Journal of Vertebrate Biology

Open Access

J. Vertebr. Biol. 2023, 72: 23006

DOI: 10.25225/jvb.23006

RESEARCH PAPER

The abundance and diversity of rodents in forest sites invaded and uninvaded by *Maesopsis eminii* trees in Amani Nature Reserve, Tanzania

Leticia J. MUSESE[1,2]*, Charles J. KILAWE[3] and Amani S. KITEGILE[1]

[1] *Department of Wildlife Management, Sokoine University of Agriculture, Morogoro, Tanzania; e-mail: musese.letecia@udsm.ac.tz, akitegile@sua.ac.tz*

[2] *Department of Zoology and Wildlife Conservation, University of Dar es Salaam, Dar es Salaam, Tanzania*

[3] *Department of Ecosystems and Conservation, Sokoine University of Agriculture, Morogoro, Tanzania; e-mail: ckilawe@sua.ac.tz*

Received 14 January 2023; Accepted 16 June 2023; Published online 8 September 2023

Abstract. The Eastern Arc Mountain forests are recognised as the richest forests for biodiversity in mainland Africa. However, disturbances, particularly invasive plants, reduce the capacity of these forests to support biodiversity conservation. This study investigated the abundance, diversity and community composition of rodents in forest sites invaded and uninvaded by *Maesopsis eminii* in Amani Forest Nature Reserve. Rodents were captured through a capture-mark-recapture technique, using 300 Sherman traps located in invaded and uninvaded forest sites. A generalised linear model was applied to assess patterns in rodent community composition in invaded and uninvaded forest sites. The results indicated that the invasion by *M. eminii* significantly affected the diversity and assemblage of rodents, thereby reducing the abundance of *Beamys hindei*, suggesting that the invasive tree may be affecting various aspects of the rodent's life. We recommend taking measures to prevent the spread of *M. eminii* into the uninvaded parts of the reserve to reduce habitat loss for rodents and other native species.

Key words: Eastern Arc Mountains, East Usambara Mountains, invasive species, rodents, native species

Introduction

The Eastern Arc Mountains (EAMs) of Africa are one of the most biologically diverse areas in the world (Mittermeier et al. 2011). Unfortunately, over 70% of its forests are degraded due to illegal timber harvest, forest fires, expansion for agriculture, mining and biological invasions (Burgess et al. 2000, Newmark 2002, Hulme et al. 2013). As a result, ≥ 800 vascular plants and ≥ 96 vertebrate species occurring nowhere else in the world may be at risk of extinction (Myers et al. 2000, Burgess et al. 2007, Newmark & McNeally 2018). The protected forests in the EAMs provide important habitat for rare flora and fauna. However, forest degradation, particularly caused by invasive plants, reduces the capacity of these forests to support biodiversity conservation (Hall et al. 2009, Kilawe et al. 2022).

Maesopsis eminii Engl. is a lowland rainforest tree species commonly known as an umbrella tree (Fig. 1). The tree species is native to Africa (Binggeli & Hamilton 1993, Mbuya et al. 1994, Epila et al. 2017) but has been successfully introduced in Australia,

* *Corresponding Author*

Latin America, and Asia continents (CABI 2016). In Tanzania, the species' natural range is limited to the rain forest of Bukoba and Geita Districts (Binggeli 1989, Geddes 1998). Soon after its introduction in East Usambara, Tanzania, *M. eminii* started to spread into the natural forest (Binggeli et al. 1993). The most recent data show that the species accounted for more than 15% of large trees in the sub-montane part of the forest (Geddes 1998, Frontier Tanzania 2001) and 50% of trees in agroforestry systems (Hall et al. 2010). The spread of *M. eminii* in East Usambara is fostered by effective dispersals; trumpeter hornbill (*Bycanistes buccinators*), silvery-cheeked hornbill (*Bycanistes brevis*), fruit bats (*Eidolon helvum*) and blue monkey (*Cercopithecus mitis*) (Binggeli 1989, Cordeiro et al. 2004, Epila et al. 2017); absence of natural predators; rapid vegetative growth; prolific seed production; high seed germination rate; tolerance to drought, pest and stress (Binggeli 1989).

Fig. 1. *Maesopsis eminii* trees (white stems) in Amani Forest Nature Reserve.

Generally, there is insufficient information regarding the impact of invasive plants on mammals, particularly rodents. It has been found that invasive plants can negatively affect animal communication (Harvey & Fortuna 2012, Stewart et al. 2021), limit food supply (Malo et al. 2013), or expose animals to predators. Studies conducted in Europe and

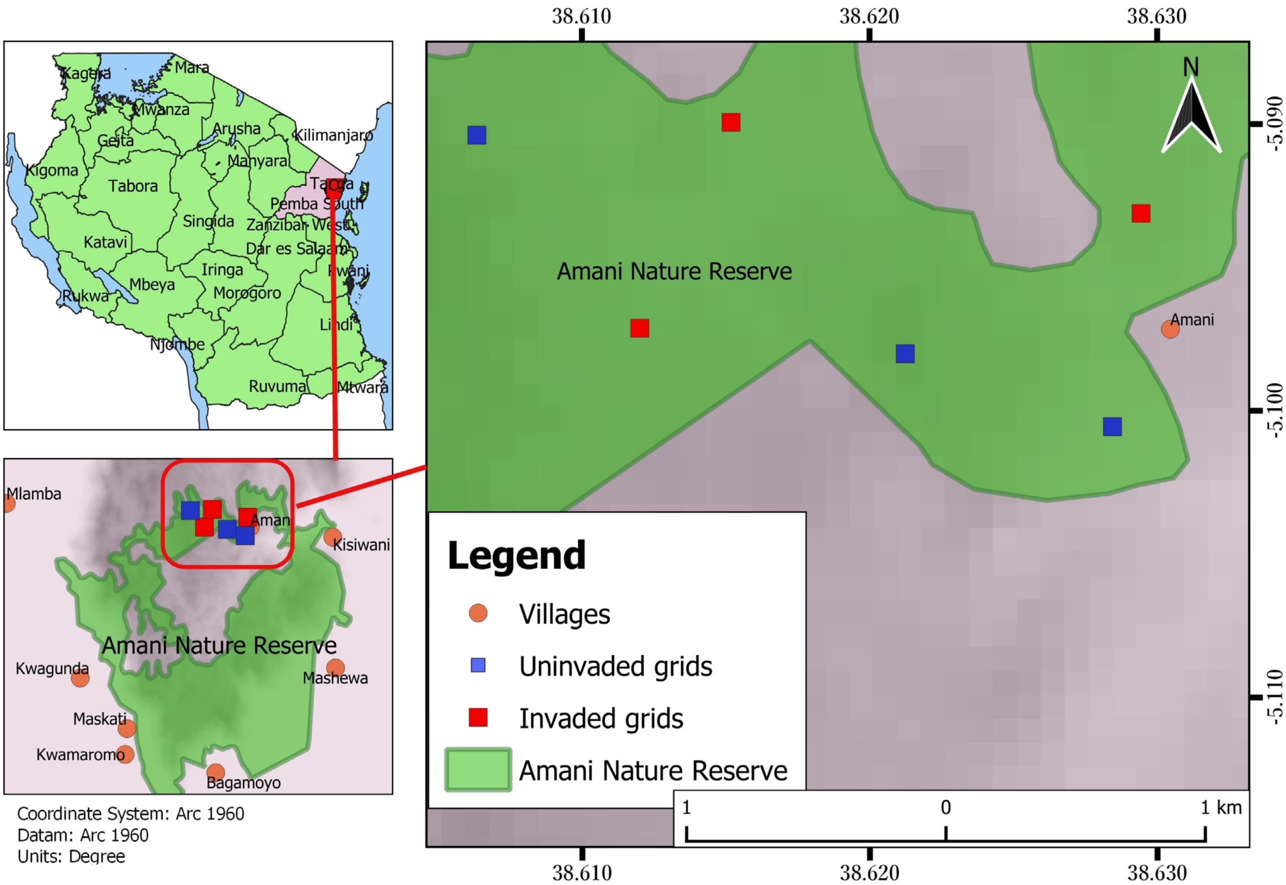

Fig. 2. A map of the study area showing the position of East Usambara Mountain in Tanzania and a land cover map of Amani Forest Nature Reserve.

North America found that invasive grasses, such as *Ammophila arenaria* and *Bromus tectorum*, as well as invasive shrubs like *Rhododendron ponticum* and *Rhamnus cathartica*, reduced the quality of mammal forage (Johnson & De León 2015) and the density, abundance, and richness of rodents (Smith et al. 2017, Guiden & Orrock 2019, Kluever et al. 2019). However, not all invasive plants negatively impact small mammals; some positive effects of invasive plants have also been reported. For example, invasive shrubs *R. ponticum* and *R. cathartica* have been found to increase the abundance of rodents (Malo et al. 2013, Guiden & Orrock 2019) and invasive shrubs, *Lonicera maackii* has been found to reduce rodents' risks against predators (Mattos & Errock 2010).

There is a conflicting account of the impacts of *M. eminii* on residence plant communities. Some scholars argue that the species impoverishes the understory scrub and herb vegetation of the forest's ecosystem, elevates soil pH and accelerates soil erosion (Binggeli 1989, Macfadyen 1989, Geddes 1998, Mugasha et al. 2000, Mwendwa et al. 2019). On the other hand, other studies found that *M. eminii* did not affect native tree species in any way (Hall 1995, Holmes 1995, Nero & Mohamed 2005) and had a high mortality rate in the original area of introduction (Kilawe et al. 2018). Generally, there is insufficient information regarding the impact of *M. eminii* on biodiversity, particularly rodents; therefore, further investigation is required.

This study aimed to determine the relationship between *M. eminii* invasions and rodent community structure in Amani Forest Nature Reserve (AFNR) to have a sound basis for decision-making about managing the invasive tree and the forest ecosystem. We hypothesised that rodent abundance and diversity would be higher in uninvaded than invaded forest sites.

Material and Methods

Study area

The study was conducted in the AFNR in the East Usambara Mountains, located between 5°06'-5°13' S and 38°32'-38°41' E, spanning an area of 8,360 hectares and rising between 190-1,130 m a.s.l. (Fig. 2). This endemic species-rich natural forest is distinguished by two rainy seasons with high relative humidity, with extensive rains from March to May and short rains from October to December (Burgess et al. 2007). The average daily temperature is 24 °C (highest) and 16.30 °C (lowest). AFNR is one of the world's 25 biodiversity hotspots of tropical forests (WTO 2001) and hence a core conservation area. It is a vital habitat for endemic plants such as *Saintpaulia ionantha* subsp. *pendula* (IUCN SSC East African Plants Red List Authority 2014) endemic vertebrates such as *Artisornis moreaui* (Bird Life International 2018), *Parhoplophryne usambarica*, *Nectophrynoides frontierei* (IUCN SSC Amphibian Specialist Group 2014) and *Afrotyphlops usambaricus* (Howell et al. 2021). AFNR is also an important habitat for Montane forest-adapted rodents, such as the soft-furred mouse (*Montemys delectorum*) (Bryja et al. 2013). Despite its importance in biodiversity conservation, AFNR is

Table 1. The number of rodents (measured as the minimum-number-known-alive) and abundance of vegetation in invaded and uninvaded forest sites of the Amani Forest Nature Reserve.

Variables	Uninvaded	Invaded
Rodents		
Montemys delectorum	222	196
Beamys hindei	21	3
Lophuromys kilonzoi	2	5
Aethomys chrysophilus	0	2
Grammomys dolichurus	1	0
Vegetation		
Maesopsis eminii (% basal area)	4.17%	74%
Native tree species (% basal area)	92.39%	25.99%
Per cent canopy cover (%)	57%	25%
Leaf litter depth (cm)	3.7	2.6
Herbaceous cover (%)	15%	21%

currently threatened by anthropogenic activities such as farming, illegal logging, and the introduction of non-native plants such as *M. eminii* (Hulme et al. 2013).

Data collection

Rodent survey

The rodent survey was conducted in six 40 × 100 m plots, systematically located in forest sites invaded and uninvaded by *M. eminii*. According to Hall et al. (2010), there is no part of AFNR without *M. emiinii*. Therefore, we defined an invaded site as the presence of *M. eminii* at high abundance (≥ 56% basal area of all stems) and uninvaded as the presence of native plants at high abundance (≥ 56% basal area of all stems). It is widely accepted that species with relative abundance ≥ 56% are considered dominant (Avolio et al. 2019). A dominant species can influence environmental conditions, community diversity and/or ecosystem function (Avolio et al. 2019). In our survey, we found that *M. eminii* had an average cover (basal area) of 74% in invaded and only 4% in uninvaded sites (Table 1).

The plots were spaced at least 1,000 m apart in each uninvaded and invaded forest site. Ademola et al. (2021) pointed out that 600 m between plots was sufficient to prevent the migration of small rodents. Five line transects measuring 100 m and spaced 10 m apart were established in each plot. In each transect, a Sherman trap of 7.6 × 8.9 × 22.9 cm dimension was placed in the trapping station at an interval of 10 m. We obtained 50 trapping stations per plot, 150 per site and 300 trapping stations for the whole study area. Trapping stations were marked by codes written on ribbons for identification purposes. The Sherman traps were baited with peanut butter mixed with maise flour to attract rodents. Traps with existing dry leaf litter were hidden to protect them from rain and direct sunlight.

Traps were placed for three consecutive nights at each site per month from April 2020 through June 2021 and inspected between 7:00 a.m. and 11:00 a.m. The Capture-Mark-Recapture (CMR) technique was applied to all captured rodents. A cotton bag was used to remove captured animals from the traps, and protective gear, particularly gloves and masks, was used during animal handling. The trapping station, capture date, sex and weight of trapped rodents were recorded. Trapped rodents were marked with number codes generated by the CMR software MARK (Borremans et al. 2015) and released after all measurements were completed. An expert from the Institute of Pest Management, Sokoine University of Agriculture, identified species. Rodents found dead in traps were preserved in alcohol (70%) and then transferred to the Institute of Pest Management, Sokoine University of Agriculture laboratory for preservation. For each plot, a vegetation survey was conducted in each site to determine the abundance of all plants, names, understory, and canopy cover.

Vegetation survey

A vegetation inventory was conducted to characterise the composition and structure of the forest sites where the rodent survey was conducted. It was not feasible to assess all trees in a plot (40 × 100 m); instead, we established a smaller sub-plot, 20 × 20 m, at the centre of each plot for vegetation survey. In each plot for each sub-plot, the following information was recorded; tree names, number, and diameter of all trees with a diameter ≥ 5 cm using a measuring tape. The percentage canopy cover (PCC) was calculated using a canopy capture smartphone application. In this procedure, a snapshot was taken, and the vertical perpendicular distance from the forest floor was obtained (Oliveira et al. 2021). Leaf litter depth and herbaceous plant cover were recorded in 10 quadrats (1 × 1 m) randomly placed in each subplot. Litter depth was measured with a ruler at the four corners of each quadrat following the procedures recommended by Yeong et al. (2016). Ten independent people visually estimated the herbaceous cover, as described by Sow et al. (2013).

Data analysis

The number of rodents was computed as the minimum-number-known-alive (MNKA) according to Krebs (1966) from the number of individual rodents captured from April 2020 through June 2021. Rodent species diversity was computed according to Shannon-Wiener diversity (H’) (Shannon & Wiener 1949) using the ‘vegan’ R package (R Core Team 2022). Statistical comparison of the Shannon diversity index of the two rodent sampling areas (invaded and uninvaded forest sites) was done by Hutcheson’s t-test (Hutcheson 1970). The Hutcheson t-test was conducted using the ‘ecolTest’ R package (R Core Team 2022).

To determine if *M. eminii* invasion resulted in changes in species community composition in the forest, we compared species counts in the invaded and uninvaded forest sites using the multivariate extension of generalised linear models ‘manyglm’ function (Zuur et al. 2010, Warton et al. 2012) in the ‘mvabund’ package (Wang et al. 2012, 2017) in the

Table 2. Species diversity in invaded and uninvaded forest sites of Amani Forest Nature Reserve.

S/N	Diversity index	Uninvaded forest site	Invaded forest site
	Simpson diversity index	0.195	0.049
	Shannon-wiener index of diversity (H′)	0.436	0.132

Table 3. Univariate tests for rodent species abundance between invaded and uninvaded forest patches.

Species	Dev	Pr (> Dev)
Aethomys chrysophilus	2.503	0.480
Beamys hindei	10.789	0.004**
Grammomys dolichurus	1.531	0.480
Lophuromys kilonzoi	1.093	0.480
Montemys delectorum	1.554	0.480

Significant codes: *significant at 0.05.

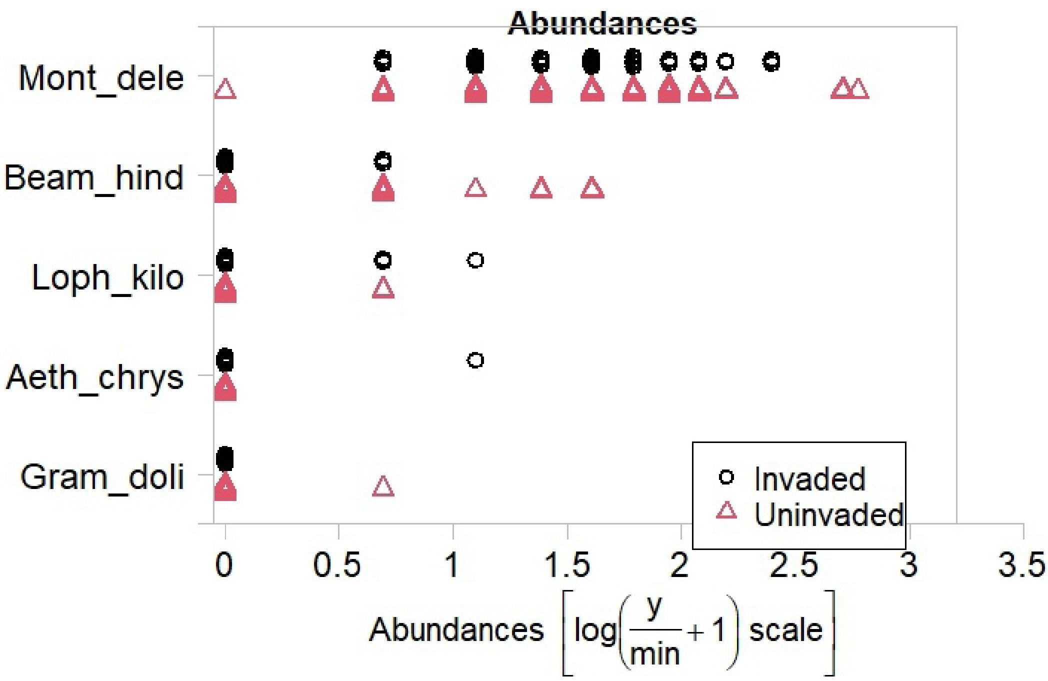

Fig. 3. A plot of the rodent abundance in invaded and uninvaded forest sites where: Gram_doli = *Grammomys dolichurus*, Aeth_chry = *Aethomys chrysophilus*, Loph_kilo = *Lophuromys kilonzoi*, Beam_hind = *Beamys hindei* and Mont_dele = *Montemys delectorum*.

R software (R Core Team 2022). This model-based approach allows for hypothesis testing, identifying species that expressed an invasion effect, predicting the abundance of each rodent species but without confounding location and dispersion effects due to the misspecification of the mean-variance relationship (Warton et al. 2012). The effect of invasion on the assemblage was evaluated using the 'anova.manyglm' function with the *P*-value calculated from 999 bootstraps via PIT-trap resampling. The option in the 'anova.manyglm' function was used to assess whether the assemblages in the invaded forest site differed from the uninvaded forest site. We fitted a multivariate generalised linear model with a negative binomial distribution (O'Hara & Kotze 2010) with invasion categories (invaded/uninvaded) as the predictor variable and abundance data as the response variable for mvabund analyses. During the analysis, both numerous rodents (e.g. *M. delectorum*, *Beamys hindei* and *Lophuromys kilonzoi*) and those with occurrence at low abundance (*Aethomys chrysophilus* and *Grammomys dolichurus*) species were included. Hence, the model for the abundance of rodents of species '*j*' found at site '*i*' (Y_{ij}) is negative binomial

(NB): $Y_{ij} \sim NB\ (\mu_{jkl}, \varphi_j)$ (equation 1) where site '*i*' is in transect '*k*' and it received invasion '*l*'. The over-dispersion parameter 'φ_j' is constant across sites but can vary across species, and the mean of 'Y_{ij}' is 'μ_{jkl}'a log-linear function of transect and invasion: $\log(\mu_{jkl}) = intercept_j + transect_{jk} + invasion_{jl} + transect \times invasion$ (equation 2). The model is based on the key assumption that 'Y_{ij}' are independent across forest sites. The appropriateness of the model assumptions was checked by directly plotting the mean-variance relationship (Wang et al. 2012). Data analysis followed data exploration protocols, including visualising outliers, normality tests, and independence between response and variables, as described by Zuur et al. (2010).

Ethical considerations

The research clearance for this study was granted by the Tanzania Commission for Science and Technology (COSTECH) (reference: RCA 2020/198) with research permit No. 2020-434-NA-2020-198, Tanzania Wildlife Research Institute (TAWIRI) (reference: TWRI/RS-342/2016/244) and Tanzania Forest Service (TFS) Agency (reference: AC: 198/305/01/47) and Sokoine University of Agriculture (reference: SUA/ADM/R.1/8/57). Handling of rodents followed the American Society of Mammalogists (ASM) guidelines for the use of wild mammals in research and education, particularly, Sikes and Animal Care and Use Committee of the American Society of Mammalogists 2016.

Results

Rodents species abundance and diversity

A total of 452 individual rodents were captured for fifteen months of the study, starting April 2020 through June 2021. Generally, rodents were more abundant in uninvaded than invaded forest sites (Table 1). The most common rodent species were *M. delectorum*, followed by *B. hindei*, whereas *G. dolichurus* and *A. chrysophilus* had lower occurrence. Generally, rodents were more abundant in uninvaded than invaded forest sites (Table 1). *Montemys delectorum* and *B. hindei* were more abundant in uninvaded than invaded sites, while *L. kilonzoi* showed greater abundance in invaded than uninvaded forest sites. *Grammomys dolichurus* was only found in the uninvaded, whereas *A. chrysophilus* was only found in the invaded forest sites.

Results revealed that rodent species diversity was greater in uninvaded than invaded forest sites (Table 2). Hutcheson's t-test on the Shannon-Weiner diversity index showed a significant difference in the diversity of rodent species between the invaded and uninvaded forest sites ($t = 2.6131$, $P = 0.009$).

The impacts of invasion on rodents' abundance

Overall, the GLM analyses indicated a significant difference in the number of rodents between invaded and uninvaded forest sites ($Dev = 17.47$, $P = 0.005$). A univariate test revealed that *B. hindei* had a significantly greater abundance in uninvaded than invaded forest sites (Table 3, Fig. 3).

Discussion

The results of this study reveal that rodents occurred in higher abundance and diversity in uninvaded than invaded forest sites as hypothesised. The invasive tree may be affecting various aspects of the rodent's life. For example, the sites invaded by *M. eminii* were more open and with more herbaceous cover than uninvaded, potentially affecting rodents' movement, exposure to predators, nesting areas, and food availability. It has been found that invasive plants can limit food supply, expose the animals to predators (Malo et al. 2013) or affect animal communication (Harvey & Fortuna 2012, Stewart et al. 2021). Information is transmitted from plants to animals as either signals and/or incidental cues that animals detect (Schaefer & Ruxton 2011). Hence, invasive plants can interfere with animal communication by altering the habitat or emitting signals and cues, generating an array of effects that can change animal behaviour (Stewart et al. 2021).

Montemys delectorum was the most common of five rodent species recorded in this study, implying that AFNR could be a suitable habitat for this species. It is important to note that *M. delectorum* inhabits burrows between the roots of large forest trees and under large logs forests (Kingdon 2015). Hence, it is commonly found in forests with high tree density, such as natural montane forests (Bryja et al. 2013, Cassola 2016). Our findings are consistent with Carleton & Stanley (2012) and Ralaizafisoloarivony et al. (2014), who found *M. delectorum* to be the most common rodent species in the forests of the East and West Usambara Mountains. *Montemys delectorum* was also discovered dominating the forests of the Ukaguru Mountains (Ademola et al. 2021) and Uluguru Mountains (Chidodo et al. 2020), implying that the species is stable and abundant in the Eastern Arc Mountains' montane forests. Rodent species are abundant in montane forests because of high humidity and soil moisture maintained by a close canopy cover and high tree density.

Furthermore, the abundance of *M. delectorum* and *B. hindei* was higher in the uninvaded forest site than in the invaded forest site, implying that plant invasion may have had a negative effect on these species' abundance because these are habitat specialists adapted to forested areas with close canopies and vegetation cover. *Maesopsis eminii* invasion in AFNR was reported to impoverish understory shrub and herb vegetation and alternated canopy structure (Mwendwa et al. 2019), which are known to be suitable environment characteristics for both *M. delectorum* and *B. hindei*. It has been described that deep leaf litter of closed forests provides suitable foraging and nesting areas for *M. delectorum* (Happold 2013, Monadjem et al. 2015, Thomas et al. 2022) while *B. hindei* have been reported to be common in areas with dense shrub layers and closed canopies (FitzGibbon et al. 1995). Clusella-Trullas & Garcia (2017) reported that invasive plants have a negative impact on the abundance of native fauna because they directly or indirectly affect food resources for animal communities. Although low species abundance is typical in plant-invaded sites, increased animal abundance in invaded sites has also been reported (Schlaepfer et al. 2010). More *L. kilonzoi* were found in invaded forest sites than in uninvaded forest sites suggesting that invasion had partial or no effect on the abundance of it in invaded forest sites. This finding is likely due to its high ability to tolerate habitat disturbances, as Ralaizafisoloarivony et al. (2014) pointed out. The observed low and increased abundance of rodents in invaded sites is because the impacts of invasive species vary depending on the characteristics of the resident species, communities and ecosystems (Vilà et al. 2011). As a result, the overall pattern of how invasive plants affect animal abundance is unclear (Hayes & Holzmueller 2012, Schirmel et al. 2015). However, species abundance provides valuable data to indicate changes in animal species between invaded and uninvaded areas (Clusella-Trullas & Garcia 2017).

The finding of this study shows that the occurrence of *M. eminii* was negatively associated with the abundance of rodent species, specifically *B. hindei*. The invasion of *M. eminii* opens the once closed forest and reduces the density and area covered by native tree species changing vegetation structure, canopy cover, ground cover and moist soil (Musila & Leonhartsberger 2006), which are major habitat requirements for *B. hindei* (FitzGibbon et al. 1995). There are limited studies for comparison, but Stewart et al. (2021) reported that plant invasion can influence plant-animal communication, such as animal behaviour. Thus, the influence of plants on animals remains a signal that may be identified from information conveyed from plants to animals (Schaefer & Ruxton 2011) and is a key pathway via which invasive plants can affect native animals (Harvey & Fortuna 2012). A favourable link between an invasive plant *M. eminii* and the abundance of rodents in AFNR is most likely owing to changes in forest structure, such as the reduction of understory vegetation, which exposes the rodents to predators. Invasive plants limit the establishment of native food plants, limiting the local food supply for native small rodents (Malo et al. 2013). Other species, such as *M. delectorum*, *L. kilonzoi*, *G. dolichurus* and *A. chrysophilus*, showed no significant association with *M. eminii* invasion, implying that the effects of invasive plants vary by species. Kluever et al. (2019) observed that invasive plants can have different effects on the same or different groups of rodents. Although this study did not confirm the association between *M. eminii* invasion and *L. kilonzoi*, Dando (2019) and Makundi (2009) reported that *L. kilonzoi* is currently threatened by the replacement of forested areas by exotic tree plantations.

This study's results further reveal that rodent diversity was higher in uninvaded than invaded forest sites, as hypothesised. We speculate that changes in vegetation cover caused by invasion have possibly reduced niche availability for diverse rodent species. This idea is supported by Freeman et al. (2014), who discovered that changes in vegetation cover due to plant invasion reduce rodent niche availability, resulting in low rodent diversity in invaded sites. *Maesopsis eminii* has significantly outcompeted native plants in AFNR, changing the vegetation cover of the invaded area (Hall 2010). Low rodent species diversity in plant-invaded sites, particularly invasive shrubs and grasses, has also been reported by Hejda et al. (2009), Ostoja & Schupp (2009) and Freeman et al. (2014) in some regions of Central Europe and USA. Our findings contradict those of Packer et al. (2016), who found no significant difference between *Rubus fruticosus* invaded and uninvaded sites in South Australia. Thus, the impacts of invasion vary among different levels of ecological complexity; hence, a need to explore the link between invasion and different ecosystems.

Conclusions

This study presented evidence that the invasion of AFNR by *M. eminii* is associated with a decline in the abundance and diversity of rodent species. If left unmanaged, *M. eminii* could lead to a loss of habitat for rodents and other native species, threatening the capacity of the forest to support biodiversity. We recommend preventing the spread of *M. eminii* into the uninvaded parts of the reserve and implementing control measures in invaded sites. The future introduction of the plant outside its ecological range should be avoided or carefully implemented.

Acknowledgements

We are grateful to the African Centre of Excellence for Innovative Rodent Pest Management and Biosensor Technology Development (ACE IRPM and BTD), Pest Management Centre (PMC), and Sokoine University of Agriculture (SUA) for their financial assistance. We acknowledge the Tanzania Commission for Science and Technology (COSTECH), the Tanzania Wildlife Research Institute (TAWIRI), and Tanzania Forest Services Agency (TFS) for permission to conduct this research. We would also want to thank Dr Christopher Sabuni, Resta Maganga, Ginethon Muhaphi, Sadick Kahangwa, Salim Fadhili, Bakari Mbamku, Ibrahim Ramadhan, Hassan Mtui, Aloyce Mkongewa, John John, Martin Kalistus, and Barnabas Malila for assisting in data collection. The authors have declared no conflicts of interest.

Author Contributions

Conceptualisation: L.J. Musese, C.J. Kilawe and A.S. Kitegile; methodology and data collection: L.J. Musese; data analysis: L.J. Musese, C.J. Kilawe and A.S. Kitegile; writing-original draft preparation: L.J. Musese; writing-review and editing: L.J. Musese, C.J. Kilawe and A.S. Kitegile; supervision: C.J. Kilawe and A.S. Kitegile. All authors have read and gave final approval for publication.

Literature

Ademola O.J., Vanden Broecke B., Leirs H. et al. 2021: Effects of forest disturbance on the fitness of an endemic rodent in a biodiversity hotspot. *Ecol. Evol. 11: 2391–2401.*

Avolio M.L., Forrestel E.J., Chang C.C. et al. 2019: Demystifying dominant species. *New Phytol. 223: 1106–1126.*

Binggeli P. 1989: The ecology of *Maesopsis* invasion and dynamics of the evergreen forest of the East Usambaras, and their implications for forest conservation and forestry practices. In: Hamilton A.C. & Bensted-Smith R. (eds.), Forest conservation in the East Usambara Mountains. *IUCN, Gland, Tanzania: 269–300.*

Binggeli P. & Hamilton A.C. 1993: Biological invasion by *Maesopsis eminii* in the East Usambara forests, Tanzania. *Opera Bot. 121: 229–235.*

Binggeli P., Ruffo C.K., Taylor D. et al. 1993: Seed banks in the forest soils. In: Hamilton A.C. & Bendsted-Smith R. (eds.), Forest conservation in the East Usambara Mountains. *IUCN, Gland, Tanzania: 307–311.*

Bird Life International 2018: *Artisornis moreaui. The IUCN Red List of Threatened Species 2018: e.T103771879A129556131. https://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T103771879A129556131.en*

Borremans B., Sluydts V., Makundi R.H. & Leirs H. 2015: Evaluation of short-, mid- and long-term effects of toe clipping on a wild rodent. *Wildl. Res. 42: 143–148.*

Bryja J., Mikula O., Patzenhauerová H. et al. 2013: The role of dispersal and vicariance in the Pleistocene history of an East African mountain rodent, *Praomys delectorum. J. Biogeogr. 41: 196–208.*

Burgess N.D., Butynski T.M., Cordeiro N.J. et al. 2007: The biological importance of the Eastern Arc Mountains of Tanzania and Kenya. *Biol. Conserv. 134: 209–231.*

Burgess N.D., Clarke G.P., Madgwick J. et al. 2000: Biodiversity values – mammals. *The IUCN Forest Conservation Programme, Coastal Forests of Eastern Africa, Cambridge, UK.*

CABI 2016: *Maesopsis eminii* (umbrella tree). *CABI Compedium, Wallingford, UK. https://doi.org/10.1079/cabicompendium.32199*

Carleton M.D. & Stanley W.T. 2012: Species limits within the *Praomys delectorum* group (Rodentia: Muridae: Murinae) of East Africa: a morphometric reassessment and biogeographical implications. *Zool. J. Linn. Soc. 165: 420–469.*

Cassola F. 2016: *Praomys delectorum. The IUCN Red List of Threatened Species 2016. e.T18114A22418403. doi:10.2305/IUCN.UK.2016-2.RLTS.T18114A22418403.en*

Chidodo S., Kilawe C.J., Mnyone L.L. et al. 2020: Factors affecting the composition of rodent assemblages in the North Uluguru Mountains, Tanzania. *J. Vertebr. Biol. 69: 20047.*

Clusella-Trullas S. & Garcia R.A. 2017: Impacts of invasive plants on animal diversity in South Africa: a synthesis. *Bothalia 47: a2166.*

Cordeiro N.J., Patrick D.A.G., Munisi B. et al. 2004: Role of dispersal in the invasion of an exotic tree in an East African submontane forest. *J. Trop. Ecol. 20: 449–457.*

Dando T. 2019: *Lophuromys kilonzoi. The IUCN Red List of Threatened Species 2019: e.T47998388A47998395. http://dx.doi.org/10.2305/IUCN.UK.2019-3.RLTS.T47998388A47998395.en*

Epila J., Verbeeck H., Otim-Epila T. et al. 2017: The ecology of *Maesopsis eminii* Engl. in tropical Africa. *Afr. J. Ecol. 55: 679–692.*

FitzGibbon C.D., Leirs H. & Verheyen W. 1995: Distribution, population dynamics and habitat use of the lesser pouched rat, *Beamys hindei. J. Zool. (Lond.) 236: 499–512.*

Freeman E.D., Sharp T.R., Larsen R.T. et al. 2014: Negative effects of an exotic grass invasion on small-mammal communities. *PLOS ONE 9: e108843.*

Frontier Tanzania 2001: Amani Nature Reserve: a biodiversity survey. *East Usambara Conservation Area Management Programme, Technical Paper 52, Forestry and Beekeeping Division, Dar es Salaam, Tanzania and Vantaa, Finland.*

Geddes R.N. 1998: *Maesopsis* invasion of the tropical forest in the East Usambara Mountains, Tanzania. *PhD Thesis, School of Agricultural and Forest Sciences, University College of North Wales, Bangor, UK.*

Guiden P.W. & Orrock J.L. 2019: Invasive shrubs modify rodent activity timing, revealing a consistent behavioral rule governing diel activity. *Behav. Ecol. 30: 1069–1075.*

Hall J.B. 1995: *Maesopsis eminii* and its status in the East Usambara Mountains. *East Usambara Catchment Forest Project Technical Report 13, Dar es Salaam, Tanzania and Helsinki, Finland.*

Hall J.B. 2010: Future options for *Maesopsis*: agroforestry asset or conservation catastrophe? In: Bongers F. & Tennigkeit T. (eds.), Degraded forests in Eastern Africa: management and restoration. *Earthscan, London, UK: 221–246.*

Hall J., Burgess N.D., Lovett J. et al. 2009: Conservation implications of deforestation across an elevational gradient in the Eastern Arc Mountains, Tanzania. *Biol. Conserv. 142: 2510–2521.*

Hall M.J., Gillespie W.T. & Mwangoka M. 2010: Comparison of agroforests and protected forests in the East Usambara Mountains, Tanzania. *Environ. Manag. 48: 237–247.*

Happold D.C.D. 2013: Ecology of African small mammals. Recent research and perspectives. In: Dennys C., Granjon L. & Poulet A. (eds.), African small mammals. *IRD Editions, Paris, France: 27–691.*

Harvey J.A. & Fortuna T.M. 2012: Chemical and structural effects of invasive plants on herbivore-parasitoid/predator interactions in native communities: invasive plants and multitrophic interactions. *Entomol. Exp. Appl. 144: 14–26.*

Hayes S.J. & Holzmueller E.J. 2012: Relationship between invasive plant species and forest fauna in Eastern North America. *Forests 3: 840–852.*

Hejda M., Pyšek P. & Jarošík V. 2009: Impact of invasive plants on the species richness, diversity and composition of invaded communities. *J. Ecol. 97: 393–403.*

Holmes J. 1995: Natural forest hand book for Tanzania. *Sokoine University of Agriculture, Morogoro, Tanzania.*

Howell K., Menegon M., Beraduccii J. & Ngalason W. 2021: *Afrotyphlops usambaricus*. *The IUCN Red List of Threatened Species 2021: e.T22476309A22476315. https://dx.doi.org/10.2305/IUCN.UK.2021-3.RLTS.T22476309A22476315.en*

Hulme P.E., Burslem D.F.R.P., Dawson W. et al. 2013: Aliens in the Arc: are invasive trees a threat to the Montane Forests of East Africa? In: Foxcroft L.C., Pyšek P., Richardson D.M. & Genovesi P. (eds.), Plant invasions in protected areas. *Springer Science + Business Media Dordrecht, Germany: 145–165.*

Hutcheson K. 1970: A test for comparing diversities based on the Shannon formula. *J. Theor. Biol. 29: 151–154.*

IUCN SSC Amphibian Specialist Group 2014: *Nectophrynoides frontierei*. *The IUCN Red List of Threatened Species 2014: e.T54839A16949680. https://dx.doi.org/10.2305/IUCN.UK.2014-1.RLTS.T54839A16949680.en*

IUCN SSC East African Plants Red List Authority 2014: *Saintpaulia ionantha* subsp. *pendula*. *The IUCN Red List of Threatened Species 2014: e.T158463A778373. https://dx.doi.org/10.2305/IUCN.UK.2014-1.RLTS.T158463A778373.en*

Johnson M.D. & De León Y.L. 2015: Effect of an invasive plant and moonlight on rodent foraging behaviour in a coastal dune ecosystem. *PLOS ONE 10: 1–12.*

Kilawe C.J., Mchelu A.H. & Emily C.J. 2022: The impact of the invasive tree *Cedrela odorota* on the electric blue gecko (*Lygodactylus williamsi*) and its habitat (*Pandanus rabaiensis*) in Kimboza Forest Reserve, Tanzania. *Glob. Ecol. Conserv. 38: e02225.*

Kilawe C.J., Mtwaenzi I.H. & Mwendwa B.A. 2018: *Maesopsis eminii* Engl. mortality in relation to tree size and the density of indigenous tree species at the Amani Nature Reserve, Tanzania. *Afr. J. Ecol. 1–4.*

Kingdon J. 2015: The kingdon field guide to African mammals, 2nd ed. *Bloomsbury Publishing, London, UK.*

Kluever B.M., Smith T.N. & Gese E.M. 2019: Group effects of a non-native plant invasion on rodent abundance. *Ecosphere 10: 1–16.*

Krebs C.J. 1966: Demographic changes in fluctuating populations of *Microtus californicus. Ecol. Monogr. 36: 239–273.*

Macfadyen A. 1989: A brief study of the relationships between *Maesopsis* and some soil properties in the East Usambaras. In: Hamilton A.C. & Bensted-Smith R. (eds.), Forest conservation in the East Usambara Mountains, Tanzania. *IUCN and Forest Division, Ministry of Lands, Natural Resources and Tourism, Gland and Cambridge: 333–343.*

Makundi R.H. 2009: The mysteries of the rats. *Sokoine University of Agriculture, Pest management center, Morogoro, Tanzania.*

Malo A.F., Godsall B., Prebble C. et al. 2013: Positive effects of an invasive shrub on aggregation and abundance of a native small rodent. *Behav. Ecol. 24: 759–767.*

Mattos K.J. & Orrock J.L. 2010: Behavioral consequences of plant invasion: an invasive plant alters rodent antipredator behavior. *Behav. Ecol. 21: 556–561.*

Mbuya L.P., Msanga H.P., Ruffo C.K. et al. 1994: Useful trees and shrubs for Tanzania: identification, propagation and management for agricultural and pastoral communities. *Technical handbook no. 6, Regional Soil Conservation Unit/SIDA, Nairobi.*

Mittermeier R.A., Turner W.R., Larsen F.W. et al. 2011: Global biodiversity conservation: the critical role of hotspots. In: Zachos F. & Habel J. (eds.), Biodiversity hotspots. *Heidelberg Springer, Berlin, Germany: 3–22.*

Monadjem A., Taylor P.J., Denys C. & Cotterill F.P.D. 2015: Rodents of Sub-Saharan Africa. A biogeographic and taxonomic synthesis. *Walter de Gruyter, Berlin, Germany.*

Mugasha A.G., Mgangamundo M.A. & Zahabu E. 2000: Is *Maesopsis eminii* a problem in East Usambara? In: Lyons E.E. & Miller S.E. (eds.), Invasive species in Eastern Africa. *ICIPE Science Press, Nairobi: 59–64.*

Musila S.N. & Leonhartsberger P. 2006: Fruit productivity and other life history traits of *Maesopsis eminii* at a forest edge and in a closed habitat of Amani, East Usambara Mts.-Tanzania. *https://citeseerx.ist.psu.edu/document?repid=rep1&type=pdf&doi=865c6cacc72522ddc51dcd6d38f9ef2a4b2c39fa*

Mwendwa B.A., Kilawe C.J. & Treydte A.C. 2019: Effect of seasonality and light levels on seed germination of the invasive tree *Maesopsis eminii* in Amani Nature Forest Reserve, Tanzania. *Glob. Ecol. Conserv. 21: e00807.*

Myers N., Mittermeier R.A., Mittermeier C.G. et al. 2000: Biodiversity hotspots for conservation priorities. *Nature 403: 853–858.*

Nero B.F. & Mohamed M.M. 2005: Seedling dynamics under *Maesopsis* tree canopy in different forest conditions at Amani Nature Reserve (ANR). *Tropical Biological Association, Cambridge, UK.*

Newmark W.D. 2002: Conserving biodiversity in East African forests: a study of the Eastern Arc Mountains. *Springer-Verlag, Berlin and Heidelberg, Germany.*

Newmark W.D. & McNeally P.B. 2018: Impact of habitat fragmentation on the spatial structure of the Eastern Arc forests in East Africa: implications for biodiversity conservation. *Biodivers. Conserv. 27: 1387–1402.*

O'Hara R.B. & Kotze D.J. 2010: Do not log-transform count data. *Methods Ecol. Evol. 1: 118–122.*

Oliveira C.F.J., Ferreguetti C.A., Santos R. et al. 2021: Leaf litter depth and low canopy cover affect the detectability of the Brazilian lancehead *Bothrops jararaca* (Wied-Neuwied, 1824) (Viperidae) in the Atlantic Forest. *North-West J. Zool. 17: 39–43.*

Ostoja S.M. & Schupp E.W. 2009: Conversion of sagebrush shrublands to exotic annual grasslands negatively impacts small mammal communities. *Divers. Distrib. 15: 863–870.*

Packer J.G., Delean S., Kueffer C. et al. 2016: Native faunal communities depend on habitat from non-native plants in novel but not in natural ecosystems. *Biodivers. Conserv. 25: 503–523.*

R Core Team 2022: R: a language and environment for statistical computing. *R Foundation for Statistical Computing, Vienna, Austria.*

Ralaizafisoloarivony A.N., Kimaro N.D., Kihupi I.N. et al. 2014: Vegetation habitats and small mammals in a plague endemic area in Western Usambara Mountains, Tanzania. *Tanzan. J. Health Res. 16: 194–205.*

Schaefer H.M. & Ruxton G.D. 2011: Plant-animal communication. *Oxford University Press, Oxford, UK.*

Schirmel J., Bundschuh M., Entling M.H. et al. 2015: Impacts of invasive plants on resident animals across ecosystems, taxa, and feeding types: a global assessment. *Glob. Change Biol. 22: 594–603.*

Schlaepfer M.A., Sax D.F. & Olden J.D. 2010: The potential conservation value of non-native species. *Conserv. Biol. 25: 428–437.*

Shannon C.E. & Wiener W. 1949: The mathematical theory of communication. *Urbana, University of Illinois Press, USA.*

Smith T.N., Gese E.M. & Kluever B.M. 2017: Evaluating the impact of an exotic plant invasion on rodent community richness and abundance. *West. N. Am. Nat. 77: 515–525.*

Sow M., Mbow C., Hély C. et al. 2013: Estimation of herbaceous fuel moisture content using vegetation indices and land surface temperature from MODIS Data. *Remote Sens. 5: 2617–2638.*

Stewart S.P., Hill A.R., Stephens A.P. et al. 2021: Impacts of invasive plants on animal behavior. *Ecol. Lett. 24: 891–907.*

Thomas M.S., Soka E.G. & Mulungu S.L. 2022: Influence of vegetation structure, seasonality, and soil properties on rodent diversity and community assemblages in west Mount Kilimanjaro, Tanzania. *Ecol. Evol. 12: e9211.*

Vilà M., Espinar J.L., Hejda M. et al. 2011: Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecol. Lett. 14: 702–708.*

Wang Y., Naumann U., Warton D.I. et al. 2017: mvabund: statistical methods for analysing multivariate abundance data. *R package version 3. https://doi.org/10.1111/j.2041-210X.2012.00190.x*

Wang Y., Naumann U., Wright S.T. et al. 2012: Mvabund – an R package for model-based analysis of multivariate abundance data. *Methods Ecol. Evol. 3: 471–474.*

Warton D.I., Wright S.T. & Wang Y. 2012: Distance-based multivariate analyses confound location and dispersion effects. *Methods Ecol. Evol. 3: 89–101.*

WTO 2001: Sustainable development of ecotourism: a compilation of good practices. *World Tourism Organization, Madrid, Spain.*

Yeong K.L., Reynolds G. & Hill J.K. 2016: Leaf litter decomposition rates in degraded and fragmented tropical rain forests of Borneo. *Biotropica 48: 443–452.*

Zuur A.F., Ieno E.N. & Elphick C.S. 2010: A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol. 1: 3–14.*