Assessing the likelihood that burrowing gerbils in the central Namib are ecological engineers

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Declaration

I, (Halleluya Natanael Shaanika), hereby declare that the work contained in the thesis entitled “Assessing the likelihood that burrowing gerbils in the central Namib are ecological engineers” is my own original work and that I have not previously in its entirety or in part submitted it at any university or higher education institution for the award of a degree.

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List of Abbreviations

EC: Electrical Conductivity

EIA: Environmental Impact Assessment

GPS: Global Positioning System

LA1: Low Density Active site 1

MET: Ministry of Environment and Tourism (now Ministry of Environment, Forestry and Tourism)

NCE: Namibia Chamber of Environment

NERMU: Namib Ecological Restoration and Monitoring Unit

OC: Organic Carbon

OM: Total Organic Matter

PAM: Plant Available Moisture

PAN: Plant Available Nutrients

PCQ: Point-Centered Quarter Method

SU: Swakop Uranium

TOC: Total Organic Content

TSF: Tailing Storage Facility

WRD: Waste Rock Dump

Disclaimer

This thesis is presented in seven main chapters, with chapter 5 and 6 prepared as stand-alone manuscripts for publication in the Journal of Arid Environments and Namibia Journal of Environment, respectively. Being prepared for submission to external journals, Chapters 5 and 6 are formatted differently to the rest of the thesis, which follows a standard layout and the Harvard VI citation style. Some unavoidable duplication also occurs as a result of this, particularly in the form of part of the introduction, general description of the study area, methods and materials, and some of the concepts in chapter 2 are repeated. To avoid too unnecessary duplication of information, the references of chapters 1 to 4, 7, and those of the two manuscripts were combined as one list provided in Chapter 8.

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Dedication

I would like to dedicate this thesis to “*wise-man*” Prof. Theo Wassenaar for his unwavering and constant support, and time spent infusing the skills of critical thinking in me, a lesson I greatly value and appreciate.

Abstract

Like many other fossorial rodents, gerbils are known to modulate their environments by changing the soil characteristics and conditions via their activities such as ground bioturbation, foraging, defecating and urinating. They play an important ecological engineering role because they can affect water hydraulic conductivity and water holding capacity, mineralization rates, thus plant-available-nutrients and moisture stored in the soil profile. If the bioturbation activities of gerbils affect water availability in the hyper arid environment, gerbils may create patches of favourable micro-sites for vegetation establishment and growth, and thus also affect the structure and function of the vegetation community at the landscape scale. The main objective of this study was to test whether the gerbil species are significantly improving the growth of vegetation through their burrowing activities on the Husab gravel plains in central Namib. In this way I wanted to verify whether they play a functional ecological engineering role in the ecosystem. Firstly, the study mapped out the spatial distribution and density of vegetation patches with and without burrows on the Husab gravel plains of the central Namib and then selected specific areas for in-depth experimental study. The focus was on the effects of gerbils' burrowing activities by comparing soil nutrients and moisture, and vegetation characteristics between contrasting sites (active burrow patches, inactive burrow patches, no-burrow vegetation patches and their control sites) on the Husab gravel plains. This study revealed that: (1) the spatial distribution and density of vegetation patches with and without burrows is not uniform and that the gerbils mostly prefer the grassy plain over other habitats. (2) The spatial distribution of density of their burrow patches can be explained by soil substrates such as surface cover and hardness. (3) Gerbils through their burrowing activities increase the hydraulic conductivity and soil's fertility-related variables together with the vegetation cover, abundance and biomass. Thus, it can be concluded that gerbils significantly improve primary productivity through changing the conditions and characteristics of the soil on their burrow patches and this may have a knock-on effect on other organisms at the landscape level. Thus, gerbils may be considered to be essential ecological engineers in the central Namib.

Keywords: burrow patches, bioturbation, ecological engineering, central Namib, vegetation productivity.

Chapter 1

General background

Gerbils (Subfamily: Gerbillinae) are a group of fossorial rodents that are widespread throughout the world's desert regions. In the Namib Desert, clusters of gerbil burrows are everywhere on gravel plains, most often associated with patches of denser vegetation. In general the small mammals including, the gerbil species (with body weight ranges from 30 g to 140 g) have been identified as ecological engineers because they change soil characteristics and conditions through their activities such as tilling, stirring and churning of soils, foraging, defecation and urination (Jones et al., 1994; Xu et al., 2012; Xu et al., 2015). This is known as bioturbation and results in a more heterogeneous soil structure, improved aeration and water infiltration and, an improvement in soil fertility and vegetation productivity (Malizia et al., 2000; Gabet et al., 2003; Xu et al., 2012). The burrow systems of small mammals increase the soil surface permeability and enhances water infiltration rate (hydraulic conductivity) as well as increase the amount of plant-available moisture (PAM) stored in the soil profile (Laundre, 1993). The gerbil species (such as *Gerbilliscus setzeri* [Chevret and Dobigny, 2005]) dig their burrows in colonies (Skinner and Chimimba, 2006), and theoretically, this may result in higher water infiltration rate, because of the exaggerated effect of soil surface permeability. This could be an important aspect in drylands where annual rainfall is lower and evapotranspiration is higher.

Studies on fossorial engineers have been conducted in regions with a wide range of annual precipitation values (see section on small fossorial mammals as engineers below for a comprehensive review of these studies). The majority of these studies have reported positive ecosystem effects such as improvements of both PAM and plant-available nutrients (PAN), with especially water limited environments (e.g. Bragg et al. 2005; Davidson and Lightfoot 2008; Yoshihara et al., 2009; Yoshihara et al. 2010) appearing to benefit from the bioturbation. All of these studies were carried out in regions with more than 200 mm annual precipitation, where moisture, although scarce, is enough and evaporation is slow enough to lead to the reported improvements of PAM and PAN. In drier environments (arid and hyper-arid) water availability represents an overriding control on ecosystem processes that determine plant productivity (Whitford, 2002). Theoretically, gerbils could be playing an engineering role in such really dry environments as well by increasing the water holding capacity and, thus the PAM and PAN of the soil. This would benefit the vegetation and ultimately could also allow grazing ungulates to exist and forage in areas where they would not normally thrive. Eldridge and Whitford (2014) suggested that the spatial changes in both soil texture and vegetation structure as a result of soil disturbance by small mammals is likely to have measurable effects on fauna in semi-arid regions.

The presumed engineering role by the gerbils on the gravel plains of the central Namib is part of an Environmental Impact Assessment (EIA) done for the Husab mine in the past (Metago Environmental Consulting Engineers and Scientists, 2010). The study suggested that there is a potential that the Namib gerbils could be playing a functional engineering role that may result in a significant impact on the ecosystem. However the central Namib is characterised by very dry climate conditions. The average annual precipitation on the central Namib Desert gravel plains ranges from only ~20 to ~80 mm, and both potential evapo-transpiration (at ~ 3,500 mm pa) and intra-seasonal and inter-annual rainfall variability are extreme (Lancaster et al., 1984 and Eckardt et al., 2013). Such low and unpredictable rainfall may place a limit on the gerbils' ability to be ecological engineers. In addition, physical processes in arid environments can result in vegetation patterns (Yizhaq et al., 2019) that mimic the patch-scale effects that are typical for fossorial mammals in these environments. At the study site it was observed that there were also many and widely distributed denser vegetation patches that do not have burrows on them. These patches could have been the result of natural mechanisms such as hydrological overland flow. Hydrological overland flow is the passage of water from one part (patches without vegetation) of the landscape to another (sink areas of vegetation patches) (Reaney et al., 2014). This is a form of catchment runoff response and it is controlled by soil roughness along with uneven topography, soil structure and hardness (Govers et al., 2000 and Morbidellil et al., 2012). Water overland flow often results in the formation of patches after strong seasonal rainfall variability especially in arid regions where moisture availability for plant growth is limited (Newman et al. 2006; Smith and Goodrich, 2006; Yizhaq et al. 2019). Hydrological overland flow mechanism may be the main mechanism that causes the formation of vegetation patches in water limited environments (Yizhaq et al., 2019). One Namib-specific study on ecological engineering by gerbils by Cox (1987) revealed a correlation between the gerbil burrow colonies

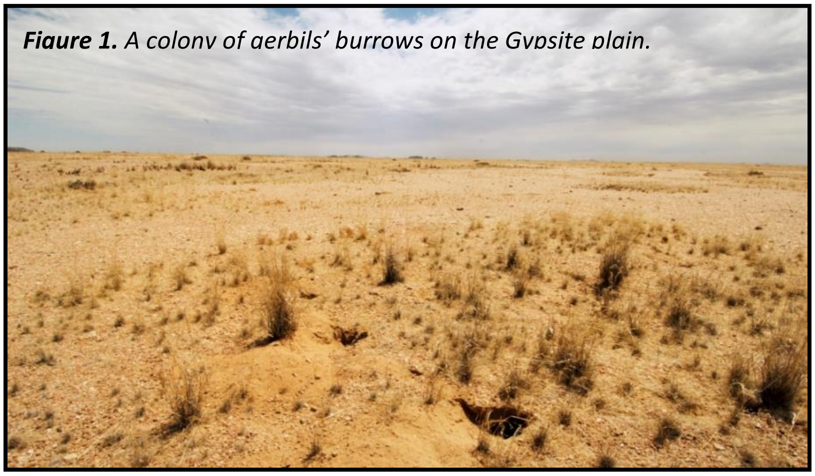


Figure 1. *A colony of gerbils' burrows on the Gypsite plain.*

and vegetation patches. On the Namib gravel plains, the connection between burrow colonies and vegetation is easy to make – grass germinates and grows in circle-shaped cluster (colonies) of about 5 m diameter that are often associated with the burrows of gerbil species (Figure 1) (Henschel, 2009). Cox (1987) showed that larger denser stands of perennial grasses with gerbil burrow colonies tend to survive for longer after the rainy season when compared to adjacent areas with no burrows or where scattered single burrows occur (associated with smaller sparse stands of perennial grasses) and concluded that these rodents must be the main creators of the denser vegetation patches. However, Cox (1987) did not separate the possible role of physical processes in being the driver of the vegetation patterns and plant productivity in general. Therefore, the aim of my study was to fill this gap in order to determine whether the gerbils do or do not improve vegetation establishment and growth on the gravel plains of the central Namib.

The EIA study that was done for the Husab mine recognised that the mine has the potential to significantly affect the presumed ecological engineering role of the gerbils by influencing the spatial extent of the occurrence, distribution, and density of the gerbils' burrows through time (Metago Environmental Consulting Engineers and Scientists, 2010). The EIA study hypothesised that the gerbils, through their ecological engineering, measurably benefit the vegetation (mainly grass) productivity through increasing the PAM, organic matter, and inorganic nutrient levels of soils. This results in the increase of grass biomass at the landscape scale, therefore allowing larger herbivores to have an extended presence in that area. If the bioturbation role of the gerbils is the key to maintaining primary productivity on the gravel plains, Husab's mining activities will have a wider detrimental effect on the ecosystem in the future. The EIA study recommended that a study should be done to assess the extent of the role of the gerbils in maintaining biodiversity on the Husab gravel plains and adjacent areas.

Additionally, if gerbils are ecological engineers, they could play a role in successfully restoring the effects of mining. Restoration of a complex disturbed ecosystem can be a challenge. In future any attempt at restoration of ecological structure and function will be strengthened if it can be shown that the burrowing fossorial animals are functionally important facilitators for the recovery of a disturbed ecosystem, thus opening up the potential to utilize their functional roles in some way. If the gerbils are ecological engineers their functional role would be possibly useful to monitor the recovery of disturbed habitats. Theoretically, if colonial gerbils arrives on a recovering habitat, the likelihoods of success may be higher compare to when they are not present. Given the risks of failure associated with restoration in general and with arid land restoration specifically (Aronson et al., 1993), it is important to approach such an initiative with caution and realistic evidence based knowledge. Therefore, it is important to understand the interdependence of gerbils and vegetation, because such knowledge will help ecologists to contain and mitigate impacts, and plan effective ecological restoration. It is also important to investigate the spatial pattern and distribution of gerbils' burrows to identify areas of high priority that requires proper management and to provide for a better quantification of the functional role of burrowing animals in the central Namib.

I was therefore interested to determine a patch-scale mechanism of the gerbils' burrows as they can be the engineers of the vegetation patches which occurs in various shapes including fairly circle (Cox, 1987), stripe and polygon (Watson, 1980). However, the engineering effect has to be considered at the landscape level rather than at the patch-scale, therefore I decided to determine the spatial extent and distribution of vegetation patches with and without gerbil burrow colonies on them on the Husab gravel plains and adjacent areas.

The thesis is arranged in seven main parts. After the description of the general background (Chapter 1), I present a literature review (Chapter 2) of ecological engineering in general and small fossorial mammals in particular, and as well as gerbils as ecological engineers. Chapter 2 also deals with an assessment of the ecology of the Namib gerbils and the possibility that species other than gerbils could be digging the burrows. In Chapter 3 I present a patch-scale conceptual model of the hypothesised engineering role of the gerbils and the research questions developed from the main question before providing a general description of the research design and study area in Chapter 4. Chapter 5 is a draft manuscript prepared for submission to the Journal of Arid Environments, focusing on the potential functional engineering role of the gerbils including their bioturbation knock-on effect on vegetation productivity. In Chapter 6, a second manuscript prepared for the Namibian Journal of the Environment, I look at the spatial distribution of vegetation patches with and without gerbil burrow colonies on them across various habitats on the

Husab gravel plains and adjacent areas. Chapter 7 is a synthesis of the main findings as presented in Chapters 5 and 6, in the context of the specific objectives I communicate in Chapters 5 and 6. Chapter 8 contains the list of references cited in this study including the two manuscripts prepared for publication.

Chapter 2

Literature review

What is ecological engineering?

Various examples of the kinds of organisms' impacts on the physical environment have progressively accumulated in the ecological literature, but there has been almost no attempt to look for general rules (Thayer, 1979 and Naiman et al., 1988). Therefore, ecological textbooks have rarely included such effects among the list of important forces which are shaping ecological populations and communities or influencing functioning of ecosystems (Wright and Jones, 2006). Instead they have only focused on interactions such as competition and predation, or emphasized metabolically regulated nutrient and energy flows (Wright and Jones, 2006). It was to incorporate this variety of abiotic environmental alteration by organisms through their bioturbation activities that the concept of ecological engineering was proposed by Jones et al. (1997).

The process through which organisms create and maintain their environments is well known as ecological engineering and the organisms responsible are called ecological engineers. Ecological engineers are organisms that directly or indirectly modulate the availability of resources by causing physical state changes in biotic or abiotic materials for the benefit of other species in ecosystems (Jones et al., 1994, 1997). This type of engineering has both negative and positive effects on species richness and abundance on a small scale, but collectively the net effects are probably positive on a larger (ecosystem) scale surrounding the engineered environments (Jones et al., 1997). Ecological engineers affect the physical space in which other species live and their direct effects can last longer than the lifetime of the organism, thus engineering effects can persist for decades even after the engineer is dead or has relocated (Hastings et al., 2007).

Species vary in their ability to act as ecological engineers. Therefore, six criteria according to which most significant engineering species can be assessed formally was introduced by Jones et al. (1994) as follows: (1) lifetime per capita activity of individual organisms; (2) population density, (3) spatial distribution of the population (both locally and regionally); (4) length of time a population has been present at a site; (5) durability of constructs, artefacts, and impacts in the absence of the original engineer and (6) number and types of resource flows that are modulated by the constructs and artefacts, and the number of other species dependent on these flows. However, an organism does not need to fulfil all six criteria to be regarded as an engineer, because the significant ecosystem effects can arise from various combinations (Berkenbusch and Rowden, 2003).

Jones et al. (1994) distinguished between two types of engineering species namely autogenic and allogenic. Autogenic engineers change the environment through their own physical structures, for example their living and dead tissues and are an integral part of the engineered habitat. Allogenic engineers include both animals and plants that change the environment by changing living or non-living materials from one physical state to another, primarily by mechanical means. A critical characteristic of an ecological engineer is that it must change the availability, quality, quantity, distribution of resources utilised by other biota, excluding the biomass provided directly by engineers (Jones et al., 1994, 1997). Therefore, engineering is not the direct provision of resources in the form of meat, fruits, leaves or dead bodies (Jones et al., 1994).

There are many ways in how organisms can engineer their aquatic, terrestrial or wetland environments. Beavers provide a striking and well known example of how organisms influence the aquatic or wetland ecosystems structure and dynamics in a hierarchical technique (Naiman et al., 1988). Beavers primarily modify stream morphology and hydrology by cutting wood and building dams. The results of their activities retain sediment and organic matter in the channel, create and maintain wetlands, modify nutrient cycling and decomposition dynamics, modify the structure and dynamics of the riparian zone, influence the character of water and materials transported downstream, and ultimately influence plant and animal community composition and diversity (Naiman and Melillo, 1984; Naiman et al., 1988). Beavers' activities influence invertebrates' community structure and function by replacing running-water species by pond species (primarily a response to finer sediments and a decrease in speed of water flow) (Naiman et al., 1988).

However the engineering role of organisms such as the small fossorial mammals on the terrestrial ecosystems for example in drylands is very important, because their bioturbation activities might influence several resources that could have positive knock on effects on other organisms. Below is the description of bioturbation by small fossorial mammals as ecological engineers in general and their potential effects on dryland environments.

Small fossorial mammals as ecological engineers

Many small fossorial mammals such as mole rats (Jones et al., 1994), rabbits (*Oryctolagus cuniculus L.*) (Willot et al., 2000), badgers (*Meles meles*) (Hutchings et al., 2001), pocket gophers (*Geomys bursarius*) (Reichmana and Seabloom, 2002), plateau zokors (*Myospalax fontanierii*) (Zhang et al., 2003), prairie dogs and kangaroo rats (Davidson and Lightfoot, 2006), tuco-tucos (*Ctenomys minutus*) (Galiano et al., 2014) gerbil species (*Rhombomys opimus*) (Xu et al., 2015), plateau pika (*Ochotona Curzoniae*) (Yu et al., 2017) and aardvarks (*Orycteropus afer*) (Haussmann et al., 2018) are regarded to play a significant engineering role in ecosystems. The small fossorial mammals' burrow systems affect the soil texture, aeration, bulk density, soil nutrient concentration, water infiltration rate and holding capacity and nutrient dynamics of soils and consequently the composition and abundance of vegetation (Reichmana and Seabloom, 2002; Villarreal et al., 2008; Yoshihara et al., 2009; Albanese et al., 2010; Kuznetsova et al., 2013; Flemming et al., 2014). The bioturbation by the small fossorial mammals is known as a key form of natural disturbance and a major driver for dynamic variation of ecosystem function because it often alters a soil's physical and biotic processes, which improves soil biodiversity in mesic ecosystems (Reichmana and Seabloom, 2002; James et al., 2009; Flemming et al., 2014; Yu et al., 2017). In addition small mammal's burrows can be used as shelters by other various vertebrate and invertebrate organisms (Whittington-Jones et al., 2011; Kuznetsova et al., 2013).

Soil characteristics, particularly soil moisture, are important drivers of the ecology of dryland environments and the impact of burrowing activities by small fossorial mammals tend to be diverse and more pronounced in arid soils where resource availability is a limiting factor for plant growth (Whitford, 2002 and Albanese et al., 2010). Theoretically, this is because the bioturbation by small mammals is likely to unlock the eco-hydrological process by increasing hydraulic conductivity and thus increase of soil moisture stored in the soil profile which results in benefit for vegetation. This can have a long term significant impact in hyper-arid lands where water is a major limiting factor for primary productivity. The engineered structures of small fossorial mammals together with effects of their bioturbation activities may persist for decades with generally larger total impacts on vegetation (Jones et al., 1994; Bragg et al., 2005; Haussmann et al., 2018). It could be hypothesized that their biotic and abiotic impacts may either increase through time as resources are increasingly accumulating in their burrow systems (Haussmann et al., 2018) or become smaller as burrows erode and fill-in (Haussmann et al., 2018).

There are various mechanisms through which small fossorial mammals engineer their environments. For example, pocket gophers, aardvarks and plateau zokors excavate massive burrow systems and deposit soil in abandoned tunnels and on the ground surface (Reichman and Seabloom 2002; Zhang et al., 2003; Haussmann et al., 2018). They increase the formation, aeration and mixing of soil, nutrient availability, and enhance infiltration (limiting erosion) of water into the soil, thus benefiting the vegetation (Reichman and Seabloom 2002; Zhang et al., 2003; Haussmann et al., 2018). The extensive excavations of the pocket gophers and plateau zokors influence a variety of nutrients and soil conditions that promotes species diversity and primary productivity in the grasslands and arid shrub lands of North America (Wang et al., 1993; Jones et al., 1994; Reichman; Seabloom, 2002). Food that is preserved in the burrows of great gerbils (*R. opimus*), a colonial rodent species of Gurbantonggut Desert (semi-arid) in China, is helpful for the growth of microbes especially for fungi, which in turn can accelerate the decomposition of the soil organic matter (Schlesinger et al., 1990; Jiang et al., 2007; Xu et al., 2015). Their burrows are also used as shelters by organisms such as jerboas, hamsters, shrews, birds, toads, hedgehogs, snakes, and lizards (Xu et al., 2015).

Mole rats are also known to create impressive and cratered landscapes (having more than one holes) through their burrowing activities with effects on soil formation, plant and animal species composition in South African lowland fynbos (Jones et al., 1994). Similarly, earthworms create burrows, mix and cast soils which result in the change of minerals, soil organic composition and moisture which in turn affect nutrient cycling which had an impact on the plant population dynamics and community composition (Jones et al., 1994).

In general if small fossorial mammals increase the water infiltration rate, thus soil moisture, and improve nutrient conditions of the soil through their burrowing activities, the colonial gerbil species are likely to be playing an important functional engineering role in hyper-arid lands. This is, because collectively the effect of their bioturbation activities is likely to be large enough that they may improve vegetation productivity for the benefit of other organisms. The following section therefore deals with the aspect of gerbil species as ecological engineers.

Gerbils as ecological engineers

A number of gerbil species such as the southern African species *G. setzeri*, *Gerbillurus vallinus* and *Gerbilliscus leucogaster*, but also species from various other dryland environments (e.g. Mongolian gerbil (*Meriones unguiculatus*) [Liu and Zhong, 2007] and Indian gerbils (*Tatera indica* and *Meriones hurrianae* [Goyal and Gosh, 1993; Chevret and Dobigny, 2005]), often build burrows in groups (Skinner and Chimimba, 2006). This colonial burrowing results in a high intensity of soil disturbance, facilitating deeper and faster infiltration of water, consequent lower evaporation rates and increased PAM and PAN (Xu et al., 2015) which can be an important phenomenon for hyper-dryland environments where annual rainfall input is low and evapo-transpiration is high. Several studies conducted between 1982 and 2016 (e.g. by Jones et al., 1994; Zhang, 2003; Xu et al., 2012; Xu et al., 2015) showed that, similar to prairie dogs, kangaroo rats and plateau zokors, the extensive networks of colonial burrows have particularly strong direct and indirect positive effects on hydraulic conductivity and water holding capacity, and through this on soil nutrients (Cox, 1987; Laundre, 1993; Gabet et al., 2003; Yoshihara, 2009; Xu et al., 2015).

In South Africa, Korn and Korn (1989) confirmed that the Highveld gerbils (*Gerbilliscus brantsii*) are necessary for the maintenance of a high species diversity of plants at Nylsvley, but not for plant productivity. They found that the total biomass (dry weight) and annual production of aboveground plant matter was significantly lower on burrows colonies than off them, but vice versa was true for plant species diversity.

The results of the effect of gerbils burrowing activities may be the other way around in hyper-arid environments, that the colonial gerbils may be engineering their habitats and improve vegetation productivity on the patch-scale for the benefit of other species at ecosystem level. However, these patches of vegetation may be developed naturally by other means rather than by ecological engineering such as bioturbation activities of gerbils. Below is a description of the vegetation patterning occurring in dryland ecosystems.

Vegetation patterning in dryland environments

In general there are various patterns of vegetation that could be made primarily by other mechanisms than ecological engineering in dryland environments. Two main types of polygonal vegetation patterns have been described in semi-arid regions: mainly spotted patterns caused by wind, while banded patterns form by water flow as a result of redistribution of plant material and seed (Aguiar and Sala, 1999; Merino-Martin et al., 2015). The latter, in the form of overland flow may be the predominant mechanism in arid environments (Yizhaq et al., 2019). The connection of patches depends on the total annual rainfall input (Aguiar and Sala, 1999). For my study area, this raises the possibility that the vegetation patterns might be primarily caused by hydrological processes that create favourable conditions for grass survival and that the gerbils simply dig their burrows where they find soft substrates and vegetation. The various resources provided by the vegetation patches for other organisms could thus be the result of a physical process together with the gerbils being just facilitators of growth of patches by improving the soil moisture conditions.

Similar polygonal vegetation patterns for arid regions have been described in other parts of the world as well as in Namibia. Ollier and Seely (1977), and Watson (1980) observed that the networks of polygonal patches of *Stipagrostis gonatostachys* and other short-lived grasses near Gobabeb are bounded by straight lines with little regularity. They stated that the patterns described here are different from simple mud cracks. They also described three types of polygons, which they called A, B and C. In type A polygons, the grass *S. gonatostachys* grows inside the polygons rather than on bounding lines. In type B, same grass species grow along the lines but not within the polygons and Type C polygons support a slight growth of *S. gonatostachys* within the polygons and a more dense growth along the lines. Goudie (1970), Ollier and Seely (1977), and Watson (1980) concluded that the polygonal patterns of *Stipagrostis gonatostachys* and other short-lived grasses result from subsurface fissures filled with sandy surface material that either permit greater infiltration and storage of moisture (favouring plant growth), or create excessively drained microsites preventing growth of plants.

Ollier and Seely (1977) suggested that the patterned ground is not the result of active processes continuing at the present time, but was created at a specific time when the soil substrates (calcrete) dried out. However, the bounding lines are utilized by burrowing animals (such as the gerbils) which may modify and maintain the difference between lines and internal of the polygons, but the burrowing animals are not the main creators of the polygons although they can be the secondary promoting agents of the polygon formation (Ollier and Seely 1977; Mugatha, 2014). Theoretically, the burrows being constructed in bounding lines may increase hydraulic conductivity, by enabling water to infiltrate faster and even deeper than where there are no burrows. This may allow the soils in drylands to hold moisture for extended period, which could be an added advantage for plant growth. These polygons are used by small mammals for several reasons: (1) the area is covered with denser vegetation tend to be cooler than the sparsely covered ones, (2) there is an accessible food supply in the form of seeds, fruits and leaves; (3) it saves time and energy for foraging and minimize the predation risk from their enemies by not foraging far from their burrows (Prakash, 1981; Brown and Heske, 1990; Busch et al., 2000; Brown and Ernes, 2002; Xu et al., 2013). Consequently, the vegetation productivity increases as a result of raised in PAM and PAN due to the gerbils' bioturbation activities (Bates and Jackson, 1984; Malizia et al., 2000; Gabet et al., 2003; Xu et al., 2012) in the polygons.

In the central Namib the denser vegetation patches (circle-shaped) are all over the gravel plains and most have gerbil burrow colonies on them. The following section is the description of denser vegetation patches and the possibility that the Namib gerbils may be either causing them or improving their formation in terms of vegetation establishment and growth.

Vegetation patches and the possible engineering role of gerbils in their formation in the central Namib

Anecdotal reports and personal observations suggest that the cover of vegetation growing on patches with gerbils' burrows is higher than where the burrow patches are absent, across the gravel plains in the central Namib. However, only one previous study investigated whether gerbils are ecological engineers. In particular, Cox (1987) tested the hypothesis that vegetation circles on the gravel plains are the result of rodent disturbance of the soil. Cox (1987) found that water infiltration rate, percentage vegetation cover and species diversity were higher on the burrow patches than off them. The development of vegetation circles probably begins with the excavation of tunnels systems and nest chambers by gerbils, because soil disturbance by rodents tended to increase the permeability of the soil to water, thus favouring growth of denser stands of annual grasses after periods of rain (Cox, 1987). Additionally, eventual collapse of the tunnels and nest chambers also creates a depression, evident in some of the recently abandoned gerbil nests, which favours water accumulation (Cox, 1987). Collapse of the tunnels and chambers may also be caused by large ungulates i.e. mountain zebra and gemsbok, attracted to colony sites by an abundance of annual grasses (Cox, 1987). Wind erosion eventually removes fine soil materials from the surface heaps, leaving a lag gravel deposit, and fills the central depression with sandy material which is still very porous (Cox, 1987). Thus, the soil system is restructured in a way favouring the infiltration and storage of water for many years, a period well beyond that at which surface evidence of the former gerbils' colonies has been obliterated, results in extended benefit for the vegetation (Cox, 1987). Cox (1987) provided valuable information which postulates that gerbils' bioturbation activities results in the formation of vegetation patches in the central Namib, but it is not inclusive to tell whether the gerbils are ecological engineers.

The review of the central Namib ecology by Louw and Seely (1982) suggested that soil disturbance by rodents tend to increase the permeability of the soil to water, favouring the growth of denser stands of annual grasses after periods of rain. Louw and Seely (1982) further suggested that patchy use of the ground by Namib gerbil species may contribute to higher vegetation cover and vegetation species diversity through alteration of the substrate. Louw and Seely (1982) suspected that the fossorial animals responsible for the burrow colonies which give rise to the vegetation circles could probably be the gerbil species (e.g. *G*. *setzeri*). There is a possibility that the burrow colonies made by gerbil species could have a significant impact on the ecosystem across the landscape on the gravel plains of the Namib.

Although *G*. *setzeri* is assumed to be playing an ecological engineering role, probably because it is well known to be colonial and that it is endemic to the Namib (Stuart and Stuart, 1995; Skinner and Chimimba, 2006), it is not the only gerbil species that is colonial and occurs on the gravel plains of the central Namib. There are other colonial and non-colonial gerbil species that are also dwellers of the Namib Desert. The ecology of these species is explained in depth within the following section.

Ecology of the Namib gerbil species

Different species of gerbils with diverse ecology occur in the Namib Desert (Table 1), not all of which live in colonies. The following review was done with the aim of summarising the ecology of all those gerbil species that inhabit the central Namib, to determine which species is the most likely cause of the burrow colonies we encountered.

Gerbil species are mostly arid environment dwellers (Ramantswana, 2013). Gerbils are the most abundant small mammals in the Namib (Griffin, 1990). Six species of gerbils have been recorded in the Namib Desert (Griffin, 1990): *Desmodillus auricularis*, *Gerbilliscus paeba*, *G. tytonis*, *G. setzeri*, *Gerbillurus vallinus*, and *G. leucogaster* (see Figure 2)*. D*. *auricularis* live in complex and wide burrow structures and can be found on bare ground (Ramantswana, 2013). It is often confused with the pouched mouse (*Saccostomus* *campestris*) which occurs in many areas of the central Namib especially after good rains (Griffin, 1990). *D*. *auricularis* occurs along the northern and eastern edge of the sand sea and in the Kuiseb River bed, where the river directly borders the gravel plains (Griffin, 1990). Although some individuals of *G*. *paeba* occur on sandy soils with little grass cover (Ramantswana, 2013), they seem to prefer semi-hard substrates of the gravel plains and localized drainage courses with some grass cover (Griffin, 1990). This is similar to the habitats that are encountered in my study area, but *G*. *paeba* live in simple burrows with only one entrance, which is hidden under vegetation and not with sand (Ramantswana, 2013).

G. tytonis prefers the vegetation-less habitat of the Namib sand sea (Griffin, 1990) and lives in simple burrows (Skinner and Chimimba, 2006). *G*. *setzeri* (hairy footed gerbil) prefers semi-compacted sparsely vegetated gravel plains, on shallow calcareous soils with a slight gypsum crust and with a grit blanket (Dempsters et al., 1998). *G*. *setzeri* is endemic to the Namib Desert, ranging northwards from the Kuiseb River to southern Angola and lives in complex, network burrows with the maximum depths of 21.4 m (Downs and Perrin, 1990a; Dempsters, et al., 1998; Henschel, 2009). *G*. *leucogaster* similarly lives in complex burrows that they dig in smooth barren substrates. *G*. *vallinus* inhabit areas of consolidated soils, bare gravel plains, dry riverbeds or shallow sand overlying gravels with scant vegetation (Dempsters, et al., 1999). They live in complex branched burrows with depths of about 1.5 m (Dempsters, et al., 1999; Skinner and Chimimba, 2006).

With the exception of *G. tytonis* which is non-colonial, all species can be colonial, but only three (*G. vallinus*, *G. leucogaster* and *G. setzeri*) are exclusively colonial (Table 1). Regarding these three species, only the distribution of *G*. *setzeri* overlaps with my study area. When combined with its habitat preferences, these two characteristics suggest that *G. setzeri* is therefore the most likely species that is digging the clusters of burrows that we encountered. I set up 25 Sherman-live traps over five nights and at different colonies of actively used burrows, and four specimens that were trapped were identified by Dr. Eiseb as *G*. *setzeri* (see Table 8 and Figure 19 in the appendix). *G*. *setzeri* occurs only on the adjacent gravel plains of the Namib Desert (Downs and Perrin, 1990a) where surface water is scarce. *G*. *setzeri* is granivorous and mainly depend on their food intake for water (Down and Perrin, 1990a; Dempsters, et al., 1999). They store their food by burying them (Down and Perrin, 1990a). There is no sufficient information available on the diet of *G*. *setzeri*, but they are mostly prefer arthropods, leafy and seed materials (Dempsters, et al., 1999). In general, low and fluctuating population of rodents resulted from low primary and insect productivity which is caused by low rainfall input (Perrin and Boyer, 2000).

Therefore, rainfall drive the system by regulating primary productivity, thus gerbil species population (Perrin and Boyer, 2000).

Table 1: *A summary description of six gerbil species occurs in the Namib Desert. G. setzeri is the most likely species that is involved in excavating the burrow clusters in my study area, because of the combined set of properties in bold.*

Gerbil species	Habitat	Burrow structure	Food source	Colonial/not colonial	Distribution includes study area
D. auricularis	Gravel plains and hard ground with grass	Live in simple burrow	Seeds, mostly of grasses	Colonial or non-colonial	No
G. tytonis	Vegetation-less habitat	Live in simple burrow	Seeds and insects	Non-colonial	No
G. vallinus	Restricted to area of consolidate soils	Complex (branched) burrow	Seeds and insects	Colonial	No
G. leucogaster	Smooth barren substrates	Complex burrow	Seeds, fruits and partly insects	Colonial	No
G. setzeri	**Semi-compacted vegetation-less gravel plains**	**Complex and wide burrow structure**	Seeds and insects	**Colonial**	**Yes**
G. paeba	Have widest habitat tolerance	Simple burrow	Seeds and insects	Colonial or non-colonial	Yes

Source: Dempsters et al. (1998), Stuart and Stuart (1995), Dempsters et al. (1999), Skinner and Chimimba (2006), and Henschel (2009).

The map below indicates the spatial distribution of the gerbil species occurs in the Southern of Africa including the study area.

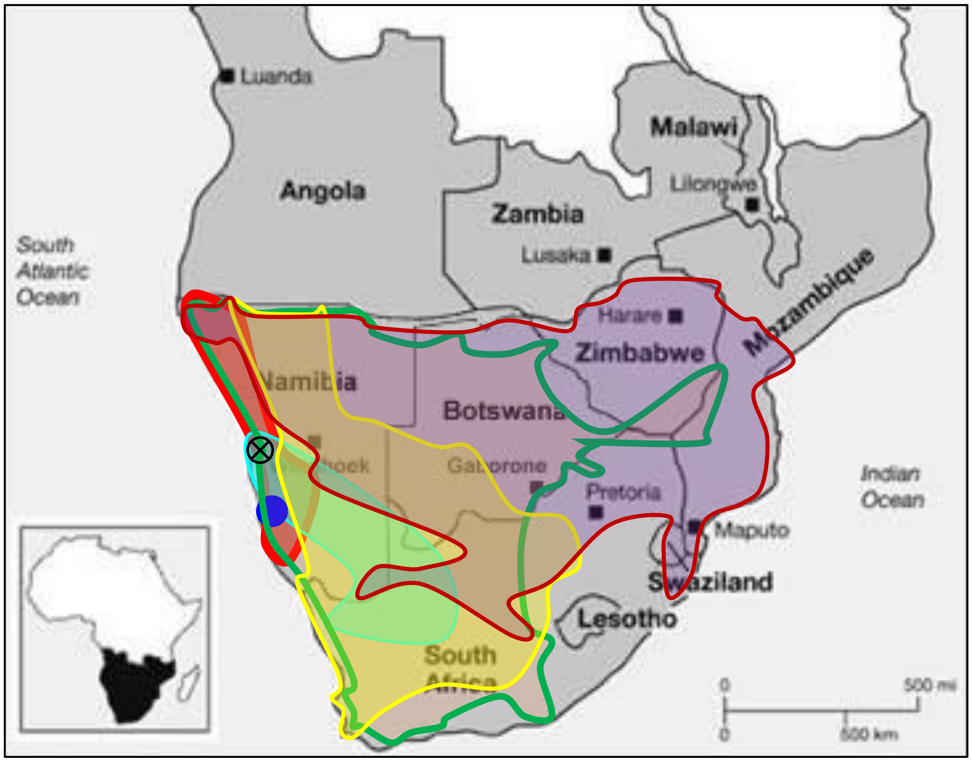


Figure 2. *The spatial distribution of southern African Gerbil species highlighted in this proposed study. A map redrawn from Stuart and Stuart (1995), Skinner and Chimimba (2006), Ramantswana (2013).*

Key:

⊗	*Study area*
●	*G. tytonis*
🟩	*G. paeba*
🟥	*G. setzeri*
🟦	*G. vallinus*
🟨	*D. auricularis*
🟪	*G. leucogaster*

Other central Namib burrowing species that could be excavating burrows

It is clear from personal observation that a number of different small fossorial species are constructing burrows on the gravel plains of the Namib Desert, at least some of who's (such as pouched mouse [*S. campestris*]), burrows are about the same size as those of gerbils. Some species' burrows are larger than the gerbils' ones, including the aardvark (*Orycteropus afer*), mongoose (*Cynictis penicillata*), ground squirrel (*Xerus princeps*), cape ground squirrels (*Xerus inauris*), cape porcupine (*Hystrix africaeaustralis*), cape hare (*Lepus capensis*), cape fox (*Vulpes chama*) and meerkats (*Suricata suricatta*) (Coetzee, 1970; Cox, 1987 and Ewacha et al, 2016). There are also species that dig smaller burrows than the gerbils' burrows. This includes a range of species such as scorpions e.g. *Parabuthus gracilis* and *Parabuthus nanus* (Prendini and Esposito, 2010), spiders, lizards (*Pedioplanis husabensis*, *Pedioplanis namaquensis*, *Meroles suborbitalis, Pedioplanis cf. inornata*), geckos and tenebrionid beetles. However, none of these species make burrows that are of the same shape and in patches, which is unique to the gerbils on the gravel plains of the central Namib (Stuart and Stuart, 1995).

The above sections contain general information towards the potential that gerbils can be ecological engineers in the central Namib. There are possibly two options that gerbils can be ecological engineers, with the first one that the gerbils are the main creators of vegetation patches. The second option is that vegetation patches existence may be originally the results of physical mechanism and then gerbils later get attracted by the denser patches of vegetation, which they will utilise for their shelters (burrows) and improve the growth of these patches. Below I propose two conceptual models and describe more about the theoretical mechanisms that may be involved in each model for the formation of vegetation patches.

Chapter 3

The conceptual models of vegetation patches as gerbil-engineered

The following text refers to the proposed theoretical conceptual models as represented by Figure 3A and B. These models explains how, at the patch-scale, the gerbils might be involved in either creating the vegetation patches or enhancing an existing physical patch-creating process. In the current study I suggest that gerbils are in fact ecological engineers because they are able to modify the soil physical properties, resource distribution, quality and quantity, and create habitat for other species. The gerbils have the ability to unlock and facilitate eco-hydrological processes on the patches (the patch is represented by the grey background of the models), which may positively affect productivity and biodiversity at the landscape scale in arid environments (Figure 3A and B).

The purpose of the conceptual models was to define the theoretical mechanism(s) involved and to allow specific predictions to be made. The conceptual models consists of several components that are either drivers or response agents. The main driver of interest is the presence of gerbils' burrow colonies of approximately 5 m diameter and 10 - 15 m apart from each other, which has abundant effects on other components that result in increased vegetation (Figure 3A and B). This patch-scale effect is indicated by the mechanisms and components that are depicted on a grey background. The total effect of the patches then translates to effects on the landscape scale, which are the components outside the grey background (Figure 3A and B).

The engineering mechanism that I propose in this study occurs on the patch-scale, where the gerbils' bioturbation activities results in enhanced PAM and PAN over about the same area as the patch of burrows. The engineering effect then occurs on a landscape scale as the sum of vegetation biomass on the patches. The total mass of living matter per unit area referred to as biomass and it changes with changing environmental factors. Biomass is usually expressed on a dry matter basis (Ball et al., 2001). Under favourable environmental conditions such as on the patches of the gerbils' burrows and water sink areas, vegetation could yield higher biomass as opposed to when conditions are unfavourable in areas without burrow patches.

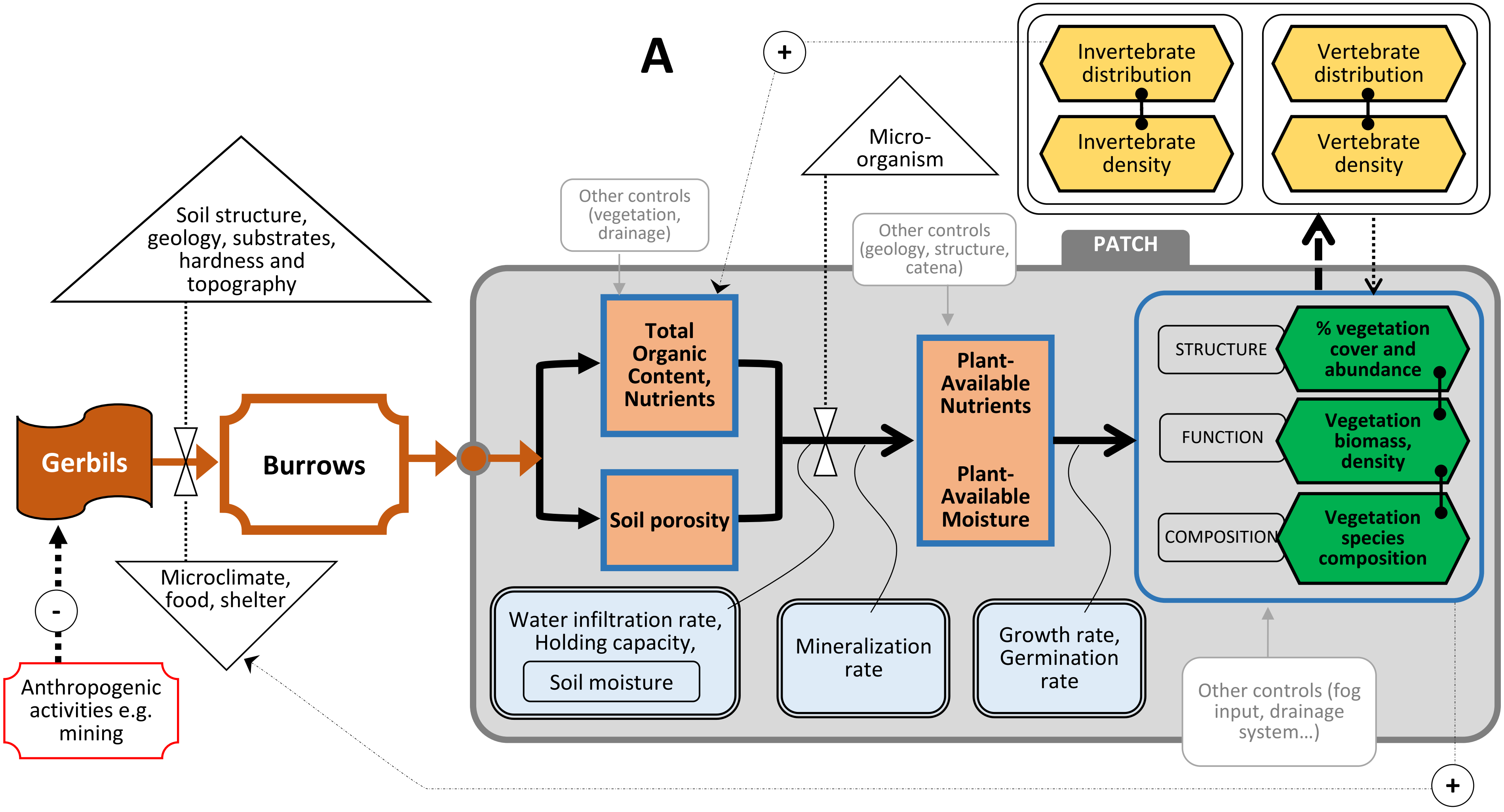
Theoretically, there are two options, both of which may include gerbils as engineers. In the first, the gerbils are altering bare substrate around their burrow colonies in a way that lead to better growing conditions for vegetation, thus causing the patches (Figure 3A). In the second option the patches could exist before the gerbils get there, with the gerbils either being neutral users of the patches or maintaining and improving the existing patch effect (Figure 3B).

In terms of the first option, the variation in soil physical characteristics, microclimate, food, shelter influence the nature of the habitats that prompt gerbils to dig burrows and enhance germination, plant growth and reproduction processes, resulting in patches of vegetation that in turn becomes the gerbils' food supply in the forms of seeds, fruits, and leaves (Brown and Heske, 1990; Brown and Ernes, 2002), and a food supply for a variety of other consumers, some of which may also represent food for gerbils (Figure 3A).

In terms of the second option, the model proposes that rainfall input indirectly results in the presence of vegetation patches through its influence on hydrological overland flow which determine the distribution of the amount of water recharge into the soil (Figure 3B). Theoretically, hydrological overland flow may directly result in patches rich in soil fertility related variables such as organic matter due the accumulation of humus being deposited by water (Figure 3B). As a result, vegetation establishes on patches rich in PAN and PAM, and subsequently food availability, such as insects, seeds, termites, ants, fresh leaves and arthropods increases (Figure 3B). This will attract the gerbils to invade the patches and excavate their burrows (Figure 3B). This option is supported by a known phenomenon in extremely arid areas where temporal and spatial variation of rainfall causes patchiness in the pattern of primary production and this likely to increase species diversity at the regional scale (Louw and Seely, 1982; Eckardt et al., 2013). Water is a strong driver of ecosystem function, productivity, and diversity in arid and semi-arid ecosystems (Eldridge et al., 2010). Water availability varies profoundly in space and through time, and consequently, soil moisture has a patchy distribution, varying across entire catchments or watersheds at landscape scale to individual plants or groups of plants at small spatial scale (Bochet et al., 1999). The distribution and redistribution of water in turn influences patterns of vegetation, which in many areas, is tightly controlled by deposition processes from areas upslope, and through complex interactions between individual plants and biotic and abiotic components of the interspaces (Cerdà et al., 1997; Bochet et al., 1999; Eldridge et al., 2002; Eldridge et al., 2010). Thus, the overland water flow mechanism is an important mechanism in the formation of vegetation patches but it may not be the only explanation (Yizhaq et al., 2019). Other biotic mechanisms such as the gerbils' burrowing activities may be secondary agents and can potentially improve vegetation patch formation (Figure 3B).

In general the burrows excavated in colonies by the gerbils may have a direct influence on the soil porosity, water distribution and redistribution by improving the hydrophobicity (ability to absorb water) capacity of the soil crust during the rainy season (Figure 3A and B). Water distribution and redistribution may be affected by physical habitat alterations of ecological engineers (Jones et al., 1994).

In hyper arid environments, water is the major potential limiting factor for primary productivity (Brown and Ernes, 2002; Belnap, 2011). Therefore, even if soil organic matter may be available in adequate quantity, the decomposition and mineralization rates tend to be lower than in other biomes because of insufficient soil moisture content. The models proposes that gerbils are engineering arid environments by favourably altering the soil moisture pattern for vegetation (Figure 3A and B). It happens because the fossorial lifestyle of the gerbils and the activities that are associated with their lifestyle (e.g. digging a network of tunnels) may influence the ecosystem in diverse ways. In particular, the gerbils' activities will have two main results (Figure 3A and B): a direct increase in total organic content (TOC) and nutrients e.g. Nitrogen (N), Phosphorus (P), Calcium (Ca), Magnesium (Mg), Potassium (K) through deposition of faecal pellets, hoarding food, urination, and the sub-surface introduction of plant and insect detritus. The effect on soil moisture will occur through an increased soil porosity and water holding capacity (TOC is associated with higher water retention properties), as well as through deeper infiltration and consequent lower evaporation rates (Laundre, 1993).



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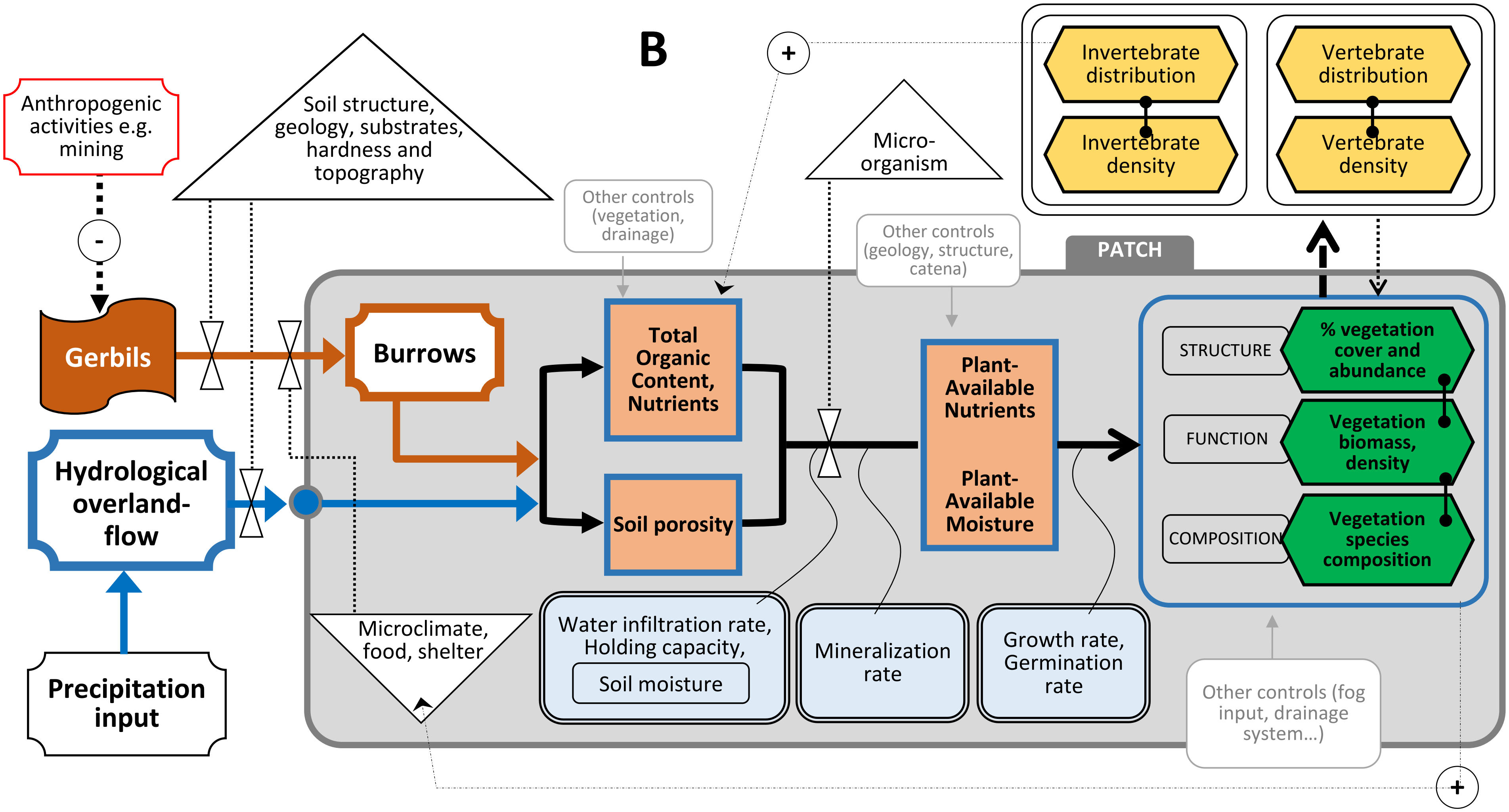

Figure 3 continued...

→ Direct influence (1)
→ Indirect influence (2)
→ Feedback (3)
⧗ Controller (4)
▨ Patch-scale dynamics (7)
●—● These variables are possibly related (8)
▢ Other controls... Factors not forming part of the current study (9)
🟨 🟩 🟧 ▢ Coloured rectangles represent variables that could be measured in the current study (10)
● Gerbils as the main creators of vegetation patches (5)
● Hydrologic overland-flow as the main causative agent of vegetation patches (6)

The grey coloured round rectangle (7) represents the predicted process, physical properties, explanatory and objectives variables occurring on the patches of burrows made by gerbil species on the central Namib gravel plains. The black solid straight-line connectors (8) with round shaped endpoints connect properties, variables that are related and may thus be redundant for modelling purposes. The black dotted lines point to specific controllers (4) e.g. microorganisms are modulators for mineralization and decomposition rates. The solid curved connectors link a process with a measurable variable that would indicate the presence and extent/magnitude of the process. Thickness of the path arrows indicates the size of effect one variable has on other, the thicker the arrow the stronger the causative effect and vice-versa.

Figure 3. *The hypothesized conceptual model of gerbils as ecological engineers. Path arrows represent predicted cause-and-effect relationships between variables, including direct, indirect and feedback. Dash and solid path arrows indicate uncertain and certain causative effects by either biotic or abiotic factor on other variables. The orange burrow pathway (A) and the blue hydrological overland flow pathways (B) are two alternative explanations for the existence of the patch (grey background). The hypothesised engineering function occurs on the patch itself via the effects of either or both pathways on soil and hydrology. The functional relationships among the components are described in the text.*

Although mineralization rate in a hyper arid desert is slow compared to other biomes, these are likely to increase as the increased soil moisture stimulates microbial mineralization processes. The burrow systems of small mammals increase aeration of the soil profile stimulates the microorganisms to function at their best, leading to concomitant promotion of mineralization rate (Laundre, 1993). Additionally, because it is expected that the water holding capacity will also increase, the mineralization processes can occur for a longer period. Collectively, these processes will result in increased PAM (Yoshihara, 2009) and PAN, which will stimulate increased vegetation growth (Malizia, et al., 2000 and Villarreal et al., 2008) on the patches. As a result of increase in soil moisture, PAM and PAN may promote processes such as germination and growth rate of vegetation and will thus directly influence the three major primary attributes of biodiversity (compositional, structural and functional) by increasing percentage vegetation cover, vegetation density, biomass, abundance, and by altering species composition (Figure 3A and B).

The spatial pattern of burrow colonies has impacts on the vegetation (primary producers) at the patch scale (grey background of Figure 3A and B). Hence, the percentage of vegetation cover, vegetation density and biomass, and species composition have an impact on the distribution of secondary and tertiary consumers (invertebrate and vertebrate organisms) at the landscape scale (everything outside the grey background of Figure 3A and B). Therefore, in arid regions, the spatial pattern of burrow colonies can fundamentally affect the spatial distribution of primary and secondary producers through time (Louw and Seely, 1982; Wesche et al., 2007; Yoshihara et al., 2010).

Overall, the presence (habitat preferences by gerbils) of gerbils' burrows may be directly influenced by drivers that operate at a larger spatial and temporal scale, such as the soil structure and type, topography, hardness, catena, microclimate, food, shelters and even including geology and soil substrate patterns which also influence hydrological overland flow (Figure 3A and B). The extent to which fossorial mammals may influence soil processes depend on the soil structure and related properties such as hardness (Laundre and Reynolds, 1993). Additionally, mining could have a direct impact on the occurrence and distribution of gerbils across the landscape (Figure 3A and B).

Several other factors can affect the size and direction of changes in the components on the burrow patches, such as the soil organic content, nutrients, PAN and PAM may be influenced by other natural controls such as geology, structure, and catena (Figure 3A and B). The percentage of vegetation cover, vegetation density, vegetation biomass, and species composition in the ecosystem may be influenced by other controls, such as variability in fog (Eckardt and Schemenauer, 1998) and the type of drainage system on the landscape scale (Figure 3A and B), but their combined effects would probably be lesser than the engineering effects of the gerbils.

Both Figure 3A and B proposes the presence of positive feedbacks which actually serve to support the gerbils' presence, but collectively they are unlikely to be large enough to destabilise the system, because the size of their effect is tightly controlled by limitation of moisture in the xeric environment. The vertebrate and invertebrate distribution and density could have a direct positive feedback to the soil organic matter, which may influence the vegetation indirectly via increases in PAN and PAM (Figure 3A and B). Altogether, vegetation density, abundance and biomass, species composition, percentage of vegetation cover, and invertebrate and vertebrate animal's distribution and density have a direct positive feedback to the food availability in ecosystems (Figure 3A and B). This results in direct and indirect positive feedback to the gerbils (Figure 3A and B).

The main prediction of the model is that gerbils either act as the original creators of vegetation patches (Figure 3A) or they are major biotic secondary causative agents during the transition between different states of the ecosystem, by adding vital nutrients to the system and, most importantly, by unlocking and promoting eco-hydrological processes (Figure 3B). Theoretically, this may positively alter biodiversity structure, composition and function in arid environments (Figure 3B). Specifically, the model is suggesting that soil total organic content, plant available moisture and plant-available nutrients, percentage of vegetation cover, vegetation density and biomass will be higher on the patches of gerbils' burrows than in areas without burrows (Figure 3A and B).

Therefore, the overarching key question was whether the patches of gerbils' burrows are positively associated with higher values of biomass different from what occurs where there are no burrow patches present? The research questions that follow from the overarching question are:

1) Is the difference between patch and control in terms of percentage vegetation cover, vegetation abundance, and vegetation biomass on average significantly higher on patches with burrows than those without burrows?
2) Is the difference between patch and control in terms of soil total organic carbon, organic matter, hydraulic conductivity, soil fertility related variables, salinity and sodicity related variables on average significantly higher on patches with burrows than those without burrows?
3) Is there a significant difference on average in terms of soil texture between the areas with and without burrow patches?
4) Is the density of vegetation patches with and without burrows on them different or uniform among various habitats, and if not, is there a possibility that their distribution can be explained by soil substrate characteristics?

There are various ways in which these questions can be approached. The following chapters describe the methods that were applied in this study.

Chapter 4

Research design

A detailed pilot study was conducted in November 2018 and January 2019 to determine the best approach that was followed by the in-depth data collection in February 2019 – February 2020.

The goal of the study was to gather empirical evidence that support the hypothesis whether the gerbils in the central Namib are ecological engineers or not. Unfortunately, the size of the study area and the need for many replications to make it statistically valid precludes a random sampling approach. Therefore, the first step taken was to map the spatial distribution and density of vegetation patches with and without burrows across the study area. Thereafter, I selected specific areas for in-depth experimental study. Therefore, this was a two-phase study with phase 1 (chapter 6) as the prerequisite of phase 2 (chapter 5). The two chapters are presented in the opposite sequence from that of the field work phases because the logic of my argument was that the Namib colonial gerbil species could be changing the environment by improving soil surface permeability and soil fertility on a patch-scale, leading to increased vegetation establishment and growth (this represents phase 2 and chapter 5). However, to be considered ecological engineers, they will have to change the environment at a landscape scale. To establish whether they have a landscape level effect, it is necessary to determine the spatial extend and density of their burrows (this represents phase 1 and chapter 6).

Therefore, the procedure comprised of two phases: (1) the burrow spatial density pattern, in which a survey was carried out, followed by mapping the distribution of vegetation patches with and without burrows on them relative to soil substrate characteristics. (2) The experimental part, in which the vegetation cover percentage was measured, vegetation abundance, several soil variables and hydraulic conductivity in replicated patches of different categories and their corresponding controls.

The specific areas considered for in-depth study were divided into two categories which constituted of low and high density, primarily based on the distribution density pattern of active and inactive burrow vegetation patches and vegetation patches without burrows. Five sites were equally selected based on the type of vegetation patches (with active burrows, with inactive burrows, and without burrows) from both low and high density areas, resulting in a total of 30 sampling sites, each site with 5 experimental points paired with their respective controls (an area of similar size about 30 - 40 m away from a vegetation patch [treatment]).

General description of the study area

The study was conducted on the gravel plains of the Husab area in the central Namib adjacent to the Husab Uranium mine (Figure 4). The mine is located about 60 km east of Swakopmund, in the Namib Desert along the Khan River (Figure 4). There is an extreme variation in moisture availability in the central Namib. The area has an arid climate and receives occasional rainfall during the months of November – April, with annual rainfall ranges from 5 to 50 mm with a long term average of 30 mm per annum (Lancaster et al., 1984; Barnes et al., 1997; Eckardt et al., 2013). Rainfall patterns are sporadic with an increase from west (10 mm along the coast) to the east (60 mm at 100 km inland) (Shanyengana et al., 2002). Sporadic rainfall is often important for seed germination, rapid growth rate and improved reproductive output for most vegetation in the central Namib (Henschel and Seely, 2000). Conversely, fog and dew are the most important primary sources of water for many plants in the central Namib (Henschel and Seely, 2000; Shanyengana et al., 2002). Unlike rainfall, fog events and the amount decreases with an increase in distance from the coast (west) towards inland (east) (Henschel and Seely, 2000; Shanyengana et al., 2002).

The average sunshine hours per day range between 9 to 10 hours, which results in an annual average temperature of 18 to 19ºC. The high-temperature conditions cause a high average annual evaporation rate of between 3000 – 3200 mm per annum (Lancaster et al., 1984). The study area is classified into four habitats namely: rocky outcrop, gypsite plain, grassy plain, plains drainage channels and hard undulating plain. The area is characterized by grasses and scattered shrubs. The common vegetation found within the mine vicinity includes *Stipagrostis* (grass) species, *Arthraerua leubnitziae* (shrub), *Euphorbia virosa* (shrub), *Euphorbia virosa* (shrub), *Acacia erioloba* (tree), *Commiphora saxicola* (tree) *Zygophyllum stapffii* (shrub), *Welwitschia mirabilis* (Giess, 1998). Ungulates such as *Antidorcas marsupialis* (springbok), *Equus zebra hartmannae* (Hartmann's mountain zebra), *Tragelaphus strepsiceros* (kudu) and *Oryx gazella* (gemsbok) are found in the area (Seely and Pallet, 2008). The dominant geology in the area is made up of marble koppes, gypcrete layers, rocky outcrops (hills), calcrete, highly weathered mica schist and red granite bedrock and, unconsolidated and consolidated gravel plains sand (Abrams et al., 1997). The following map is an overview of the entire study area for this study.

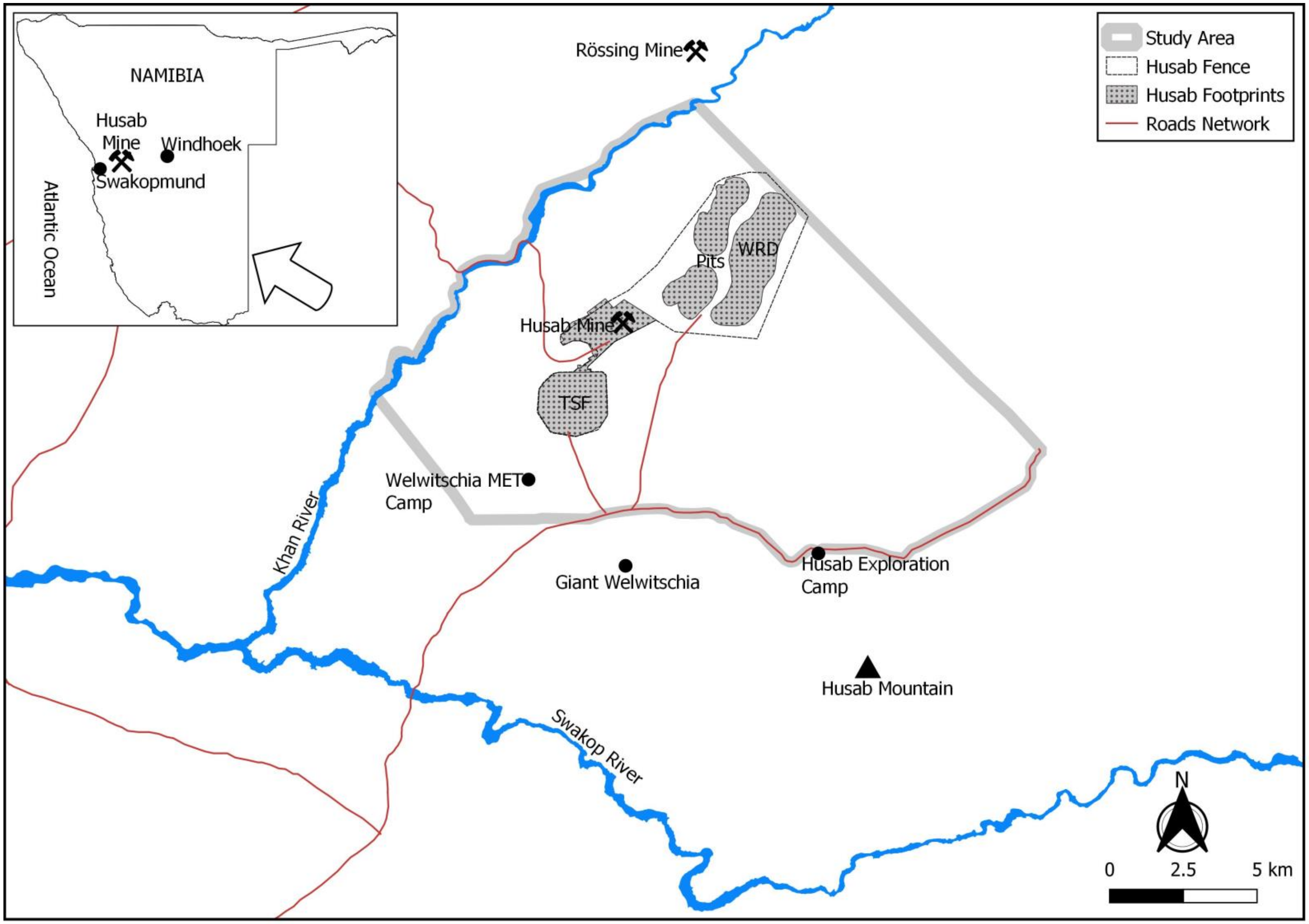

Figure 4. *A map of the study area. The map is showing the Husab mine (located about 60 km east of Swakopmund) including the adjacent main landscape features, giant Welwitschia, Welwitschia camp of the Ministry of Environment and Tourism (MET), Husab exploration camp, Husab mountain, Rössing mine, Khan and Swakop river). The greyish line represents the boundary of the study area which includes the gravel plains (habitat for the gerbils). The Husab mine footprint includes the fence, Tailing Storage Facility (TSF), offices and processing-plant (located by the footprint nearby and north of the TSF), Pits and Waste Rock Dump (WRD). See text for further detail on study area.*

Chapter 5

The following chapter was prepared as a manuscript to be submitted to the Journal of Arid Environments

Aspects of gerbils burrowing activity and their potential ecological engineering role on a gravel plain in the central Namib Desert

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Author’s contribution

HS conceived and designed the research, TW conceived and guided the design, TW and SE supervised the research, HS implemented the work, analysed data and wrote the manuscript, TW and SE edited the manuscript, TW guided data analysis

Abstract

Burrowing small mammals are often considered to be ecological engineers as their burrowing activities alter the soil conditions by potentially changing resource availability and affecting habitat conditions for other species. Post excavation, burrows may strongly have an impact on the local vegetation communities through several mechanisms, including resource trapping, altered plant-available moisture and nutrients, and amelioration of microclimatic conditions at the landscape scale. The main objective of this study was to determine whether the gerbils are significantly improving the growth of vegetation at a patch-scale through their burrowing activities. The study focused on the effect of gerbil burrowing activities by comparing soil physical and chemical properties and vegetation characteristics between contrasting vegetation patches with and without burrows on the Husab gravel plains in the central Namib. The key findings of this study are that on average, vegetation cover, abundance and biomass (each time expressed as the difference between a vegetation patch and a nearby un-vegetated control) were significantly higher on the patches with burrows than on patches without burrows. The burrow patches also showed higher hydraulic conductivity, potassium content, organic matter and carbon than patches without burrows. Our results show that gerbils are significantly improving the primary productivity through changing the conditions and characteristics of the soil at patch-scale. Theoretically, this may have a positive knock-on effect on the larger grazers at the landscape level.

Key words: burrow patches, bioturbation, ecological engineering, central Namib, plant-available moisture and nutrient, vegetation productivity.

Introduction

Gerbils (*Gerbilliscus* spp.) are a group of fossorial desert rodents that are known to change the soil characteristics and conditions through their activities such as foraging, defecation and urination. This is known as bioturbation, which involves the tilling, stirring and churning of soils by living organisms, usually resulting in heterogeneity of soil structure and aeration (Malizia et al., 2000; Gabet et al., 2003). Many bioturbating species, including gerbils are considered to be ecological engineers because they promote mineralization rates, water holding capacity, organic matter (OM), organic carbon (OC) and inorganic nutrient levels of soils which benefits vegetation (Jones et al., 1994; Xu et al., 2015) and thus also a range of other organisms that depend on these changed soil characteristics and vegetation. Jones et al. (1997) suggested that "ecological engineers are organisms that directly or indirectly modulate the availability of resources to other organisms other than themselves by causing physical state changes in biotic or abiotic materials".

Because the gerbils of Namibia's central Namib Desert may increase hydraulic conductivity within their burrow patches, and because their burrow patches are often found in denser stands of vegetation, Cox (1987) considered them to be ecological engineers. Personal observation suggests that Cox's (1987) deduction has some merit: denser patches of grass of about 5 m diameter are often associated with the typical burrows of gerbils (Figure 5) (Henschel, 2009). Cox (1987) argued that these stands of perennial grasses occur because the gerbils' burrows change soil conditions such that the grasses survive for longer after the rainy season. Louw and Seely (1982) also postulated that soil disturbance by rodents tended to increase the permeability of the soil to water, favouring the growth of denser stands of perennial grasses after periods of rain in the central Namib. Theoretically, this could allow grazing ungulates such as zebras and oryx to exist and forage in areas where they could not normally thrive.

***Figure 5**. A colony of gerbils' burrows on the Gypsite Plain. The specific gerbil species that are responsible for digging the burrows on the gravel plains of the central Namib are unknown. Both Louw and Seely (1982) and Cox (1987) suspected that it could be Gerbilliscus setzeri.*

There is strong evidence that many gerbil species are often engineering their environment toward the benefit of other species. For instance, studies such as those by Xu et al. (2012; 2015), Zhang (2003) and Jones et al. (1994) showed that gerbils' networks of burrows, their foraging activities and the nutrient deposition that occurs through urination and defecation have direct and indirect positive effects on other organisms in the ecosystem. Cox (1987), Laundre (1993), Gabet et al. (2003), Yoshihara (2009), and Xu et al. (2015), all reported that the water infiltration rate, water holding capacity and soil nutrients are often higher on the gerbil burrow patches than off them. The burrows of the gerbils can enhance hydraulic conductivity which results in an increase of the amount of plant-available moisture stored in the soil profile (Yoshihara et al., 2009). This effect is even more important in the hyper-arid environment, where any factor (such as the bioturbation activities of gerbils) that can affect water availability could create favourable micro-sites for vegetation establishment (Louw and Seely, 1982; Jones et al., 1994; Xu et al., 2015). The food hoarded in gerbils' burrows is also helpful for the growth of microbes, especially for fungi (Jiang et al., 2007), which in turn can accelerate the decomposition of soil organic matter (Schlesinger *et al*., 1990). This can significantly contribute to the fertility level of the soils and result in increases of plant-available nutrients (PAN) (Xu et al., 2012).

However, most other studies on gerbils as ecological engineers (e.g. Bragg et al., 2005; Davidson and Lightfoot, 2008; Yoshihara et al., 2010) have been done in regions with more than 200 mm annual rainfall. The average annual precipitation for the central Namib gravel plains ranges from 5 to 50 mm (Lancaster et al., 1984 and Eckardt et al., 2013). Such low and unpredictable rainfall may place a limit on the potential for gerbils to be ecological engineers. In addition, both Cox (1987) and Louw and Seely (1982) (the only two Namib-specific publications on gerbils as engineers) included only vegetation patches with burrows in their design, but there are also many vegetation patches that clearly do not have any burrows intermingled with those with burrows (Figure 6).

Similar polygonal vegetation patterns for arid regions have been described in other parts of the world as well as in Namibia. Goudie (1970), Ollier and Seely (1977), and Watson (1980) found that the polygonal networks of *Stipagrostis gonatostachys* and other short-lived grasses result from subsurface fissures filled with sandy surface material that either permit greater infiltration and storage of moisture (favouring plant growth), or create excessively drained microsites preventing growth of plants. Two main types of polygonal vegetation patches have been described in semi-arid regions: mainly spotted patterns occur when wind is the main driver of the process, while banded patterns form when water is the dominant redistributor of plant material and seed (Aguiar and Sala, 1999; Merino-Martin et al., 2015). The latter, in the form of overland flow, may be the predominant mechanism in arid regions (Yizhaq et al., 2019), with the discreteness and connectedness of patches being a function of the total annual rainfall input (Aguiar and Sala, 1999). For our study area, this raises the possibility that the vegetation patches might be primarily caused by hydrological processes that create conditions favourable to grass survival and that the gerbils simply dig their burrows where they find soft substrates and vegetation. The various resources provided by the vegetation patches for other organisms could thus be the result of a physical process with the gerbils being just a neutral user of the patches.

***Figure 6**. Patches of vegetation without burrows (at the time of taking the picture, this comprised only dried grass stumps and some shrubs). The main causative agent of these patches on the gravel plains of the central Namib is unknown, but we are suspecting that it could be the hydrological overland flow – a well-known vegetation formation phenomenon in arid ecosystems (Newman et al., 2006; Smith and Goodrich, 2006; Yizhaq et al., 2019).*

The gerbils' presumptive importance in ecosystem function means that impacts on them could have detrimental effects on other species. This issue was raised in a biodiversity impact assessment done for the Husab Mine, a uranium mine located in the Namib-Naukluft National Park adjacent to our study area (Metago Environmental Consulting Engineers and Scientists, 2010). However, the importance of the mine's impact on the gerbils was uncertain because the size of the engineering effect by the gerbils was unknown. Additionally, we have an interest in clarifying key functional features of the arid ecosystem, to enable better conservation management and assessment of risks to biodiversity related to land use and climate change. More immediately, the gerbils' burrowing activities may assist future restoration of mine or other disturbed areas by increasing the depth of the substrate utilized by the plants, and by ameliorating some of the critical soil physical and chemical properties (Wright, 2006 and Yoshihara et al., 2009). Fossorial rodent *Parotomys brantsii* have shown to create hotspots of increased soil fertility that encourage plant establishment (Desmet and Cowling, 1999). Thus, we considered it important to understand how gerbils and vegetation are interdependent and how this relationship may assist to contain and mitigate impacts and to plan effective ecological restoration and conservation management.

The aim of this paper was to collect empirical evidence that may help us to understand whether the gerbils are significantly improving the growth of vegetation through their burrowing activities. In this way we wanted to verify if they are playing a functional ecological engineering role on the central Namib gravel plains.

Methods and materials

Study area

The study was conducted between June 2019 and February 2020 on the gravel plains west of the Husab Mountain in the central Namib about 60 km east of Swakopmund (-22.64681° S, 14.59987° E) (Figure 7). The central Namib is hyper-arid with extreme variation in moisture availability for all biota. Mean annual rainfall ranges from 5 mm at the coast itself to about 50 mm at the study area itself, with advective fog contributing a further nominal amount of moisture annually (Lancaster et al., 1984 and Eckardt et al., 2013). The year preceding our study was relative dry with a total rainfall of 15.9 mm (as measured at the nearby Husab mine).

Although the dominant geomorphological feature is the large plains consisting mostly of deep silty gravel with shallow pedogenic calcrete and gypcrete layers (Dixon, 1994), the parent geology of the study area is evident as rocky outcrops of marble, conglomerates, highly weathered mica schist and different types of granite bedrock. Pedogenic gypcretes occur on the highest parts of the gravel plain catena as a shallow, thin and fractured layer. Apart from the gravel plains, the main geomorphological features are rocky outcrops of marble, conglomerates, highly weathered mica schist and different types of granite bedrock. The low annual precipitation means that vegetation is sparse and, with the exception of perennial shrubs that are limited to drainage lines, mostly ephemeral. The study area was subdivided into several habitats by Wassenaar and Mannheimer (2010), four of which are relevant for the gerbils because they are characterized by substrates that are appropriate for digging by fossorial animals: the gypsite plain, grassy plain, plains drainage channels and hard undulating plain. The grassy plain and plains drainage channels are both dominated by soft to intermediate gravel plains sand surface cover, unlike the hard undulating plain and gypsite plain which have a harder surface cover type.

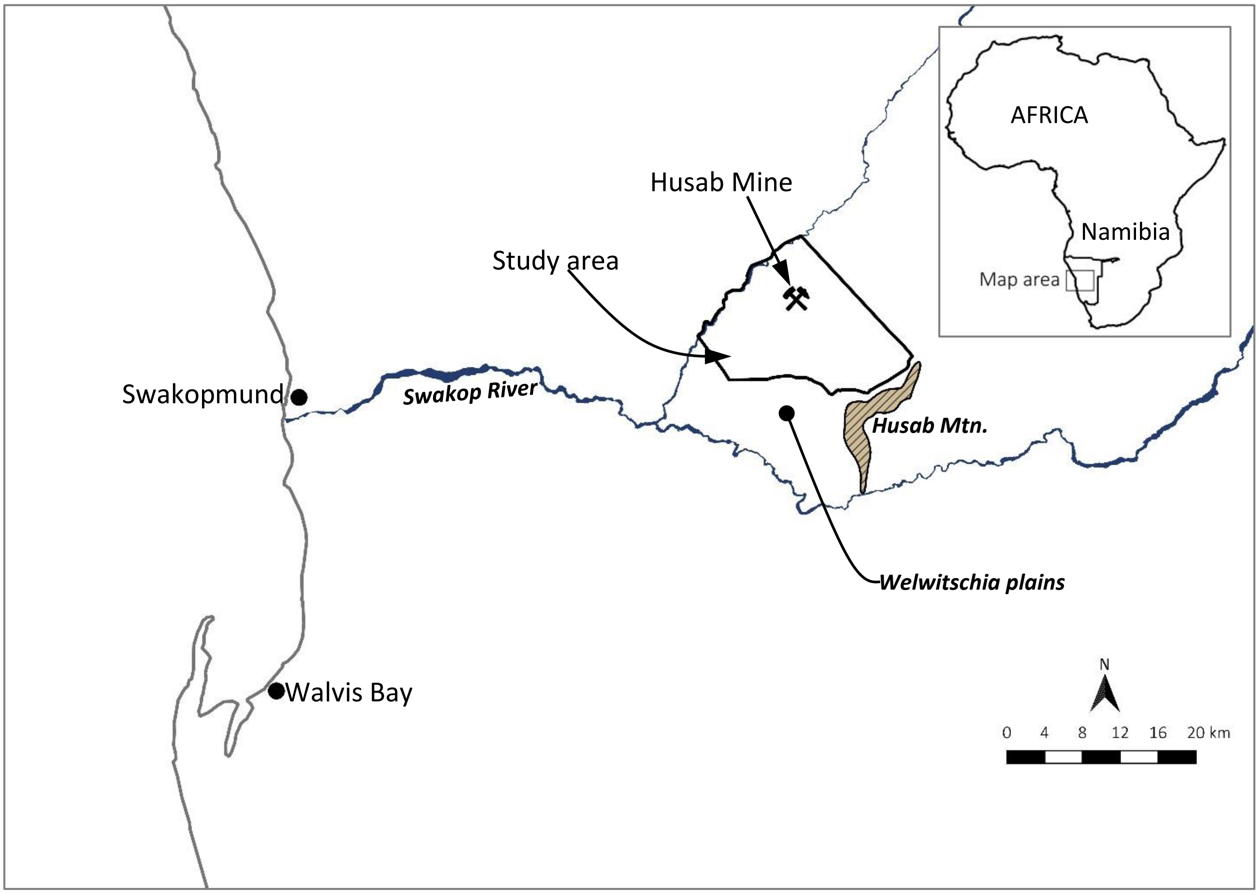


Figure 7. *The location of our study area in the central Namib, about 60 km east of Swakopmund.*

Experimental design

Based on a study that was conducted in parallel with this one and that mapped the spatial distribution and density of vegetation patches (Shaanika et al., Chapter 6), we arbitrarily distinguished between areas that had relatively high or relatively low density of patches.

To determine whether the gerbils significantly improve vegetation growth and could thus be considered ecological engineers, we compared several variables that reflect ecosystem properties, such as productivity (vegetation biomass, percentage cover and abundance), hydraulic conductivity, soil depth (measured as the depth from the soil surface to the hard layer of calcrete or gypcrete), and soil chemical (organic C, N, P, K, Mg, Ca) and physical (organic matter, pH, electrical conductivity [EC], salinity and texture) properties among patches with and without burrows.

Our basic hypothesis was that vegetation patches would, on average, differ from their immediate environment, and that the magnitude of the difference will also be a function of the presence or absence of burrows. We therefore measured the variables both on patches with and without burrows, and on a control site of similar dimensions to each patch, about 20 m away from the patch on the bare gravel plain. The main value we wanted to determine was the difference between each patch and its control. First, based on our informal observations, we expected that patch minus control would always be positive, at least for those variables that reflect soil fertility (N, P, K, organic C and vegetation biomass, abundance and cover). Second, we expected that if gerbils were modulating their environment, the difference between patch and control would on average be larger on patches with burrows than those without burrows. Third, we furthermore differentiated between actively used and inactive burrows, reasoning (with less certainty) that active burrow patches would show the largest effect because any improvement in soil chemical properties will have been leached out in older, unused burrows.

Finally, like many biological phenomena in the desert, the patches as well as the gerbils themselves will likely cluster in places where the substrate and other conditions are more favourable. Hence we expected that the average difference between patch and control, and specifically where vegetation patches associated with burrows, will be larger in areas with a relatively high density of patches than areas with a low density. Theoretically, the areas with a high density of burrow vegetation patches may yield higher biomass than areas with low density as a result of more bioturbation activities.

Data collection

The size of the study area and the need for many replications to make it statistically valid required a semi-random sampling approach. In a study (Shaanika et al., Chapter 6) that we conducted in parallel with the current one, we used a GIS to identify areas with relatively low and relatively high densities of vegetation patches in each of the three categories of active, inactive and no burrows. We then placed five sampling sites of 1 km^2 per density class for each patch category in such a way that each sampling site covered a high or low density area respectively (Figure 8). Within each sampling site, five sampling main-points were randomly selected from a regular grid of points generated by QGIS (Sherman, 2015). A 100 m search area around each sampling main-point was divided into four quarters. Within this search area we selected the closest vegetation patch for the specific patch category in two directly opposing quarters for measurements (Figure 9). In each quarter we established a patch-control pair with one of the area being a vegetation patch (treatment) and the other one a similar-sized area (control) about 30 - 40 m away from the vegetation patch in a random compass direction (Figure 9).

In the centre of each patch-control pair we first recorded habitat and substrate type and measured before measuring hydraulic conductivity with a mini-disc-infiltrometer (consist of two chambers, which are filled with water, the upper chamber controls the suction rate [Devices, 1998 and Kargas, et al., 2017]) and a stop-watch. We then divided each patch-control pair into five 1 m^2 quadrats (Figure 9). In each quadrat we measured total vegetation cover (the sum of the areas of the surface projection of an idealised oval of all individual plant canopies in square meter) and abundance (the number of individual plants rooted inside the quadrat). At first we distinguished between growth forms, but since about 99% of the plants we encountered here were grass polls and none of the material included inflorescences, we ignored this distinction for analysis. We then collected all vegetation material, including roots and litter in labelled paper bags for biomass measurement. Biomass was measured with an FZ-1200i Super Hybrid Sensor (by A&D company of Tokyo in Japan) electronic balance after drying the bagged samples for 48 hours at 50°C in a Labcon drying oven.

Soil Analysis

Soil samples (2 kg) were gathered in paper bags with a small-garden-shovel from the centre of each of the patch-control pairs. The deepest depth excavated was measured with a tape-measure. We pooled soil samples from the two patch and two control points per sampling point, ending up with ten 2 kg samples per patch category and density class. The soil samples were submitted to a private analytical laboratory in Windhoek for the measurement of chemical and physical properties. Methods used to determine chemical and physical properties are summarized in table 2.

Table 2: *The methods that were used for the analysis of soil samples.*

Variables	**Method details**	**Units**
Total nitrogen	Modified Kjeldahl method	Mg N/kg
Organic carbon	Colorimetric Walkley–Black	% m/m C
Organic matter	Calculated from organic carbon, factor = 1.724	% m/m OM
Phosphorus	UV–Vis spectrophotometer (UV mini–1240)	Mg P/kg
pH	Saturated paste electrometric	
Conductivity	Saturated paste electrometric	mS/m
Sodium, magnesium, calcium, potassium	Water soluble – saturated extract followed by inductively coupled plasma - optical emission spectrometry	Meq/L
Sand, silt, clay	Pipette method: Sand (2 mm – 53 µm), Silt (53 – 2 µm), Clay (<2 µm)	%

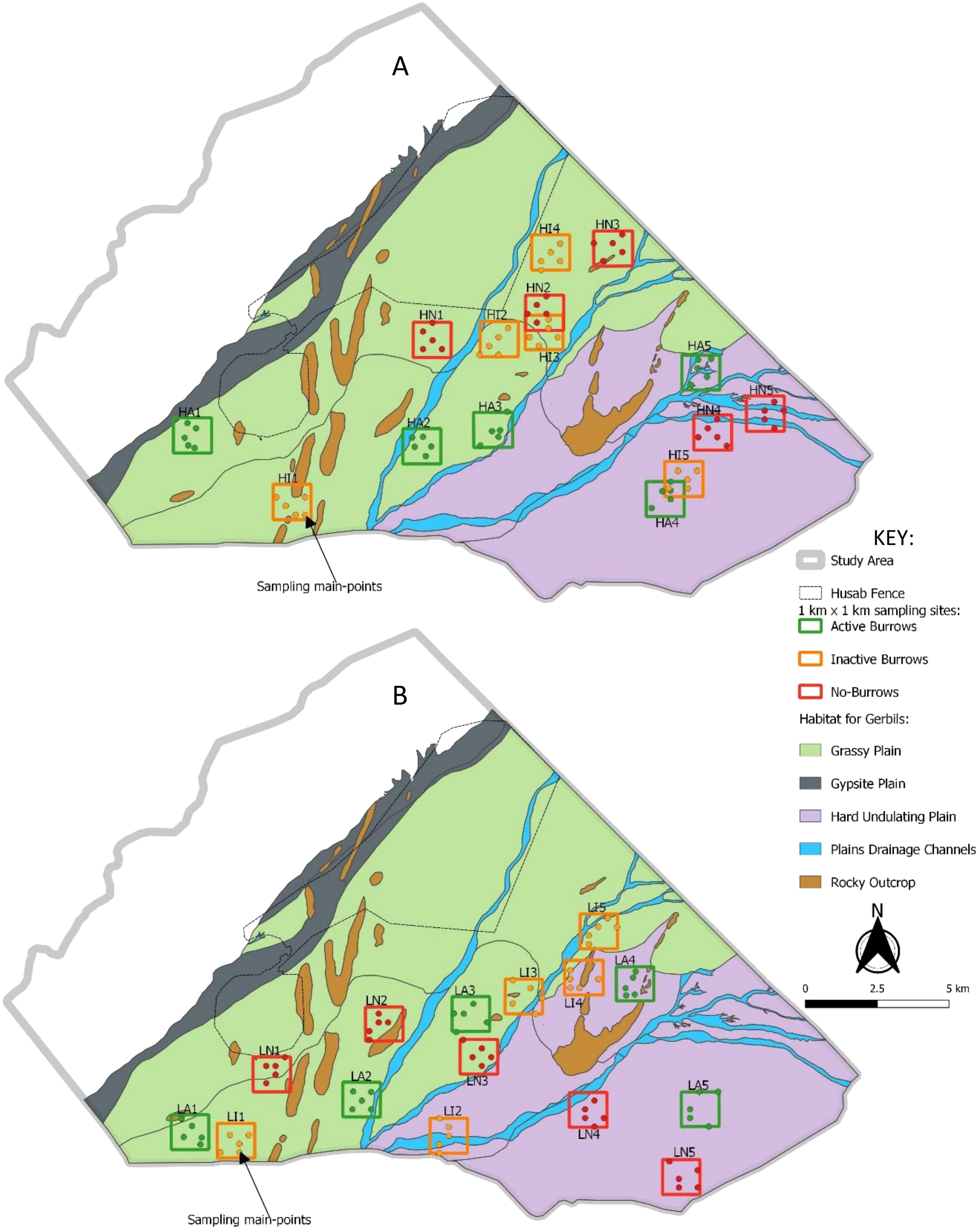


Figure 8. *The outline of the study area showing location of sampling sites for areas with a relatively (A) high and (B) low density of vegetation patches. Each sampling site per patch is coded with a specific id number ranges from 1 to 5 e.g. LA1 = Low Density Active site 1.*

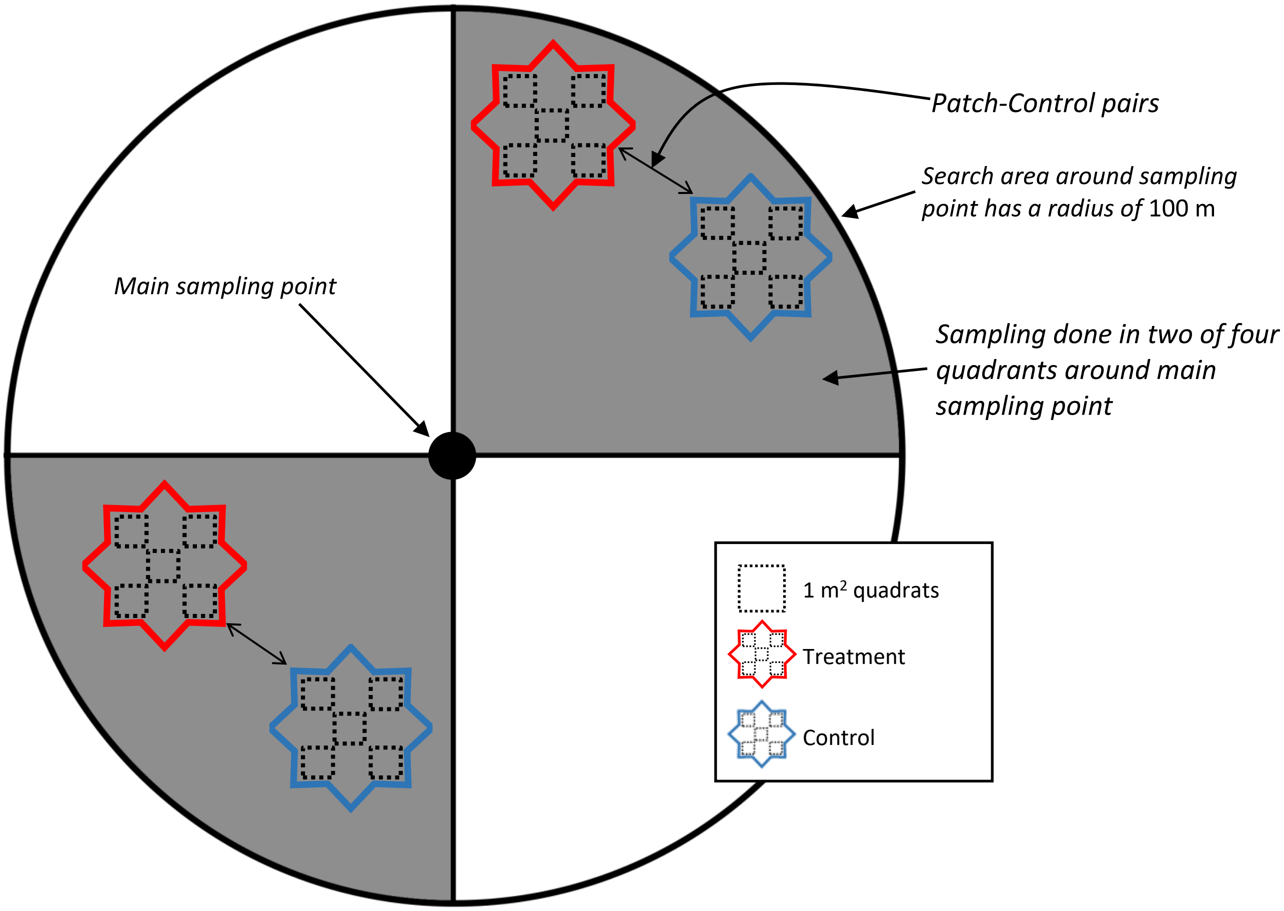


Figure 9. *The diagram shows the sampling main-points divided into four quarters surrounded by a circle of approximately 100 m radius around a point and the selected closest vegetation patches together with their proximity control points in two directly opposing quarters. The patch-control pairs were repeated for each patch category.*

Data analysis

For each variable we calculated the average of the two differences (patch-control) per sampling point between each patch and its respective paired control and then the average across all five sampling points within a sampling site. We thus effectively had five replicate values per patch category and density class. We present our data on graphs as a combination of the mean per patch category and density class calculated for the five replicates as described above, overlain on data points representing all paired differences for each category and class.

Normality of data was determined using the Shapiro-Wilk test; data that were normally distributed (vegetation biomass and abundance, and hydraulic conductivity, soil depth, and all soil physical and chemical properties except Ca and EC) were subjected to a one-way analysis of variance (ANOVA), and to a Kruskal-Wallis test if the distribution was not normal (percentage vegetation cover, Ca and EC). Post Hoc multiple comparisons were done using Tukey's Honestly Significant Difference (HSD). IBM SPSS Statistics for Windows, version 26 (IBM Corp., Armonk, N.Y., USA) was used for statistical analysis. A 95% level of confidence was regarded as significant.

Results

Overall the mean of patch-control differences in terms of vegetation cover, abundance and biomass were positive among all the categories of patches, which means that on average patches had more vegetation than the surrounding environment (Figure 10). This was also the case for hydraulic conductivity (Figure 11) where all patch categories showed faster infiltration on average than their control areas. The mean of patch-control differences were also positive for phosphorus (Figure 12E), pH (Figure 13C) and percentage sand and soil depth (Figure 14C, E), but negative or mostly negative for all other soil chemical and physical variables with an exception of OM and OC in both density categories of inactive burrow patches which was positive (Figures 12, 13 and 14).

The mean of patch-control differences in terms of vegetation cover were significantly higher in both density categories of inactive burrow patches than the rest (Table 3). Regarding vegetation abundance the mean of patch-control difference was significantly higher in high density inactive burrow patches than the rest (Table 3). The mean of patch-control difference in terms of vegetation biomass was significantly higher in the high density of inactive burrow patches than high and low density of no-burrow vegetation patches (Table 3). The average of vegetation biomass of the inactive burrow patches was 51.7 g compared to 17.7 g of patches without burrows. On average the gerbils improved the vegetation biomass by 190% (more than 3 times) on the inactive burrow patches compared to patches without burrows.

The mean of patch-control differences in terms of hydraulic conductivity, content of silt, and sand were varied among all patch categories and density classes, but the hydraulic conductivity and content of sand on the patches was higher than zero on average for both density categories (Figures 11 and 14A, C). The mean of patch-control differences in terms of content of silt were lower than zero on average for both density categories (Figure 14A). The mean of patch-control differences in terms of hydraulic conductivity were significantly different overall, with the high density inactive burrow patches being significantly higher than both density categories of no-burrow vegetation patches (Table 3).

The mean of patch-control differences in terms of silt content were significantly different overall, with both density categories of active burrow patches being significantly higher than both density categories of no-burrow vegetation patches (Table 3). Similarly, the mean of patch-control differences in terms of silt content were also significantly lower in low density of inactive burrow patches than high density of no-burrows vegetation patches (Table 3). Additionally, the mean of patch-control differences in terms of sand content were significantly different overall, with both density categories of no-burrow vegetation patches being significantly higher than both density categories of active burrow patches (Table 3).

Regarding OM and OC the mean of patch-control differences were varied among all patch categories and density classes with content of OM and OC in both density categories of inactive burrows higher than zero compared to the rest (Figure 12C, D). Overall the mean of patch-control differences were significantly different, with the content of OM and OC being significantly higher in both density categories of inactive burrow patches than high density of the no-burrow vegetation patches (Table 3). In terms of K the mean of patch-control differences were also varied among all patch categories and density classes, with all patch categories and density classes (except for high density of inactive burrow patches and low density of active burrow patches close or equal to zero) lower than zero (Figure 12A). The mean of patch-control differences were significantly different, with the content of K being significantly higher in both density categories of inactive burrow patches than high density of the no-burrow vegetation patches (Table 3). The mean of patch-control differences in terms of N, P, Na, pH, EC, Ca, Mg, content of clay and soil depth showed similar patterns across all patch categories and density classes (Figures 12 and 13, 14B, D) and none were significantly different (Table 3).

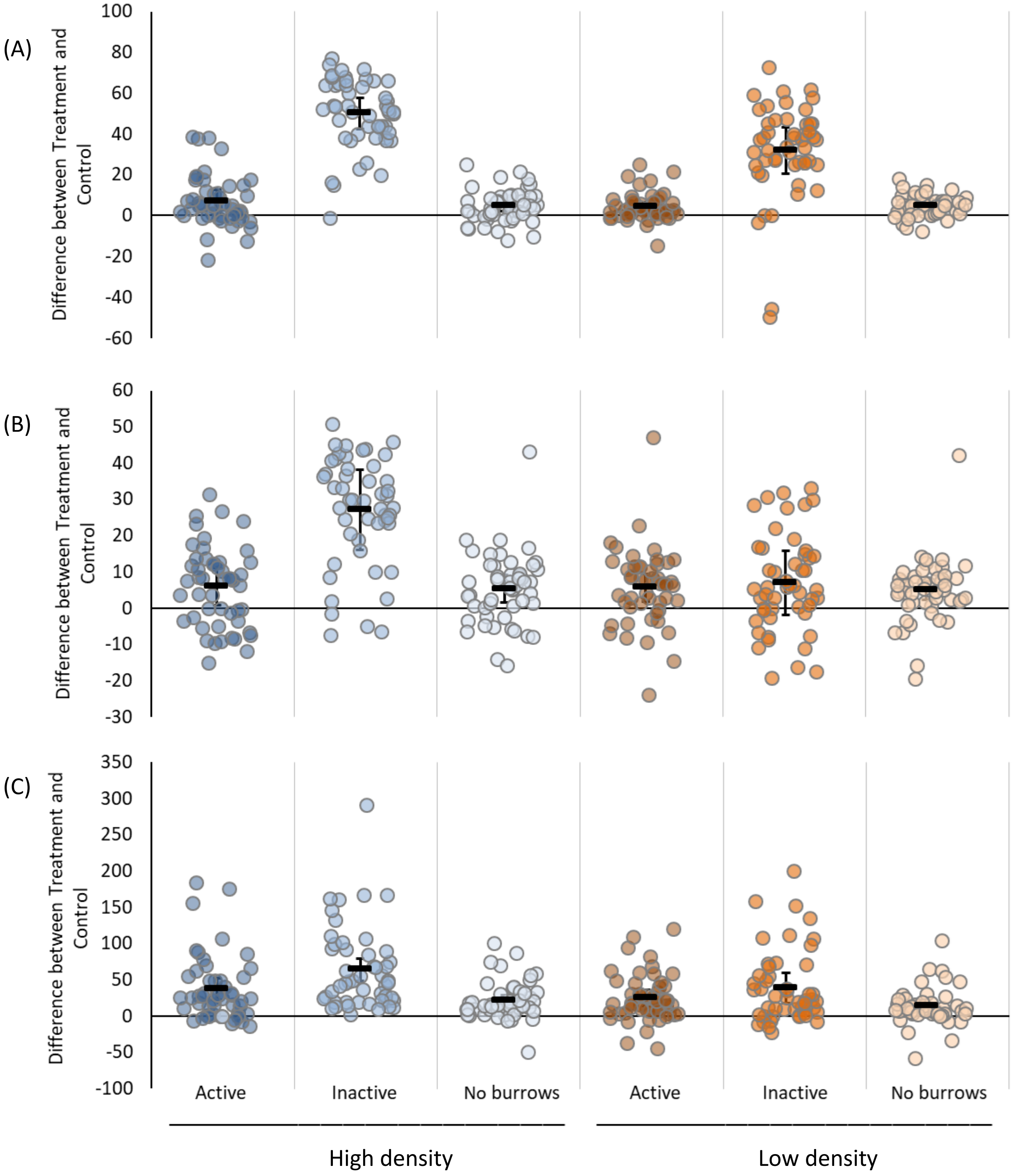


Figure 10. *The mean difference ± 95% confidence interval (CI) (horizontal bar and error bars) between patch and control sites in terms of vegetation (A) cover (%), (B) abundance, (C) biomass (g) among the high and low density of active and inactive burrow patches, and no-burrows vegetation patches on the Husab gravel plains of the central Namib. Coloured circles represent all paired differences between patch and control sites. To save space the x-axis is shared by all sub-plots.*

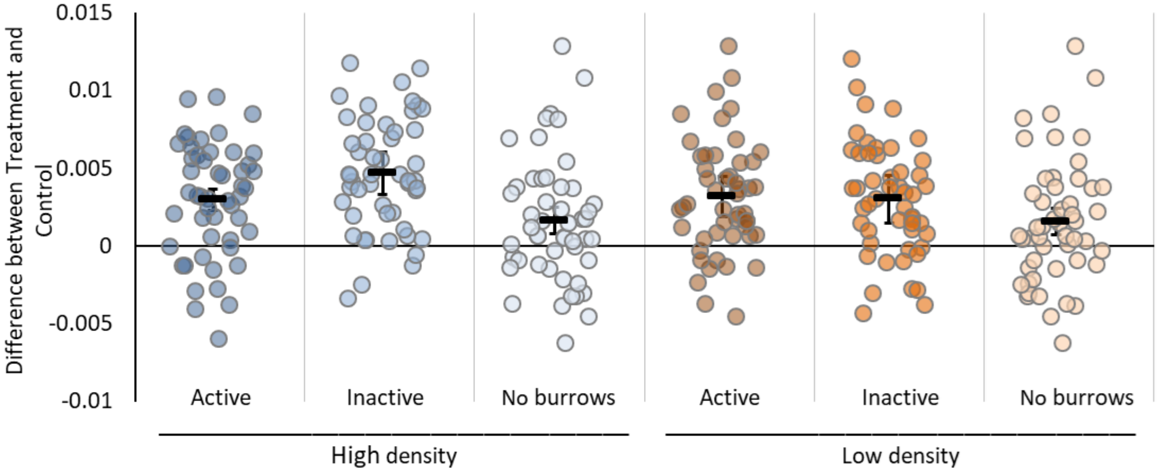
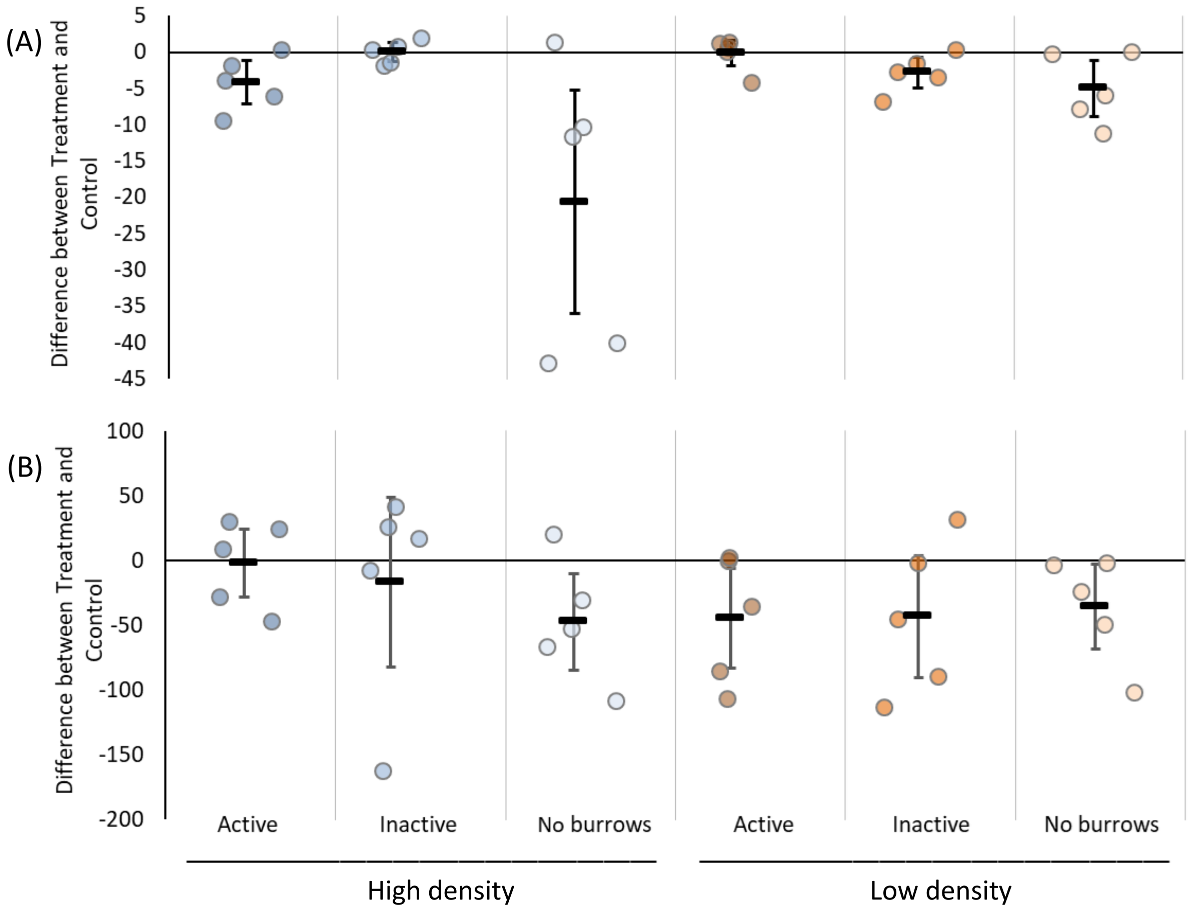


Figure 11. *The mean difference ± 95% confidence interval (CI) (horizontal bar and error bars) between patch and control sites in terms of hydraulic conductivity (m/s) among the high and low density of active and inactive burrow patches, and no-burrows vegetation patches on the Husab gravel plains of the central Namib. Coloured circles represent all paired differences between patch and control sites.*



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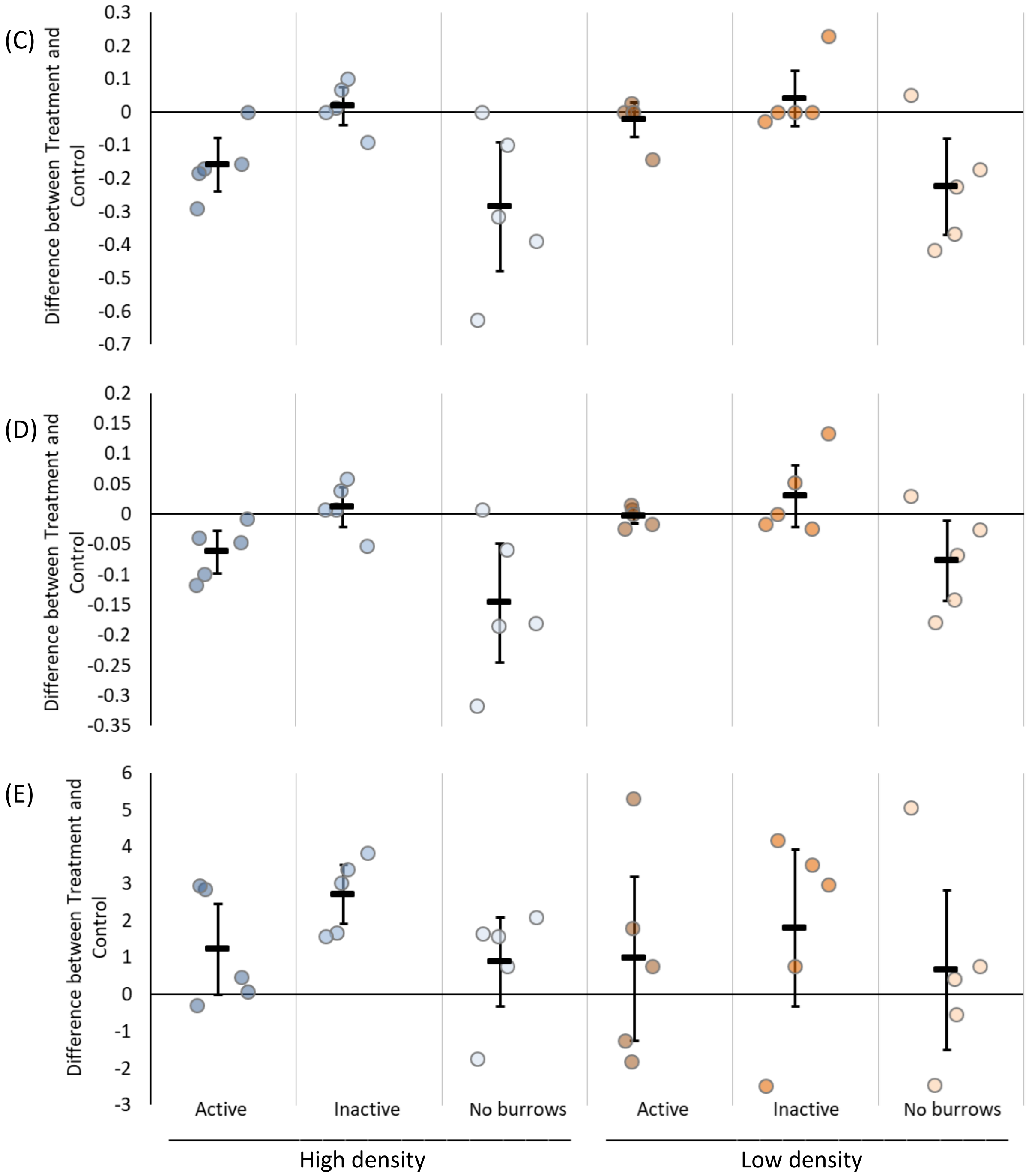
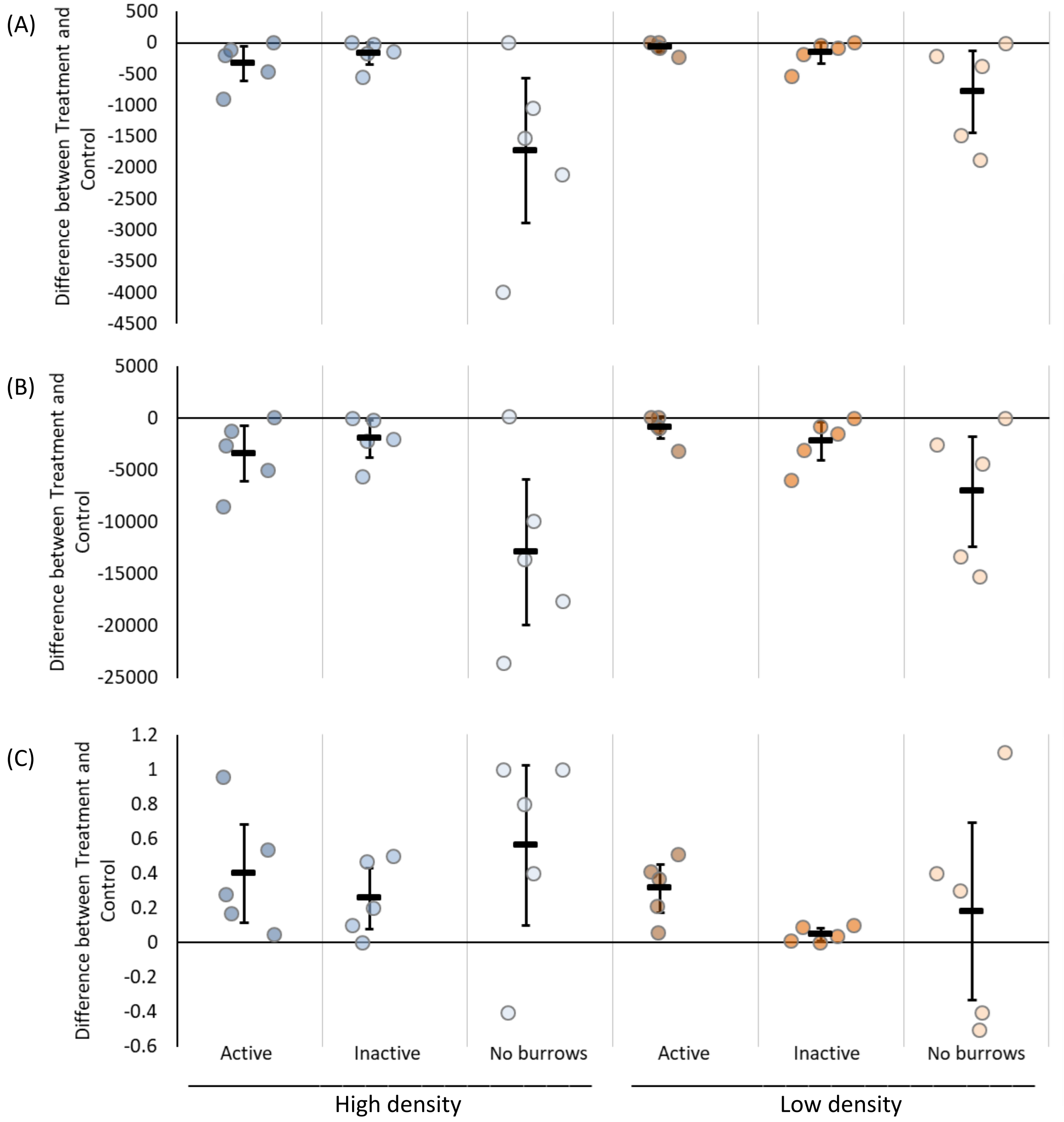


Figure 12. *The mean difference ± 95% confidence interval (CI) (horizontal bar and error bars) between patch and control sites in terms of (A) potassium (meq/L), (B) nitrogen (mg N/kg), (C) organic matter (% m/m OM), (D) organic carbon (% m/m C), (E) phosphorus (mg P/kg) among the high and low density of active and inactive burrow patches, and no-burrows vegetation patches on the Husab gravel plains of the central Namib. Coloured circles represent all paired differences between patch and control sites. To save space the x-axis is shared by all sub-plots.*



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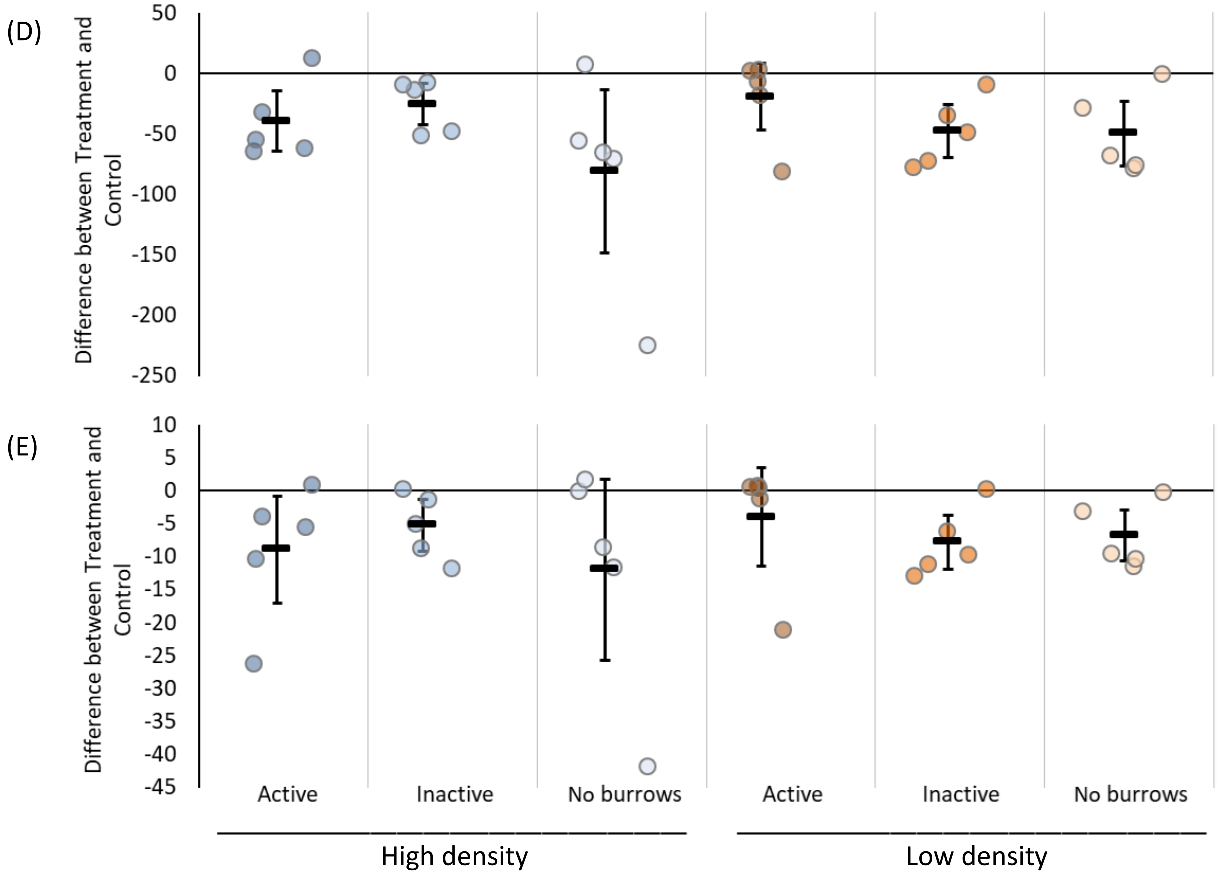
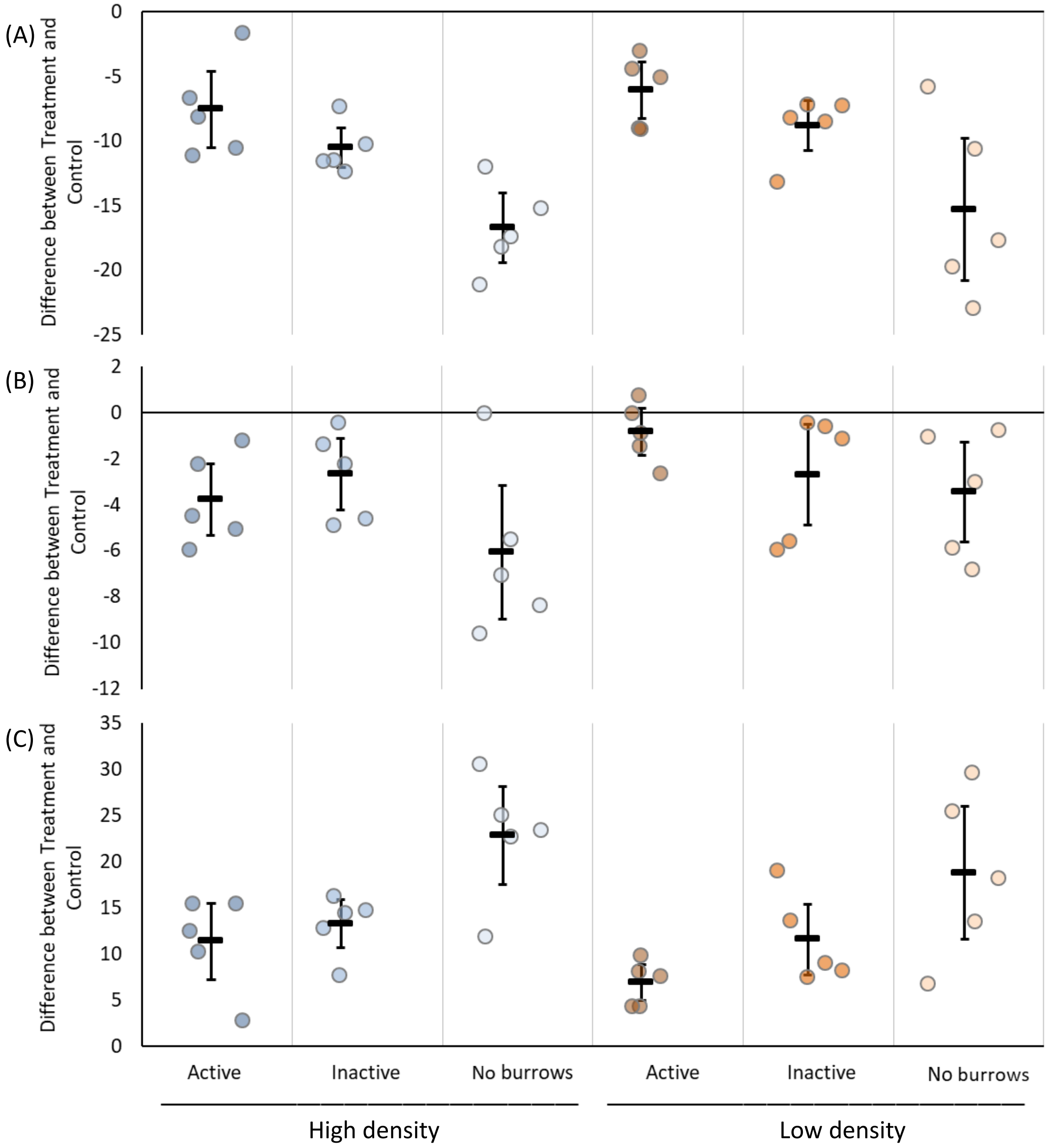


Figure 13. *The mean difference ± 95% confidence interval (CI) (horizontal bar and error bars) between patch and control sites in terms of (A) sodium (meq/L), (B) conductivity (mS/m), (C) pH, (D) calcium (meq/L), (E) magnesium (meq/L) among the high and low density of active and inactive burrow patches, and no-burrows vegetation patches on the Husab gravel plains of the central Namib. Coloured circles represent all paired differences between patch and control sites. To save space the x-axis is shared by all sub-plots.*



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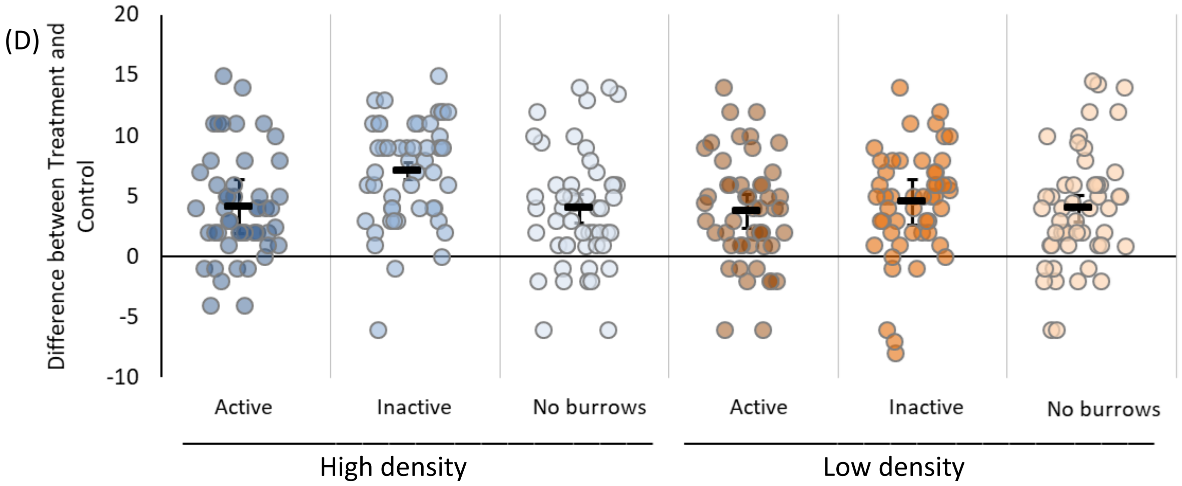

Figure 14. *The mean difference ± 95% confidence interval (CI) (horizontal bar and error bars) between patch and control sites in terms of percentage (%) concentration of (A) silt (53-2 µm), (B) clay (<2 µm), (C) sand (2 mm-53 µm), (D) soil depth (cm) among the high and low density of active and inactive burrow patches, and no-burrows vegetation patches on the Husab gravel plains of the central Namib. Coloured circles represent all paired differences between patch and control sites. To save space the x-axis is shared by all sub-plots.*

Table 3: *The summary of statistical results for each variable. Superscript asterisks (**) indicate significant differences.*

Variable	Test	Statistical Results	Multiple Comparison
Cover (%)	K-W	(H=20.30, df=5, P=0.00)	HI, LI > rest; HI > LI
Abundance	ANOVA	($F_{5, 24} = 2.96$, $P < 0.01$) ***	HI > rest
Biomass (g)	ANOVA	($F_{5, 24} = 5.51$, $P < 0.01$) ***	HI > HN, LN
Organic matter (OM)	ANOVA	($F_{5, 24} = 4.51$, $P < 0.01$) ***	HI, LI > HN
Organic carbon (OC)	ANOVA	($F_{5, 24} = 4.24$, $P < 0.01$) *	HI, LI > HN
Nitrogen (N)	ANOVA	($F_{5, 24} = 0.55$, $P>0.05$)	
Phosphorus (P)	ANOVA	($F_{5, 24} = 0.60$, $P > 0.05$)	
Potassium (K)	ANOVA	($F_{5, 24} =3.27$, $P < 0.05$) *	HI, LI > HN
Sodium (Na)	ANOVA	($F_{5, 24} = 0.93$, $P > 0.05$)	
Magnesium (Mg)	ANOVA	($F_{5, 24} = 0.47$, $P > 0.05$)	
Calcium (Ca)	K-W	(H=4.76, df=5, P > 0.05)	
Conductivity (EC)	K-W	(H=6.93, df=5, P > 0.05)	
pH	ANOVA	($F_{5, 24} = 0.96$, $P > 0.05$)	
Sand	ANOVA	($F_{5, 24} = 4.98$, $P < 0.01$) ***	HN > HA, LA; LN > LA
Silt	ANOVA	($F_{5, 24} = 5.98$, $P < 0.01$) ***	HA, LA > HN, LN; LI > HN
Clay	ANOVA	($F_{5, 24} = 1.92$, $P > 0.05$)	
Hydraulic conductivity	ANOVA	($F_{5, 24} = 3.39$, $P < 0.05$) *	HI > HN, LN
Soil depth	ANOVA	($F_{5, 24} = 0.64$, $P > 0.05$)	

High density: Active (HA), Inactive (HI), No-Burrows (HN)
Low density: Active (LA), Inactive (LI), No-Burrows (LN)

Discussion

In general, the three types of patches had more vegetation (from personal observation) than the surrounding environment. Our study found clear evidence that gerbils are improving variables related to soil fertility (increased OM and OC, increased K), soil moisture and plant productivity on vegetation patches with burrows over no-burrow vegetation patches. This was surprising because from personal observation, the vegetation cover, abundance, and shoot system on the burrow patches and no-burrows vegetation patches showed a similar pattern. Yet, we recorded higher vegetation cover, abundance and biomass on the inactive burrow patches than off them including the no-burrow vegetation patches. The increased plant productivity was very high, with biomass more than three times higher on inactive burrow patches than on patches without burrows. This is the first study to compare the vegetation biomass between the patches with and without burrows on them.

In connection with our companion paper (Shaanika et al., Chapter 6) where the design of this study was derived, it is likely that the gerbils are not the main creators of the vegetation patches, because there were greater densities of no-burrow vegetation patches compared to the ones with burrows across the study area. This suggests that the patches may be originally created by other natural physical mechanism, with the gerbils probably colonizing the softer soil substrates associated with vegetation patches (Shaanika et al., Chapter 6) and improving soil conditions and characteristics stated above which significantly benefit the plant growth. It is therefore clear that the gerbils are improving plant productivity with old burrow patches yielding higher biomass than the rest of the patches.

We expected the active burrow patches to yield higher vegetation biomass, cover and abundance because any improvement in soil chemical properties will have been leached out of inactive burrow patches. However, our results show that the enriching effects of burrowing activities probably increase through time, and may persist for years even after the engineer is dead or has relocated. In addition the higher density of burrows tended to have a superior impact over low density burrow patches, possibly because of higher bioturbation of soil. The burrows may persist for an extended period and their impacts on the vegetation may increase through time as the resources (plant-available-moisture and nutrients) are increasingly accumulated in the burrows (Bragg et al., 2005 and Haussmann et al., 2018).

The gerbils have improved the vegetation biomass by 190% over vegetation patches without burrows. This means that the gerbils through their burrowing activities have increased vegetation productivity 3 times more than the abiotic processes could have done. Therefore, the gerbils modified, modulated and maintained the natural land, which resulted in suitable microsites for vegetation establishment and growth. Small rodents through their burrowing activities are constructing resource-rich patches with a distinct microclimate that have potential knock-on effects on the plant community structure, function and composition (Laundre, 1993; Romañach, et al., 2005; Xu et al., 2015). This resulted in higher average plant productivity on the small rodents burrow patches than off them (Gutterman et al., 1990; Zinnel and Tester, 1990).

The gerbils through their burrowing activities had a significant influence on variables, most of which related to the soil fertility and moisture, essential for flora establishment and growth. OM, OC, K, hydraulic conductivity and silt were significantly higher on the burrow patches than on no-burrow vegetation patches. An improved concentration of silt on the burrow patches, probably promoted the water infiltration rate which were higher on the burrow patches than off them. This shows that the gerbils are playing a critical functional role toward the benefit of the vegetation on the gravel plains of the central Namib. Because an increase of the organic matter potential contribute to the formation of nutrients such as K, essential for healthy plant growth on the burrow patches than off them (Jiang et al., 2007; Davidson and Lightfoot, 2008; Xu et al., 2015). The dead materials and seed that is always trapped by the burrows (Bragg et al., 2005; Yoshihara et al., 2009; Guo et al., 2012; Haussmann et al., 2018; Davies et al., 2019) could result in higher content of organic matter which contribute to soil fertility and consequently improved vegetation establishment and growth. The burrows of the gerbils increase the soil's porosity, resulting in faster and deep infiltration of water into the soil and thus minimize the loss of too much water due to excess evaporation than on undisturbed areas. Thus, burrows increase the soil surface permeability which increases hydraulic conductivity and subsequently enriches moisture stored in the soil profile (Bates and Jackson, 1984; Malizia et al., 2000; Gabet et al., 2003; Wright, 2006; Yoshihara et al., 2009; Xu et al., 2012; Xu et al., 2015) which benefits vegetation growth and survival. It is therefore clear that the gerbils contribute to the soil fertility and moisture related variables which measurably benefit vegetation productivity on the gravel plains of the Namib Desert – a desert which is characterised by hyper-arid climate.

The gerbils do not affect other variables which are also related to soil fertility such as N and P, and those related to soil texture, salinity and sodicity i.e. clay content, soil depth Na, Mg, Ca, EC and pH. On average the gerbil species could possibly contribute to the concentration of N and P on their burrow patches. However, the rate of mineralization of N and P may require slightly more moisture to happen, unlike for K. The arid climate condition of the central Namib may limit the role of the gerbils to facilitate the mineralization rate formation of N and P, because it may require abundant moisture to happen. In the hyper arid environments water is the major limiting factor for mineralization rate, therefore even if the soil organic matter may be available in adequate quantity, the decomposition and mineralization rate tend to be lower, because of insufficient soil moisture content (Brown and Ernes 2002; Belnap, 2011).

However, on average this did not undermine the critical effect of the gerbils to improve the vegetation productivity on the gravel plains of the central Namib Desert. Overall, the gerbils through their burrowing activities significantly influenced variables related to soil fertility and improved vegetation productivity on their burrow patches on the gravel plains of the central Namib Desert. We do not have data on the potential knock-on effects of vegetation on other organisms on the gravel plains. But, theoretically, the improved vegetation productivity as a result of the gerbils' burrowing activities would benefit the larger ungulate grazers on the gravel plains of the central Namib. Personal observation showed that there were ants, termites, lizards and snakes (horn adders) on the actively used burrow patches. These organisms may be using the burrows as their shelters or foraging areas. Overall, the gerbils are potentially playing ecological engineering functional role on the gravel plains of the central Namib D*es*ert.

Conclusion

We conclude from the current results that the gerbils significantly alter a number of variables related to soil fertility, soil moisture and vegetation productivity. The results indicate that the bioturbation role of the gerbils is the key to maintaining primary productivity and thus will enrich biodiversity on the gravel plains of the central Namib. This study confirm that the gerbils are significantly improving the growth of vegetation, thus primary productivity. Therefore, the gerbil species play a significant role at the patch scale as ecological engineers on the gravel plains of the central Namib. There is a potential that the improved vegetation productivity as a result of gerbils burrowing activities would benefit the larger ungulate grazers at the landscape scale. This was explored in a companion paper (Chapter 6).

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Chapter 6

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The spatial distribution of gerbils' burrow and no-burrow vegetation patches on a gravel plain in central Namib Desert

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Author's contribution

HS conceived and designed the research, TW guided the design, TW and SE supervised the research, HS implemented the work, analysed data and wrote the manuscript, TW and SE edited the manuscript, TW guided data analysis

Abstract

Gerbils through their bioturbation activities influence soil conditions and characteristics, and often create suitable microsites for plant establishment and growth. Indeed the gerbils through bioturbation activities are known to affect water availability and soil fertility, which result in suitable patches for vegetation establishment and growth. This is critical for the development and maintenance of spatial heterogeneity in terms of primary production and secondary producers through time in arid ecosystems. The specific objectives were to determine whether the spatial distribution and density of vegetation patches with and without burrows on them varied or was uniform among various habitats, and if not, whether their distribution can be explained by soil substrate characteristics on the Husab gravel plains. This study was conducted to map the distribution of density of the vegetation patches with and without burrows on them. The key findings of this study are that the distribution density of vegetation patches with and without burrows on them varies among different habitats. It is concluded that the gerbils prefer the grassy plain over other habitats and that the spatial distribution of density of their burrow patches and no-burrow vegetation patches can be explained by the soil substrate characteristics.

Key words: bioturbation, burrow patches, central Namib, gerbil, soil biodiversity, spatial distribution, and vegetation patches.

Introduction

Most of the hyper-arid central Namib Desert is covered by sparsely distributed vegetation, with the perennial flora generally limited to drainage channels and other structures (such as rocky outcrops) where soil moisture is presumably adequate for plant survival. The bare gravel plains in between drainage lines usually support only a minor cover of annual grasses and a few herbs after adequate rains, most of which dry up and disappear fairly quickly. However, in addition to the shrubs and perennial grasses in drainage lines, denser perennial vegetation (mostly grasses) grow in patches that form clear circular and polygonal patterns. These patches of vegetation of about 5 m diameter are often associated with colonies of ca. 8 cm diameter burrows, which are probably constructed by gerbils (most likely the endemic species *Gerbilliscus setzeri*) (Louw and Seely, 1982; Cox, 1987). The large difference between vegetation on the burrow patches when compared to adjacent areas further suggested that the gerbils, through their burrowing activities, might be modulating the environment by creating suitable microsites for vegetation establishment and growth (Louw and Seely, 1982; Cox, 1987, Shaanika et al., Chapter 5) and shelters for other invertebrate and vertebrate animals.

However, focused personal observation shows that there are also abundant and widely distributed patches that do not have burrows on them, with slight apparent difference between these and burrow patches in terms of vegetation cover. It is therefore possible that the vegetation patches may be primarily the result of other mechanisms, with the gerbils colonizing the softer soil substrates associated with naturally formed vegetation patches (Goudie, 1970; Ollier and Seely, 1977; Watson, 1980). Elsewhere, hydrological overland flow is considered to be the main mechanism in the formation of vegetation patches on bare ground, mostly level surfaces in arid ecosystems (Yizhaq et al., 2019). Overland flow often favours the formation of vegetation patches after strong seasonal rainfall in arid regions where soil moisture availability is limited for plant growth (Newman et al., 2006; Smith and Goodrich, 2006; Yizhaq et al., 2019). The density and shapes of these patches are presumably a function of total annual rainfall, which means that the higher the rainfall, the denser the patches and the more they connect (Aguiar and Sala, 1999). Most importantly, the overland flow results in suitable germination sites and growing conditions, similar to what Louw and Seely (1982) and Cox (1985) have described as an engineering action by gerbils.

Clearly this will matter when deciding how much attention to give to impacts on gerbils as a result of mining or similar disturbances. Mining activities can cause large impacts on biodiversity through the removal of soil surface and vegetation cover (Cooke and Johnson, 2002; Wassenaar, et al., 2013; Mahalik, 2018). This type of impact may be raised if the affected component is functionally important as an ecological engineer. If gerbils do indeed modulate the environment for the benefit of larger ungulates such as zebra and oryx (in numbers that cannot be sustained without the perennial vegetation patches), any impacts to the gerbils will have detrimental knock-on effects on a larger part of biodiversity.

In a companion paper (Shaanika et al., Chapter 5), we explored the issue of the strength of the evidence related to the engineering role of the gerbils. We concluded that they are probably not the main originators of the vegetation patches, but also that their burrows have a significant positive effect on several variables related to soil fertility and vegetation productivity when compared to patches without burrows. This means that as far as the mechanism is concerned, they can indeed be viewed as ecological engineers and that the spatial pattern and extent of their burrows on a landscape scale can fundamentally affect the spatial pattern of primary and secondary producers through time (Wesche et al., 2007 and Yoshihara et al., 2010). Therefore, an important part of the context for the larger issue of the importance of their role in the central Namib has to do with the spatial distribution of their burrows, the density of their burrow colonies and their association with specific habitats and substrate types. If the burrow patches are limited to only a few places, their total functional role would not be as significant, even if they can predictably be considered to be engineers.

In the current study we therefore looked at the spatial distribution of vegetation patches in general, as well as burrow colonies specifically as a reflection of habitat suitability for the gerbils and their relationship with key environmental aspects such as the soil substrates. The extent to which rodents may influence soil processes through digging their burrows depends on the soil structure and hardness of the substrates (Laundre and Reynolds, 1993; Giannoni et al., 1996; Shenbrot et al., 1997). Most small fossorial mammals prefer softer substrates (Ebensperger and Bozinovic, 2000). We were interested to determine whether the gerbils of the Namib are also affected by such physical habitat characteristics and whether that may place a limit on the total extent of their engineering effect.

The results of this study will assist in the evaluation of impacts that mining has on the Namib Desert's ecosystem and will provide more options to manage the impacts and may be useful for restoration and monitoring processes. The aim of this paper was to establish the spatial extent and distribution of vegetation patches with and without gerbil burrow colonies on them across various habitats on the Husab gravel plains and adjacent areas. The specific objectives were to determine whether the density of vegetation patches with and without burrows on them varied or were uniform among various habitats, and if not, whether their distribution can be explained by soil substrate characteristics.

Methods and materials

Study area

The study was conducted on the gravel plains west and north of the Husab Mountain in the central Namib, adjacent to the Husab Uranium mine (Figure 15). The plains are popularly known as the Welwitschia Plains, for the large population of the plant species *Welwitschia mirabilis* that occurs there. The mine is located about 60 km east of Swakopmund (-22.64681° S, 14.59987° E), in the Namib Desert along the Khan River (Figure 15).

The central Namib has a hyper-arid climate with annual rainfall ranging from 5 mm at the coast to about 50 mm in the eastern part of our study area (Lancaster et al., 1982 and Eckardt et al., 2013). Although fog may precipitate on about 50 days per year (Lancaster et al., 1984 and Olivier, 1995), the total amount of moisture it provides to the biota remains low. The low annual precipitation means that vegetation is sparse, with the exception of perennial shrubs that are limited to drainage lines and mostly perennial grasses in circular and polygonal patches on bare gravels.

Common plant species include *Stipagrostis* species, *Arthraerua leubnitziae*, *Euphorbia virosa*, *Vachellia erioloba*, *Commiphora saxicola*, *Zygophyllum stapffii* and *Welwitschia mirabilis* (Giess, 1998). As part of an environmental impact assessment done for the adjacent Husab Mine, the whole study area was subdivided into twelve habitats, four of which are relevant for the current study, namely the gypsite plain,

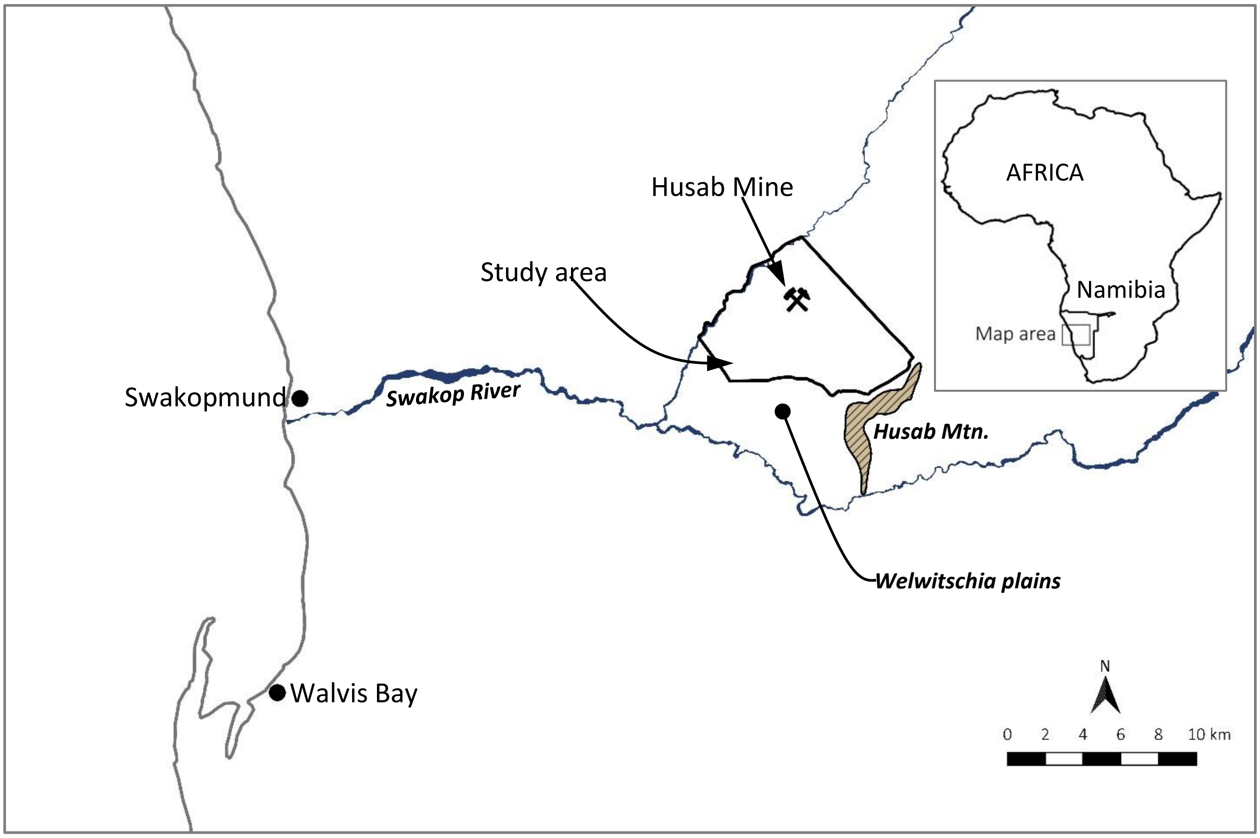

Figure 15. *A map of the central Namib region, showing the location of our study area relative to the main regional towns and rivers.*

grassy plain, plains drainage channels and hard undulating plain (Wassenaar and Mannheimer, 2010). We considered these four habitats to be suitable for gerbil species because they cover the largest part of the gravel plain and all are characterized by substrates that are suitable for digging by fossorial animals. The grassy plain and plains drainage channels are dominated by a soft to intermediately hard gravelly sand cover, while the hard undulating and gypsite plains are characterised by a relatively harder surface cover but still accessible to fossorial animals.

The substrates described above overlie extensive calcrete and gypcrete layers (Watson, 1979; Dixon, 1994; Heine and Walter, 1996) and in places also granitic gneisses. The pedogenic gypcretes occur on the highest parts of the gravel plain catena. Apart from the gravel plains, the main geomorphological features are marble hills, conglomerates, quartz gravels, highly weathered mica schist and different types of granite bedrock that originated during the Damara-Orogeny (Stanitstreet et al., 1991; Heine and Walter, 1996).

Data Collection

The data collection was done between February and March 2019. To minimize the search time and maximize the amount of information collected for the effort, we searched for vegetation patches on a grid of regular points placed across the four habitats described above (Figure 16). We used a plug-in in Quantum Geographic Information System (QGIS) software (Sherman, 2015) to generate 469 regular points spaced 500 m apart. Because a large part of the study area (covered by the mine itself) was not accessible, we could not equalise sampling intensity in all four habitat types, with especially the gypsite plain being relatively under-sampled. The sampling points were transferred to a handheld GPS (Global Positioning System) device (GARMIN GPSMAP64s) for navigation from point to point in the field, which was done using a fat-wheel-bicycle as transport. At each sampling point, we conducted a search for the nearest vegetation patches within a 100 m radius in each of four quadrants surrounding the point (Figure 17). We classified vegetation patches into three categories: without burrows, with active burrows and with inactive burrows (Table 4) and measured the distance from the regular sampling point to each closest patch in the specific category (Figure 17). If a quadrant did not have any patch of a specific category within the 100 m radius, we recorded its distance as 100 m. At each regular sampling point, we observed, assessed and recorded a set of variables that collectively described the habitat and in particular the type and characteristics of surface cover (Table 4) and counted the number of burrows. However the rocky-outcrops were omitted during the phase of data collection because they are composed of hard rocks impossible for the gerbils to inhabit.

Table 4: *The variables that were observed, assessed and recorded at each sampling point during the survey.*

Variable	**Category of variable**	**Description**
Habitat type	Grassy plain	Soft to intermediate gravel plains sand surface cover
	Hard undulating plain	Weathered rocks dominated area, but softer covers were also present
	Gypsite plain	Hills and valleys surface covered by harder rocks, but softer covers were also present
	Plain drainage channels	Very soft sand surface cover, perennial shrubs are common
Surface cover type	Thick layer of gravel plains sand	Deeper layer of loose sand (>5cm deep)
	Thin layer of gravel plains sand	Shallow layer of loose sand (≤5cm)
	Gypcrete	Evaporitic crust associated with gypsum strata and soft sand, in general found about 10 cm below the surface.
	Highly weathered granite and mica schist rocks	Thin layer of weathered fragments of granite and mica schist rocks
Surface hardness type	Soft	Shallow to deeper layer of loose sand
	Intermediate	Deeper layer of compacted sand
	Hard	Rocks
Patch type	Active burrows	Open burrows associated with the recent soil bioturbation signs, fresh or dry seeds, plant debris, new faecal droppings, and no spider web at the entrance
	Inactive burrows	Collapsed and filled burrows associated with old seeds and plant debris, old faecal drops, and spider web at the entrance
	No-burrows	Vegetation patches without burrows on them

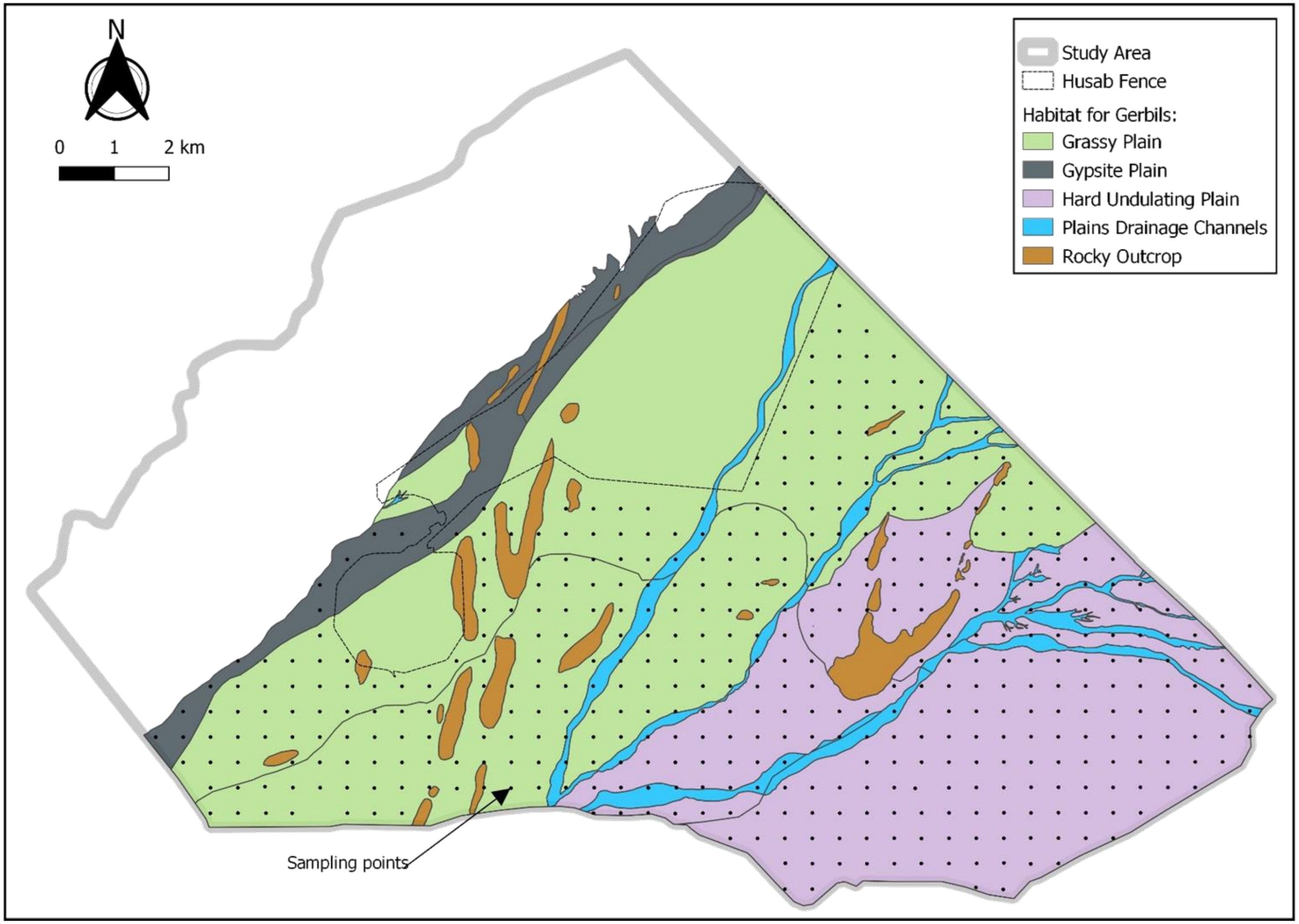

Figure 16. *A map of the study area, showing the habitats described in the text and the regular survey design (adapted from Wassenaar and Mannheimer, 2010). Each dot represents a sampling point at which a number of measurements were made and observations recorded.*

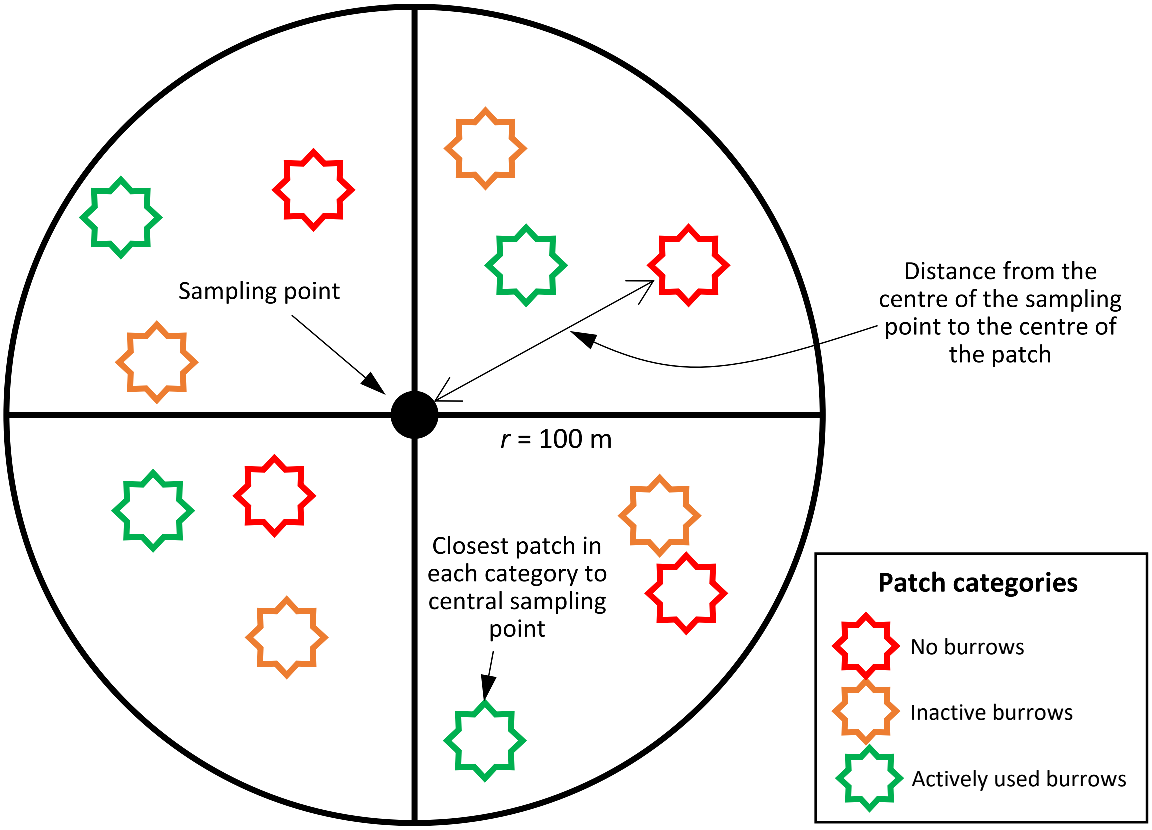

Figure 17. *A diagram showing the basic data collection design. We used a Point-Centre-Quarter method to determine the density of each of three patch types. Each differently-coloured star-shaped symbol represents a vegetation patch type. We measured the distance from the central sampling point to the closest vegetation patch in each of the four quadrants to determine the sampling-point-specific density for each type.*

Data analysis

We calculated the total number and percentage of sampling points with and without vegetation patches, and mean values for the number of burrows (active and inactive combined) per patch of vegetation. The density of each type of patch was also calculated per sampling point using the formula for density $1/(\bar{x}_d)^2$, whereby $\bar{x}_d$ represent average distance (Cottam and Curtis, 1956). Subsequently, the density data, together with each point's coordinates, habitat and substrates, were imported into Quantum Geographic Information System (QGIS Version 3.4) (Sherman, 2015) to yield maps of the spatial distribution of density of each patch type. We overlaid the density data on the habitat maps and used QGIS to assign specific sampling points to habitat type.

Our data were not normally distributed (Shapiro-Wilk's test), and we thus used a One-way Kruskal-Wallis (K-W) test to test whether there were significant differences in terms of the mean density of vegetation patches with active and inactive burrows and no-burrows among various habitats and substrates. Similar test was performed to test for differences in terms of the mean number of burrows per patch of vegetation among various habitats and substrates. The statistical program IBM SPSS version 26 was used for data analyses. A 95% level of confidence was regarded as significant.

Results

In total, 300 (64%) of the 469 regular sampling points we visited had vegetation patches in the search area around it. Most of the vegetation patches around these 300 sampling points had inactive burrow patches (at 74% of the 300 points), followed by patches without burrows (at 62% of the 300 points). Only 11% of the points had patches with active burrows. The no-burrow vegetation patches had highest densities than inactive burrow ones (Figure 18; Table 5). Active burrow patches were located nearly exclusively on the grassy plains (Figure 18). Inactive burrow patches also appeared to be more on the grassy plains than on the other habitats, while no-burrow vegetation patches were found more or less everywhere (Figure 18).

Due to the small area and few samples taken on the gypsite plain and plains drainage channels (Figure 18; Table 5), we found no active burrow vegetation patches and only small numbers of inactive and no-burrow vegetation patches on the gypsite plain and plains drainage channels. The visual spatial pattern that is evident from the maps in Figure 18 was confirmed by statistical tests. Overall, the mean density of the three patch categories (Table 5) and the number of burrows per patch of vegetation (active and inactive combined) (Table 6) was not uniform among the habitats, surface cover or surface hardness categories. With the exception of the active burrow patches (all contrasts) and no-burrow patches (in terms of surface hardness), differences in patch density were significant among all habitats and surface characteristics (Table 7). In terms of habitat type, grassy plain always had significantly higher patch density than the rest (Table 7). For surface characteristics the gypcrete and harder surfaces had significantly higher patch density than all the others and soft surfaces respectively (Table 7). Similarly, the mean number of burrows per patch also differed among habitats and surface characteristics. For habitat type, grassy plains had significantly more burrows per patch (Table 7). In terms of surface cover type, gypcrete surfaces tended to have significantly more burrows per patch than both thick and thin gravel plains sand, and surfaces that were classified as hard and intermediately soft had higher numbers than soft surfaces (Table 7).

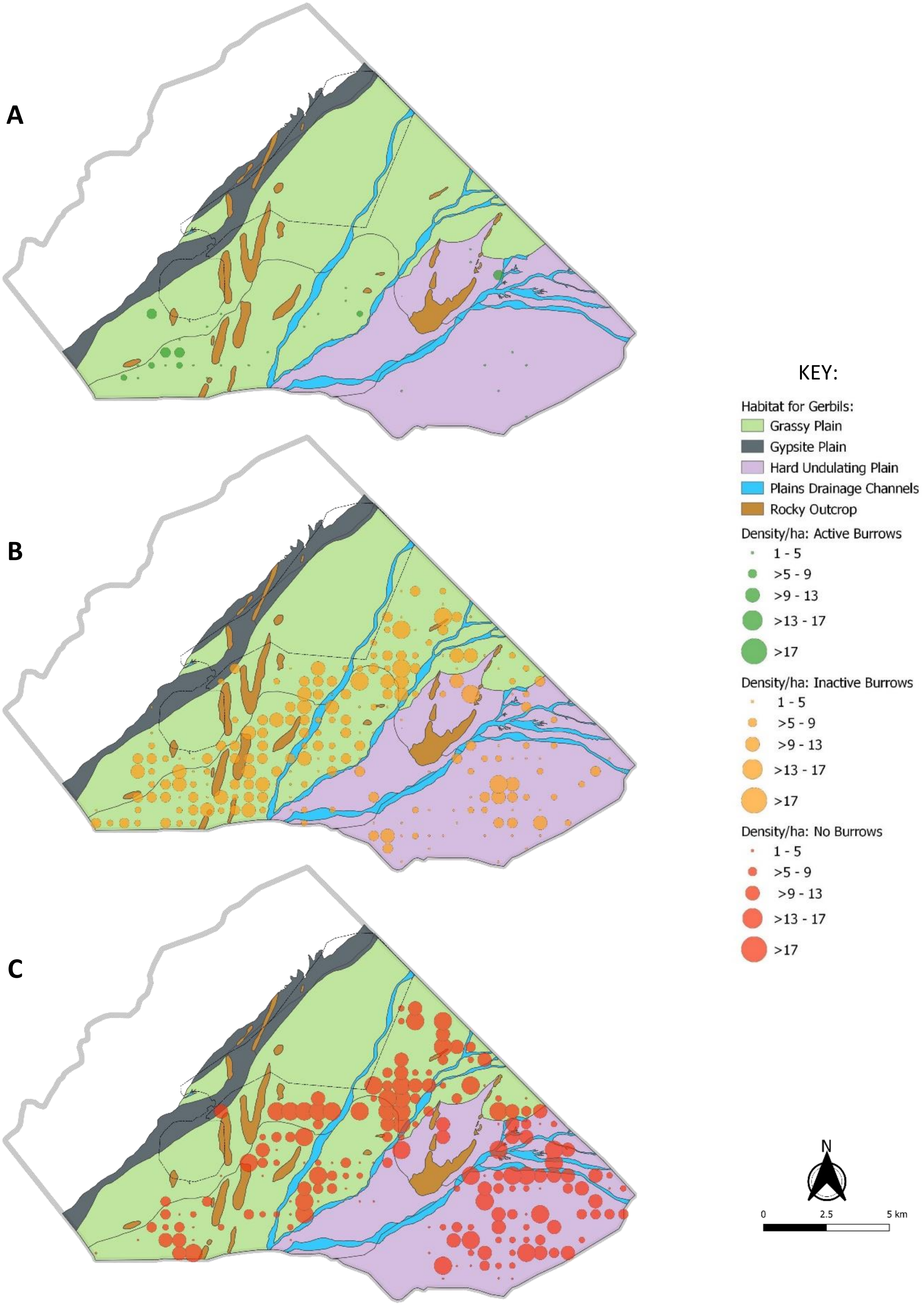

Figure 18. *The spatial distribution density/ha of (A) active burrow patches, (B) inactive burrow patches and (C) no-burrows vegetation patches across various habitats on the Husab gravel plains.*

Table 5: *The mean density/ha of active and inactive burrow patch, and no-burrow vegetation patch per habitat, surface cover and hardness.*

	Mean density/ha (±95% CI, n)		
Habitat	**Active Burrows**	**Inactive Burrows**	**No-Burrows**
Hard Undulating Plain	0.10 (±0.64, 211)	4.13 (±14.76, 211)	15.31 (±47.87, 197)
Grassy Plain	0.48 (±1.84, 227)	12.72 (±22.95, 227)	45.91 (±151.01, 226)
Plain Drainage Channels	0.67 (±0.39, 20)	1.74 (±3.79, 20)	20.32 (±53.82, 35)
Gypsite Plain	0 (±0, 11)	0.75 (±1.91, 11)	5.93 (±19.27, 11)
Surface cover type			
Thick layer of gravel plains sand	0.27 (±1.41, 377)	6.89 (±17.24, 377)	28.73 (±117.46, 377)
Thin layer of gravel plains sand	0.096 (±0.35, 29)	3.13 (±4.83, 29)	20.51 (±52.43, 30)
Gypcrete	0.096 (±0.35, 17)	39.59 (±43.40, 17)	94.49 (±142.77, 17)
Highly weathered granite rocks	0.10 (±0.57, 45)	9.76 (±17.98, 45)	25.77 (±53.00, 44)
Highly weathered mica schist rocks	0 (±0, 1)	0 (±0, 1)	1.70 (N/A, 1)
Surface hardness type			
Soft	0.56 (±2.93, 394)	8.30 (±40.17, 394)	31.56 (±238.34, 394)
Intermediate	0.096 (±0.71, 29)	3.13 (±9.65, 29)	20.51 (±104.85, 30)
Hard	0.19 (±1.12, 46)	9.55 (±35.69, 46)	25.23 (±105.03, 45)

Table 6: *The mean number of gerbil burrows (active and inactive combined) per patch of vegetation among the habitat, surface cover and hardness type.*

Variable	**Mean number (95% CI, n) of burrows per patch of vegetation**
Habitat	
Hard undulating plain	0.68 (±1.73, n = 422)
Grassy plain	2.12 (±3.34, n = 454)
Plain drainage channels	0.68 (±1.59, n = 40)
Gypsite plain	0.41 (±1.37, n = 22)
Surface cover type	
Thick layer of gravel plains sand	1.24 (±2.63, n = 754)
Thin layer of gravel plains sand	1.12 (±2.03, n = 58)
Gypcrete	3.59 (±4.19, n = 34)
Highly weathered granite rocks	1.82 (±2.85, n = 90)
Highly weathered mica schist rocks	0 (±0, n = 2)
Surface hardness type	
Soft	1.24 (±2.63, n = 754)
Intermediate	2.03 (±3.21, n = 92)
Hard	1.78 (±2.83, n = 92)

Table 7: *The summary of statistical results for each variable. The superscript stars (**) represent the significant results.*

Variable	Patch category	Test	Results	Multiple Comparison
Mean density of burrows per hectare				
Habitat	Active burrows	K-W	H = 6.28, df = 3, P > 0.05	
	Inactive burrows	K-W	H = 63.33, df = 3, P < 0.01	Grassy plains**>rest
	No-burrows	K-W	H = 15.44, df = 3, P < 0.01	Grassy plains**>rest
Surface cover type	Active burrows	K-W	H = 1.35, df = 4, P > 0.05	
	Inactive burrows	K-W	H = 39.87, df = 4, P < 0.01	Gypcrete layers**>rest
	No-burrows	K-W	H = 15.94, df = 4, P < 0.01	Gypcrete layers**>rest
Surface hardness type	Active burrows	K-W	H = 1.16, df = 2, P > 0.05	
	Inactive burrows	K-W	H = 9.15, df = 2, P < 0.01	Hard**>Soft
	No-burrows	K-W	H = 5.02, df = 2, P > 0.05	
Mean number of burrows per patch of vegetation				
Habitat	Active and inactive burrows combined	K-W	H = 52.56, df = 3, P < 0.01	Grassy plains**>rest
Surface cover type	Active and inactive burrows combined	K-W	H = 25.87, df = 3, P < 0.01	Gypcrete layers**>thick and thin layer of gravel plains sand
Surface hardness type	Active and inactive burrows combined	K-W	H = 16.78 , df = 2, P < 0.01	Hard and intermediate**>Soft

Discussion

Our first results that came through were the absolute number of vegetation patches in general. We recorded patches at 64% (300 of 469) of the regular sampling points we visited. This was unexpected because the patches are not immediately obvious during casual observation, especially after some years without rain. The low-rainfall that is characteristic of this hyper-arid region clearly places a limit on primary productivity. Arid ecosystems are usually characterised by sparsely distributed clumps of low vegetation cover and growth (Huenneke et al., 2001), but our results in the current study and in Shaanika et al. (Chapter 5) suggest that there are mechanisms that may extend total vegetation biomass over large areas beyond what can be expected from the low moisture levels.

Although we don't have data on total numbers or productivity, the vegetation patches collectively must be contributing a significant amount to the perennial vegetation productivity on the plains. This would remain to be the case even in the absence of gerbils. However, we previously showed that even though the patches are most likely the result of surface hydrological processes, the gerbils still improved plant biomass by 190% (i.e. > three times) over vegetation patches without burrows (Shaanika et al., Chapter 5). The increased productivity is most likely a direct result of a positive impact by the gerbils on a number of variables related to soil fertility and vegetation productivity (Shaanika et al., Chapter 5). Gerbil species elsewhere in the world are known to significantly improve the fertility and primary productivity of arid environments through their burrowing activities (Malizia et al., 2000; Jiang et al., 2002; Gabet et al., 2003; Xu et al., 2012; Xu et al., 2015). Here we show that this effect is probably quite large when considering the extent of the vegetation patches with burrows. It is therefore clear that the gerbils must be playing a significant engineering role on the gravel plains of the Namib.

The density of vegetation patches was however not uniform across the area, being significantly affected by both substrate characteristics and habitat. In our study area it was particularly the grassy plain (which also had the most patches with intermediate-soft substrates) that stood out with three times more burrows per patch and at least twice the patch density on average than the next closest habitat. Patches that were characterised by layers of gypcrete immediately below the surface also tended to have a much higher density of patches overall and about two or three times more burrows than other surface classes. This is probably because of the gypcretes, which are cracked and fissured along multiple planes, providing many opportunities for the digging of structurally inclusive burrows. Additionally, although we expected softer surfaces to have more evidence of gerbils (reasoning that these are probably easier to dig into), the gerbils appear to rather prefer the somewhat harder surfaces presumably because their tunnels will not collapse as easily there. The distribution of small fossorial animals is often influenced by habitats, based on the availability of food resources and the physical nature of the soil substrates (Brown and Ernes, 2002; Busch et al., 2000; Vijayan et al., 2007; Yoshihara, et al., 2009; Albanese et al., 2010; Traba et al., 2010).

Conclusion

Our results suggest that the total positive effect of gerbils on plant productivity, and by extension therefore on herbivore presence on these hyper-arid plains, is quite likely significant. As such they can be considered as critical to the functioning of the Namib's hyper-arid ecosystem, although their presumed indirect role in facilitating the extended presence of large herbivores here should ideally still be quantified.

As a result of their habitat preferences (they appear to prefer the grassy plain and surfaces with somewhat harder substrates, particularly with gypcrete layers), the variation in spatial patterns of burrow colonies may influence the distribution of primary production through time. Theoretically, they may thus have positive knock-on effects on the larger grazers, allowing them to thrive where they would not normally be sustained in numbers. Taken together with our companion study (Shaanika et al., Chapter 5), our results support the deduction by Louw and Seely (1982) and Cox (1985) that the gerbils of the central Namib are important ecological engineers, even though they probably do not directly cause the formation of vegetation patches as has previously been assumed. As such the places that they prefer, particularly the grassy plains and areas with gypcrete layers, are more important from an ecological functioning perspective than what these habitats are usually considered to be (e.g. Wassenaar and Mannheimer, 2010).

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Chapter 7

Synthesis

There are many and widely distributed patches of vegetation (mainly grasses) associated with gerbils' burrow colonies on the gravel plains of the central Namib Desert. The study by Cox (1987) and the review of Namib ecology by Louw and Seely (1982) proposed that these vegetation patches were originally created by the gerbils through their burrowing activities and consequent improvement of hydrological characteristics on the circular patches. Gerbils, through their burrowing activities, might thus be modulating the environment by creating suitable microsites for vegetation establishment and growth (Louw and Seely, 1982; Cox, 1987). This type of key functional role would meet the requirements of ecological engineering and the gerbils to be defined as ecological engineers.

However, it is also clear that there are many vegetation patches without burrows on them, suggesting that either they had burrows in the past which have since disappeared, or there is a second mechanism that may explain their formation. Although I cannot evidently exclude the possibility that these patches had burrows a long time ago, their widespread distribution and their high density on especially the hard undulating plains suggest that they are more likely to have been formed by a physical process. In this regard, other studies (Newman et al., 2006; Smith and Goodrich, 2006; Yizhaq et al., 2019) have observed similar forms of vegetation patches in other water limited (arid and semi-arid) environments, and they concluded that these patches where caused by hydrological overland flow – a well-known mechanism in the formation of vegetation patches in arid lands. The question remained whether gerbils are neutral inhabitants of pre-existing patches, or whether there was still a potential that they may be ecological engineers on the patches?

My first overarching aim was therefore to determine whether, on a patch scale, the gerbils are significantly improving the growth and productivity of plants through their burrowing activities when compared to patches without burrows, thus to verify if they are playing a functional ecological engineering role on the Husab gravel plains of the central Namib. This is the first study to compare vegetation patches with and without burrow colonies on them in terms of vegetation productivity in the hyper-arid environment.

I found that, on all patch types, the average plant productivity was always higher than on the bare control areas. I also found that those variables that reflect soil fertility and soil moisture were significantly higher on patches with burrows, in particular inactive burrows, than those without burrows. In addition, the gerbils' burrows, especially the active burrow patches appear to increase the content of silt, which may favour water infiltration rate and the soil's water holding capacity. Most importantly, inactive burrow patches had, on average, more than three times more plant biomass than patches without burrows. This suggest that the gerbils' effect on at least the patch scale is large enough to be called engineering in terms of Jones et al. (1994) criteria for ecological engineers. The consistently higher values on inactive burrow patches than active ones indicate that the effect of Namib gerbils' burrowing activities can last for long after the gerbils have died or relocated. Overall, this study shows that the gerbils are significantly improving primary productivity and that this is happening as a result of the gerbils' effect on soil fertility and soil texture that favours improved soil moisture.

According to Jones et al. (1994), the effect of ecological engineering has to be measured at an ecosystem level. To determine the extent of their effect and whether there are factors that limit their occurrence, I measured the spatial extent and distribution of vegetation patches of all three patch types (with active and inactive burrows and without burrows) across various habitats and substrates on the Husab gravel plains. Through this, I wanted to determine whether their patch-scale effect would convert to an ecosystem-level effect.

The spatial distribution of the density of all vegetation patches and the number of burrows per patch varied significantly among different habitats and were influenced by the soil substrate characteristics. However, vegetation patches of all types were common and widespread (Figure 18B and C, Chapter 6). Out of the 300 points that I encountered with vegetation patches, 74 % of them were associated with inactive burrow colonies, 11 % with active burrow colonies and 64 % had no burrows on them. Considering the extent of the Namib's gravel plains and their overlap with the geographic distribution of the gerbils (assuming that it is *G. setzeri*), together with the greatness of the gerbils' effect (the contribution of patches with inactive burrows was three times more than patches without burrows on them), their engineering effect must be widespread in the Namib in general and must have an ecosystem-level effect on not only primary productivity but also the distribution of large mammal herbivores. In addition, because they favour certain habitats and substrates, their spatial distribution may influence the landscape-scale distribution of primary productivity and all other organisms that depend on that.

I do not have data on productivity during high rainfall periods because my study was conducted during the dry season (my study was preceded by a relatively dry year with only 15.9 mm falling in total). It is possible that during the years of good rain, both the vegetation patches with and without burrows may contribute to the productivity on ecosystem level. However, my results reflect the ecologically more important situation of an extremely dry period where biomass becomes critical.

The critical characteristic of an ecological engineer is that it must alter the availability, quality, quantity, and distribution of resources utilised by other biota (Jones et al., 1994, 1997). The Namib gerbils have equally fulfilled this characteristic, resulting in higher plant productivity on both the patch-scale and ecosystem-scale. Although I did not measure their effect on diversity of other organisms such as insects (which have been shown to be positively affected by ground squirrels in the Namib [Ewacha et al., 2016]), their direct role in improving productivity is possibly functionally more important. I therefore conclude that the colonial gerbils are playing a functional ecological engineering role on the Husab gravel plains of the central Namib Desert.

Theoretically, their effect on primary productivity will have a positive knock-on effect on the larger grazers such as zebras and oryx, allowing them to thrive in areas where they could not normally do well in the absence of the gerbils. A logical extension of my study would be to confirm this assumption through the measurement of the impact of vegetation productivity on the larger grazers on the Husab gravel plains. This study was conducted within the fog zone and there is a potential that fog might have an impact on the engineering effect of gerbils, thus vegetation productivity. To test this hypothesis, I further recommend that the same study should be conducted across the fog gradient. The findings of this study has disclosed that the gravel plains of the central Namib support a functional process which is critical for the biodiversity and an important aspect for the conservation management. The ongoing functional process should be monitored to observe if there is a temporal change of the magnitude of the impact, spatial distribution and density of the gerbil burrowing activities and vegetation patches in general. The functional role of burrowing gerbils on the disturbed and recovering areas should be also monitored during and post-mining activities for successful restoration. In future if the impact studies for the Husab mine would have to be re-done or evaluated, the presumed impact of burrowing gerbils from the past should be considered as the key functional aspect for the maintenance of biodiversity on the Husab gravel plains.

Chapter 8

References

Abrams, M.M., Jacobson, P.J., Jacobson, K.M. and Seely, M.K. (1997). Survey of soil chemical properties across a landscape in the Namib Desert. *Journal of Arid Environments*, 35(1), pp. 29-38.

Aguiar, M.R. and Sala, O.E. (1999). Patch structure, dynamics and implications for the functioning of arid ecosystems. *Trends in Ecology & Evolution*, 14(7), pp. 273-277.

Albanese, S., Rodríguez, D., Dacar, M.A. and Ojeda, R.A. (2010). Use of resources by the subterranean rodent *Ctenomys mendocinus* (*Rodentia ctenomyidae*), in the lowland Monte desert, Argentina. *Journal of Arid Environments*, 74(4), pp. 458-463.

Andersen, D.C. and MacMahon, J.A. (1985). Plant succession following the Mount St. Helens volcanic eruption: facilitation by a burrowing rodent, *Thomomys talpoides*. *American Midland Naturalist*, pp. 62-69.

Aronson J, Floret C, Le Floc'h E, Ovalle C. and Pontanier R. (1993). Restoration and rehabilitation of degraded ecosystems in arid and semi-arid lands: Review from the South. *Restoration Ecology* 1(1), pp. 8-17.

Ball, D., Collins, M., Lacefield, G., Martin, N., Mertens, D., Olson, K., Putnam, D., Undersander, D. and Wolf, M. (2001). Understanding Forage Quality. *American Farm Bureau Federation Publication.*

Barnes, R.D., Fagg, C.W. and Milton, S.J. (1997). *Acacia erioloba: monograph and annotated bibliography*. Oxford Forestry Institute, University of Oxford.

Bates, R.L. and Jackson, J.A. (1984). Dictionary of geological terms, New York, NY, Bantam Doubleday Dell Publishing Group.

Belnap, J. (2011). Biological phosphorus cycling in dryland regions. In *Phosphorus in action*. Soil Biology, Springer, Berlin, Heidelberg. pp. 371-406.

Berkenbusch, K. and Rowden, A.A. (2003). Ecosystem engineering—moving away from 'just-so' stories. *New Zealand Journal of Ecology*, pp. 67-73.

Bian, J., Wang, Q. and Shi, Y. (1991). Experimental analysis of the relationship between plant component on zokor mounds and the original vegetation. *Alpine meadow ecosystem*, 3, pp. 181-188.

Blume, H.P. (2011). Charles Darwin and the discovery of bioturbation in the year 1837. *Annals of Agrarian Science*, 9(1), pp. 66-69.

Bochet, E. (2015). The fate of seeds in the soil: a review of the influence of overland flow on seed removal and its consequences for the vegetation of arid and semiarid patchy ecosystems. *Journal of Soil Science,* 1, pp. 131–146.

Bochet, E., Rubio, J.L. and Poesen, J. (1999). Modified topsoil islands within patchy Mediterranean vegetation in SE Spain. *Catena*, 38(1), pp. 23-44.

Bornman, C.E.J. (1972). *Welwitschia mirabilis*: observations on general habit, seed, seedling, and leaf characteristics. *Madoqua*, 2(1), pp. 53-66.

Boyer, D.C. and Perrin, M.R. (1996). Habitat selection by the gerbils *Gerbillurus paeba* and *G. tytonis* in the Namib Desert dunes. *South African Journal of Wildlife Research-24-month delayed open access*, 26(3), pp. 71-76.

Bragg, C.J., Donaldson, J.D. and Ryan, P.G. (2005). Density of Cape porcupines in a semi-arid environment and their impact on soil turnover and related ecosystem processes. *Journal of Arid Environments*, 61(2), pp. 261-275.

Brown, J.H. and Ernest, S.M. (2002). Rain and rodents: complex dynamics of desert consumers: although water is the primary limiting resource in desert ecosystems, the relationship between rodent population dynamics and precipitation is complex and nonlinear. *Journal of Biological Science*, 52(11), pp. 979-987.

Brown, J.H. and Heske, E.J. (1990). Control of a desert-grassland transition by a keystone rodent guild. *Journal of Biological Science*, 250(4988), pp. 1705-1707.

Brown, J.H. and Heske, E.J. (1990). Temporal changes in a Chihuahuan Desert rodent community. Department of Biology, University of New Mexico, 59, pp. 290-302.

Busch, C., Antinuchi, C.D., del Valle, J.C., Kittlein, M., Malizia, A.I., Vassallo, A.I. and Zenuto, R.R. (2000). Population ecology of subterranean rodents. *Life underground: The biology of subterranean rodents*, pp. 183-226.

Cameron, G.N., Spencer, S.R., Eshelman, B.D., Williams, L.R. and Gregory, M.J. (1988). Activity and burrow structure of Attwater's pocket gopher (*Geomys attwateri*). *Journal of Mammalogy*, 69(4), pp. 667-677.

Canals, R.M., Herman, D.J. and Firestone, M.K. (2003). How disturbance by fossorial mammals alters N cycling in a California annual grassland. *Journal of Ecology*, 84(4), pp. 875-881.

Carlisle, D., Merifield, P.M., Orme, A.R., Kohl, M.S., Kolker, O. and Lunt, O.R. (1978). *Distribution of calcretes and gypcretes in southwestern United States and their uranium favorability, based on a study of deposits in Western Australia and South West Africa (Namibia)*, 29(78). University of California.

Cerdà, A. (1997). The effect of patchy distribution of *Stipagrostis tenacissima L.* on runoff and erosion. *Journal of Arid Environments*, 36(1), pp. 37-51.

Chevret, P. and Dobigny, G. (2005). Systematics and evolution of the subfamily Gerbillinae (Mammalia, Rodentia, Muridae). *Molecular phylogenetics and evolution*, 35(3), pp. 674-688.

Christiansen, F.W. (1963). Polygonal fracture and fold systems in the salt crust, Great Salt Lake Desert, Utah. *Science*, 139(3555), pp. 607-609.

Clark, K.L., Branch, L.C., Hierro, J.L. and Villarreal, D. (2016). Burrowing herbivores alter soil carbon and nitrogen dynamics in a semi-arid ecosystem, Argentina. *Soil Biology and Biochemistry*, 103, pp. 253-261.

Coetzee, C.G. (1970). The distribution of mammals in the Namib Desert and adjoining inland escarpment. *Scientific Papers of the Namib Desert Research Station*, 1970(40), pp. 23-36.

Comparatore, V.M., Maceira, N.O. and Busch, C. (1991). Habitat relations in *Ctenomys talarum* (Caviomorpha, Octodontidae) in a natural grassland. *Zeitschrift für Säugetierkunde*, 56(2), pp. 112-118.

Cooke, J.A. and Johnson, M.S. (2002). Ecological restoration of land with particular reference to the mining of metals and industrial minerals: A review of theory and practice. *Environmental Reviews*, 10(1), pp. 41-71.

Cottam, G. and Curtis, J.T. (1956). The use of distance measures in phytosociological sampling. *Journal of Ecology*, 37(3), pp. 451-460.

Cox, G.W. (1987). The origin of vegetation circles on stony soils of the Namib Desert near Gobabeb, South West Africa, Namibia. *Journal of Arid Environments*, 13, pp. 237-243.

Davidson, A.D. and Lightfoot, D.C. (2006). Keystone rodent interactions: prairie dogs and kangaroo rats structure the biotic composition of a desertified grassland. *Ecological geography*, 29(5), pp. 755-765.

Davidson, A.D. and Lightfoot, D.C. (2008). Burrowing rodents increase landscape heterogeneity in a desert grassland. *Journal of Arid Environments*, 72(7), pp. 1133-1145.

Davies, G.T.O., Kirkpatrick, J.B., Cameron, E.Z., Carver, S. and Johnson, C.N. (2019). Ecosystem engineering by digging mammals: effects on soil fertility and condition in Tasmanian temperate woodland. *Royal Society open science*, 6(1), pp. 180-621.

Dempsters, E. R., Perrin, M. R., & Downs, C. T. (1999). *Gerbilliscus vallinus*. *Mammalian Species*, (605), pp. 1-4.

Dempsters, E. R., Perrin, M. R., & Downs, C. T., Griffin, M. (1998). *Gerbilliscus setzeri*. *Mammalian Species*, 604, pp. 1-4.

Desmet, P.G. and Cowling, R.M. (1999). Patch creation by fossorial rodents: a key process in the revegetation of phytotoxic arid soils. *Journal of Arid Environments*, 43(1), pp. 35-45.

Devices, D. (1998). Measuring soil hydraulic conductivity with a disk infiltrometer. Application Note. AN7002-10. USA.

Dixon, J.C. (1994). Aridic Soils, Patterned Ground and Desert pavements.

Dong, Q.M., Zhao, X.Q., Wu, G.L., Shi, J.J. and Ren, G.H. (2013). A review of formation mechanism and restoration measures of “black-soil-type” degraded grassland in the Qinghai-Tibetan Plateau. *Environmental Earth Sciences*, 70(5), pp. 2359-2370.

Downs, C.T. and Perrin, M.R. (1990a). The effect of diet on water and energy turnover rates of four *Gerbillurus* species in captivity. *Journal of Zoology*, 222(2), pp. 215-233.

Ebensperger, L.A. and Bozinovic, F. (2000). Energetics and burrowing behaviour in the semifossorial degu *Octodon degus* (Rodentia: Octodontidae). *Journal of Zoology*, 252(2), pp. 179-186.

Eckardt, F.D. and Schemenauer, R.S. (1998). Fog water chemistry in the Namib Desert, Namibia. *Atmospheric Environment*, 32(14-15), pp. 2595-2599.

Eckardt, F.D., Soderberg, K., Coop, L.J., Muller, A.A., Vickery, K.J., Grandin, R.D., Jack, C., Kapalanga, T.S. and Henschel, J. (2013). The nature of moisture at Gobabeb, in the central Namib Desert. *Journal of Arid Environments*, 93, pp. 7-19.

Eldridge, D.J. and Whitford, W.G. (2014). Disturbances by desert rodents are more strongly associated with spatial changes in soil texture than woody encroachment. *Plant and soil*, 381(1-2), pp. 395-404.

Eldridge, D.J., Bowker, M.A., Maestre, F.T., Alonso, P., Mau, R.L., Papadopoulos, J. and Escudero, A. (2010). Interactive effects of three ecosystem engineers on infiltration in a semi-arid Mediterranean grassland. *Ecosystems*, 13(4), pp. 499-510.

Eldridge, D.J., Zaady, E. and Shachak, M. (2002). The impact of disturbance on runoff and sediment production and its implications for the management of desert ecosystems. *Landscape Ecology*, 17, pp. 587-97.

Ewacha, M.V., Kaapehi, C., Waterman, J.M. and Roth, J.D. (2016). Cape ground squirrels as ecosystem engineers: modifying habitat for plants, small mammals and beetles in Namib Desert grasslands. *African journal of Ecology*, 54(1), pp. 68-75.

Feller, C., Brown, G.G., Blanchart, E., Deleporte, P. and Chernyanskii, S.S. (2003). Charles Darwin, earthworms and the natural sciences: various lessons from past to future. *Agriculture, Ecosystems and Environment*, 99(1-3), pp. 29-49.

Fleming, P.A., Anderson, H., Prendergast, A.S., Bretz, M.R., Valentine, L.E. and Hardy, G.E.S. (2014). Is the loss of Australian digging mammals contributing to a deterioration in ecosystem function? *Mammal Review*, 44(2), pp. 94-108.

Gabet, E.J., Reichman, O.J. and Seabloom, E.W. (2003). The effects of bioturbation on soil processes and sediment transport. *Annual Review of Earth and Planetary Sciences*, 31(1), pp. 249-273.

Galiano, D., Kubiak, B.B., Overbeck, G.E. and de Freitas, T.R. (2014). Effects of rodents on plant cover, soil hardness, and soil nutrient content: a case study on tuco-tucos (*Ctenomys minutus*). *Journal of Mammalogy*, 59(4), pp. 583-587.

Gang, W. and Guozhen, D. (1990). Niche analysis of species in vegetative succession on zokor mounds. *Chinese Journal of Ecology*, 1, pp. 01.

Gharajehdaghipour, T., Roth, J.D., Fafard, P.M. and Markham, J.H. (2016). Arctic foxes as ecosystem engineers: increased soil nutrients lead to increased plant productivity on fox dens. *Scientific reports*, 6(1), pp.1-7.

Giannoni, S.M., Borghi, C.E. and Roig, V.G. (1996). The burrowing behavior of *Ctenomys eremophilus* (Rodentia, Ctenomyidae) in relation with substrate hardness. *Mastozoologia Neotropical*, 3(2), pp. 161-170.

Giess, W. (1998). A preliminary vegetation map of Namibia. *Dinteria*, 4, pp. 5-114.

Gómez-García, D., Azorín, J., Giannoni, S.M. and Borghi, C.E. (2004). How does *Merendera montana* (L.) Lange (Liliaceae) benefit from being consumed by mole-voles? *Plant Ecology*, 172(2), pp. 173-181.

Gonnet, J.M. and Ojeda, R.A. (1998). Habitat use by small mammals in the arid Andean foothills of the Monte Desert of Mendoza, Argentina. *Journal of Arid Environments*, 38(3), pp. 349-357.

Goudie, A. (1970). Climate, weathering, crust formation, dunes, and fluvial features of the Central Namib Desert, near Gobabeb, South West Africa. *Journal of Arid Environments*, 2(1), pp. 15-31.

Govers, G., Takken, I. and Helming, K. (2000). Soil roughness and overland flow. *Agronomie*, 20(2000), pp. 131-146.

Goyal, S.P. and Ghosh, P.K. (1993). Burrow structure of two gerbil species of Thar desert, India. *Acta Theriologica*, 38, pp. 453-453.

Griffin, M. (1990). A review of taxonomy and ecology of gerbilline rodents of the central Namib Desert, with keys to the species (Rodentia: Muridae). *Journal of Ecology*, 25, pp. 83-98.

Guo, Z.G., Zhou, X.R., Hou, Y. (2012). Effect of available burrow densities of plateau pika (*Ochotona curzoniae*) on soil physicochemical property of the bare land and vegetation land in the Qinghai-Tibetan Plateau. *Journal of Ecology*, 32, pp. 104–110.

Gurney, W.S.C. and Lawton, J.H. (1996). The population dynamics of ecosystem engineers. *Journal of Ecology*, pp. 273-283.

Gutterman, Y., Golan, T. and Garsani, M. (1990). Porcupine diggings as a unique ecological system in a desert environment. *Journal of Ecology*, 85(1), pp. 122-127.

Hagenah, N. and Bennett, N.C. (2013). Mole rats act as ecosystem engineers within a biodiversity hotspot of the Cape Fynbos. *Journal of Zoology*, 289(1), pp. 19-26.

Hambleton-Jones, B.B. (1983). *The geology and geochemistry of some epigenetic uranium deposits near the Swakop River, South West Africa* (No. PER--78). Nuclear Development Corporation of South Africa (Pty.) Ltd.

Hastings, A., Byers, J.E., Crooks, J.A., Cuddington, K., Jones, C.G., Lambrinos, J.G., Talley, T.S. and Wilson, W.G. (2007). Ecosystem engineering in space and time. *Journal of Ecology*, 10(2), pp. 153-164.

Hauptfleisch, M.L., Vinte, M.P. and Blaum, N. (2017). A comparison of the community dynamics of bioturbating small mammals between livestock and wildlife farming areas in the Kalahari, Namibia. *Namibian Journal of Environments*, 1, pp. A-39.

Haussmann, N.S., Louw, M.A., Lewis, S., Nicol, K.J., Van der Merwe, S. and le Roux, P.C. (2018). Ecosystem engineering through aardvark (*Orycteropus afer*) burrowing: Mechanisms and effects. *Ecological Engineering*, 118, pp. 66-72.

Heine, K. and Walter, R. (1996). Gypcretes of the central Namib Desert, Namibia. *Palaeoecology of Africa*, 24, pp. 173-201.

Henschel, J. R. and Seely, M. K. (2000). Long-term growth patterns of *Welwitschia mirabilis*, a long-lived plant of the Namib Desert. *Plant Ecology*, 150(1-2), pp. 7–26.

Henschel, J. (2009). Phase-2 Environmental Baseline Study of Vertebrates in Mining License Area 140 (ml140) of the Langer Heinrich Uranium mine, pp. 17-23.

Heth, G. (1989). Burrow patterns of the mole-rat *Spalax ehrenbergi* in two soil types (terra-rossa and rendzina) in Mount Carmel, Israel. *Journal of Zoology*, 217(1), pp. 39-56.

Huenneke, L.F., Clason, D. and Muldavin, E. (2001). Spatial heterogeneity in Chihuahuan Desert vegetation: implications for sampling methods in semi-arid ecosystems. *Journal of Arid Environments*, 47(3), pp. 257-270.

Hutchings, M.R. and Harris, S. (2001). Defecation and urination patterns of badgers (*Meles meles*) at low density in south west England. *Journal of Mammalogy*, 46(1), pp. 87-96.

James, A.I., Eldridge, D.J. and Hill, B.M. (2009). Foraging animals create fertile patches in an Australian desert shrubland. *Ecological geography*, 32(5), pp. 723-732.

Jiang, H.P., Wu, N. and Yang, W.K. (2007). Effects of *Rhombomys opimus* on microbial quantity, soil moisture, content and soil nutrient content in a desert. *Arid Zone Restoration*, 24, pp. 187-192.

Johnson, D.L. (2002). Darwin would be proud: bioturbation, dynamic denudation, and the power of theory in science. *Geology and Archaeology: An International Journal*, 17(1), pp. 7-40.

Jones, C.G., Lawton, J.H. and Shachak, M. (1994). Organisms as ecosystem engineers. *Ecosystem Management*. Springer, New York, NY, pp. 130-147.

Jones, C.G., Lawton, J.H. and Shachak, M. (1997). Positive and negative effects of organisms as physical ecosystem engineers. *Journal of Ecology*, 78(7), pp. 1946-1957.

Kargas, G., Londra, P.A. and Valiantzas, J.D. (2017). Estimation of near-saturated hydraulic conductivity values using a mini disc infiltrometer. *Water Utility Journal*, 16, pp. 97-104.

Knight, L. I. (2013). *Cytosystematics of Gerbils* (Doctoral dissertation, Stellenbosch: Stellenbosch University). pp. 2-5.

Koide, R.T., Huenneke, L.F. and Mooney, H.A. (1987). Gopher mound soil reduces growth and affects ion uptake of two annual grassland species. *Journal of Ecology*, 72(2), pp. 284-290.

Korn, H. and Korn, U. (1989). The effect of gerbils (*Gerbilliscus brantsii*) on primary production and plant species composition in a southern African savanna. *Journal of Ecology*, 79(2), pp. 271-278.

Kurek, P., Kapusta, P. and Holeksa, J. (2014). Burrowing by badgers (*Meles meles*) and foxes (*Vulpes vulpes*) changes soil conditions and vegetation in a European temperate forest. *Ecological Research*, 29(1), pp.1-11.

Kuznetsova, T.A., Kam, M., Khokhlova, I.S., Kostina, N.V., Dobrovolskaya, T.G., Umarov, M.M., Degen, A.A., Shenbrot, G.I. and Krasnov, B.R. (2013). Desert gerbils affect bacterial composition of soil. *Microbial Ecology*, 66(4), pp. 940-949.

Lancaster, J., Lancaster, N. and Seely, M.K. (1984). Climate of the central Namib Desert. *Journal of Arid Environments*, 14(1), pp. 5-61.

Lang, W.B. (1943). Gigantic drying cracks in Animas Valley, New Mexico. *Science*, 98(2557), pp. 583-584.

Laundre, J.W. and Reynolds, T.D. (1993). Effects of soil structure on burrow characteristics of five small mammal species. *The Great Basin Naturalist*, pp. 358-366.

Laundre, J.W. (1993). Effects of small mammal burrows on water infiltration in a cool desert environment. *Journal of Ecological*, 94(1), pp. 43-48.

Laundre, J.W. (1998). Effect of ground squirrel burrows on plant productivity in a cool desert environment. *Rangeland Ecology & Management/Journal of Range Management Archives,* 51(6), pp. 638-643.

Lavelle, P., Barot, S., Blouin, M., Decaëns, T., Jimenez, J.J. and Jouquet, P. (2007). Earthworms as key actors in self-organized soil systems. *Ecosystem Engineers: Plants to Protists*, pp. 405.

Lawton, J.H. (1994). What do species do in ecosystems? *Oikos*, pp. 367-374.

Liu, W., Wan, X. and Zhong, W., 2007. Population dynamics of the Mongolian gerbils: seasonal patterns and interactions among density, reproduction and climate. *Journal of Arid Environments*, 68(3), pp. 383-397.

Laycock, W.A. and Richardson, B.Z. (1975). Long-term effects of pocket gopher control on vegetation and soils of a subalpine grassland. *Rangeland Ecology & Management/Journal of Range Management Archives*, 28(6), pp. 458-462.

Louw, G.N. and Seely, M.K. (1982). Ecology of desert organisms. Evolutionary ecology of deserts, pp. 140-143.

Luna, F. and Antinuchi, C.D. (2006). Cost of foraging in the subterranean rodent *Ctenomys talarum*: effect of soil hardness. *Journal of Zoology*, 84(5), pp. 661-667.

Mahalik, G. (2018). Environmental impacts of mining on biodiversity of Angul-Talcher open mining site, Odisha. Scholars Academic Journal of Biosciences (SAJB), 4(3A), pp. 224-227.

Malizia, A.I., Kittlein, M.J. and Busch, C. (2000). Influence of the subterranean herbivorous rodent (*Ctenomys talarum*) on vegetation and soil. *Zeitschrift fur Saugetierkunde*, 65(3), pp. 172-182.

Merino-Martín, L., Moreno-de las Heras, M., Espigares, T. and Nicolau, J.M. (2015). Overland flow directs soil moisture and ecosystem processes at patch scale in Mediterranean restored hillslopes. *Catena*, 133, pp. 71-84.

Metago Consulting Environmental Engineers and Scientists (Pty) Ltd. (2010). Environmental Impact Assessment (EIA) For The Proposed Husab Mine (Previously Called Rössing South). [online] South Africa: EIA Report, pp. 5-6. Available at: www.metago.co.za [Accessed 27 Oct. 2010].

Mielke, H.W. (1977). Mound building by pocket gophers (Geomyidae): their impact on soils and vegetation in North America. *Journal of Biogeography*, pp. 171-180.

Milton, S.J. (2001). Rethinking ecological rehabilitation in arid and winter rainfall regions of southern Africa: meeting report. *South African Journal of Science*, 97(1-2), pp. 47-48.

Morbidellil, R., Corradinil, C., Saltalippil, C., Flammini, A. and Govindaraju, R.S. (2012). The role of slope on the overland flow production. *River Basin Management*, 7(172), pp. 63.

Mugatha, S.M. (2004). The influence of land use patterns on diversity and abundance of rodents in Gachoka division of Mbeere district, Kenya. Msc Thesis University of Nairobi, pp. 15-16.

Naiman, R.J. and Melillo, J.M. (1984). Nitrogen budget of a subarctic stream altered by beaver (*Castor canadensis*). *Journal of Ecology*, 62(2), pp. 150-155.

Naiman, R.J., Johnston, C.A. and Kelley, J.C. (1988). Alteration of North American streams by beaver.

Biological Science, 38(11), pp. 753-762.

Nauyoma, T. (2014). Environmental factors associated with *Juttadinteria albata* (*L. Bolus*) population structure and assessment of its performance in trial planting at Sendelingsdrif Mine. *Master dissertation*. University of Namibia, Namibia.

Nevo, E. (1979). Adaptive convergence and divergence of subterranean mammals. *Annual review of ecology and systematics*, 10(1), pp. 269-308.

Newman, B.D., Wilcox, B.P., Archer, S.R., Breshears, D.D., Dahm, C.N., Duffy, C.J., McDowell, N.G., Phillips, F.M., Scanlon, B.R. and Vivoni, E.R. (2006). Ecohydrology of water-limited environments: A scientific vision. *Water resources research*, 42(6), pp. 231-236.

Olivier, J. (1995). Spatial distribution of fog in the Namib. *Journal of Arid Environments*, 29(2), pp. 129-138.

Ollier, C.D. and Seely, M.K. (1977). Patterned ground near Gobabeb, central Namib Desert. *Journal of Arid Environments*, 10(3), pp. 213-214.

Ollier, C.D. (1977). Outline geological and geomorphic history of the central Namib Desert. *Journal of Arid Environments*, 10(3), pp. 207-212.

Perrin, M.R. and Boyer, D.C. (2000). Seasonal changes in the population dynamics of hairy-footed gerbils in the Namib Desert. *South African Journal of Wildlife Research-24-month delayed open access*, 30(2), pp. 73-84.

Prakash, I. (1981). Ecology of the Indian desert gerbil (*Meriones hurrianae*). *Central Arid Zone Research Institute*, Jodhpur and Printed at the Harvard Press. pp. 12-13.

Prendini, L. and Esposito, L.A. (2010). A reanalysis of Parabuthus (Scorpiones: Buthidae) phylogeny with descriptions of two new Parabuthus species endemic to the Central Namib gravel plains, Namibia. *Zoological Journal of the linnean society*, 159(3), pp. 673-710.

Ramantswana, T. M. (2013). *Comparative geographic variation of selected southern African gerbils* (*Doctoral dissertation*, Stellenbosch: Stellenbosch University), pp. 1-7.

Reaney, S.M., Bracken, L.J. and Kirkby, M.J. (2014). The importance of surface controls on overland flow connectivity in semi-arid environments: Results from a numerical experimental approach. *Hydrological Processes*, 28(4), pp. 2116-2128.

Reichman, O.J. and Seabloom, E.W. (2002). The role of pocket gophers as subterranean ecosystem engineers. *Trends in Ecology & Evolution*, 17(1), pp. 44-49.

Rietkerk, M., Boerlijst, M.C., van Langevelde, F., HilleRisLambers, R., de Koppel, J.V., Kumar, L., Prins, H.H. and de Roos, A.M. (2002). Self-organization of vegetation in arid ecosystems. The American Naturalist, 160(4), pp. 524-530.

Romañach, S.S., Seabloom, E.W., Reichman, O.J., Rogers, W.E. and Cameron, G.N. (2005). Effects of species, sex, age, and habitat on geometry of pocket gopher foraging tunnels. *Journal of Mammalogy*, 86(4), pp. 750-756.

Rosenzweig, M.L. and Winakur, J. (1969). Population ecology of desert rodent communities: habitats and environmental complexity. *Journal of Ecology*, 50(4), pp. 558-572.

Schlesinger, W.H., Reynolds, J.F., Cunningham, G.L., Huenneke, L.F., Jarrell, W.M., Virginia, R.A. and Whitford, W.G. (1990). Biological feedbacks in global desertification. *Science*, 247(4946), pp. 1043-1048.

Scholz, H. (1963). Studies on the formation of soil between Rehoboth and Walvis-Bay (No. Thesis S368). Bonn University. Bonn (Alemania).

Scholz, H. (1972). The soils of the central Namib Desert with special consideration of the soils in the vicinity of Gobabeb. *Madoqua*, 2(1), pp. 33-51.

Schooley, R.L., Bestelmeyer, B.T. and Kelly, J.F. (2000). Influence of small-scale disturbances by kangaroo rats on Chihuahuan Desert ants. *Journal of Ecology*, 125(1), pp. 142-149.

Seely, M. and Pallet, J. (2008). Ecology of the Namib. Secrets of a desert uncovered. Venture Publications, P O BOX 21593, Windhoek.

Shaanika, N. H., Wassenaar, T. D. and Eiseb, S. J. (2020). Aspects of gerbils burrowing activity and their potential ecological engineering role on a gravel plain in central Namib Desert (*Masters dissertation*, chapter 5, manuscript prepared for the *Journal of Arid Environments*, Namibia University of Science and Technology) pp. 29-59.

Shaanika, N. H., Wassenaar, T. D. and Eiseb, S. J. (2020). The spatial distribution of gerbils' and no-burrow vegetation patches on a gravel plain in central Namib Desert. (*Masters dissertation*, chapter 6, manuscript prepared for the *Namibia Journal of Environment*, Namibia University of Science and Technology) pp. 56-73.

Shanyengana, E. S., Henschel, J. R. and Seely, M. K. (2002). Exploring fog as a supplementary water source in Namibia. *Atmospheric Research*, 64(64), pp. 251–259.

Shenbrot, G.I., Krasnov, B.R. and Khokhlova, I.S. (1997). Biology of Wagner's gerbil (*Gerbillus dasyurus*) in the Negev Highlands, Israel. *Journal of Mammalogy*, 61(4), pp. 467-486.

Sherman, G., (2015). Quantum Geographic Information System. Open Source Geospatial Foundation Project. Disponível em:< http://www. qgis. org/>. Acesso em, 27.

Skinner J.D. and Chimimba C.T. (2006). Mammals of Southern Africa. 3rd Ed. Cambridge. Cambridge University Press, pp. 104-107.

Smith, R.E. and Goodrich, D.C. (2006). Rainfall excess overland flow. *Encyclopedia of hydrological sciences*.

Stanistreet, I.G., Kukla, P.A. and Henry, G. (1991). Sedimentary basinal responses to a late Precambrian Wilson cycle: The Damara orogen and Nama foreland, Namibia. *Journal of African Earth Sciences (and the Middle East)*, 13(1), pp. 141-156.

Stuart, C. and Stuart, T. (1995). Field guide to the mammals of southern Africa. Gerbils (*Gerbillinae*): University of Pretoria, pp. 104-107.

Thayer, C.W. (1979). Biological bulldozers and the evolution of marine benthic communities. *Science*, 203(4379), pp. 458-461.

Traba, J., Acebes, P., Campos, V.E. and Giannoni, S.M. (2010). Habitat selection by two sympatric rodent species in the Monte desert, Argentina. First data for *Eligmodontia moreni* and *Octomys mimax*. *Journal of Arid Environments*, 74(2), pp. 179-185.

Vijayan, S., Kotler, B.P., Mukherjee, S., Brown, J.S. and Bouskila, A. (2007). Influence of cover on the foraging behavior of Negev Desert gerbils. *Basic and Applied Dryland Research*, 1, pp. 51-66.

Villarreal, D., Clark, K.L., Branch, L.C., Hierro, J.L. and Machicote, M. (2008). Alteration of ecosystem structure by a burrowing herbivore, the plains vizcacha (*Lagostomus maximus*). *Journal of Mammalogy*, 89(3), pp. 700-711.

Walsberg, G.E. (2000). Small mammals in hot deserts: some generalizations revisited. *Biological Science*, 50(2), pp. 109-120.

Wang, Q., Bian, J. and Shi, Y. (1993). Influence of plateau zokor mounds on the vegetation and soil nutrients in an alpine meadow. *Acta Theriologica Sinica*, 13(1), pp. 31-37.

Wassenaar, T.D., Henschel, J.R., Pfaffenthaler, M.M., Mutota, E.N., Seely, M.K. and Pallett, J. (2013). Ensuring the future of the Namib's biodiversity: Ecological restoration as a key management response to a mining boom. *Journal of arid environments*, 93, pp. 126-135.

Wassenaar, T.D. and Mannheimer C.M. (2010). Biodiversity Impact Assessment at Swakop Uranium's Husab Project. Unpublished Specialist Report to Metago Environmental Engineers and Swakop Uranium, as part of a comprehensive Environmental Impact Assessment.

Watson, A. (1979). Gypsum crusts in deserts. *Journal of Arid Environments*, 2(1), pp. 3-20.

Watson, A. (1980). Vegetation polygons in the central Namib Desert near Gobabeb. *Journal of Arid Environments* 11(4), pp. 315-325.

Watson, A. (1985). Structure, chemistry and origins of gypsum crusts in southern Tunisia and the central Namib Desert. *Sedimentology*, 32(6), pp. 855-875.

Watson, A. (1988). Desert gypsum crusts as palaeoenvironmental indicators: A micro-petrographic study of crusts from southern Tunisia and the central Namib Desert. *Journal of Arid Environments*, 15(1), pp. 19-42.

Wesche, K., Nadrowski, K. and Retzere, V. (2007). Habitat engineering under dry conditions: the impact of pikas (*Ochotona pallasi*) on vegetation and site conditions in southern Mongolian steppes. *Journal of Vegetation Science*, 18(5), pp. 665-674.

Whitford, W.G. (2002). Ecology of Desert Systems. Academic Press, London. *Journal of Arid Environments*, 73(9), pp. 821-827.

Whittington-Jones, G.M., Bernard, R.T. and Parker, D.M. (2011). Aardvark burrows: a potential resource for animals in arid and semi-arid environments. *African Zoology*, 46(2), pp. 362-370.

Wilkinson, M.J. (1988). The Tumas Sandstone Formation of the central Namib Desert. Palaeoenvironmental implications. *Collection Palaeoecology of Africa and the surrounding islands*, 19, pp. 139-150.

Willden, R. and Mabey, D.R. (1961). Giant desiccation fissures on the Black Rock and Smoke Creek deserts, Nevada. *Science*, 133(3461), pp. 1359-1360.

Willott, S.J., Miller, A.J., Incoll, L.D. and Compton, S.G. (2000). The contribution of rabbits (*Oryctolagus cuniculus L.*) to soil fertility in semi-arid Spain. *Biology and Fertility of Soil*s, 31(5), pp. 379-384.

Wright, J.P. and Jones, C.G. (2006). The concept of organisms as ecosystem engineers ten years on: progress, limitations, and challenges. *Biological Science*, 56(3), pp. 203-209.

Wright, N.I. (2006). Ecological impacts of Highveld gerbils (*Gerbilliscus brantsii*) on a rehabilitated ash disposal site (Doctoral dissertation, North-West University). pp. 56.

Wu, R., Chai, Q., Zhang, J., Zhong, M., Liu, Y., Wei, X., Pan, D. and Shao, X. (2015). Impacts of burrows and mounds formed by plateau rodents on plant species diversity on the Qinghai-Tibetan Plateau. *Journal of Rangeland*, 37(1), pp. 117-123.

Xu F, Liu W. and Qiao H. H. (2013). Relationships between vigilance, foraging and other behaviors of the great gerbil (*Rhombomys opimus*). *Arid Land Geography*, 36(1): pp. 118–124.

Xu, W., Liu, W., Yang, W., Tang, C. and Blank, D. (2012). *Rhombomys opimus* contribution to the "fertile island" effect of tamarisk mounds in Junggar Basin. *Ecological Research*, 27(4), pp. 775-781.

Xu, W., Liu, W., Yang, W., Wang, M., Xu, F. and Blank, D. (2015). Impact of great gerbils (*Rhombomys opimus*) on desert plant communities. *Journal of Arid Lands*, 7(6), pp. 852-859.

Yizhaq, H., Stavi, I., Swet, N., Zaady, E. and Katra, I. (2019). Vegetation ring formation by water overland flow in water-limited environments: Field measurements and mathematical modelling. *Ecohydrology*, 12(7), pp. e2135.

Yoshihara, Y., Okuro, T., Buuveibaatar, B., Undarmaa, J. and Takeuchi, K. (2010). Clustered animal burrows yield higher spatial heterogeneity. *Plant Ecology*, 206(2), pp. 211-224.

Yoshihara, Y., Okuro, T., Undarmaa, J., Sasaki, T. and Takeuchi, K. (2009). Are small rodents key promoters of ecosystem restoration in harsh environments? A case study of abandoned croplands on Mongolian grasslands. *Journal of Arid Environments*, 73(3), pp. 364-368.

Yu, C., Jia, T.T., Pang, X.P. and Guo, Z.G. (2016). Effects of plateau pika (*Ochotona Curzoniae*) disturbing soil carbon and nitrogen distribution in alpine meadow. *Ecological Sciences*, 53, pp. 208-218.

Yu, C., Zhang, J., Pang, X.P., Wang, Q., Zhou, Y.P. and Guo, Z.G. (2017). Soil disturbance and disturbance intensity: Response of soil nutrient concentrations of alpine meadow to plateau pika bioturbation in the Qinghai-Tibetan Plateau, China. *Journal of Soil Sciences*, 307, pp. 98-106.

Yurkewycz, R.P., Bishop, J.G., Crisafulli, C.M., Harrison, J.A. and Gill, R.A. (2014). Gopher mounds decrease nutrient cycling rates and increase adjacent vegetation in volcanic primary succession. *Ecological Sciences*, 176(4), pp. 1135-1150.

Zhang, Y. (2000). Studies on the pattern of animal-plant interaction: the effects of plateau zokor on the biogeochemical cycling of alpine meadow ecosystem and its response to the chemical defense of plants. *PhD Dissertation*. *Graduate University of the Chinese Academy of Sciences*, *Beijing.*

Zhang, Y., Dong, S., Gao, Q., Liu, S., Liang, Y. and Cao, X. (2016). Responses of alpine vegetation and soils to the disturbance of plateau pika (*Ochotona curzoniae*) at burrow level on the Qinghai–Tibetan Plateau of China. *Ecological Engineering*, 88, pp. 232-236.

Zhang, Y., Zhang, Z. and Liu, J. (2003). Burrowing rodents as ecosystem engineers: the ecology and management of plateau zokors (*Myospalax fontanierii*) in alpine meadow ecosystems on the Tibetan Plateau. *Mammal Review*, 33(3-4), pp. 284-294.

Zhang, Y., Zhou, X. and Cincotta, R.P. (1994). Study of diversity and succession pattern of plant communities on zokor mound. *Ecological Sciences*, 14, pp. 42-49.

Zinnel, K.C. and Tester, J.R. (1990). Effects of plains pocket gophers on root biomass and soil nitrogen. *In Proceedings of the 12th North American Prairie Conference: recapturing a vanishing heritage. University of Northern Iowa, Cedar Falls.* pp. 2-3.

Appendix

Table 8: *A summary of characteristic of the gerbil specimens that were captured in the field during the phase of data collection.*

Place: Welwitschia gravel plains sand adjacent to the Husab mine			
Species id number	**Species name**	**Body features**	**Length (mm)**
GS1	*G. setzeri*	Head body length	127
		Tail length	140
		Hind foot	33.6
GS2	*G. setzeri*	Head body length	120
		Tail length	135
		Hind foot	30.5
GS3	*G. setzeri*	Head body length	130
		Tail length	150
		Hind foot	35
GS4	*G. setzeri*	Head body length	130
		Tail length	160
		Hind foot	37.5

Figure 19. *The endemic G. setzeri that was camera-trapped at different angles next to its burrow (A and B) and live trapped (C) during the night on the Husab gravel plains of the central Namib Desert.*