons and along the entire elevation gradient. The high abundance of *M. delectorum* may be attributed to interspecific competition which leads to differences in abundance among the species and it enables highly competitive species to successfully colonize the area. The population of *Montemys delectorum* varied spatially along elevation and temporally between seasons. We observed greater population at low and mid- elevations compared to higher elevations which could be due to environmental and climatic factors in the area. The low and mid-elevations provide ample resources, including food and cover, for small mammals while the higher elevations are characterised by environmental and climatic limiting factors such as lower temperature, intense humidity and rocky soil, thus resulting in reduced food resources and cover (Richard *et al*., 2022).

The presence of high canopy cover reduces predation risks (Rey *et al*., 2002; Rose *et al*., 2020). The increased population of *M. delectorum* during the wet seasons was attributed to the higher primary productivity, thus resulting from increased rainfall. The rainfall triggers the vegetation growth which leads to an increase in food resources and cover for the animals. Some studies such as that by Ernest *et al*. (2000) have widely documented the positive relationship between precipitation, plant production, cover and rodent population. As the findings of the current study clearly reveal, there was similar relationship between the precipitation and *M. delectorum* population notably when the area experienced unusual rainfall during the dry season, thus resulting in population increase. After the rainfall, vegetation grows with an increase in canopy and ground cover that support the survival of small mammals (Joneidi *et al*., 2020).

The breeding pattern and sex ratio of the dominant rodent, *M. delectorum,* at MRNFR fluctuate throughout the year. The presence of the actively breeding females throughout the year can be explained by the availability of food and cover year-round in MRNFR, a tropical forest that receives a substantial amount of rainfall in Tanzania (Williamson *et al*., 2014). Due to sufficient rainfall, the primary productivity is high, thus providing enough food for *M. delectorum* throughout the year although there were breeding peaks in the wet season due to abundance of food and cover. The breeding peak along the elevation gradient was observed from September to March in the higher elevations with harsh climates. This is due to the climatic conditions, particularly temperature, which are favorable for the survival of the juvenile mammals during this time. The study suggests that the rodents undergo physiological, mental, and physical stress in very low temperatures, which inhibits their reproduction (Robertson & Wilsterman, 2020). The sex ratio differences were not significant in the low and high elevations while the sex ratio in the mid- elevation was 0.6 with more females than males, possibly due to climatic conditions. Consequently, the females are likely to forage more than males in search of the mates and food for their young. Female require more energy during lactating, thus making them more susceptible to being caught more in the traps compared to males. During the breeding season, the females have a higher energy requirement than males and, hence forage more (Steinlechner & Puchalski, 2003).

6.2 Conclusion

The present study has yielded significant findings regarding the small mammal populations in Mount Rungwe Nature Forest Reserve

(MRNFR) in Tanzania. The research identified the diverse array of small mammal species, including the endangered shrew *Myosorex kihaulei* which was previously believed to be endemic in Udzungwa Mountains. The presence of *Myosorex kihaulei* in MRNFR expands its known geographical distribution. Additionally, the *Graphiurus sp.,* was observed across all elevation gradients and the recent genomic data suggests significant genetic divergence from the known *Graphiurus* species.

The study demonstrated that the changes in elevation had the profound impact on the diversity and abundance of small mammals at MRNFR. The mid- and lower elevations exhibited higher levels of the species diversity and abundance compared to the higher elevations. This indicates that the aspect of elevation influenced the biotic and abiotic characteristics of the area thereby shaping the species composition. Furthermore, the study revealed that the rodents in MRNFR displayed omnivorous feeding behavior with distinct food preference observed among different rodent species. The coexistence of the species with high niche breadth and overlap, which results from the availability of abundant resources suggests that the competition among species is minimized in the area.

The dominant species, *Montemys delectorum*, in MRNFR exhibited the spatial and temporal fluctuations in its population. In comparison with other species, the adaptability of *M. delectorum* in MRNFR was evident. However, its population and breeding pattern varied in response to changes in elevation and availability of precipitation. The continuous rainfall in MRNFR sustains high population number of *M. delectorum*.

In summary, this study provides the valuable insights into the ecology of small mammals in the Rungwe Nature Forest Reserve, which can potentially inform the development of the effective conservation management strategies for the area. The recorded species should be considered in the future management plans and the findings of the study can serve as the baseline data for further research, thus contributing to the conservation and preservation of this important ecosystem.

6.3 Implication of the study

The study of small mammals in Mount Rungwe Nature Forest Reserve carries several significance implications across various domains which include:

Conservation Implications: Understanding the small mammal community in Mount Rungwe Nature Forest Reserve is crucial for conservation efforts. Identifying species richness, population trends, and habitat preferences can inform conservation strategies aimed at preserving biodiversity within the reserve. Conservation implications may include habitat management practices, such as maintaining key habitat features preferred by small mammals especially the endangered *M. kihaulei.*

Policy Recommendations: Findings from the study can contribute to policy formulation and decision-making processes related to natural resource management, protected area governance and protection of endangered species. Recommendations may include development of wildlife corridors to promote connectivity between fragmented habitats.

Public Health: Small mammals can serve as reservoirs for zoonotic diseases, making their study relevant to public health concerns. Investigating the population dynamics of rodents in the study area can help assess potential risks to human health and inform disease surveillance and management strategies.

Ecosystem Functioning: Small mammals play critical roles in ecosystem functioning, including seed dispersal, predation, and nutrient cycling. Understanding their ecological roles and interactions with other species can provide insights into broader ecosystem dynamics within Mount Rungwe Nature Forest Reserve. Implications may include recognizing the importance of small mammals in maintaining ecosystem resilience and considering their conservation in the context of broader landscape-level management strategies.

Education and Outreach: Findings from the study can be used to enhance public awareness and appreciation of the biodiversity and ecological importance of Mount Rungwe Nature Forest Reserve. Education and outreach initiatives aimed at local communities, tourists, and policymakers can highlight the value of small mammal conservation and encourage support for conservation efforts. By engaging stakeholders and fostering a sense of stewardship, the study can contribute to long-term sustainability and conservation of the reserve's natural resources.

6.4 Recommendations

The research findings from the present study contribute to scientific knowledge of the ecology of the small mammals in the MRNFR and conservation efforts. The following recommendations are made:

i. The outcomes of the study should call for an update of the General Management Plans (GMP) for MRNFR in attempt to include the richness and distribution of small mammals in the Rungwe Forest.

ii. The study recorded the shrew, *Myosorex kihaulei,* which was previously only known from the Udzungwa Mountains. It is recommended that more researches should be conducted in order to investigate its population distribution, habitat and species biology in detail. Additionally, the conservation measures should be enhanced as it is listed as an endangered species by IUCN.

iii. Given the collection of *Graphiurus* sp. which was quite different from the known *Graphiurus* species, further studies are recommended to explore the species' genomics and distribution.

iv. The study recommends further research on the coexistence mechanisms of the species. Due to insufficient data, the study confined itself to the analysis of the diet composition of the four most captured species and it could not do so for other species which were either not captured in the snap traps or in low numbers, thus preventing diet analysis. Furthermore, the number of rodents caught for the diet analysis was not sufficient to perform the seasonal diet analysis.

v. The study recommends further investigation of other coexistence mechanisms such as interspecific interactions, life history differences, and pest/predator pressure, which determine the coexistence of the rodents in MRNFR as only one coexistence mechanism was tested due to limited resources.

vi. The long-term studies of the impact of climate change on small mammal populations in MRNFR is recommended so as to anticipate the potential range shifts, altered community dynamics and potential implications for ecosystem functioning.

References

Ademola, O. J., Massawe, A. W., Mulungu, L. S., Hieronimo, P., Makonda, F. B. S., & Makundi, R. H. (2022). Habitat type impacts small mammal diversity in the Ukaguru Mountains, Tanzania. *Mammalia*, *86*(2), 123–133. https://doi.org/10.1515/mammalia-2020-0158

Ademola, O. J., Massawe, A. W., Mulungu, L. S., & Makundi, R. H. (2022). Dietary composition of rodents across different habitats in the Ukaguru Mountains, Tanzania. *African Journal of Ecology*. https://doi.org/10.1111/aje.13042

Avolio, M. L., Forrestel, E. J., Chang, C. C., la Pierre, K. J., Burghardt, K. T., & Smith, M. D. (2019). Demystifying dominant species. *New Phytologist*, *223*(3), 1106–1126. https://doi.org/10.1111/nph.15789

Clausnitzer, V., Churchfield, S., & Hutterer, R. (2003). Habitat occurrence and feeding ecology of Crocidura montis and Lophuromys flavopunctatus on Mt. Elgon, Uganda. *African Journal of Ecology*, *41*(1), 1–8. https://doi.org/10.1046/j.1365-2028.2003.00386.x

Cuypers, L. N., Sabuni, C., Šumbera, R., Aghová, T., Lišková, E., Leirs, H., Baird, S. J. E., Goüy de Bellocq, J., & Bryja, J. (2022). Biogeographical Importance of the Livingstone Mountains in Southern Tanzania: Comparative Genetic Structure of Small Non-volant Mammals. *Frontiers in Ecology and Evolution*, *9*. https://doi.org/10.3389/fevo.2021.742851

Devi, A., & Jain, K. (2020). The Impact of Dominance on Adaptation in Changing Environments. *Genetics*, *216*(1), 227–240. https://doi.org/10.1534/genetics.120.303519

Ernest, S. K. M., Brown, J. H., & Parmenter, R. R. (2000). Rodents, plants, and precipitation: spatial and temporal dynamics of consumers and resources. *Oikos*, *88*(3), 470–482. https://doi.org/10.1034/j.1600-0706.2000.880302.x

Gebrezgiher, G. B., Makundi, R. H., Meheretu, Y., Mulungu, L. S., & Katakweba, A. A. S. (2022). A Decade-Long Change in the Elevational Distribution of Non-Volant Small Mammals on Mount Meru, Tanzania. *Diversity*, *14*(6), 454. https://doi.org/10.3390/d14060454

Hanney, P., & Morris, B. (1962). Some Observations upon the Pouched Rat in Nyasaland. *Journal of Mammalogy*, *43*(2), 238–248. https://doi.org/10.2307/1377095

Happold, D. C. D. (2013). Mammals of Africa : Rodents, Hares and Rabbits. In *Mammals of Africa : Rodents, Hares and Rabbits: Vol. III*. Bloomsbury Publishing. https://doi.org/10.5040/9781472926937

Harmáčková, L., Remešová, E., & Remeš, V. (2019). Specialization and niche overlap across spatial scales: Revealing ecological factors shaping species richness and coexistence in Australian songbirds. *Journal of Animal*

Ecology, *88*(11), 1766–1776. https://doi.org/10.1111/1365-2656.13073

Joneidi, H., Azizi, N., Osati, K., & Bandak, I. (2020). The effects of precipitation variability on the canopy cover of forage species in arid rangelands, Iran. *Arabian Journal of Geosciences*, *13*(18), 931. https://doi.org/10.1007/s12517-020-05901-x

Lema, R., & Magige, F. J. (2018). The influence of agricultural activities on the diversity of rodents in Kindoroko forest reserve and surrounding areas, North Pare Mountains, Tanzania. *Tanzania Journal of Science*, *44*(1), 97–106.

Lunghi, E., Manenti, R., Cianferoni, F., Ceccolini, F., Veith, M., Corti, C., Ficetola, G. F., & Mancinelli, G. (2020). Interspecific and interpopulation variation in individual diet specialization: Do environmental factors have a role? *Ecology*, *101*(8). https://doi.org/10.1002/ecy.3088

McCain, C. M. (2004). The mid-domain effect applied to elevational gradients: species richness of small mammals in Costa Rica. *Journal of Biogeography*, *31*(1), 19–31. https://doi.org/10.1046/j.0305-0270.2003.00992.x

Mwasapi, B. S., & Rija, A. A. (2022). Local habitat characteristics influence abundance and community structure of rodents in a regenerating Lulanda reserved forest, southern Tanzania. *Restoration Ecology*, *30*(1). https://doi.org/10.1111/rec.13501

Rahman, A. ur, Khan, S. M., Ahmad, Z., Alamri, S., Hashem, M., Ilyas, M., Aksoy, A., Dülgeroğlu, C., & Shahab Ali, G. K. (2021). - Impact of multiple environmental factors on species abundance in various forest layers using an integrative modeling approach. *Global Ecology and Conservation*, *29*, e01712. https://doi.org/10.1016/j.gecco.2021.e01712

Reid, R. E., Greenwald, E. N., Wang, Y., & Wilmers, C. C. (2013). Dietary niche partitioning by sympatric Peromyscus boylii and P. californicus in a mixed evergreen forest. *Journal of Mammalogy*, *94*(6), 1248–1257. https://10.0.6.108/13-MAMM-A-104.1

Rey, P. J., Garrido, J. L., Alcántara, J. M., Ramírez, J. M., Aguilera, A., García, L., Manzaneda, A. J., & Fernández, R. (2002). Spatial variation in ant and rodent post-dispersal predation of vertebrate-dispersed seeds. In *Functional Ecology* (Vol. 16).

Richard, U., Byamungu, R. M., Magige, F., & Makonda, F. B. S. (2022). Microhabitat, altitude and seasonal influence on the abundance of non-volant small mammals in Mount Rungwe forest nature reserve. *Global Ecology and Conservation*, *35*, e02069. https://doi.org/10.1016/J.GECCO.2022. E02069

Robertson, C. E., & Wilsterman, K. (2020). Developmental and reproductive physiology of small mammals at high altitude: challenges and evolutionary innovations. *Journal of Experimental Biology*, *223*(24). https://doi.org/10.1242/jeb.215350

Rose, K. M., Friday, J. B., Oliet, J. A., & Jacobs, D. F. (2020). Canopy openness affects microclimate and performance of underplanted trees in restoration of high-elevation tropical pasturelands. *Agricultural and Forest Meteorology*, *292–293*, 108105. https://doi.org/10.1016/j.agrformet. 2020. 108105

Ssuuna, J., Makundi, R. H., Isabirye, M., Sabuni, C. A., Babyesiza, W. S., & Mulungu, L. S. (2020). Rodent species composition, relative abundance, and habitat association in the Mabira Central Forest Reserve, Uganda. *Journal of Vertebrate Biology*, *69*(2). https://doi.org/10.25225/jvb.20021

Steinlechner, S., & Puchalski, W. (2003). Mechanisms for Seasonal Control of Reproduction in Small Mammals. In *Environmental Signal Processing and Adaptation* (pp. 233–250). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-642-56096-5_11

Varty, N. (1990). Ecology of the small mammals in the riverine forests of the Jubba Valley, Southern Somalia. *Journal of Tropical Ecology*, *6*(2), 179–189.

Williamson, D., Majule, A., Delalande, M., Mwakisunga, B., Mathé, P. E., Gwambene, B., & Bergonzini, L. (2014). A potential feedback between landuse and climate in the Rungwe tropical highland stresses a critical environmental research challenge. *Current Opinion in Environmental Sustainability*, *6*(1), 116–122. https://doi.org/10.1016/J.COSUST.2013.11.014

Wirminghaus, J. O., & Perrin, M. R. (1992). Diet of small mammals in the southern African temperate forest. *Israel Journal of Zoology*, *38*, 353–361. https://doi.org/10.1080/00212210.1992.10688682

Kuhusu Tasnifu Hii

Utafiti huu unakusudia kuelezea ikolojia ya mamalia wadogo katika hifadhi ya msitu wa asili ya mlima Rungwe ambao ni mlima wa pili kwa urefu kusini mwa Tanzania. Utafiti ulijikita katika miinuko tofauti ya mlima, iliyojumuisha misitu ya chini na ya kati ya milima, misitu ya mianzi na maeneo ya milima ya nyasi na vichaka. Jumla ya mamalia wadogo 3 184 kutoka katika spishi 12 walirekodia. Kwa ujumla, utafiti huu umefafanua ikolojia ya mamalia wadogo katika msitu wa mlima Rungwe na hivyo kuongeza uelewa wa ikolojia yao. Utafiti umeonyesha jinsi mamalia wadogo wanavyoathiriwa na mwinuko, hali ya hewa na makazi. Matokeo mengine ya kuvutia katika tafiti hii ni kupatikana kwa spishi ya *Graphiurus sp*. nov. (Rungwe) ambayo ni spishi mpya kulingana na takwimu za maumbile. Pia utafiti uliweza kurekodi *Myosorex kihaulei* ambaye yupo hatarini kutoweka. Utafiti huu umefichua bioanuai kubwa katika mlima Rungwe na kwa hivyo inapendekeza juhudi zaidi za uhifadhi.