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Factors affecting the composition of rodent assemblages in the North Uluguru Mountains, Tanzania

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Abstract. The Uluguru Mountains, which are part of the Eastern Arc Mountains, is a hotspot for diversity and an important area for the conservation of biodiversity in Tanzania, but faces increasing disturbance due to anthropogenic activities leading to a high rate of forest degradation and fragmentation. Changes in habitat structure have caused significant changes in the faunal assemblage of the region. However, information on these effects in the Uluguru Mountains is currently lacking. We conducted a survey of the small rodent assemblage on the Uluguru Mountains in three different habitats: forest, fallow, and cultivated land along two elevation gradients: 900-1,400 and 1,500-2,000 m a.s.l. Additionally, we recorded the habitat structure for each transect by looking at grass cover, tree density and shrub density. Generalised linear mixed models were used to examine the effects of habitat structure on both species richness as well as abundance. Our results revealed that, even while species richness remained similar over the whole study area, the species composition significantly changed depending on habitat structure. This finding arose particularly from changes in the numbers of *Praomys delectorum* and *Mastomys natalensis*, with the latter more abundant in cultivated and fallow land but not in forest, where *P. delectorum* is more abundant. This outcome may indicate that an increase in forest degradation and expansion of agriculture could have an impact on rodent assemblage and potentially on their population dynamics.

Key words: habitat type, habitat structure, habitat patches, habitat disturbance

Introduction

The Uluguru Mountains of Eastern Tanzania are one of the component blocks of the Eastern Arc Mountains, which range from the Taita Hills in Southern Kenya to the Udzungwa Mountains in central Tanzania and are a hotspot for biodiversity (Stanley et al. 2005, 2011, Burges et al. 2007, Rovero et al. 2014). Due to their large degree of endemism, with at least 16 endemic vertebrate and 135 endemic plant taxa, the Uluguru Mountains are considered to be among the 10 most important tropical forests sites for conservation on the African continent (Burgess et al. 2002). Sadly, they are experiencing a high rate of forest degradation and fragmentation caused by the intensification of

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agriculture (Mugatha 2004, Fischer & Wilkinson 2005, Fischer et al. 2011, Lema & Magige 2018) and recurrent wildfires (Bracebridge 2005, Burgess et al. 2007), which can have potential detrimental effects on the biodiversity.

Habitat structures, such as vegetation type and cover have been found to have a large impact on the community structure and population dynamics of rodents (Ecke et al. 2002, Carrilho et al. 2017, Weldy et al. 2019, Chidodo et al. 2020, Ssuuna et al. 2020, Welegerima et al. 2020). This effect is mainly because vegetation type and cover determine the availability of resources which affects both the abundance and diversity of rodent species (Ecke et al. 2002, Ssuuna et al. 2020, Welegerima et al. 2020). The loss of forest habitat may, therefore, lead to changes in the population dynamics and eventually lead to the extinction of forest-specific rodent species. This outcome may cascade through the ecosystem in the case that species play key ecological roles, for example if they are keystone species in food webs, or play a role in seed dispersal (Wolff & Sherman 2007).

However, habitat disturbance does not necessarily lead to a lower species richness. For example, areas with intermediate levels of habitat degradation in the Brazilian Atlantic rainforest had a higher small mammal richness compared to conserved parts of the forest (Vera y Conde & Rocha 2006), and similar results have been found in shortgrass prairie ecosystems in Colorado (Thompson & Gese 2013) and Sudanian savannah in southwestern Senegal (Konečný et al. 2010). Notably, Caro (2001) and Konečný et al. (2010) reported that species richness and abundance were greater outside than inside national parks, which could be linked to lower population densities of certain species in parks and the effect of traditional agriculture, which may support the presence of species typical of deforested landscapes. In deforested pine plantations in Yunnan in China, small mammal richness and diversity were higher in younger than older plantations (Men et al. 2006, Yang et al. 2014). Similarly in Malaysia, small mammal communities were not clearly differentiated among forest types in (primeval forest, fallow areas and rubber plantation), except in new fallow areas where human-associated rats occurred (Nakagawa et al. 2006). These differences in species richness and diversity response patterns are likely to be the result of species-specific responses to forest vegetation-induced changes along succession gradients after disturbance, as demonstrated by several authors (Etcheverry et al. 2005, Fisher & Wilkinson 2005, Men et al. 2006, Robitaille & Linley 2006, Scott et al. 2006). Nonetheless, studies focusing on the link between forest degradation and rodent communities in tropical Africa are still scarce (see Ssuuna et al. 2020 for a rare example). Therefore, it is important to study how small rodent species richness varies among different habitat types and how habitat structure affects the abundance of specific rodent species. This information is important in the case of the Uluguru Mountains and may lead to a better targeted conservation plan.

Material and Methods

Study Area

This study was conducted in the Mlimani ward found in the Northern part of the Uluguru Mountains. The mountains are situated within Morogoro Urban, Mvomero, and Morogoro Rural Districts in Tanzania (Fig. 1). The Uluguru Mountains experience a bimodal rainfall pattern with a short and long rainy season. The average temperatures for the coolest and warmest months are 24 °C and 26.5 °C, respectively. There are three major types of landform in the North Uluguru Mountains: Steep Mountains, Piedmonts, and Peneplains. The soils are acidic lithosols and ferralisols (Lovett & Pocs 1993), that have developed from granulite, gneiss, and migmatite bedrocks (Griffiths 1993). The mountains contain at least 135 plant species, 16 vertebrate species (shrews, rodents, and birds) found nowhere else (Burgess et al. 2002). About 10% of the species are threatened and/or trade restricted according to IUCN. Most of the mountains were nationally gazetted since 1909 (IUCN 2013), but an area of about 24,115 km^2 was formally reserved as the Uluguru Nature Forest Reserve (UNFR) in 1998 (Chamshama et al. 2004). Some parts of the mountains are not formally protected and are accessible for a variety of purposes by communities living at lower altitudes. Intensive cultivation and recurrent wildfires outside of the reserved forest remove the regenerating vegetation and increase landscape heterogeneity (Frontier-Tanzania 2005, Binkley et al. 2007). Ethics permission and clearance was granted by Sokoine University's ethics board (ref. SUA/ADM/R.1/8/234).

Study Design

The study area was stratified into two altitudinal ranges of 900-1,400, and 1,500-2,000 m a.s.l.

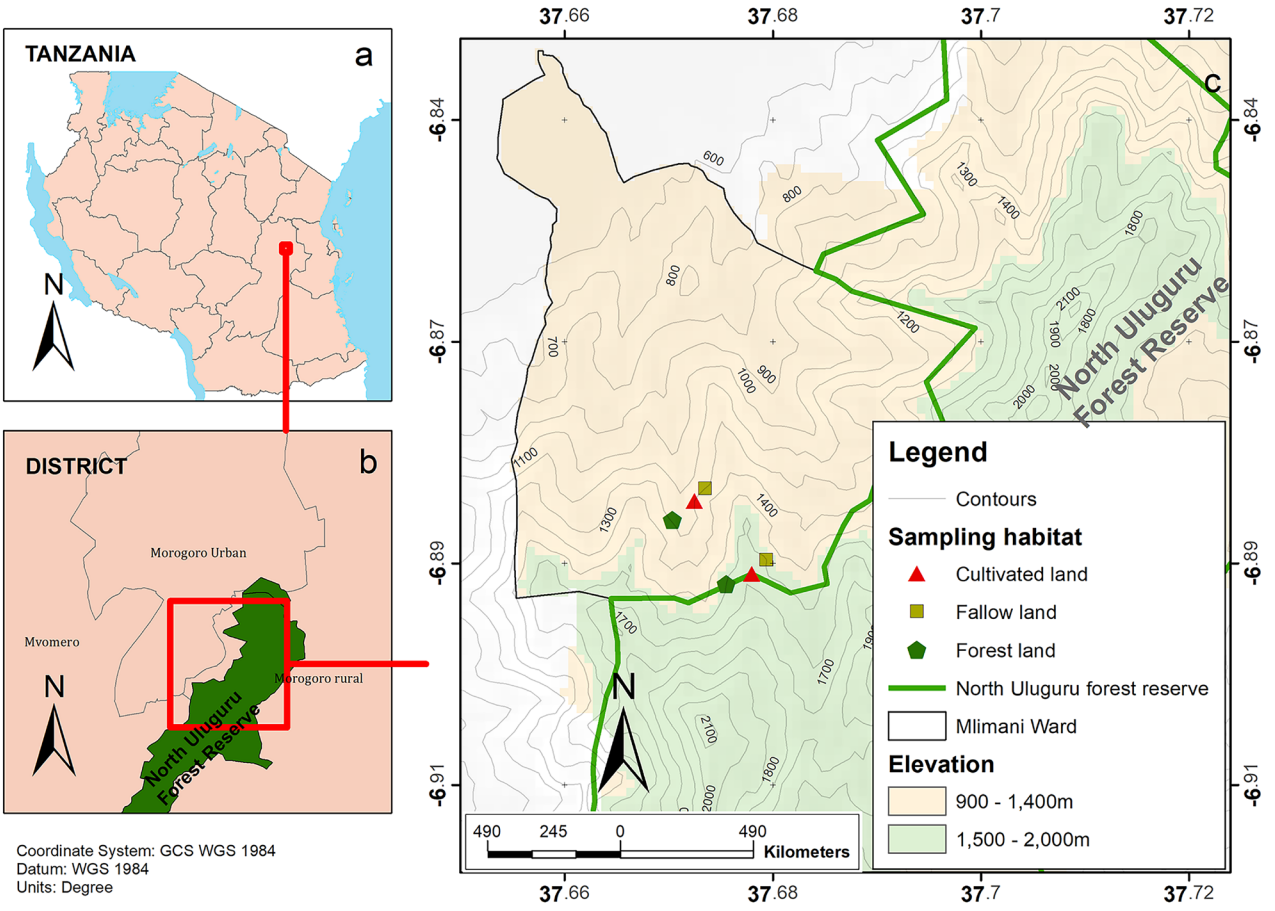

Fig. 1. Study area showing the location of habitat types in the Uluguru Mountains.

(Fig. 1). In each stratum, three potential rodent habitats were selected, namely: forest, fallow land, and cultivated land. The forest was defined as a continuous strand of trees with no evidence of farming or settlement. Fallow land was a discontinuous strand of trees with evidence of farming activities, settlement, and/or recurrent wildfire. Cultivated land was considered as land that was used for farming for at least eight months in each year. In each habitat type, five lines transect, 50 m long, were established. In each transect, nine Sherman live traps (23 × 9 × 8 cm; H.B. Sherman Traps, Inc., Tallahassee, Florida) were placed at a spacing of 10 m resulting in a total of 45 traps per habitat, with 270 traps across the whole study area.

Data Collection

Rodent trapping

Rodent assessments were conducted during the short dry season (19 October 2018 to 24 February 2019) as well as during the long rainy season (19 March 2019 to 24 June 2019). The traps were set for three consecutive nights in each habitat and a mixture of peanut butter and maize bran was used as bait. The traps were checked every morning before 9.00 a.m. All captured rodents were identified to species level, marked by toe clipping, weighed, and their sex identified visually.

Habitat structure

The line-intercept method, as recommended by Fiala et al. (2006), was used to measure the habitat structure in each trapping line transect. The density of trees and shrubs was assessed at the transect level (50 m long × 10 m wide belt around the line of traps) resulting in five transects per habitat type. In each transect, trees and shrubs with diameter > 50 mm and height > 1.5 m were counted and identified to species level while the density of herbs was assessed at a five grids of 1 × 1 m, which were randomly selected from each 50 × 10 m transect. Again, at each trapping station the understory height was measured using a measuring stick with a 300 mm disc fixed to the tip. Understory was defined as a layer that comprises shrubs, grass, and herbs that grow beneath the forest canopy. The percentage understory cover was assessed at a plot of 5 × 5 m marked at each trap station. Visual assessment was used to estimate the

percentage understory cover. The slope gradient and aspect of each habitat were measured at the start, centre, and end of transect using Suunto Hypsometer (Suunto) and Garmin GPSMAP 64s (Garmin), respectively.

Data Analysis

The main interest of this study was to examine the effects of habitat structure on rodent presence. We used the number of unique individuals that were captured during each season without taking recaptures into account. Generalized linear mixed effect models (GLMM), with a Poisson error distribution, were used to test the effect of habitat structure (grass cover, shrub density and tree density) on species richness and abundance of the different species. We placed all the habitat structure measurements in each line transect within all the six different plots (fallow, cultivated and forest on both elevation levels) independently in a principal component analysis (PCA). Some of the habitat structure variables were collinear, therefore we ran a PCA on the habitat structure measurements, taken for each line-transect within all the six fields, before we constructed the models. We used the Kaiser-Guttman criterion (eigenvalue > 1; Kaiser 1991, Peres-Neto et al. 2005) to select the number of components to retain, which resulted in two important principal components (see Results). Additionally, our explanatory analysis revealed that there were no differences in species richness or abundance between the two different seasons and we combined data for both seasons for further analysis.

Table 1. Rodent species abundance distribution across habitats.

	Habitats		
	Agriculture	Fallow	Forest
Dasymys incomtus	0	6	0
Grammomys surdaster	4	3	2
Lophuromys kilonzoi	11	12	6
Mastomys natalensis	20	10	0
Mus musculus	4	2	0
Praomys delectorum	0	0	54

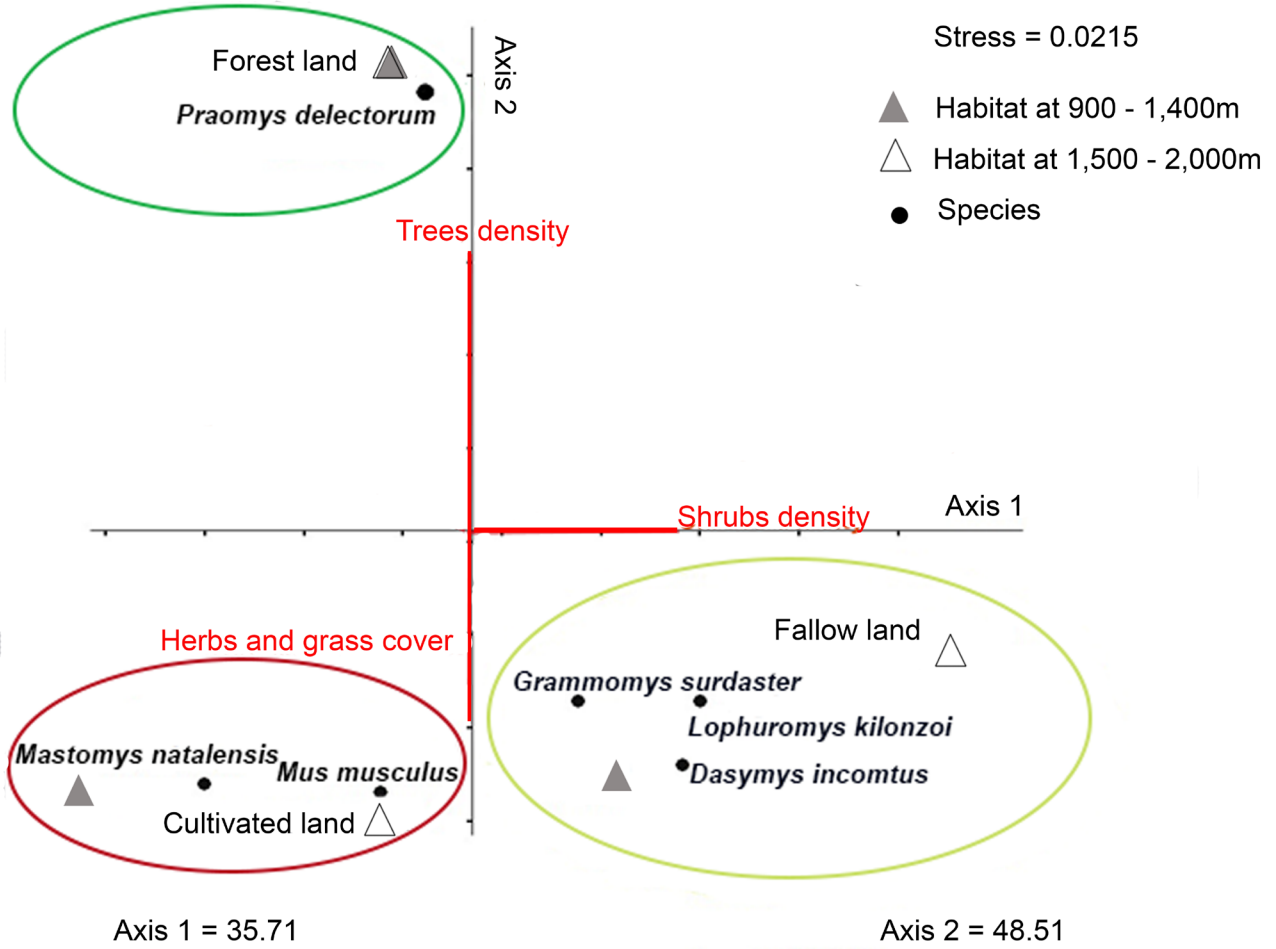

Fig. 2. Principal components analysis (PCA) biplots of rodent species and habitats in community space (first two axes). Habitats are represented by triangles and dots represent rodent species.

Species richness

A GLMM was constructed with the number of unique species trapped in each transect as response variable, with a Poisson error distribution. We included the two principal components as fixed effects, while habitat and elevation were included as random effects to account to the nested design of the study. Non-significant interaction were deleted from the final model.

Abundance

For each species we created a separate GLMM where we used the number of unique individuals that were trapped at each transect as the response variable. However, less than 10 individuals were trapped for three species throughout the whole study period, which was too low for further analysis (Table 1). Therefore, the effects of habitat structure were focused on the abundance of the three most common species: *Praomys delectorum*, *Mastomys natalensis* and *Lophuromys kilonzoi* (Table 1). Statistical analysis was performed using R version 3.6.0 (R Core Team 2013) with the R package "lmer4" (version 1.1-21; Bates et al. 2015).

Table 2. Results from principal component analysis showing the correlation of the three different habitat variables for PC1 and PC2.

Component	PC1	PC2
Grass cover	–0.711	0.073
Shrub density	–0.089	0.977
Tree density	0.698	0.199
Proportion of variance (%)	0.532	0.340
Eigenvalue	1.597	1.019

Results

Principal component on the habitat structure

PCA reduced the number of variables describing habitat structure to two principal components, explaining 87.2% of the total variance. The first component was positively correlated with tree density and negatively with grass cover (Table 2). This outcome suggests that transects with a high PC1 score predominantly comprised forest with the habitat dominated by high tree density with low levels of grass cover (Table 2), while transects with a low PC1 score were mainly cultivated and fallow areas, dominate by grasses (Fig. 2). The second principal component was positively correlated with shrub diversity, where transects with a high PC2 score had a higher shrub density compared to transects with a lower PC2 score. While elevation was not included in the PCA, inspection of the data revealed that PC2 correlated negatively with elevation, where transects with a high PC2 score were mostly at the lower end of the elevation gradient (Table 2).

Species richness

Over the entire study (810 trap-nights), we captured six different species of rodents and an overall total of 134 unique individuals. The species caught were *Praomys delectorum* (Thomas, 1910) (n = 54), *Mastomys natalensis* (Smith, 1834) (n = 30), *Lophuromys kilonzoi* (Verheyen et al., 2007) (n = 29), *Grammomys surdaster* (sensu Bryja et al. 2017) (n = 9), *Mus musculus* (Linnaeus, 1958) (n = 6), *Dasymys incomtus* (Sundevall, 1847) (n = 6) (Table 1). The GLMM revealed that species richness did not change along the PC1 axis (estimation ± SE: –0.006 ± 0.109, Z = –0.053, p = 0.958) nor the PC2 axis (–0.149 ± 0.136, Z = –1.099, p = 0.272). This finding suggests that rodent species richness did not differ between grassland areas and forest landscapes and that shrub density had no overall effect on the number of rodent species that were present in the study area.

Abundance

Rodent species abundance was significantly associated with habitat structure (Fig. 2). The ordination plot revealed three clusters of rodents, where cluster one was dominated by *P. delectorum* which increased in abundance positively with an increase in tree density (r = 0.845) and slope (r = 0.527) but negatively with an increase in herbs and grass cover (r = –0.631). Three species (i.e. *L. kilonzoi, D. incomtus*, and *G. surdaster*) co-occurred in cluster two. The abundance of these species increased with an increase in herbs and grass cover (r = 0.631) and negatively with tree density (r = –0.781). Cluster three comprised two species, *M. natalensis* and *M. musculus*, which increased with herbs/grass cover (r = 0.781) but decreased with an increase in shrubs diversity (r = –0.725). The distance between fallow and cultivated land was limited and the two habitat types shared rodent species.

Our model revealed that PC1 was a significant predictor of the abundance of *P. delectorum* (0.431 ± 0.192, Z = 2.246, p = 0.025; Fig. 3A), suggesting that this species was more abundant in forests, where the tree density was large and the amount of grasses covering the area was low. PC2 (reflecting mainly

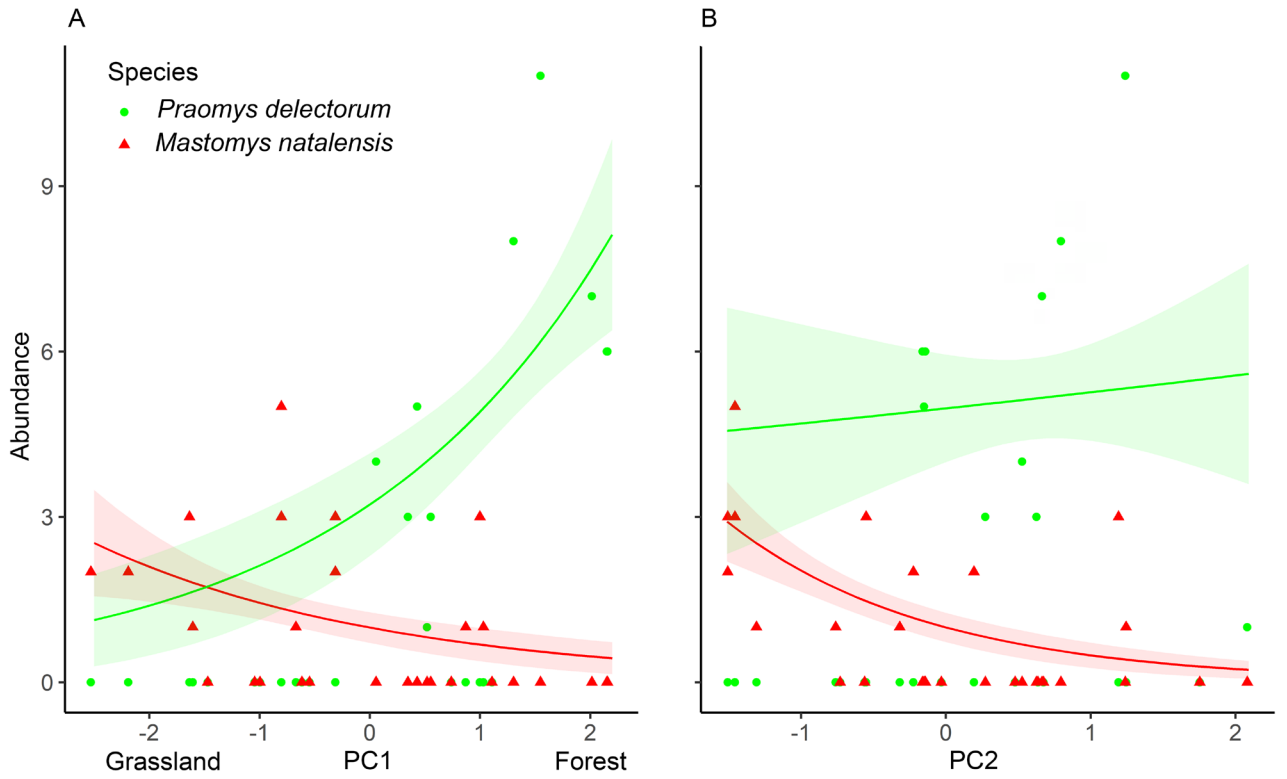

Fig. 3. The predicted effect and the standard error of the two habitat variables (PC1 and PC2) on the abundance of *Praomys delectorum* (green circles) and *Mastomys natalensis* (red triangle).

shrub density), had no effect on the abundance of *P. delectorum* (0.067 ± 0.221, Z = 0.304, p = 0.761; Fig. 3B). The model showed that PC1 was significantly negatively correlated with *M. natalensis* abundance (–0.574 ± 0.182, Z = –3.150, p = 0.002; Fig. 3A), indicating that *M. natalensis* is more abundant in grasslands compared to forests. Additionally, we found that PC2 was also significantly negatively correlated with *M. natalensis* abundance (–0.935 ± 0.227, Z = –4.112, p < 0.001; Fig. 3B) suggesting that areas with a high shrub diversity had a negative effect on the abundance of *M. natalensis*. Neither PC1 (–0.416 ± 0.331, Z = –1.257, p = 0.209) nor PC2 (–0.062 ± 0.316, Z = –0.196, p = 0.844) was significantly associated with the abundance *L. kilonzoi*, suggesting that these habitat variables had a limited effect on the abundance of *L. kilonzoi* in the study area.

Discussion

Our study demonstrated that, while variation in habitat structure did not influence rodent species richness, it did affect community assemblage and the abundance of some rodent species in the Uluguru Mountains. The results further suggested that *M. natalensis* replaces *P. delectorum* in human-altered habitats. We showed that habitat structure (trees density, grass cover and shrubs density) may affect rodent assemblage, potentially playing a role in shaping the presence and abundance of both *M. natalensis* and *P. delectorum* in the Uluguru Mountains. Notably, *P. delectorum* occurred more frequently in areas with a high tree density and a limited grass cover, which are typical of montane forests (Bryja et al. 2014). These areas were not preferred by *M. natalensis*, which instead was found more frequently in locations dominated by grasses that characterise fallow and agricultural land (Lyamuya 2017). Taken together, these findings suggest that *P. delectorum* and *M. natalensis* prefer different habitat types, with *P. delectorum* a primarily forest dweller whereas *M. natalensis* is mostly associated with agricultural fields in the Uluguru Mountains. These findings correspond with previous work in other montane areas in Tanzania. For instance, 85% *P. delectorum* captured on the Kilimanjaro Mountain were trapped in forest areas, while about 75% of *M. natalensis* was captured in agriculture lands (Mulungu et al. 2008). Similar results were obtained from the Usambara Mountain, Tanzania, were *P. delectorum* was more abundant in forest habitat compared to *M. natalensis*, which was captured more frequently in cultivated fields (Hieronimo et al. 2014, Ralaizafisoloarivony et al. 2014).

In the only other survey of small mammals in Uluguru, Stanley et al. (1998) found relatively high numbers of *Hylomyscus arcimontensis*, a species that we did not capture in the current study. This discrepancy could be due to the fact that this species is specialised to pristine montane forests above 2,000 m, i.e. the habitat that we did not sample in the current study.

The influence of tree density on *P. delectorum* might be linked to the microclimate (cool and humid) while grass cover provides *M. natalensis* with adequate food items, nesting sites and protection from predators (Kingdon 2003, Wolff & Sherman 2007). This finding indicates that the association may be mainly determined by species-specific preferences and food availability, suggesting that rodent species diversity may be driven by habitat heterogeneity/diversity in this region (Tews et al. 2004). Our results also imply that some rodent species prefer dense shrub habitat, which may provide protection from predators and access to nesting sites (Wolff & Sherman 2007), with flexibility in diet facilitating adaptation to this habitat (Bantihun & Bekele 2015).

We additionally showed an association between shrub density and the abundance of *M. natalensis*, though not in *P. delectorum*. This habitat structure was also found to correlate with elevation, where areas with a low shrub density tended to occur at higher elevations. This result indicates that *M. natalensis* is also abundant on agricultural land at higher elevations on the Uluguru Mountains. It is at these higher elevations that forest degradation is becoming more problematic. A prediction of this finding is that when forest areas are replaced by agricultural landscapes, *M. natalensis* may readily enter these new human-altered habitats, especially at high elevations, while *P. delectorum* will tend to disappear (Makundi et al. 2003). This outcome will have a negative impact on the biodiversity of the Uluguru Mountains as well as a deleterious effect on farmers, since *M. natalensis* is a notorious pest species with the potential to cause pre- and post-harvest damage (Mulungu 2017).

Strikingly, habitat structure did not predict the abundance of *L. kilonzoi*. This species occurs abundantly in fallow land with high shrub density, which is an intermediate habitat type between forest and agricultural land. These results suggest that *L. kilonzoi* may be as a habitat generalist species that can adapt relatively easily to a range of habitat types (Ssuuna et al. 2020).

Conclusion

A primary conclusion of this study if that the structure of rodent species assemblages in the Uluguru Mountains varied among habitat types. Alteration of the environment for human use has seemingly resulted in significant changes in the rodent species assemblages in those environments. *Praomys delectorum* was restricted to forest habitats, whereas *Mastomys natalensis* was abundant in cultivated land, suggesting that *M. natalensis* may have the capacity to replace *P. delectorum* in human-altered habitats. The current study indicated that rodent species assemblages are influenced by habitat structure. Therefore, an increase in forest degradation and expansion of agriculture is predicted to have an impact on rodent assemblage and potentially on their population dynamics.

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