Disentangling the effects of two co-occurring biotic modifiers on vegetation properties in a semi-arid savannah ecosystem

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A B S T R A C T

Biotic modifiers are species that strongly alter environmental conditions, and that often shape local communities. When more than one biotic modifier co-occurs, the potential for interactive effects exists, where the effects of one species may negate or enhance the impacts of a second biotic modifier. Here we test for an interactive effect of aardvark (*Orycteropus afer*) burrows and tree presence on soil (soil temperature, moisture and compaction) and understorey vegetation properties (plant cover, species richness and composition) in a semi-arid savanna. Aardvark burrowing altered abiotic conditions, with soil temperature and compaction being lower, and soil moisture higher, in burrow entrances than at the burrow mounds and control microsites. In addition, the impact of aardvark burrowing on soil moisture and soil compaction was mediated by the occurrence of trees. In contrast, vegetation cover and species richness were independently affected by burrowing and trees, while vegetation composition was only affected by the occurrence of trees, but not by burrowing. This research suggests that co-occurring biotic modifiers can have both independent and interactive effects, and disentangling their impacts will help understand the mechanisms underlying dryland plant communities.

1. Introduction

Biotic modifiers are species that substantially alter environmental conditions (Linder et al., 2012). These species can create or destroy microhabitats by changing disturbance regimes, microclimatic conditions and the distribution of resources (Linder et al., 2012). The impacts of these species may create favourable habitats for other species in areas that would otherwise be unsuitable (Stachowicz, 2001). For example, in arid steppes burrowing by marmots (*Marmota bobak*) creates habitats suitable for salt-tolerant specialist species and affects the dispersal of these species in the landscape (Valkó et al., 2021). Biotic modifiers are typically also considered to be ecosystem engineers (sensu Jones et al., 1994), with the former classification being more inclusive than the latter, by not strictly requiring an organism to show impacts on environmental conditions extending beyond its lifespan (Linder et al., 2012). While the impacts of biotic modifiers may be positive (i.e. facilitative), neutral or negative (i.e. competitive) for individual species (Jones et al., 1997), at the community- and landscape-levels the presence and activity

of biotic modifiers typically increase environmental heterogeneity and species richness (Romero et al., 2015), by creating habitat patches with unique environmental conditions, resulting in microhabitat mosaics that potentially support different biotic communities (Pickett and Cadenasso, 1995).

Trees are important biotic modifiers that can strongly modulate light and moisture regimes (Linder et al., 2012; Stachowicz, 2001). For example, because tree canopies intercept solar radiation, they typically lower evapotranspiration and buffer against heat gain and loss (Davis et al., 2019; De Frenne et al., 2019). As a result, tree canopies reduce temperature extremes and contribute to more consistent thermal regimes in the understorey than in nearby open habitats (De Frenne et al., 2019). Some trees may also potentially increase the availability of soil moisture and nutrients to understorey plants through, for example, hydraulic lift, a process by which water moves from deeper to shallower soil layers by roots (Sardans and Peñuelas, 2014). Therefore, by providing a more stable and more resource-rich environment, trees may facilitate a higher species richness and herbaceous biomass under their

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canopies than in adjacent areas (Tessema and Belay, 2017). However, in addition to these beneficial effects, trees can also have negative impacts on herbaceous plant species through competition for light and soil resources. For example, in semi-arid savannahs encroaching tree species can decrease species richness and herbaceous vegetation cover, and alter vegetation composition due to shading (Bussa and Shibru, 2020; Randle et al., 2018).

At finer spatial scales burrowing mammals also play an important role as biotic modifiers by creating distinct microhabitats when constructing burrows for shelter and foraging (Eldridge and Mensinga, 2007; Eldridge et al., 2009). Burrows typically provide a cooler microclimate than ambient conditions (Whittington-Jones et al., 2011) and, due to their shape, trap rainfall (Laundre, 1993) and litter (James et al., 2009), increasing soil moisture and soil carbon locally. Burrowing also contributes to the mixing of soils by bringing sediment from deeper within the soil profile up to the surface (Reichman and Seabloom, 2002). As a result, excavated soils generally have a lower bulk density and differ in other physical and chemical properties from undisturbed surrounding soils (Butler and Sawyer, 2012; Mallen-Cooper et al., 2019; Whitford and Kay, 1999). Therefore, the activities of burrowing mammals create unique microhabitats that generally differ in plant species composition from surrounding undisturbed areas (Eldridge and Whitford, 2009; Kurek et al., 2014; Louw et al., 2019; Whitford and Kay, 1999).

In semi-arid environments both trees and burrowing mammals often create more favourable microhabitats for plant establishment. Under the canopy of trees, ameliorated microclimatic conditions and higher soil fertility may also increase plant basal cover (Abdallah and Chaieb, 2012). In contrast, burrowing activities typically reduce plant cover in and around burrows relative to undisturbed surrounding areas due to physical disturbances and the burial of short stature plants (Eldridge and Simpson, 2002; Van Staalduinen and Werger, 2007). However, the bare soil associated with freshly excavated burrows provides opportunities for the establishment of pioneer species and potentially other plant species not occurring in the surrounding undisturbed areas. This creates potential colonization sites and typically increases plant diversity in the landscape (Obidziński and Kieltyk, 2006; Whittington-Jones, 2006). Seed germination and seedling establishment is often also enhanced in burrows and underneath the canopy of trees in semi-arid environments, due to the accumulation of resources and the generally cooler and moister conditions in these microhabitats (Fleming et al., 2014; McLaren and McDonald, 2003). Shading by trees specifically benefits shade-tolerant species, at a cost to the shade-intolerant species more typical of open areas (Jakobsson et al., 2019; Nieto-Lugilde et al., 2015; Rossi and Villagra, 2003). As such, shrubs generally benefit from the shade of trees in semi-arid environments, but perennial forbs and grasses more commonly occur in adjacent, open sites (Rossi and Villagra, 2003). Therefore, through their impacts as biotic modifiers, both trees and burrowing mammals may influence the distribution and composition of vegetation in semi-arid areas, with trees being more likely to facilitate shade-tolerant species and burrowing mammals typically facilitating earlier successional plant species.

A relatively poorly studied aspect of biotic modifiers is their potential interactive effects. For example, Gunnison's prairie dogs (*Cynomys gunnisoni*) and banner-tailed kangaroo rats (*Dipodomys spectabilis*) co-occur in the Chihuahuan desert grasslands of North America. Their combined impacts increase landscape heterogeneity and plant species richness more than when either occurs by itself (Davidson and Lightfoot, 2008). Furthermore, in a semi-arid Mediterranean grassland three biotic modifiers, *Stipa* tussocks, biological soil crusts and European rabbits (*Oryctolagus cuniculus*), have an interactive effect on water infiltration. *Stipa* tussocks increase infiltration rates, but the availability of water for interception by *Stipa* is altered by biological soil crusts and rabbit disturbances. Biological soil crusts generally increase the flow of water to *Stipa* tussocks, but rabbits disturbing the soil surface may break up biological soil crusts, thereby, reducing water flow to *Stipa* tussocks and lowering infiltration (Eldridge et al., 2010). Therefore, in arid and

semi-arid environments, there appears to be particular potential for interactive effects between different co-occurring biotic modifiers, as abiotic conditions are more extreme and the modulation of environmental conditions by one biotic modifier may be greatly influenced by the presence of another.

Where burrowing animals and trees co-occur, they may have interactive effects on their abiotic environment and biotic communities. Although these biotic modifiers differ in their function and the way they alter their environment, the one may influence the impacts of the other. For example, burrows could potentially have much lower soil temperatures when compared to undisturbed surrounding soils when burrows are in the open, whereas more similar soil temperatures are expected between burrows and undisturbed soils when underneath the canopy of a tree. The aim of this study was therefore to determine if the impacts of burrowing by medium-sized mammals, chiefly aardvark (*Orycteropus afer*), are altered by the presence of trees, chiefly black thorn (*Senegalia mellifera*), in the semi-arid savannah systems of the Kalahari Desert, South Africa. To test this, we examined the impacts of burrowing on physical soil properties (soil temperature, soil moisture and soil compaction) and vegetation properties (vegetation cover, species richness and vegetation composition) when burrows were underneath and away from trees for three different burrow age classes (fresh, abandoned and collapsed). We hypothesized that the abiotic and biotic impacts of aardvark burrows will be greater in the absence of trees than in the presence of trees, as environmental amelioration by trees may outweigh any additional microhabitat effects that aardvark burrows may have.

2. Materials and methods

2.1. Study site

Khamab Kalahari Reserve is a 95 000 ha game reserve located within the semi-arid savannah of the Kalahari Desert (25°29′S 23°15′E). The reserve receives annual rainfall of c. 330 mm, with precipitation chiefly limited to summer months (Collinson and Brett, 2008). Mean minimum temperatures are 0 °C and 18 °C for winter and summer respectively, with mean maximum temperatures of 22 °C and 34 °C for those seasons (Collinson and Brett, 2008). The soil in the reserve is primarily well-aggregated and freely draining wind-blown sand of the Kalahari Group (Collinson and Brett, 2008). These sands are up to 1.2 m deep in some areas in the reserve (Collinson and Brett, 2008).

The reserve's vegetation is characterised by a co-dominance of tree and grass species, with relatively low plant cover that varies across the reserve (1–15% tree cover, 1–50% shrubs and 5–70% grasses; Brown and Bezuidenhout, 2010). The survey area for this study was primarily located within the *Vachellia erioloba - Senegalia mellifera* woodland community. The most common tree species in this community are *Vachellia erioloba*, *Senegalia mellifera*, *Vachellia luederitzii* (Mimosaceae), *Boscia albitrunca* (Capparaceae), and *Grewia flava* (Malvaceae), while the grassy layer is dominated by *Stipagrostis uniplumis*, *Schmidtia pappophoroides* and *Eragrostis lehmanniana* (Poaceae) (Brown and Bezuidenhout, 2010). The reserve's vegetation is classified as Molopo Bushveld, within the Eastern Kalahari Bushveld Bioregion (Mucina et al., 2014).

2.2. Study species

Aardvark are nocturnal mammals that feed on ants and termites (Smithers, 1971; Taylor et al., 2002). Aardvark disturb the soil surface and vegetation by making shallow surface scrapes and by constructing burrows for foraging (Dean and Milton, 1991) and for shelter (Smithers, 1971). Foraging burrows can vary considerably in size, with small burrows being only deep enough to cover the animal's head, but large burrows being up to 2 m deep (Taylor et al., 2002). Temporary burrows are used for shelter for up to a few days, while permanent burrows are used for an extended period and may become very large (Taylor and Skinner, 2003, recorded a burrow of 6.1 m in length) over time

(Smithers, 1971). Aardvark burrowing may have different effects on soil and vegetation in different environments, but generally increases soil moisture, and decreases species richness and vegetation cover in semi-arid and arid environments (Louw et al., 2019; Whittington-Jones, 2006).

Senegalia mellifera is a very thorny small tree occurring in bushveld and semi-arid areas. Soil nutrients are generally higher underneath the canopy of this nitrogen-fixing species than in open areas (Ward et al., 2018). However, even though there is a higher nutrient content underneath their canopies *Senegalia mellifera* trees are known to supress the grass layer (Richter et al., 2001). This tree often becomes an encroacher in semi-arid areas and may form impenetrable stands in overgrazed areas (Stafford et al., 2017).

2.3. Burrow selection and classification

Medium-sized burrows (entrance diameter 28–68 cm) were located opportunistically within the southern portion (c. 5000 ha) of Khamab Kalahari Reserve during March 2016. To distinguish burrows from feeding scrapes and natural depressions, only excavations with a tunnel shape structure and a roof were considered (Fig. 1). It is likely that the majority of surveyed burrows were originally created by aardvark as they are the main excavators in the reserve, with many other animals subsequently utilizing these burrows (Skinner and Chimimba, 2005; Smithers, 1971). Sampled burrows were separated by at least 10 m, with a total of 71 sites sampled.

Data were gathered at three microsites associated with each burrow site: 1) at the burrow entrance (i.e. below the edge of the tunnel roof), 2) at the impacted area around the burrow, and 3) at a control site close to the burrow. The impacted area was the area opposite the burrow entrance, where soil was deposited by the burrower (i.e. the excavated soil mound). The control area for each burrow was chosen 2 m away from the burrow at a 90° angle to the orientation of the burrow tunnel (to avoid sampling the surface potentially above the burrow tunnel), where there were no visible signs of burrowing disturbance. Data from this study have been previously analysed, but in a different context (see Louw et al., 2019).

Of the burrows surveyed, 27 were located under trees (chiefly *Senegalia mellifera*), with the other 44 burrows occurring away from trees. Burrows were classified to be associated with trees when canopy cover of trees over burrows was at least 10%. The average canopy cover over burrows associated with trees was 56% (range: 10–90%) and when not associated with trees was 0.02% (range: 0–1%). As an indication of the duration of time since burrowing ceased, burrows were classified into one of three "burrow age" categories: recently abandoned or currently used burrows (hereafter "fresh" burrows), abandoned burrows, and collapsed burrows (presumed to have been deserted for a longer period than abandoned burrows). Underneath the canopy of trees, 52% of the burrows sampled were fresh, 22% abandoned and 26% collapsed. These proportions were similar for burrows in the open: 41% of the burrows

sampled were fresh, 27% abandoned and 32% collapsed.

2.4. Soil and vegetation data collection

Soil and vegetation characteristics of all microsites were examined using the same method, with a quadrat of 0.25 m^2 surveyed in each burrowing microsite. This quadrat size was chosen to accommodate measurements within narrow burrow entrances. Three physical soil characteristics were measured at each burrowing microsite: 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) soil temperature at 2 cm depth using a hand-held RTD thermometer (Eutech Instruments; RSA). At each burrowing microsite all vascular plants were identified to species level where possible, and aerial cover for each species was visually estimated.

2.5. Statistical analyses

Generalized linear mixed effect models (GLMMs) were used to analyse soil moisture, soil temperature, soil compaction, vegetation cover, observed species richness and the occurrence of locally widespread species, after testing that our data met the assumptions of these models. Soil compaction data were analysed using a quasibinomial distribution since c. 26% of our measurements were at the lower range of values that can be determined by the penetrometer and to account for overdispersion. Vegetation cover data were also analysed using a quasibinomial distribution, species occurrence data using a binomial distribution, observed species richness data using a Poisson distribution, and soil moisture and temperature with a Gaussian distribution. Burrowing microsites (i.e. burrow entrance, impacted area and control), the presence of trees (i.e. present or absent) and burrow age (i.e. fresh, abandoned and collapsed) were set as fixed effects. The location of each burrow (and its associated microsites) were set as a random effect to account for potential unmeasured differences in environmental conditions across the study area. In all models the interaction between burrowing microsite and tree presence was included as a predictor variable. Since soil temperatures typically vary strongly between warmer and cooler times of the day (Whittington-Jones et al., 2011), the interaction of time, burrowing microsite and tree presence was included as a predictor variable.

Non-metric Multidimensional Scaling ordination and Permutational Multivariate Analysis of Variance (Quinn and Keough, 2002) were used to test for differences in species composition between burrow entrances, impacted areas and controls in the presence and absence of trees (including the interaction between burrowing microsite and tree presence). For vegetation cover, species richness, species occurrence and species composition, trees that were associated with burrows were excluded from the data used in the analyses and we only considered the
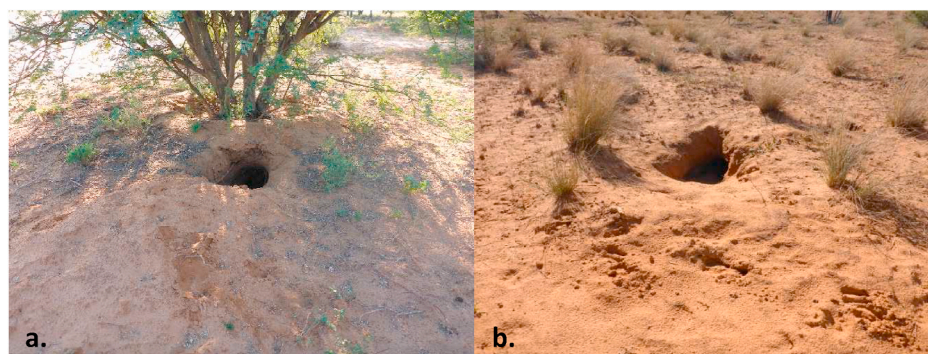

Fig. 1. Exemplar burrows in Khamab Kalahari Reserve a) underneath the canopy of trees and b) in the open. The diameter of the burrows was c. 40–50 cm.

understorey vegetation. Analyses were implemented using the lme4 package (Bates et al., 2015), MASS package (Venables and Ripley, 2002) and vegan package (Oksanen et al., 2015) in R statistical software (R Core Team, 2015).

3. Results

Soil temperature was significantly cooler in burrow entrances than in the impacted areas and controls, with the magnitude of the temperature difference depending on time of day (Burrow microsite:Time: Chi^2 = 22.05, p < 0.001, Fig. 2, Table 1). There was one exception where burrow entrances had similar temperatures to impacted areas and the controls, and this was only in the morning and where burrows were underneath the canopy of trees. Soil temperature, however, did not differ significantly underneath or away from trees and there was no significant interaction between trees and burrowing microsite. Soil moisture was higher at the burrow entrances under trees than in the controls, and there was a significant interaction between the presence of trees and burrowing microsite (Burrow microsite:Tree interaction: Chi^2 = 5.83, p = 0.05, Fig. 3a, Table 1), with significantly higher soil moisture in the impacted areas than control sites, but only when impacted areas were in the presence of trees. Soil compaction was affected by burrowing, with this effect also being mediated by the presence of trees (Burrow microsite:Tree interaction: Chi^2 = 7.44, p < 0.05, Fig. 3b, Table 1), where soil compaction was lowest in burrow entrances (irrespective of the presence of trees) and highest in impacted areas (but only in the absence of trees). Burrow age did not have a significant effect on soil temperature, moisture or compaction.

A total of 32 vascular plant species were recorded. Burrowing significantly decreased vegetation cover (Chi^2 = 9.94, p < 0.01, Fig. 3c,

Table 1
The effects of tree presence, mammal burrows and burrow age on soil and vegetation characteristics in a semi-arid savannah in South Africa. Models also included the locations of associated microsites as a random effect to account for the spatial clustering of sets of microsites.

| Response variable	Fixed effects	Chi^2	Df	P
Temperature	Burrow microsite	248.52	4	***
	Time	78.12	1	***
	Tree	2.99	3	
	Burrow age	0.90	2	
	Burrow microsite:Time	22.05	2	***
	Burrow microsite:Tree	1.39	2	
	Time:Tree	0.38	1	
	Burrow microsite:Time:Tree	3.85	2	
Moisture	Burrow microsite	24.32	2	***
	Tree	2.85	1	
	Burrow age	3.12	2	
	Burrow microsite:Tree	5.83	2	*
Compaction	Burrow microsite	66.09	2	***
	Tree	1.34	1	
	Burrow age	2.83	2	
	Burrow microsite:Tree	7.44	2	*
Vegetation cover	Burrow microsite	9.94	2	**
	Tree	13.81	1	***
	Burrow age	27.74	2	***
	Burrow microsite:Tree	0.23	2	
Species richness	Burrow microsite	23.89	2	***
	Tree	7.42	1	**
	Burrow age	17.98	2	***
	Burrow microsite:Tree	0.24	2	

$p \leq 0.05$.
$p < 0.01$.
$p < 0.001$.
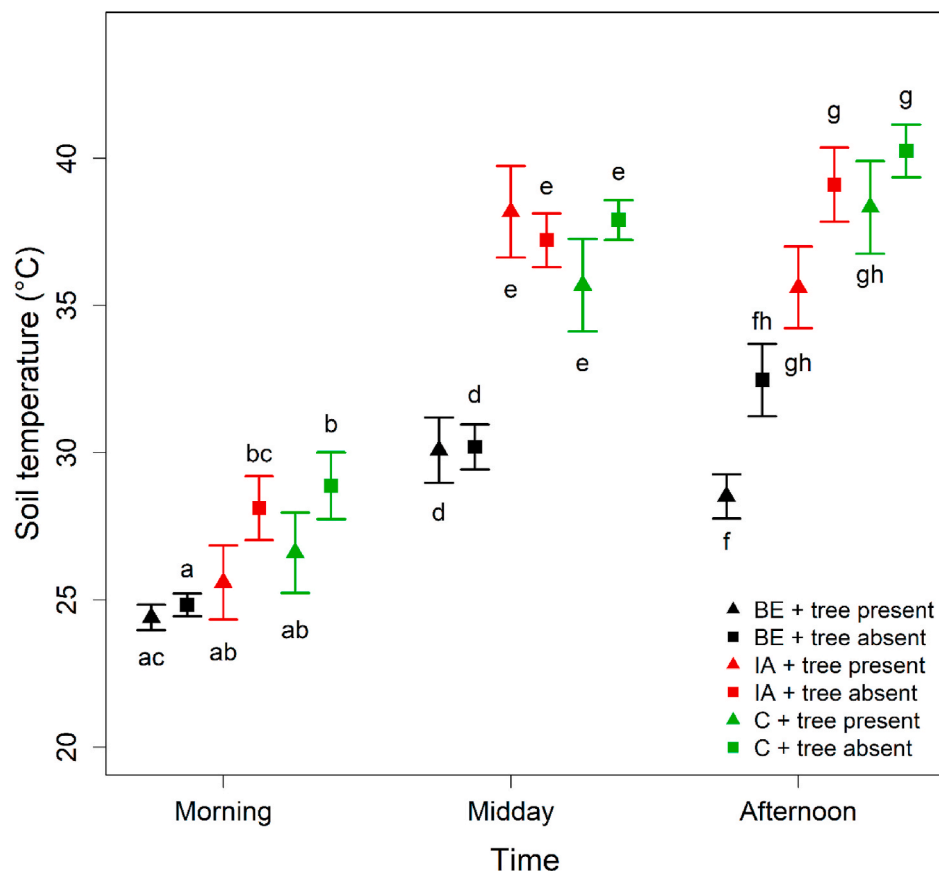
Fig. 2. Soil temperature (mean ± SE) recorded at burrowing microsites (BE = burrow entrance, IA = impacted area and C = control). Temperature was recorded at three intervals: Morning (7h25 – 10h25), Midday (10h25 – 12h45), Afternoon (12h55 – 16h00). Data for burrows where trees were present are shown with a triangular symbol and for where trees are absent are shown with a square symbol. Microsites within each time category not sharing a letter differ significantly.
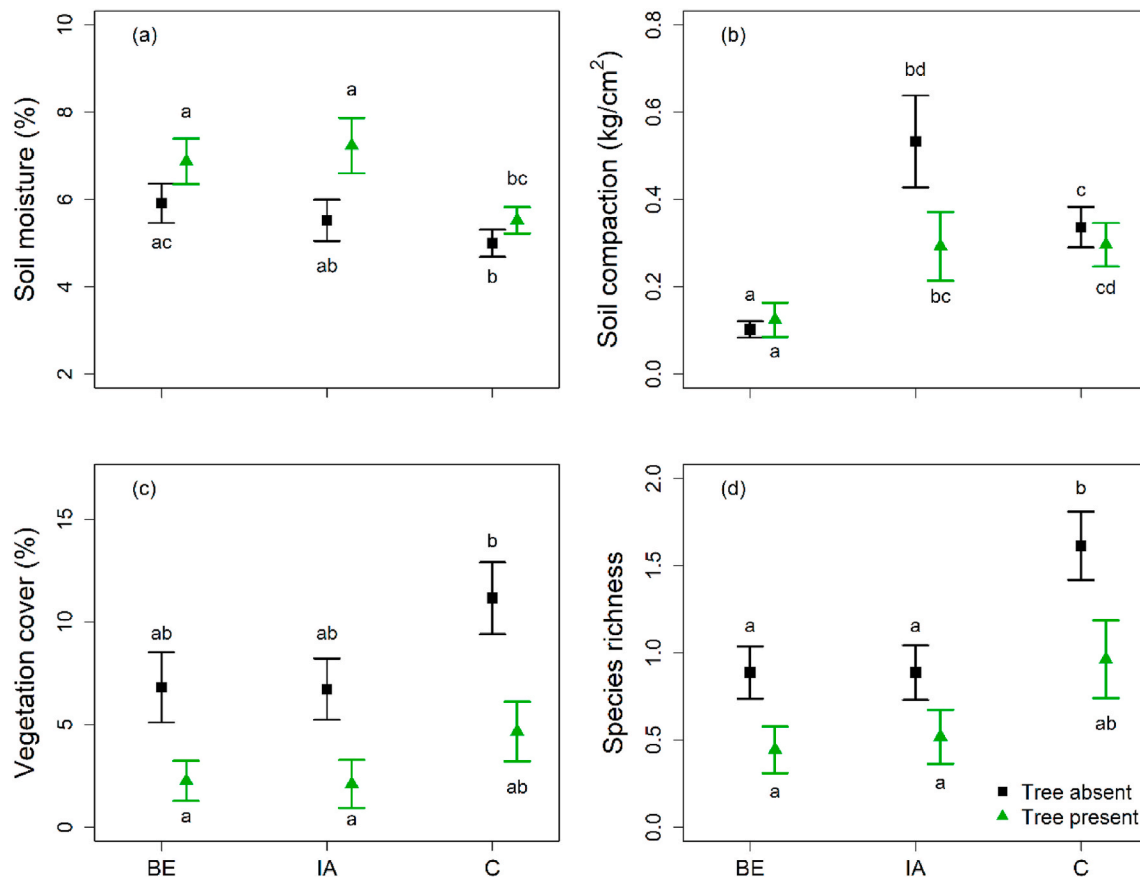
Fig. 3. Mean ± SE of a) soil moisture, b) soil compaction, c) vegetation cover and d) species richness recorded in burrowing microsites (BE = burrow entrance, IA = impacted area and C = control) in the presence and absence of trees. Microsites not sharing a letter differ significantly.

Table 1), with vegetation cover being lower in burrow entrances and impacted areas in the presence of trees when compared to controls away from trees (Chi^2 = 13.81, p < 0.001, Table 1). Vegetation cover was also significantly lower in fresh than abandoned and collapsed burrows (Chi^2 = 27.74, p < 0.001, Table 1, Supplementary Information Table S.1). Significantly more plant species occurred at the controls than at the other burrowing microsites (Chi^2 = 23.89, p < 0.001, Fig. 3d, Table 1), with significantly more species in controls away from trees than other burrowing microsites underneath or away from trees (Chi^2 = 7.42, p < 0.01, Table 1). Additionally, significantly fewer species also occurred at fresh than abandoned and collapsed burrows (Chi^2 = 17.98, p < 0.001, Table 1, Table S.1). For both vegetation cover and species richness, there was no significant statistical interaction between the presence of trees and burrowing microsite (Table 1).

Species composition differed underneath and away from trees (F = 4.78, R^2 = 4.09%, p < 0.001), and differed with burrow age (F = 1.81, R^2 = 3.09%, p < 0.05). However, species composition did not differ significantly between burrowing microsites. There was also no significant interaction for species composition between trees and burrowing microsite. Only 11% of the variation in species composition was explained by the predictor variables (Fig. 4, Table S.2).

The most widespread species sampled were *Acanthosicyos naudinianus* (Cucurbitaceae) that occurred in 10%, *Schmidtia pappophoroides* (Poaceae) in 17% and *Stipagrostis uniplumis* (Poaceae) in 33% of the quadrats. *Acanthosicyos naudinianus* and *Schmidtia pappophoroides* occurred more frequently in controls than burrow entrances and impacted areas (*Acanthosicyos naudinianus*: Chi^2 = 27.04, p < 0.001, *Schmidtia pappophoroides*: Chi^2 = 38.73, p < 0.001, Table S.3; Table S.4). *Schmidtia pappophoroides* also occurred significantly less often at fresh than abandoned burrows (Chi^2 = 8.31, p < 0.05, Table S.3; Table S.5).

Stipagrostis uniplumis occurred more frequently in the controls than impacted areas (albeit marginally significant; Chi^2 = 5.70, p = 0.06, Table S.3; Table S.4) and when in the absence of trees (Chi^2 = 10.60, p < 0.01, Table S.3; Table S.6).

4. Discussion

In contrast to expectations, the ameliorating impacts of aardvark burrows on abiotic properties was not always greater in the absence of trees, but varied with either similar, greater or smaller effects in the absence of trees. Both burrowing and trees had significant impacts on the understorey plant community, but there were no significant interactive effects. Therefore, although some of the abiotic impacts (soil moisture and compaction) of burrows differed between tree-shaded and exposed sites, biotic effects of burrowing and trees were independent of one another. This study, therefore, suggests that these two biotic modifier species can have both interactive and independent effects in this semi-arid ecosystem.

In our study, soil temperatures were lower in burrow entrances and the ameliorating effect of burrows became more pronounced as ambient temperatures increased through the day. Burrows play an important role as thermal refugia for organisms in arid and semi-arid environments, where the range of ambient temperatures are high and burrows have smaller thermal fluctuations (Bennett et al., 1988; Roper et al., 2001). Similarly, underneath trees soil temperatures were lower, albeit non-significantly, when compared with soils away from trees (in agreement with Abdallah and Chaieb, 2012). Soil moisture was higher at burrow entrances than undisturbed surrounding soils, possibly due to the accumulation of moisture in burrows (Bulova, 2002; Laundre, 1993), which may be due to reduced evaporative water loss as a result of lower
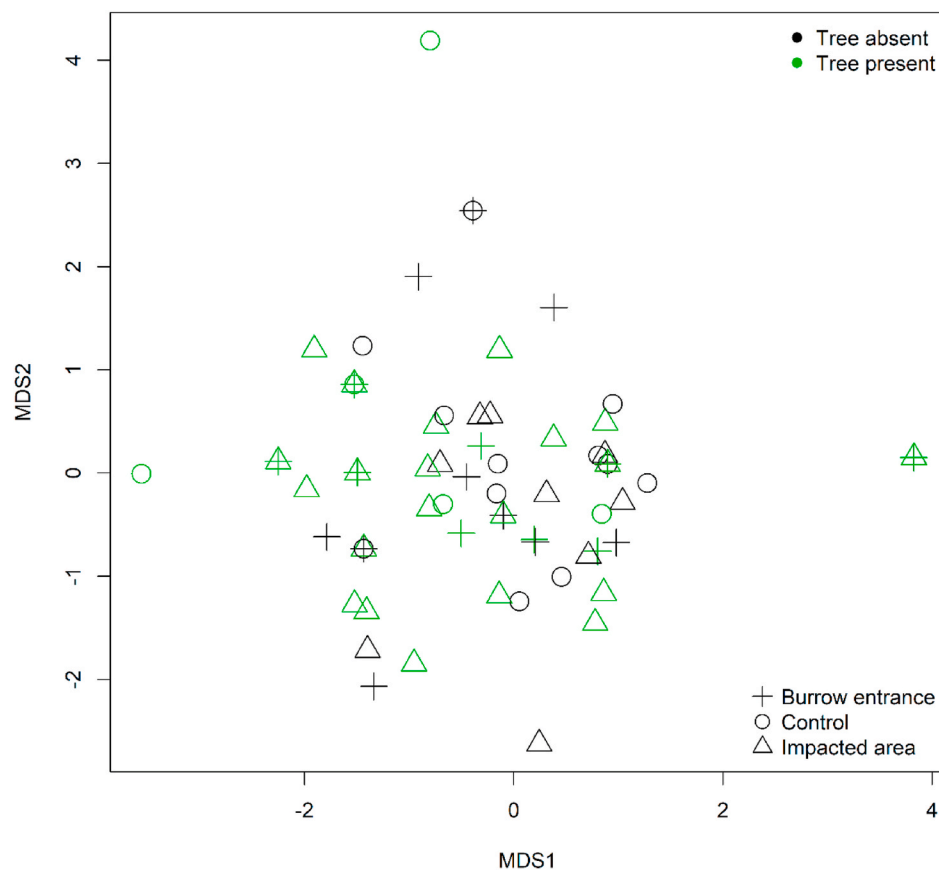
Fig. 4. Non-metric multidimensional scaling ordination of plant species composition in burrow entrances, impacted areas and controls in the presence and absence of trees. Symbols indicate the different microsites (i.e. + = "Burrow entrance", △ = "Impacted area", ○ = "Control"). Black = burrow not associated with a tree, green = burrow associated with a tree.

burrow soil temperatures (Bulova, 2002; Laundre, 1993). Contrary to expectation, however, the increase in soil moisture due to burrowing was more pronounced in the presence of trees, with impacted areas also having a higher soil moisture than undisturbed surrounding areas. We expected the difference between burrowing microsites and controls to be greater in the absence of trees where there is no ameliorating effect of trees, but clearly this is not always the case. Interestingly, in the middle of the day, soil temperatures at burrows without trees were significantly lower than soil temperatures at trees without burrows. This suggests that burrows cool the soil more on a microscale than trees, potentially providing better heat refugia than trees, particularly during times of the day that animals are likely to seek shelter from the sun. Soil moisture, however, did not differ significantly between burrows without trees and trees without burrows, suggesting that burrows and trees have similar moisture capturing abilities.

By digging in burrow entrances and loosening soil, aardvark decreased soil compaction, affecting another key soil property for plant establishment (Whitford and Kay, 1999). In contrast, when trees were absent, aardvark burrowing increased soil compaction at impacted areas surrounding burrows. Most burrows that were associated with trees occurred under *Senegalia mellifera*, a very thorny small tree, which may have excluded trampling and grazing by larger mammal species, thereby protecting burrow mounds. Indeed, although mound soils are generally looser than undisturbed surrounding soils, the increased compaction at burrow mounds in the absence of trees may be attributed to antelope being attracted to, and able to access, burrows away from trees for water after rain (pers. obs.). Since soils underneath *S. mellifera* generally have a higher fertility (Ward et al., 2018) and potentially lower grazing pressure due its thorny low canopy, a higher vegetation cover would be expected. However, we observed the opposite, possibly due to both

shading and the production of secondary metabolites by *S. mellifera* (e.g. tannins and essential oils) that inhibit germination and supress the growth of understorey plants (Ward et al., 2018). Therefore, burrowing affects soil conditions, and depending on the soil property being studied, trees may alter the abiotic conditions beyond the impacts of burrowing or lessen the impacts of burrowing.

Although aardvark burrowing created cooler and moister microhabitats, burrows supported fewer species and lower vegetation cover than surrounding areas (Bruun et al., 2005; Whittington-Jones, 2006). Burrow creation and maintenance by burrowing mammals can cause physical damage to plants (Alkon, 1999), often killing seedlings and even established plants (Wiegand et al., 1997), potentially outweighing the abiotic microhabitat benefits of burrows. In addition, because burrows at this site were created in sandy soils, there was probably an increased need for aardvark to maintain burrow entrances to avoid burrow collapse (Shenbrot et al., 2002), leading potentially to more frequent negative impacts of burrowing on the plants occurring in and around burrows. Furthermore, vegetation cover and species richness were consistently (albeit non-significantly) lower under trees than away from trees. Therefore, both of these biotic modifiers have negative impacts on vegetation, but these effects are independent of one another.

Although burrows generally differ in plant species composition (Coggan et al., 2018), burrows at our site had a similar species composition to undisturbed surrounding soils. Species composition did however differ underneath the canopy of trees and away from trees, although this only explained a small proportion of the variation in community composition. Species composition also differed between burrow age classes, as fresh burrows supported simpler plant communities with lower species richness and vegetation cover than abandoned and collapsed burrows, where burrowing had ceased for a longer time.

The three most widespread species in our samples were all perennial species and occurred less frequently at burrows. Indeed, burrow disturbances often favour the establishment of pioneers and annual plant species (Obidziński and Kieltyk, 2006; Wesche et al., 2007). Additionally, one of the three widespread species, *Stipagrostis uniplumis* (a perennial grass), occurred more frequently in the absence of trees, possibly due to competition with trees for light (Richter et al., 2001). *Stipagrostis uniplumis* has been reported to be particularly intolerant to shade, and has even been shown to die due to self-shading from its own standing dead biomass (Zimmermann et al., 2010).

The temporal extent of the impacts of the two biotic modifiers in this study system differ strongly, with burrows likely having a much shorter lifespan than trees (see e.g. Goodman et al., 2018). Both biotic modifiers also likely have differing impacts on their environment depending on their "age": this is demonstrated for burrow age in this study and has been shown for tree and shrub size in other arid systems (Wang et al., 2020). These temporal effects also have the potential for interactive effects since, although not tested in our study, tree roots likely play an important role in improving the structure and, therefore, longevity of burrows in sandy soils. As a result, the effect of burrows on vegetation properties may possibly have a longer duration underneath the canopy of trees than when burrows are created away from trees. The difference in burrow durability may enhance heterogeneity by creating a shifting mosaic of patches, where burrow effects underneath trees are possibly longer-lived and burrows away from trees probably collapse more easily and converge with the undisturbed surrounding area at a faster rate. Therefore, in addition to monitoring the interactive effects of co-occurring biotic modifiers, we advocate that the monitoring of temporal patterns of their co-occurrence are also important considerations to better understand their potential cumulative interactive impacts.

Species that act as biotic modifiers may strongly affect abiotic conditions, increasing environmental heterogeneity and creating unique combinations of conditions. While our understanding of the species- and location-specific impacts of these species is developing (e.g. Decker et al., 2019; Louw et al., 2019; Momberg and le Roux, 2020), there is considerable potential for interactive effects between biotic modifiers. Moreover, very few studies have examined the interactive effects of biotic modifiers that vary greatly in form and function (e.g. vascular plants and vertebrates) as our study did (although see Eldridge et al., 2010). Based on our results, it may be necessary to include multiple biotic modifiers in studies, as diverse biotic modifiers may not necessarily act independently. In addition, it may be particularly important to test for interactive effects between multiple biotic modifiers, especially where biotic modifiers have strong impacts on biotic or abiotic characteristics, since the loss of these species may have particularly complex and/or unforeseen impacts.

CRediT authorship contribution statement

M.A. Louw: Conceptualization, Formal analysis, Investigation, Data curation, Writing – original draft, Methodology. **N.S. Haussmann:** Conceptualization, Methodology, Writing – review & editing, Funding acquisition. **P.C. le Roux:** Conceptualization, Formal analysis, Writing – review & editing, Methodology.

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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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jaridenv.2021.104504.

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