

The Giant Root-rat (*Tachyoryctes macrocephalus*) as a Synanthropic Landscape Engineer in the Bale Mountains, Southeast Ethiopia

Dissertation zur Erlangung des Doktorgrades der Naturwissenschaften (Dr. rer. nat.)

vorgelegt am Fachbereich Biologie der Philipps-Universität Marburg

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des Fachbereichs Biologie der Philipps-Universität Marburg

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Marburg, an der Lahn, Mai 2023

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Declaration of the author contributions

The thesis ‘**The Giant Root-rat (*Tachyoryctes macrocephalus*) as a Synanthropic Landscape Engineer in the Bale Mountains, Southeast Ethiopia**’ is based on the work I carried out from January/February 2020 to February 2023 at the University of Marburg, under the supervision of Prof. Dr. Nina Farwig and Dr. Dana G. Schabo. **Chapters 2 - 4** of this thesis include three independent scientific manuscripts, each with co-authorship, and have been published, submitted or will be published. The contributions of the authors for each manuscript are stated as following:

Chapter 2 – The activity of a subterranean small mammal alters Afroalpine vegetation patterns and is positively affected by livestock grazing

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Summary

Subterranean rodents particularly can act as ecosystem engineers by shaping the landscape due to soil perturbation and herbivory. Human activities, such as settlement establishment and livestock grazing, also profoundly impact ecosystem structure and functioning. In the face of growing local landuse changes, understanding the effects of rodents engineering on biodiversity and how these effects are modulated by environmental factors and human activities is important to predict future changes, and even to reconstruct ecosystem history, as well as to implement sustainable management strategies.

Subterranean rodent engineering leads to increased landscape heterogeneity and nutrient availability for plants. Rodents also directly impact vegetation through foraging and burying small plants underneath mounds. As such, engineering activities of rodents affect plant and animal communities and ecosystem structure and functioning. However, rodent engineering activities and thus their effects are influenced by environmental conditions, vegetation and human activities. The effects of rodents and underlying mechanisms even became more complex in the areas where the distribution of engineering rodents and livestock grazing overlaps. This is because both rodents and livestock affect, and are affected by vegetation, on the one hand, and plant responses to such interactive disturbances depend on their functional traits, on the other hand. Disentangling this complex interplay between subterranean rodents, vegetation, human activities and their environment remains challenging.

In this thesis, I analysed the interplay of abiotic conditions, vegetation structural and functional composition and human land-use and the burrow density of the giant root-rat (*Tachyoryctes macrocephalus* RÜPPELL 1842), a subterranean rodent endemic to the Afroalpine ecosystem of the Bale Mountains in south-east Ethiopia. I first examined the effects of giant root-rat on plant species richness and vegetation cover and *vice-versa*, and how these reciprocal effects might be modulated by temperature, habitat wetness and livestock grazing. Secondly I focussed

on the interplay between root-rat disturbance and human disturbance by working along a gradient of human activities. Finally, to understand the mechanisms through which root-rat engineering and human settlement and livestock grazing influence plant community assembly, I evaluated the changes in functional trait diversity and composition of vegetation communities along gradients of the engineering disturbances and human activities.

My thesis showed that increasing root-rat burrow density led to decreased vegetation cover; and reciprocally, increasing vegetation cover leads to decreased root-burrow density. Increasing livestock grazing intensity indirectly, via its negative effect on vegetation cover, leads to increased root-rat burrow density. Furthermore, increasing both root-rat engineering and human activities result in increased overall plant species functional dispersion. However, root-rat disturbances filtered plants with higher seed mass, stolonifereous vegetative organ and prostrate stem shot growth form, while human disturbances filtered species with larger leaf area and higher leaf nitrogen content.

This thesis promotes our understanding of the interplay between engineer rodents, human disturbances and local environmental conditions in shaping ecosystem structure and functioning. The thesis also demonstrates that giant root-rats play a synanthropic engineering role that affects vegetation structure and ecosystem processes in the critically important alpine ecosystem of the Bale Mountains. My findings also suggest that giant root-rats might have been benefited from human settlement and livestock grazing, as they reduce vegetation cover and height, particularly in enlarging the rodent's open habitat.

Chapter 1: General introduction

Human-induced land use change, and overexploitation of the natural environment are the main causes of current biodiversity loss and disruption of ecosystem processes globally (Díaz et al. 2019). High-altitude mountain regions, such as Alpine biomes, which contain higher rate of endemism and provide critically important ecosystem services such as water, are the most fragile and vulnerable ecosystems to such change drivers (Williams et al. 2004; MA 2007; Johansson & Granström 2014). In order to preserve and restore biodiversity and ecosystem processes, appropriate conservation strategies are needed (Bruner et al. 2001). Developing such strategies, in turn, requires an understanding of biodiversity structure and functioning, as well as processes shaping these biodiversity features, the linkages between biodiversity and ecosystem processes, and mechanisms underlying (MA 2007).

Ecosystem engineer species drive structures of plant and animal communities and ecosystem dynamic properties (Jones, Lawton & Shachak 1997; Romero, Gonçalves-Souza, Vieira & Koricheva 2015). Particularly, herbivorous subterranean rodents have a high impact on ecosystems due to a joint effect of soil perturbation and herbivory (Hagenah & Bennett 2013; Jones et al. 1997). The creation of subterranean tunnel systems by rodents with deposition of soil mounds at the ground surface facilitates sediment transport, alters nutrient availability, soil texture and moisture content, and creates habitats for other animal and plant species (Huntly & Reichman 1994; Zhang & Liu 2003). Most importantly, through their continually burrowing activities, they also create mima mounds – rounded dome-shaped structures with an individual structure measuring up to 27 m in diameter and 1.5 m high (Beyene 1986; Sillero-Zubiri et al. 1995; Šklíba et al. 2017; Wraase et al. 2023). Such mosaics of nutrients and soil conditions and landscape heterogeneity created by subterranean rodents are known to boost plant species diversity (Hagenah & Bennett 2013). However, tunnelling and mound creation itself reduces the overlying vegetation because short, ground layer plant species are buried (Mokotjomela,

Schwaibold & Pillay 2009; Reichman & Smith 1985). In addition, subterranean rodents also impact vegetation directly as they feed on plant material, with consequences for plant community composition and structure. Through direct herbivory, rodents are known to reduce plant cover and diversity on top of their burrows (Šklíba et al. 2017).

The direction and magnitude of the impacts of subterranean animals in shaping and maintaining vegetation patterns depend on a number of factors, including local soil characteristics and climatic conditions (e.g. Hagenah & Bennett 2013; Jones et al. 1997). Firstly, the activities of subterranean rodents seem to be negatively related to temperature in arid and semi-arid regions (Huntly & Reichman 1994), but are positively linked in the high altitude (Vlasatá et al. 2017). Secondly, soil moisture determines rodent burrowing activity, as it defines the energy needed for the excavation (Lovegrove 1989; Vleck 1979). Finally, while subterranean rodents shape vegetation patterns, their burrow density is at the same time strongly determined by vegetation structure, diversity and composition of their habitat (Huntly & Reichman 1994; Zhang & Liu 2003). For instance, the activities of rodents in dry regions are shown to increase with increasing vegetation cover (Zhang & Liu 2003) and plant productivity is also shown to positively affect the abundance of rodents (Šklíba et al. 2017).

The above-mentioned complex interplay between subterranean rodents, abiotic factors and vegetation patterns is modified by human land-use, such as livestock grazing. Soil compaction due to the presence of livestock may impact the construction and maintenance of their foraging tunnels (Vial, Macdonald & Haydon 2011). Additionally, selective removal and damage of plants by livestock grazing and threading, alter plant community composition and reduce plant biomass (Vial 2011). As a consequence, in addition to inducing food competition, livestock activities can cause alterations of suitable habitats for rodent species and their abundance, distribution and ecological functions. In contrast to the negative effects of livestock grazing on subterranean rodents (Vial 2011; Vial et al. 2011), some other studies show that livestock

grazing, especially following burning of shrubby vegetation, influence the distribution of many rodent species due to enlargement of their natural, open-landscape habitat (Miehe & Miehe 1994). So far, studies investigating the interplay between subterranean rodents and their environment have mostly looked at distinct relationships between few of the above-mentioned factors (e.g. Šklíba et al. 2017; Vial et al. 2011b; Vlasatá et al. 2017). However, to gain a comprehensive picture of how subterranean rodents shape an ecosystem, analyses taking the complexity of the interrelations among environmental factors, land use, rodent activities, and vegetation patterns are needed.

1.2 Aims of the thesis

With this thesis, I (i) examine the influences of environmental factors (soil moisture and temperature) and human activity related to livestock grazing on the reciprocal effects between vegetation and the ecosystem engineering activities of an endemic subterranean rodent, the giant root-rat (*Tachyoryctes macrocephalus*) in the Afroalpine grassland and moorland ecosystem of the Bale Mountains, southeastern Ethiopia; (ii) examined the influences of human activities related to settlement establishment and livestock grazing on the reciprocal effects between vegetation and the ecosystem engineering activities of the giant root-rat; and (iii) evaluated the changes in functional trait diversity and composition of vegetation communities along gradients of root-rat engineering disturbances (fresh burrow density, old burrow density and presence of mima mound) and human activities (settlement and livestock grazing).

I undertook this thesis research in the Afroalpine ecosystem of the Bale Mountains in Southeastern Ethiopia, starting in December 2020. The Bale Mountains represent the largest area of Afroalpine vegetation over 3,000 m asl in Africa (Yalden 1983). Elevation in the Bale Mountains ranges between 1,500 and 4,377 m asl. The area experiences two rainy seasons, with lighter rains from March to June and the heavy rainy season from July to October, and a dry season between November and February; mean annual rainfall is approximately 1,000 mm

(Miehe & Miehe 1994). The lowest and maximum recorded temperature in the Bale mountains is -15 °C and 26 °C, respectively (Miehe & Miehe 1994; OBARD 2007). The soils in the Bale Mountains are entirely volcanic in origin and mainly derived from the basaltic and trachytic parent rock, are fairly fertile silty loams of reddish-brown to black colour (Hillman 1986; Miehe & Miehe 1994).

Five broad vegetation zones occur in the Bale Mountains and the surrounding areas, namely the northern grasslands (a flat area at an altitude of 3000 m a.s.l.), the northern dry Afromontane forest (2900-3400 m a.s.l.), ericaceous forest (3400-3800 m a.s.l.), the Afro-alpine moorland and grassland (3800-4377 m a.s.l.), and the southern Hareenna forest (1500-3200 m a.s.l.; Hillman 1986; Miehe & Miehe 1996; NH 2004; OARDB 2007). Vegetation in the Afroalpine ecosystem include open grassland, grassland dotted with *Artemisia afra* shrub, *Helichrysum* dwarf-scrub, *Alchemilla* meadow, *Lobelia rhychopetalum*, and wetlands, such as alpine lakes, rivers, swamps and seasonal wetland grasslands (Tallents 2007).

Similar to many other alpine ecosystems in Africa, more rapid ecosystem changes have been detected in the Bale Mountains over the past 40 years due to human activities (Tallents 2007; Johansson & Granström 2014; BMNP 2017). Reber et al. (2018) have recorded a total of 870 settlements (207 permanently inhabited, 449 seasonally inhabited, and 214 uninhabited) in the Afroalpine zone of the Bale Mountains. Socio-economic survey conducted in 2013 show 863 households, each having an average of four people, in the study area (BMNP, unpubl. data). For this study, I considered distance from settlement and livestock dung abundance as proxies for overall human activities. The Bale mountains also represent the world's oldest known high-altitudinal residential site (Ossendorf et al. 2019). The Bale Mountains region is included in Conservation International's Eastern Afro-Montane Biodiversity Hotspot, with the BMNP being recognized as the single most important conservation area in Ethiopia (Williams et al. 2004).

The giant root-rat (*Tachyoryctes macrocephalus*, RÜPPELL 1842, family Spalacidae; Šumbera et al. 2018), a subterranean rodent, is one of the several small mammal species restricted to the Afroalpine belt of the Bale mountains (Sillero-Zubiri and Gottelli 1995). The species is restricted to <1,000 km² area at altitudes from 3,000 to 4,150 m above sea level (asl; Šumbera et al. 2018), where it is the main prey of the endangered Ethiopian wolf (*Canis simensis*) and numerous raptor species, such as golden eagle (*Aquila chrysaetos*), lesser-spotted eagle (*A. pomarina*), tawny eagle (*A. rapax*), Verreaux's eagle (*A. verreauxi*) and augur buzzard (*Buteo rufofuscus*) (Sillero-Zubiri et al. 1995; Asefa 2007). The giant root-rats are diurnal species and occur with a density of 63 animals per ha (Yalden 1985). Root-rat abandoned old burrows are used by grass rats (Šklíba et al. 2017).

Giant root-rats construct extensive large underground burrow systems. An individual root-rat burrow system extends up to 34 m, which branches into short tunnels that comprise nesting and food caching and defecation chambers (Beyene 1986; Sillero-Zubiri et al. 1995; Yaba et al. 2011). The root-rats produce through types of burrow marks: fresh burrows, old burrows, and mima mounds. Fresh burrows are easily distinguished from old burrows in that the former are freshly open or plugged holes that are currently active. However, root-rat old burrows are abandoned burrows, with holes open or plugged with weathered soil, partially or wholly covered by vegetation regrowth, and sometimes occupied by other small rodents. Mima mounds are rounded dome-shaped structures formed by continually burrowing activities of giant root-rat that measure up to 27 m in diameter and 1.5 m high (Beyene 1986; Sillero-Zubiri et al. 1995; Šklíba et al. 2017; Wraase et al. 2023). Areas around root-rat mima mounds, which are their favoured habitats, are characterized by the predominance of bare soil, as they eject soil from their burrow systems when excavating, and when plugging their burrow holes at night for thermoregulation (Yalden 1975). They also graze and gather vegetation for bedding around burrows, which further alter the landscape (Beyene 1986; Yaba et al. 2011). As a result, GRRs

have been known to cause changes in plant species diversity and composition (Tallents & Macdonald 2011; Šklíba et al. 2017). Despite the vital ecological engineering role it plays, the species is currently classified by the IUCN as endangered mainly due to habitat loss and degradation brought about by livestock overgrazing (Lavrenchenko & Kennerley 2016; BMNP 2017).

In chapter 2, I predicted: i) reduced vegetation cover and plant species richness in areas with elevated root-rat burrow density; and ii) increased plant species richness and vegetation cover, directly or indirectly via root-rat burrow density, but a decrease with increasing surface temperature and habitat wetness, but decreased with increasing livestock grazing intensity. In the reverse effect (effects of vegetation on root-rat), I expected: i) a decrease in root-rat burrow density with increasing plant cover due to the need for open spaces and an increase in root-rat burrow density with increased plant species richness due to the need to access and select high quality resources; and ii) an increase of root-rat burrow density with, directly or indirectly via species richness and vegetation cover, increasing surface temperature, habitat wetness, and livestock grazing intensity.

In chapter 3, I expected that 1) livestock grazing intensity would be higher at permanent human settlement areas than at seasonal settlement and decline with increasing distance from settlement; ii) permanent settlement and increasing grazing directly and indirectly lead to decreased vegetation cover which in turn leads to increased giant root-rat burrow density, but lead to decreased plant species richness that in turn results in decreased root-rat burrow density, and 3) giant root-rats would have negative reciprocal effects on vegetation cover and species richness, which in turn are influenced by human activities, as plant biomass damage caused by giant root-rat burrowing and foraging activities would reduce vegetation cover and plant species richness.

In chapter 4, I predicted (i) increased functional trait diversity (functional trait divergence) with increasing root-rat engineering and human activities (distance from settlement and livestock grazing intensity) since both disturbances are expected to create habitat heterogeneity and increased resources (space and nutrients). (ii) I also predicted that plant seed mass, leaf area and leaf nitrogen content would increase with root-rat engineering and human disturbances, while stolonifereous and prostrate traits would be positively associated with root-rat engineering disturbances.

Because this is a cumulative dissertation, chapters 2 - 4 can be read independently as the scientific background, methods and the results are presented and discussed independently in each chapter. In addition, the material and methods sections across these chapters are repetitive to maintain this independence. Please also consider that even though here I refer to the work done by me and write in first person, the three chapters are the result of collaborations with other researchers. The author contributions for each chapter can therefore be found within the section “Declaration of the author contributions”.

Chapter 2: The activity of a subterranean small mammal alters Afroalpine vegetation patterns and is positively affected by livestock grazing

2.1 Abstract

Subterranean rodents can act as ecosystem engineers by shaping the landscape due to soil perturbation and herbivory. At the same time, their burrow density is affected by environmental conditions, vegetation and anthropogenic factors. Disentangling this complex interplay between subterranean rodents and their environment remains challenging. In this study, I analysed the interplay of abiotic conditions, vegetation patterns and human land-use and the burrow density of the giant root-rat (GRR; *Tachyoryctes macrocephalus*), a subterranean rodent endemic to the Afroalpine ecosystem of the Bale Mountains in south-east Ethiopia. Specifically, I examined the effects of GRR on plant species richness and vegetation cover and *vice-versa*, and how these reciprocal effects might be modulated by temperature, habitat wetness and grazing. My results showed that increasing GRR burrow density led to decreased vegetation cover, and that effects of GRR on vegetation cover were slightly stronger than *vice-versa*. Considering the reciprocal causation models, I found that increasing plant species richness led to increased GRR burrow density, while GRR burrow density decreased as vegetation cover increased. Increases in habitat wetness and livestock grazing intensity also directly led to increased GRR burrow density. My results stress the importance of subterranean ecosystem engineers on vegetation and highlight the vulnerability of these complex interactions to human activity.

Keywords: Ecosystem engineering, giant root-rat, subterranean rodent, soil mound, habitat wetness, plant species richness, *Tachyoryctes macrocephalus*, vegetation cover

2.2 Introduction

Ecosystem engineer species constantly create habitats and therefore drive structures of plant and animal communities and ecosystem dynamics (Jones, Lawton & Shachak 1997; Romero, Gonçalves-Souza, Vieira & Koricheva 2015). Particularly, herbivorous subterranean rodents have a high impact on ecosystems due to a joint effect of soil perturbation and herbivory

(Hagenah & Bennett 2013; Jones et al. 1997). The creation of subterranean tunnel systems by rodents with deposition of soil mounds at the ground surface facilitates sediment transport; alters nutrient availability, soil texture and moisture content; and creates habitats for other animal and plant species (Huntly & Reichman 1994; Zhang & Liu 2003). Studies have found that such mosaics of nutrients and soil conditions created by subterranean rodents boost plant species diversity (Hagenah & Bennett 2013). However, tunnelling and mound creation itself reduces the overlying vegetation because short, ground layer plant species are buried (Mokotjomela, Schwaibold & Pillay 2009; Reichman & Smith 1985). In addition, subterranean rodents also impact vegetation directly as they feed on plant material, with consequences for plant community composition and structure. Through direct herbivory, rodents are known to reduce plant cover and diversity on top of their burrows (Šklíba et al. 2017).

The direction and magnitude of the impacts of subterranean animals in shaping and maintaining vegetation patterns depend on a number of factors, including local soil characteristics and climatic conditions (e.g. Hagenah & Bennett 2013; Jones et al. 1997). Firstly, the activities of subterranean rodents seem to be negatively related to temperature in arid and semi-arid regions (Huntly & Reichman 1994), but are positively linked in the high altitude (Vlasatá et al. 2017). Secondly, soil moisture determines rodent burrowing activity, as it defines the energy needed for the excavation (Lovegrove 1989; Vleck 1979). Finally, while subterranean rodents shape vegetation patterns, their burrow density is at the same time strongly determined by vegetation structure, diversity and composition of their habitat (Huntly & Reichman 1994; Zhang & Liu 2003). For instance, the activities of rodents in dry regions are shown to increase with increasing vegetation cover (Zhang & Liu 2003) and plant productivity is also shown to positively affect the abundance of rodents (Šklíba et al. 2017).

The above-mentioned complex interplay between subterranean rodents, abiotic factors and vegetation patterns is modified by human land-use, such as livestock grazing. Soil compaction

due to the presence of livestock may impact the construction and maintenance of their foraging tunnels (Vial, Macdonald & Haydon 2011). Additionally, selective removal and damage of plants by livestock grazing and threading, alter plant community composition and reduce plant biomass (Vial 2011). As a consequence, in addition to inducing food competition, livestock activities can cause alterations of suitable habitats for rodent species and their abundance, distribution and ecological functions. In contrast to the negative effects of livestock grazing on subterranean rodents (Vial 2011; Vial et al. 2011), some other studies show that livestock grazing, especially following burning of shrubby vegetation, influence the distribution of many rodent species due to enlargement of their natural, open-landscape habitat (Miehe & Miehe 1994). So far, studies investigating the interplay between subterranean rodents and their environment have mostly looked at distinct relationships between few of the above-mentioned factors (e.g. Šklíba et al. 2017; Vial et al. 2011b; Vlasatá et al. 2017). However, to gain a comprehensive picture of how subterranean rodents shape an ecosystem, analyses taking the complexity of the interrelations among environmental factors, land use, rodent activities, and vegetation patterns are needed.

In this study, I examined the ecosystem engineering role of the endemic giant root-rat (GRR; *Tachyoryctes macrocephalus*, RÜPPELL 1842), an Afroalpine specialist rodent in the Bale Mountains, south-eastern Ethiopia. GRRs, via their burrowing and herbivory activities, strongly shape the Afroalpine landscape of the Bale Mountains, where they have a long history of interaction with humans (Miehe & Miehe 1994; Ossendorf et al. 2019) and where the number of people is still rising (BMNP [Bale Mountains National Park] 2017). Its subterranean and above-ground herbivory activities in the immediate vicinity of the burrow opening cause changes in soil properties and vegetation structure (Sillero-Zubiri et al. 1995). Currently the GRR is classified by the IUCN as globally endangered due to habitat change/degradation induced by livestock grazing (Lavrenchenko & Kennerley 2016). Understanding the

interactions among environmental factors, human activities and GRR activities in structuring the Afroalpine ecosystem has been identified as one of the top priority research topics by the BMNP management to aid effective management decisions (BMNP 2017). Thus, the GRR is a perfectly suitable species to understand the linkages between abiotic conditions, vegetation patterns, rodent burrow density and human land-uses. Previous research on the impact of the GRR on vegetation in some parts of the Afroalpine zone of the Bale Mountains have shown that burrowing activity of GRR causes altered plant species composition and reduced cover (Šklíba et al. 2017; Yaba, Mekonnen, Bekele & Malcolm 2011). However, so far, it is poorly understood how these effects might be influenced by environmental factors and land-use across the species distribution range. My aims were to determine the role of GRRs as ecosystem engineers through the interrelations between environmental conditions, land-use, GRR burrow density, and vegetation variables. More specifically, I analysed, using path analysis: i) the direct and indirect effects of temperature, habitat wetness, livestock grazing and GRR burrow density on plant species richness and vegetation cover, and ii) the direct and indirect effects of temperature, habitat wetness, livestock grazing, plant species richness and vegetation cover on GRR burrow density. Comparing the effect of the GRR burrow density on vegetation and *vice-versa*, I aimed to reveal which factor is more strongly influenced by the other. I hypothesize: i) reduced vegetation cover and plant species richness in areas with elevated GRR burrow density; ii) increased plant species richness and vegetation cover, directly or indirectly via GRR burrow density, but a decrease with increasing surface temperature and habitat wetness, but decreased with increasing livestock grazing intensity; iii) a decrease in GRR burrow density with increasing plant cover due to the need for open spaces and an increase in GRR burrow density with increased plant species richness due to the need to access and select high quality resources; and iv) an increase of GRR burrow density with, directly or indirectly via species richness and vegetation cover, increasing surface temperature, habitat wetness, and livestock grazing intensity.

2.3 Materials and methods

2.3.1 Study area

The study was conducted in the Afroalpine ecosystem of the BMNP across the Sanetti Plateau and Web Valley in south-eastern Ethiopia (Fig. 1), during the dry season in January/February 2020. The Bale Mountains represent the largest area of Afroalpine vegetation in Africa (Miehe & Miehe 1994; Yalden 1983) and encompass an elevation range of 1,500–4,377 m asl. There are two rainy seasons, with short rains from March to June and the long rains from July to October, and a dry season between November and February; mean annual rainfall is approximately 1,000 mm (Miehe & Miehe 1994). The BMNP is included in Conservation International's Eastern Afromontane Biodiversity Hotspot (BMNP 2017).

2.3.2 Study species

The giant root-rat (GRR) is one of the 13 to 14 African root-rat species of the genus *Tachyoryctes* Rüppel, 1842 in the family Spalacidae (Šumbera et al. 2018). It is easily distinguished from the other congeneric species by its large body mass (around 1 kg) and eyes on top of the head, considered as an adaptation to detect predators in open habitats (Šumbera et al. 2018; Yalden 1975).

GRR is endemic to <1,000 km² area in the Bale Mountains of Ethiopia at altitudes from 3,000 to 4,150 m asl (Bryja et al. 2019), where it is the main prey of the endangered Ethiopian Wolf (*Canis simensis*) and numerous raptor species (Sillero-Zubiri, Tattersall & Macdonald 1995). GRRs are naturally confined to open, Afroalpine *Helichrysum* dwarf-shrub heathlands, seasonally waterlogged short grassland and swamps (Sillero-Zubiri et al. 1995; Tallents & Macdonald 2011). The species is diurnal and constructs large underground burrows including an extensive tunnel system (Bryja et al. 2019; Sillero-Zubiri et al. 1995). The burrow system of an individual GRR may extend to 34 m (Beyene 1986; Yaba et al. 2011; Yalden 1975). The tunnels are characterized by extensive soil perturbation aboveground and have holes through which GRRs are able to forage and bask on the ground surface (Beyene 1986; Bryja et al. 2019;

Sillero-Zubiri et al. 1995). During foraging, GRR stays with its back in the hole and collects plants surrounding it (Vlasatá et al. 2017). It largely feeds on *Alchemilla abyssinica*, an abundant forb species in the area (Vlasatá et al. 2017).

2.3.3 Study design

To assess the interplay between environmental conditions, livestock grazing, vegetation and GRR burrow density, I established eight study locations scattered over an area of 1,000 km². Three locations were established in the Web Valley and five in the Sanetti Plateau of the BMNP (Fig. 1). I chose suitable localities for study locations in accessible areas with flat terrain, encompassing major habitat types known to host populations of the target species, before going to the field. The pairwise distance between study locations ranged from 5–30 km. At each study location, I defined two (n= 3 locations) to three (n=5 locations) transects of 1.5 km length in different directions, to maximize representation of various habitats (see Tallents & Macdonald 2011), at a minimum angle of 100 degrees. Major habitat types covered by study locations and transects included: open-grassland, grassland dotted with *Artemisia afra* shrub, *Helichrysum* dwarf-scrub, *Alchemilla* meadow, *Lobelia rhychopetalum*, and wetlands, such as alpine lakes, rivers, swamps and seasonal wetland grasslands (Tallents & MacDonald 2011). Along each transect, I established three 25 m × 25 m plots at a minimum distance of 500 m from each other, and placed plots within a homogeneous habitat type, at least 5 m away from habitat edges. Due to logistic constraints, one location was missing one plot within one transect. Overall, I thus had 62 plots covering an area of 38,750 m².

2.3.4 Data collection

At each plot, I recorded data on GRR burrow density, vegetation patterns, livestock grazing and habitat wetness. As indicator for GRR burrow density I counted the numbers of: a) GRR fresh burrows, which are surrounded by or plugged with fresh soil; b) old burrows, which are abandoned GRR burrows, with holes open or plugged with old soil, without freshly perturbed

soil, partially or wholly covered by vegetation regrowth, and sometimes occupied by other small rodents (Sillero-Zubiri et al. 1995), and c) the proportion of the plot area covered by GRR soil perturbation. The often smaller diameter of other rodents holes and presence of rodents' droppings and pathways connecting burrow openings were used to distinguish fresh and old GRR burrows (Šklíba et al. 2017). As density of fresh burrows, old burrows and the proportion of perturbed soil cover were positively correlated, only the density of fresh burrows was incorporated in further analyses (Spearman's correlation test, $\rho > 0.65$, $P < 0.001$). To estimate livestock grazing on the plateau, I recorded the number of cow droppings within the 25 m \times 25 m plots. I estimated habitat wetness, as an ordinary variable, at each plot as absent (1), seasonally waterlogged (2), along perennial rivers drainage line (3), and wetland (4).

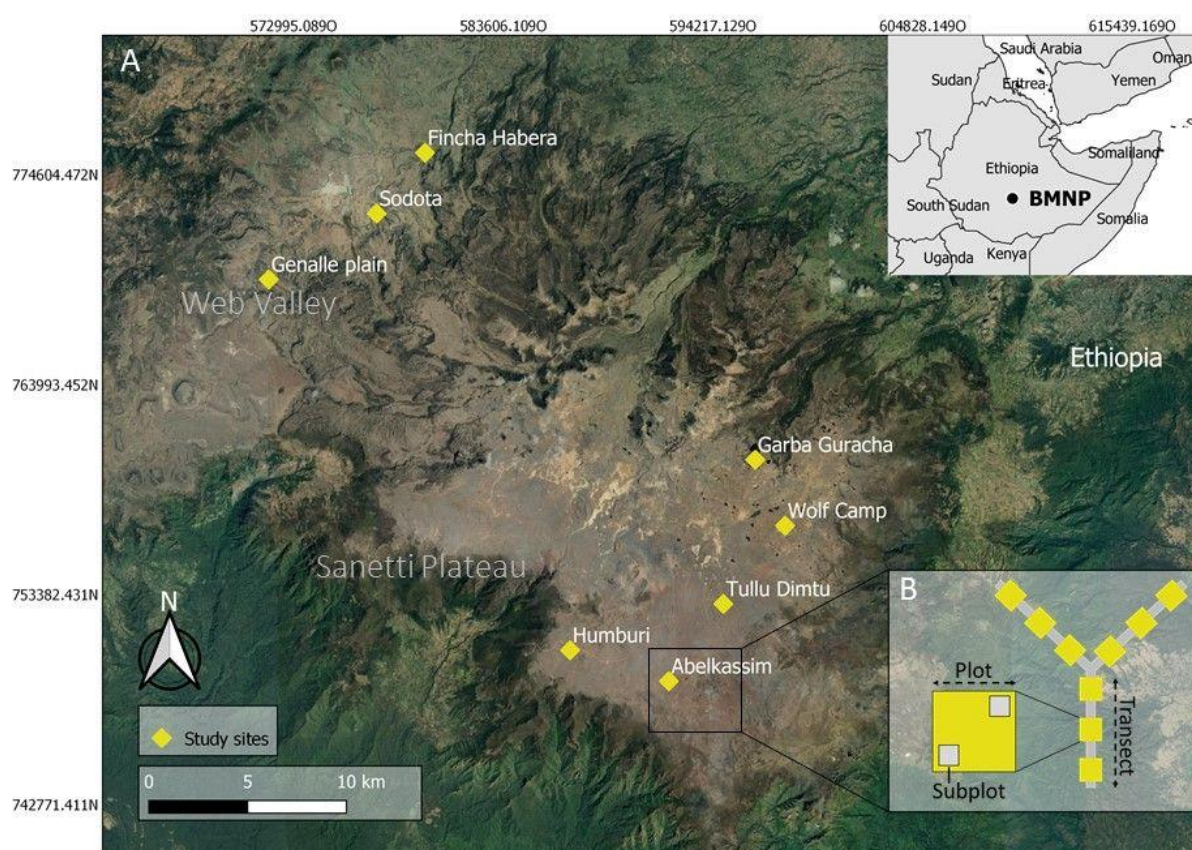


Fig. 1. (A) Overview map of the Bale Mountains National Park (BMNP) in southern Ethiopia with eight study locations; and (B) Detailed map showing the set-up of one study location with three transects of 1.5 km length and 3 study plots along each transect (for detailed description see Methods section “Study area”).

To record vegetation data, I established two 10 m \times 10 m subplots at opposite corners of each 25 m \times 25 m plot, the first subplot being randomly selected. In each of these subplots, I identified all plants to species level, except senescent plants which were not recorded and grasses which were recorded as a single morpho-species. I recorded estimated cover of each species in 5% intervals and subsequently summed cover estimations of all species recorded on a subplot. For further analyses, I calculated the mean number of species and summed vegetation cover on the plot level. I also calculated the Shannon diversity at the 25 m \times 25 m plot scale, but excluded it from the analysis as it was correlated to species richness (correlation coefficient = 0.75). To make sure that GRR burrow density matches vegetation sampling, I also recorded GRR burrow density at the 10 m \times 10 m plots. GRR burrow density as well as vegetation parameters positively correlated between the two plot sizes (all correlation coefficient > 0.83, Supplementary file Table S1). Therefore, as I recorded all other environmental data on the 25 x 25 m scale, I used GRR burrows and estimated vegetation parameters on the 25 m \times 25 m plot level for further analyses.

In addition, I derived temperature data for each plot using remote sensing data and temperature records from ten weather stations positioned over the whole BMNP and covering the time period from January to December 2017. For remote sensing data, I used thermal Landsat-8 satellite imagery in 30 m resolution from the USGS Earth Explorer (www.earthexplorer.com). Then, the bi-monthly Landsat-8 imagery and daily local temperature recordings were aggregated to monthly means and were spatially predicted for the whole study area (Wraase et al. In press).

2.3.5 Data analyses

I *a priori* defined sets of two alternative path models to disentangle the effect of GRR burrow density on vegetation patterns and *vice-versa* using Shipley's test of directed separation (Shipley 2009). In a first set of path models, I analysed the direct and indirect effects of

temperature, habitat wetness, livestock grazing and GRR burrow density on plant species richness and vegetation cover, whereby two separate models were calculated for plant species richness and vegetation cover as response variables (path models “effect of GRR burrow density on vegetation patterns”). In a second set of path models, I reversed the direction of causal paths between vegetation patterns and GRR burrow density, and analysed the direct and indirect effects of temperature, habitat wetness, livestock grazing and vegetation cover or plant species richness on GRR burrow density (path models “effect of vegetation patterns on GRR burrow density”). Again, separate models were run for plant species richness and vegetation cover, resulting in a total of four path models. Prior to the analysis, all predictor variables were tested for collinearity using Spearman’s correlation test (Supplementary file Table S2). The analyses were conducted in the R environment (R Core Team 2020).

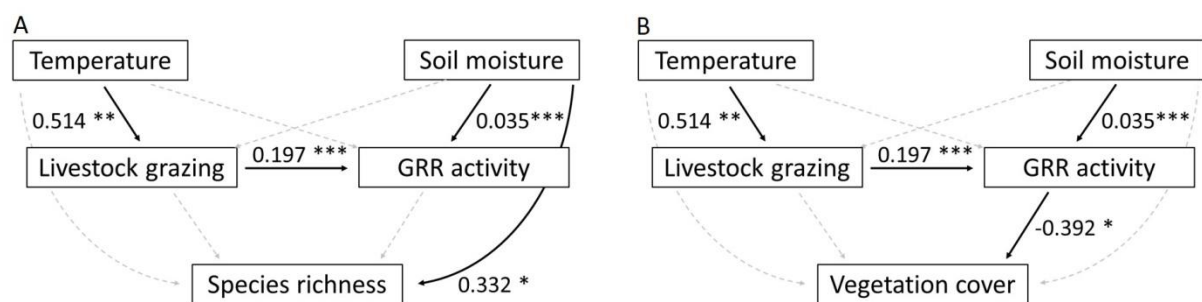


Fig. 2. Path models testing for the effect of giant root-rat (GRR) burrow density on vegetation patterns, showing relationships between temperature, habitat wetness, livestock grazing, GRR burrow density and (A) plant species richness and (B) vegetation cover. Significant paths are depicted by solid, black arrows. Values show standardized effect sizes with asterisks indicating the significance levels (* $P < .05$, ** $P < .01$, *** $P < .001$). Dotted, grey arrows indicate non-significant relationships.

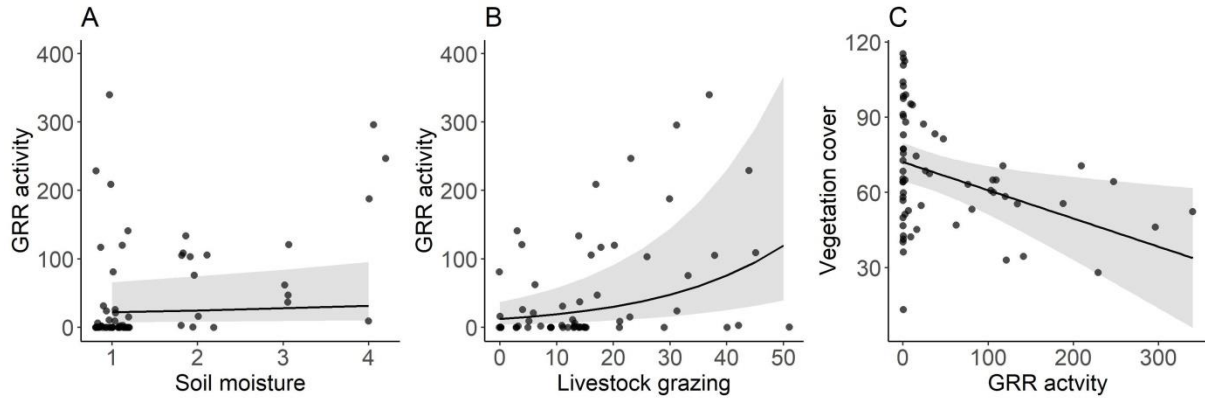


Fig. 3. Increasing giant root-rat (GRR) burrow density with increasing habitat wetness (A) and livestock grazing intensity (B) and decreasing vegetation cover with increasing GRR burrow density (C). Shown are effects of model outputs and 95% intervals based on generalized mixed effects models and underlying raw data.

Each path model consisted of three mixed effects regressions, testing the initially assumed relationships between the variables (see Figs 2–5). I used generalized- and linear mixed effect models (GLMM and LMM, respectively), including transects nested within study locations as random effects in each regression. Analysing the effect of GRR burrow density on vegetation patterns, the first regression was a GLMM with a negative binomial family to correct for overdispersion, which analysed the effect of temperature and habitat wetness on livestock grazing (package `glmmTMB`, function `glmmTMB`, Brooks et al. 2017). The second regression included livestock grazing as fixed effect with GRR burrow density as response, using a GLMM accounting for zero-inflation. The third regression included GRR burrow density as fixed effect, and either plant species richness or vegetation cover as response variables in two separate LMMs with normal error distribution (R package `NLME`, function `lme`; Pinheiro et al. 2021). For the models with interchanged path direction, revealing the effect of vegetation on GRR burrow density, the first regression was identical as for previous path models. The second regression modelled species richness or vegetation cover including livestock grazing as fixed effect using LMMs, in two separate path models. The third regression included species richness

or vegetation cover as additional predictor variables, predicting GRR burrow density, using GLMMs with Poisson distribution accounting for zero-inflation. The model diagnostics were made using the DHARMA package (Hartig 2022).

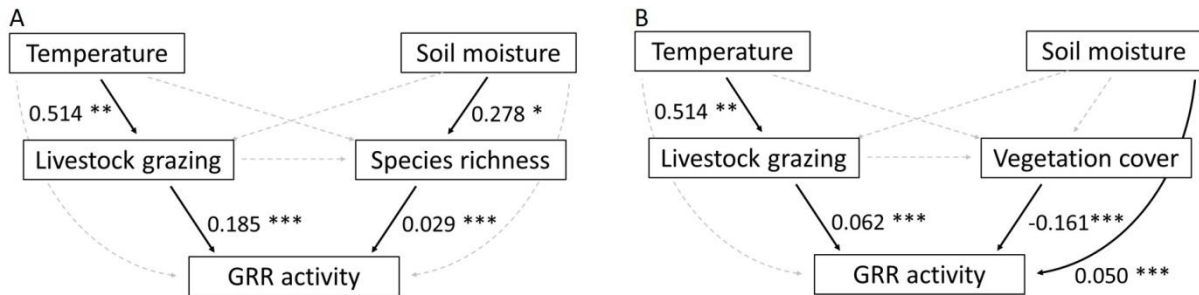


Fig 4. Path models testing the effects of vegetation patterns on giant root-rat (GRR) burrow density, showing: relationships between temperature, habitat wetness, livestock grazing with (A) species richness, and (B) vegetation cover on GRR burrow density. Significant paths are depicted by solid, black arrows. Values show standardizes effect sizes with asterisks indicating the significance levels (* $p < .05$, ** $p < .01$, *** $p < .001$). Dotted, grey arrows indicate non-significant relationships.

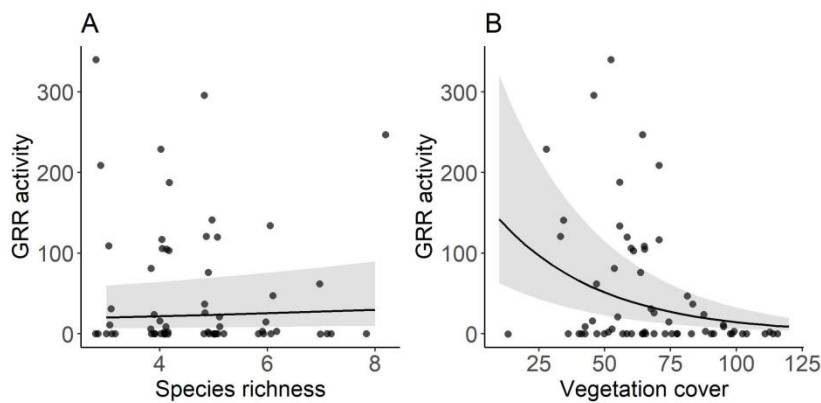


Fig. 5. Increasing giant root-rat (GRR) burrow density with increasing species richness (A) and decreasing GRR burrow density with increasing vegetation cover (B). Shown are effects of model outputs and 95% intervals based on generalized mixed effects models and underlying raw data.

A model-wide comparison of effect sizes across the regressions was achieved by scaling path coefficients, which is appropriate for path analysis including non-normally distributed response variables. In a regression with normally-distributed response, I standardized the path coefficient by the ratio of the standard deviation of the predictor over the standard deviation of the response. For non-normally distributed response variable, I followed the observation-empirical approach by Lefcheck (2021). For the estimated path coefficients of each regression in a path model, I derived the p -values using the `cftest` function from the `multcomp` package (Hothorn et al. 2021). If a response variable was hypothesized to be independent from a predictor variable, a d-separation test was applied to test this independence claim. For each claim I tested if the response was independent from the predictor by testing if its partial slope deviated significantly from zero, using the LMM or GLMM applied for that response in the path model. For each path model separately, the null-probabilities of all independence claims were combined using C-statistics (Shipley 2009). A Chi^2 test was run on the C-statistics to derive a model-wide p -value (Shipley 2009). I also estimated the indirect effects of temperature, habitat wetness and livestock grazing on each vegetation variable via GRR burrow density, as well as on GRR burrow density via each vegetation variable (Shipley 2009). I tested the significance of these indirect effects using the Sobel Test in a freely available online application provided by Soper (2021).

I compared both competing sets of path models (effect of GRR burrow density on vegetation patterns *vs.* effect of vegetation patterns on GRR burrow density) using the Akaike's information criterion (AIC) as model selection technique for d-separation tests (Shipley 2009).

2.4 Results

The number of GRR fresh burrow ranged from 0 to 340 across plots (mean \pm SD: 48.78 ± 79.43), with a density of 780.50 ± 1270.81 burrows per ha. I recorded 38 plant species across all plots, with species richness per plot varying between three and eight species (4.72 ± 1.25). Vegetation cover ranged from 13% to 115 % (68.03 ± 22.86). The number of cow dungs ranged

between 0 and 51 (16.23 ± 14.03). Across plots, the temperature varied between 2.6 °C and 8.3 °C (5.2 ± 1.5).

2.4.1 Path models: Effect of GRR burrow density on vegetation

While habitat wetness had a direct positive effect on plant species richness, I neither found a significant effect of temperature nor of livestock grazing or GRR burrow density on plant species richness (Fig. 2A; Table 1). I found a direct and negative effect of increasing GRR burrow density on vegetation cover (Figs. 2B & 3C). However, neither a direct effect of increasing temperature nor of grazing or habitat wetness on vegetation cover was observed (Table 1). Yet, I found significant indirect negative effects of habitat wetness and livestock grazing, both via GRR burrow density, on vegetation cover (Supplementary file Table S3). Both path models with the different vegetation variables reproduced the data well as proven by the Chi-square test for independence (path model for species richness: Chi-square = 13.04, $P = 0.22$; vegetation cover: Chi-square = 9.48; $P = 0.48$).

Table 1. Results of path models analysing the effects of temperature, habitat wetness, livestock grazing and GRR burrow density on plant species richness and vegetation cover. Given are values of unstandardized path coefficients and their standard errors (Ustd. Estimate \pm SE), standardized path coefficients (Std. Estimate) and R^2 . Values of Std. Estimates with asterisk indicate significant effects at significance levels of * = $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

Variables	Ustd. Estimate \pm SE	Std. Estimate	R^2
Level 1: Livestock grazing			0.37
Habitat wetness	0.204 ± 0.132	0.245	
Temperature	0.249 ± 0.083	0.514**	
Level 2: GRR burrow density			0.38
Livestock grazing	0.046 ± 0.003	0.197***	

Habitat wetness	0.121 ± 0.024	0.035***
Temperature	0.044 ± 0.056	0.022
Level 3: Plant species richness		0.51
GRR burrow density	-0.003 ± 0.002	-0.208
Livestock grazing	-0.004 ± 0.015	-0.036
Habitat wetness	0.474 ± 0.187	0.332*
Temperature	0.136 ± 0.164	0.163
Level 3: Vegetation cover		0.20
GRR burrow density	-0.113 ± 0.044	0.044*
Livestock grazing	0.040 ± 0.278	0.023
Habitat wetness	2.352 ± 3.578	0.090
Temperature	1.134 ± 2.471	0.074

2.4.2 Path models: Effect of vegetation on GRR burrow density

I found a positive effect of plant species richness on GRR burrow density (Fig 4A & Fig. 5A), and a negative effect of vegetation cover on the rodent's burrow density (Fig 4B & Fig. 5B; Table 2). Livestock grazing had a positive direct influence on GRR burrow density in both path models, as well as habitat wetness in the path model testing the effect of plant species richness on GRR burrow density (Table 2). No indirect effect of grazing either through species richness or vegetation cover on GRR burrow density was detected (in all cases, Sobel test statistic = -1.27–0.31; $P = 0.204$ –0.762; Supplementary file Table S2). The assumptions of both path models were supported by the Chi-square test for independence (path model for species richness: Chi-square = 14.33, $P = 0.16$; vegetation cover: Chi-square = 10.46; $P = 0.40$).

Table 2. Results of path models analysing the effects of temperature, habitat wetness, livestock grazing and plant species richness, or vegetation cover on GRR burrow density. Given are values of unstandardized path coefficients and their standard errors (Ustd. Estimate \pm SE), standardized path coefficients (Std. Estimate) and R^2 . Values of Std. Estimates with asterisk indicate significant effects at significance levels of * = $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

Variables	Ustd. Estimate \pm SE	Std. Estimate	R^2
Level 1: Livestock grazing			0.37
Habitat wetness	0.204 \pm 0.132	0.245	
Temperature	0.249 \pm 0.083	0.514**	
Level 2: Species richness			0.51
Livestock grazing	-0.011 \pm 0.014	-0.109	
Habitat wetness	0.398 \pm 0.018	0.278*	
Temperature	0.172 \pm 0.612	0.206	
Level 3: GRR burrow density			0.29
Species richness	0.079 \pm 0.024	0.029***	
Livestock grazing	0.049 \pm 0.003	0.185***	
Habitat wetness	0.051 \pm 0.032	0.013	
Temperature	0.005 \pm 0.057	0.002	
Level 2: Vegetation cover			0.15
Livestock grazing	-0.234 \pm 0.269	-0.131	
Habitat wetness	-1.057 \pm 3.462	-0.040	
Temperature	2.354 \pm 2.592	0.154	

Level 3: GRR burrow density **0.18**

Vegetation cover	-0.025 ± 0.001	-0.161***
Livestock grazing	0.017 ± 0.002	0.062***
Habitat wetness	0.204 ± 0.018	0.050***
Temperature	-0.051 ± 0.048	-0.021

2.4.3 Comparison of path models

I compared both sets of path models for each of the vegetation variables, i.e., plant species richness or vegetation cover. The path model testing the effect of plant species richness on GRR burrow density (AIC: 75.04) showed a slightly better AIC value than the model testing the effect of GRR burrow density on species richness (AIC: 78.33; Δ AIC: 3.29). In contrast, the path model testing the effect of GRR burrow density on vegetation cover (AIC: 62.46; Δ AIC: 3.02) produced slightly better AIC values, than that testing the effect of vegetation cover on GRR burrow density (AIC: 65.48).

2.5 Discussion

My results show that increasing GRR burrow density led to decreased vegetation cover. Considering the reciprocal causation models, I found that increasing plant species richness led to increased GRR burrow density, while GRR burrow density decreased as vegetation cover increased. The latter finding is particularly interesting, because GRR's preference of sites with lower vegetation cover has been less known unlike the well-known decrease of vegetation cover by root-rat activity (Šklíba et al. 2017). However, the AIC statistics of the alternative models are too similar to make any conclusion(s) about which causal effect is more likely; hence, both directions are presumably at equilibrium. Increases in habitat wetness and livestock grazing intensity also directly led to increased GRR burrow density.

In line with my prediction, my results showed that vegetation cover decreased with increasing GRR burrow density. Obviously, both bioturbation and direct herbivory of GRR lead to reduced vegetation cover, in agreement with reports of previous studies on other species (Hausmann, 2017; Wu et al. 2015). My findings are also in line with studies on the GRR (Beyene 1985; Sillero-Zubiri et al. 1995; Šklíba et al. 2017; Yalden 1975) and reduced *A. abyssinica*, GRR's favoured food plant, at active GRR burrows. Yet, I did not find a significant effect of GRR burrow density on plant species richness, which partly contradicts out initial prediction but is in line with many similar studies demonstrating inconsistent results (Hausmann 2017; Jones et al. 1997; Romero et al. 2015; Wu et al. 2015). My result in this regard may suggest that plant damage during mound excavation and foraging does not lead to reduced species richness. This might be true in the latter case because subterranean rodents are well-known to be food generalists (Nevo 1999). Studies on food consumption of GRRs (Beyene 1986; Yaba et al. 2011) showed that they feed on any available plants around burrows even though they amply forage on abundantly available herb plant species (e.g. *A. abyssinica*) and grasses (Vlasatá et al. 2017). This suggests that GRR might be a food generalist predominantly foraging on abundantly available forbs, which in turn might minimize the risk of local extinction of rare species and may explain the lack of impact of the rodent's burrow density on plant species richness.

Analysing vegetation effects on GRR burrow density, I found increased GRR burrow density with increasing plant species richness and with decreasing vegetation cover. The increased GRR activity with increasing plant species richness is not clear, because, as discussed above, GRRs feed on any available plants around burrows (Beyene 1986; Yaba et al. 2011). Despite this, Šklíba et al. (2020) showed that GRRs shifted their home ranges, during the late dry season when forage was in short supply, from shorelines into the wetlands to increase their food supply. Thus, given the positive associations I found between habitat wetness and both GRR burrow density and plant species richness, my result of GRR's association with richness could be a by-

product of GRR's preference for microhabitats, such as wetlands that are characterized by high species richness (Sillero-Zubiri et al. 1995; Yalden 1975). The increased GRR burrow density with decreasing vegetation cover clearly reveals GRR's preference for open habitats (Sillero-Zubiri et al. 1995; Vlasatá et al. 2017). In fact, they are morphologically, physiologically and behaviourally adapted to life in open Afroalpine habitats (Bryja et al. 2019; Sillero-Zubiri et al. 1995; Yaba et al. 2011). Overall, my results demonstrate that effects of GRR on vegetation cover were stronger than *vice-versa*, and that the cause-effect relationship between plant species richness and GRR was only in one direction (richness on GRR).

The significant positive effect of livestock grazing on GRR burrow density is in agreement with my prediction and has not been well known although previously suggested (Šklíba et al. 2017), and fits with the rodent's preference for open habitats (Beyene 1986; Lavrenchenko & Kennerley 2016). A study on Plateau Zokor (*Myospalax baileyi*) in the Tibetan Plateau, China, has also shown such increase in burrow density with increasing livestock grazing activity, but the effects were found to be dependent on the seasonality, grazing system and stocking rate of grazing practices (Wang et al. 2020). My result, however, is in contrast to results of other studies reporting a non-significant or negative effect of livestock grazing on GRR and other subterranean rodents (e.g. Fuhlendorf et al. 2001; Vial et al. 2011). These inconsistencies in results across studies indicate a spatiotemporal context-dependence of the complex interplays between livestock grazing, vegetation patterns and subterranean rodents. In my study system, the effect of livestock grazing on GRR is assumed to be attributable to a livestock herbivory-induced decrease in vegetation cover (Vial 2011). The GRR could thus, potentially benefit from livestock-induced enlargement of their habitat. Yet, my results are based on assessments in the dry season; grazing intensity and its effects on GRR burrow density may differ in the wet season, when food abundance for livestock is higher (Vial 2011). In addition, my study did not cover the potential effects of other domestic animals. Thus, my result should be interpreted cautiously because, despite the long-time associations of humans and GRRs in the Bale

Mountains (Ossendorf et al. 2019), concerns over the increasing livestock grazing encroachments in the Bale mountains have been growing (BMNP 2017; Vial 2011). Particularly, unregulated overstocking of livestock has been considered as the major threat to several globally threatened species, including the GRR. Thus, future research should focus on the spatiotemporal intensity of domestic animals grazing tolerable by the GRRs to inform management decisions.

The increased GRR burrow density with increasing habitat wetness found in my study is consistent with my prediction and findings in other studies (Sillero-Zubiri et al. 1995; Šklíba et al. 2017, 2020; Vlasatá et al. 2017) that reported that wetland habitats are dry-season preferred habitats of GRRs. This habitat type provides better forage quality, and easily workable soil (Sillero-Zubiri et al. 1995; Šklíba et al. 2020; Vlasatá et al. 2017). A similar positive association between moisture and mound density has been reported for Plateau Zokor (Zhang & Jikeliu 2003). In contrast to my prediction, but in consistence with findings on the GRR (Vlasatá et al. 2017) and on other species (e.g. Hagenah and Bennett 2013; Hart et al. 2021), I did not observe any effect of temperature on GRR burrow density. My result could be attributed to the species' adaptation to local climatic conditions within its range.

2.6 Conclusion

With my study on GRR, I could show the reciprocal impact of a subterranean ecosystem engineering rodent on its environment, and *vice versa*. Surprisingly, I found positive influences of human activities in terms of livestock grazing on GRR burrow density. My results highlight the complex interplay between environmental factors, humans and ecosystem engineering species, especially in light of an extreme environment such as Afroalpine ecosystem. Given the unregulated ongoing human activity in the Afroalpine ecosystem of the Bale mountains, research focusing on the influences of different grazing seasons and stocking rate on the GRR and its engineering role would be important to inform effective ecosystem management.

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Data Availability

All relevant data are within the manuscript.

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Competing interests

The authors have declared that no competing interests exist.

Chapter 3: Human activities modulate reciprocal effects of a subterranean ecological engineer rodent, *Tachyoryctes macrocephalus*, on Afroalpine vegetation cover

3.1 Abstract

Human activities, directly and indirectly, impact ecological engineering activities of subterranean rodents. As engineering activities of burrowing rodents are affected by, and reciprocally affect vegetation cover via feeding, burrowing and mound building, human influence such as settlements and livestock grazing, could have cascading effects on biodiversity and ecosystem processes such as bioturbation. However, there is limited understanding of the relationship between human activities and burrowing rodents. The aim of this study was therefore to understand how human activities influence the ecological engineering activity of the giant root-rat (*Tachyoryctes macrocephalus*), a subterranean rodent species endemic to the Afroalpine ecosystem of the Bale Mountains of Ethiopia. I collected data on human impact, burrowing activity and vegetation during February and March of 2021. Using path analysis, I tested (1) direct effects of human settlement on the patterns of livestock grazing intensity, (2) direct and indirect impacts of humans and livestock grazing intensity on the root-rat burrow density, and (3) whether human settlement and livestock grazing influence the effects of giant root-rat burrow density on vegetation and *vice versa*. I found lower levels of livestock grazing intensity further from human settlement than in its proximity. I also found a significantly increased giant root-rat burrow density with increasing livestock grazing intensity. Seasonal settlement and livestock grazing intensity had an indirect negative and positive effect on giant root-rat burrow density, respectively, both via vegetation cover. Analysing the reciprocal effects of giant root-rat on vegetation, I found a significantly decreased vegetation cover with increasing density of giant root-rat burrows, and indirectly with increasing livestock grazing intensity via giant root-rat burrow density. My results demonstrate

that giant root-rats play a synanthropic engineering role that affects vegetation structure and ecosystem processes. These effects may be a mechanism through which engineering rodents create stable and resilient ecosystem structure and processes.

Keywords: Bioturbation, grazing intensity, human settlement, rodent burrow, synanthropic association.

3.2 Introduction

Human-induced land use change is the main cause of biodiversity loss and disruption of ecosystem processes globally (Díaz et al. 2019). One of the most extensive land-use types worldwide, and thus one of the most detrimental for biodiversity, is livestock production (Eldridge et al. 2016; FAO 2018; Filazzola et al. 2020) although certain types of livestock production can be less detrimental than intensive crop agriculture or urbanization (Olivier et al. 2020). Currently, livestock grazing occupies 26% of global terrestrial land cover (FAO 2018). The increasing global livestock population (Bar-On et al. 2018), but declining extent and productivity of rangelands, has resulted in changes in traditional grazing practices in Africa (FAO 2018), such as rotational grazing and seasonal movements, to partly sedentary grazing systems (Bagchi et al. 2006; Reitalu et al. 2010). In contrast, seasonal grazing systems that are evenly distributed across rangelands, livestock grazing intensity in sedentary grazing systems and its influences on biodiversity are largely concentrated to nearby human settlements, declining as a function of increasing distance from settlement areas (Bagchi et al. 2006; Reitalu et al. 2010; Dunne et al. 2011).

Livestock have strong direct and indirect effects on biodiversity and ecosystem processes, mainly through grazing, trampling, defecation and urination (Eldridge et al. 2016; Narantsetseg et al. 2018; Maestre et al. 2022). For example, grazing by livestock directly creates bare soil, and indirectly causes soil loss via wind and rain erosion, and by facilitating the rapid runoff of rainfall (FAO 2018). Moreover, grazing by livestock removes plant biomass, thereby directly

reducing plant cover and eliminating grazing intolerant species (Tessema et al. 2011), and indirectly by creating open spaces for gap-colonizing plant species and promoting the dominance of unpalatable and grazing tolerant species (Tessema et al. 2011; Eldridge et al. 2016; Pavlů et al. 2018; Niu et al. 2019). Livestock trampling causes soil compaction and disruption of surface layers, which indirectly reduce infiltration and increase runoff and soil loss (Dunne et al. 2011; FAO 2018). Further, through trampling, livestock also directly reduces vegetation cover and height, regeneration and recovery from grazing impacts by damaging seedlings and vegetative organs (Eldridge et al. 2016). Livestock trampling also indirectly affects vegetation via changes in soil properties (Tessema et al. 2011). Finally, livestock dung deposition and urination affect nutrient cycling and can cause nutrient overloading which affects vegetation structure and diversity by facilitating encroachment of exploitive native and/or non-native plant species that may lead to biotic homogenization (Bokdam 2001; Dunne et al. 2011; Pavlů et al. 2018). Therefore, livestock production may result in changes in vegetation structure and composition, and reduced or increased plant species diversity, depending on the intensity of grazing, trampling, and degree of resistance of the regional species pool to different grazing intensities (Eldridge et al. 2016; FAO 2018).

Apart from the effects on soil and vegetation, these direct and indirect effects of human activities related to settlement establishment and livestock grazing cascade to wild animals, affecting their distribution, abundance and behaviour (Wang et al. 2020). Subterranean small rodents that are adapted to living in savannah and alpine grassland ecosystems are particularly known to be susceptible to human activities (Vial et al. 2010; Wang et al. 2019, 2020). For example, habitat loss and degradation caused by human settlement—via space use for house building—and livestock husbandry—via grazing and trampling—lead to deterioration of habitat quality for rodents (Bakker et al. 2009). Moreover, livestock grazing can lead to competition for food with rodents (Zhang & Liu 2003; Niu et al. 2019), and livestock trampling

can destroy burrow systems (Šklíba et al. 2017). Despite these generally presumed negative effects, livestock grazing and trampling activities can also have positive effects on subterranean rodents inhabiting grasslands through facilitation of habitat by reducing vegetation height and cover (Bakker et al. 2009; Asefa et al. 2022).

Effects on subterranean rodents can also cascade through the system, as many burrowing rodents are ecosystem engineers, transforming ecosystems through their feeding and burrowing activities (Beyene 1986; Jones et al. 1997; Davidson et al. 2012). They can directly reduce vegetation cover and diversity through consumption of plants and burrowing and mound building activities that bury vegetation under the excavated soil (Wang et al. 2019; Šklíba et al. 2017). Ejection of soil, decomposed cached foods and defecations from their underground tunnels onto the ground surface lead to redistribution of soil moisture and air, alteration of nutrient availability, and increased microhabitat heterogeneity (Reichman & Seabloom 2002; Zhang & Liu 2003; Haussmann 2017). Thus, by providing new spaces and nutrient rich microhabitat, subterranean rodents facilitate colonization by new plant species, potentially leading to increased diversity (Jones et al. 1997; Reichman & Seabloom 2002; Hagenah & Bennett 2013; Šklíba et al. 2017). At the same time, while subterranean rodents shape vegetation patterns, their activity strongly depends on vegetation (Huntly & Reichman, 1994; Zhang & Liu, 2003). For instance, the activities of rodents in dry regions are shown to increase with increasing vegetation cover (Zhang & Liu, 2003), and plant productivity is also shown to positively affect the abundance of rodents (Šklíba et al., 2017). On the other hand, the activities of rodents in alpine regions are shown to decrease with increasing vegetation cover (Wang et al. 2020; Asefa et al. 2022). Thus, given the direct and indirect effects of human activities both on vegetation and subterranean rodents, this natural interplay between vegetation and rodents is sensitive to human activities (Jones 2012; Eldridge & Soliveres 2023). Many of the burrowing rodents are critically endangered and vulnerable in many parts of the world, and

as many of them are ecosystem engineers, their decline has a disproportionately large effect on other components of the habitats they live in, such as on soil properties and vegetation dynamics (Valkó et al. 2022; Eldridge & Soliveres 2023). In addition to their impact on soil and vegetation, engineer rodents also impact other animals relying on vegetation for food, shelter and reproduction (Jones 2012). Yet, there have been limited understandings on the nature and extent of such complex interactions between human activities, vegetation and subterranean rodents (Valkó et al. 2022; Eldridge & Soliveres 2023); specifically, how the effects of human activities on vegetation affect rodents engineering activities and its reciprocal effects on vegetation.

In this study, I examined the influences of human activities on the reciprocal effects between vegetation and the ecosystem engineering activities of an endemic subterranean rodent, the giant root-rat (*Tachyoryctes macrocephalus*, RÜPPELL 1842) in the Afroalpine grassland and moorland ecosystem of the Bale Mountains in southeastern Ethiopia. Human associations with giant root-rats in the Bale Mountains date back to 43–47 thousand years ago, where the middle Stone Age foragers used to hunt the root-rats (Ossendorf et al. 2019) although the root-rats are neither hunted nor considered as pest in the present times. Consequently, it has been supposed that giant root-rats have a synanthropic association with human activities (Ossendorf et al. 2019). In recent decades, the numbers of human settlements and livestock in the mountains have grown rapidly (Johansson & Granström 2014; Vial et al. 2010), with some scenarios even showing the grazing level to approach the ecosystem collapse threshold (Vial et al. 2011; BMNP 2017). There are two types of settlements in the mountains: permanent settlement, and seasonal settlements which occur in the wetter months, from April to August, when livestock are moved from lower pastures where agricultural crops are being grown (Hillman 1986; BMNP 2017). As such, livestock grazing intensity and other possible human activities would differ between settlement types and vary along the distance from settlements. Here, I evaluated:

1) livestock grazing intensity in relation to human settlement type, differentiating between traditional seasonal vs permanent, and along a distance gradient from the settlements, 2) the direct and indirect (via vegetation variables) effects of human settlement type, distance from settlement and livestock grazing intensity on giant root-rat burrow density; and 3) the indirect influences of human settlement and livestock grazing intensity on the reciprocal effects of giant root-rat burrowing activities on vegetation cover and plant species richness. I predicted that: 1) livestock grazing intensity would be higher at permanent human settlement areas than at seasonal settlement and decline with increasing distance from settlement, 2) permanent settlement and increasing grazing directly and indirectly lead to decreased vegetation cover which in turn leads to increased giant root-rat burrow density, but lead to decreased plants species richness that in turn results in decreased root-rat burrow density, and 3) giant root-rats would have negative reciprocal effects on vegetation, which in turn are influenced by human activities, on vegetation, as plant biomass damage caused by giant root-rat burrowing and foraging activities would reduce vegetation cover and plant species richness.

3.3 Material and methods

3.3.1 Study area

This study was conducted in the Afroalpine ecosystem of the Bale Mountains National Park in southeastern Ethiopia (6.508–7.178N, 39.508–39.928E; Fig. 1), between December 2020 and February 2021. With elevation ranging between 1,500 and 4,377 m asl, the Bale Mountains represent the largest area of Afroalpine vegetation over 3,000 m asl in Africa (Yalden 1983). The area experiences two rainy seasons, with lighter rains from March to June and the main rainy season from July to October, and a dry season between November and February; mean annual rainfall is approximately 1,000 mm (Miehe & Miehe 1994). The lowest and maximum recorded temperature in the Bale mountains is -15 °C and 26 °C, respectively (Miehe & Miehe 1994; OBARD 2007). The soils in the Bale Mountains are entirely volcanic in origin and mainly

derived from the basaltic and trachytic parent rock, are fairly fertile silty loams of reddish-brown to black colour (Hillman 1986; Miede & Miede 1994). The Bale Mountains region is a global biodiversity hotspot area hosting a high level of endemism, including many local endemics such as the giant root-rat (BMNP 2017). In the region, rock-shelters were repeatedly occupied by humans in prehistoric times and represent the world's oldest known high-altitudinal residential site. Those prehistoric high-altitude residents used to forage on the locally endemic giant root-rats (Ossendorf et al. 2019). Similar to many other alpine ecosystems in Africa, more rapid ecosystem changes have been detected in the Bale Mountains over the past 40 years (Tallents 2007; Johansson & Granström 2014; BMNP 2017). Reber et al. (2018) have recorded a total of 870 settlements (207 permanently inhabited, 449 seasonally inhabited, and 214 uninhabited) in the Afroalpine zone of the Bale Mountains. Socio-economic survey conducted in 2013 show 863 households, each having an average of four people, in the study area (BMNP, unpubl. data). Permanent settlers live and use the area throughout the year, while seasonal settlement occurs in the wetter months, from April to August, when livestock are moved from lower pastures where agricultural crops are being grown and thus human activities are higher (Hillman 1986).

3.3.2 Study species

The giant root-rat (*Tachyoryctes macrocephalus*, RÜPPELL 1842, family Spalacidae; Šumbera et al. 2018) is a rodent species endemic to the Bale Mountains of Ethiopia (Yalden 1985; Yalden & Largen 1992; Lavrenchenko & Kennerley 2016). The species is restricted to <1,000 km² area at altitudes from 3,000 to 4,150 m above sea level (asl; Šumbera et al. 2018), where it is the main prey of the endangered Ethiopian Wolf (*Canis simensis*) and numerous raptor species, such as golden eagle (*Aquila chrysaetos*), lesser-spotted eagle (*A. pomarina*), tawny eagle (*A. rapax*), Verreaux's eagle (*A. verreauxi*) and augur buzzard (*Buteo rufofuscus*) (Sillero-Zubiri et al. 1995; Asefa 2007). The giant root-rats are diurnal species and occur with a density of 63 animals per ha (Yalden 1985). They construct extensive large underground burrow systems. An

individual root-rat burrow system extends up to 34 m, which branches into short tunnels that comprise nesting and food caching and defecation chambers (Beyene 1986; Sillero-Zubiri et al. 1995; Yaba et al. 2011). Burrow holes are used to expel soil, as well as decomposed cached foods and defecations, and to access aboveground vegetation for feeding. Unused burrow holes are plugged in by soil backfilling while all active fresh holes are plugged in during night time for thermoregulation (Beyene 1986; Šklíba et al. 2017; Šumbera et al. 2018). It is via these burrowing and feeding activities that giant root-rats impact ecosystem processes and vegetation structure and diversity (Asefa et al. 2022). Despite the vital ecological engineering role it plays, the species is currently classified by the IUCN as endangered mainly due to habitat loss and degradation brought about by livestock overgrazing (Lavrenchenko & Kennerley 2016; BMNP 2017).

3.3.3 Data collection

To examine the relationships between human settlement, livestock grazing, vegetation variables and giant root-rat burrow density, I worked across the entire distribution range of the giant root-rat that is scattered over an area of 1,000 km². Six study sites were selected systematically, between 5 to 20 km apart, to cover all major sections (eastern, central, and western sections; Fig. 1) and vegetation types of the Bale Mountains' Afroalpine ecosystem (open grassland, grassland dotted with *Artemisia afra* shrub, *Helichrysum* dwarf-scrub, *Alchemilla* meadow, *Lobelia rhychopetalum*, and wetlands, such as alpine lakes, rivers, swamps and seasonal wetland grasslands; Tallents 2007). At each site, I selected two adjacent settlements (3–5 km apart) that were known to be established 30 years ago (Hillman 1986; BMNP 2017), one of them being permanent and one seasonal. Starting at the centre of each settlement, I established three 1.5 km long transects at an angle of 80–120° (see the inset map on Fig. 1). Along each transect, I established six 25 m × 25 m plots at a distance of 250 m from each other. I determined the size of plots and distance from one another to standardize and make comparable with our

recent study (Asefa et al. 2022). Plots were placed within a uniform habitat type and at least 15 m away from any habitat edge. In total, there were 216 plots covering an area of 13.5 ha.

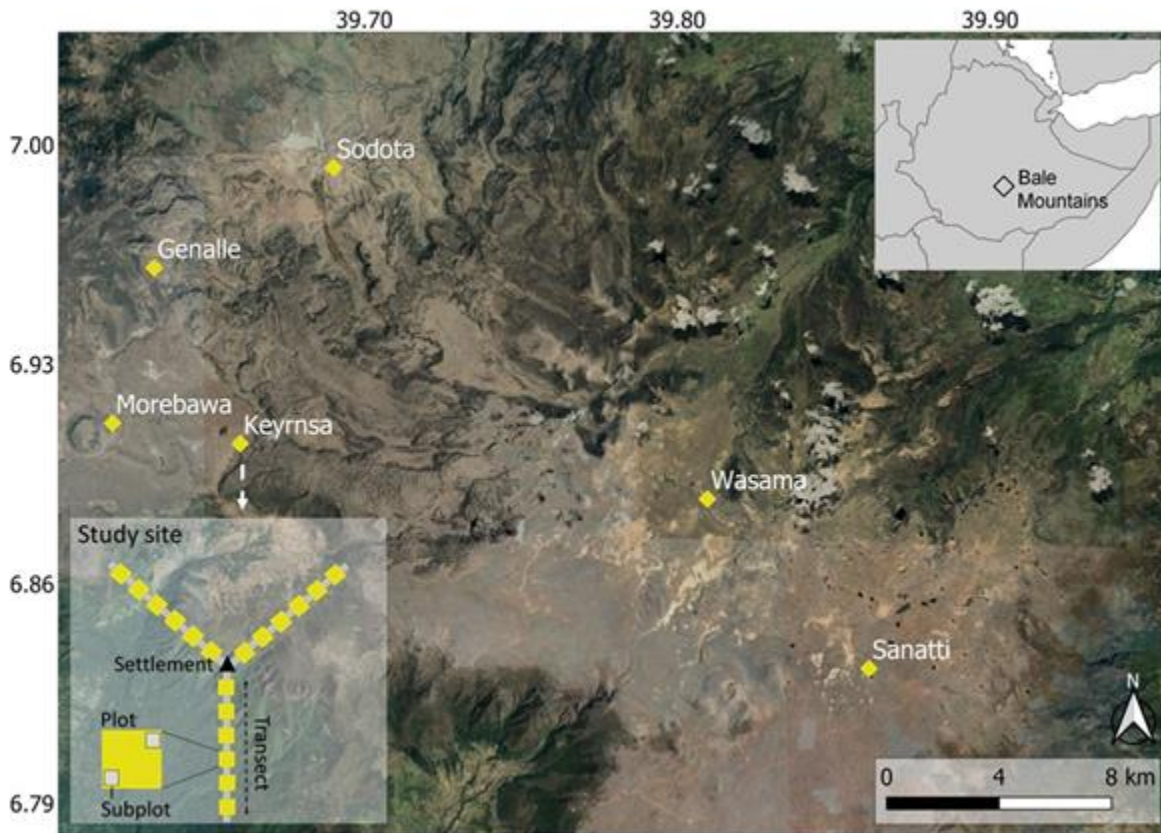


Fig. 1. Overview map of the Bale Mountains National Park and its location in southeast Ethiopia (top-right inset) and the six study sites, and detailed inset map (bottom-left) showing the set-up of one study location with three transects of 1.5 km length, six study plots along each transect and two subplots within each plot (for detailed description see Methods section “Study area”).

I undertook data collection during the late dry season (February and March) of 2021, but my intended wet season sampling was not possible due to logistic and security reason. At each plot, I recorded (1) two proxy variables characterizing and quantifying the intensity of grazing and other possible human activities: (1.a) settlement type (seasonal vs permanent settlement at center), and (1.b) distance from the settlement, a proxy for grazing intensity and for other possible human activities; (2) abundance of livestock dung (cattle and horses), a proxy for

livestock grazing intensity; (3) giant root-rat burrow density; and (4) vegetation variables. For giant root-rat burrow density, I used only fresh burrows as my main interest was to reflect the species' current burrowing activity and link it to current human activities and vegetation patterns. Giant root-rat fresh burrows are easily distinguished from old burrows in that the former are freshly open or plugged holes that are currently active. However, giant root-rat old burrows are abandoned burrows, with holes open or plugged with weathered soil, partially or wholly covered by vegetation regrowth, and sometimes occupied by other small rodents (Sillero-Zubiri et al. 1995; Šklíba et al. 2017; Asefa et al. 2022). I recorded vegetation data within two 10 m × 10 m subplots established at opposite corners of each plot. The size of plots and subplots were chosen to be comparable to our recent study (Asefa et al. 2022). In each of these subplots, I identified all plants to species level, except grasses which were collectively recorded as a single morpho-species, and estimated, in 5% intervals, percentage cover of each species. Based on Miehe and Miehe's (1994) elevational distribution of plants species in the montane and alpine areas, about 10 grass species are expected to occur in the study area, which collectively have an average cover of 15-20%. This grouping of grasses to a single morpho-species may consistently underestimate species richness and modulate diversity values, but I could not avoid this potential bias because many grasses were overgrazed and difficult to identify at species level during my survey. I also recorded percentage cover of overall vegetation. For analyses on the plot level, I averaged cover values of overall vegetation converted into proportion and combined species lists obtained from the two subplots and calculated the cumulative number of species (species richness).

3.3.4 Data analysis

I used path analyses to simultaneously quantify and test (1) the effects of human settlement type differentiating between traditional seasonal vs permanent, and distance from settlement on livestock grazing intensity; (2) the direct and indirect effects of settlement type, distance from settlement, livestock grazing and vegetation variables (i.e. vegetation cover and plant species

richness) on giant root-rat burrow density; and (3) the potential influences of human activities on the reciprocal effects of giant root-rat burrow density on the vegetation variables. Thus, to disentangle the effect of vegetation patterns on giant root-rat burrow density and *vice-versa*, I defined two sets of path models, each consisting of two path models involving one of the two vegetation variables as a predictor or response (Shipley 2009; for detail see also Figs. 2–5). For each path model, I fitted three multiple regression models using the glmmTMB R package (Brooks et al. 2017). I conducted all analyses in the R environment (R Core Team 2020) and the full R-script of all analyses is given in Supporting Information 1.

I first fitted each regression using generalized linear mixed-effects models (GLMM), specifying transect nested within site as random variables, to account for their potential effects on the response variables that would not be explained by the fixed-effect variables. Whenever model convergence problems were detected, I updated such models by changing the default optimizer `nlminb()` to the `BFGS()` option from `optim()` function of the glmmTMB R package (Brooks et al. 2017), which led to model convergences in all cases (Brooks et al. 2017). I then used diagnostic plots in the DHARMA R package (Hartig 2021) and tested each fitted model for uniformity, dispersion, zero-inflation, homoscedacity, and outliers. Whenever significant violations in any of these assumptions were detected, I revised model structure and rerun again by adding zero-inflation and/or dispersion model components, depending on the diagnostic test results (Brooks et al. 2017; Hartig 2021). This model revision solved the assumption problems detected. Summary of model specification and error distribution used for all finally fitted regression models are provided on Table 1 and briefly described as follows.

For path models in which giant root-rat burrow density was a response, the first regression modelled the effects of settlement type and distance from settlement on livestock dung abundance using GLMM, with a negative binomial error distribution in the glmmTMB R package (Brooks et al. 2017). In the second regression, I included settlement type, distance from settlement and livestock dung abundance as fixed effects and either vegetation cover (modelled

using beta-family error distribution) or plant species richness (modelled using negative binomial error distribution) as a response. I fitted these regressions with a dispersion component added to each model. Finally, I analysed the effects on giant root-rat burrow density of settlement type, distance from settlement, livestock dung density and either vegetation cover or plant species richness, using a zero-inflated GLMMs (Table 1). For the second set of path models analysing the reciprocal effects of giant root-rat burrow density on vegetation variables and the influences of human activities on the effects, I reversed path directions between each of the two vegetation variables and giant root-rat burrow density. Here, I fitted three regression models for each path model and the first regression was identical as for previous path models. The second regression, which was also identical across the two path models in this set, modelled giant root-rat burrow density as a response using a GLM with negative binomial error distribution, and settlement type, distance from settlement and livestock dung abundance as fixed effects. In the final regression models, I included settlement type, distance from settlement, livestock dung abundance and giant root-rat burrow density as fixed effects, and either vegetation cover or plant species richness as a response (for details on model specifications see Table 1).

For each final regression model, described above, I checked for multicollinearity among predictors using the ‘performance’ R package (Lüdtke 2021); this confirmed lack of collinearity problem, in all models collinearity values ranged between 1.00–1.67. Thus, I obtained raw (unstandardized) regression coefficients and associated *p*-values of each predictor, as well as standardized path coefficients, using the ‘MuMIn’ R Package (Barton 2022). Finally, I obtained coefficient estimates of the indirect effect of each predictor on the response variable in each path model, as the product of the standardized path coefficients of two sequential paths in a model (Shipley 2009; for detail on the causal models, see Figs. 2–5). I tested the statistical significance of each indirect effect using the Sobel Test (Soper 2021). I also obtained

conditional and/or marginal R-squared values using the package ‘performance’ (Lüdtke 2021), to assess the proportion of variation of the response explained by the model.

Table 1. Description of regression model structure fitted using glmmTMB for path models analysing the effects of human activities and vegetation variables on giant root-rat burrow density (a), and the effects of human activities and giant root-rat burrow density on vegetation variables (b). Each regression model consists of fixed effects, random effects – indicated as “1|site/transect”, and, where applicable, zero-inflation and dispersion model components that are incorporated via ziformula and dispformula functions, respectively.

Response variable	Regression model structure
<i>(a) Effects of human activities and vegetation variables on giant root-rat burrow density</i>	
Level 1: Livestock dung abundance	Dung ~ settlement type + distance from settlement + (1 site/transect), family = nbinom2
Level 2(a): Vegetation cover	Vegetation cover ~ settlement type + distance from settlement + dung + (1 site/transect), dispformula = ~ dung, family = beta_family
Level 2(b): Plant species richness	Richness ~ settlement type + distance from settlement + dung + (1 site/transect), dispformula = ~ dung, family = nbinom2
Level 3(a): Giant root-rat burrow density	Giant root-rat burrow density ~ settlement type + distance from settlement + dung + vegetation cover + (1 site/transect), ziformula = ~ settlement type + dung + vegetation cover, family = nbinom2
Level 3(b): Giant root-rat burrow density	Giant root-rat burrow density ~ settlement type + distance from settlement + dung + plant species richness + (1 site/transect), ziformula = ~ settlement type + dung, family = nbinom2

(b) Effects of human activities and giant root-rat burrow density on vegetation variables

Level 1: Livestock dung abundance $\text{Dung} \sim \text{settlement type} + \text{distance from settlement} + (1|\text{site/transect}), \text{family} = \text{nbinom2}$

Level 2: Giant root-rat burrow density $\text{Giant root-rat burrow density} \sim \text{settlement type} + \text{distance from settlement} + \text{dung} + (1|\text{site/transect}), \text{ziformula} = \sim \text{settlement type}, \text{dispformula} = \sim \text{dung} + \text{settlement type} + \text{distance from settlement}, \text{family} = \text{nbinom2}$

Level 3(a): Vegetation cover $\text{Vegetation cover} \sim \text{settlement type} + \text{distance from settlement} + \text{dung} + \text{giant root-rat burrow density} + (1|\text{site/transect}), \text{family} = \text{beta_family}$

Level 3(b): Plant species richness $\text{Richness} \sim \text{settlement type} + \text{distance from settlement} + \text{dung} + \text{giant root-rat burrow density} + (1|\text{site/transect}), \text{dispformula} = \sim \text{dung}, \text{family} = \text{nbinom2}$

3.4 Results

I recorded a mean (\pm SE) number of 53.28 ± 4.21 livestock dung per plot, ranging from 0–500 across plots and density of 852.48 ± 67.36 per ha. I counted a mean number of 30.76 ± 4.12 giant root-rat burrows per plot (range: 0–333 burrows), with a density at 492.16 ± 65.92 burrows per ha. Mean proportion of vegetation cover was 0.43 ± 0.12 (range: 0.00–0.92). I recorded a total of 68 plant species across plots, with a range of 2 to 24 species and a mean number of 10.57 ± 0.26 of species per plot.

3.4.1 Human activities and their effects on vegetation

The regression models analysing the effects of human settlement type, distance from settlement and livestock grazing intensity on vegetation explained 51–100% of the total variation in the response variable (Table 2 and 3). I found a decreased livestock dung abundance with increasing distance from settlement areas ($Z = -11.189$, $P < 0.001$), and a non-significant effect of settlement type on dung abundance ($Z = 0.302$, $P > 0.05$) (Table 2 and 3). I found a significantly higher vegetation cover at seasonal human settlement areas compared with that at permanent settlement areas ($Z = 2.200$, $P < 0.01$; Table 2), while I found decreased vegetation cover with increasing livestock dung abundance ($Z = -3.222$, $P < 0.01$, Table 2). Although the direct positive effect of distance from settlement on vegetation cover was non-significant (see Table 2), it had a significant indirect positive effect due to its negative association with livestock dung abundance (Sobel test = 2.644, $P < 0.05$, Table 4) that in turn also had a negative effect on vegetation cover. Regarding the effects of human activities on plant species richness, I found significantly lower richness at seasonal settlements compared with that at permanent ones ($Z = -2.068$, $P < 0.05$; Table 3).

Table 2. Results of regression models analysing the effects of settlement type (seasonal vs permanent), distance from settlement, livestock dung abundance and vegetation cover on giant root-rat burrow density. Given are unstandardized regression coefficients and their standard errors (Unstd. Est. \pm S.E.), standardized path coefficients (Std. Est.), and marginal/conditional R^2 values. Z-values with asterisk indicate significant effects at levels of * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

Variables	Unstd. Est. \pm S.E.	Std. Est.	Z-value
Level 1: Abundance of livestock dung (Conditional/marginal R^2: 0.51/0.32)			
Intercept	4.5638 \pm 0.2025		22.533***
Settlement type (seasonal)	0.0340 \pm 0.1127	0.0199	0.302
Distance from settlement	-0.0014 \pm 0.0001	-0.6558	-11.189***
Level 2: Vegetation cover (Conditional/marginal R^2: 1.00/0.64)			
Intercept	-0.3309 \pm 0.1514		-2.186*
Settlement type (seasonal)	0.2544 \pm 0.1156	0.2165	2.200*
Distance from settlement	0.0002 \pm 0.0001	0.1453	1.488
Livestock dung abundance	-0.0045 \pm 0.0014	-0.4149	-3.222**
Level 3: Giant root-rat burrow density (Conditional/marginal R^2: 0.23/0.11)			
Intercept	4.3281 \pm 0.5002		8.654***
Settlement type (seasonal)	-0.3546 \pm 0.2363	-0.0885	-1.501
Distance from settlement	0.0003 \pm 0.0003	0.0622	0.933
Livestock dung abundance	0.0047 \pm 0.0038	0.1266	1.219
Vegetation cover	-1.8808 \pm 0.6132	-0.1671	-3.067**

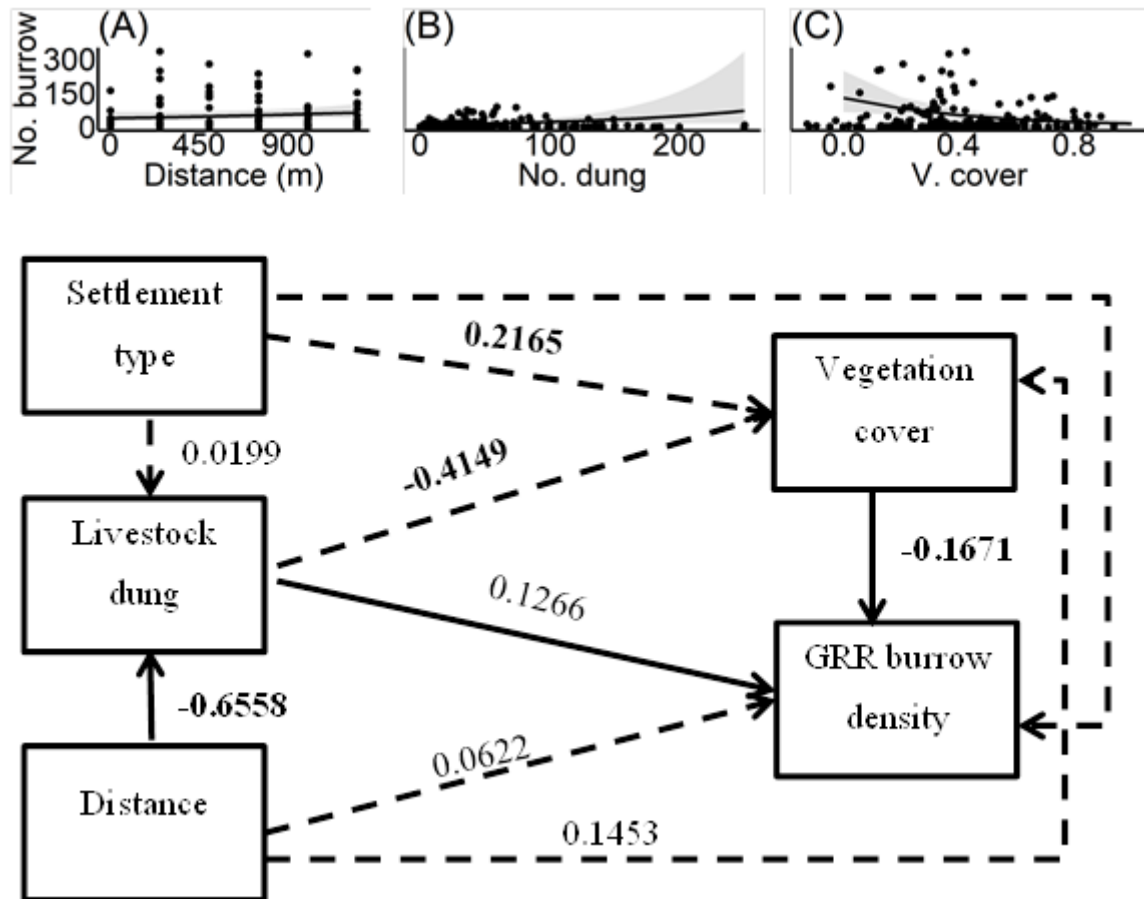


Fig. 2. Standardized path coefficients of the direct effects of settlement type (seasonal), distance from settlement, livestock dung abundance and vegetation cover on giant root-rat burrow density. Path coefficients indicated in bold font or path in solid line denote statistically significant effect at $P < 0.05$. The inset figures show the relationships of distance from settlement (A), livestock dung abundance (B) and vegetation cover (C) with giant root-rat burrow density.

Table 3. Results of regression models analysing the direct effects of settlement type (seasonal vs permanent), distance from settlement, livestock dung abundance (proxy for grazing intensity) and plant species richness on giant root-rat burrow density. Given are unstandardized regression coefficients and standard errors (Unstd. Est. \pm S.E), and standardized coefficients (Std. Est.), Z-values, and marginal/conditional R^2 values of each regression model depending on if random effects were included in the models (see methods for details). Z-values with asterisk indicate significant effects at levels of * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

Variables	Unstd. Est. \pm S.E.	Std. Est.	Z-value
Level 1: Abundance of livestock dung (Conditional/marginal R²: 0.51/0.32)			
Intercept	4.5638 \pm 0.2025		22.533***
Settlement type (seasonal)	0.0340 \pm 0.1127	0.0199	0.302
Distance from settlement	-0.0014 \pm 0.0001	-0.6558	-11.189***
Level 2: Plant species richness (Conditional/marginal R²: 1.00/0.10)			
Intercept	2.4340 \pm 0.1118		21.768***
Settlement type (seasonal)	-0.0884 \pm 0.0434	-0.0686	-2.038*
Distance from settlement	0.00001 \pm 0.00001	0.0501	0.040
Livestock dung abundance	-0.0010 \pm 0.0006	0.0755	-1.605
Level 3: Giant root-rat burrow density (Conditional/marginal R²: 0.24/0.05)			
Intercept	3.2425 \pm 0.5977		5.425***
Settlement type (seasonal)	-0.3524 \pm 0.2816	-0.1387	-1.252
Distance from settlement	0.0002 \pm 0.0003	0.0734	0.675
Livestock dung abundance	0.0043 \pm 0.0039	0.1828	1.091
Plant species richness	0.0306 \pm 0.0341	0.0931	0.898

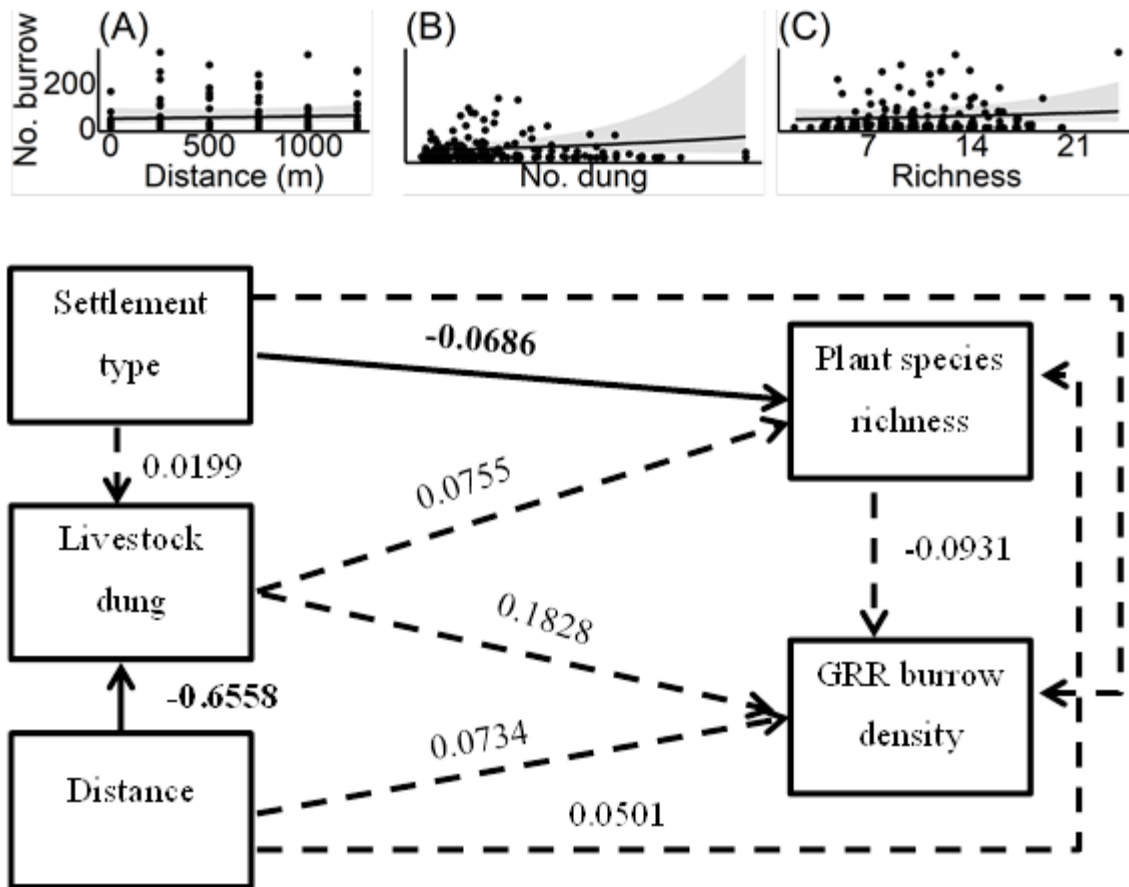


Fig. 3. Standardized path coefficients of the direct effects of settlement type, distance from settlement, livestock dung abundance and plant species richness on giant root-rat burrow density. Path coefficients indicated in bold font, above a solid line path, denote statistically significant effect at $P < 0.05$. The inset figures show the relationships of distance from settlement (A), livestock dung abundance (B) and plant species richness (C) with giant root-rat burrow density.

Table 4. Estimated coefficients of indirect effects (IE) on giant root-rat burrow density of settlement type (seasonal) and distance from settlement (Distance) via livestock dung abundance and vegetation variables, and of livestock dung abundance via vegetation variables.

*: $P < 0.05$.

Predictor	Mediator	Response	IE	Sobel test statistic
<i>Path model 1: Effects of human activities and vegetation cover on giant root-rat burrow density</i>				
Settlement type	Livestock dung	Vegetation cover	-0.0083	-0.3
Distance	Livestock dung	Vegetation cover	0.2721	2.644*
Settlement type	Livestock dung	Root-rat burrow density	0.0013	-0.302
Distance	Livestock dung	Root-rat burrow density	-0.0445	-2.056*
Settlement type	Vegetation cover	Root-rat burrow density	-0.0139	-2.211*
Distance	Vegetation cover	Root-rat burrow density	-0.0093	-1.387
Livestock dung	Vegetation cover	Root-rat burrow density	0.0266	2.165*
<i>Path model 2: Effects of human activities and plant species richness on giant root-rat burrow density</i>				
Settlement type	Livestock dung	Plant species richness	0.0015	0.295
Distance	Livestock dung	Plant species richness	-0.0495	-1.412
Settlement type	Livestock dung	Root-rat burrow density	0.0036	0.291
Distance	Livestock dung	Root-rat burrow density	-0.1199	-1.099
Settlement type	Plant species richness	Root-rat burrow density	-0.0064	-0.825
Distance	Plant species richness	Root-rat burrow density	0.0047	0.736
Livestock dung	Plant species richness	Giant root-rat burrow density	0.0070	0.758

3.4.2 Effects of human activities on giant root-rat burrow density

The regression model in the path models analysing the effects of human settlement, livestock grazing and vegetation on giant root-rat burrow density explained 23–24% of the total variation

in the response variables (Tables 2 and 3). Considering the path model examining the effects of settlement, livestock dung abundance and vegetation cover on giant root-rat burrow density, a significant direct effect was found only for increasing vegetation cover that led to decreased root-rat burrow density ($Z = -3.222$, $P < 0.01$). I found that increasing livestock dung abundance and indirectly via vegetation cover (Sobel test = 2.165, $P < 0.001$; Table 4; Fig. 2) led to increased giant root-rat burrow density ($Z = 2.096$, $P < 0.05$; Table 2). Seasonal settlement type (Sobel test = -2.211, $P < 0.05$), compared with permanent settlement type, and distance from settlement (Sobel test = -1.387, $P < 0.05$) had significant indirect negative effects on giant root-rat burrow density, both via vegetation cover (Table 4). Increasing livestock dung abundance resulted in increased vegetation cover that in turn resulted in increased giant root-rat burrow density (Sobel test = 2.165). In the second path model including plant species richness, I did not find a significant direct and/or indirect effect of settlement type, distance from settlement, livestock dung abundance, or plant species richness on giant root-rat burrow density (Tables 3 and 4; Fig. 3).

Table 5. Results of path models analysing the effects of giant root-rat burrow density on plant species richness and vegetation cover. Given for each regression model are conditional/marginal R^2 values depending on if random effects were included in the models (see methods for details) and values of unstandardized regression coefficients and their standard errors (Unstd. Est. \pm S.E.), and standardized path coefficients (Std. Est.). Z-values with asterisk indicate significant effects at significance levels of * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

Variables	Unstd. Est. \pm S.E.	Std. Est.	Z-value
Level 1: Livestock dung abundance (Conditional/marginal R^2: 0.51/0.32)			
Intercept	4.5638 \pm 0.2025		22.533***
Settlement type (seasonal)	0.0340 \pm 0.1127	0.0199	0.302

Distance from settlement	-0.0014 ± 0.0001	-0.6558	-11.189***
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Level 2: Giant root-rat burrow density (Conditional/marginal R²: 0.21/0.05)

Intercept	3.4871 ± 0.5355		6.512***
Settlement type (seasonal)	-0.3445 ± 0.2974	-0.0717	-1.158
Distance from settlement	0.0002 ± 0.0003	0.0403	0.710
Livestock dung abundance	0.0057 ± 0.0054	0.1283	1.050

Level 3(a): Vegetation cover (Conditional/marginal R²: 0.86/0.72)

Intercept	-0.3332 ± 0.1647		-2.022*
Settlement type (seasonal)	0.2671 ± 0.1015	0.1671	2.631**
Distance from settlement	0.0004 ± 0.0001	0.1878	2.486*
Livestock dung abundance	-0.0022 ± 0.0012	-0.3821	-4.700***
Giant root-rat burrow density	-0.0022 ± 0.0009	-0.1674	-2.605**

Level 3(b): Plant species richness (Conditional/marginal R²: 1.00/0.12)

Intercept	2.4230 ± 0.1119		21.644***
Settlement type (seasonal)	-0.0933 ± 0.0434	-0.1323	-2.152*
Distance from settlement	-0.0001 ± 0.0006	-0.0012	-0.015
Livestock dung abundance	-0.0011 ± 0.0006	-0.1641	-1.702
Giant root-rat burrow density	0.0006 ± 0.0004	0.0944	1.566

Table 6. Estimated coefficients of indirect effects (IE) on plant species richness and vegetation cover of settlement type (seasonal) and distance from settlement (Distance) via livestock dung abundance and giant root-rat burrow density, and of livestock dung abundance via giant root-rat burrow density. *: P < 0.05.

Predictor	Mediator	Response	IE	Sobel test statistic
<i>Path model 1: Effects of human activities and giant root-rat burrow density on vegetation cover</i>				
Settlement type	Livestock dung	Vegetation cover	-0.0076	-0.298
Distance	Livestock dung	Vegetation cover	0.2506	1.818*
Settlement type	Root-rat burrow density	Vegetation cover	0.0012	1.047
Distance	Root-rat burrow density	Vegetation cover	-0.0067	-0.643
Livestock dung	Root-rat burrow density	Vegetation cover	-0.0215	-0.969
<i>Path model 2: Effects of human activities and giant root-rat burrow density on plant species richness</i>				
Settlement type	Livestock dung	Plant species richness	-0.0033	-0.298
Distance	Livestock dung	Plant species richness	0.1076	1.218
Settlement type	Root-rat burrow density	Plant species richness	-0.0068	-0.917
Distance	Root-rat burrow density	Plant species richness	0.0038	0.609
Livestock dung	Root-rat burrow density	Plant species richness	0.0121	0.863

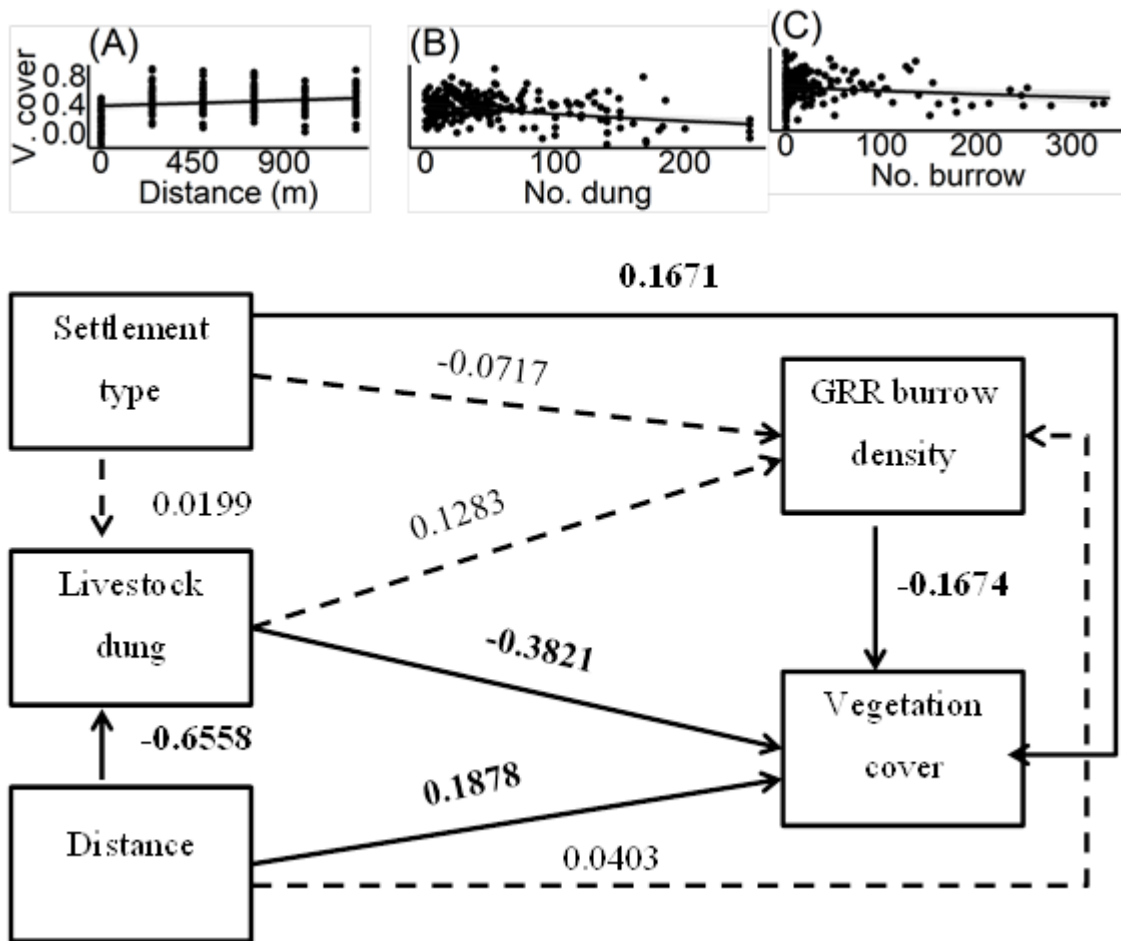


Fig. 4. Standardized path coefficients of the direct effects of settlement type (seasonal), distance from settlement, livestock dung abundance and giant root-rat burrow density on vegetation cover. Path coefficients indicated in bold font, above a solid line path, denote statistically significant effect at $P < 0.05$. The inset figures show the relationships of distance from settlement (A), livestock dung abundance (B) and giant root-rat burrow density (C) with vegetation cover.

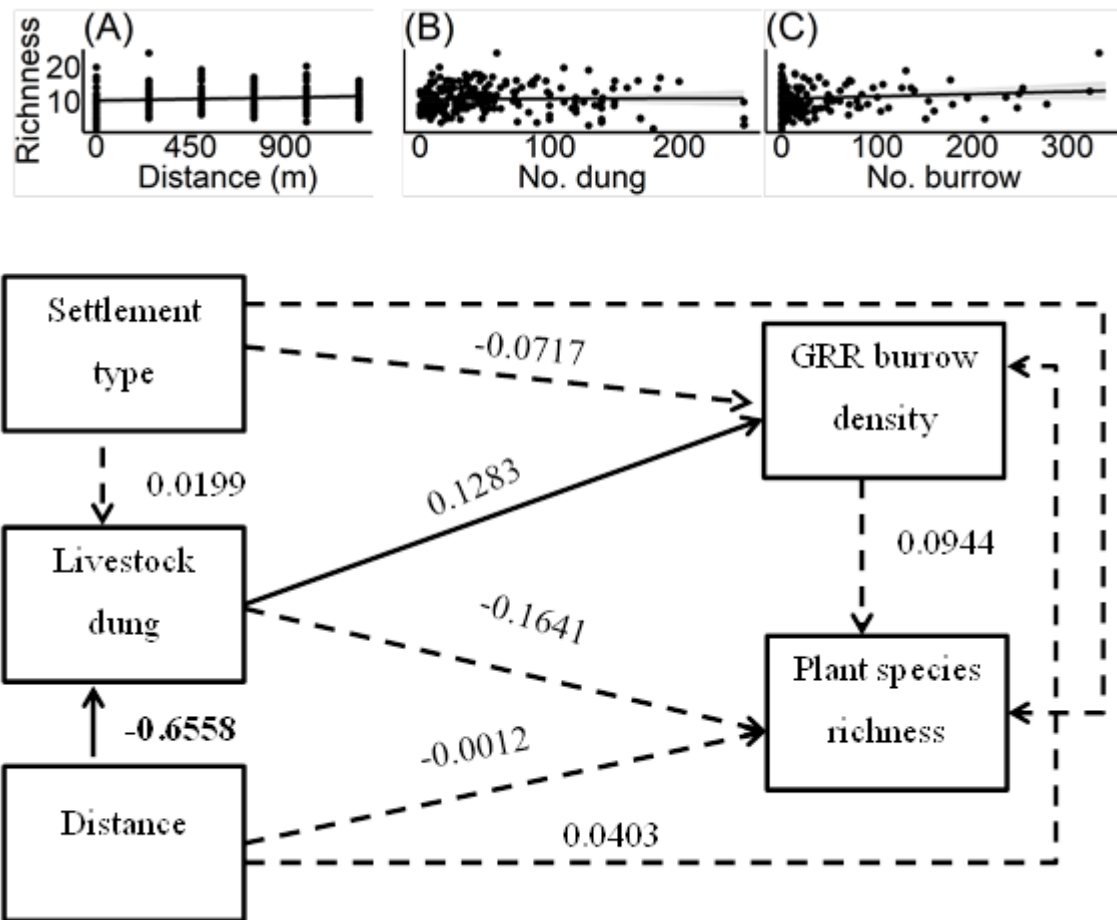


Fig. 5. Standardized path coefficients of the direct effects of settlement type (seasonal), distance from settlement, livestock dung abundance and giant root-rat burrow density on plant species richness. Path coefficients indicated in bold font, above a solid line path, denote statistically significant effect at $P < 0.05$. The inset figures show the relationships of distance from settlement (A), livestock dung abundance (B) and giant root-rat burrow density (C) with plant species richness.

3.4.3 Influences of human activities on reciprocal effects of giant root-rat on vegetation

In the path models analysing the reciprocal effects of giant root-rat on vegetation, regression models explained 21–100% of the total variations in the response variables (Tables 5). Examining the reciprocal effect of giant root-rat burrow density on vegetation cover, I found a significantly decreased vegetation cover with increasing giant root-rat burrow density ($Z = -2.605$, $P < 0.05$; Table 5; Fig. 4). I also found higher vegetation cover at the seasonal settlement

type, compared to the permanent settlement type, increased vegetation cover with increasing distance from settlement (Table 5). Considering the reciprocal effect of giant root-rat burrow density on plant species richness, I neither found a significant direct effect of giant root-rat burrow density on plant species richness, nor of the direct or indirect effect of settlement type, distance from settlement, or livestock dung abundance (Table 5 and 6; Fig. 5).

3.5 Discussion

My results demonstrate that giant root-rat burrow density and vegetation cover reciprocally affect each other and are modulated by human activities. In line with my predictions, I found increased livestock dung abundance with decreasing distance from settlement, suggesting heavier grazing intensity near settlements. Increasing livestock dung abundance in turn led to decreased vegetation cover, and indirectly via vegetation cover led to increased giant root-rat burrow density. This positive association of giant root-rat burrow density with livestock grazing intensity and decreasing distance to human settlement sites is an interesting finding of my study that revealed the root-rat's synanthropic association, a phenomenon that has not been well studied, although previous research has indicated a potential synanthropic association (Ossendorf et al. 2019) as the root-rats are known to prefer sites with lower vegetation cover (Tallents 2007; Šklíba et al. 2017; Asefa et al. 2022). Aligning with previous research, my results indicate giant root-rats reciprocally negatively affected vegetation cover, with human activities modulating this reciprocal association.

My finding of increased giant root-rat burrow density with livestock grazing intensity, indirectly via reduced vegetation cover, is in line with results of our recent independent study on giant root-rats (Asefa et al. 2022). This finding suggests that livestock grazing-induced decreases in vegetation cover potentially benefit habitat occupancy of subterranean small rodents, including giant root-rats that are adapted to life in grassland ecosystems (Šumbera et al. 2018). In fact, giant root-rats are found to be very abundant even in heavily degraded areas caused by livestock grazing around settlement areas (Tallents 2007; Šklíba et al. 2017). Similar

studies on other subterranean rodents, such as the Plateau zokor (*Myospalax baileyi*) in the Chinese Tibetan Plateau (Wang et al. 2019, 2020) and black-tailed prairie dogs (*Cynomys ludovicianus*, Knowles 1986), have also reported positive effects of livestock grazing on rodents. Besides this positive effect of livestock grazing on giant root-rat habitat, it is also possible that livestock grazing affects nutrient cycling, by increasing the availability of nitrogen for rapid regrowth of the grazed plants, which results in increased biomass of young, palatable plant tissues (Hobbs 1996; Tallents 2007). This can improve the quality of food for herbivorous rodents, such as giant root-rats. Despite this, some other studies showed that heavy livestock grazing negatively impacts a marsupial ecosystem engineer (Neilly & Schwarzkopf 2018; Eldridge & Soliveres 2023).

Consistent with my second prediction, livestock dung abundance also appeared to modulate the association of distance from settlement with giant root-rat burrow density, as shown by the indirect, via livestock dung abundance, negative effect of distance from settlement on giant root-rat burrow density (see Table 4). This result is a consequence of heavier livestock grazing intensity around settlement areas, thereby reducing vegetation cover and creating open habitat for giant root-rats and other rodents (see also Reitalu et al. 2010). This association of giant root-rats with human settlement appears to be stronger at permanent settlement areas, as shown in my finding of decreased giant root-rat burrow density at seasonal settlement sites due to higher vegetation cover at seasonal than at permanent settlements (see Table 2 and 4). The fostering effects of settlement abandonment on vegetation cover have also been reported in many studies elsewhere (e.g. Pavlů et al. 2018; Mayer et al. 2019) and can be attributed to colonization of grazing-induced degraded areas by disturbance-tolerant plant species that exploit abundantly available resources and to relaxation from damages due to temporary grazing abandonment (Bokdam 2001; Niu et al. 2019). My above findings highlight the presence of a synanthropic association of giant root-rats, which has not been revealed prior to this study. My findings of an overall positive effect of livestock grazing on giant root-rat have to be interpreted with

caution for three main reasons. Firstly, my study did not consider the potential effects of sheep and goats which are reported to affect subterranean rodents differently, mainly via browsing, to that of large-sized livestock (cattle and horses) (Wang et al. 2019, 2020). Secondly, my study period encompassed only the dry season. However, since food abundance both for livestock and giant root-rat is higher during the wet season, grazing intensity and its effects on giant root-rat burrow density may differ in the wet season (Vial et al. 2011; Šklíba et al. 2017), which likely is weaker association in the wet season as more food available. In addition, Šklíba et al. (2017) have found that giant root-rats show a slight differences in their mobility between dry and wet seasons, their engineering activities and impacts can also differ between wet season. And, thirdly, habitat modification and degradation due to livestock overgrazing has been considered as the major threat to the giant root-rat (Lavrenchenko & Kennerley 2016; BMNP 2017). This may suggest that the positive association of giant root-rats with livestock grazing intensity I found, as also reported by Šklíba et al. (2017), may not necessarily mean that grazing is always beneficial to giant root-rats, rather may suggest giant root-rats' reliance on underground parts of plants as a food source where aboveground vegetation is degraded (for detail on feeding habit of giant root-rat, see Yaba et al. 2011). Thus, it seems that livestock grazing is likely a detrimental threat to survival of giant root-rats when the impacts involve both aboveground and belowground vegetation biomass. In order to avoid the potential negative impacts of the currently growing unregulated grazing practices in the Bale Mountains on the giant root-rats and other co-occurring endemic rodents, planning and implementation of grazing management policy should rely on understanding of thresholds of grazing level beneficial and tolerable to giant root-rats. In the path model including species richness as a predictor, the lack of significant effect of plant species richness on giant root-rat burrow density contradicts my expectation and the positive relationship found in our recent study on giant root-rat (Asefa et al. 2022). The discrepancy in results of these studies seem to be due to differences in the sampling approach, more wetland habitats were sampled in the previous study which in turn

was positively associated with higher plant species richness (Asefa et al. 2022). Yet, I believe that my present finding is more plausible; particularly, considering the food generalist behaviour of the giant root-rats (Beyene 1986; Yaba et al. 2011), plant species richness may play minimal role in determining the rodents' distribution.

Analysing the reciprocal effects of giant root-rat burrow density on vegetation variables and the effects of human activities, my findings showed that increasing giant root-rat burrow density led to decreased vegetation cover. This finding is consistent with the well-known negative effects of subterranean rodents on vegetation cover (Beyene 1985; Wu et al. 2015; Haussmann 2017; Šklíba et al. 2017; Asefa et al. 2022; see also Valkó et al. 2021 for a similar species, the Steppe Marmot (*Marmota bobak*) and is attributed to vegetation biomass removal by giant root-rat's bioturbation and direct feeding. Through this reciprocal effect, giant root-rats' engineering does not only affect vegetation but also positively affects the giant root-rats themselves, because the reduction in vegetation cover they cause eventually creates higher quality habitat. This supposition holds true, in light of findings of previous studies (Yalden 1975; Miede & Miede 1992; Šklíba et al. 2017; Wraase et al. 2022) that giant root-rats' own long-term burrowing activity plays an important role in their habitat selection. Despite the significant effects of giant root-rat burrow density on vegetation cover, I found a non-significant effect on plant species richness, which is in line with finding of our previous study on giant root-rat (Asefa et al. 2022), as well as studies on other rodents elsewhere (e.g. Wu et al. 2015).

Overall, my results showed that vegetation and giant root-rat reciprocally affect each other and human activities related to settlement and livestock grazing influence these natural reciprocal relationships, which likely hold true for other subterranean rodents. Here, human activities interactively caused decreased vegetation cover that in turn led to increased giant root-rat burrow density, although these effects are more pronounced at permanent settlements. Reciprocally, giant root-rat engineering is found to further reduce vegetation cover that has continuously been affected by human activities, thereby enhancing their habitat suitability

(Šklíba et al. 2017; Wraase et al. 2022). These results highlight that giant root-rats play a synanthropic ecological engineering role in shaping vegetation cover by reducing cover but leading to increased cover after abandoning their burrows (see Šklíba et al. 2017); thereby contributing to our understanding of the effects of subterranean burrowing herbivore animals on ecosystem structure and processes in the face of growing biodiversity loss due to global (e.g. climate change) and local (e.g. human activities) change drivers. Despite this, results of this study should be interpreted cautiously, because I considered only present engineering activity of giant root-rats. Similar to many subterranean engineer rodents across the globe (e.g. Jones et al. 1997; Reichman & Seabloom 2002; Davidson et al. 2012), giant root-rats create a mosaic of sites differing in the age of the engineered burrow marks, which are known to differ in vegetation and soil characteristics (Šklíba et al. 2017). Contrary to the negative effects of present engineering I found in my study, past engineering activities of subterranean rodents are often known to positively affect vegetation cover and plant species richness due to colonization by plant species of new spaces and nutrient rich microhabitats created at old, abandoned rodent burrows (Zhang & Liu 2003; Šklíba et al. 2017). This implies that present and past engineering activities of rodents, including giant root-rats, can have antagonistic or opposite effects on vegetation variables and soil properties (Zhang & Liu 2003; Šklíba et al. 2017), a mechanism through which ecological engineering rodents likely lead to stable and resilient ecosystem structure and processes (see Jones et al. 1997). Thus, further research should focus on investigating the effects of human activities and giant root-rat past and present engineering activities on vegetation, including plant functional trait composition.

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Data availability

All relevant data are within the manuscript and its Supplementary Material files.

The original contributions and R code presented in the study will be made available online in the Dryad Digital Repository.

Conflict of interests

The authors have no conflict of interest to declare.

Chapter 4: Giant root-rat engineering and livestock grazing activities alter plant functional trait composition of an Afroalpine vegetation community in the Bale Mountains, Ethiopia

4.1 Abstract

Engineering disturbances from burrowing rodents and human activities, such as livestock grazing, profoundly impact ecosystem structure and functioning. Although we do know that human activities and rodent engineering modulate abundance, diversity and composition of plant communities, our knowledge and understanding of functional trait are positively or negatively linked to such disturbances is limited. This understanding is important to know the mechanisms through which human settlement and livestock grazing and rodent engineering influence plant community assembly. Here, I evaluated the changes in functional trait diversity and composition of vegetation communities along gradients of engineering disturbances of a subterranean endemic rodent, giant root-rat (*Tachyoryctes macrocephalus* RÜPPELL 1842) and human activities (settlement establishment and livestock grazing) in the Bale mountains of Ethiopia. I conducted RLQ and fourth-corner analyses to test for trait-environment (human activities/engineering) covariation. Overall, my results show an increase in plant functional trait diversity with increasing root-rat engineering and increasing human activities. Species functional traits, such as larger seed mass, stolonifereous vegetative propagation and prostrate stem were associated with increasing root-rat engineering along RLQ axis 1, while leaf size and leaf nitrogen content were associated with increasing human activities along axis 2. In conclusion, my study suggests that associations between plant traits, rodent engineering and human activities follow similar principles/mechanisms, i.e. these disturbances act as habitat filters that result in increased resource availability (e.g. space, light and nitrogen) and

microhabitat heterogeneity, thereby promoting species coexistence and ultimately resulting in a functional trait divergence.

Keywords: Functional trait dispersion, habitat filter, micro-habitat heterogeneity, disturbance, subterranean rodent.

4.2 Introduction

Plants are a crucial component of ecosystems as they are the primary biomass producers via photosynthesis and thus provide food directly for herbivores and indirectly for other higher order trophic levels (Díaz et al. 2019). The net primary production produced by plants provides the energy that drives most ecosystem processes (Eviner & Chapin 2003), and thus, changes in the patterns of plant community diversity and composition often results in changes in critically important ecological processes, such as the amount of net primary production, which in turn influence the extent, distribution, and diversity of organisms within ecosystems (Reichman & Seabloom 2002; Eldridge et al. 2023). Understanding the relationship of plants to environmental change caused by disturbances, e.g. rodent bioturbation, and human activities related to settlement and livestock grazing, will allow to project changes across trophic levels such as for herbivorous animals (Eldridge et al. 2023).

Subterranean rodents are particularly known as ecosystem engineers due to their extensive underground tunnel digging and mound building on the ground surface that greatly alter soil chemical and physical properties (Reichman & Seabloom 2002; Haussmann 2017), such as reduced soil particle size, redistribution of soil moisture and increased nutrient availability (Zhang et al. 2003; Escobedo et al. 2017). Furthermore, by creating a dynamic mosaic of burrow mounds varying in the age, such as fresh active burrow mounds, old abandoned burrow mounds and mima mounds, subterranean rodents engineering leads to increased microhabitat heterogeneity (Tallents & Macdonald 2011; Šklíba et al. 2017; Asefa et al. 2022). The effects of improved resource availability and increased microhabitat heterogeneity caused by rodent

engineering activities have been known to be increased plant species diversity and altered species composition (Huntly & Inouye 1988). However, rodents engineering disturbance that buries short vegetation underneath mounds and selective feeding has been shown to decrease diversity and modulate composition towards tall and unpalatable species (Jones et al. 2008; Asefa et al. 2022).

Similar to subterranean engineering rodents, human activities related to settlement establishment and livestock production have been known to impact vegetation structure and composition (Eldridge et al. 2016; FAO 2018; Filazzola et al. 2020). Livestock have strong direct and indirect effects on biodiversity and ecosystem processes, mainly through grazing, trampling, defecation and urination (Eldridge et al. 2016; Narantsetseg et al. 2018; Maestre et al. 2022). Moreover, grazing by livestock removes plant biomass, thereby directly reducing plant cover and eliminating grazing intolerant species (Tessema et al. 2011), and indirectly by creating open spaces for gap-colonizing plant species and promoting the dominance of unpalatable and grazing tolerant species (Tessema et al. 2011; Eldridge et al. 2016; Pavlů et al. 2018; Niu et al. 2019). Further, through trampling, livestock also directly reduces vegetation cover and height, regeneration and recovery from grazing impacts by damaging seedlings and vegetative organs (Eldridge et al. 2016). Finally, livestock dung deposition and urination affect nutrient cycling and can cause nutrient overloading which affects vegetation structure and diversity by facilitating encroachment of exploitive native and/or non-native plant species that may lead to biotic homogenization (Bokdam 2001; Dunne et al. 2011; Pavlů et al. 2018).

Both rodent engineering and human activities have been shown to influence plant community assembly. Besides the regional species pool (Cornell & Harrison 2014) and the dispersal ability of plants (Lebrija-Trejos et al. 2010), rodent engineering and human activities modulate the abiotic and biotic conditions and thus affects community assembly (Mayfield & Levine 2010; Escobedo et al. 2017). Thus, a species membership in a community established at a given

disturbed site is constrained by local abiotic ecological filters that select a subset of species from the regional pool and are able to arrive in the site based on their tolerance to the local environmental conditions modulated by rodent engineering or by human activities (Mayfield & Levine 2010). Furthermore, biotic filtering exerts a strong influence on the species that co-occur in a community and determining the final number and identity of species via competitive exclusion (Hardin 1960), and plant-herbivore trophic interactions that may lead to local elimination of certain plant species (Cadotte et al. 2011). However, the effects of such disturbances on vegetation community assembly operate through species' functional traits (Grime 1977). While we have a general understanding on how abiotic and biotic filtering governs community assembly, it is essential to understand whether different disturbances, including rodent engineering and human activities, modify the traits of vegetation communities through similar community assembly processes observed based on taxonomic study approaches.

A functional trait is “any of the life history, morphological, physiological or phenological features that, singly or in combination with other traits, impacts indirectly the fitness of plant species in a given environment” (Diaz et al. 2016). Functional traits are related to plant ecological strategies (Diaz et al. 2016). For example, leaf traits, such as leaf area and leaf nitrogen content, reflect leaf economic spectrum describing variation between conservative to acquisitive leaves, strategy to balance leaf construction against growth (Wright et al. 2004). Thus, studies focusing on how the diversity and composition of functional traits of plant communities are shaped by disturbances caused by rodent engineering and human activities provide important insights into mechanisms underpinning the assembly processes (Levine et al. 2016; Mouchet et al. 2010).

Rodent engineering and human activities have also been known to influence patterns of plant community functional trait diversity—i.e. a change from functional trait divergence to

convergence, and vice-versa—and functional trait composition (Eldridge et al. 2016; Escobedo et al. 2017). At local scale, rodents engineering and human activities that cause increased resource availability, such as space and nutrients, and habitat heterogeneity are expected to promote coexistence of individual plants with different traits via niche differentiation, ultimately resulting in increased functional trait diversity (Escobedo et al. 2017). On the other hand, rodents present burrowing activities and associated feeding, and livestock grazing influence environmental filtering process to select for individuals with similar traits that particularly are necessary or better adapted or resistant to that disturbance condition, likely resulting in decreased functional diversity of a community (Escobedo et al. 2017). Thus, understanding the assembly processes and underpinning mechanisms of how disturbances caused by rodent engineering and human activities affect plant functional traits is important to predict future changes.

In this study I evaluated the changes in functional trait diversity and composition of vegetation communities along gradients of engineering disturbances of a subterranean endemic rodent, giant root-rat (*Tachyoryctes macrocephalus* RÜPPELL 1842) and human activities in the Bale mountains of Ethiopia. To do so, I used six traits to identify the main dimensions of variation in leaf and growth traits and determined their association to root-rat engineering and human disturbances. Specifically, first I tested multivariate functional trait diversity in relation to disturbance, and then I identified the association between each trait and disturbance. I predicted increased functional trait diversity (functional trait divergence) with increasing root-rat engineering (fresh burrow density, old burrow density and presence of mima mound) and human activities (distance from settlement and livestock grazing intensity) since both disturbances are expected to create habitat heterogeneity and increased resources (space and nutrients). I also predicted plant seed mass, leaf area and leaf nitrogen content would increase

with root-rat and human disturbances, while stolonifereous and prostrate traits would be positively associated with root-rat engineering disturbances.

4.3. Materials and methods

4.3.1 Study area

This study was conducted in the Afroalpine ecosystem of the Bale Mountains National Park in South-Eastern Ethiopia (BMNP; 6.508–7.178N, 39.508–39.928E; Fig. 1) between December 2020 and February 2021. The Bale Mountains represent the largest area of Afroalpine vegetation over 3,000 m asl in Africa (Yalden 1983). Elevation in the Bale Mountains ranges between 1,500 and 4,377 m asl. The area experiences two rainy seasons, with lighter rains from March to June and the heavy rainy season from July to October, and a dry season between November and February; mean annual rainfall is approximately 1,000 mm (Miehe & Miehe 1994). The lowest and maximum recorded temperature in the Bale mountains is -15 °C and 26 °C, respectively (Miehe & Miehe 1994; OBARD 2007). The soils in the Bale Mountains are entirely volcanic in origin and mainly derived from the basaltic and trachytic parent rock, are fairly fertile silty loams of reddish-brown to black colour (Hillman 1986; Miehe & Miehe 1994). Vegetation types of the Bale Mountains' Afroalpine ecosystem include open grassland, grassland dotted with *Artemisia afra* shrub, *Helichrysum* dwarf-scrub, *Alchemilla* meadow, *Lobelia rhychopetalum*, and wetlands, such as alpine lakes, rivers, swamps and seasonal wetland grasslands; Tallents 2007).

Similar to many other alpine ecosystems in Africa, more rapid ecosystem changes have been detected in the Bale Mountains over the past 40 years (Tallents 2007; Johansson & Granström 2014; BMNP 2017). Reber et al. (2018) have recorded a total of 870 settlements (207 permanently inhabited, 449 seasonally inhabited, and 214 uninhabited) in the Afroalpine zone of the Bale Mountains. Socio-economic survey conducted in 2013 show 863 households, each having an average of four people, in the study area (BMNP, unpubl. data). For this study, I

considered distance from settlement and livestock dung abundance as proxies for overall human activities. The Bale mountains also represent the world’s oldest known high-altitudinal residential site (Ossendorf et al. 2019). The Bale Mountains region is included in Conservation International’s Eastern Afro-Montane Biodiversity Hotspot, with the BMNP being recognized as the single most important conservation area in Ethiopia (Williams et al. 2004).

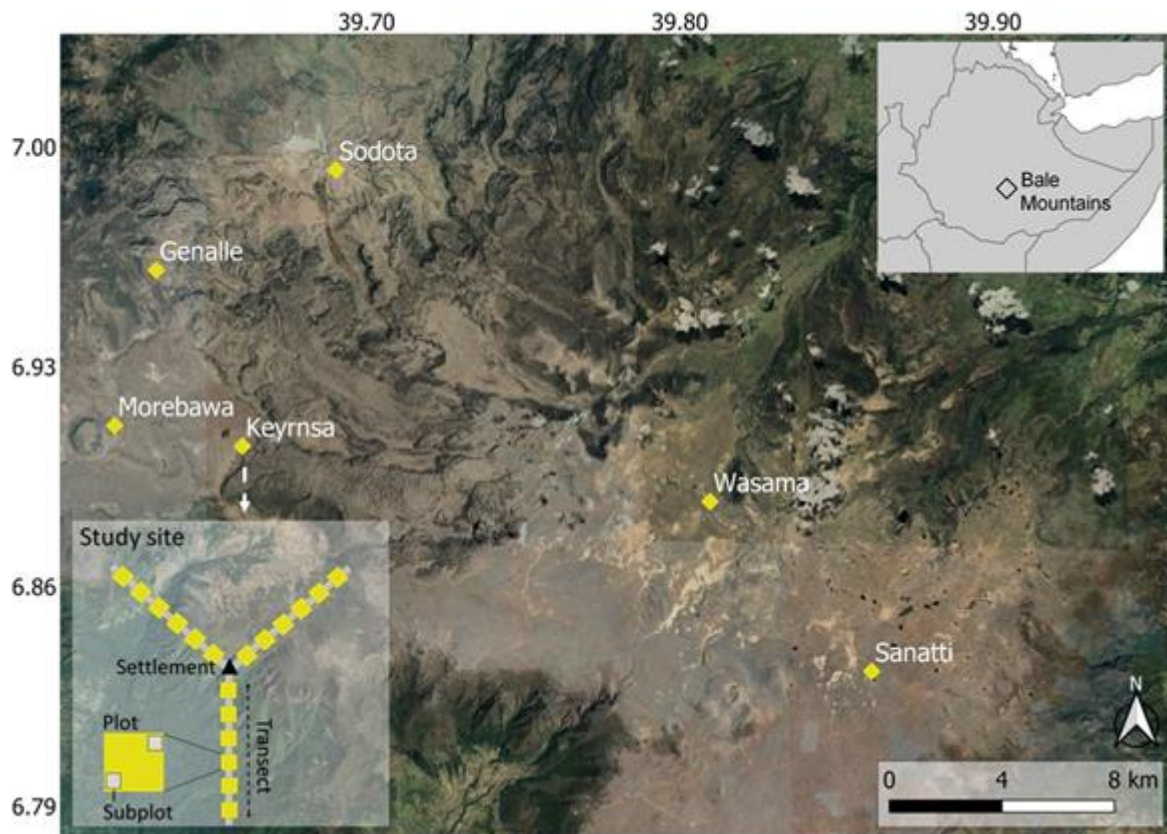


Figure 1. Overview map of the Bale Mountains National Park and its location in southeast Ethiopia (top-right inset) and the six study sites, and detailed inset map (bottom-left) showing the set-up of one study location with three transects of 1.5 km length, six study plots along each transect and two subplots within each plot (for detailed description see Methods section “Study area”).

4.3.2 Giant root-rat and its disturbances

Giant root-rat (*Tachyoryctes macrocephalus*, RÜPPELL 1842), a subterranean rodent, is one of the several small mammal species restricted to the Afroalpine belt of the Bale mountains (Sillero-Zubiri and Gottelli 1995). The species is restricted to <1,000 km² area at altitudes from 3,000 to 4,150 m above sea level (asl; Šumbera et al. 2018), where it is the main prey of the endangered Ethiopian wolf (*Canis simensis*) and numerous raptor species, such as golden eagle (*Aquila chrysaetos*), lesser-spotted eagle (*A. pomarina*), tawny eagle (*A. rapax*), Verreaux's eagle (*A. verreauxi*) and augur buzzard (*Buteo rufofuscus*) (Sillero-Zubiri et al. 1995; Asefa 2007). The giant root-rats are diurnal species and occur with a density of 63 animals per ha (Yalden 1985).

Giant root-rats construct extensive large underground burrow systems. An individual root-rat burrow system extends up to 34 m, which branches into short tunnels that comprise nesting and food caching and defecation chambers (Beyene 1986; Sillero-Zubiri et al. 1995; Yaba et al. 2011). Giant root-rats produce through types of burrow marks: fresh burrows, old burrows, and mima mounds. Fresh burrows are easily distinguished from old burrows in that the former are freshly open or plugged holes that are currently active. However, root-rat old burrows are abandoned burrows, with holes open or plugged with weathered soil, partially or wholly covered by vegetation regrowth, and sometimes occupied by other small rodents. Mima mounds are rounded dome-shaped structures formed by continually burrowing activities of giant root-rat that measure up to 27 m in diameter and 1.5 m high (Beyene 1986; Sillero-Zubiri et al. 1995; Šklíba et al. 2017; Wraase et al. 2023). Areas around root-rat mima mounds, which are their favoured habitats, are characterized by the predominance of bare soil, as they eject soil from their burrow systems when excavating, and when plugging their burrow holes at night for thermoregulation (Yalden 1975). They also graze and gather vegetation for bedding around burrows, which further denudes the landscape (Beyene 1986; Yaba et al. 2011). As a result,

GRRs have been known to cause changes in plant species diversity and composition (Tallents & MacDonald 2011; Šklíba et al. 2017).

4.3.3 Data collection

4.3.3.1 Human activities, root-rat burrow density and plant species abundance

To examine the relationships between human settlement, livestock grazing, giant root-rat burrow density and plant functional traits, I systematically selected six study sites, between 5 to 20 km apart, spanning across the entire distribution range of the giant root-rat. At each site, I selected two adjacent settlements (3–5 km apart) that were known to be established 30 years ago (Hillman 1986; BMNP 2017). Starting at the centre of each settlement, I established three 1.5 km long transects at an angle of 80–120° (see the inset map on Fig. 1). Along each transect, I established six 25 m × 25 m plots at a distance of 250 m from each other. In total, there were 216 plots covering an area of 13.5 ha.

I undertook data collection in February and March of 2021. At each plot, I recorded (1) rodent engineering activities measured as fresh burrow density, old burrow density and presence-absence of mima mounds; (2) human activities measured as distance from settlement and abundance of livestock dung; and (3) , and (3) plant species and species-specific cover.

I recorded plant species identity and species-specific cover data within two 10 m × 10 m subplots established at opposite corners of each plot. In each of these subplots, I identified all plants to species level, except grasses which were collectively recorded as a single morpho-species, and estimated, in 5% intervals, percentage cover of each species. For analyses on the plot level, I averaged cover values of each species obtained from the two subplots. Species occurring only in one plot, and grasses which were recorded as a single morphospecies were excluded from analysis. Thus, my data finally contained 61 species recorded across 216 plots.

4.3.3.2 Plant trait selection and data

I selected six plant traits which are known to having ecological functions related to resource use and acquisition, growth, survival and reproduction and thus influencing species responses to environmental changes caused by abiotic or biotic disturbances (Díaz et al. 2016). These traits were: 1) adult plant maximum height (cm), 2) leaf area (mm²), 3) stem shoot growth form, three categories: acaulescent (without aboveground stem), prostrate or erect, 4) dispersal mode, in three categories: seed alone, seed and rhizome and seed and stolones, 5) leaf nitrogen content (mg/g), and 6) seed mass (mg).

Adult plant height is a measure of whole plant size and indicates ability to pre-empt resources, and therefore outcompete them. It also relates to plant resistance to damages from herbivory and burrowing activities of subterranean rodents (Díaz et al. 2016). Stem shoot growth form can also be linked with plant mechanical strength and resistance to biotic filters (Chave et al. 2009; Zanne et al. 2010). I extracted information on species-specific maximum plant height and stem shoot growth form from botanical descriptions provided in the flora of Ethiopia and Eritrea (Edwards et al. 1995, 1997, 2000; Hedberg et al. 1989, 2003, 2004, 2006).

Leaf area, one-sided surface area of an individual lamina, is a measure of leaf size and is relevant for light interception and has important consequences for leaf energy and water balance (Farquhar et al. 2002). For leaf area estimation, I extracted information on minimum and maximum sizes of leaf length (L) and leaf width (W) the leaf blade (i.e. excluding petioles), as well as information on leaf shape type, from the flora of Ethiopia and Eritrea (Edwards et al. 1995, 1997, 2000; Hedberg et al. 1989, 2003, 2004, 2006). In the case of compound leaves, single leaflets were treated as analogous to simple leaves with the exception of highly dissected pinnae for which I used the entire pinnae. Then, I estimated LA using Montemgory formula: Leaf area = cLW, where c is a correction factor to account for differences in leaf shape type among species. I used c values, ranging between 0.55—0.79, reported by Schrader et al. (2021),

as their analysis is based on global level datasets that encompass larger number of species and all the 10 leaf shape types I identified within my community samples (see Supporting information 1). In some cases, a species is characterized by having an intermediate shape between two shape types, e.g., elliptic to orbicular, in which case I used average values.

Leaf nitrogen mass is directly related to photosynthesis and respiration and reflects a trade-off between two different costs that increase with higher nitrogen (to acquire N, and potentially suffer more herbivory), on the one hand, and the greater photosynthetic potential that higher nitrogen allows, on the other hand (Díaz et al. 2016). For most species, I compiled data on leaf nitrogen content from the TRY Plant Trait Database³⁰ (Kattge et al. 2022; <https://www.try-db.org>, accessed 20 February 2023), and for the remaining species for which traits are not included in the TRY database I extracted from published literature.

Seed mass (mass of an individual seed plus any additional structures that assist dispersal and do not easily detach) indexes species along a dimension describing the trade-off between seedling competitiveness and survival on the one hand, and dispersal and colonization ability on the other (Thompson et al. 1993). I compiled data on seed mass for all species from Seed Information Database (<https://ser-sid.org/> accessed April 2023). Similarly, vegetative dispersal is an adaptation to resist to/recovery from herbivory damages and an adaptation strategy to compensate the erratic seed production and seedling establishment in alpine habitats (Choler 2005). I compiled information on vegetative dispersal from flora of Ethiopia and Eritrea (Edwards et al. 1995, 1997, 2000; Hedberg et al. 1989, 2003, 2004, 2006).

Species names were standardized according to The World Flora Online database (www.worldfloraonline.org/; accessed April 2023), and each species and its synonyms, subspecies or local variety is represented by a single value for each trait. The number of observations per trait and species range from a single one to hundreds. Thus, I calculated the

geometric mean of all the records of a trait compiled. All data were unit-standardized and subjected to error detection and quality control (see below). Accordingly, I excluded trait records measured on juvenile plants and on plants grown under non-natural environmental conditions, duplicate trait records for same species on a particular trait, and potential outliers – trait records with a distance of >3 standard deviations from the mean of species (Diaz et al. 2016). The remaining dataset was used to calculate species mean trait values.

4.3.4 Statistical analysis

To investigate whether disturbance by rodents and humans increases functional diversity, I calculated functional dispersion (FDis) based on principal coordinates analysis (PCoA) of a Hill-Smith dissimilarity matrix (FDis; Laliberté & Legendre 2010). FDis is the mean distance of each species to the centroid of all species in the community, weighted by its abundance. Thus, a decrease in FDis means that community composition has shifted towards species that are more similar to each other, i.e. convergence, in response to increased disturbance. I used FDis because it is independent of species richness and takes into account species abundance; moreover, it can be used for multiple traits, as well as for continuous and categorical trait values (Laliberté & Legendre 2010). I calculated FDis using ade4 package (Dray & Dufour 200). I then examined the relationship between FDis and disturbance by rodents and humans using a beta regression with logit-link function using the betareg package (Cribari-Neto & Zeileis 2010). I fitted this without random effect as a model with random component (transect nested within site) showed singularity. I started with the full model and used AICc for model selection and averaging at a threshold of >2 . Then, I performed an automated model selection with subsets of the supplied ‘global’ model including all five predictor variables, using dredge function of MuMin package (Barton 2022). Thus, based on models with $\Delta\text{AICc} < 2$, I calculated model-averaged parameters, along with standard errors and confidence intervals, using model.avg function of package MuMin (Barton 2022). I also obtained sum of AICc weights

from all subsets of selected models (i.e. models with $\Delta\text{AICc} < 2$) containing a given predictor, from a set of models fitting all possible combinations of predictors.

To directly measure the link between species traits and environmental data, I used Dray and Legendre's (2008) novel version of the fourth-corner analysis provided in *ade4* package (Dray & Dufour 2007). Accordingly, I first conducted separate ordinations of the three tables: ordination of table L, which was done by a correspondence analysis (CA); table R, done by a hillsmith function with row weights of table L; and table Q, done by a hillsmith function with the column weights of table L (Dray & Dufour 2007; Dray & Legendre 2008). To evaluate the global, or their joint multivariate relationship, significance of the trait-environment relationships, I conducted RLQ analysis using outputs of the ordinations described above. The RLQ analysis is a three-tables co-inertia analysis that tends to maximize the covariance between the sample site scores constrained by the environmental variables of table R and the species scores constrained by the traits of table Q (Dray & Legendre 2008). Finally, I undertook the fourth-corner analysis. In the fourth-corner procedure, a matrix L with species abundances is related to a matrix R with variables describing the extent of giant root-rat and human disturbances at the sample plots and a matrix Q describing species traits (Dray & Dufour 2007). The environmental matrix (R) contained the three root-rat disturbance variables: presence/absence of mima mound, root-rat old burrow density and root-rat fresh burrow density, and the two human activities: distance from settlement and livestock grazing intensity. The trait matrix (Q) was composed of six species traits: three continuous variables – plant adult height, leaf area and leaf nitrogen content, and three categorical variables: stem growth form (acaulescent, erect, and prostrate), and mode of propagation (seed only, seed and rhizome, and seed and stolones). I used the permutation model 6, with 999 permutations (Dray & Legendre 2008), which permutes all species within an entire column and row of the L matrix to test the null hypotheses of the observed pattern would be different from random. To evaluate the

global, or their joint multivariate relationship, significance of the traits-environment relationship, I applied a multivariate test using `fourthcorner2` function of the `ade4` package. The significance of observed statistic was tested based on 999 Monte-Carlo permutations (Dray & Dufour 2007). To measure the strength and significance of the links between individual trait and environmental variable, I used a Pearson correlation coefficient for two quantitative variables, a Pearson χ^2 for two qualitative variables and a Pseudo-F for one quantitative variable and one qualitative variable (Dray & Dufour 2007). I conducted all analyses in the R environment (R Core Team 2020).

4.4 Results

In assessing the effects of root-rat engineering and human disturbances on plant community FDis, as measured using AICc, of the total 32 models with different combinations of predictor variables considered, the “null” model was ranked 29th and the “full” model 8th in terms of their fit to the data (Table 1). This shows that the strong explanatory power of the predictors and justifies the rationale to using model averaging approach. Four models had $\Delta\text{AICc} < 2$, which also contained all the five predictor variables explaining the FDis (Table 1).

FDis ranged between 0.059–0.2534 (mean \pm SE: 0.154 ± 0.003). FDis significantly increased with increasing disturbance caused both by root-rat fresh burrow density ($Z = 3.698$, $P < 0.001$) and with decreasing distance from settlement areas ($Z = 3.442$, $P < 0.001$). Other predictors of rodent disturbance, i.e. old burrows and mima mounds, and human disturbance, i.e. dung abundance, showed non-significant relationship to plant FDis (Table 2).

Table 1. Subsets of models (with $\Delta\text{AICc} < 2$) examining the effects of giant root-rat engineering and human disturbances on FDis of 61 Afroalpine plant species in the Bale Mountains of Ethiopia. Human disturbance variables: Distance = distance from settlement; dung = abundance of livestock dung; root-rat disturbance variables: fresh mound = giant root-rat fresh

burrow density; mima mound = presence-absence of mima mound; old mound = giant root-rat old burrow density.

Model rank	Model	df	logLik	AICc	Δ AICc	AICc Wi
1	Distance + fresh mound	4	389.678	-771.2	0	0.252
2	Distance + fresh mound + old mound	5	390.601	-770.9	0.25	0.223
3	Distance + fresh mound + mima mound	5	390.189	-770.1	1.07	0.148
4	Distance + dung + fresh mound	5	389.789	-769.3	1.87	0.099
8	Full model [Distance + dung + fresh mound + mima mound + old mound + settlement type]	7	390.748	-767.0	4.21	0.031
29	Null model	2	377.765	-751.5	19.69	0.000

Table 2. Sum of AICc weights (AICc Wi) and model averaged parameter estimates for the effects of giant root-rat and human disturbance activities of functional trait diversity of 61 Afroalpine plant species in the Bale Mountains of Ethiopia. N: number of containing models; NA: not available.

Predictor	Sum of AICc Wi (N)	Unstd. Estimate \pm SE	z value
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Intercept	NA	-1.626e-01 \pm 4.37e-02	37.019***
Root-rat fresh burrow density	1.00 (4)	3.39e-04 \pm 3.41e-05	3.698***
Root-rat old burrow density	0.64 (1)	-5.65-04 \pm 4.11e-04	1.365
Root-rat mima mound (Present)	0.20 (1)	-4.68e-02 \pm 4.62e-02	1.008
Distance from settlement	1.00 (4)	-1.80e-04 \pm 5.19e-05	3.442***
Livestock dung abundance	0.31 (1)	2.16e-04 \pm 4.68e-05	0.458

The general association between plant traits and disturbance measures (root-rat and human) was larger than expected under random community assembly (observed: 0.578, expected: 0.231, $P < 0.05$; Fig. 2). The first axis of the RLQ summarised most of the projected inertia between traits and disturbance metrics (eigenvalues = 0.55; % total inertia = 87.7%), while the value was 9.1% (eigenvalues: 0.06) for the second axis (see Fig. 2). These results show that there was thus clear evidence for a strong link between traits and disturbance variables in the data set. From the figure 2, it is evident that distance from settlement and dung abundance are related (both associated with humans, i.e. more dung, less distance) and associated with the first axis of the RLQ. Root-rat variables were also related to each other, but associated with the second axis (Fig. 2). Considering the associations of individual functional trait and environmental variables, while larger seed mass and stolones vegetative propagation and prostrate stem shoot form traits were associated with increasing root-rat engineering disturbance, larger leave size and increased nitrogen content were associated with increasing human disturbances (Table 3; Fig. 2). As depicted on figure S3, certain species were found to be characteristics of specific traits (Supporting information 2); these associations are discussed in detail in the Discussion section.

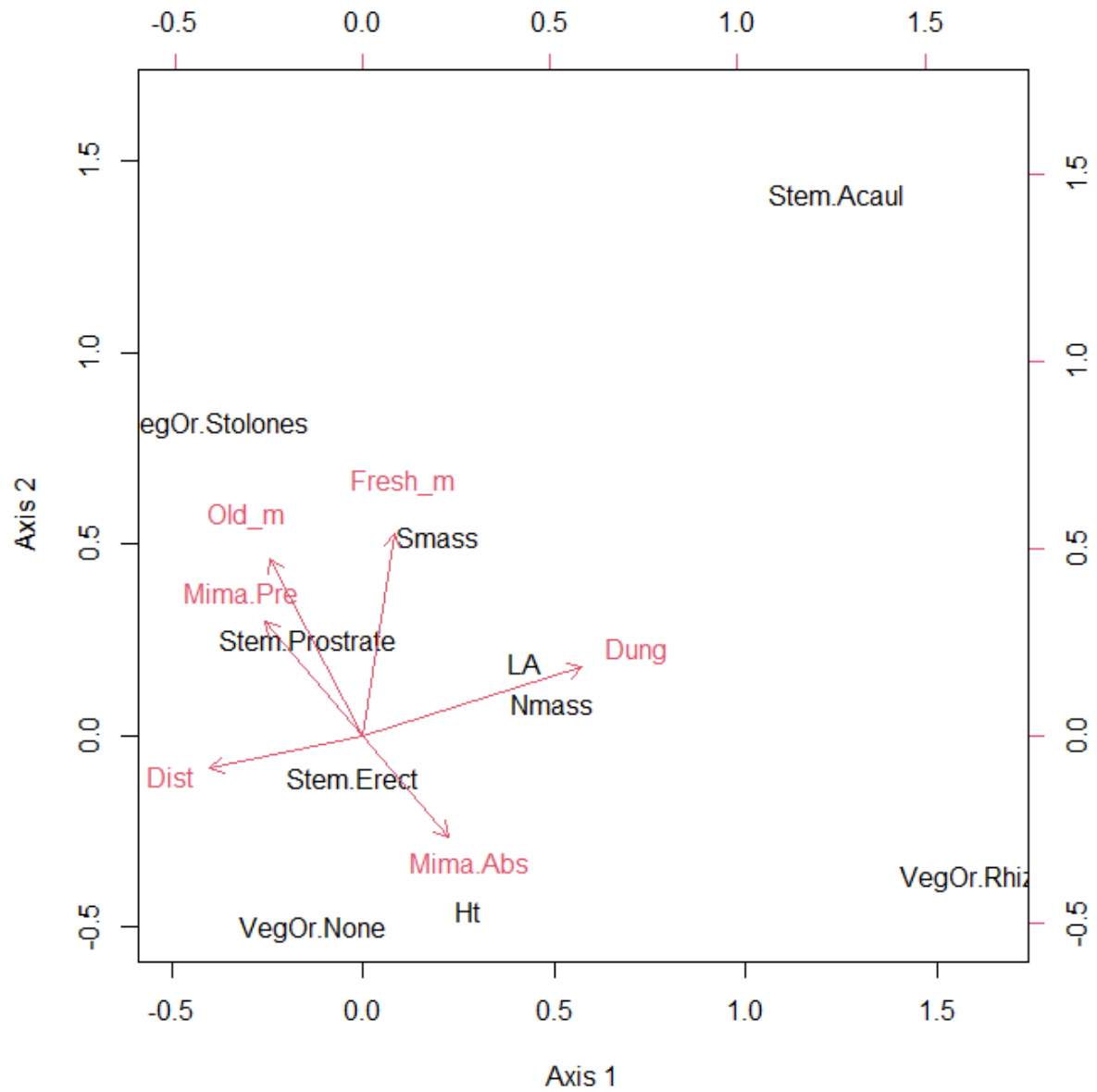


Fig. 2. A biplot of disturbance variables and plant trait variables along the first two RLQ axes. Abbreviations for disturbance variable: Mima.Pre = root-rat mima mound present; Mima.Abs = mima absent; Old_m = root-rat old burrow density; Fresh_m = root-rat fresh burrow density; Distance = distance from settlement. Abbreviations for traits: VegOr.None: no vegetative

propagation; VegOr.Stolones = vegetation propagation via stolones; VegOrg.Rhizome = vegetative propagation via rhizomes; Ht = plant adult height; Nmass = leaf nitrogen content; LA = leaf area; Stem.Acau = acaulescent stem shoot growth form.

Table 3. Fourth-corner analysis evaluating the associations of plant species' functional traits and giant root-rat engineering and human activity variables in the Afroalpine ecosystem of the Bale Mountains, Ethiopia. Given are significant positive (+) or negative (-) relationships at significance level of $P < 0.05$; marginal significant correlations $P < 0.1$ are given in brackets, and circle represent non-significant relationship.

Variables	Leaf area	Height	Leaf nitrogen	Seed mass	Propagation: seed alone	Propagation: seed rhizome	Propagation: and seed stolones	Stem: acaulescent	Stem: erect	Stem: prostrate
Mima mound (absent)	○	○	○	○	○	○	○	○	○	○
Mima mound (present)	(+)	○	○	○	○	○	+	○	○	○
Root-rat old burrow density	○	(-)	○	○	○	(+)	○	○	(+)	○
Root-rat fresh burrow density	(+)	○	(+)	(+)	○	○	○	○	(+)	○
Distance from settlement	-	○	-	○	○	○	○	○	○	○
Livestock dung	+	○	+	○	○	○	+	○	○	○

4.5 Discussion

In this study, I identified associations between plant functional diversity and composition with disturbances by root-rats and humans. I found a positive association between FDis and disturbances both by root-rats and humans, with survival and reproductive traits positively associated with root-rat engineering and acquisitive traits positively associated with human disturbances. These findings suggest that both human activities and rodent engineering disturbances act as habitat filters that promote species coexistence, ultimately resulting in a functional trait divergence (Escobedo et al. 2017; Boet et al. 2020). However, root-rat and human disturbances had varying degrees of associations with individual traits. For example, while increasing root-rat disturbance was positively associated with increased seed mass and plants with prostrate and stolones vegetative organs, increasing human disturbance was associated with larger leaf size, increased leaf nitrogen content and increased seed mass (see Table 3 & Fig. 2).

My finding of increased FDis with increasing root-rat engineering and human activities is in line with my prediction. However, this increase in FDis was found to be significant only with increasing root-rat fresh burrow density and decreased distance from settlement. Previous studies (e.g. Chambers et al. 1990; Choler 2005) have suggested that disturbances from human activities and rodents engineering are important to maintain or enhance the structural and functional diversities of Arctic and Alpine meadow vegetation communities. Thus, my result likely indicates that the filtering process through which both disturbances operate involves the creation of habitat heterogeneity and increasing resources.

My analysis of the associations of individual functional trait and environmental variables showed interesting patterns reflecting the different roles of root-rat and human disturbances in shaping plant functional traits. In line with my prediction, my results showed strong association of larger seed mass, stolonifereous vegetative propagation and prostrate stem shoot form with increasing root-rat disturbances (Fig. 2). These results show rodent-induced and human-

induced disturbances favour different traits. Burrowing mammals affect plants through two mechanisms: modifying microtopography and soil properties and creation of new spaces (Choler 2005; Haussmann 2017). In my study area, Šklíba et al. (2017) have reported that giant root-rat mounds are less compact and contain higher concentrations of nutrients despite soils from deeper horizons are usually nutrient-poor. These authors attributed these higher nutrient concentrations the species unique behaviour. The root-rats gather large amount of plant material as food and nest bedding. Old nest bedding, mixed in various proportions with soil and faeces, is then disposed of both aboveground and in abandoned tunnels, which likely causes an increase in nutrient concentrations (Beyene 1986; Yaba et al. 2011; Šklíba et al. 2017). In addition, the decomposition of biomass buried under mounds can also increase the availability of nutrients (Huntly & Reichman 1994). Thus, the increased resource availability with increasing root-rat engineering may explain my findings of strong associations of certain traits with root-rat disturbances (see Choler 2005; Escobedo et al. 2017; Boet et al. 2020). My result is similar to previous studies in my study area showing that root-rat engineering-induced patches have notably benefited stolonifereous, prostrate rosette species, such as *Alchemilla abyssinica*, *Helichrysum gofense* and *Euryops prostrates*, and larger seed (see Fig. 2 & Fig. S1). The latter two species are Bale endemic and have been recorded only at root-rat mima mound sites (Miehe & Miehe 1994; Tallents & MacDonald 2011). Prostrate stem shoot growth is particularly known to be important trait that enable species to withstand the extremes of day-time light, all-day wind pressure and night-time cold prevailing in alpine areas, such as my study area (Grime 1997; Diaz et al. 2016). Stolonifereous trait is one of commonly known traits of alpine plants that serve as a reproduction strategy to reduce resource allocation to seed production to (Choler 2005; Severin et al. 2020). My finding of positive association of seed mass with root-rat disturbances can be explained by the fact that these disturbances filter species according to their seed size as large seeds facilitate survival through the early stages of recruitment, and higher establishment in the face of rodent herbivory and burrowing disturbances (Westoby et al. 2002;

Muller-Landau 2010). In summary, my finding regarding seed size agrees with findings of the study by Šklíba et al. (2017), who reported strong association of plant species with relatively larger seed mass, such as *Urtica simensis*, *Carduus nyassanus* and *Salvia merjamie*, with root-rat fresh mounds. The former two species are also characterized by mechanical defence against herbivores, similar to the high abundance of unpalatable plants observed in the Tibetan plateau as a consequence of the activity of the plateau zokors (*Myospalax baileyi*; Zhang & Liu 2003; Wang et al. 2019, 2020).

Larger leaf size and higher leaf nitrogen content in terms of mass are strongly associated with human activities (Fig. 2). This result is in line with my prediction and is unsurprising, since human activities related to livestock production are globally known to favour plant with resource acquisitive traits (Grime 1997; Wright et al. 2004; Dunne et al. 2011). Overall, removal of plant biomass by livestock directly reduces plant cover and height, and indirectly creates open spaces for gap-colonizing plant species and promoting the dominance of unpalatable and grazing tolerant species (Tessema et al. 2011; Eldridge et al. 2016; Pavlů et al. 2018; Niu et al. 2019). In addition, livestock dung deposition and urination leads to increased nitrogen nutrient (Bokdam 2001; Dunne et al. 2011; Pavlů et al. 2018). Therefore, it is plausible to state that human activities related to livestock grazing sorts species in favour of those with acquisitive leaf economic spectrum. As shown on figure S3, characteristic species with such acquisitive leaf economic spectrum and are associated with human activities include: *Crepis rueppelii*, *Haplocarpha rueppelii*, *Kniphofia foliosa*, *Potentilla dentate* and *Umbilicus bostryoides*. All these species are known to be weedy growing in degraded areas (see Edwards et al. 1995, 1997, 2000; Hedberg et al. 1989, 2003, 2004, 2006).

4.6 Conclusion

In conclusion, I found increased overall plant species FDis with increasing both root-rat engineering and human activities. However, combinations of some traits were related with either root-rat or human disturbances. Root-rat disturbances filtered plants with higher seed

mass, stolonifereous vegetative organ and prostrate stem shot growth form, while human disturbances filtered species with larger leaf area and higher leaf nitrogen content. From these findings, it is possible to conclude that two plant strategies can be revealed: traits related to survival and reproduction strategies are associated with root-rat disturbances, while leaf traits related to economic spectrum related to acquisitive resource use strategy are associated with human disturbances (Díaz et al. 2016). A recent global review by Eldridg & Soliveres (2023) has highlighted the importance of soil-disturbing vertebrates to rehabilitate degraded landscapes. Therefore, identification of such associations between plant traits and disturbance can help predicting changes under future environmental change and on which trait-disturbance associations to focus in effective ecosystem mismanagement.

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Data availability

All relevant data are within the manuscript and its Supplementary Material files.

The original contributions and R code presented in the study will be made available online in the Dryad Digital Repository.

Conflict of interests

The authors have no conflict of interest to declare.

Chapter 5: Synthesis

Understanding the role of landscape engineering by subterranean rodents in shaping biodiversity patterns and ecosystem functioning, and how this is modulated by human activities, is important to forecast future fates and to respond proactively to undesirable consequences. In this thesis, I found a positive relationship between giant root-rat burrow density activity and human activities, especially livestock grazing, and both reducing vegetation cover and functional trait diversity of alpine vegetation community.

5.1 Effects of root-rat engineering on vegetation cover and plant species richness

In Chapters 2 and 3, I found a reciprocal relationship between giant root-rat engineering and vegetation cover and this relationship is modulated by human activities and environmental conditions. In these chapters, I found decreases in vegetation cover with increasing root-rat burrow density and *vice-versa*. However, no significant effect of root-rat was found on plant species richness. Obviously, both bioturbation and direct herbivory of the root-rat lead to reduced vegetation cover, in agreement with reports of previous studies on other species (Haussmann, 2017; Wu et al. 2015), as well as with studies on the root-rat (Beyene 1985; Šklíba et al. 2017). Yet, the lack of a significant effect of root-rat on plant species richness is unexpected, because rodent bioturbation creates habitat heterogeneity, thereby enhancing species diversity (Jones et al. 1997). However, many similar studies have demonstrated inconsistent results (Haussmann 2017; Jones et al. 1997; Romero et al. 2015; Wu et al. 2015). Thus, this lack of effect in the present study may be related to a food generalist nature of the root-rat (Beyene 1986; Yaba et al. 2011) which may minimize the risk of local extinction of rare species and may explain the lack of impact of the rodent's burrow density on plant species richness. Considering the reciprocal effect of vegetation effects on the root-rat, increased root-rat burrow density with decreasing vegetation cover clearly reveals root-rat's preference for open habitats (Sillero-Zubiri et al. 1995; Vlasatá et al. 2017) since they are morphologically,

physiologically and behaviourally adapted to life in open Afroalpine habitats (Bryja et al. 2019; Sillero-Zubiri et al. 1995). Furthermore, root-rat burrow density was found to increase as distance to settlement decreases. This result is a consequence of heavier livestock grazing intensity around settlement areas, thereby reducing vegetation cover and creating open habitat for giant root-rats and other rodents. Overall, the above findings suggest that giant root-rats might have been benefited from human settlement and livestock grazing, as they reduce vegetation cover and height, particularly in enlarging the rodent's open habitat.

5.2 Impacts of giant root-rat engineering and livestock grazing on plant functional traits

In chapter 4, I identified associations between plant functional diversity and composition with disturbances by root-rats and humans. I found an increase in functional diversity with increasing disturbances both by root-rats and humans. These findings suggest that both rodent engineering and human disturbances act as habitat filters that promote species coexistence, ultimately resulting in a functional trait divergence (Escobedo et al. 2017; Boet et al. 2020). However, traits modulating plant survival and reproduction, namely higher seed mass and prostrate stem form and stolones vegetative organs, showed a positive association with root-rat engineering, while acquisitive traits (leaf area and leaf nitrogen content) showing a positive association with human disturbances. Interestingly, common stoloniferous, prostrate species associated with root-rat burrows also locally endemic to the Bale Mountains, likely suggesting a co-evolutionary relationship between them and the root-rat. The association of acquisitive leaf traits with human disturbances is as expected since human activities related to livestock production are globally known to favour unpalatable plant with resource acquisitive traits (Grime 1997; Wright et al. 2004; Dunne et al. 2011). Overall, findings of my thesis in this chapter reveal two plant strategies: traits related to survival and reproduction strategies are associated with root-rat disturbances, while leaf traits related to economic spectrum related to acquisitive resource use strategy are associated with human disturbances (Díaz et al. 2016).

5.3 Conclusion

Findings of my thesis highlight the presence of a synanthropic association of giant root-rats, which has not been revealed prior to this study despite the recent report that the association of humans and root-rats date back to middle Stone Age foragers. However, my findings of an overall positive effect of human activities on giant root-rat have to be interpreted with caution because of two main reasons. Firstly, my study did not consider the potential effects of sheep and goats which are reported to affect subterranean rodents differently, mainly via browsing, to that of large-sized livestock (cattle and horses). And, secondly, habitat modification and degradation due to livestock overgrazing has been considered as the major threat to the giant root-rat. Here, the positive association of giant root-rats with livestock grazing intensity thus may not necessarily mean that grazing is always beneficial to giant root-rats, rather may suggest giant root-rats' reliance on underground parts of plants as a food source where aboveground vegetation is degraded. It seems that livestock grazing is likely a detrimental threat to survival of giant root-rats when the impacts involve both aboveground and belowground vegetation biomass.

Soil-disturbing vertebrates are known to play important role in rehabilitation of degraded landscapes. Therefore, identification of the associations between plant traits and root-rat and livestock grazing disturbances can help predicting changes under future environmental change and on which trait-disturbance associations to focus in effective ecosystem mismanagement.

6. Perspectives

The Bale Mountains region is the largest alpine ecosystem in Africa with a uniquely high number of endemic animals and plants and the major source of perennial rivers for millions of people and their livestock in the Horn of Africa. The mountains are year-round, as well as seasonally, used as pasture. This use has been currently growing rapidly, which has resulted in increased endangerment of several endemic animals, including the giant root-rat. Given the role of the root-rats as landscape engineers, having better understanding of what they do, what the effects of their activities and how their activities and effects on ecosystem are influenced by environmental and human activities is critically important to develop strategies that ensure persistence of the root-rats and sustainable use and conservation of the alpine ecosystem. While I have attempted to address these questions in chapter 2–4, still there are several possibilities for additional studies which I discuss in the following subsections.

6.1 Temporal variations in the relationships between root-rat, human activities and vegetation

Although I found an overall positive effect of livestock grazing on giant root-rat, this finding may only applies to dry season environmental conditions and human activities. The effects of livestock on burrowing animals are known to be dependent on the seasonality, grazing system and stocking rate of grazing practices (Wang et al. 2020). In the study area, during wet season, vegetation cover and species richness increase, food abundance both for livestock and giant root-rat is higher and number of livestock and thus grazing intensity becomes higher. Thus, a similar study to my thesis would be valuable to elucidate how the relationships between the root-rat, grazing and vegetation may vary in temporal fashion. Furthermore, in my thesis I did not cover grass species, which are the resources used by livestock and the root-rats too. Thereofre, examining the relationships among the root-rat, vegetation including grass species

and livestock grazing would enormously advance our knowledge on the engineering role of the root-rat.

6.2 Determining habitat preference of the root-rat in relation to wetlands

Wetlands, such seasonal or permanent streams, rivers, marshes and swamps, are among the major constituent land cover types of the Afroalpine ecosystem of the study area (Tallents 2007). These wetlands are not only the preferred grazing areas for livestock, but also are the prime habitats for the root-rats (Sillero-Zubiri et al. 1995; Šklíba et al. 2017, 2020; Vlasatá et al. 2017). In chapter 2 of this thesis, I also found increased root-rat burrow density with increasing habitat wetness rodents. However, overgrazing by livestock has substantially decreased the wetlands (Tallents 2007). A recent study by Stephen et al. (2019) shows that wetland extent more than doubles between wet and dry seasons and that only 4% of the Afroalpine zone is saturated year-round. Therefore, a study on temporal variability of root-rat distribution in relation to the wetlands condition and livestock grazing level is helpful to predict the response of the rodents to changing extent of the wetlands.

6.3 Characterization and quantification of giant root-rat burrowing marks

Of the key questions might be asked about zoogenic ecosystem engineering include the types and extent of land scape signatures they leave, rate of formation and decay of the structural signatures, and the local- and landscape-level effects such signatures have on biodiversity and ecosystem processes. In chapter 2–4 of my thesis, I have addressed most of these questions. However, there are areas that need further research. For example, giant root-rat mima mounds are the most visible landscape signature in the study area. However, characteristics of the mima mounds are remained little explored, but see Wraase et al. (2023). For instance, the length, width and height of the mima mounds and how they vary in relation to major substrate (habitat) types, to my knowledge, have not been sufficiently investigated. Similarly, dimensions of burrow mounds (of a single hole) and the volume of soil excavated per hole per day by

individual root-rat needs to be understood. Finally, detailed investigations of the relevance of the root-rats engineering for other animals and the effects on soil physical and chemical properties is needed. This topic has been tackled by previous authors (Beyene 1986; Yaba et al. 2011; Šklíba et al. 2017), but their study areas were limited to vey small areas.

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Supplementary material

Supplementary files chapter 2

Supplementary file Table S1. Spearman's correlation coefficients between each pairs of variables analysed

Variables	No. fresh holes	Temperature	No. cow dung	Soil moisture	Vegetation cover
Temperature	0.04				
No. cow dung	0.36*	0.48*			
Soil moisture	0.50*	0.08	0.27*		
Vegetation cover	0.29*	0.07	0.01	-0.11	
Plant species richness	0.07	0.04	0.09	0.17	0.18

*statistically significant correlation

Supplementary file Table S2. Direct, indirect and total effects and relative effect size (RE; given as the ratio of the indirect effect to the direct effect) of temperature, soil moisture, livestock grazing and GRR activity on plant species richness and vegetation cover. The direct effects are the standardized path coefficients provided in Table 1 and 3, while the standardized indirect effects were calculated as described in the methods section. Total effects were the sum of the direct and indirect effects. Values of direct and indirect effects indicated by with asterisk (*) denote significant effects at $P < 0.05$ significance levels.

Predictors	Direct	Indirect	ER	Predictors	Direct	Indirect	ER
(a) Effects on species richness via GRR				(c) Effects on GRR via species richness			
Soil moisture	0.332*	-0.007	0	Soil moisture	0.013	0.008	0.6
Temperature	0.163	-0.005	0	Temperature	0.002	0.006	3.0
Livestock grazing	-0.036	-0.041	1.1	Livestock grazing	0.185	-0.003	0.0
(b) Effects on vegetation cover via GRR				(d) Effects on GRR via vegetation cover			
Soil moisture	0.09	-0.014*	0.2	Soil moisture	0.05	0.006	0.1
Temperature	0.074	-0.009	0.1	Temperature	-0.021	-0.025	1.2
Livestock grazing	0.023	-0.077*	3.3	Livestock grazing	0.062	0.021	0.3

Supplementary materials chapter 4

Supporting information TS1. List of plants, their height and area estimation. For details and abbreviations, see methods section in the main text.

Species name	Species code	Height max (cm)	Leaf length (L, cm)	Leaf width, (W, cm)	Leaf shape	L*W	MP, c	Leaf area, (cm ² ; = c*L*W*)
<i>Agrocaria melanantha</i>	AG.MEL	70	8.25	3.30	linear-lanceolate	27.23	0.71	19.33
<i>Alchemilla abyssinica</i>	AL.ABY	6	8.25	4.50	reniform-orbicular,	37.13	0.75	27.84
<i>Alchemilla microbetula</i>	AL.MIC	6	2.5	2.30	ovate	5.75	0.67	3.85
<i>Alchemilla pedata</i>	AL.PED	15	4.5	4.50	oblong-elliptic	20.25	0.71	14.38
<i>Anagallis serpens</i>	AN.SER	40	1.25	1.00	obovate	1.25	0.79	0.99
<i>Anthemis tigrensensis</i>	AN.TIG	60	3.5	0.95	oblong or elliptic	3.33	0.71	2.36
<i>Arabis alpina</i>	AR.ALP	60	3.7	1.15	spathulate to oblong	4.26	0.70	2.98
<i>Arabis thalina</i>	AR.THA	25	1.45	0.60	spathulate to elliptic,	0.87	0.68	0.59
<i>Artemisia abyssinica</i>	AR.ABY	60	2.5825	2.58	ovate	6.67	0.67	4.47
<i>Artemisia afra</i>	AR.AFR	100	5.5	0.30	ovate	1.65	0.67	1.11
<i>Cardamine hirsuta</i>	CA.HIR	45	6.75	0.80	ovate to orbicular	5.40	0.75	4.05
<i>Cardamine obliqua</i>	CA.OBL	120	9.5	3.50	elliptic to suborbicular	33.25	0.75	24.94
<i>Carduus nyassanus</i>	CA.NYA	150	27	10.50	oblanceolate	283.50	0.64	181.44
<i>Cerastium afromontanum</i>	CE.AFR	75	2.325	0.45	Ovate to lanceolate	1.03	0.69	0.71
<i>Cineraria abyssinica</i>	CI.ABY	100	3	0.04	ovate	0.12	0.67	0.08
<i>Conium maculatum</i>	CO.MAC	250	20	17.00	oblong-lanceolate	340.00	0.72	243.10
<i>Cotula abyssinica</i>	CT.ABY	20	2.25	0.90	linear	2.03	0.71	1.44
<i>Crepis rueppelli</i>	CR.RUP	35	20	3.00	oblanceolate	60.00	0.64	38.40
<i>Cynoglossum lanceolatum</i>	CY.LAN	70	7.5	2.13	lanceolate, oblong-lanceolate or linearlanceolate,	15.94	0.72	11.48
<i>Dispacus pinnatifidus</i>	DI.PIN	300	12.5	5.25	lanceolate	65.63	0.70	45.94
<i>Erophila verna</i>	ER.VER	9.5	1.3	3.79	obovate, spatulate, oblanceolate, lanceolate, oblong	4.92	0.69	3.40
<i>Erigeron alpinus</i>	ER.ALP	50	5.25	0.65	linear-oblong or elongate-lanceolate	3.41	0.71	2.43

<i>Euryops prostratus</i>	EU.PRO	15	0.8	0.13	oblong-linear,	0.10	0.72	0.07
<i>Gallium acrophyllum</i>	GA.ACR	30	0.7	0.13	(ob)lanceolate	0.09	0.64	0.06
<i>Geranium arabicum</i>	GR.ARA	10	0.85	0.40	ovate - lanceolate	0.34	0.69	0.23
<i>Gnaphalium rubriflorum</i>	GN.RUB	40	2.5	0.30	spathulate, obtuse or subacute	0.75	0.70	0.53
<i>Haplocapa rueppelii</i>	HA.RUP	13	7.5	4.25	elliptical	31.88	0.69	21.99
<i>Hebenstretia angolensis</i>	HE.DET	50	3.375	0.24	linear or linear-lanceolate;	0.80	0.71	0.57
<i>Hedbergia abyssinica</i>	HE.ABY		2.1	0.20	elliptic to lanceolate	0.42	0.71	0.30
<i>Helichrysum citrispinum</i>	HE.CIT	75	0.7	0.15	linear-lanceolate or oblong	0.11	0.71	0.07
<i>Helichrysum cymose</i>	HE.CYM	120	9.5	1.35	oblong-lanceolate	12.83	0.72	9.17
<i>Helichrysum forsskahlii</i>	HE.FOR	75	1.2	0.38	lanceolate or linear	0.45	0.71	0.32
<i>Helichrysum gofense</i>	HE.GOF	15	2.375	0.28	oblong-linear, linear or linear-lanceolate	0.65	0.72	0.47
<i>Helichrysum splendidum</i>	HE.SPL	75	1.5	0.50	linear-oblong or lanceolate	0.75	0.71	0.53
<i>Kniphofia foliosa</i>	KN.FOL	40	60	3.65	linear lanceolate	219.00	0.71	154.40
<i>Lythrum rotundifolium</i>	LY.ROT	30	1.25	0.75	obovate to orbicular or oblong-elliptical,	0.94	0.70	0.66
<i>Malva verticillata</i>	MA.VER	300	27	27.00	cordiform or reniform	729.00	0.55	400.95
<i>Myocotes keniensis</i>	MY.KEN	5	1.875	0.09	oblong or lanceolate	0.16	0.72	0.11
<i>Plantago afra</i>	PL.AFR	50	4.5	0.25	linear or linear-lanceolate;	1.13	0.71	0.79
<i>Potentilla dentata</i>	PO.DEN	40	5.6	2.30	oblong to lanceolate	12.88	0.73	9.34
<i>Ranunculus multifidus</i>	RA.MUL	100	6.75	5.13	ovate	34.59	0.67	23.18
<i>Ranunculus oreophytus</i>	RA.ORE	40	1.5	1.15	Elliptic	1.73	0.69	1.19
<i>Ranunculus stagnalis</i>	RA.STA	33	1.65	3.13	lobed	5.17	0.55	2.84
<i>Rumex nepalensis</i>	RU.NEP	100	12.5	6.00	ovate	75.00	0.67	50.25
<i>Salvia merjamie</i>	SA.MER	100	10.5	3.90	oblong, elliptic or ovate	40.95	0.70	28.54
<i>Satureja pseudosimensis</i>	SA.PSE	35	0.75	0.65	ovate	0.49	0.67	0.33
<i>Satureja punctata</i>	SA.PUN	100	0.85	0.45	circular to ovate	0.38	0.70	0.27
<i>Scabiosa columbaria</i>	SC.COL	70	9	2.00	ovate or obovate	18.00	0.67	12.06
<i>Sedum baleensis</i> M. Gilbert (1985)	SE.BAL	0.5	1.1	0.35	linear	0.39	0.71	0.27

<i>Sedum mooneyi</i> M. Gilbert (1985)	SE.MOO	1	0.41	0.40	obovate	0.16	0.67	0.11
<i>Senecio schultzii</i>	SE.SCH	30	15.5	2.25	linear-oblong to oblanceolate	34.88	0.71	24.87
<i>Senecion unionis</i>	SE.UNI	35	5.8	0.16	linear or oblong	0.93	0.72	0.67
<i>Sonchus melanolepis</i>	SO.MEL	45	6	1.60	linear	9.60	0.71	6.82
<i>Swertia abyssinica</i>	SW.ABY	65	3.25	1.70	oblanceolate, elliptic	5.53	0.67	3.67
<i>Swertia kilimangerica</i>	SW.KIL	150	6	2.35	obovate	14.10	0.67	9.45
<i>Trifolium acaule</i>	TR.ACA	5	0.7	0.30	obcordate to oblanceolate	0.21	0.62	0.13
<i>Umbilicus botryoides</i>	UM.BOT	38	9	9.00	peltate, \pm circular, concave	81.00	0.70	56.70
<i>Urtica simensis</i>	UR.SIM	100	8.5	5.50	subcordate	46.75	0.55	25.71
<i>Veronica abyssinica</i>	VE.ABY	40	3	2.30	ovate	6.90	0.67	4.62
<i>Veronica glandulosa</i>	VE.GLA	50	2.125	1.05	ovate to elliptic	2.23	0.68	1.52
<i>Polygonum afromontanum</i>	PO.AFR	100	2.5	0.50	ovate-elliptic	1.25	0.68	0.85

Supporting material 2

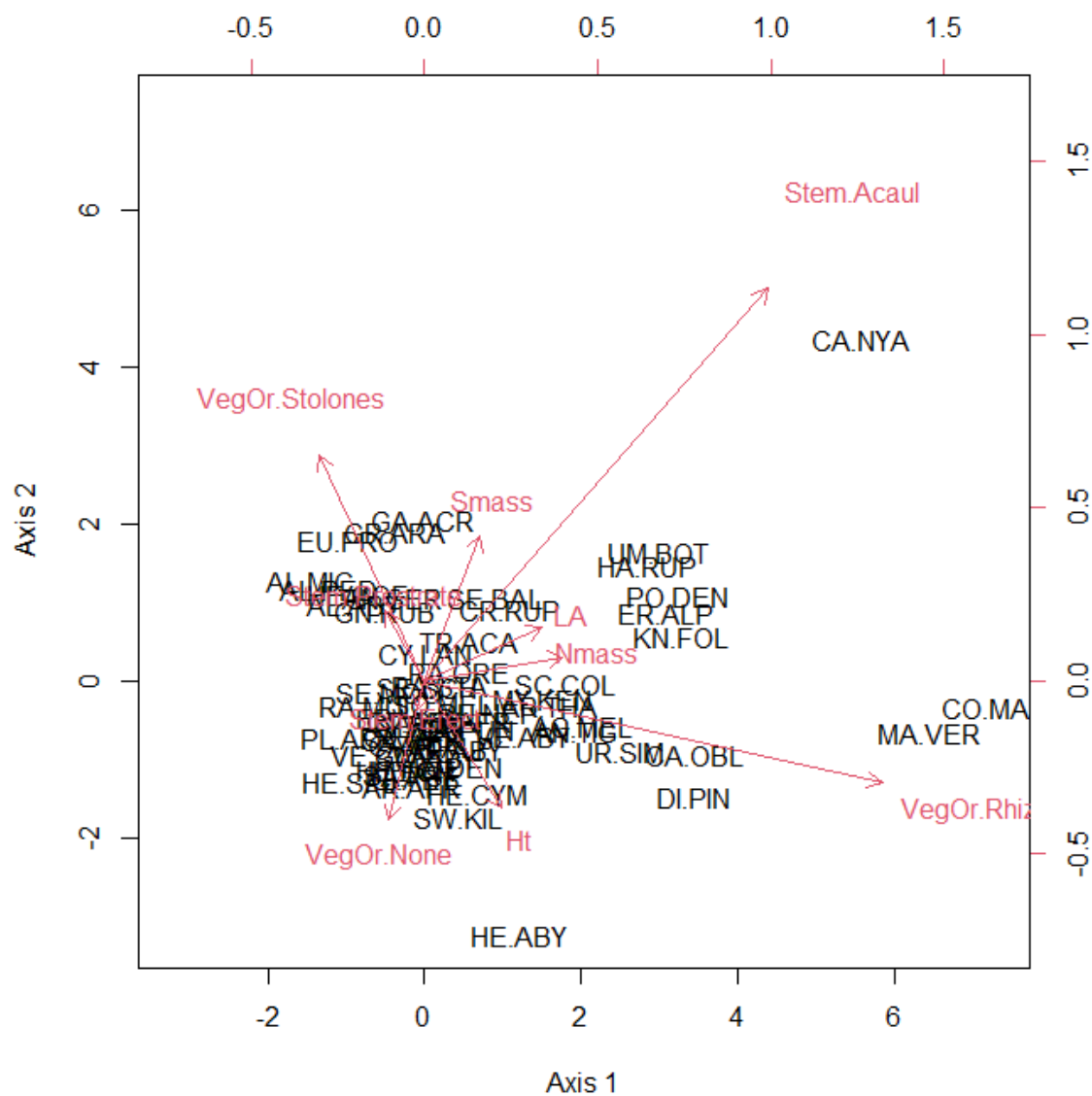


Fig. S1. A biplot of plant species and trait variables along the first two RLQ axes. Full names of plant species are provided in supplementary material TS1.

Deutsche Zusammenfassung

Unterirdisch-lebende Nagetiere können als Ökosystemingenieure fungieren, indem sie die Landschaft durch Bodenperturbation und Herbivorie verändern. Auch menschliche Aktivitäten wie die Errichtung von Siedlungen und die Beweidung mit Vieh haben tiefgreifende Auswirkungen auf die Struktur und die Funktion von Ökosystemen. Angesichts zunehmender lokaler Landnutzungsänderungen ist es wichtig, die Auswirkungen von Bioturbation durch Nagetiere auf die biologische Vielfalt zu verstehen und zu untersuchen, wie diese Auswirkungen durch Umweltfaktoren und menschliche Aktivitäten moduliert werden. So können künftige Veränderungen vorhersagen, die Nutzungsgeschichte der Ökosysteme rekonstruieren sowie nachhaltige Bewirtschaftungsstrategien umgesetzt werden. Bioturbation unterirdischer Nagetiere führt zu einer größeren Heterogenität der Landschaft und einer besseren Nährstoffverfügbarkeit für Pflanzen. Nagetiere wirken sich auch direkt auf die Vegetation aus, indem sie nach Nahrung suchen und Pflanzen unter ihren Bauten vergraben. Somit wirkt sich die Bioturbation von Nagetieren auf Pflanzen- und Tiergemeinschaften sowie auf die Struktur und das Funktionieren von Ökosystemen aus. Die Bioturbationsaktivität der Nagetiere und damit auch ihre Auswirkungen werden jedoch von Umweltbedingungen, der Vegetation und den menschlichen Aktivitäten beeinflusst. Besonders in Gebieten, in denen sich die Verbreitung von Nagetieren und Weidevieh überschneidet, sind die Auswirkungen von Nagetieren und die zugrunde liegenden Mechanismen noch komplexer. Dies liegt zum einen daran, dass sowohl Nagetiere als auch Nutztiere die Vegetation beeinflussen und von ihr beeinflusst werden, und zum anderen daran, dass die Reaktionen der Pflanzen auf solche interaktiven Störungen von deren funktionellen Eigenschaften abhängen. Dieses komplexe Wechselspiel zwischen unterirdisch-lebenden Nagetieren, der Vegetation, menschlichen Aktivitäten und ihrer Umwelt zu entschlüsseln, bleibt eine Herausforderung.

In dieser Arbeit analysierte ich das Zusammenspiel von abiotischen Bedingungen, struktureller und funktioneller Zusammensetzung der Vegetation und menschlicher Landnutzung mit der Aktivität der endemischen Art *Tachyoryctes macrocephalus* (RÜPPELL 1842), einem unterirdisch-lebenden Nagetier, das im afroalpinen Ökosystem der Bale Mountains in Südost-Äthiopien endemisch ist. Zunächst untersuchte ich die Auswirkungen von *T. macrocephalus* auf den Reichtum an Pflanzenarten und die Vegetationsbedeckung und umgekehrt, und wie diese wechselseitigen Auswirkungen durch die Temperatur, die Feuchtigkeit des Lebensraums und die Beweidung durch Vieh moduliert werden. Zweitens konzentrierte ich mich auf die Wechselwirkung zwischen Störungen durch *T. macrocephalus* und menschlichen Aktivitäten, indem ich entlang eines Gradienten menschlicher Besiedlung arbeitete. Um die Mechanismen zu verstehen, durch die *T. macrocephalus*, menschliche Besiedlung und Beweidung Pflanzengemeinschaften beeinflussen, habe ich die Veränderungen in der Vielfalt funktioneller Merkmale und der Zusammensetzung von Vegetationsgemeinschaften entlang eines Gradienten von Bioturbation von *T. macrocephalus* und menschlichen Aktivitäten untersucht.

In meiner Arbeit konnte ich zeigen, dass eine zunehmende Dichte von *T. macrocephalus* zu einer Abnahme der Vegetationsdecke führt und umgekehrt eine zunehmende Vegetationsdecke zu einer Abnahme der Dichte von *T. macrocephalus*. Eine zunehmende Beweidungsintensität führt indirekt über ihre negative Auswirkung auf die Vegetationsdecke zu einer erhöhten Dichte von *T. macrocephalus*. Darüber hinaus führt eine Zunahme sowohl der Dichte von *T. macrocephalus* als auch der menschlichen Aktivitäten zu einer Zunahme der funktionellen Vielfalt von Pflanzenarten. Die Störungen durch *T. macrocephalus* führten jedoch dazu, dass Pflanzen mit größerer Samenmasse, stoloniferen vegetativen Organen und gestreckten Wuchsformen herausgefiltert wurden, während menschliche Störungen Arten mit größerer Blattfläche und höherem Blattstickstoff herausfilterten.

Diese Arbeit fördert unser Verständnis des Zusammenspiels zwischen Bioturbation von Nagetieren, menschlichen Störungen und lokalen Umweltbedingungen bei der Gestaltung der Struktur und Funktionsweise von Ökosystemen. Die Arbeit zeigt auch, dass *T. macrocephalus* eine synanthrope landschaftsgestaltende Rolle spielt, die sich auf die Vegetationsstruktur und die Ökosystemprozesse in dem besonderen alpinen Ökosystem der Bale Mountains auswirkt. Meine Ergebnisse deuten auch darauf hin, dass *T. macrocephalus* von der Besiedlung durch den Menschen und der Beweidung mit Vieh profitiert haben könnte, da hierdurch die Vegetationsdecke und -höhe reduziert wird, was insbesondere den offenen Lebensraum der Nagetiere vergrößert.

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Erklärung

Ich versichere, dass ich meine Dissertation mit dem Titel „The Giant Root-rat (*Tachyoryctes macrocephalus*) as a Synanthropic Landscape Engineer in the Bale Mountains, Southeast Ethiopia“ selbstständig ohne unerlaubte Hilfe angefertigt und mich dabei keiner anderen als der von mir ausdrücklich bezeichneten Quellen und Hilfsmittel bedient habe.

Diese Dissertation wurde in der jetzigen oder einer ähnlichen Form noch bei keiner anderen Hochschule eingereicht und hat noch keinen sonstigen Prüfungszwecken gedient.

Marburg, den 30.05.2023

Addisu Asefa Mitiku