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# Termite mounds create heterogeneity in invertebrate communities across a savanna rainfall gradient

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# Abstract

Termite mounds create nutrient hotspots that serve as key resource areas for savanna vegetation and mammalian herbivores. However, despite the key ecological roles performed by termite mounds, few studies have investigated their influence on invertebrate communities, and none have examined such effects across environmental gradients. We hypothesised that termite mounds would support greater numbers of invertebrates than the surrounding savanna matrix and that assemblages would differ in composition due to the enhanced nutritional quality of vegetation on mounds. We also predicted that the differences between on-mound and off-mound invertebrate diversity would be more pronounced in areas where the difference in nutritional value between mounds and the savanna matrix vegetation was most prominent. We tested these hypotheses in Kruger National Park, South Africa, by sampling ground- and grass-dwelling invertebrate herbivores, omnivores and detritivores on and at various distances away from termite mounds at three savanna sites of varying vegetation quality across a rainfall gradient. All invertebrate groups sampled responded to termite mounds, but mound influence varied across trophic groups (Orthoptera showed the clearest patterns), diversity measures (changes in abundance rather than species richness) and with mean annual rainfall (strongest effects at the highest rainfall site). Orthoptera were more abundant on mounds, particularly at the wettest site, and there was a positive relationship between mound size and Orthoptera species richness. Ant assemblage composition on mounds differed from that off mounds and beetle abundance was greater on mounds, possibly as a result of concentrated mammalian herbivore activity and faecal deposition on mounds. Our results suggest that termite mounds are not only important nutrient and foraging hotspots for vertebrates, but that they also introduce heterogeneity in invertebrate communities, especially in nutrient-poor savannas.

**Keywords:** Coleoptera, Formicidae, heterogeneity, Kruger National Park, *Macrotermes*, nutrient hotspots, Orthoptera, ants, beetles, grasshoppers

# Introduction

Understanding the relationship between environmental heterogeneity and biodiversity patterns is important for describing and predicting patterns of species assembly and drivers of ecosystem processes (Du Toit, Rogers & Biggs 2003; Tews *et al.* 2004; Parr & Andersen 2006). The spatial heterogeneity of environmental resources causes the composition of species assemblages to change in complex ways across landscapes. Increased heterogeneity may increase the diversity of available niches and facilitate the co-occurrence of competing species, resulting in increased species richness (Du Toit & Cumming 1999; Palmer 2003; van Rensburg *et al.* 2004). Environmental heterogeneity and the processes creating it are of particular interest in savannas, which are globally widespread and inherently complex due to the co-dominance of trees and grass and the frequency of spatially varying disturbances such as fire and herbivory (Scholes & Archer 1997).

Ecosystem engineers such as termites are important drivers of fine-scaled environmental resource partitioning, and generate high levels of spatial heterogeneity across savanna landscapes through activities that alter local environmental conditions (Dangerfield, McCarthy & Ellery 1998). Some fungus-growing termites (Blattodea: Termitoidae) construct large epigeal nests, which are considered keystone structures in savannas because of the profound effects they have on surrounding soil properties, vegetation communities and mammalian grazing patterns. Soils on and around termite mounds are often nutrient-enriched (Seymour *et al.* 2014) and harbour distinct floristic communities with higher levels of foliar nutrients (Moe, Mobæk & Narmo 2009; Sileshi *et al.* 2010; Davies *et al.* 2014b). Mammalian and insect herbivores are consequently attracted to mounds and forage on the nutrient-rich vegetation growing on them (Mobæk, Narmo & Moe 2005; Levick *et al.* 2010; Davies *et al.* 2016a; Davies *et al.* 2016b), sometimes leading to altered fire patterns (Sileshi *et al.* 2010) and influencing the structure of savanna ecosystems.

The extent to which termite mounds influence surrounding vegetation, and consequently mammalian herbivory patterns, is, however, not uniform across landscapes, with mounds in nutrient-poor savannas exerting a greater effect on their surroundings than those in nutrient-rich savannas (Davies *et al.* 2014b; Muvengwi *et al*. 2017). Mean annual precipitation is an important determinant of savanna vegetation quality, with high rainfall savannas experiencing greater rates of soil leaching and denitrification that results in vegetation of poorer nutritional quality compared with drier savannas (Scholes & Archer 1997). Consequently, termite mounds in high rainfall savannas can serve as nutritional hotspots. This is in stark contrast to their otherwise nutrient-poor surroundings (Erpenbach *et al.* 2013; Davies *et al.* 2014b). These findings demonstrate the need to examine termite mounds across environmental gradients when attempting to understand their potential for introducing heterogeneity in these systems (Davies 2013).

Substantial work has been carried out in African and Indian savanna systems on the role of termite mounds, constructed by various fungus-growing species, in introducing heterogeneity to soil properties, vegetation and herbivory patterns (e.g. Jouquet *et al*. 2017; Levick *et al.* 2010; Okullo & Moe 2012; Sileshi *et al.* 2010; Seymour *et al.* 2014; Davies *et al.* 2016b). Yet, the effects on invertebrate diversity around mounds have received comparatively little attention. This despite invertebrates representing the majority of global animal diversity and biomass, and performing critical roles in savanna ecosystem functioning (Kim 1993; Dangerfield *et al.* 1998; Braack & Kryger 2003). Termitophiles are invertebrates that are directly associated with termites and live inside their mounds, and have captured the attention of entomologists since the early 1900s (e.g. Warren 1919). However, to our knowledge only two studies have examined invertebrate diversity in response to an altered external environment around termite mounds, as opposed to within them. Pringle *et al.* (2010) found aerial and arboreal invertebrates to occur in greater abundances near mounds than further away and suggested that mounds act as local centres from which arthropods disperse. In contrast, Nduwarugira *et al.* (2016) found spider communities to be generally unresponsive to termite mounds. Given the paucity of studies, and mixed results, there remains a need to understand the effects of mounds on invertebrate communities across landscapes and functional groups (e.g. herbivorous, predatory and omnivorous invertebrates), especially given the varied responses of vegetation and mammalian herbivory across rainfall gradients (Davies *et al.* 2014a, 2016b). Furthermore, effects of termite mounds on ground- and grass-dwelling invertebrate diversity remains unexplored.

Here, we assess whether termite mounds built by termites in the genus *Macrotermes*, and mostly by *M. falciger*, influence the diversity of several ground- and grass-dwelling invertebrate groups, and how these patterns might vary across a rainfall gradient. Although effects were expected to vary across taxa, we predicted that mounds would enhance invertebrate diversity by providing universally favourable resources (e.g. nutritious vegetation, an increase in available prey species and an increased variety of microhabitats and shelter for invertebrates).

We selected grasshoppers (Orthoptera) because they represent important invertebrate herbivores (Sinclair 1975; van der Plas & Olff 2014), predicting that their abundance and species richness would be highest on termite mounds where vegetation is of higher nutritional value than the surroundings. We also sampled beetles, with particular attention given to Scarabaeinae (true dung beetles) because these detritivores were expected to respond positively to increased mammalian herbivore presence, and subsequent dung deposition (a food resource), on and around termite mounds. Lastly, we assessed ant diversity on and off mounds because they are a dominant invertebrate group, highly abundant in savannas and relatively sensitive to changes in environmental conditions (Folgarait 1998; Philpott *et al.* 2010). Ant diversity has previously been shown to increase with net primary productivity in savanna systems (Parr *et al.* 2004), and as such, ant diversity was expected to be highest on mounds because of the generally higher productivity associated with higher quality mound soil and vegetation. Since our predictions for termite mound effects were based largely on nutritional differences in vegetation, we also expected herbivorous insect groups, i.e. grasshoppers, to respond more strongly than other groups (Loaiza *et al.* 2011; Cárdenas *et al.* 2014). Finally, since mound effects on vegetation communities and mammalian herbivory patterns vary across rainfall gradients, with stronger effects recorded in higher rainfall sites (Davies *et al.* 2014b, 2016a), we predicted similarly stronger effects on invertebrate communities at the highest rainfall site.

# Methods

## Study area

The study took place in three savanna sites in the southern region of the Kruger National Park, South Africa. The driest site, Skukuza (25°02'S, 31°30'E), was characterised by *Acacia nigrescens* and *Combretum apiculatum* thickets and received a mean rainfall of 550 mm.year-1 (Gertenbach 1983). Dominant grasses on termite mounds included *Panicum maximum* and *Urochloa mosambicensis*, while in the surrounding savanna matrix *P. maximum*, *Pogonarthria squarrosa*, *Digitaria eriantha* and *Brachiaria nigropedata* were common (Davies *et al.* 2014b). The highest rainfall site, Pretoriuskop (25°12'S, 31°16'E), was an open tree savanna dominated by *Terminalia sericea* and *Dichrostachys cinerea* (Gertenbach 1983) and had a mean rainfall of 750 mm.year-1 (Gertenbach 1983). *Cynodon dactylon* and *P. maximum* were dominant grasses on termite mounds, while the savanna matrix was characterised by *Setaria sphacelata*, *Loudetia simplex*, *P. squarrosa* and *Schizachyrium sanguineum* (Davies *et al.* 2014b). The third site, Napi (25°06'S, 31°27'E), fell within a transitional zone between Skukuza and Pretoriuskop and was characterized as a woodland savanna dominated by *Combretum collinum* and *C. zeyheri* and had a mean rainfall of 650 mm.year-1 (Gertenbach 1983). Common grasses on termite mounds were *P. maximum* and *U. mosambicensis*, whereas *D. eriantha*, *Eragrostis rigidior* and *P. squarrosa* were commonin the savanna matrix (Davies *et al.* 2014b).

*Mound selection and characteristics*

Within each savanna site, we selected 10 termite mounds built by the genus *Macrotermes*, which was apparent based on the physical characteristics of the mounds. Although not directly sampled from every mound studied, the overwhelmingly dominant species in the region was *M. falciger* (Davies *et al*. 2014a). Termite mounds are incredibly long-lasting structures that remain on the landscape for millennia, much exceeding the lifetime of the individual colony that built them (Erens *et al.* 2015). Due to repeated recolonization by termite colonies (Collins 1980; Darlington 1985), mound effects on soils are also long-lasting, making the identity of the building species of less importance than the structures themselves. Selected mounds were spaced at least 40 m from the nearest neighbouring mound because mounds in our study site have been shown to influence herbivory patterns up to 20 m from their centre (Levick *et al.* 2010; Davies *et al.* 2016a); a 40 m spacing therefore ensured that effects measured at a given mound were not influenced by surrounding mounds. For each mound we recorded the mean diameter (taken as the mean of the north-south and east-west axes of the mound periphery, which was defined as the location where the mound slope became horizontal and/or comparable to that of the surrounding savanna matrix) and the percentage of vegetation cover (proportion of the mound covered by grass).

## Invertebrate sampling

Sampling took place during the austral summer (January 2012) when invertebrate activity is at its peak in southern African savannas (Swart, Richardson & Ferguson 1999; Parr *et al.* 2004). Orthoptera were sampled by sweep netting (∅400 mm net), with 24 sweeps performed at each of the following distance intervals: 1) on the mound, 2) around the mound at a radius of 10 m; and 3) a radius of 20 m from the mound (Fig. S1). While all Orthoptera were used for abundance scores, only adult specimens were used for species richness and community composition analyses because of difficulties associated with identifying nymphs to species level.

Beetles and ants were sampled with pitfall traps (∅ 55 mm, volume 150 ml) containing a propylene glycol-water solution as a fluid and preservation agent. Traps were placed along transects radiating from the centre of each mound in six directions and were left open for five days. The starting transect direction was chosen at random and subsequent transects were spaced 60˚ apart. This circular arrangement was used to account for possible directional influences. Each transect consisted of four pitfall traps, one at each of the following distance intervals: 1) on the mound approximately midway between the peak and the base, 2) at the base of the mound, 3) 10 m from the mound, and 4) 20 m from the mound (Fig. S1). Thus, there were a total of six pitfall traps at each distance interval per mound. Rain covers (plastic lids, ∅ 270 mm) were placed over the traps to prevent flooding. Apart from distinguishing between overall beetle abundance and that of Scarabaeinae (true dung beetles), beetles were not identified and were therefore not included in any analysis of species richness. Ants were identified to species and morphospecies.

## Analysis

Mound vegetation data were arcsine transformed to meet assumptions of normality and a one-way analysis of variance (ANOVA) was used to determine whether mound diameter and vegetation cover differed among sites.

We constructed candidate sets of linear mixed effects models with Poisson error distributions using the R package *lme4* to assess variation in the abundance of Orthoptera, beetles and ants, as well as the species richness of Orthoptera and ants in relation to site (rainfall), distance from the mound and mound diameter. The interaction between site and distance from the mound was also included in the model sets to assess how the strength of mound spatial influence varied across the rainfall gradient. Mound identity was modelled as a random effect in all models. Model selection was then performed using sample-size-corrected Akaike Information Criterion (AIC*c*) and the Akaike weights of the constructed models (see Tables S1, S3, S5, S7 and S8). The significance of variables present in the most parsimonious model for each dataset were assessed using a Type 3 Wald Chi-squared test in the R package *car*.

We compared differences in Orthoptera and ant species assemblages across sites (aggregated across distance intervals) and distance intervals (aggregated across sites). The data were fourth root transformed to balance rare and common species’ contributions to community structure, after which Bray-Curtis similarity measures and two-way crossed analyses of similarity (ANOSIMs) were used in the software package PRIMER v 5.2.9 (Clarke & Warwick 2001). One-way ANOSIMs were used to compare assemblages among distance intervals within each site separately. ANOSIM produces an R-statistic as a measure of dissimilarity between assemblages, which ranges from -1 (indicating more variation within rather than between assemblages) to 1 (highly dissimilar assemblages). Values of 0 indicate highly similar assemblages. Non-metric multi-dimensional scaling (nMDS) ordinations were used for visual illustration of assemblage variation across sites and distance intervals. An indicator value (IndVal) analysis (Dufrene & Legendre 1997) was performed using the R package labdsv (http://ecology.msu.montana.edu/labdsv/R) for the ant and Orthoptera data to determine whether any species were characteristic of a particular distance interval or site. Species with a significant (p < 0.05) IndVal value of > 0.70 were considered to be adequate indicators for a particular distance or site (subjective benchmark; McGeoch *et al*. 2002).

# Results

## Mound characteristics

Termite mound diameter differed across the rainfall gradient (ANOVA, F2,27 = 10.17, p < 0.01), with the smallest mounds found at the highest rainfall site (Pretoriuskop: 6.65 ± 0.11 m, mean diameter ± SE). The intermediate and driest sites had larger mounds of similar size (Napi: 8.74 ± 0.21 m; Skukuza: 9.61 ± 0.11 m). The amount of grass cover on mounds did not differ significantly across the three sites (F2,27 = 1.75, p = 0.19).

## Orthoptera

We collected 1 014 individual Orthoptera across all sites, of which 81% were nymphs. Orthoptera abundance displayed a negative pattern with increasing rainfall, with most individuals sampled around mounds (all distance intervals combined) at the driest site (Skukuza: 41.40 ± 5.10, mean ± SE per mound), followed by the intermediate site (Napi: 33.00 ± 3.86) and lastly the wettest site (Pretoriuskop: 27.00 ± 2.82). However, site alone did not adequately explain changes in Orthoptera abundance (χ2 = 0.65, df = 2, p = 0.72). In contrast, distance from termite mound had the greatest influence on Orthoptera abundance across sites (χ2 = 17.95, df = 2 p < 0.01), with significantly more individuals sampled on termite mounds than at 10 m (z = 4.55, p < 0.01) or 20 m (*z* = 6.28, p < 0.01) away from mounds. Mean annual rainfall influenced the pattern of higher Orthoptera abundance on mounds, evidenced by the significant interaction between site and distance to mound (χ2 = 27.53, df = 4, p < 0.01), with the strongest patterns recorded at the wettest site, Pretoriuskop (Fig. 1a).

Twenty-six species of adult Orthoptera, as well as seven unknown morphospecies, were identified (Table S2). Distance from mound (χ2 = 8.99, df = 2, p < 0.05) and mound diameter (χ2 = 6.79, df = 1, p < 0.01) significantly influenced Orthoptera species richness, with higher species richness on mounds compared with the 10 m (z = 2.43, p < 0.05) and 20 m distance intervals (z = 2.31, p = 0.05), and larger mounds hosting more species than smaller ones (z = 2.47, p < 0.05). Site (rainfall) was not a significant driver of species richness, although there was a decreasing trend in species richness with increasing rainfall, with a mean of 6.50 ± SE of 0.76 species per mound sampled at the driest site, Skukuza, followed by 5.70 ± 0.76 species at the intermediate site, Napi, and 3.40 ± 0.49 species at the wettest site, Pretoriuskop.

Orthoptera species assemblages differed little between sites and the only significant difference occurred between the extreme rainfall sites (Skukuza *vs.* Pretoriuskop: R = 0.16, p < 0.01, two-way crossed ANOSIM), although the effect size was small and the difference was likely not biologically meaningful. Distance from mounds also had little influence on Orthoptera assemblages when aggregated across sites, with only a weak difference between the base of the mound and 20 m away from mounds (R = 0.09, p < 0.05; Table S4), or within individual sites, where only a weak difference between on the mound and 20 m away from mounds was recorded at the driest site, Skukuza (R = 0.19, p < 0.05). No indicator species were identified for a particular site or distance interval.

## Beetles

We collected 1 117 beetles across all sites, with site (χ2 = 29.87, df = 2, p < 0.01), distance from mound (χ2 = 41.49, df = 3, p < 0.01) and the interaction between site and distance (χ2 = 18.31, df = 6, p < 0.01) significantly affecting beetle abundance. There were significantly more beetles at the intermediate and driest sites (Napi: 46.40 ± 3.10; Skukuza: 40.20 ± 3.10, mean ± SE per mound), than the wettest site (Pretoriuskop: 22.00 ± 3.50). The intermediate site (Napi) had the most pronounced difference in abundance, with beetle abundance being much higher on and around the base of mounds compared with the 10 m and 20 m distance intervals (Fig. 1b). Scarabs comprised 29.20 % of all beetles sampled at Napi, 19.30 % at Pretoriuskop and 15.10 % at Skukuza (n = 240 scarabs across all sites).

## Ants

We collected 21 019 ants across all sites, with site (χ2 = 83.25, df = 2, p < 0.01) and distance from mound (χ2 = 1569.14, df = 3, p < 0.01) significantly influencing abundance. Ant abundance increased with rainfall, with the most individuals sampled at Pretoriuskop (1049.90 ± 49.31, mean ± SE per mound), followed by Napi (725.20 ± 110.87) and then Skukuza (326.80 ± 54.02). Patterns in ant abundance with distance from mound varied across sites, with a significant interaction between site and distance from mound (χ2 = 1351.18, df = 6, p < 0.01). The clearest effect was observed at the intermediate rainfall site, Napi, with higher ant abundance on and around the base of mounds compared with low abundance at both distance intervals away from mounds (Fig. 1c).

We identified 90 ant morphospecies from 32 genera (Table S6). Site was the only variable that significantly influenced ant species richness (χ2 = 131.5, df = 2, p < 0.01), with more species sampled at high rainfall sites (Pretoriuskop, highest rainfall: 24.46 ± 0.46 per mound; Napi, intermediate rainfall: 11.88 ± 0.40; Skukuza, lowest rainfall: 13.74 ± 0.30).

Ant assemblages at the wettest site, Pretoriuskop, differed significantly from assemblages at the drier sites (Napi: R = 0.84, p < 0.01; Skukuza: R = 0.80, p < 0.01), which in turn differed less from each other, although still significantly so (R = 0.43, p < 0.01). Termite mounds influenced ant assemblages, with composition on and off mounds differing across all sites (R = 0.23, p < 0.01). The largest differences were recorded at Skukuza and Pretoriuskop between assemblages on the mound and 20 m away (Fig. 3), whereas at the intermediate site, Napi, differences in ant assemblages with increasing distance from mounds were less pronounced and assemblages 10 m and 20 m away from mounds were equally dissimilar to those on mounds (Fig. 3). The nMDS plots in Fig. 3 should be interpreted with caution given the stress levels of > 0.2 (Clarke 1997). However, they serve as a useful visualisation tool and we base our interpretation of community composition change with distance from mounds predominantly on the R statistics from the ANOSIM (Fig. 3).

The wet and intermediate sites, Pretoriuskop and Napi, had several reliable ant indicator species at the site level, while the dry savanna, Skukuza, had none (Table 1). No indicator species were found for either of the four distance categories (on mound, base of mound, 10 m and 20 from mound) within each site. However, some indicator species were found when the distance categories were combined into an ‘on mound’ (on mound and base of mound) and ‘off mound’ (10 m and 20 m) category. The wettest site, Pretoriuskop, was the only site to have indicator species for both the ‘on mound’ and ‘off mound’ categories, while the intermediate site only had an ‘on mound’ indicator species, and the driest site only had on ‘off mound’ indicator species (Table 1).

# Discussion

Our results demonstrate that termite mounds promote savanna diversity through their influence on a range of invertebrate groups. We further show that mound effects vary with both functional group and environmental context: herbivores (Orthoptera) showed the clearest patterns of high abundance on mounds and decreasing abundance with distance from mounds, and mound effects were most pronounced in wetter, nutrient-poor savanna sites. Therefore, termite mounds enhance productivity in savannas not only through changes in edaphic conditions, vegetation nutrition and composition, mammalian and insect herbivory patterns and fire regimes (Mobæk *et al.* 2005; Levick *et al.* 2010; Sileshi *et al.* 2010; Seymour *et al.* 2014; Davies *et al.* 2016a; Davies *et al.* 2016b), but also through changes in invertebrate diversity and community structure.

*Mounds promote invertebrate diversity*

The suggestion that termite mounds act as local centres from which arthropods disperse (Pringle *et al.* 2010) is largely supported by our finding of higher invertebrate abundance on and around mounds compared with the surrounding matrix. Mounds served as key resource areas for savanna arthropods and influenced their diversity in multiple ways, with grasshoppers showing the clearest responses. Increased grasshopper abundance on mounds, which was particularly evident at the wettest site where the surrounding vegetation quality was generally poor, matches our predictions of mounds benefitting invertebrate herbivores through enhanced vegetation quality known to benefit mammalian and insect herbivores (Loaiza *et al.* 2011; Davies *et al.* 2014b, 2016b). However, mounds did not affect Orthoptera species richness or assemblage composition, suggesting the that benefit of mound vegetation is not species specific for these invertebrate herbivores, as is also the case for mammals where almost all species are similarly attracted to mound vegetation (Mobæk *et al.* 2005). However, we were only able to identify a small proportion of our Orthoptera specimens, due to the predominance of nymphs in the dataset, and mound effects on Orthoptera species richness and composition warrants further investigation.

Beetle abundance was similarly positively affected by termite mounds, with the clearest patterns being evident at the intermediate rainfall site, Napi. The high beetle abundance around mounds at Napi was largely driven by a high number of scarabs sampled here. Napi also had the greatest mammalian herbivore biomass across our sites, with concurrent high grazing intensity on and around mounds (Davies *et al.* 2016a). It is therefore possible that beetles, and particularly scarabs, were attracted to mounds at this site due to increased mammalian dung around mounds, which could serve as a food resource. Although mammalian herbivores might be expected to spend more time feeding on mounds at the wettest site (Pretoriuskop) given the poorer quality of matrix vegetation here, the combination of low herbivore biomass and small mound size (Davies *et al.* 2016a) at this site likely led to less dung being deposited at these mounds, and subsequently lower beetle abundance and less distinct patterns of beetle abundance with distance from mounds here.

Ant abundance was also highest on mounds at the intermediate rainfall site, Napi. Although not directly tested here, it is possible that the high abundance of invertebrates (Orthoptera, beetles and ants) at this intermediate site was fostered by the combination of large mound size (leading to more suitable habitat to house and/or shelter insects in mound vegetation or soil) and increased herbivore dung (i.e., increased food availability). In addition, changes to vegetation structure, and consequently microclimate, can influence ants, with ant communities strongly structured by litter cover and bare ground elsewhere in Kruger (Parr *et al.* 2004). Indeed, *Ocymyrmex* sp. 1 was identified as an indicator species of mounds at our intermediate site, Napi. This ant genus is well known for its thermophilic characteristics, and the habitat specificity of this species on mounds at this intermediate site was likely promoted by the high on-mound grazing pressure by mammalian herbivores here. Increased grazing likely increased *Ocymyrmex* habitat suitability by reducing vegetation height, increasing sun exposure and raising soil surface temperatures.

Although less apparent, ant abundance was also higher at the base of mounds at the wettest site, Pretoriuskop, but was unchanged across distance categories at the driest site, Skukuza. Greater ant abundance on or near mounds at the wetter sites suggests that mounds here represent more productive habitats that can sustain larger ant populations, although it is unclear from our data exactly which resources attracted ants to mounds at these sites. In contrast, ant species richness was largely unaffected by distance to termite mounds at all sites, although fewer species were sampled on mounds than off them at the driest and wettest sites. This finding concurs with other studies (e.g., Hoffmann 2010) that have found ant species richness to be less affected by disturbance than either abundance or composition. Ant assemblages at the extreme sites on the rainfall gradient (Skukuza and Pretoriuskop) became increasingly dissimilar with increasing distance from mounds (assemblages on mounds were most different from those 20 m away), mirroring findings for soil and vegetation properties (Jouquet *et al.* 2006; Moe, Mobæk & Narmo 2009; Sileshi & Arshad 2012). Additionally, mounds did not host consistent indicator species across the rainfall gradient, and only the wettest site had indicator species for both the on-mound and off-mound categories. This lack of consistent indicator species suggests that termite mounds create heterogeneous habitats that favour different and varied ant species across savanna types, rather than benefitting only a few select species, thereby introducing a large amount of heterogeneity to savanna ecosystems.

*Mound effects vary across the rainfall gradient*

As the nutritional quality of herbaceous savanna vegetation decreases with increasing rainfall, mammalian herbivores become increasingly dependent on termite mounds for quality forage (Davies *et al.* 2016a). Our results suggest a similar increasing mound dependency for some insect groups with decreasing vegetation nutrition: most clearly for Orthoptera, but with ants also displaying variable responses across the rainfall gradient. In contrast, beetle abundance showed the opposite pattern, with the fewest individuals and weakest effect of mounds at the wettest site, Pretoriuskop. Instead, the overall pattern of increased beetle abundance around mounds at the drier sites follows large-scale differences in mammalian herbivore biomass across our sites, which was highest at the intermediate site followed by the driest site. This correlation with mammalian biomass suggests that beetles are either influenced by similar factors regulating larger-scale mammalian herbivores (e.g. matrix vegetation quality) or that they benefit directly from increased mammalian herbivore biomass (e.g. benefiting from the higher volume of mammalian dung deposits). The clear increase in beetle abundance, albeit largely driven by scarabs, on mounds at the intermediate site where mammalian herbivory is strongly concentrated on mounds (Davies *et al.* 2016a) suggests the latter, i.e. a direct benefit of increased dung availability.

*Conclusion*

Our results demonstrate that termite mounds influence invertebrate diversity across a range of trophic groups and suggest that their influence is manifest through multiple interactions between the abiotic (e.g. soil properties, fire regimes and annual rainfall) and biotic (e.g. vegetation properties and herbivory patterns) environment. By quantifying the effects of termite mounds on invertebrate communities across an environmental gradient, we provide support for the importance of termite mounds in maintaining heterogeneous invertebrate communities, with implications for savanna biodiversity and the generation of fine-scaled heterogeneity beyond that already established for vegetation and mammalian herbivory patterns. Although we investigated effects of mounds across a rainfall gradient, future work that assesses whether annual (e.g. drought) or seasonal changes in rainfall alter these observed responses in invertebrate communities would be further enlightening. Additional research could also explore which microhabitat alterations on mounds (vegetation structure, soil porosity, increased food availability (i.e. herbivore dung or more nutritious vegetation)) are most influential to the observed patterns of invertebrate diversity.

Our findings add to a growing body of evidence suggesting that areas containing large termite mounds and/or high densities of mounds could be of particular importance for biodiversity conservation, and that protecting and maintaining such areas could conserve a range benefits associated with these structures. In light of our findings, mounds are particularly important to consider for Orthoptera conservation in areas of high rainfall. How termite mounds complement other drivers of fine-scaled heterogeneity (e.g. grazing lawns away from mounds) and whether they represent unique habitats for invertebrates that cannot be replaced by other drivers are open questions that warrant further investigation and may further highlight the need to consider termite mounds in conservation planning.

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# Table 1. Ant species identified as indicators of a particular distance categories or site. Species with a significant (denoted with an asterix) indicator value > 0.70 were considered.

|  |  |  |  |
| --- | --- | --- | --- |
| **Site** | **Scale** | **Indicator species** | **Indicator value** |
| Pretoriuskop | site | *Pheidole* sp.2 | 0.82\* |
|  | site | *Pheidole* sp.9 | 0.70\* |
|  | on mounds | *Pheidole* sp*.* 6 | 0.70\* |
|  | off mounds | *Bothroponera crassa* | 0.81\* |
| Napi | site | *Crematogaster* sp*.*2 | 0.82\* |
|  | site | *Monomorium albopilosum* | 0.85\* |
|  | site | *Monomorium* sp.4 | 0.74\* |
|  | site | *Tapinoma* sp.1 | 0.70\* |
|  | on mounds | *Ocymyrmex* sp.1 | 0.72\* |
|  | off mounds | *-* | - |
| Skukuza | site | **-** | **-** |
|  | on mounds | *-* | *-* |
|  | off mounds | *Monomorium junodi* | 0.73 |

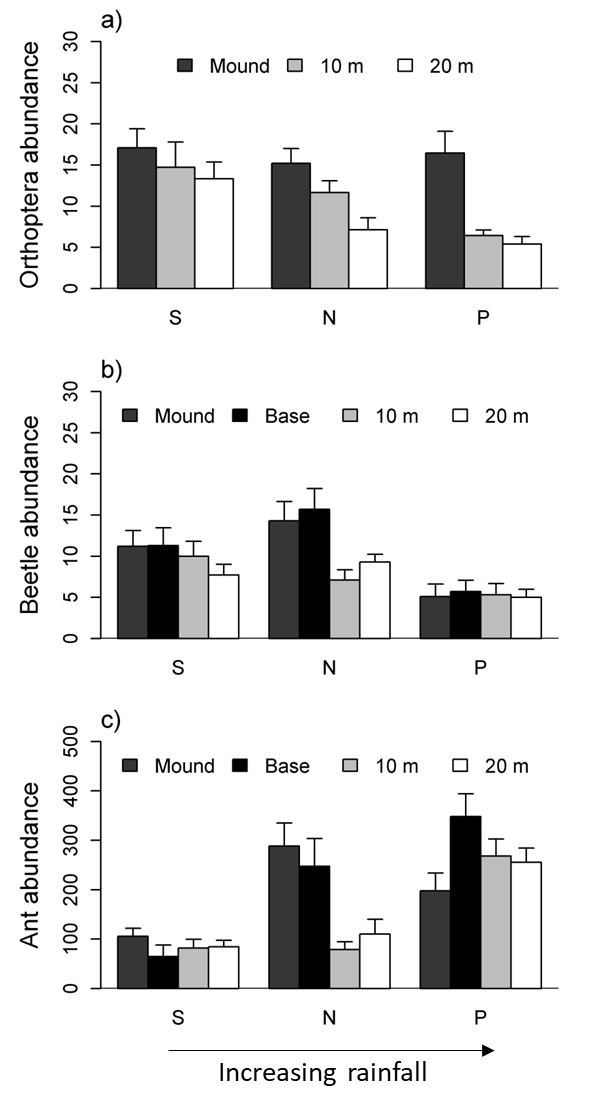
**Figure legends**

**Figure 1.** Mean abundance of a) Orthoptera, b) beetles and c) ants across distance intervals from termite mounds at three sites in the Kruger National Park, South Africa: Skukuza (S), Napi (N) and Pretoriuskop (P). Sites are arranged in order of increasing mean annual precipitation. Error bars denote standard error (SE). Orthoptera were sampled by sweep netting on and around the base of mounds collectively, and at 10 m and 20 m from mounds. Ants and beetles were sampled with pitfall traps on mounds, around the base of mounds, at 10 and at 20 m away from mounds.

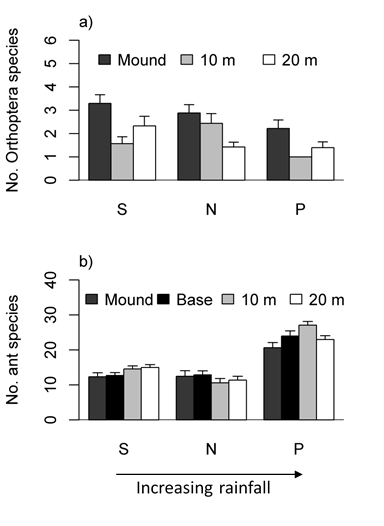
**Figure 2.** Mean species richness of a) Orthoptera and b) ants across three distance categories from termite mounds at three sites in the Kruger National Park, South Africa: Skukuza (S), Napi (N) and Pretoriuskop (P). Sites are arranged in order of increasing mean annual precipitation. Error bars denote standard error (SE). Orthoptera were sampled by sweep netting on and around the base of mounds collectively, and at 10 m and 20 m from mounds. Ants and beetles were sampled with pitfall traps on mounds, around the base of mounds, at 10 and at 20 m away from mounds.

**Figure 3.** Non-metric multidimensional scaling (nMDS) ordinations of ant assemblages sampled at distance categories from termite mounds at three sites across a rainfall gradient in Kruger National Park, South Africa: a) Skukuza, b) Napi and c) Pretoriuskop. Ordinations are displayed on the left with corresponding bar graphs on the right representing changes in the R-statistic (with values ranging from 0 (most similar) to 1 (most dissimilar)) from a one-way ANOSIM between assemblages on mounds and at various distances away from mounds. Assemblages at 10 m and 20 m differed significantly (p < 0.05, denoted by \*) from those found on mounds across all sites.

**Figure 1**



**Figure 2**

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**Figure 3**