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Abstract. A study was conducted in Mabira Central Forest Reserve in Uganda to determine rodent species composition, relative abundance, and habitat association. A total of 1,030 rodents belonging to 14 species were captured on 10,584 trap nights. Rodent species recorded include: *Lophuromys stanleyi, Hylomyscus stella, Praomys jacksoni, Mastomys natalensis, Lophuromys ansorgei, Lemniscomys striatus, Aethomys hindei, Mus triton, Mus minutoides, Deomys ferrugineus, Gerbilliscus kempi, Rattus rattus, Grammomys kuru,* and *Hybomys univittatus.* Overall, *L. stanleyi* (23.7%) was the most dominant species followed by *H. stella, P. jacksoni,* and *M. natalensis.* Species richness and evenness was highest in the regenerating forest habitat and least in the intact forest habitat. Rodent abundance was significantly affected by habitat type. The regenerating forest habitat had the highest number of animals, while the lowest numbers were observed in the depleted forest habitat. Species diversity was higher in regenerating forest habitat and lowest in the intact forest. The three habitats appeared distinct in terms of rodent species composition and there was a strong association between the two trapping grids in the same habitat type. All ordination plots showed that different rodent species consistently associated with distinct habitats. Habitat type and seasonal changes influenced rodent composition, relative abundance and habitat association. Composition of rodent community reflected the level of habitat degradation and can be used as a proxy for evaluating the biodiversity of lowland tropical forests.

Key words: African ecology, small mammal community, lowland tropical forest, Rodentia

Introduction

The government of Uganda has shown commitment to conserve its forest resources through investment in a variety of initiatives, including gazetting national tree planting days, and creation of the National Forestry Authority (NFA). However, a trend of tree loss has worsened due to continued

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forest encroachment through conversion of forest to other land uses, such as agriculture, urbanization, timber cutting, charcoal burning, and livestock grazing. Overall, the forest estate in Uganda has been reduced by 3.05 million ha in a span of 25 years (Ministry of Water and Environment 2016). Continued forest encroachment leads to habitat disturbance, which often results in alterations in the community structure of small mammals. At the same time, species coexistence has been shown to be maximized at an intermediate level of disturbance (Byrom et al. 2015). Forests that experience an intermediate level of disturbance tend to show higher species richness and diversity, as compared to those exposed to a high level of disturbance. Disturbance can be considered as events that promote alterations in system structure, reduce species competition, and change resource availability, though certain tolerant species can persist even in highly disturbed areas (Vera & Rocha 2006).

Forests are key habitats for many native fauna species (Ministry of Water and Environment 2016), including rodents. Frequent logging, agricultural cultivation in and around the forest, and animal rearing can disrupt the entire ecosystem, with some species becoming rare, while others become locally extinct. Environmental variation can drive changes in rodent population dynamics, thereby facilitating the coexistence of competing species (Adler & Drake 2008). These impacts can also lead to both temporal and spatial changes (Ruokolainen et al. 2009), which can affect species rates of increase, both directly or indirectly, mediated through species interactions.

Many Ugandan forests are under pressure due to human activities (Kayanja & Byarugaba 2001, Obua et al. 2010, Ministry of Water and Environment 2017). This impact has led to a worrying scenario of a reduction in forest estate from 24% of the total land area in 1990 to 9% in 2015 (Ministry of Water and Environment 2016), which impacts on forest ecosystems, and the population dynamics of small mammals (Getachew & Afework 2015). Records further indicate that the forest estate outside protected areas declined from 68% of the total forest land area in 1990 to 61% in 2005, and down to 38% in 2015. Over the same period, protected forests lost 46% of protected woodlands (Ministry of Water and Environment 2016).

Mabira Central Forest Reserve (MCFR) is a protected Tropical High Forest (THF) supporting a high diversity of biota including rodents. Due to continued anthropogenic activities in the forest, there are two main vegetation types; young and colonizing forest (27%), and mature mixed forest (52%). Large sections of Mabira forest patches: Mabira, Nandagi, Namananga, Namakupa, Namawanyi and Kalagala falls have experienced a trend of increased levels of human incursions (Ministry of Water and Environment 2017). The forest cover change index illustrates the disappearance of numerous small forest islands in the areas to the East, North, and North-East of the reserve and from the river valleys of the North (Mitchell 2010).

Habitat structure influences the structure of small mammal communities in tropical forests (Tews et al. 2004, Guerta & Cintra 2014). Furthermore, habitat structure and seasonal changes significantly affect small mammal abundance and habitat preferences (Getachew & Afework 2015). Despite continued forest destruction in Uganda, few studies have directly examined the effects of disturbance on small mammal communities. Sollmann et al. (2015) found forest structure to influence total abundance of species and abundance of some individual species. Some of the major disturbances in Afro-tropical forest ecosystems are human mediated (Obua et al. 2010). They decrease the extent of canopy cover, with a reciprocal change in understory vegetation, which has been reported to enhance small mammal diversity in tropical forests (Cusack, unpublihed data).

Most research on small mammals in Uganda has been conducted either in mountainous regions of the Albertine Rift or on agricultural land (Delany 1975, Thorn & Kerbis Peterhans 2009, Mayamba et al. 2019, 2020). A number of other surveys on mammalian diversity in Uganda forest reserves have been previously conducted, including Davenport et al. (1996a) who reported on small mammals in Ugandan forests, as well as Basuta & Kasenene (1987), and Lunde & Sarmiento (2002). However, in all these studies, the focus has rarely been on the community structure of rodents in Ugandan forested areas that experience anthropogenic impacts.

Documenting the differences and similarities in the number of species among different habitats will provide insight into the structural composition of natural communities. Observed patterns may improve understanding of ecological

processes and guide future research aimed at managing species diversity (Shukor et al. 2001). Assessment of the conservation status of any fauna requires knowledge of its diversity, endemism, distribution, biology and habitat requirements, as well as information on threats faced. Vegetation structure and anthropogenic stressors can impact the diversity, distribution, and resilience of a small mammal community (Venance 2009, Byrom et al. 2015). Notably, a study by Linzey et al. (2012) showed that populations in undisturbed habitats were self-regulating, while those in disturbed habitats were not. Forests with an intermediate level of disturbance show higher values for species richness and diversity, as compared to those exposed to a high disturbance level. Disturbances can be considered as events that promote alterations in systems structures, reduce species competition, and change resource availability (Vera & Rocha 2006, Hall & Miller 2012). A study by Getachew & Afework (2015) on the diversity and habitat association of small mammals in the Aridtsy forest in Ethiopia concluded that habitat structure and season

significantly affect small mammal abundance and habitat preferences.

Despite the recent changes in forest cover and land use in Uganda, little is known about the current status of rodents in previously forested areas, heavily degraded forests and lightly degraded forest regions. The aim of this study was to determine the rodent species composition, relative abundance, and habitat association in the MCFR, in relation to habitat disturbance.

Material and Methods

Study site
The study was conducted in MCFR (31,293 ha), specifically in the Namananga, Namawanyi, and Mabira-Wakisi sections (Fig. 1) from September 2018 to August 2019. The extent of forest cover change in these sections is evident and well documented. MCFR is one of Uganda's largest surviving forests (Davenport et al. 1996b) and the only tract of forest of its kind remaining in the central region of the country. It is located
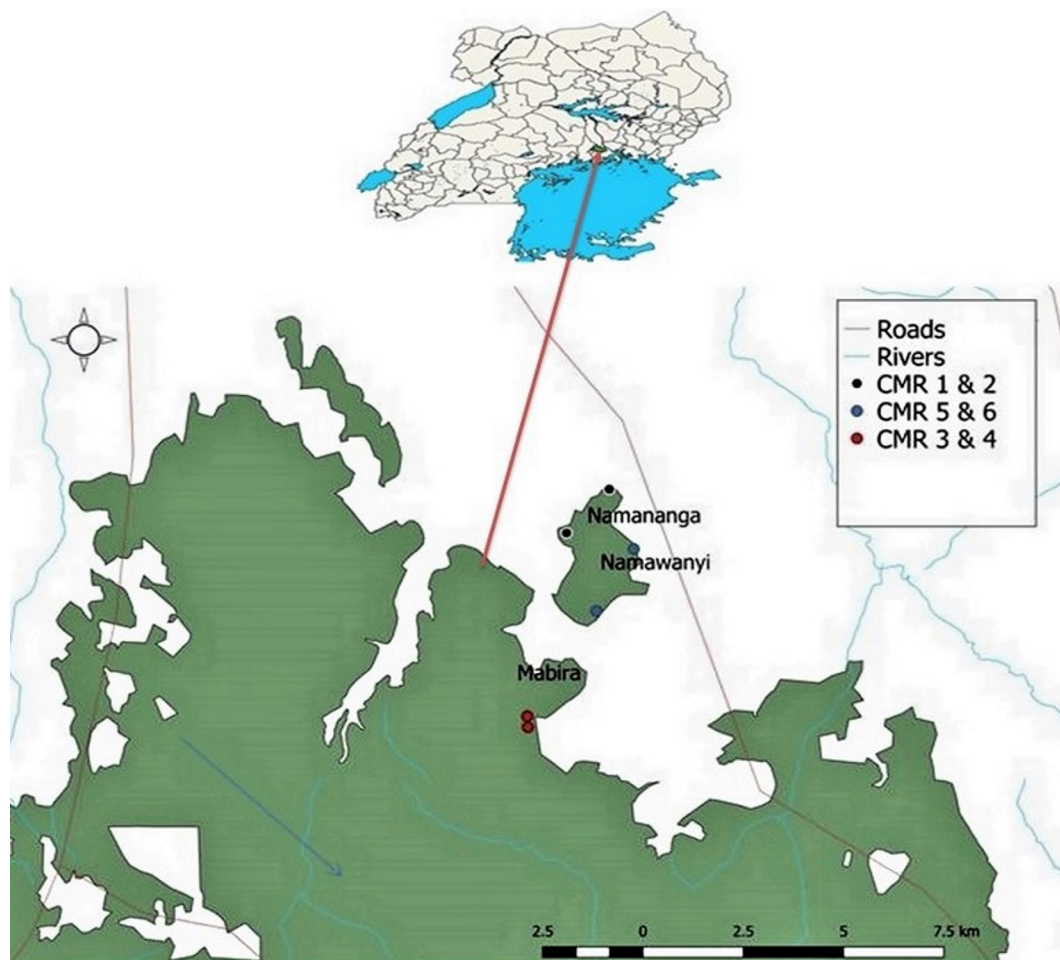
Fig. 1. Map showing location of the study sites: Namananga, Namawanyi, and Mabira-Wakisi sections of Mabira Central Forest Reserve (MCFR).

Table 1. Rodent species captured during the study period in the regenerating, intact, and depleted forest habitats of Mabira Central Forest Reserve (MCFR), Central Uganda, from 2018-2019.

Species	Number of rodents in IF (%)	Number of rodents in RF (%)	Number of rodents in DF (%)	Overall number (%)
Aethomys hindei (Thomas, 1902)[1]	0	34 (7.3)	26 (10.7)	60 (5.8)
Deomys ferrugineus Thomas, 1888	11 (3.4)	0	0	11 (1.1)
Grammomys kuru (Thomas & Wroughton, 1907)[2]	0	1 (0.2)	0	1 (0.1)
Hybomys univittatus (Peters, 1876)	1 (0.3)	0	0	1 (0.1)
Hylomyscus stella (Thomas, 1911)	171 (53.1)	3 (0.6)	1 (0.4)	175 (17.0)
Lophuromys stanleyi Verheyen, et al. 2007[3]	14 (4.3)	158 (33.9)	72 (29.8)	244 (23.7)
Lophuromys ansorgei de Winton, 1896[4]	0	32 (6.9)	71 (29.3)	103 (10.0)
Lemniscomys striatus (Linnaeus, 1758)	0	38 (8.2)	57 (23.6)	95 (9.2)
Mastomys natalensis (Smith, 1834)	2 (0.6)	120 (25.8)	9 (3.7)	131 (12.7)
Mus minutoides Smith, 1834[5]	4 (1.2)	31(6.7)	0	35 (3.4)
Mus triton (Thomas, 1909)	0	11 (2.4)	3 (1.2)	14 (1.4)
Praomys jacksoni (de Winton, 1897)[6]	119 (37.0)	28 (6.0)	2 (0.8)	149 (14.5)
Rattus rattus (Linnaeus, 1758)	0	2 (0.4)	1 (0.4)	3 (0.3)
Gerbilliscus kempii (Wroughton, 1906)	0	8 (1.7)	0	8 (0.8)
Total Captured	322 (100)	466 (100)	242 (100)	1030 (100)
Total trap nights	3528	3528	3528	10584
Evenness_e^H/S	0.41	0.54	0.53	
Species richness	7	12	9	14
SDI	0.58	0.79	0.76	

IF: intact forest, RF: regenerating forest, DF: depleted forest, SDI: Simpson's Diversity Index.

[1] It may also represent *Aethomys kaiseri*. The identification is based on the known distribution of both species in Monadjem et al. (2015).

[2] Based on Bryja et al. (2017), it was the only species of *Grammomys* in the ecologically similar Minziro forest in Tanzania.

[3] It was the only species of the *Lophuromys flavopunctatus* (= *aquillus*) species complex in the Minziro forest (Sabuni et al. 2018). It is also known from the Ruwenzori Mountains and it may be the most common Ugandan species from this group. Alternatively, it might represent *L. margarettae*, known from the Kakamega forest in Kenya (J. Bryja et al., unpublished data), but the two species are most readily distinguished using genetic data.

[4] Based on the distribution in Monadjem et al. (2015). It is the only species from the *Lophuromys sikapusi* complex occurring in the lowland Kakamega forest in Kenya.

[5] It may also represent *M.* cf. *gratus* (sensu Bryja et al. 2014), which was confirmed in both Minziro and Kakamega forests (J. Bryja et al., unpublished data), but the two species are distinguishable mainly using genetic data.

[6] Some specimens may represent *Praomys misonnei*. However, all individuals examined had nine (9) palatal ridges, typical for *Praomys jacksoni*, which is an abundant species in both the Minziro and Kakamega forests (Mizerovská et al. 2019, J. Bryja et al., unpublished data).

between 0°24'-0°35' N, and 32°52'-33°07' E, 54 km from Kampala city, traversing Mukono, Buikwe, and Kayunga districts (Ministry of Water and Environment 2017). The forest lies between 1,070 and 1,340 m a.s.l., and receives two peaks in rainfall from March to May and September to November, with a mean annual rainfall of 1,200 to 1,500 mm, and average temperatures of 26°C (Fungo et al. 2013). Namananga forest reserve is located close to Kangulumira trading centre (Fig. 1), with one part of the reserve in a swamp dominated by *Learsia hexandra* and the forested expanse dominated by *Brousonetia papyrifera*. Small cultivated fields and areas of human settlement fringe the reserve. The reserve undergoes natural regeneration as well as tree planting, with average tree height less than 15 m. Namawanyi forest reserve is also located close to Kangulumira trading centre (Fig. 1), and is dominated by *Brosonetia papyrifera* with few indigenous trees and is fringed by cultivated fields. This reserve has high levels of disturbance, with many sections completely depleted and transforming into bush/grassland, and experiencing seasonal bush burning. The
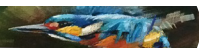
Fig. 2. Namawanyi fields: depleted forest/bushed grassland.

Fig. 3. Namananga fields: regenerating forest.

Wakisi forest section of the reserve represents an intact section and is part of the Mabira forest main block with relatively limited levels of disturbance.

Sampling design

Three habitats, spaced at a distance of at least 3 km were selected subjectively from MCFR. Habitat A is the regenerating forest (Namananga section) with abandoned patches of cabbage and pawpaw gardens (Fig. 3), habitat B is the intact/undisturbed forest (Mabira-Wakisi section) without or very limited disturbance (Fig. 4), habitat C (Fig. 2) is bush-grassland/bush-fallow/abandoned agricultural fields (Namawanyi section): formerly a forest but now reduced due to agricultural activities, and affected by burning, especially in February and March.

Trapping procedure

A Capture-Mark-Recapture (CMR) exercise was conducted on a monthly basis from September 2018 to August 2019. A total of 49 Sherman live traps (H.B. Sherman Traps, Inc., Tallahassee, FL, USA) were set in each of the six (6) grids of the size of 60 × 60 m, each containing seven parallel lines spaced 10 m apart, with 10 m between traps, each parallel line having seven trapping stations. The trapping stations were marked using labelled bamboo poles (2 m long) for easy identification, and were identified using coordinates labelled A to G, and numbered 1 to 7. Two grids with at least 500 m between them were laid in each of the three study sites. Animal trapping was conducted following the procedure by Aplin et al. (2003), with traps baited with a mixture of ghee, peanut butter, ripe bananas, and maize grains. They
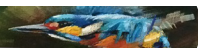
Fig. 4. Mabira-Wakisi fields: intact forest.

were set for three consecutive nights on a monthly basis. All trap stations were inspected early in the morning on each day of trapping.

Data collection and analysis
Captured animals were gently removed from traps into a cloth bag, and weighed using a Pesola balance. Species identification was based on morphometric measurements and recent distributional data based on Stanley & Foley (2008), Happold et al. (2013), Bryja et al. (2014, 2017), Monadjem et al. (2015), Sabuni et al. (2018), and Mizerovská et al. (2019). For more details see notes in Table 1. In cases where species identification was not confirmed by DNA analysis, we believe that species identification was unambiguous and with high reliability and that subsequent analyses of community diversity and structure were not significantly affected by occasional incorrect species identification.

Each individual animal captured was uniquely toe clipped using sterilized scissors and released at the point of capture. All specimens (clipped toes) were labelled, preserved in absolute alcohol for future reference, and deposited at the Zoology Department, Makerere University. For each captured animal, observations recorded included: grid location and grid number, trapping station, date, toe clipping code, species, sex, and body weight.

The rodent community structure was described as relative composition based on the trappable rodent species at the study sites. Species composition was analysed using StataIC12 software and presented

as percentage based on the relative abundance of each species over the study period. The number of animals captured in each site were counted and trap success was calculated on the basis of the total number of rodents trapped divided by the product of the number of traps used and number of trapping nights (Ralaizafisoloarivony et al. 2014), that is,

$$\text{Trap success} = \frac{N}{N_t \times N_n} \times 100$$

where N = total number of rodents trapped, N_t = number of traps used and N_n = total trap nights. Mean monthly abundance across the three habitats was calculated, while the species richness across the three habitats was analysed using rarefaction curves. In order to meet assumptions of normality and homogeneity of variance (Wilcoxon 1945), normality checks were performed using the Shapiro-Wilk W test, and the monthly differences in rodent species abundance across the three habitats were tested using analysis of variance (One-way ANOVA) in stataIC12.

Using both R-studio and PAST Statistics software, diversity measures: species richness, Simpson Diversity Index (SDI), evenness, and dominance were estimated. Richness was defined as the number of species in each of the three habitats, and diversity estimates of rodent species were based on the SDI since it comprises both species richness and evenness and gives greater weight to dominant species in a sample. The SDI was computed using the formula:

$$D = 1 - \frac{\sum n\,(n-1)}{N\,(N-1)}$$

where n is the number of individuals of different species, N is total number of individuals of all the species.

Renyi diversity profiles were plotted using PAST software to obtain a visual perspective of rodent diversity differences in the three habitats under study. An area is considered more diverse than the other if all its Renyi diversities range maximally. One-way ANOVA with Fisher LSD was performed in order to compare the effects of habitat type and seasonal changes on the total monthly rodent abundance.

PAST was used to analyse rodent habitat association. The Bray-Curtis similarity index and Correspondence Analysis (CA) (Chahouki & Zare 2012), were used to analyse rodent habitat association at both habitat and grid level. When conducting the CA, rare species were excluded.

Ethical clearance
This study was approved by Sokoine University of agriculture: ref. no: PFC/D/2017/0009, Uganda Wildlife Authority (UWA): ref. no: UWA/COD/96/05, National Forest Authority (NFA): ref. no: NFA/N/2.1/18, license no: 292, and Uganda National Council for Science and Technology (UNCST): ref. no: NS73ES.

Results

Species composition and relative abundance
A total of 1,030 rodent captures were made in 10,584 trap nights (9.7% trap success). Out of the number of rodents captured, 322, 466, and 242 rodent individuals were trapped in the intact, regenerating, and depleted forest habitats, respectively. These comprised 14 rodent species (Table 1).

Overall, *Lophuromys stanleyi* was the most abundant rodent species, with 244 (23.7%) individuals and 158 (33.9%), 14 (4.3%), and 72 (29.8%) individuals in the regenerating, intact, and depleted forest habitats, respectively. This was followed by *Hylomyscus stella* (175 inds., 17.0%), *Praomys jacksoni* (149 inds., 14.5%), and *Mastomys natalensis* (131 inds., 12.7%). The least frequently captured species over the entire period of study were *Gerbilliscus kempi* (8 inds., 0.8%), *Rattus rattus* (3 inds., 0.3%), *Grammomys kuru* (1 ind., 0.1%), and *Hybomys univittatus* (1 ind., 0.1%) (Table 1). *L. stanleyi* was the most dominant in the regenerating forest, followed by *M. natalensis*, and *Aethomys hindei*. *H. stella* dominated the intact forest habitat, followed by *P. jacksoni* and *Deomys ferrugineus*, while *L. stanleyi* was also dominant in the depleted forest habitat, followed by *Lophuromys ansorgei*, and *Lemniscomys striatus*, respectively. Two species of the genus *Mus* were mainly captured in the regenerating forest with greater numbers of *Mus minutoides* (31 inds., 6.7%), as compared to *Mus triton* (11 inds., 2.4%). Species richness and evenness was highest in the regenerating forest habitat, followed by the depleted forest habitats, and the intact forest habitat, respectively (Table 1).

Rarefaction curves for the study habitats showed the curves for the regenerating, and intact forest approached the asymptote, while that of the depleted forest habitat was still increasing. Furthermore, the regenerating forest habitat had the highest number of species, followed by the depleted and intact forest, respectively (Fig. 5).

**Table 2.** Analysis of variance (total abundance).

Source	Degrees of freedom	Sum of squares	Mean squares	F	Pr > F
Model	3	3819.33	1273.11	26.33	< 0.001
Error	32	1547.56	48.36		
Corrected Total	35	5366.89			
Computed against model Y = Mean (Y), R^2 = 0.712, Akaike´s AIC = 143.39					

Table 3. Bray-Curtis similarities in rodent composition among the trapping habitats and species communities in the study.

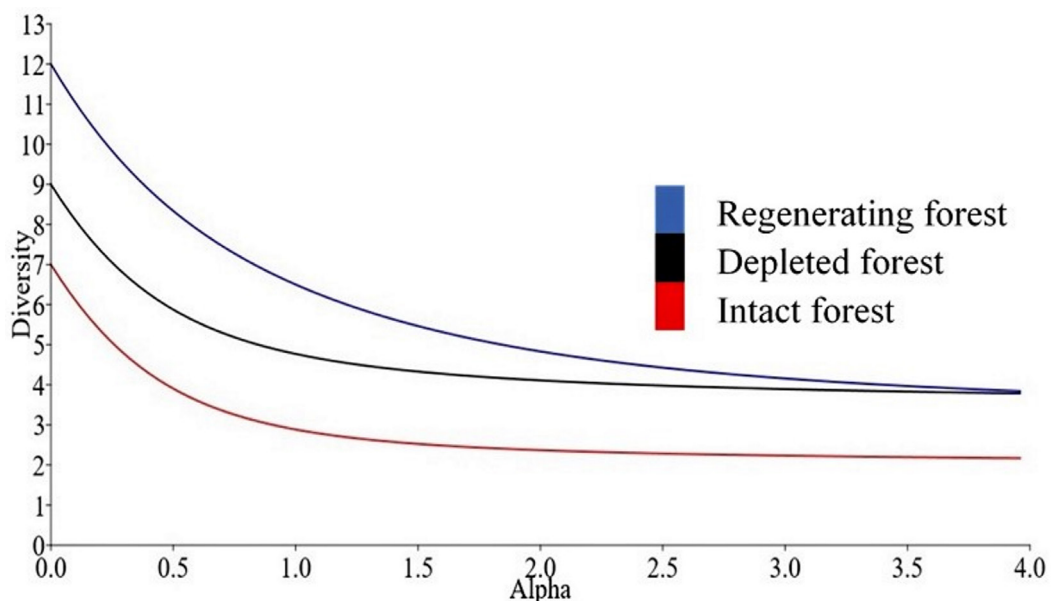| Habitat	Regenerating habitat	Intact habitat	Depleted habitat
Regenerating habitat	1	0.13	0.53
Intact habitat	0.13	1	0.07
Depleted habitat	0.53	0.07	1
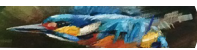
Table 4. Bray-Curtis similarities in rodent composition among the trapping grids and species communities in the study.

Grid	CMR1	CMR2	CMR3	CMR4	CMR5	CMR6
CMR1	1.00	0.61	0.11	0.19	0.45	0.48
CMR2	0.61	1.00	0.08	0.15	0.41	0.51
CMR3	0.11	0.08	1.00	0.83	0.05	0.02
CMR4	0.19	0.15	0.83	1.00	0.13	0.09
CMR5	0.45	0.41	0.04	0.13	1.00	0.65
CMR6	0.48	0.51	0.02	0.09	0.65	1.00
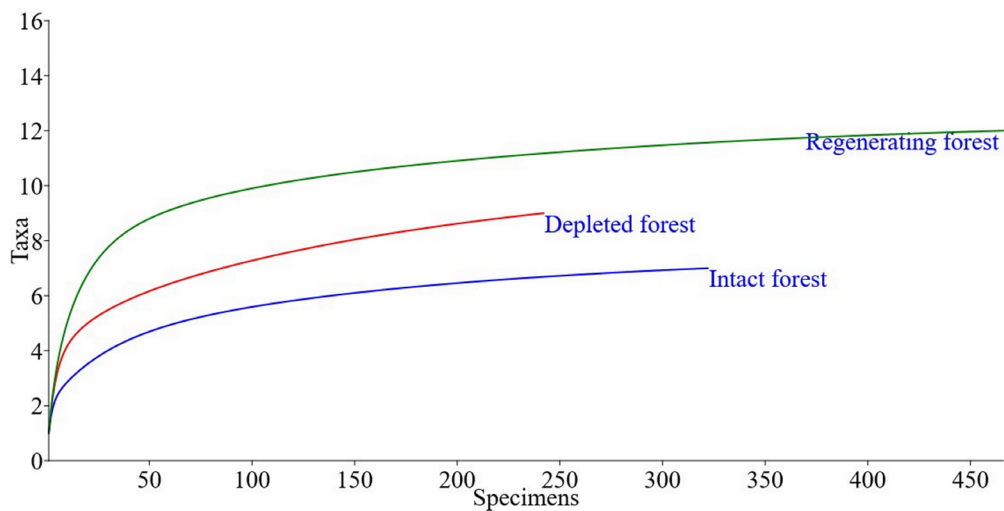
Fig. 5. Rarefaction curves for the three study habitats in Mabira Central Forest Reserve (MCFR).

Fig. 6. Renyi diversity profiles for the three study habitats in Mabira Central Forest Reserve (MCFR).

Both the Renyi diversity profiles (Fig. 6) and the SDI (Table 1) indicated that species diversity was highest in the regenerating forest habitats (D = 0.79), followed by depleted forest habitats (D = 0.76) and were lowest in the intact forest habitats (D = 0.58).
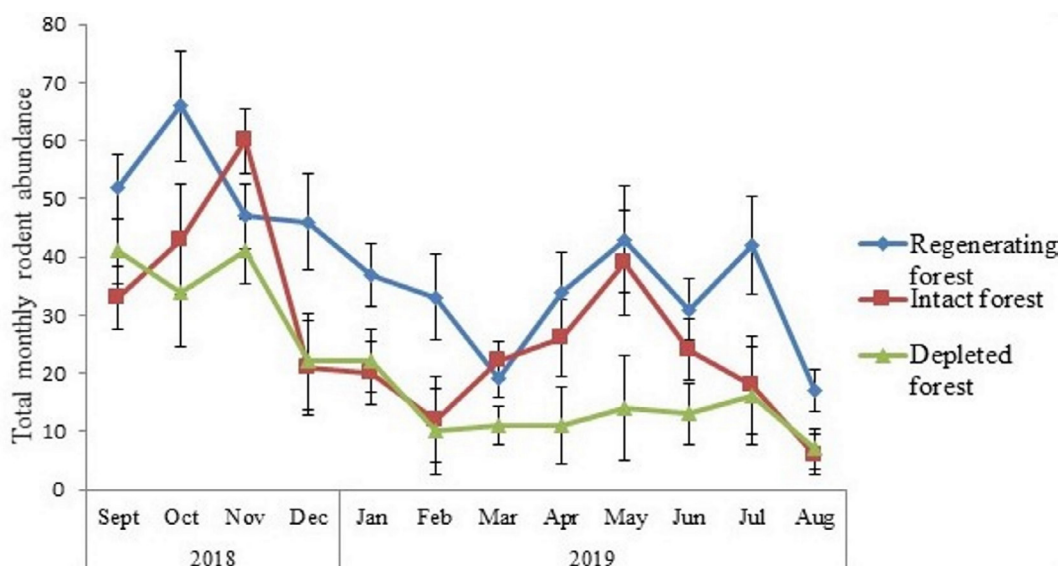
Fig. 7. Mean (±SE) monthly rodent abundance across the three habitats over the study period.
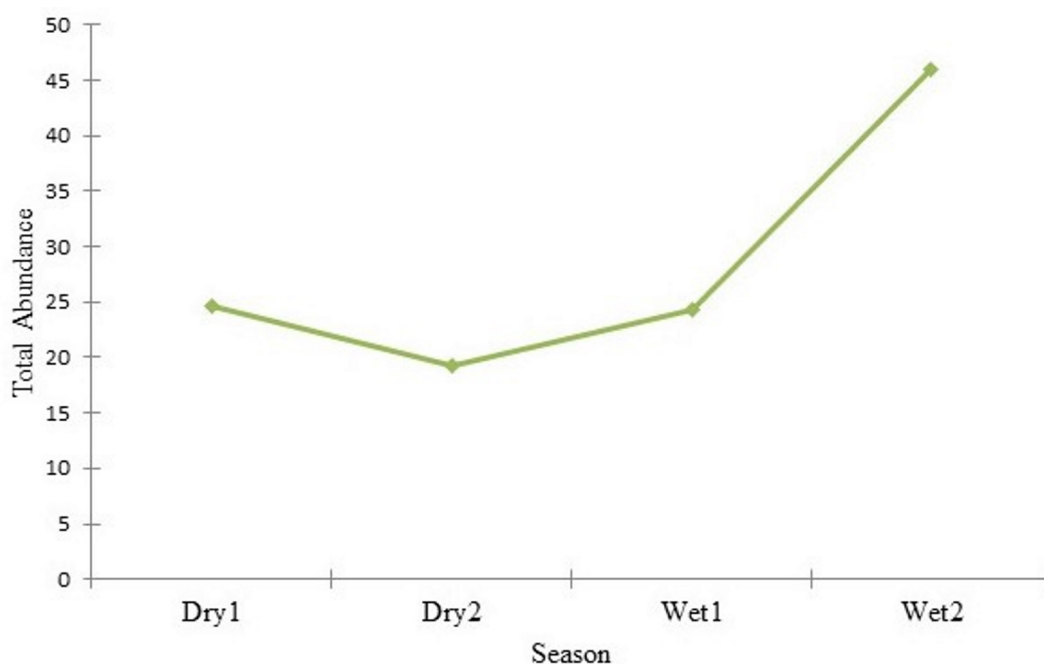

Fig. 8. Graph showing the mean rodent abundance based on season.

Overall, abundance was higher in 2018 as compared to 2019, and the average monthly abundance was 29 ± 6/0.5 ha animals captured. A relatively higher abundance was recorded in the months of September 42 ± 6/0.5 ha, October 48 ± 10/0.5 ha and November 49 ± 6/0.5 h) in 2018, and in May 32 ± 9/0.5 ha and July 25 ± 8/0.5 ha in 2019 (Fig. 7).

Effect of seasonal changes on rodent abundance
Changes in seasons explained about 71.2% of the variation in rodent total abundance (Table 2). There was a significant difference in rodent abundance based on season ($F_{(3,35)}$ = 26.33, $p < 0.001$) whereby wet season 2 (Mean = 46 ± 2.32) had a higher number of rodents compared to other seasons (mean wet season 1 = 24.33 ± 2.32; dry 1 = 24.67 ± 2.32; and dry 2 = 19.22 ± 2.32). As the wet season progressed, total rodent abundance significantly increased (Fig. 8). All rodent species were most abundant during the wet season, and least abundant during the dry season.

Rodent habitat association
Overall, more rodents were captured in the regenerating forest habitat 466 (45.2%) compared to the other habitat types; intact forest: 322 (31.3%) and depleted forest: 242 (23.5%) habitats. There was a significant difference in the distribution of rodents across the different habitats (χ^2 (26) = 1000.00, $p < 0.001$), and seasons (χ^2 (39) = 134.77, $p < 0.001$).
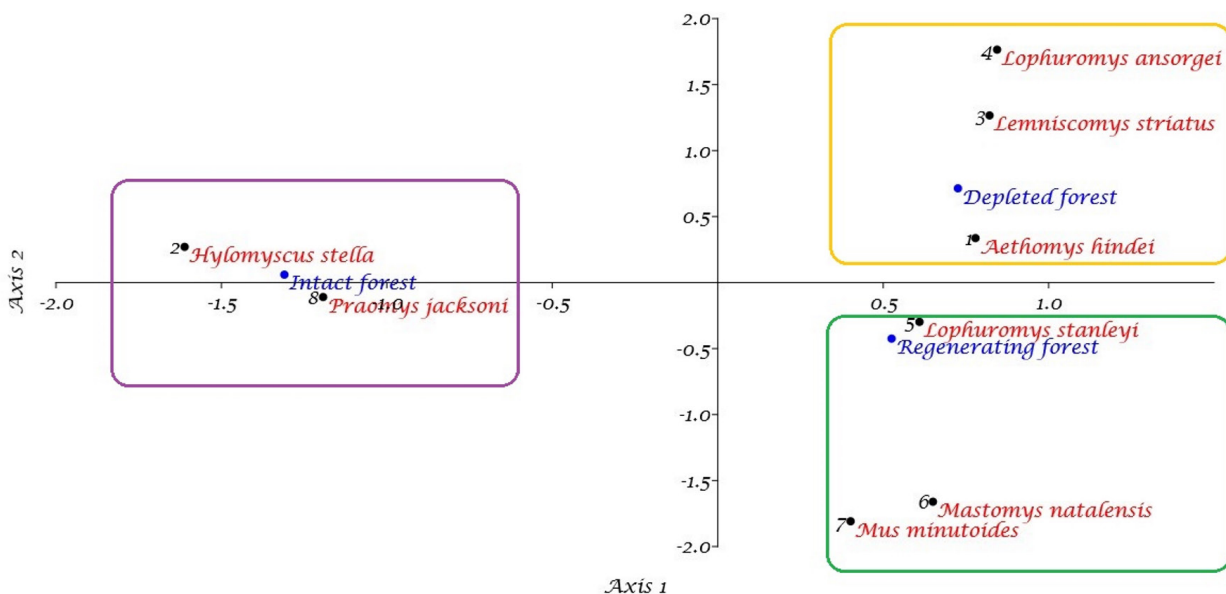
Fig. 9. Ordination plots showing rodent species associated with different habitat types. Axis 1 and 2 explained 79.4% and 20.6% of variation in rodent association, respectively.
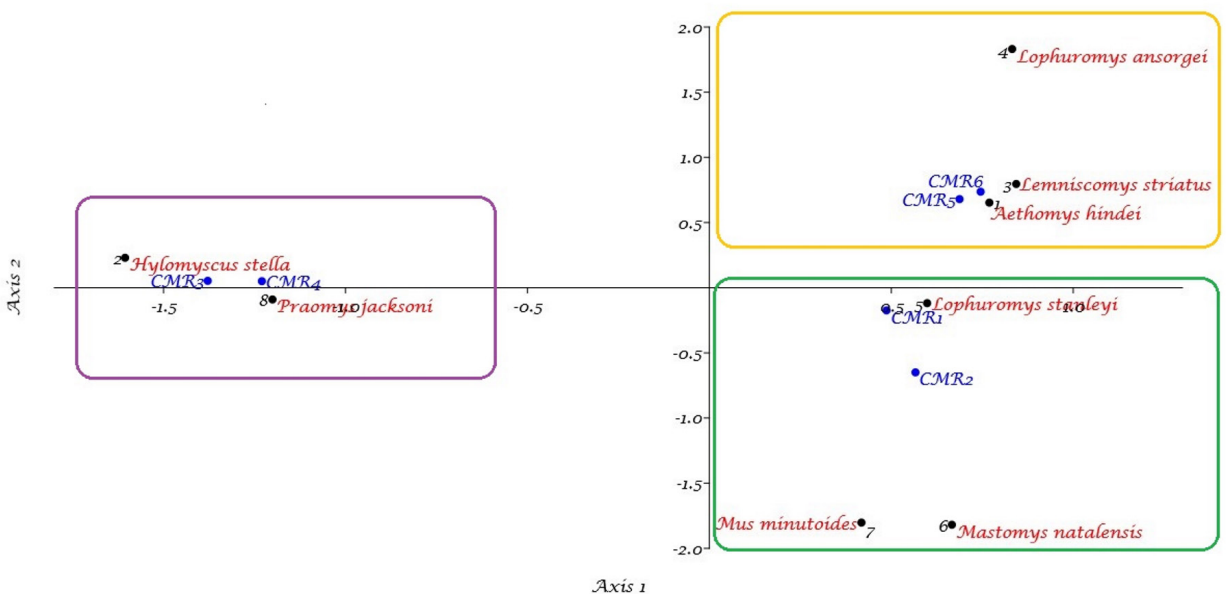
Fig. 10. Ordination plots showing rodent species associated with different trapping grids. Axis 1 and 2 explained 70.5% and 20.2% of variation in rodent association, respectively. Axes 3, 4, and 5 explained only 9.3% of the total variation in rodent association.

The results in Table 3 indicate that the three habitats were distinct (correlation values ≤ 0.50). On the other hand, results in (Table 4) indicate that there were strong relationships between CMR1 and 2 (0.61), CMR3 and 4 (0.83), and CMR5 and 6 (0.65). Thus, the three trapping habitats were broadly different in rodent species composition.

Rodent species were distinct amongst the three trapping habitats, and similar between trapping grids within the same habitat. The plots showed that different rodent species associate with distinct habitats. *H. stella* and *P. jacksoni* were
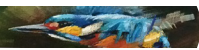
associated with the intact forest habitats, while *L. stanleyi*, *M. natalensis,* and *M. minutoides* were associated with the regenerating forest habitat, and *L. striatus*, *L. ansorgei*, and *A. hindei* were associated with the depleted forest habitat (Figs. 9, 10).

Discussion

Species composition and relative abundance

The results of this survey illustrate the importance of the Mabira forest in supporting small mammals (rodents) in Uganda. Other studies in tropical

lowland forests have focused on small mammal distributions. Stanley & Foley (2008) in their survey of small mammals of the Minziro forest recorded several rodent species, including *Hylomyscus stella*, *Praomys jacksoni*, *Mus triton*, *Hybomys univittatus*, among others. Other studies have focused on particular species, for instance Wawera & Odanga (2004), who observed *P. jacksoni* and *H. stella* in the tropical lowland forest in Kakamega, Kenya. However in the current study in MCFR, rodent species, such as *Lemniscomys striatus*, *Aethomys hindei*, *Gerbilliscus kempi*, and *Mastomys natalensis*, were also captured. In total, 14 species were recorded from the three study sites. Results showed differences in species composition among habitats, with a higher diversity index for the regenerating forest habitat, followed by the depleted forest habitat, and intact forest habitat.

The high diversity in the regenerating forest could be attributed to the fact that such habitats have a high diversity of plants which colonize the gaps created by disturbance. Such diversity in plant species may translate into increased food availability that attracts rodents, leading to increased rodent diversity. This finding is consistent with the findings from a number of previous studies (Vera & Rocha 2006, Leis et al. 2008). Such differences could also be explained by human activity, which alters habitat characteristics, thus impacting rodent communities (Hoffmann & Zeller 2005). In the current study, we attribute the low diversity (low species richness and abundance) in the depleted forest habitat to human activities, including frequent cultivation, cattle grazing, bush burning, charcoal burning, and deforestation (Nature Uganda 2011).

Rarefaction curves for the study habitats showed the curves for the regenerating and intact forest approached the asymptote, implying that an adequate level of sampling had been conducted with the chances of capturing more new species limited. For the depleted forest habitat, the rarefaction curve was still rising, implying that with more sampling, there was a possibility of capturing additional new species. The regenerating forest habitat had the highest number of species, followed by the depleted and intact forest, respectively. This finding could be attributed to the fact that forests with an intermediate level of disturbance tend to show higher values of species richness and diversity in comparison with those exposed to a high level of disturbance. Disturbances can
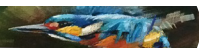
be considered as events that promote alterations in systems structures, reduce species competition, and change resource availability (Vera & Rocha 2006, Hall & Miller 2012).

The current study indicated that *Lophuromys stanleyi* was the most abundant rodent species with a 23.7% contribution to total captures in the three habitats. This species is considered as an opportunistic rodent species that tends to colonize mainly depleted and regenerating forest habitats with dense vegetation (Yalden 1988). The higher abundance of *L. stanleyi* in regenerating and depleted forest habitats compared to the intact forest further confirms that the *Lophuromys* group are highly adaptive to changing and new environments, and tend to colonize disturbed habitats (Massawe et al. 2005).

H. stella was reported second in abundance, with over 17% contribution to total captures, which occurred entirely in the intact forest habitat. A similar observation was made for *P. jacksoni*. These species are reported to be primarily forest dwellers, occurring in a variety of intact tropical high forests or in forest habitats with minimal levels of disturbance. *P. jacksoni* occurs in a variety of forested habitats including primary and secondary forest (Monadjem et al. 2015). The current findings concur with previous studies carried out in Uganda and Tanzania (Stanley & Foley 2008, Happold et al. 2013, Mizerovská et al. 2019).

The relatively high number of *M. natalensis* (over 12.7% contribution), especially in the regenerating forest habitats, affirms that it is a generalist rodent species and has the widest distribution of any African rodent. It is typically associated with agricultural fields and homes, but also occurs in natural savannah and grasslands, often sharply increasing in abundance after some form of disturbance (Monadjem et al. 2015). This species is reported by various authors, occurring in both disturbed and undisturbed habitats. The high abundance of *M. natalensis* in the regenerating forest habitats affirms the theory that this species adapts to new environments and tends to colonize disturbed habitats (Massawe et al. 2005, Makundi et al. 2010).

The existence of *A. hindei* in both the regenerating and depleted habits confirms its behaviour of a generalist herbivorous species found in woodlands that can inhabit and colonize any habitat under

cultivation, typically inhabiting bush thickets (Kingdon 1974). It has a broad distribution in Africa (Monadjem et al. 2015). In the current study, a relatively high number of *Lophuromys ansorgei* was captured in the regenerating and depleted forest habitats due to the presence of dense vegetation in the fallow areas and abandoned garden patches in the regenerating forest, which results in a relatively cool environment conducive to *L. ansorgei*.

Season effect on rodent abundance

There was significant variation in monthly rodent abundance over the entire study period. Generally, higher abundances was recorded in the wet season (September, October in 2018, and May, July in 2019), and lower abundances in the dry season (December in 2018, and February, March, June in 2019). The monthly changes in rodent abundance recorded in this study conform to theories that suggest rodent populations are highly dynamic and driven by multiple environmental factors (Leirs 1992). Rainy seasons are usually followed by rapid growth of vegetation, which provides cover and food (Getachew & Afework 2015), hence there was typically higher trap success during the two wet seasons compared with the dry seasons. Different habitats were represented by contrasting vegetation structure and degree of cover, which significantly influenced species composition and abundance across habitats. Depleted habitats were associated with rice fields and other mixed crop fields, and these are associated with rodent population outbursts during the harvest period, characterised by rapid population increase (Mulungu et al. 2003). In the current study, it was noted that human activities changed with respect to different months and seasons, and these temporal patterns in activity could have played a role in regulating the rodent population across habitats.

Rodent habitat association

Overall, more individuals were captured in the regenerating forest habitats compared to the intact and depleted forest habitats. This finding is in line with the intermediate disturbance hypothesis, which predicts that local species diversity is maximized at an intermediate level of disturbance (Bongers et al. 2009), assuming that in the regenerating forest, there was an intermediate level of disturbance compared to other forest habitats.

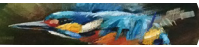The three habitats seemed to be distinct in terms of rodent associations, except for the depleted and regenerating forest habitat. However, there was a similarity between the regenerating and depleted forest habitats, which could be attributed to the fact that some abandoned farm patches within the regenerating habitat resemble parts of the depleted habitats, potentially attracting similar species.

Specialized rodent species showed a significant association with specific habitats. For example, *H. stella*, *Deomys ferrugineus*, and *P. jacksoni* were exclusively associated with the intact forest habitats, while *L. stanleyi* was mainly associated with the regenerating and bushed-depleted forest habitats. This finding confirms the observation that different rodent species have different habitat requirements, with some habitat specialists and others, generalists. *H. stella* appears to be a forest dweller, while others are more plastic in habitat use, such as *L. stanleyi*. The current findings are in agreement with earlier studies (Stanley & Foley 2008, Monadjem et al. 2015, Mizerovská et al. 2019). Basuta & Kasenene (1987) pointed out that some rodent species, such as *P. jacksoni*, are habitat specific and are mainly associated with closed forest habitats. Intermediate levels of habitat disturbance tends to create an environment with diverse vegetation and multiple microhabitats that attract a wider range of rodent species. However, continuous and heavy habitat disturbance reduces overall diversity by eliminating sensitive late-succession species (Bongers et al. 2009).

The results of the present study further indicate a significant variation in the rodent population distribution among different habitat types and seasons, which could be attributed to differences in habitat characteristics in each of the three study habitats. In the regenerating and depleted forest habitats, there was dense vegetation cover, which appears to provide good shelter for rodents and accounts for higher capture rates, as compared to the intact forest with a closed canopy with little understory vegetation.

Conclusion

The nature of habitat and seasonal changes influence rodent composition, diversity, abundance, and habitat association. An understanding of these characteristics of rodent species within a given ecosystem is key information for conservation and management of rodent species. The composition of rodent communities reflects the level of habitat degradation and can be used as a proxy for evaluating the biodiversity of lowland tropical forests.
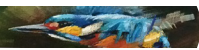
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