**Ecosystem engineering through aardvark (*Orycteropus afer*) burrowing: mechanisms and effects**

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**Research Highlights**

- Three microsites were studied (burrow entrance, soil mound, control)
- Species richness differs between microsites
- The nature of this effect is dependent on the state of degradation of the burrow
- Species composition is weakly affected by burrowing activities
- Aardvark burrowing increases variation in soil and vegetation characteristics

**Abstract**

Burrowing mammals are often considered to be ecosystem engineers as burrowing disturbs the soil, thereby potentially changing resource availability and affecting habitat conditions for other species. After their excavation, burrows may strongly impact local plant communities through several mechanisms, including resource trapping, altered chemical and physical soil properties, and amelioration of microclimatic conditions. We studied ecosystem engineering by aardvark (*Orycteropus afer*) burrowing by comparing soil and vegetation characteristics between three microsites (burrow entrances, excavated soil mounds and adjacent control sites). We were able to identify several engineering effects and distinguish between potential mechanisms. Burrow soils were cooler, drier and less compact than the other microsites, with all three microsites representing unique combinations of abiotic conditions. Mean species richness was higher at older burrows than mounds and non-burrowed controls, despite burrows having a smaller seedbank and not differing in soil fertility from mounds and control sites. However, the opposite was observed at fresh burrows and mounds, where control plots contained more species on average than the other two types of microsites. Burrow age and microsite type also affected species composition, although only a small proportion of species were significantly associated with specific microsites and just two species were limited to a single microsite type. We suggest that trampling and the physical digging action at burrow entrances, and burial by deposited soil at mounds, prevents the establishment of many plant species at active burrows. However, once abandoned, burrow entrances provide good physical conditions for seedling survival, allowing the establishment of more species. Therefore, as suggested previously for other ecosystem engineers, it is important to explicitly consider the age and degradation processes of engineered

structures. In addition, our results highlight biologically-important differences in engineering impacts between burrow entrances, where soil is removed, and mounds, where soil is deposited. Such microscale differences are important to consider when examining bioturbation or, more generally, ecosystem engineering.

## 1. Introduction

Burrowing activites are an important form of natural disturbance in many ecosystems, and burrowing animals are often considered to be ecosystem engineers (Bragg et al., 2005; Gálvez-Bravo et al., 2009; Whittington-Jones et al., 2011; Desbiez and Kluyber, 2013). By creating discrete patches of disturbance, burrowing animals can increase abiotic heterogeneity at the landscape-level, generating novel microhabitats. These abiotic impacts of individual burrowing animals vary in size, but in some regions burrowing animals are thought to be the dominant geomorphic agents, displacing more sediment through their digging than all abiotic processes combined (Thorn, 1978; Butler, 1992). Through the creation of unique microhabitats and the disruption of the existing vegetation, burrowing disturbances can affect plant community characteristics. Indeed, burrowing may allow the establishment of species that would otherwise not be able to occur in an undisturbed landscape, increasing landscape-scale species richness and altering species composition (Wesche et al., 2007; Kurek et al., 2014).

Burrowing mammals can operate as ecosystem engineers through several engineering mechanisms, including ameliorating physical conditions, altering soil chemistry, and concentrating resources and seeds. Burrows can ameliorate physical environmental properties such as air temperature (Pike and Mitchell, 2013), soil texture (Mielke, 1977), bulk density (Whitford and Kay, 1999) and water infiltration rates (Grinnell, 1923; Laundre, 1993), leading to the formation of microenvironments that are abiotically favourable (Yair, 1995; see also Whitford and Kay, 1999). Burrowing also plays an important role in soil geochemical processes,

as the mixing and displacement of soil alters the chemical properties of the soil, including

organic matter content and general nutrient status (Eldridge and Whitford, 2009; Kurek et al.,

2014; Yu et al., 2017). Burrows can also act as traps for seeds (Boeken et al., 1995), litter (James

et al., 2009) and water (Shachak et al., 1991; Laundre, 1993), locally increasing resource

availability. The disturbance caused by mammal burrowing consequently may result in the

formation of resource-rich patches with a distinct microclimate and soil chemistry, with potential

knock-on effects for plant community structure.

The ecological consequences of engineering by burrowing mammals are diverse. For

example, burrow excavation can have a negative effect on plant cover (Wiegand et al., 1997), but

burrows are also often associated with increased plant species richness and biomass (Wesche et

al., 2007; Kurek et al., 2014). Because burrowing often alters soil physical and chemical

properties, burrows tend to support different plant communities than undisturbed surroundings.

Indeed, burrowed areas often suppport a higher number of pioneer and short-lived species

(Wesche et al., 2007; Kurek et al., 2014), as well as more alien species (Eldridge and Simpson,

2002), than unburrowed areas. Burrows can also offer shelter to a variety of animals other than

the original excavator by ameliorating environmental extremes in temperature and moisture

(Whittington-Jones et al., 2011). By potentially affecting animal and plant species diversity, the

presence of burrows in a landscape can also affect diversity-dependant ecosystem services

(Ceballos and Ehrlich, 2009).

The persistence of engineered structures contributes to determining their impacts, with

structures with greater longevity generally having larger total impacts on communities (Jones et

al., 1994). Some types of burrows (and indeed other forms of bioturbation) may persist for

extended periods (Bragg et al., 2005), and it could be hypothesized that their biotic and abiotic impacts will increase through time (e.g. as resources are increasingly accumulated within the burrow). It could, however, also be hypothesized that, as burrows erode and fill-in, their effects become smaller relative to undisturbed areas. It is, therefore, important to explicitly consider burrow age (or, more generally, engineered structures' stage of degradation) when examining the impacts of burrowing animals to determine if there are temporal shifts in the strength of the engineering mechanisms or effects.

This paper, therefore, had two aims. First, three potential engineering mechanisms of mammal burrows were tested, namely (1) burrows change soil physical properties, (2) burrows act as seed traps, and (3) burrowing changes soil fertility. Second, we documented the biotic impacts of burrows and burrow-related soils relative to unburrowed control plots, examining plant species richness, cover and composition. For both aims, the impact of the stage of burrow degradation was explicitly examined to test for temporal variation in the strength of mechanisms and effects. We address these aims by examining burrows excavated by aardvark (*Orycteropus afer*) within a relatively species-rich mesic grassland.

## 2. Materials and methods

### 2.1. Study area

Rietvlei Nature Reserve is a 3870 ha grassland nature reserve, located in the south-eastern suburbs of Pretoria, South Africa. The area receives a mean annual rainfall of approximately 720 mm, mostly in summer (Marais, 2004). Temperatures vary between 4°C (mean winter minimum) and 27°C (mean summer maximum) (Marais, 2004). The vegetation comprises grassland, with

scattered bush clumps restricted to relatively warmer sites within the reserve. More than 600 vascular plant species have been recorded in the reserve (Marais, 2004), most of which are grass and herbaceous species. The reserve contains c. 80 mammal species (Marais, 2004). The aardvark (*Orycteropus afer*) is the largest of the burrowing species on the reserve and creates large, easily-identifiable burrows.

## 2.2.    *Study species*

Aardvark are medium-sized (50 to 80 kg; Kingdon, 1971), solitary burrowers that feed nocturnally, mostly on ants and termites (Melton, 1976). They occur ubiquitously throughout sub-Saharan Africa in all biomes except deserts (Skinner and Smithers, 1990). Aardvark are well adapted to excavating soils, pushing the soil back with their hind feet and tail as they dig (Melton, 1976), leaving large claw marks in compact soils (Bragg et al., 2005). Three types of burrows are constructed by aardvark: relatively shallow foraging burrows, larger temporary shelters and more complex burrows used for permanent residence (Smithers, 1971). Their burrows are used by a variety of other animals (Smithers, 1971). In other systems, aardvark burrows show ameliorated temperature and moisture regimes compared to outside soils (Whittington-Jones et al., 2011) and therefore have the potential to provide thermal and moisture refugia to both plant (Wiegand et al., 1997) and animal species (Whittington-Jones et al., 2011). In addition, aardvark have the potential to directly affect plant species composition by facilitating seed dispersal (Milton and Dean, 2001).

***2.3.    Field sampling and laboratory experiments***

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120    *2.3.1 Burrow selection and classification .*

121        An extensive burrow survey was performed during April 2015. A stratified random

122    sampling approach was applied, with the reserve's management blocks being used as strata.

123    Within each management block a team of eight to 14 people systematically searched a randomly

124    selected 1 ha plot for burrows. A total of 32 ha, or approximately 1% of the reserve, was

125    searched in this manner. To distinguish burrows from feeding scrapes and natural depressions,

126    only excavations with a tunnel-shape structure and roof were recorded. Because no other

127    medium-sized burrowers occur at Rietvlei, all burrows large enough to shelter an aardvark were

128    considered aardvark burrows. A total of 203 burrows, distributed across the reserve, were

129    identified in this manner. Of these, 60 burrows were randomly selected for sampling during April

130    and May 2015.

131        Each burrow was paired with an undisturbed control site 2 m from the burrow entrance in

132    a direction perpendicular to the orientation of the burrow. In addition to burrows and controls,

133    measurements were also taken on the mounds of excavated soil associated with each burrow.

134    Burrows and mounds were classified as fresh (i.e. recently or currently in use), abandoned, or

135    collapsed, based on the level of soil disturbance (see Figure 1). Fresh burrows showed evidence

136    of recent soil disturbance, including animal tracks and scrapes. Abandoned burrows showed no

137    signs of recent soil disturbance but still had an intact structure, while in collapsed burrows a

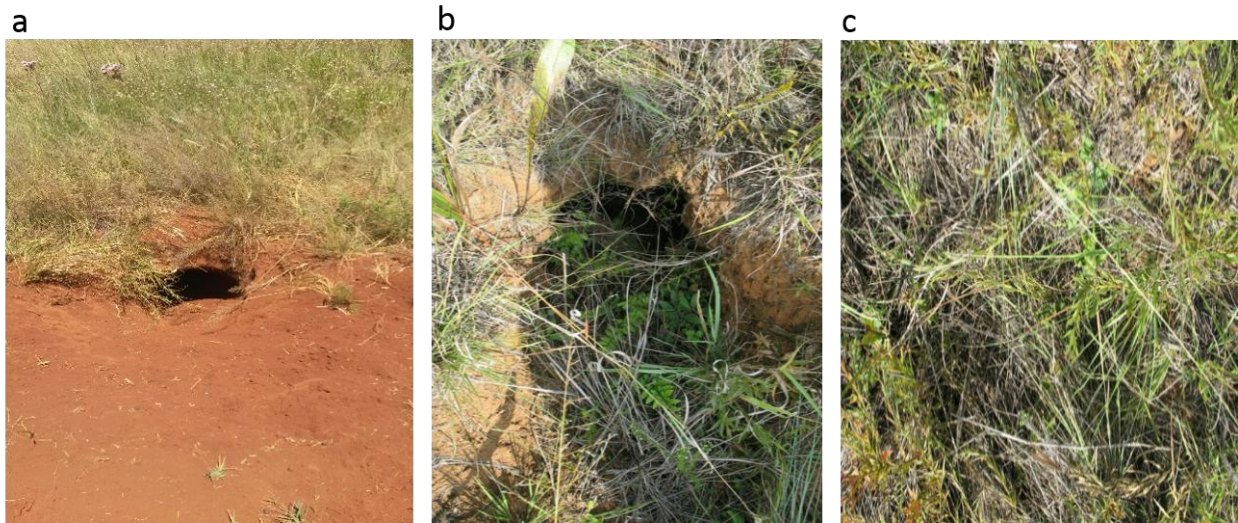138    portion (or portions) of the tunnel roof had fallen in.

Fig 1. The three stages of burrow degradation: a.) a fresh burrow, with evidence of recent soil excavation, b.) an overgrown, abandoned burrow and c.) a collapsed burrow, where vegetation cover is obscuring a fallen in section of the tunnel roof

### 2.3.2. Field data collection

At each burrow, mound and control, the following soil measurements were taken: (1) volumetric water content within the top 3.8 cm of the soil (TDR 300 soil moisture meter; Spectrum technologies; USA), (2) soil resistance to penetration at 5 mm depth (as a measure of soil compaction) using a hand-held pocket penetrometer (Geotest; USA) and (3) instantaneous soil temperature at 2 cm depth using a hand-held RTD thermometer (Eutech Instruments; RSA). From each burrow, mound and control, the top 2 cm of the soil profile was sampled over an area of 100 cm$^2$ for seed bank analyses. A further 1.3 L of topsoil (collecting down to a maximum depth of 10 cm) was collected from half of the sites for soil fertility analyses. Lastly, all vascular plant species were identified within a 2500 cm$^2$ quadrat and their aerial cover estimated. At the

burrow, samples and measurements were taken below the edge of the tunnel roof, avoiding more heavily shaded areas deeper within the burrow, where plants are unlikely to establish. The approximate centres of mounds were sampled.

### 2.3.3. *Soil seed bank and fertility experiments*

A germination experiment was conducted to compare the size and richness of the soil seed banks between burrows, mounds and controls. The topsoil samples collected for seed bank analyses were placed in pots on top of a layer of coarse quartz sand. Pots were kept under shelter and were watered every second (summer and spring) or third (winter) day and monitored for six months (June to November 2015). Individual pot positions were randomized every two weeks. Seedlings were removed once they could be identified to genus level (or family for grasses).

A phytometer experiment was conducted using radishes (*Raphanus sativus*) to estimate soil fertility (see Dietrich et al., 2013). A standard volume of soil (c. 300 ml) was placed in pots on top of c. 100 ml quartz sand, and two radish seeds were planted in each pot. Pots were kept under shelter outside and were watered every second day. In pots where both seeds germinated, the later emerging seedling was removed. Neither of the two seeds germinated in one pot, and that sample was excluded from further analyses. Pot positions were randomized every two weeks. After three months the roots and leaves of all germinated radishes were harvested, dried for 7 days at 70 °C and weighed, with total radish biomass serving as a measure of soil fertility.

## 2.4 *Statistical analyses*

Generalized linear mixed effect models were used to analyse the data, assuming a Poisson distribution for species richness and abundance data, a binomial distribution for cover and soil compaction data, and a Gaussian distribution for all other response variables. Microsite, burrow age and time of day (only for analysis of temperature) were included as fixed effects, with burrow location included as a random effect to account for spatial clustering of sets of microsites (i.e. the spatial grouping of a burrow and its associated mound and control plot). The interaction between burrow age and microsite type (and microsite type and time of day for analyses of temperature) was also tested, but was only retained when the interaction term significantly improved the model.

The influence of microsite type and burrow age on species composition was examined using non-metric multidimensional scaling (NMDS) and statistically tested using a permutational multivariate analysis of variance (PERMANOVA). Above-ground vegetation composition data were standardized using the Wisconsin double standardization (as suggested by Oksanen et al., 2016). The seedling composition data were not similarly transformed as it caused non-convergence of the NMDS algorithm. $Chi^2$ analyses were used to test if the occurrence patterns of common species (defined as occurring in more than three quadrats) differed from an even distribution.

All analyses were conducted using R statistical software (R Core Team, 2016), with the use of the vegan package (Oksanen et al., 2016) for NMDS and PERMANOVA analyses and the lme4 package (Bates et al., 2015) for generalized linear mixed effect models.

# 3. Results

Soil temperature differed significantly between burrows, mounds and controls, with this effect depending on the time of the day (Figure 2, Table 1). Burrow entrances were cooler than mounds or controls, with the temperature differences between microsites being smaller during the cooler part of the day. Both soil moisture and soil compaction were significantly lower at burrows than mounds and controls (Figure 3a, b, Table 1). Burrow age did not significantly affect soil temperature, moisture or compaction (Table 1).
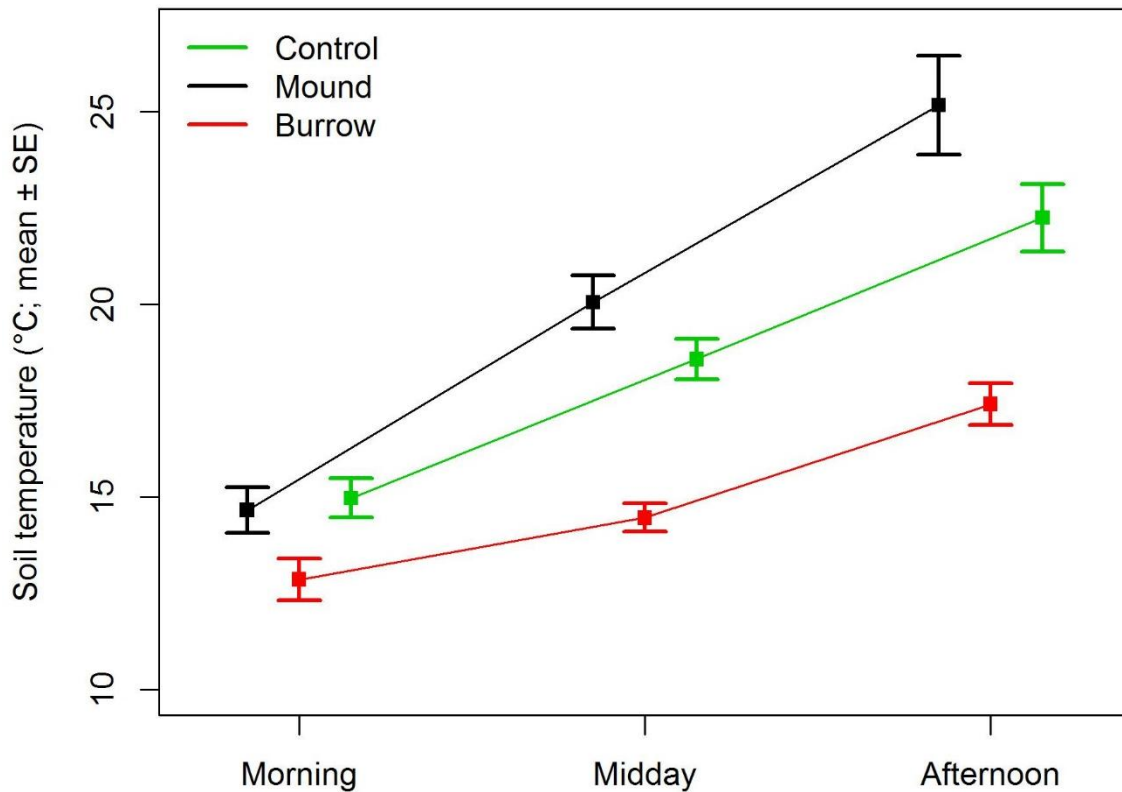


Fig 2. Soil temperature progression at the three microsites. Morning: 07:15 to 10:05, Midday: 10:05 to 12:10, Afternoon: 12:10 to 15:45
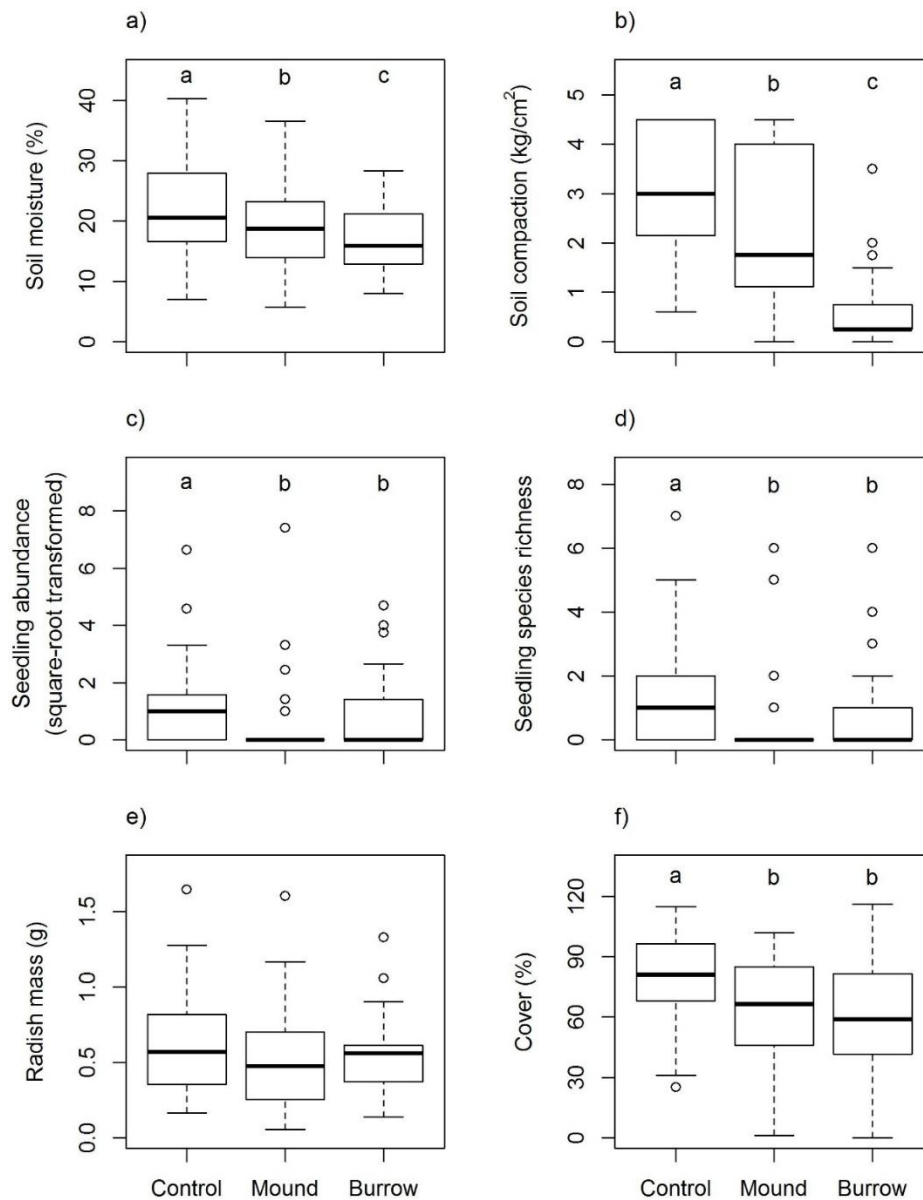
Fig 3. Soil and vegetation characteristics at the three microsites: a.) soil moisture, b.) soil
compaction, c.) seedling abundance, d.) seedling species richness, e.) radish biomass and f.) total
plant cover. Significant differences between microsites are indicated by lower case letters.
Shown are median values (thick lines), interquartile range (box) and range (whiskers). Empty
circles are outliers.

Table 1: Results from generalized linear mixed effect models of the effects of burrowing on soil and vegetation characteristics. Models also included burrow location as a random effect to account for the spatial clustering of sets of microsites at each burrow.

| Response variable | Fixed effects | $\text{Chi}^2$ | df | p |
|---|---|---|---|---|
| Temperature | Microsite | 135.74 | 2 | *** |
| | Time | 103.19 | 1 | *** |
| | Age | 2.82 | 2 | |
| | Microsite:Time | 23.80 | 2 | *** |
| Moisture | Microsite | 51.31 | 2 | *** |
| | Age | 2.84 | 2 | |
| Compaction | Microsite | 25.62 | 2 | *** |
| | Age | 2.11 | 2 | |
| Seedling abundance | Microsite | 36.18 | 2 | *** |
| | Age | 1.31 | 2 | |
| Belowground species richness | Microsite | 19.73 | 2 | *** |
| | Age | 1.21 | 2 | |
| Radish biomass | Microsite | 1.27 | 2 | |
| | Age | 2.42 | $1^{\#}$ | |
| Aboveground vegetation cover | Microsite | 17.01 | 2 | *** |
| | Age | 5.62 | 2 | |
| Aboveground species richness | Microsite | 12.79 | 2 | ** |
| | Age | 6.02 | 2 | * |
| | Microsite:Age | 15.01 | 4 | ** |

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

[#] No samples from fresh burrows were used for the phytometer experiment.

Seedlings germinated from 69 of the 180 soil seed bank samples, and analyses of seed bank characteristics were limited to these pots. Significantly more seedlings germinated from the control plots than either the burrows or mounds (Figure 3c, Table 1). However, the number of seedlings did not differ between burrows and mounds, and burrow age did not affect the number of seedlings (Table 1). In addition, significantly more species (Figure 3d) germinated at controls than at burrows or mounds (again, with no difference between burrows and mounds, and no

effect of burrow age; Table 1). Lastly, seed bank composition (Figure 4a, Table 2) and radish biomass (Figure 3e, Table 1) did not differ significantly between burrows, mounds and controls or age classes.
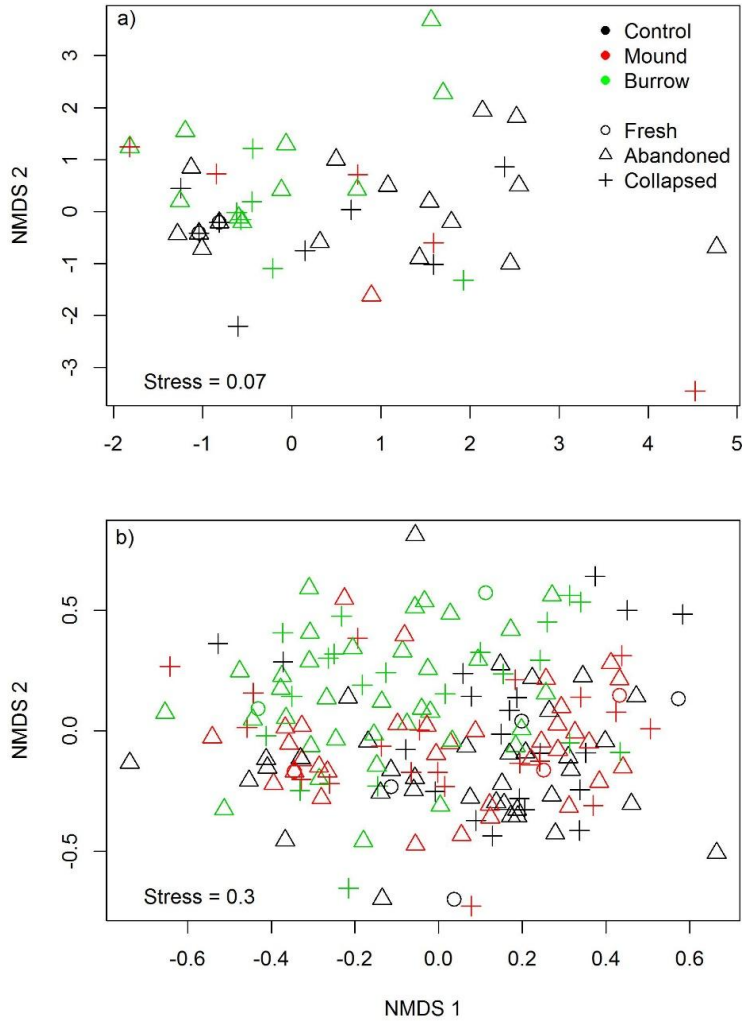


Fig 4. Species composition of a.) seedlings and b.) standing vegetation at the three microsites (indicated by symbol colour) and for the three burrow age classes (indicated by symbol shape).

Table 2: Results from PERMANOVA analyses of the effects of burrowing mammals on above- and below-ground species composition.

| | Fixed effect | F | $R^2$ (%) | p |
|---|---|---|---|---|
| Above-ground | Microsite | 4.14 | 4.54 | *** |
| | Age | 1.73 | 1.90 | * |
| Below-ground | Microsite | 1.44 | 4.17 | |
| | Age | 1.18 | 4.42 | |

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Aboveground vegetation cover differed significantly between burrows, mounds and controls, with mean cover being lowest in burrows and highest in control plots (Figure 3f, Table 1). Burrow age had no effect on vegetation cover. Both microsite (burrow, mound, control) and burrow age had a significant effect on species richness, with the impact of microsite depending on burrow age (Table 1). Fresh burrows and mounds had fewer species than either abandoned or collapsed burrows or mounds (Figure 5). In addition, fresh burrows had fewer species than their control sites, with the opposite observed at abandoned and collapsed burrows (Figure 5). Species composition differed significantly (albeit weakly) between burrows, mounds and controls, and was also affected by burrow age (Figure 4b, Table 2).
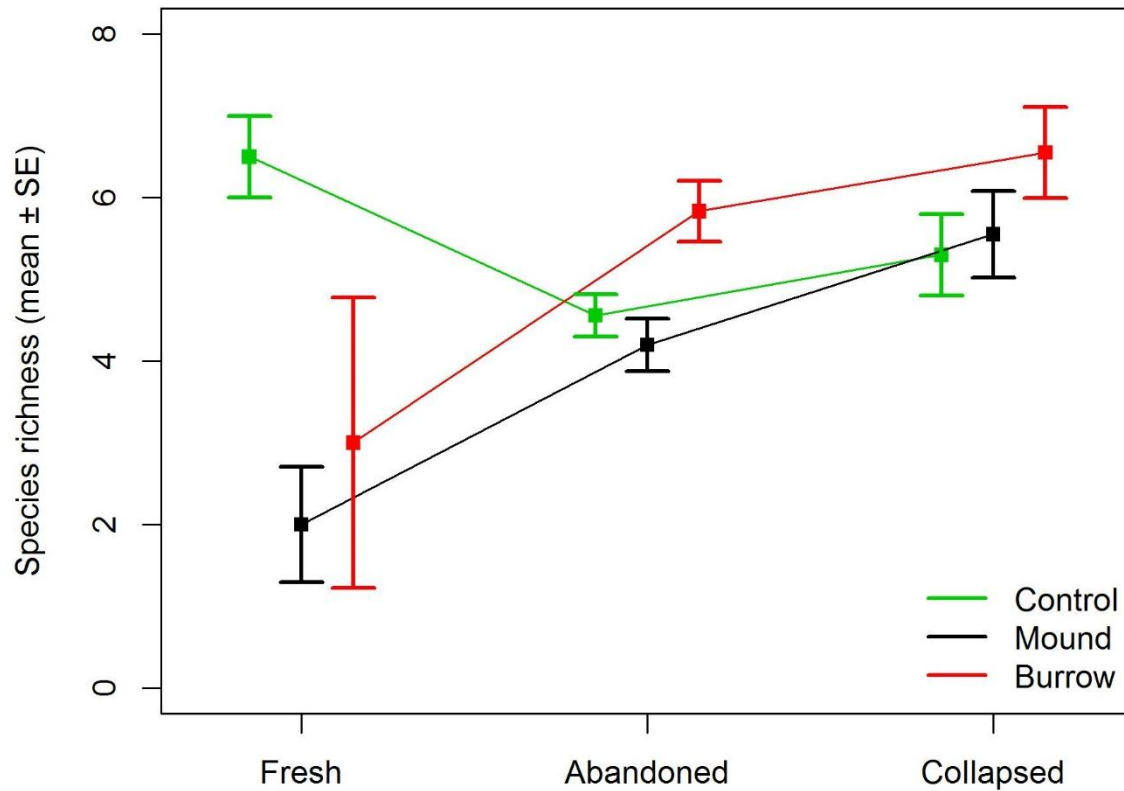
Fig 5. Species richness at the three microsites for the three burrow age classes.

A total of 166 species were recorded in the aboveground vegetation, of which only 46 species occurred in more than three plots (Table 3). Eight species were disproportionately often associated with burrows (Table 3). Of these eight species, two were alien species which were both recorded more frequently than expected at burrow entrances. Another two species occurred exclusively at burrows (two fern species; *Cheilanthes viridis* and *Pellaea calomelanos*). Only one species was found significanly less often at burrows than at mounds and controls (Table 3).

Table 3: Average cover (%) of common plant species (i.e. >3 occurrences) occurring at burrows, mounds and controls (with the total number of occurrences per microsites in parentheses). Plant species shown in bold are unique to a specific microsite. n = 60 for each microsite. Significant p-values indicate species where a species' occurrence across microsites differed significantly from what would be expected by chance (as determined by a $Chi^2$ analysis).

| Plant species | Burrow | Mound | Control | p |
|---|---|---|---|---|
| *Acalypha angustata* | 1.3 (6) | 1.4 (8) | 1.0 (8) | |
| *Aristida congesta* | 0.1 (2) | 0.1 (1) | 0.2 (1) | |
| *Bidens bipinnata* | 0.4 (5) | 0.1 (4) | 0.1 (2) | |
| *Bidens pilosa* | 0.8 (5) | 0.5 (2) | 0.02 (1) | |
| *Campuloclinium macrocephalum* | 0.9 (12) | 0.4 (5) | 0.4 (5) | |
| ***Cheilanthes viridis*** | **6.4 (13)** | 0.0 (0) | 0.0 (0) | *** |
| *Commelina africana* | 0.3 (3) | 0.2 (3) | 0.2 (1) | |
| *Conyza bonariensis* | 1.3 (9) | 0.5 (5) | 0.2 (2) | |
| *Conyza podocephala* | 0.6 (6) | 0.5 (7) | 1.0 (7) | |
| *Conyza sp.1* | 0.7 (6) | 0.1 (2) | 0.0 (0) | * |
| *Cymbopogon excavates* | 0.4 (3) | 1.2 (3) | 3.1 (9) | |
| *Cynodon dactylon* | 8.1 (26) | 12.3 (27) | 5.3 (16) | |
| *Eragrostis chloromelas* | 2.4 (15) | 8.7 (25) | 17.8 (36) | ** |
| *Eragrostis curvula* | 0.2 (1) | 2.4 (5) | 1.4 (4) | |
| *Eragrostis lehmanniana* | 3.9 (17) | 11.5 (25) | 13.0 (21) | |
| *Eragrostis plana* | 0.1 (2) | 0.3 (1) | 0.1 (1) | |
| *Eragrostis tef* | 0.1 (1) | 0.4 (3) | 4.2 (7) | |
| *Helichrysum rugulosum* | 1.2 (6) | 2.3 (10) | 2.9 (12) | |
| *Hermania depressa* | 0.02 (1) | 0.4 (2) | 0.1 (1) | |
| *Heteropogon contortus* | 0.3 (3) | 1.0 (1) | 1.8 (5) | |
| *Hilliardiella oligocephala* | 1.8 (11) | 1.0 (6) | 0.7 (8) | |
| *Hyparrhenia hirta* | 1.4 (6) | 0.8 (7) | 2.0 (6) | |
| *Hypoxis iridifolia* | 0.0 (0) | 0.3 (2) | 0.4 (3) | |
| *Hypoxis sp.1* | 0.7 (3) | 0.4 (2) | 0.3 (3) | |
| Morpho *sp.1* | 0.7 (4) | 0.3 (1) | 0.0 (0) | |
| Morpho *sp.2* | 1.1 (4) | 1.4 (5) | 1.2 (4) | |
| *Oenothera rosea* | 0.4 (4) | 0.1 (2) | 0.2 (5) | |
| *Oenothera sp* | 0.4 (4) | 0.1 (1) | 0.0 (0) | |
| *Oxalis corniculata* | 1.3 (23) | 0.3 (3) | 0.3 (6) | *** |
| *Panicum natalense* | 0.5 (3) | 1.4 (5) | 2.1 (4) | |
| *Pelargonium luridum* | 0.1 (2) | 0.02 (1) | 0.1 (1) | |
| ***Pellaea calomelanos*** | **0.4 (4)** | 0.0 (0) | 0.0 (0) | * |
| Poaceae *sp.1* | 1.1 (3) | 1.0 (1) | 4.7 (4) | |

| | | | | |
|---|---|---|---|---|
| *Pollichia campestris* | 1.2 (6) | 0.0 (0) | 0.02 (1) | ** |
| *Schkuhria pinnata* | 0.4 (4) | 0.7 (4) | 0.3 (2) | |
| *Senecio inornatus* | 0.5 (7) | 0.7 (6) | 1.1 (12) | |
| *Senecio sp.1* | 0.5 (9) | 0.02 (1) | 0.1 (2) | ** |
| *Setaria sphacelata* | 0.02 (1) | 0.2 (3) | 0.1 (1) | |
| *Solanum tomentosum* | 0.3 (5) | 0.2 (6) | 0.2 (5) | |
| *Tagetes minuta* | 1.1 (13) | 0.2 (4) | 0.03 (2) | ** |
| *Teucrium trifidum* | 0.3 (4) | 0.02 (1) | 0.0 (0) | |
| *Themeda triandra* | 0.3 (1) | 1.6 (4) | 0.7 (2) | |
| *Thesium utile* | 0.1 (2) | 0.3 (2) | 0.0 (0) | |
| *Urochloa panicoides* | 0.1 (2) | 0.3 (1) | 0.02 (1) | |
| *Verbena bonariensis* | 5.0 (15) | 1.0 (8) | 0.5 (3) | ** |
| *Verbena brasiliensis* | 0.6 (5) | 0.5 (3) | 0.5 (4) | |

## 4. Discussion

Burrows, mounds and control sites differed significantly in abiotic and biotic characteristics, highlighting how burrowing animals can increase fine-scale heterogeneity within a landscape. In addition, some of the effects of burrowing were dependant on the stage of burrow degradation. Therefore, in this system where burrows are continuously being created and abandonded, aardvark appear to be creating a shifting mosaic of habitat conditions.

Fresh burrows and mounds had lower species richness than controls, presumably as a result of the physical digging action and unearthing of roots at burrow entrances and burial of vegetation at mounds. However, in contrast, abandoned and collapsed burrows had higher plant species richness than their adjacent mounds and control sites. Therefore, as burrows are abandoned and collapse, the favourable environmental conditions associated with burrows outweigh the negative effects of the disturbance of the burrowing action. Our results are in agreement with Gutterman et al. (1990), who found that plant species richness, biomass and density reached maximum levels once porcupine diggings were partially filled.

7          This influence of microsite type and burrow age is also evident in species composition, where both variables had significant, albeit small, impacts on the plant community composition. Interestingly, there was not an effect of burrow age on plant cover, with burrows and mounds having consistently lower vegetative cover than controls. This suggests, since cover and richness are not tighly linked within burrows in this system, that within older burrows the higher species richness may be driven by a high total abundance of small individual plants (i.e. allowing the co-existence of more species than would be possible if the plants were larger).

A number of mechanisms can potentially account for these engineering effects. Burrows may trap seeds (Boeken et al., 1995), change soil fertility (Yu et al., 2017), create favourable microclimates (Pike and Mitchell, 2013), and provide protection from herbivory and/or fires. We explored the first three mechanisms, but cannot exclude protection from herbivores or from frequent winter fires as an engineering mechanism. Our results do not indicate that burrows trap seeds, in contrast to, for example, Bragg (2005). In fact, we found the opposite to be true, as a higher abundance and richness of seedlings germinated from the mound and control soils than the burrow soils. The results from the phytometer experiment suggest that the lower abundance of germinated seeds from burrow soils cannot be ascribed to differences in soil fertility, but are probably a true reflection of smaller seed banks within burrows, at least in the entrance areas of the burrow where we measured. Since burrows at our study site often had steeply sloping entrances, it is possible that burrows actually trapped more seeds, but that these seeds moved further into the deeply shaded portion of burrows where plant establishment is not possible due to lack of sunlight. For aardvark, and generally for other burrowing mammals, excavations made for nesting and denning (i.e. burrows) are typically deeper, tunnel-like structures, while foraging

scrapes and diggings are shallower and smaller. Differences between the size and structure of these different types of excavations likely strongly affect their ecological impacts, and highlight how differences in engineered structures must be accounted for when examining the landscape-level influence of an ecosystem engineer.

Although we did not test for specific soil nutrients, the phytometer results suggest that there are no differences in soil fertility between burrow, mound and control soils. This is in contrast to results from Yu et al. (2017), who found that pika (*Ochotona curzoniae*) burrowing has beneficial effects on soil nutrient storage, and Kurek et al. (2014), who showed that badger and fox burrowing increases nutrient availability. Eldridge and Whitford (2009) attribute the build-up of nutrients in areas where burrowing animals congregate to the accumulation of faeces, food and nesting material. Again, because we took our measurements at the relatively steep entrances of burrows, an accummulation mechanism is unlikely. In addition, aardvark feed mostly on termites and are not known to take other food into their burrows or defecate in their burrows. Another potential mechanism of nutrient increase at burrows is through the redistribution of nutrients from lower soil horizons (Kurek et al., 2014). This mechanism is obviously only effective in areas where nutrient concentrations increase with depth (Eldridge and Whitford, 2009), which is possibly not the case in our mesic grassland.

We attribute the increase in plant species richness in general, and the distribution of the two fern species specficially, to the physical changes in soil conditions associated with aardvark burrows. Indeed, our results show that burrows provide a cooler environment with less compact soils, providing safe sites (sensu Harper, 1977) and favourable conditions for ferns to establish. However, in contrast to findings from Whittington-Jones et al. (2011), lower soil moisture values

were found at aardvark burrows than mounds and controls. Again, this could be a result of the location of the measurements within the burrows, i.e. on the steep entranceways where water possibly dissipates more easily into the burrow. Importantly, although soil moisture was higher at mounds and controls, ferns could not establish here, suggesting that the temperature amelioration provided by burrows plays a crucial role in the establishment of ferns. An untested alternative (and potentially complementary) mechanism that could explain why ferns are restricted to burrow entrances (and could also contribute to higher species richness at that microsite) is that burrows provide species with protection from herbivores (which may be relatively unimportant for ferns) and fires (which occur annually or biennially in the study site).

Two of the six species significantly associated with burrows were alien invasive species (*Tagetes minuta* and *Verbena bonariensis*). Therefore, in addition to providing a favourable habitat for less common species to establish, the disturbance associated with burrows may also provide opportunities for some exotic species to establish. The ability of alien species to outcompete many native species in areas of increased disturbance is well-documented (e.g. Lake and Leishman, 2004; Haussmann et al., 2013), and in the case of aardvark burrowing, we suggest that the physical digging action may create better colonization opportunities for invasive species than some less resilient native species. Our results further show that aardvark burrows do not change the soil seed bank composition, suggesting that plant species are not selectively trapped, but rather selectively favoured by the improvement of germination and establishment conditions. Burrowing therefore creates patches with a distinct microclimate, increasing microscale heterogeneity in the landscape and favouring the establishment of a different combination of species to undisturbed microsites.

In addition to the impacts of burrowing on the physical condition of the soil and the vegetation, burrowing activities are likely to have other biotic and abiotic impacts. Indeed, these effects of aardvark burrows on landscape heterogeneity, and the resulting consequences for biological diversity, represent only one pathway through which this species alters ecosystem processes and the associated ecosystem service. For example, aardvark digging may reduce biological methane and carbon dioxide production associated with termite activity (Zimmerman et al., 1982; Wood, 1988), as a result of digging increasing soil aeration . Therefore, while accurate for the impact of aardvark on soil and vegetation characteristics, the results reported here may underestimate the total impact of this burrowing activity across other ecosystem properties and processes.

## 5. Conclusions

Burrowing by aardvark significantly altered abiotic conditions and biotic community characteristics, with burrow entrances, mounds of excavated soils and undisturbed control sites differing in several ways. Although we recognize the value of contrasting burrowed vs unburrowed landscapes (e.g. Gálvez-Bravo et al., 2011), it is important to note that even within a burrowed area fine-scale heterogeneity exists due to the burrowing process. This environmental heterogenity (and the knock-on effects for biological diversity) is further enhanced by burrows differing in their stage of degradation, with differences in plant species richness and community composition between fresh and older burrows. As a result, burrowing generates both spatial and temporal variation within this environment, creating a shifting mosaic of habitats differing in abiotic characteristics.

From an applied perspective, accurately predicting how climate change (and other forms of global environmental change) will influence ecosystem engineers and their interactions with other species is an important challenge. While species distribution models and mechanistic approaches may provide robust predictions about how ecosystem engineers themselves will respond to changing conditions (Menge et al., 2008; Zippay and Helmuth, 2012; Bean et al., 2014), focusing on the mechanisms through which engineers affect co-occurring species offers a potentially productive approach for examining how their ecological influence may change. In this system, for example, amelioration of physical environmental conditions appears to be an important mechanism through which aardvark impact plant species. This suggests that, under warmer conditions, the ecological importance of microclimatic buffering may increase, with burrows being more important as refugia against extreme conditions (following e.g. Cavieres et al., 2002).

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# References

Bates, D., Mächler, M., Bolker, B.M., Walker, S.C., 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software. 67, 1–48.

Bean, W.T., Stafford, R., Butterfield, H.S., Brashares, J.S., 2014. A multi-scale distribution model for non-equilibrium populations suggests resource limitation in an endangered rodent. PLoS ONE. 9, 1–9.

Boeken, B., Shachak, M., Gutterman, Y., Brand, S., 1995. Patchiness and disturbance: plant community responses to porcupine diggings in the central Negev. Ecography. 18, 410–421.

Bragg, C.J., Donaldson, J.D., 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, 261–275.

Butler, D.R., 1992. The grizzly bear as an erosional agent in mountainous terrain. Zeitschrift für Geomorphologie. 36, 179–189.

Cavieres, L., Arroyo, M.T-K., Peňaloza, A., Molina-Montenegro, M., Torres, C., 2002. Nurse effect of *Bolax gummifera* cushion plants in the alpine vegetation of the Chilean Patagonian Andes. Journal of Vegetation Science. 13, 547–554.

Ceballos, C., Ehrlich, P.R., 2009. Discoveries of new mammal species and their implications for conservation and ecosystem services. Proceedings of the National Academy of Sciences of the United States of America. 106, 3841–3846.

Desbiez, A.L.J., Kluyber, D., 2013. The role of giant armadillos (*Priodontes maximus*) as physical ecosystem engineers. Biotropica. 45, 537–540.

Dietrich, A.L., Nilsson, C., Jansson, R., 2013. Phytometers are underutilised for evaluating ecological restoration. Basic and Applied Ecology. 14, 369–377.

Eldridge, D.J., Simpson, R., 2002. Rabbit (*Oryctolagus cuniculus* L.) impacts on vegetation and soils, and implications for management of wooded rangelands. Basic and Applied Ecology. 3, 19–29.

Eldridge, D.J., Whitford, W.G., 2009. Badger (*Taxidea taxus*) disturbances increase soil heterogeneity in a degraded shrub-steppe ecosystem. Journal of Arid Environments. 73, 66–73.

Gálvez-Bravo, L., López-Pintor, A., Rebollo, S., Gómez-Sal, A., 2011. European rabbit (*Oryctolagus cuniculus*) engineering effects promote plant heterogeneity in Mediterranean dehesa pastures. Journal of Arid Environments. 75, 779–786.

Gálvez-Bravo, L., Belliure, J., Rebollo, S., 2009. European rabbits as ecosystem engineers: warrens increase lizard density and diversity. Biodiversity and Conservation. 18, 869–885.

Grinnell, J., 1923. The burrowing rodents of California as agents in soil formation. Journal of Mammalogy. 4, 137–149.

Gutterman, Y., Golan, T., Garsani, M., 1990. Porcupine diggings as a unique ecological system in a desert environment. Oecologia. 85, 122–127.

Harper, J. L., 1977. Population biology of plants. Academic Press, London.

Haussmann, N.S., Rudolph, E.M., Kalwij, J.M., McIntyre, T., 2013. Fur seal populations facilitate establishment of exotic vascular plants. Biological Conservation. 162, 33–40.

James, A.I., Eldridge, D.J., Hill, B.M., 2009. Foraging animals create fertile patches in an Australian desert shrubland. Ecography. 32, 723–732.

Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. Oikos. 69, 373–386.

Kingdon, J., 1971. East African Mammals. An Atlas of Evolution in Africa, Vol. 1, first ed. Academic Press Inc., London and New York.

Kurek, P., Kapusta, P., 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, 1–11.

Lake, J.C., Leishman, M.R., 2004. Invasion success of exotic plants in natural ecosystems: the role of disturbance, plant attributes and freedom from herbivores. Biological Conservation. 117, 215–226.

Laundre, A.J.W., 1993. Effects of small mammal burrows on water infiltration in a cool desert environment. Oecologia. 94, 43–48.

Marais, R., 2004. A plant ecological study of the Rietvlei Nature Reserve, Gauteng Province. M.Agric dissertation, University of the Free State, Bloemfontein.

Melton, D.A., 1976. The biology of aardvark (Tubulidentata-Orycteropodidae). Mammal Review. 6, 75–88.

Menge, B.A., Chan, F., Lubchenco, J., 2008. Response of a rocky intertidal ecosystem engineer and community dominant to climate change. Ecology Letters. 11, 151–162.

Mielke, H.M., 1977. Mound building by pocket gophers (Geomyidae): their impact on soils and vegetation in North America. Journal of Biogeography. 4, 171–180.

Milton, S.J., Dean, W.R.J., 2001. Seeds dispersed in dung of insectivores and herbivores in semi-arid southern Africa. Journal of Arid Environments. 47, 465–483.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, L., Solymos, P., Stevens, M.H.H., Wagner, H., 2016. Package 'vegan', version 2.4 - 1. https://cran.r-project.org/web/packages/vegan/vegan.pdf (Accessed February 2017)

Pike, D.A., Mitchell, J.C., 2013. Burrow-dwelling ecosystem engineers provide thermal refugia throughout the landscape. Animal Conservation. 16, 694–703.

R Development Core Team, 2016. R: A Language and Environment for Statistical Computing. Version 3.3.2. http://www.R-project.org (Accessed February 2017)

Shachak, M., Brand, S., Gutterman, Y., 1991. Porcupine disturbances and vegetation pattern along a resource gradient in a desert. Oecologia. 88, 141–147.

Skinner, J.S., Smithers, R.H.N., 1990. The Mammals of the Southern African Subregion, first ed. University of Pretoria Press, Pretoria.

Smithers, R.H.N., 1971. The Mammals of Botswana. Memoirs of the National Museum of Rhodesia, no. 4. National Museums of Rhodesia, Harare.

Thorn, C.E., 1978. A preliminary assessment of the geomorphic role of pocket gophers in the alpine zone of the Colorado Front Range. Geografiska Annaler. 60A, 181–187.

Wesche, K., Nadrowski, K., Retzer, 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, 665.

Whitford, W.G., Kay, F.R., 1999. Biopedturbation by mammals in deserts: a review. Journal of Arid Environments. 41, 203–230.

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

Wiegand, T., Dean, W.R.J., Milton, S.J., 1997. Simulated plant population responses to small-scale disturbances in semi-arid shrublands. Journal of Vegetation Science. 8, 163–176.

Wood, T.G., 1988. Termites and the soil environment. Biology and Fertility of Soils. 6, 228–236.

Yair, A., 1995. Short and long term effects of bioturbation on soil erosion, water resources and soil development in an arid environment. Geomorphology. 13, 87–99.

Yu, C., Pang, X.P., Wang, Q., Jin, S.H., Shu, C.C., Guo, Z.G., 2017. Soil nutrient changes induced by the presence and intensity of plateau pika (*Ochotona curzoniae*) disturbances in the Qinghai-Tibet Plateau, China. Ecological Engineering. 106, 1–9.

Zimmerman, J.P., Greenberg, J.P., Wandiga, S.O., Crutzen, P.J., 1982. Termites: a potentially large source of atmospheric methane, carbon dioxide, and molecular hydrogen. Science. 218, 563–565.

Zippay, M.L., Helmuth, B., 2012. Effects of temperature change on mussel, *Mytilus*. Integrative Zoology. 7, 312–327.