Engineering by cape ground squirrels affects biodiversity in semi-arid grasslands

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Highlights

•Environmental modifications by burrowing mammals are critical to semi-arid grasslands.

•Squirrel burrowing led to greater plant cover and richness, particularly in shrubs.

•Small mammal and invertebrate abundance and richness were higher on burrow areas.

•Squirrel activity in semi-arid grasslands increased the plant and animal diversity.

Abstract

Burrowing mammals that disproportionately affect their physical environment, creating habitat and providing resources for other organisms, are considered ecosystem engineers. Such modifications are particularly important in dry grassland environments, where low precipitation and soil nutrients limit plant growth. We tested 5 hypotheses about the impact of Cape ground squirrels (*Xerus inauris*) on plants and animals in a semi-arid grassland of South Africa. At each burrow cluster and paired control site without burrows, we estimated plant cover, height, and richness using quadrats, and invertebrate and small mammal abundance and richness using pit-fall traps and mark-recapture, respectively. We determined nitrogen concentrations in grasses on and off burrows and measured carbon and nitrogen stable isotopes in plants and squirrel hair to determine squirrel diet. Burrows had greater plant cover and richness, particularly more shrubby vegetation, but plant height and nitrogen concentrations did not differ on and off burrows. Invertebrate and small mammal abundance and richness were greater on burrows. Squirrel disturbances in semi-arid grassland improved conditions for disturbance-dependent shrubs, which were rarely consumed by squirrels but are valuable forage for antelope and provide cover for invertebrates and small mammals. By altering habitat for plants reliant on disturbance, Cape ground squirrels enhance grassland biodiversity.

Keywords: *Xerus inauris;* Semi-arid ecosystems; Ecosystem engineer; Semi-fossorial rodents; South Africa

1. Introduction

Temperate grasslands are the most threatened and least protected of all the global terrestrial biomes, as grasslands are transformed by agriculture, mining, and climate change (Carbutt et al., 2017; Prinsloo et al., 2021). Worldwide, only 4.6% of temperate grasslands are protected, despite the high levels of biodiversity in this biome (Carbutt et al., 2017).

Organisms that make strong modifications to their habitat, affecting resource availability, ecological structure, and species composition, are considered ecosystem engineers (Jones et al., 1994). While habitat loss, degradation, and climate change directly impact grasslands, the decline of animal species that are considered ecosystem engineers can have large and cascading impacts on the biodiversity and heterogeneity of native grasslands (Davidson et al., 2012; Lindtner et al., 2019). In particular, many burrowing mammals are considered to be ecosystem engineers because they have critical roles in creating and maintaining biodiversity in grasslands across the world (Davidson et al., 2012). Burrowing activities in arid and semi-arid environments can benefit plants by moving nutrients from deeper soil to the surface, reducing soil hardness, and providing a moister and cooler environment for seeds to germinate (Romero et al., 2015; Davies et al., 2019). Burrowing mammals can also promote plant growth by enriching the surrounding soil through nitrogen in their feces (Wesche et al., 2007; Gharajehdaghipour and Roth, 2018; Mallen-Cooper et al., 2019). Furthermore, burrowing activities can also benefit animals by providing them with refuge from thermal extremes and predators (Waterman, 1995; Ewacha et al., 2016). Several burrowing grassland mammals have been identified as ecosystem engineers, particularly social species where the density of social groups creates distinctive patches of habitat, such as prairie dogs (*Cynomys* spp.; Davidson et al., 2012) in North America, marmots in Eurasia (*Marmota sibirica*; Valkó et al., 2021; Suuri et al., 2022), degus (*Octodon degus*; Übernickel et al., 2021) in South America, and bettongs in Australia (*Bettongia lesueur*; Davidson et al., 2012). In the dry temperate grasslands of southern Africa, only the semi-social springhare (*Pedetes capensis*; Davidson et al., 2012) and the solitary aardvark (*Orycteropus afer*; Louw et al., 2019) have been identified as burrowing ecosystem engineers. The impact of other burrowing ecosystem engineers on the temperate grasslands of this region has not been well established, particularly social species that build large burrow structures that persist over time (Davidson et al., 2012).

In the arid Namib Desert of western Namibia, Cape ground squirrels create important thermal and predator refuge for small mammals and are thus known as ecosystem engineers in this extremely arid environment (median annual rainfall is 94 mm of rainfall, and maximum/minimum temperatures average 39 °C/-0.9 °C; Ewacha et al., 2016). However, the geographic range of this species spans both arid and semi-arid regions across southern Africa (Skurski and Waterman, 2005), including the dry temperate grasslands of central South Africa (Herzig-Straschil, 1978; Skurski and Waterman, 2005). The influence of Cape ground squirrels on biodiversity in semi-arid temperate grasslands has not been investigated, despite the importance of these grasslands and the predicted threats to their persistence (Carbutt and Martindale, 2014; Kusangaya et al., 2014). The impact of specific ecosystem engineers can vary spatio-temporally, even when providing the same engineering functions, with the result that an ecosystem engineer's community impacts may vary across their range (Louw et al., 2019; Übernickel et al., 2021). Thus, although functionally Cape ground squirrels may alter their physical habitat similarly across their range by digging burrows, the impact on other species may vary, particularly in areas with varying temperatures and rainfall (Lindtner et al., 2019; Louw et al., 2019; Lowney and Thomson, 2022).

The objective of our study was to determine the impact of Cape ground squirrels as ecosystem engineers on plant, invertebrate, and small mammal communities in the semi-arid grasslands of South Africa. Cape ground squirrels are social animals living in family groups that dig and occupy clusters of burrows (hereafter called a burrow cluster) segregated by open land with no burrows (Waterman, 1995; Ewacha et al., 2016). These burrow clusters can persist for decades, providing squirrel groups with important refuge from thermal extremes and protection from predators (Waterman, 1995; Ewacha et al., 2016). These diurnal squirrels forage at their burrows early mornings and evenings, consuming mainly bulbs, grasses, seeds, shrubs, and sometimes arthropods (Herzig-Straschil, 1978; Skurski and Waterman, 2005). For the remainder of the day, squirrels move away from their burrow cluster to forage (Waterman, 2002).

We hypothesized that Cape ground squirrel engineering in semi-arid grasslands would affect plant cover, height, and richness through digging, nutrient deposition, trimming, and/or foraging activities (Table 1). More specifically, burrowing activities could create gaps in the vegetation and bring nutrients to the surface, which could promote the growth of opportunistic plant species (digging hypothesis; Romero et al., 2015; Beca et al., 2022). Nutrient deposition by squirrels (e.g., fecal deposits) could also promote increased plant growth (nutrient deposition hypothesis; Desmet and Cowling, 1999; Davidson and Lightfoot, 2006). Under both hypotheses, we predicted greater plant cover, height, and richness on burrow clusters compared to controls. Under the nutrient deposition hypothesis, we also predicted greater nitrogen concentrations in plants found on burrow clusters compared to controls.

Table 1. Hypotheses and predictions summarizing the direct effects of Cape ground squirrels (*Xerus inauris*) on plants, invertebrates, and small mammals at the S.A. Lombard Nature Reserve (modified from Ewacha et al., 2016).

Hypotheses	Predictions
Vegetation	
1. Digging	Greater plant cover, height, and richness on burrow clusters
2. Nutrient deposition	Greater plant cover, height, and richness on burrow clusters
	Greater % nitrogen in plants on burrow clusters
3. Trimming	Lower plant height on burrow clusters
4. Foraging	Lower plant cover and height on burrow clusters
	Plant stable isotope ratios reflected in squirrel diet
Invertebrates and small mammals	
1. Burrow refuge	Greater invertebrate and small mammal abundance and species richness on burrow clusters

We also hypothesized that Cape ground squirrels could affect plant cover, height, and richness through trimming plants to improve predator visibility (trimming hypothesis) or by foraging on plant cover (foraging hypothesis; Davidson and Lightfoot, 2006; Zhong et al., 2022). Many species of rodents will reduce plant cover through trimming and foraging, impacting predator visibility, including Brant's voles (*Lasiopodomys brandtii;* Zhong et al., 2022), prairie dogs (Davidson and Lightfoot, 2006) and mole rats (Bathyergidae; Hagenah and Bennett, 2013). Under the trimming hypothesis, we predicted lower plant height on burrow clusters, but no difference in plant cover and richness between burrow clusters and controls. Under the foraging hypothesis, we predicted lower plant cover and height on burrow clusters compared to controls, but no difference in plant richness between burrow clusters and controls since the diet of these squirrels is not specialized (Herzig-Straschil, 1978). We also

predicted that stable isotope ratios of plants on burrow clusters would be reflected in the squirrel's diet.

Cape ground squirrels could also provide invertebrates and small mammals with refuge from thermal extremes and predators (burrow refuge hypothesis; Van Nimwegen et al., 2008). Under this hypothesis, we predicted greater invertebrate and small mammal abundance and richness on burrow clusters compared to controls.

2. Materials and methods

2.1. Study area

We conducted our study in austral winter (May–August) 2012 and 2013 on the S.A. Lombard Nature Reserve, a 3359 ha reserve in the semi-arid grassland ecoregion of South Africa (27°59′S, 25°359′E; Trytsman et al., 2016). The average annual temperature is 17.6 °C, ranging from −8.7 °C in winter to 40 °C in summer (Herzig-Straschil, 1978). Temperatures on the reserve for the winter of 2012 averaged a high of 22.7 °C and a low of 2.0 °C while temperatures for the winter of 2013 averaged a high of 20.2 °C and a low of 1.8 °C. Annual rainfall on the reserve averaged 509 mm (range 241–965 mm) from 1952 to 2013. Winters are dry and rainfall is typically less than 10 mm. Winter rainfall on the reserve was 17.2 mm in 2012 and 5.2 mm in 2013.

The reserve is a flat, open area with geologically distinct eastern and western areas (van Zyl, 1965; Herzig-Straschil, 1978; Pettitt and Waterman, 2011). The main ungulates found on the reserve include springbok (*Antidorcas marsupialis*), black wildebeest (*Connochaetus gnou*), gemsbok (*Oryx gazella*), red hartebeest (*Alcelaphus buselaphus*), blesbok (*Damaliscus dorcas phillipsi*), and zebra (*Equus quagga*). Our study focused on the eastern region, which is characterized by a brackish type of soil dominated by *Sporobolus* grasses with occasional shrubs, including *Pentzia calcarea*, *Lightfootia* sp., *Aristida* cf. *adscensionis*, and *Lycium* sp. (van Zyl, 1965). It is unlikely that squirrels establish their burrows based on soil and vegetation properties (Ewacha et al., 2016). Indeed, we have observed five new burrow clusters form in the S.A. Lombard Nature Reserve since 2012, and we observed shrubs subsequently growing after the burrow clusters were established (unpubl. data). Cape ground squirrels occupy the same burrow clusters over many years, maintaining old holes and forming new holes within existing burrow clusters (Herzig-Straschil, 1978; Ewacha et al., 2016). Only a single family group usually inhabits a burrow cluster (Waterman, 1995).

We examined burrow clusters that ranged between 82 and 434 m^2 (median: 143 m^2) with 26–84 openings (median: 48 openings). Other organisms, such as yellow mongooses (*Cynictis penicillata*) and meerkats (*Suricata suricatta*), may use squirrel burrows for refuge (Edwards and Waterman, 2011), but Cape ground squirrels usually establish and expand burrow clusters (Waterman and Roth, 2007; Ewacha et al., 2016).

2.2. Species sampling

We sampled nine burrow clusters occupied by Cape ground squirrels (mean of 5.4 ± 0.56 squirrels per burrow cluster) and paired control sites with no burrows, situated 50 m from the burrow cluster in a random cardinal direction. We considered 50 m to be a sufficient distance to separate controls from squirrel burrow clusters, but close enough so that burrow clusters and control sites were located in similar habitat and topography (Ewacha et al., 2016). In

2012, we determined invertebrate and small mammal abundance and species richness. In 2013, we determined small mammal abundance and species richness, gathered plant information (cover, height, and richness), and collected plant samples for stable isotope analysis.

We used 1×1 m quadrats (May–August 2013) to estimate vegetation cover of all plant species visually at the center of the burrow cluster or control site, and 5 and 10 m away from the center in the four cardinal directions (nine quadrats per burrow cluster or control site). We also measured plant (grass and shrub) height at nine equally spaced points within each quadrat (9 estimates per 9 quadrats = 81 measurements per site). We submitted pressed plant samples to the University of Pretoria Herbarium for identification to species or genus level.

To determine invertebrate abundance and richness we sampled one paired site at a time between May 25 and June 18, 2012, using pitfall traps at the center of the burrow cluster or control site, and 5 and 10 m away from the center in the four cardinal directions (nine pitfall traps per burrow cluster or control site). We buried pitfall traps (1 L) flush with the ground for two consecutive days and nights, collecting samples twice a day (morning and evening) to account for differences in temperature (during trapping, the mean maximum daily temperature was 18.6 ± 0.9 °C (mean ± SE) and the overnight mean minimum was 0.5 ± 0.9 °C). We preserved all trapped invertebrates in 70% ethanol and identified them to family level except for Caelifera (n = 7), Lepidoptera (n = 3), Diptera (n = 2), and Araneae (n = 31), which were identified to sub-order or order. We did not quantify the number of ants because traps were located at varying proximities to ant hills, which would have created bias.

To determine small mammal abundance and richness we sampled two paired sites at a time (from June 5–20, 2012, and July 20 to August 9, 2013), using Sherman traps placed at the center of the burrow cluster or control site, and 5 and 10 m away from the center in the four cardinal directions (nine traps per burrow cluster or control site). We baited each trap ($7.6 \times 8.9 \times 22.9$ cm; Sherman Inc., Florida, USA) with peanut butter and oats, added cotton wool for insulation, and live-trapped for two consecutive nights each year, opening the traps at dusk (approximately 17h00) then checking and closing them the following morning (approximately 07h00). We focused our trapping efforts on nocturnal small mammals because diurnal small mammals were not prominent within the region. Diurnal Cape ground squirrels were too large to be captured by these traps. We determined the species of each captured animal, placed a unique temporary dye mark (Rodol D; Lowenstein and Sons, New York, NY, U.S.A.) on its back for identification, and released it at the site of capture. Sherman and pitfall traps were not set at the same sites simultaneously.

2.3. Stable isotope analysis

Stable isotope ratios provide a direct measure of nutrients assimilated into a consumer's tissues (Peterson and Fry, 1987). Carbon and nitrogen stable isotope ratios vary between food sources, so they can be used to reconstruct squirrel diet. $\delta^{13}C$ values differ between plants with C_3 or C_4 photosynthetic pathways (DeNiro and Epstein, 1978), whereas $\delta^{15}N$ values vary among trophic positions (DeNiro and Epstein, 1981; Peterson and Fry, 1987).

We measured % nitrogen of plants to determine whether squirrels were contributing nutrients (e.g., feces) to the plants, and examined stable isotope ratios ($\delta^{15}C$ and $\delta^{15}N$) of plants and squirrels to determine squirrel diet. We sampled plant species with greater than 5% cover (n = 71 grass and n = 35 shrub samples) and collected hair samples from squirrel tails (n = 55

squirrels from 32 burrow clusters). We rinsed plant samples with water and washed hair samples with soapy water to remove surface oils. Samples were then dried, homogenized with scissors, weighed into tin capsules (2.5–3 mg for plants, 0.6–0.8 mg for hair), and shipped to the Chemical Tracers Laboratory, Great Lakes Institute for Environmental Research, University of Windsor for measurement of stable isotope ratios on a continuous flow isotope ratio mass spectrometer. During this process, samples were combusted and separated into CO_2 and N_2, which were measured to determine carbon and nitrogen stable isotope ratios (Derbridge et al., 2012). These values were then presented in delta notation by comparing the stable isotope ratios to an international standard, PeeDee Belemnite limestone for carbon and atmospheric N_2 for nitrogen (DeNiro and Epstein, 1978, 1981).

2.4. Statistical analysis

We transformed plant cover (log x + 0.5) to improve normality, and used a linear mixed-effects model (LMM) to determine differences in plant cover between treatment (burrow cluster vs. control) and vegetation type (grass vs. shrub), with site pair (burrow cluster and the corresponding control site) as a random effect and including an interaction between treatment and vegetation type. We determined differences in plant height and richness between burrow clusters and control sites using paired t-tests. To examine whether squirrels increased % nitrogen in plants through fecal deposition at burrow clusters, we used a paired *t*-test to compare % nitrogen of grass samples on burrow clusters versus controls (control sites had no shrubs).

We calculated invertebrate and small mammal abundances as the number of individuals captured per available trap at each burrow cluster or control site. We excluded misfires or traps disturbed by wildlife for invertebrates (6%; n = 9 traps in 2012) and small mammals (6%; n = 9 traps in 2012 and 2013). We transformed invertebrate abundance (inverse x + 0.5) to improve normality, and used LMMs to determine differences in invertebrate abundance and richness between burrow clusters and controls and between day and night, with site pair as a random effect. We also used LMMs to determine differences in small mammal abundance and richness between burrow clusters and controls, with site pair as a random effect and blocking on year (2012 and 2013).

We estimated the proportion of grass vs. shrubs in the diet of squirrels using the average $\delta^{15}N$ and $\delta^{13}C$ of each functional group in a two-source linear mixing model for each element (Philips, 2001). We applied a trophic discrimination (difference in stable isotope ratios between consumer and resource) correction to plant stable isotope ratios prior to a comparison with squirrel signatures. We used a trophic discrimination factor of 3.3 ± 1.0‰ for ^{13}C enrichment and 1.9 ± 1.0‰ for ^{15}N enrichment based on Hobbie et al. (2017), who assessed the importance of plants and fungi in the diets of Arctic ground squirrels (*Urocitellus parryii*). All analyses were completed using JMP Pro 13 (SAS Institute Inc., Cary, NC, U.S.A.).

3. Results

We identified 43 plant species total (n = 38 on burrow clusters and n = 17 on controls). The most common plant species, *Sporobolus* sp. grass, was found on both burrow clusters and controls. Common shrub species, which were mostly found on burrow clusters, included *Lycium* sp., *Pentzia calcarea*, and *Lightfootia* sp. Plant cover was higher on burrow clusters than controls ($F_{1, 24}$ = 9.95; p = 0.004) and grass cover was higher than shrub cover overall

($F_{1, 24} = 35.78$; $p < 0.001$), but the significant interaction between treatment and vegetation type ($F_{1, 24} = 20.12$; $p < 0.001$) suggested squirrels enhance shrub growth, as shrub cover was minimal at control sites (Fig. 1a). Tukey's post-hoc test on the interaction indicated no difference in % cover of shrubs on burrow clusters, grass on burrow clusters or grass on controls (all $p > 0.21$), but shrubs on controls were significantly lower than all three (all $p < 0.0001$). Plant height did not differ between burrow clusters and controls ($t_8 = 1.92$; $p = 0.091$; Fig. 1b). Plant richness was higher on burrow clusters than controls ($t_8 = -8.08$; $p < 0.001$; Fig. 1c) and the % nitrogen in grasses ($1.5 \pm 0.1\%$ overall mean $\pm$ SE) did not differ between treatments and controls (paired $t_8 = -1.27$; $p = 0.24$; Fig. 1d). Shrubs comprised only $7.6 \pm 0.7\%$ of squirrel diets (Fig. 2).
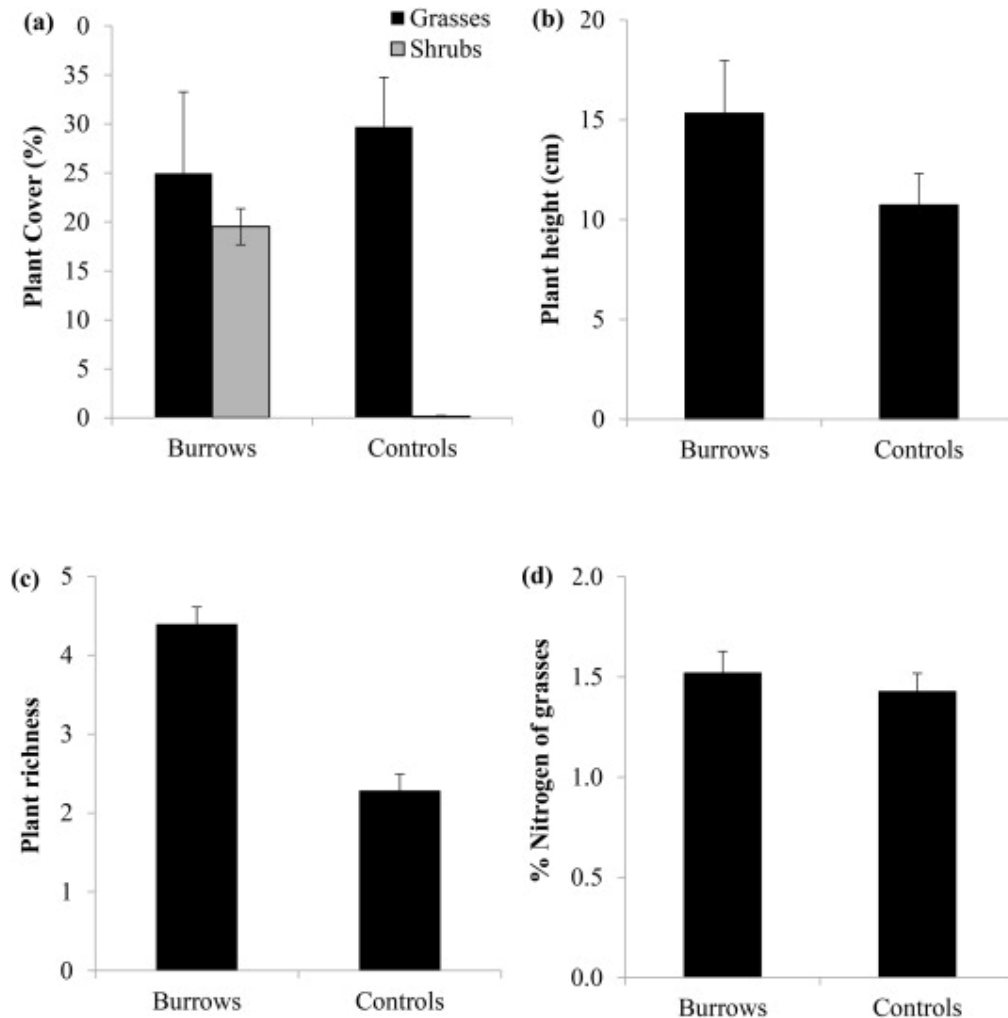
Fig. 1. Plant (a) cover, (b) height, (c) species richness, and (d) percent nitrogen (mean $\pm$ SE) on Cape ground squirrel (*Xerus inauris*) burrow clusters (n = 9) and paired controls (n = 9) at the S.A. Lombard Nature Reserve in winter 2013.
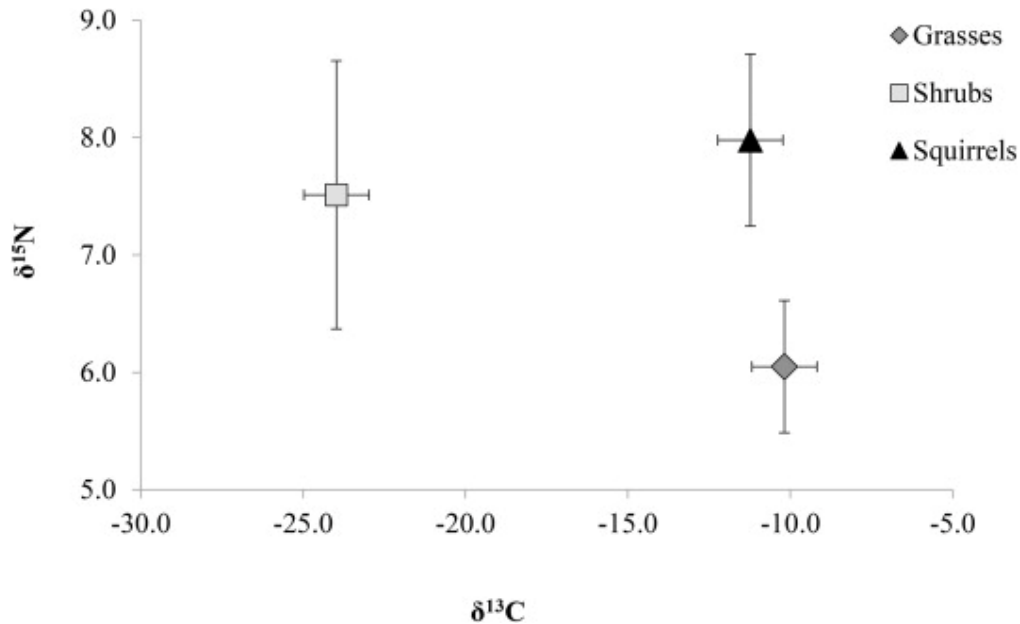
Fig. 2. Stable isotope ratios (mean ± SE) in grasses (n = 71), shrubs (n = 35), and Cape ground squirrel (*Xerus inauris*) hair (n = 55) at the S.A. Lombard Nature Reserve in winter 2013. A trophic discrimination correction was applied to plant stable isotope ratios: 3.3 ± 1.0‰ for ^{13}C and 1.9 ± 1.0‰ for ^{15}N (Hobbie et al., 2017).

We trapped 166 invertebrates (n = 115 on burrow clusters and n = 51 on controls). We identified invertebrates within the orders Coleoptera, Blattodea, Dermaptera, Orthoptera, Hymenoptera, Hemiptera, Lepidoptera, Siphonaptera, Diptera, and Araneae. Beetles (Tenebrionidae, Carabidae, and Anthicidae families) were the most abundant invertebrates captured (47% of total catch; n = 78), followed by spiders (19%; n = 31), and seed bugs (Lygaeidae family; 8%; n = 14). We captured 21 small mammals in 2012 (n = 17 at burrow clusters and n = 4 at controls) and 12 in 2013 (n = 9 at burrow clusters and n = 4 at controls). We captured two small mammal species, bushveld gerbils (*Gerbilliscus leucogaster*; 91% of total catch; n = 30) and multimammate mice (*Mastomys* spp.; 9%; n = 3). Burrow clusters had higher invertebrate abundance ($F_{1, 25}$ = 6.35; p = 0.019) and richness ($F_{1, 25}$ = 4.41; p = 0.046) than controls, and both abundance ($F_{1, 25}$ = 16.84; p = 0.0004) and richness ($F_{1, 25}$ = 24.90; p < 0.0001) were higher in day than night (Fig. 3). Burrow clusters also had higher small mammal abundance ($F_{1, 25}$ = 9.94; p = 0.004) and richness ($F_{1, 25}$ = 8.69; p = 0.007) than controls (Fig. 4).
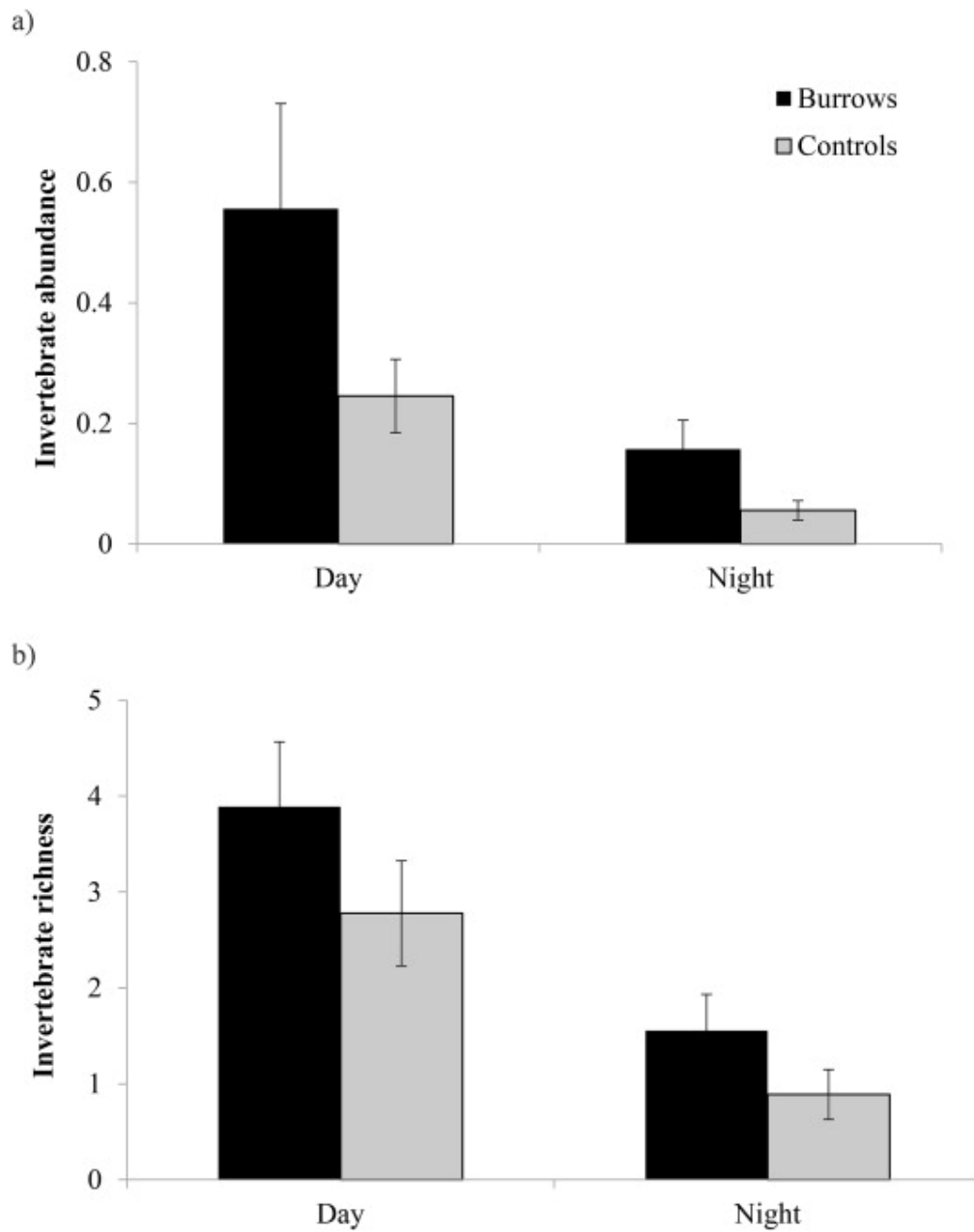
a)

b)

Fig. 3. Invertebrate (a) abundance (captures per trap) and (b) species richness (mean ± SE) on Cape ground squirrel (*Xerus inauris*) burrow clusters (n = 9) and paired controls (n = 9) at the S.A. Lombard Nature Reserve during day and night in winter 2012.
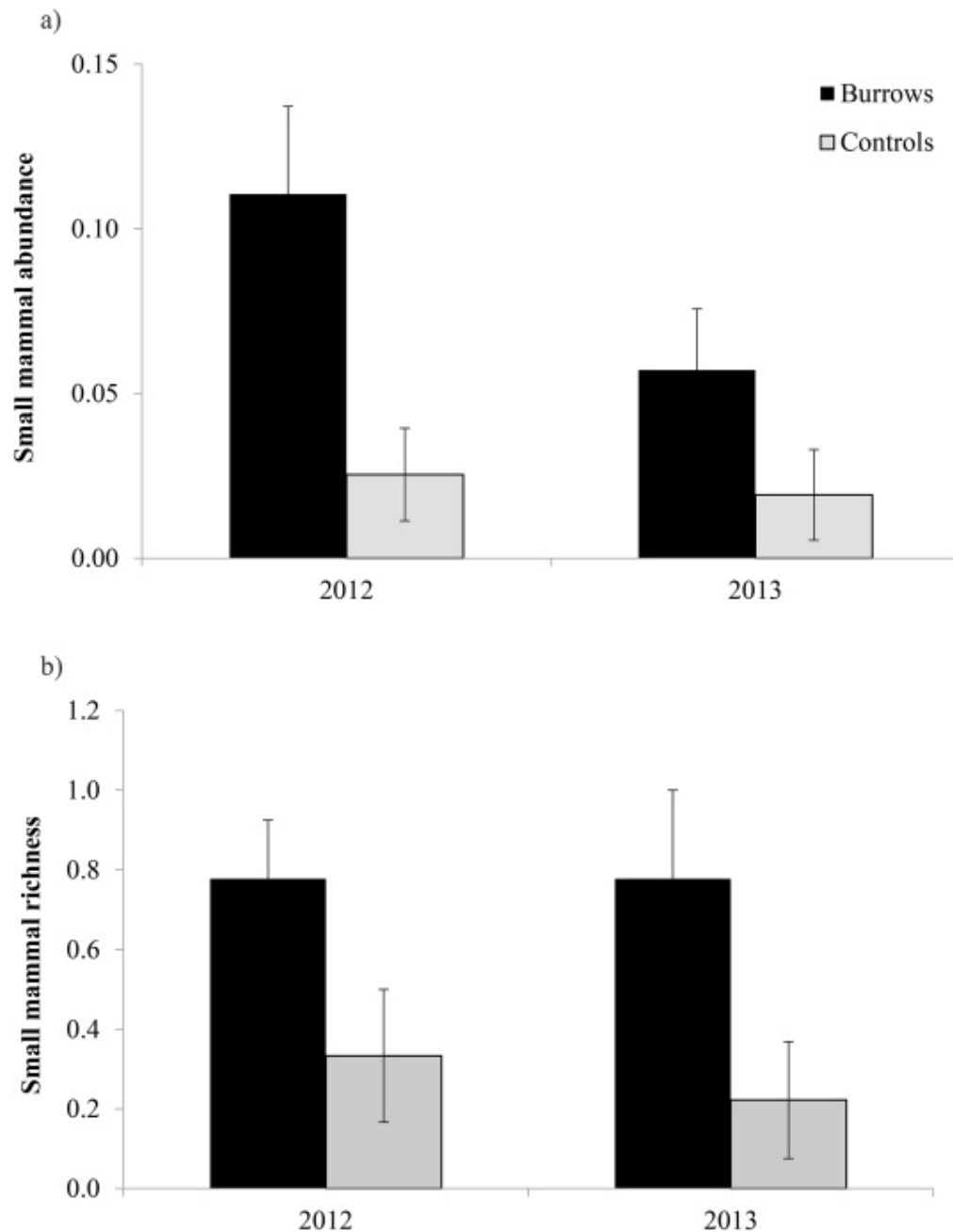
Fig. 4. Small mammal (a) abundance (captures per trap) and (b) species richness (mean ± SE) on Cape ground squirrel (*Xerus inauris*) burrow clusters (n = 9) and paired controls (n = 9) at the S.A. Lombard Nature Reserve in winter 2012 and 2013.

4. Discussion

Burrowing and foraging activities of Cape ground squirrels affected plant and animal communities, suggesting that Cape ground squirrels are ecosystem engineers within the semi-arid grasslands of South Africa. In particular, we found greater shrub cover on burrow clusters compared to controls, leading to higher plant richness on burrow clusters due to various shrub species being present (<1% shrub cover on controls), which squirrels rarely consumed. Thus, squirrels did not reduce overall plant cover on burrow clusters, rejecting the

foraging hypothesis. Plant height did not differ on and off the burrow clusters, rejecting the trimming hypothesis, nor did squirrels increase nitrogen concentrations in the plants on burrow clusters, rejecting the nutrient deposition hypothesis. Thus, the digging hypothesis best explained the impact of Cape ground squirrels on vegetation in our study area of all the hypotheses we considered (Table 1).

Grasses at our study area, including *Stipagrostis* spp., *Themeda triandra*, and *Cymbopogon plurinodis*, are dominant in undisturbed areas (van Zyl, 1965), whereas disturbance through digging activities can destabilize soil and reduce topsoil hardness, creating opportunities for disturbance-dependent and opportunistic shrub species to grow (Dean and Milton, 1991; Desmet and Cowling, 1999; Davies et al., 2019; Louw et al., 2019). Because of this disturbance through digging, burrow clusters are typically less compacted than undisturbed areas (Butler and Butler, 2009; Louw et al., 2019). Reduced soil compaction provides a more favourable microclimate for seeds to germinate and seedlings to establish due to greater water availability, soil aeration, and root space (Louw et al., 2019). Dean and Milton (1991) found that burrowing mammals, such as aardvark and Cape foxes (*Vulpes chama*), create microsites that accumulate seeds, water, and detritus, which promote seedling growth and convert *Stipagrostis*-dominated sand dunes into shrubby grasslands. In arid environments, burrowing by ecosystem engineers could be the only mechanism bringing nutrients to the surface of the soil or increasing moisture, thereby enhancing microbial and invertebrate activity (Decker et al., 2019). Similarly, disturbance by burrowing squirrels at our study area could have reduced soil compaction, providing greater opportunity for shrub species to grow.

Burrowing also promotes mixing and alters the chemical composition of the soil, which can improve soil fertility (Desmet and Cowling, 1999; Wesche et al., 2007; Decker et al., 2019; Louw et al., 2019). Indeed, Desmet and Cowling (1999) found greater soil microbial activity on burrow mounds of Brant's whistling rat (*Parotomys brantsii*) compared to control sites. Decker et al. (2019) also found that soil enzyme activity is greater in the presence of burrowing small mammals and increased rainfall in Australia. As a result, the soil around burrows sites could have higher nutrient concentrations, such as nitrogen, which can promote plant growth (Wesche et al., 2007).

In the Namib Desert, Cape ground squirrels reduced plant cover and height on burrow clusters, supporting the foraging and trimming hypotheses (Ewacha et al., 2016). The differing impacts on plant cover and height between the Highveld grassland and Namib Desert studies could be attributed to geographical variation in climate and resource availability. Our semi-arid grassland study area has higher annual rainfall, lower annual temperatures, and more nutrient-rich soils compared to the Namib Desert, thereby supporting the growth of a greater variety of plant species, including shrubs. In the Namib Desert, plant recruitment and growth are limited by weather and site conditions rather than plant competition (Milton and Dean, 2000), and the shrubs that grow on burrow clusters in the semi-arid grasslands do not grow within the Namib Desert due to a harsh dry climate and nutrient-poor soils.

We found greater invertebrate abundance and richness on burrow clusters than controls, supporting the burrow refuge hypothesis. Burrow clusters provide protection from predators, moist environments, and food sources for invertebrates (Bangert and Slobodchikoff, 2006; Davidson and Lightfoot, 2007). Invertebrates may also have been attracted to the increased shrub cover at burrow clusters. In the Namib Desert, we found higher beetle abundance and richness at the controls where plant cover and height were higher (Ewacha et al., 2016). Dean

and Milton (1995) similarly found a higher abundance and diversity of insects associated with a greater plant cover and higher diversity of perennial plants. Likewise, Blaum et al. (2009) found that shrub density is the habitat component that best predicts invertebrate assemblages, particularly for beetles, ants, and scorpions.

We found greater small mammal abundance and richness on burrow clusters compared to controls, suggesting that burrow clusters provide thermal refuge and protection from predators (the burrow refuge hypothesis; Whittington-Jones et al., 2011; Ewacha et al., 2016). We also found greater small mammal abundance on burrow clusters in the Namib Desert (Ewacha et al., 2016). Plant and arthropod communities can also affect small mammal abundance and distribution, suggesting an alternative mechanism by which burrowing ground squirrels may affect small mammals (Whittington-Jones et al., 2011; Ewacha et al., 2016). For example, Hoffmann and Zeller (2005) found that small mammal abundance and richness are lower in overgrazed regions within the Nama Karoo, Namibia due to low grass and shrub cover, shrub diversity, and arthropod abundances. Bushveld gerbils, the most common small mammal species captured at squirrel burrow clusters on our temperate grassland study area, typically dig their burrows at the base of shrubs (Skinner and Chimimba, 2005), suggesting these gerbils could have been attracted to the shrubby vegetation found at squirrel burrow clusters. Greater abundances and species richness of invertebrates and small mammals on burrow clusters can provide important food sources for other organisms in a resource-limited environment.

Based on our stable isotope results, squirrels eat a low proportion of shrubs (7.6%), thus having little impact on vegetation on the burrow clusters, which are predominantly covered by shrubs. Squirrels forage at their burrow clusters during early mornings and evenings, and otherwise spend their day foraging away from their burrow clusters (Herzig-Straschil, 1978; Waterman, 2002). Although squirrels spend little time foraging at their burrow clusters, various antelope species (wildebeest, springbok, etc.) benefit from the shrubs (e.g., *Lycium* sp. and *Pentzia* sp.) growing on the burrow clusters, particularly during the winter flowering season (van Zyl, 1965). Thus, these ungulates may benefit from the ecosystem engineering activities of ground squirrels.

Examining the impacts of ecosystem engineers in arid and semi-arid environments are particularly important since engineering is predicted to be more pronounced in harsh environments where resources are limited (Louw et al., 2019; Lowney and Thomson, 2022). Cape ground squirrels acted as ecosystem engineers at both arid and semi-arid sites (the Namib Desert and this study, respectively), but their impact on the habitat and other organisms differed by site. Squirrel burrowing in the semi-arid Highveld grassland improved conditions for disturbance-dependent shrubs, which can provide important cover for invertebrates and small mammals, and a valuable food source for antelope species. Our results suggest that an ecosystem engineer can have varying species- and community-level effects across different geographical areas and habitats even if their engineering activities are similar (Louw et al., 2019). Impacts on the surrounding biological community can vary based on environmental conditions, resource availability, and the response of the community to engineering activities.

5. Conclusion

As ecosystem engineers in semi-arid grasslands, Cape ground squirrels create important habitat for plant and animal communities. Despite their importance to such communities,

many burrowing mammals are threatened by human activities such as agriculture and mining (Davidson et al., 2012; Decker et al., 2019; Beca et al., 2022). Declines in ecosystem engineer species in grassland ecosystems could have great consequences on ecosystem functions (Decker et., 2019; Beca et al., 2022), particularly as climate change causes increased warming and reduced rainfall across the temperate semi-arid grasslands of southern Africa (Kusangaya et al., 2014).

CRediT authorship contribution statement

Michelle V.A. Ewacha: Methods, Investigation, analysis, Writing – original draft, preparation, Visualization. **James D. Roth:** Conceptualization, methods, analysis, Writing – review & editing. **Jane M. Waterman:** Conceptualization, methods, analysis, Resources, Supervision, Writing – original draft, preparation, review and editing, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

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