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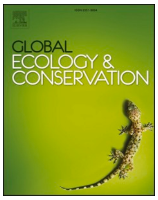

Microhabitat, altitude and seasonal influence on the abundance of non-volant small mammals in Mount Rungwe forest nature reserve

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ABSTRACT

A study on microhabitat, altitudinal and seasonal influences on small mammal abundance in Mount Rungwe Nature Forest Reserve, Tanzania was carried out from March 2019 to February 2020 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 ibeanus, 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

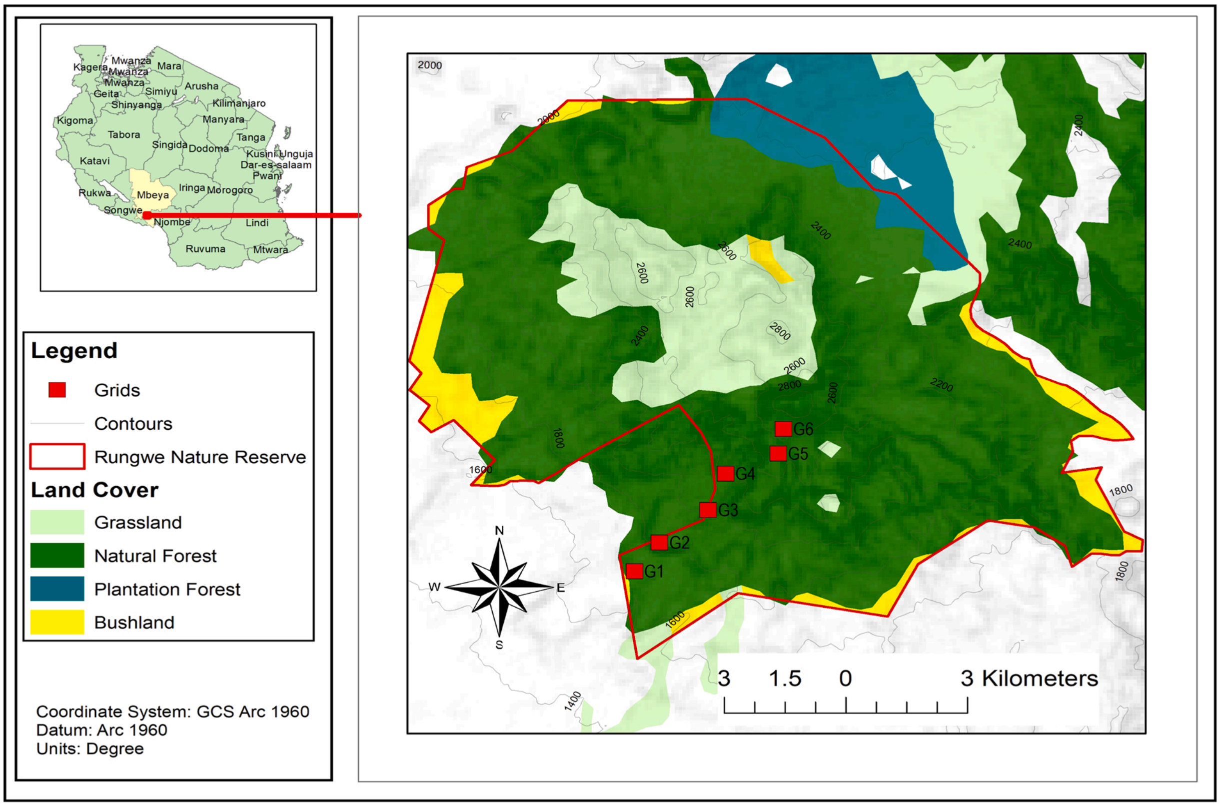


Fig. 1. Study area showing sampling points in the Mount Rungwe Forest Nature Reserve.

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 $9^0 03'$ - $9^0 12'$ S and $33^0 35'$ - $33^0 45'$ 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 -6^0 C in the highlands and 29^0 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) (1500–1900 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 Bélanger 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 ibeanus* (Osgood 1910)	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 ibeanus	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

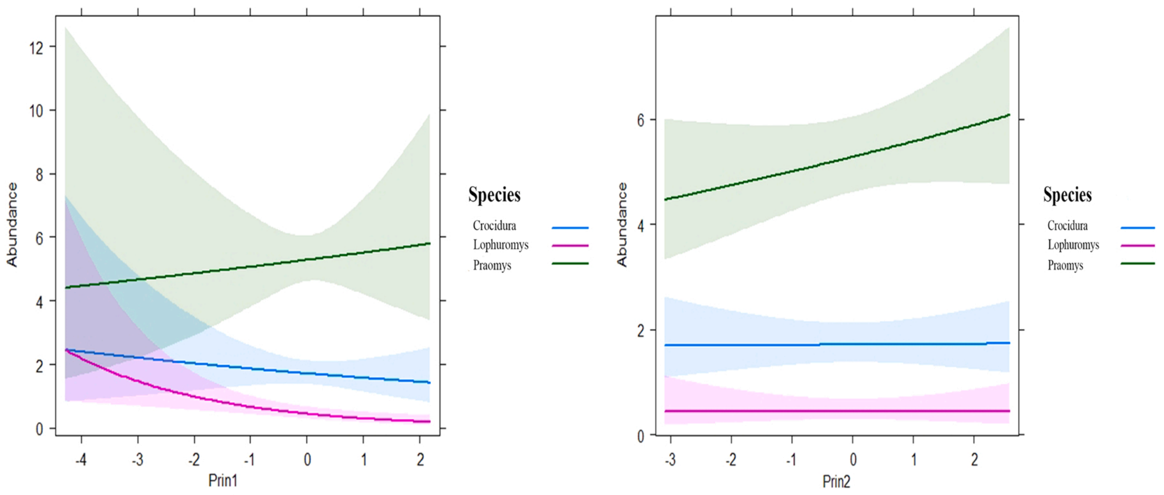
GLM results reveal that the overall (all species abundance) abundance of small mammals was not influenced by microhabitat variables along the PCA1 and PCA2 axis, but the individual (single) species abundance was influenced differently. GLM results (Fig. 2a) show microhabitat characteristics affect *P. 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



(a) (b)

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); Kamenišťák 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. ibeanus*, *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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