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Mammal burrowing in discrete landscape patches further increases soil and vegetation heterogeneity in an arid environment

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ABSTRACT

Burrowing mammal disturbances often create heterogeneity within landscapes. Aardvark (*Orycteropus afer*) are extensive burrowers in sub-Saharan ecosystems and play an important role in structuring communities in arid environments. The burrowing activities of aardvark are often associated with heuweltjies (nutrient-rich mounds differing in soil and vegetation characteristics from surrounding areas) which contribute strongly to landscape heterogeneity. This study determined the impact of aardvark burrowing and heuweltjies on soil and vegetation characteristics. Data were collected at four microsites: 1) at each burrow entrance on a heuweltjie, 2) on the burrowed heuweltjie (i.e. heuweltjie with an aardvark burrow), 3) on the nearest unburrowed heuweltjie, and 4) on the adjacent matrix. Aardvark burrowing and heuweltjies both impacted the soil and vegetation characteristics. Despite having more moderate thermal regimes than other microsites, burrow entrances were largely unvegetated. Although aardvark burrowing did not affect plant species richness on heuweltjies, it decreased vegetation cover. Vegetation composition differed between heuweltjies and the matrix, and this dissimilarity was increased further by aardvark burrowing. As a result, the combined effect of burrowing mammals and heuweltjies increases landscape heterogeneity. This emphasises the important ecosystem engineering role that aardvark have in arid environments, even where considerable abiotic heterogeneity already exists.

1. Introduction

Environmental heterogeneity plays an important role in ecosystem dynamics and contributes to the maintenance of species diversity (Butler and Sawyer, 2012; Shea et al., 2004; Tews et al., 2004; Zaitlin and Hayashi, 2012) and ecosystem functioning (Whitford and Kay, 1999). Patch creation, either through abiotic or biotic processes, increases heterogeneity in the landscape by altering local environmental conditions, creating mosaics of different microhabitats (Turner, 2005). Disturbances, including fires, floods and intense herbivory may be key drivers of heterogeneity across a range of spatio-temporal scales within many ecosystems (Turner, 2005). At relatively small spatial scales, burrowing animals can also be important agents of disturbance (Bragg et al., 2005; Whitford and Kay, 1999), creating patchiness by displacing sediment (Butler and Sawyer, 2012; Whitford and Kay, 1999) and redistributing resources in the landscape (Hansell, 1993). Through their burrowing activity, these animals may displace more soil than abiotic processes in some landscapes (Black and Montgomery, 1991; Thorn, 1978), potentially playing a key role in increasing environmental heterogeneity.

Habitat patches created by burrowing may differ strongly in soil structure, fertility and water-holding capacity from the adjacent undisturbed substrate (Zaitlin and Hayashi, 2012). In addition, burrows can provide thermal and moisture refugia, with burrow temperature and relative humidity often differing substantially from ambient conditions (Kinlaw, 1999). As a result, burrows generally support unique plant communities within landscapes (Whitford and Kay, 1999) and certain burrowing animals are considered to be ecosystem engineers (Butler and Sawyer, 2012; Zaitlin and Hayashi, 2012). Indeed, through burrowing these animals physically alter their environment and potentially influence

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the distribution and abundance of species (Kurek et al., 2014; Parsons et al., 2016). For example, pocket gophers are important ecosystem engineers as their burrowing redistributes soil nutrients, increases plant species diversity in the landscape, and affects the composition of plant and insect communities (Huntly and Inouye, 1988). Burrowing mammals therefore create new (and potentially unique) microhabitats that may be preferentially utilized by a variety of plant and animal species.

The role of burrowing mammals as ecosystem engineers is especially important in drylands (Kinlaw, 1999; Wesche et al., 2007; Wilby et al., 2001), where burrows provide a more favourable microclimate than ambient conditions by buffering thermal extremes (Anderson and Richardson, 2005; Whittington-Jones et al., 2011) and increasing relative humidity (Whittington-Jones et al., 2011). Seed germination and seedling establishment in harsh environments may be enhanced within burrows due to the accumulation of water and their generally moister, cooler environment (Gutterman et al., 1990). Seed germination may further be improved by the accumulation of organic matter (e.g. insect frass and mammal dung) in burrows in arid areas where resources are scarce (Dean and Milton, 1991). Many animals also benefit from sheltering within burrows in arid environments. For example, the southern hairy-nosed wombat (*Lasiorhinus latifrons*) avoids temperatures outside its thermal tolerance range by sheltering in burrows, simultaneously also minimizing respiratory water loss due to the higher relative humidity within burrows (Shimmin et al., 2002). Burrowing mammals may therefore play a key role in drylands by ameliorating conditions and increasing availability of limiting resources, thereby making conditions more tolerable for some species in arid environments (Crain and Bertness, 2006).

In arid African ecosystems, the aardvark (*Orycteropus afer*) is an important ecosystem engineer due to its extensive burrowing (Dean and Milton, 1991). Aardvark diggings increase seed germination by concentrating soil resources and improving soil conditions (Dean and Milton, 1991; Milton and Dean, 2015). For example, in areas with hard capped soils and sheet wash, diggings alter soil conditions and provide more favourable sites for seed germination by loosening such soils and increasing seed trapping sites (Dean and Milton, 1991). Excavated soil mounds adjacent to aardvark burrows also provide environmental conditions that differ from undisturbed vegetation (Whittington-Jones, 2006). These mounds offer bare soil for colonization by plant species that are not found in the surrounding areas, thereby increasing species diversity at the landscape scale (Whittington-Jones, 2006). By burrowing into the mounds of the seed-harvesting ant (*Messor capensis*), aardvark also affect secondary seed dispersal, increasing the survival of viable cached seeds (Dean and Yeaton, 1992). Furthermore, many dryland insect, reptile, bird and mammal species are dependent on abandoned aardvark burrows for shelter and nesting sites (Milton and Dean, 2015). As a result, disturbances by aardvark promote diversity in shrublands (Dean and Milton, 1991).

In the arid Karoo region of South Africa, large earth mounds, known as "heuweltjies", form nutrient-rich patches within the landscape (Herpel, 2008). The origin of these heuweltjies is contentious, traditionally being ascribed to termite activity (Esler and Cowling, 1995; Milton and Dean, 1990; Picker et al., 2007), but more recently attributed to differential erosion (Cramer et al., 2012). Heuweltjies are characterized by soil properties markedly different from the surrounding areas, having higher calcium carbonate levels (McAuliffe et al., 2014), higher pH, and a finer topsoil (Kunz et al., 2012) than their surroundings. The vegetation of heuweltjies is also distinctly different from that of the surrounding areas (Esler and Cowling, 1995; McAuliffe et al., 2014; Milton et al., 1992), with associated differences in plant species' performance (including plant growth rate and abundance) and interspecific plant-plant interactions (Riginos et al., 2005). Therefore, similar to aardvark burrowing, heuweltjies increase local heterogeneity and affect species diversity in the landscape. In areas where aardvark and heuweltjies co-occur, the excavating activities of aardvark are often associated with heuweltjies (Milton and Dean, 1990; Moore and Picker, 1991), providing an opportunity to study the combined effects of these two sources of heterogeneity.

The aim of this study was to determine the impact of aardvark burrowing on soil and vegetation characteristics in an arid ecosystem where heuweltjies are prominent features in the landscape. Specifically, we compared the impacts of heuweltjies (by examining unburrowed heuweltjies), and the combined impacts of heuweltjies and aardvark (by examining burrowed heuweltjies) with undisturbed matrix vegetation. Our focus was on both soil (temperature, moisture and compaction) and vegetation (species richness, vegetation cover and composition) properties.

2. Materials and methods

2.1. Study site

Tierberg Karoo Research Centre is a 100 ha research site located in the southern Great Karoo (33°10′S. 22°17′E) with an arid climate (c. 170 mm rainfall per annum; Milton et al., 1992). The mean minimum temperatures are 4.0 °C and 18.3 °C and the mean maximum temperatures are 16.0 °C and 32.4 °C for winter and summer respectively (Booi, 2011). The site is situated within the Sand River Valley on deep colluvium soils, with a mean density of 2.2 heuweltjies/ha (Milton et al., 1992). The research centre is fenced off to exclude domestic livestock and anthropogenic disturbances are minimal.

2.2. Burrow selection

Aardvark burrows were located during April 2015 by traversing the study site. To distinguish burrows from feeding scrapes and natural depressions, only excavations with a tunnel shape structure and a roof were selected (see Appendix A, Fig. A1, electronic version only). Smaller aardvark disturbances (e.g. shallow feeding scrapes) may have an effect on soil and vegetation characteristics (Dean and Milton, 1991; Wiegand et al., 1997), but were not considered for our study. Eleven burrows were found (i.e. 0.11 burrows/ha), but one was occupied by a beehive and no soil measurements could be obtained from it. Therefore, only vegetation descriptors were measured here.

2.3. Soil and vegetation data collection

All 11 burrows were located on heuweltjies and therefore we could not sample burrows away from heuweltjies. Consequently, it was not possible to test interactive effects between heuweltjies and aardvark or to determine the effect of aardvark burrowing in isolation from heuweltjies. As a result, data were collected from four microsites associated with each burrow: 1) at the entrance of the burrow, 2) on the burrowed heuweltjie (i.e. area surrounding the burrow), 3) on the nearest unburrowed heuweltjie, and 4) on the adjacent (i.e. non-heuweltjie) matrix (see Fig. A2). At the burrow entrance, measurements were taken below the edge of the tunnel roof to avoid more heavily shaded areas deeper within the burrow. For both burrowed and unburrowed heuweltjies, data were collected for the entire heuweltjie. Burrowed and unburrowed heuweltjies on average both covered 62 m^2 and did not differ significantly in size (ANOVA: $F = 0.005$, $p > 0.05$). The sampling area of the matrix was chosen *a priori* as 25 m^2, based on species-area curves for the site (Dean and Milton, 1995). Although