

ARTICLE

Context-dependent directional effects of termite mounds on soil nutrients, vegetation communities, and mammalian foraging

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Abstract

Termite mounds are keystone structures in African savannas, affecting multiple ecosystem processes. Despite the large size of termite mounds having the potential to modify conditions around them, patterns of mound-induced ecosystem effects have been assumed to be isotropic, with little attention given to how effects might vary around mounds. We measured soil nitrogen content, grass species composition, and mammalian grazing on and off termite mounds in the four cardinal directions, and across wet and dry seasons at three savanna sites varying in mean annual rainfall in South Africa's Kruger National Park. Evidence of directional effects (anisotropy) on ecosystem properties around termite mounds varied with site. Grass species composition differed between north- and south-facing slopes at the two drier sites where mounds were taller. However, differences in grazing extent and soil nitrogen content around mounds were only present at the intermediate rainfall site where mammalian herbivore biomass was highest, and mounds were of medium height. Our results suggest that termite mound effects display significant variation with direction, but that the emergence of directional effects is context dependent. Our results further suggest that such context-dependent directional effects can lead to positive feedback loops between termites, abiotic conditions, and mammalian herbivores.

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KEYWORDS

anisotropy, aspect, feedbacks, grazing, Kruger National Park, *Macrotermes*, savanna, soil nutrients, termites

INTRODUCTION

Patterns in nature are rarely omnidirectional. Instead, directional effects (i.e., anisotropy) are evident in many ecological phenomena, such as seed dispersal occurring more frequently in the direction of the prevailing wind direction (Trakhtenbrot et al., 2014), or the movement of soil particles and nutrients downslope due to gravity and associated water movement (Stieglitz et al., 2003). Vegetation patterns can also be strongly dictated by aspect, with distinct plant communities found on north- and south-facing slopes (Holland & Steyn, 1975). Directional effects are also evident in sessile organisms such as forest trees growing in directions of increased light (Aakala et al., 2016), and coral recruitment being influenced by the direction of the prevailing ocean current (Maida et al., 1995). Directional effects exhibited by large structures, such as tree canopies, could conceivably cascade to affect other organisms that are dependent on these structures. However, such cascading effects of anisotropy have been largely untested.

Termite mounds are keystone structures in savanna landscapes. Mound-building termites reorganize the physical and chemical composition of soils in and around mounds and, through their foraging, concentrate nutrients and moisture within mound soils, creating nutrient and moisture hotspots (Davies, Levick, et al., 2016; Seymour et al., 2014). These nutrient- and moisture-rich patches lead to multiple cascading effects on both vegetation and animal communities that can extend beyond the mounds themselves to influence large areas of savanna landscapes. For example, distinct woody and herbaceous plant communities, differing in species composition and nutrient content, are found on and around termite mounds (Davies, Robertson, et al., 2014; Moe et al., 2009), and there is elevated insect and mammalian herbivory on mound vegetation (Davies, Van Rensburg, et al., 2016; Levick et al., 2010). Nutrient and moisture enrichment on mounds has been assumed to be equivalent across the mound surface, that is, isotropic. Yet mounds can be large (tens of square meters), and mound structure could cause localized within-mound differences in the magnitude of mound effects, arising from, for instance, variation in shading or mound slope steepness. Such variation could lead to consistent differences in the magnitude of effects across directions (e.g., aspect effects induced by shading). Effects of mounds on their surrounding environment

have similarly been assumed to be isotropic (Sileshi & Arshad, 2012), but directional differences in intra-mound properties, or in the matrix, could cause these effects to exhibit anisotropy. For example, variable terrain around mounds could lead to increased erosion and nutrient enrichment downslope of mounds, yet such effects have not been quantified.

Termite mound effects have also been suggested to create feedback loops between termites and mammalian herbivores. Elephants (*Loxodonta africana*), for example, benefit from feeding on nutritious mound vegetation and are suggested to increase coarse woody debris around mounds through their wasteful foraging habits, which in turn assists termites through increasing food supply (Holdo & McDowell, 2004). If termite mounds exhibit directional effects that influence on-mound vegetation patterns, herbivory patterns could follow these directional patterns and potentially reinforce them by enhancing the growth of herbivory-tolerant plant species on some sides of mounds. Moreover, herbivores are more likely to deposit waste on sides of mounds where they forage, further biasing nutrient enrichment. While studies have consistently documented increased herbivory of mound vegetation (Davies, Levick, et al., 2016; Moe et al., 2009; Sileshi & Arshad, 2012), none, to our knowledge, have investigated how such herbivory might interact with intra-mound characteristics and potentially lead to variation across mound surfaces and into the surrounding matrix.

Here, we aimed to (1) determine whether termite mound effects on soil nutrients, grass species composition, and mammalian grazing patterns exhibit anisotropy, and (2) if anisotropy is present, whether directional effects differ across seasons and with mean annual rainfall. We predicted that stronger directional effects would be evident in areas with taller mounds due to increased shading effects, which would lead to increased differences between plant communities on opposite sides of termite mounds. Furthermore, we expected mounds in higher rainfall, nutrient-poor savanna sites to exhibit stronger directional effects because herbivores in these landscapes would be more reliant on mound vegetation due to stronger differences between mound and non-mound (i.e., matrix) vegetation (Davies, Levick, et al., 2016; Davies, Robertson, et al., 2014). We predicted that increased herbivory in these landscapes would be concentrated on mound slopes that had higher cover of

nutrient-rich vegetation, but that feedbacks between herbivores and directional variation in mound effects would interact with mound height to strengthen anisotropy so that the strongest directional effects would be evident around tall mounds in nutrient-poor savannas.

METHODS

Study site

The study took place in three savanna vegetation types across a rainfall gradient in southern Kruger National Park (KNP), South Africa. The three sites are at a similar latitude, and occur in a summer rainfall region, but vary in mean annual precipitation, vegetation communities and soil fertility (Table 1). All three sites occur within an undulating landscape on granitic substrate; *Macrotermes* mounds occur predominantly on crests and upper sections of hillslopes, with the dominant species being *M. falciger* and *M. natalensis* (Davies, Levick, et al., 2014). Primary grazers and mixed-feeders in the study area include white rhinoceros (*Ceratotherium simum*), buffalo (*Syncerus caffer*), plains zebra (*Equus quagga burchellii*), blue wildebeest (*Connochaetes taurinus*), impala (*Aepyceros melampus*), elephant and waterbuck (*Kobus elipsiprimnus*).

Herbivore biomass at each site was calculated using aerial census data collected between 1987 and 1993 when high spatial resolution sampling was conducted. Biomass values for grazers and mixed-feeders were obtained from the six census grid cells (each 1 km² in extent) closest to the surveyed mounds in each study site and a mean value

for each site calculated (Davies, Levick, et al., 2016). After 1993, KNP changed to a sample-based, distance-sampling aerial census approach with the resultant resolution being too coarse for use in this study. However, other than elephant, buffalo (due to the cessation of culling in 1994) and white rhino (*Ceratotherium simum*) abundance increasing, herbivore populations were stable since 1993 (SANParks unpubl, Smit et al., 2020), and we, therefore, expected patterns in relative herbivore densities between sites to be unchanged.

Experimental design

Thirty *Macrotermes* mounds were selected at each site, with all mounds located on hillcrests with similar, relatively flat topography. Within the study region, both active and inactive mounds are vegetated, so we did not discriminate between these two classes. All mounds had grass growing on them, and most (70%) had no woody vegetation. Of those that did support trees or shrubs, five had single trees growing on their northern slopes and four on their southern slopes. Because of the relatively even distribution of trees across mound sides, coupled with the majority of mounds not having any trees on them, we assumed that trees on mounds were not driving potential directional effects around mounds. Mound diameter was measured for each mound along the north–south and east–west axes, and the average diameter calculated from these measurements. Similarly, mound height was measured in each cardinal direction (to account for potential variation in slope around mounds), and mean mound height was calculated.

TABLE 1 Characteristics of the three savanna study sites in southern Kruger National Park, South Africa.

Site	MAP (mm/year)	Soil fertility	Lat./long.	Herbivore biomass (kg/km ²)	Dominant tree species	Dominant grass species
Skukuza	550	Nutrient-rich	25°02' S, 31°30' E	1568	<i>Acacia nigrescens</i> , <i>Combretum apiculatum</i>	<i>Panicum maximum</i> , <i>Urochloa mosambicensis</i> , <i>Pogonarthria squarrosa</i> , <i>Digitaria eriantha</i> , <i>Brachiaria nigropedata</i>
Napi	625	Intermediate	25°06' S, 31°27' E	3490	<i>Combretum zeyheri</i> , <i>Combretum collinum</i>	<i>Panicum maximum</i> , <i>Urochloa mosambicensis</i> , <i>Digitaria eriantha</i> , <i>Eragrostis rigidior</i> , <i>Pogonarthria squarrosa</i>
Pretoriuskop	750	Nutrient-poor	25°12' S, 31°16' E	838	<i>Terminalia sericea</i> , <i>Dichrostachys cinerea</i>	<i>Cynodon dactylon</i> , <i>Panicum maximum</i> , <i>Setaria sphacelata</i> , <i>Loudetia simplex</i> , <i>Pogonarthria squarrosa</i> , <i>Schizachyrium sanguineum</i>

Note: Herbivore biomass represents the biomass of primary mammalian grazers and mixed feeders; browsers were excluded since our study focused on the grass layer. Dominate tree and grass species are for mound and non-mound communities (Davies, Robertson, et al., 2014).

Abbreviation: MAP, mean annual precipitation.

We calculated mean shadow length produced by mounds at each site at three times of day (solar noon and the mid-points between solar noon and sunrise and sunset) for both the winter (21 June) and summer (21 December) solstices using the following equation:

$$\text{Shadow length} = H / \tan \theta,$$

where H is the mean mound height and θ is solar elevation in degrees.

Grass communities on each termite mound were surveyed using sixteen 1-m² quadrats in January 2012. Six quadrats were placed on the upper sections of mounds and 10 on the lower sections where more surface area was available. Each grass species present in the quadrat was identified, and the percentage of the quadrat that it occupied (basal cover) visually estimated. Sampling quadrats were stratified according to aspect, with half (eight) on the northern side of the mound and the other half on the southern side.

Grazing on and around termite mounds was quantified using two methods. First, grass tuft use was estimated at 10 of the 30 mounds at each site during early April 2012 (late growing season when forage is abundant) and September 2012 (late dry season when forage is most limited). However, due to a natural fire at the intermediate site in August 2012, September surveying was conducted at the driest and wettest sites in 2012 and at the intermediate site in September 2013. These savanna sites burn regularly, and we did not expect this single fire event to affect our results, especially considering that termites have been found to be largely resistant to fire (Davies et al., 2012; Hockridge et al., 2023). Tuft use was estimated by laying out distance transects in the four cardinal directions around termite mounds. On each distance transect, 4 m line transects (parallel to each other and perpendicular to the distance transect) were placed at seven distance categories starting on the mound, and then at a distance of 1, 2, 4, 8, 16, and 32 m from the mound. Grazing pressure was expected to be higher closer to mounds; hence a geometric progression with the common ratio of 2 was used for the transects. Along each 4 m line transect, the tuft of grass located closest to each 40 cm mark was identified and scored according to grazing intensity, thus 11 tufts per 4 m line transect were assessed: 308 tufts per mound. Scoring was according to the following scale: 0 = no grazing evident, 1 = very light grazing, 2 = light to moderate grazing, 3 = moderate to heavy grazing, 4 = heavy grazing, and 5 = tuft completely grazed, only roots remaining. The same observer (ABD) ranked each tuft of grass throughout the study.

Second, grazing lawn extent was measured around the 30 termite mounds at each site. Beginning in May

2012, grazing lawns were measured in the four cardinal directions from each termite mound. Measurements were then taken approximately every two months until April 2013. However, due to the fire, measurements at the intermediate site (Napi) were not recorded in September or December 2012. Lawns were defined as the area where the height of the grass layer was noticeably reduced due to grazing.

Soil samples from the top 10–15 cm of the soil layer were collected around six termite mounds at each site during April 2012. Samples were collected along the same transects used for measuring tuft use and at the same distance intervals (25 samples per mound). Samples were air dried and homogenized after collection and analyzed spectroscopically for nitrogen (N) content (in milligrams per kilogram) at the Max Planck Institute for Biogeochemistry, Jena, Germany.

Analysis

All statistical procedures were conducted in R software version 2.15.1 (R Core Team, 2017). Differences in basal cover of the dominant grass species (recorded on at least half the mounds surveyed in each site) growing on northern and southern slopes of mounds were assessed using either Wilcoxon or Student's t tests depending on the distribution (normality) of the data. Percentage basal cover was arc sine transformed before analysis.

For each grazing response variable (tuft use and grazing lawn extent), a candidate set of generalized linear mixed-effects models (GLMM) with Poisson error distributions was constructed. For tuft use, models included site, distance from mound, season and direction. For grazing lawns, we included site, sampling month and direction. For tuft use, the 4 m line transect with which each tuft was associated was modeled as a random effect and nested within termite mound identity. For grazing lawn extent, mound identity was modeled as a random effect. Models were applied using the lme4 package (Bates et al., 2007) and ranked according to sample-size-corrected Akaike information criterion (AIC_c) (Burnham & Anderson, 2002) using the package MuMIn (Barton, 2019). The most parsimonious model for each response variable was selected for further analysis (Appendix S1: Tables S1 and S2) using Type III likelihood-ratio χ^2 tests with the package car (Fox & Weisberg, 2019). Finally, multiple comparisons of means post hoc testing for mixed-effects models, using Tukey contrasts averaged across interaction terms, was used to examine pairwise comparisons with the package multcomp (Hothorn et al., 2008).

To investigate soil N content across sites, distances and directions, a candidate set of GLMMs with Poisson

error distributions was constructed with mound identity as a random effect. The best performing model (assessed using AIC_c) was selected for further analysis with Type III likelihood-ratio χ^2 tests. Multiple comparisons of means post hoc testing was used for pairwise comparisons with Tukey contrasts averaged across interactions.

RESULTS

Termite mounds were tallest at the driest site, Skukuza, with a mean (\pm SD) height of 2.20 (\pm 0.48) m, followed by Napi: 1.57 (\pm 0.66) m, and Pretoriuskop: 1.16 (\pm 0.29) m. Mound height and diameter were correlated (Spearman rank correlation: $r_s = 0.75$, $p < 0.001$, $N = 90$), as were the north–south and east–west diameters ($r_s = 0.89$, $p < 0.001$, $N = 90$). Shadow length was almost double at Skukuza relative to Pretoriuskop, and intermediate at Napi (Skukuza shadow length: 4.11 m, Napi: 2.95 m, Pretoriuskop: 2.10 m at 9:17 on 21 June, and Skukuza: 2.33 m, Napi: 1.67 m, Pretoriuskop: 1.24 m at 8:26 on 21 December). The intermediate site, Napi, had the highest mammalian herbivore biomass, followed by Skukuza. The wettest site, Pretoriuskop, had much lower (four times lower than Napi) herbivore biomass (Table 1).

Grass species on mounds

At Skukuza, *Cenchrus ciliaris* was significantly more abundant on northern slopes of termite mounds (paired Wilcoxon rank sum test, $W = 21$, $p = 0.036$), while *Panicum maximum* was significantly more abundant on southern slopes (paired Student's t test, $t = 4.145$, $df = 9$, $p = 0.003$). At Napi, significantly more *P. maximum* was recorded on southern slopes ($t = 3.285$, $df = 9$, $p = 0.009$). At Pretoriuskop, there was no significant difference in grass species cover between northern and southern slopes (Figure 1).

Tuft use

Tuft use around mounds differed significantly with direction ($\chi^2 = 50.217$, $df = 3$, $p < 0.001$) with higher use recorded south of mounds than in all other directions (S-E: $\beta = 0.215$, $SE = 0.046$, $Z = 4.694$, $p < 0.001$; S-N: $\beta = 0.306$, $SE = 0.046$, $Z = 6.625$, $p < 0.001$; S-W: $\beta = 0.193$, $SE = 0.046$, $Z = 4.201$, $p < 0.001$). The other directions did not differ from each other. The interaction between direction and site was significant ($\chi^2 = 18.435$, $df = 6$, $p = 0.005$), with direction being an important factor only at Napi. An interaction between direction and

season was included in the best model, but was not significant ($\chi^2 = 6.965$, $df = 3$, $p = 0.073$), although directional effects were more pronounced at Pretoriuskop in the dry season (Figure 2).

Grazing lawns

Grazing lawn extent around mounds varied significantly with site, sampling month, and direction (site: $\chi^2 = 30.058$, $df = 2$, $p < 0.001$; month: $\chi^2 = 2587.783$, $df = 5$, $p < 0.001$; direction: $\chi^2 = 73.030$, $df = 3$, $p < 0.001$). Grazing lawns were consistently largest at Napi (Napi-Skukuza: $\beta = 0.705$, $SE = 0.204$, $Z = 3.456$, $p = 0.002$; Napi-Pretoriuskop: $\beta = 1.158$, $SE = 0.202$, $Z = 5.733$, $p < 0.001$). Differences between Skukuza and Pretoriuskop fluctuated with season, with more extensive lawns at Pretoriuskop during the dry season (May–September) and at Skukuza during the wet season (December–April). Across seasons, however, Skukuza tended to have larger grazing lawns ($\beta = 0.452$, $SE = 0.204$, $Z = 2.222$, $p = 0.068$). Across sites, lawns were larger during the drier months, with lawn extent peaking in September. Lawns were significantly larger on the southern sides of mounds (being up to 1.5 m longer, on average, during the dry season at Napi). Lawn extent on northern and eastern sides did not differ significantly ($\beta = 0.017$, $SE = 0.014$, $Z = 1.176$, $p = 0.642$), but the western side extended significantly further than both northern ($\beta = 0.122$, $SE = 0.014$, $Z = 8.840$, $p < 0.001$) and eastern ($\beta = 0.139$, $SE = 0.014$, $Z = 9.929$, $p < 0.001$) sides. The interaction between direction and site was significant ($\chi^2 = 99.931$, $df = 6$, $p < 0.001$), with directional effects less pronounced at Skukuza. Similarly, the interaction between direction and month was significant ($\chi^2 = 48.335$, $df = 15$, $p < 0.001$), with directional differences being more pronounced during the drier months (May–September) (Figure 3).

Soil nitrogen

Soil N decreased significantly with distance from termite mounds at all three sites ($\chi^2 = 1235.122$, $df = 6$, $p < 0.001$), but there was a significant interaction between site and distance ($\chi^2 = 950.927$, $df = 12$, $p < 0.001$). A sharper decrease with distance was observed at Pretoriuskop compared with the other two sites, especially Napi. Overall, soil N content decreased significantly with each increasing distance category until 16 m into the matrix. Nitrogen levels differed significantly among the three sites ($\chi^2 = 56.146$, $df = 2$, $p < 0.001$), with Pretoriuskop and Skukuza having significantly lower N content than Napi (Napi-Skukuza: $\beta = 0.416$, $SE = 0.048$,

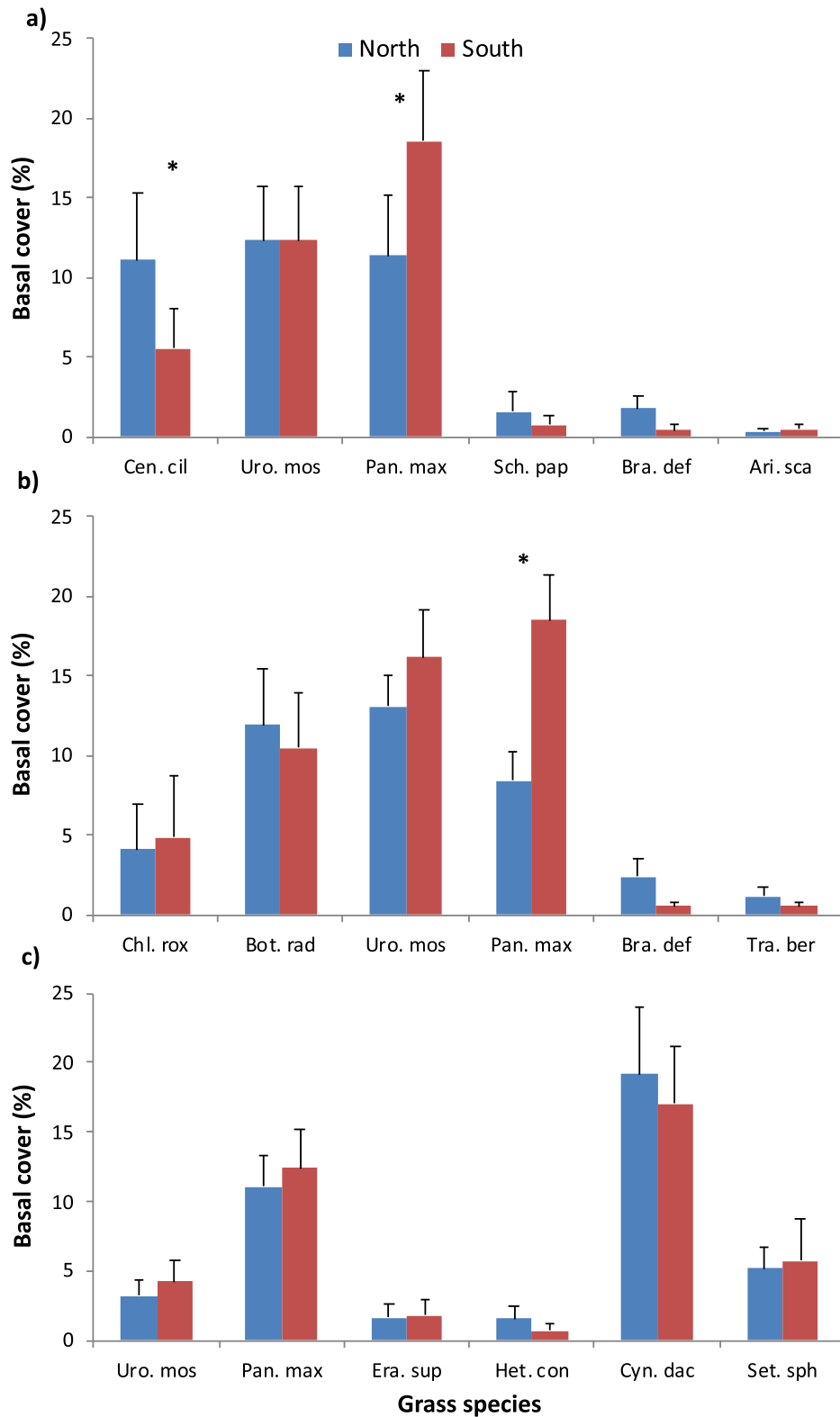


FIGURE 1 Abundance (measured as percentage basal cover; mean + SE) of the dominant grass species (recorded in at least half the termite mounds surveyed in each site) occurring on the northern and southern slopes of termite mounds in (a) Skukuza, (b) Napi, and (c) Pretoriuskop, Kruger National Park, South Africa. Grass species abbreviations are as follows: Cen. cil, *Cenchrus ciliaris*; Uro. mos, *Urochloa mosambicensis*; Pan. max, *Panicum maximum*; Sch. pap, *Schmidtia pappophoroides*; Bra. def, *Brachiaria deflexa*; Ari. sca, *Aristida scabrivalvis*; Chl. rox, *Chloris roxburghiana*; Bot. rad, *Bothriochloa radicans*; Tra. ber, *Tragus berteronianus*; Era. sup, *Eragrostis superba*; Het. con, *Heteropogon contortus*; Cyn. dac, *Cynodon dactylon*; Set. sph, *Setaria sphacelata*. An asterisk indicates that grass cover was significantly different between the north and south sides of mounds (see text for statistical results).

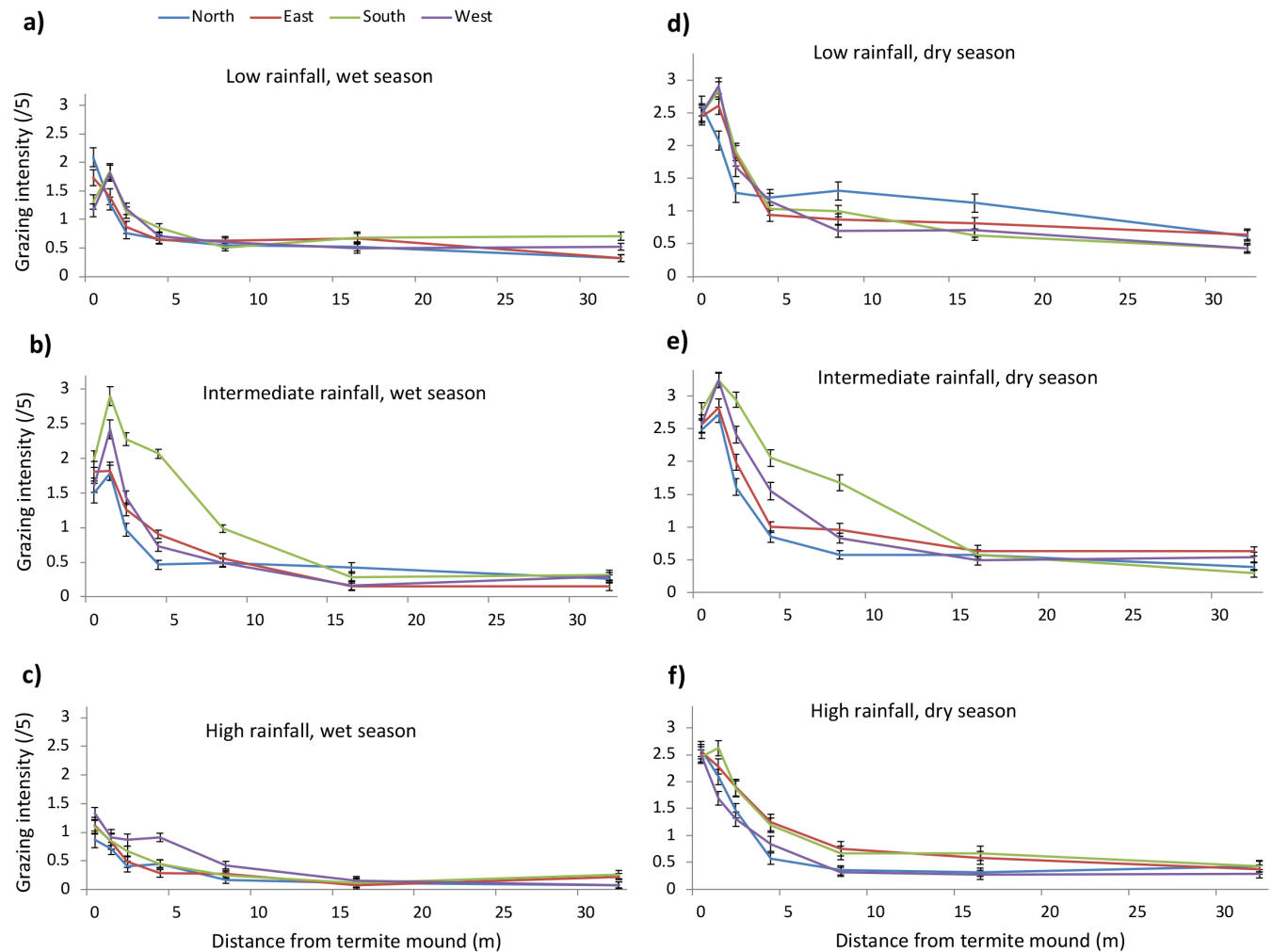


FIGURE 2 Intensity of grass tuft use (mean score out of $5 \pm$ SE) along distance transects in the four cardinal directions around termite mounds during two seasons—(a–c) the end of the wet (growing) season (April) and (d–f) the end of the dry season (September)—and at three savanna sites: (a, d) Skukuza, (b, d) Napi, and (c, e) Pretoriuskop in the Kruger National Park, South Africa. Grass tufts were ranked on a scale of 0–5 depending on the intensity of grazing.

$Z = 8.689$, $p < 0.001$; Napi-Pretoriuskop: $\beta = 0.442$, $SE = 0.048$, $Z = 9.240$, $p < 0.001$), but not from each other ($\beta = 0.027$, $SE = 0.048$, $Z = 0.549$, $p = 0.847$). Elevated N levels at Napi were driven by mound soil differences; matrix soils (32 m from mounds) did not differ among sites (Figure 4).

There were also significant differences in soil N content with direction ($\chi^2 = 70.499$, $df = 3$, $p < 0.001$) and a significant interaction between site and direction ($\chi^2 = 518.580$, $df = 6$, $p < 0.001$). Directional effects were not evident at Skukuza nor Pretoriuskop, but were clear at Napi, where significantly higher N content was recorded on southern and, to a lesser extent, western mound slopes. Northern slopes at Napi had the lowest soil N levels. Directional differences at Napi were only discernible on and close to mounds (up to 8 m). There was also a significant interaction between distance and

direction ($\chi^2 = 430.058$, $df = 18$, $p < 0.001$), with some direction transects at Napi retaining elevated N further into the matrix, particularly eastern slopes that had elevated N up to 16 m from mounds (Figure 4b).

DISCUSSION

Our results demonstrate that termite mound effects display significant variations with direction, but that the emergence of directional effects is context dependent. Significant differences in grass species composition on north- and south-facing mound slopes were evident at the drier sites but absent from the wettest site where mounds were smallest. Moreover, directional differences in grazing were evident at the intermediate rainfall site, present but weaker at the wettest site, and absent from

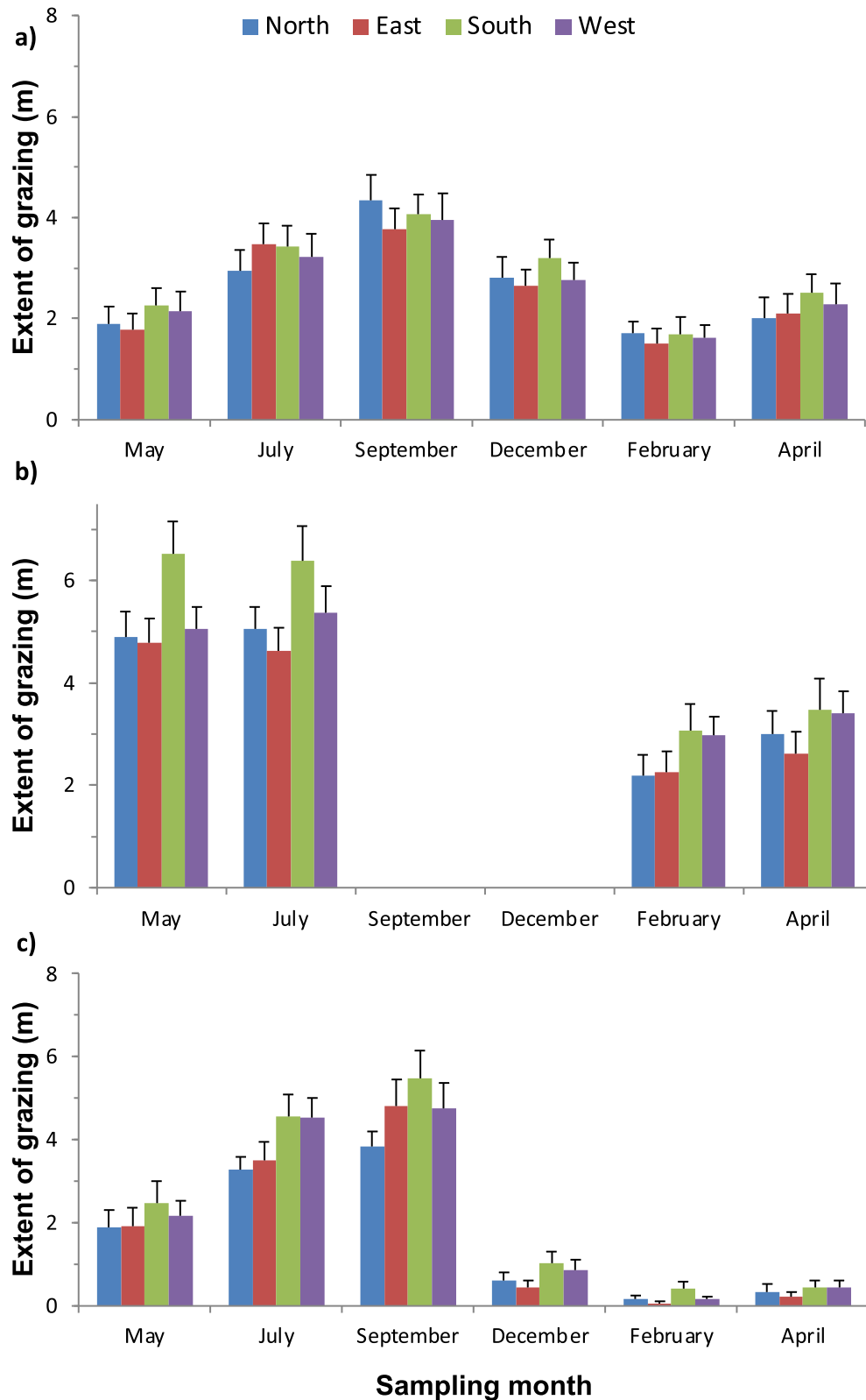


FIGURE 3 Distance of grazing lawn extent around termite mounds (mean + SE) in the four cardinal directions and at six surveying dates from May 2012 to April 2013 at three savanna sites: (a) Skukuza, (b) Napi, and (c) Pretoriuskop, in Kruger National Park, South Africa.

the driest site. Directional effects on soil N content were only evident at the intermediate rainfall site. In addition, directional effects varied seasonally, with larger

directional differences in grazing patterns during the dry season at both the intermediate rainfall and wettest site. Anisotropy in mound effects has implications for

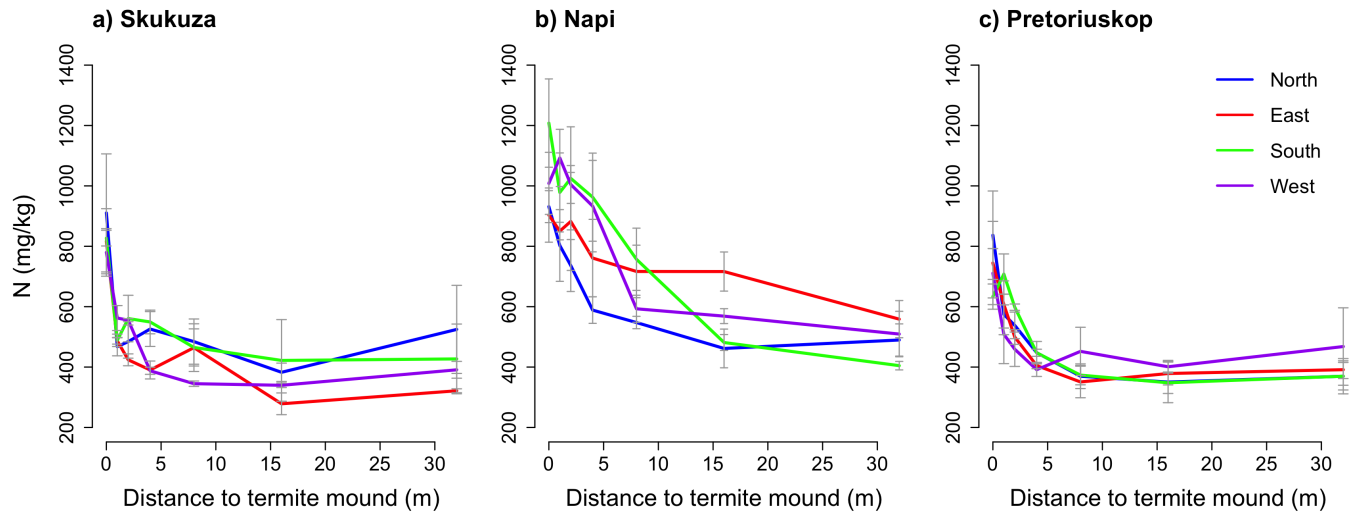


FIGURE 4 Nitrogen content (mean \pm SE) of soil samples across distance transects from termite mounds in three savanna sites and across four directions in Kruger National Park, South Africa.

termite-induced spatial heterogeneity, both in terms of the extent to which mounds influence ecosystems and in the way in which these effects are measured.

Drivers of context-dependent directional effects are likely caused by variation in mound height, mean annual rainfall, and mammalian herbivore biomass across sites. In our study, mound height varied across the rainfall gradient, with taller mounds at the driest and intermediate rainfall sites. Given their longer shadow lengths, mounds at these sites are likely tall enough to produce aspect effects through shading, altering microclimatic conditions on north- and south-facing mound slopes. South-facing slopes are then likely cooler with higher moisture content, favoring grass species adapted to such conditions, such as *P. maximum*, a shade-loving grass species that is also high in nutrients and preferred by grazers (Treydte et al., 2007). In contrast, no difference in species-specific basal cover was recorded at the wettest site, where mounds were significantly shorter, and unlikely to cause aspect effects (shadows here were >2 m shorter than the driest site). Increased cover of *C. ciliaris*, a nutritious, palatable grass that prefers warm, dry areas (van Oudtshoorn, 1999), was also recorded on north-facing slopes at the driest site, which likely resulted from the overall drier conditions here.

In addition to differences in mound height and rainfall, mammalian herbivore biomass varied across sites with the highest biomass at the intermediate rainfall site where termite mounds displayed the strongest directional variation in grazing. Here, both tuft use and grazing lawn extent were greatest on south-facing slopes, where nutritious and palatable grass species (most notably *P. maximum*) were most abundant. Although *P. maximum* was also more abundant on south-facing slopes at the driest site, and herbivore biomass at this

site was also relatively high, high *C. ciliaris* cover on north-facing slopes likely diluted directional grazing effects because it is also attractive to herbivores. Directional effects on grazing were largely absent at the wettest site during the wet season but emerged during the dry season, with increased grazing on south- and east-facing slopes. Although grass species did not vary with aspect here, south-facing slopes receive less insolation, likely enabling grasses to retain higher moisture content into the dry season, attracting grazers.

Differences in soil N content with direction were only distinguishable at the intermediate rainfall site, suggesting an intriguing feedback loop involving termites, abiotic conditions, and mammalian herbivores. Soil N content at this site was highest on south- and west-facing mound slopes, whereas soil N content did not vary with direction at the other sites. Since there is no plausible reason to expect increased termite activity on south-facing slopes at only this site, it is possible that increased N content here resulted from additional nutrient input from grazing herbivores through urine and dung deposition (dung counts are a frequently used and reliable measure of herbivore abundance (Burkpile et al., 2013; Cromsigt et al., 2009), and we therefore considered it reasonable to assume the reverse, that increased herbivory leads to increased dung deposition). Indeed, the 8-m distance of N enrichment on south-facing slopes closely matches the extent of increased tuft use and grazing lawn extent, suggesting that increased soil N is closely linked to herbivore activity. These findings suggest that the magnitude of directional variation in mound effects is mediated by abiotic drivers in the form of aspect-induced microclimatic differences that affect grass species composition, which, in turn, steer patterns of mammalian grazing and lead to directional variation in

soil N content. These interactions could then result in a feedback loop between mammalian herbivores and vegetation through soil N enrichment by herbivores when they are present in sufficient numbers, which could further entrench directional effects.

Although our study suggests the existence of a feedback loop, we were unable to mechanistically test it. Future studies using manipulative experiments (e.g., herbivore exclosures around mounds or watering experiments that mimic rainfall variation) would be illuminating to uncover the existence and mechanistic basis of our proposed feedback loop, as well as when it does and does not form. Similarly, the increased soil N 16 m from the eastern side of mounds at Napi did not match either of the herbivory datasets (tuft use or grazing lawn extent) and could therefore not be explained by the proposed feedback loop. This distance was far enough from mounds to be largely unaffected by them (Davies, Levick, et al., 2016; Davies, Robertson, et al., 2014) and was likely driven by factors we did not measure (e.g., soil nutrient patterns in the matrix).

Nonetheless, the clear evidence of directional effects around termite mounds has implications for their importance for termite-induced spatial heterogeneity, and the extent to which they shape landscapes. Previous studies have estimated termite mound influence to affect up to 30% of savanna landscapes, assuming effects to be nondirectional (Davies, Baldeck, et al., 2016; Davies, Levick, et al., 2016; Levick et al., 2010). However, these extrapolations could over- or underestimate mound effects if measurements are focused in only a few directions. Indeed, our results suggest that future studies on vegetation, nutrient, or herbivory patterns around mounds should ensure that their sampling design encompasses multiple directions around mounds, at least in study sites situated away from the equator. Termite mounds on or near to the equator are unlikely to exhibit anisotropic effects due to a subdued or absence of aspect effects, but this remains to be investigated.

Due to termite mounds being heavily used by herbivores, they are thought to be among the first sites to show signs of environmental degradation and have been suggested as useful monitoring sites (Grant & Scholes, 2006). The presence of anisotropy has implications for such monitoring; where southern sides of mounds are more intensely grazed they will likely be more useful in monitoring exercises. Furthermore, anisotropy is most evident under high herbivore pressure. When directional effects are evident, they could indicate increased herbivory (and potential over-grazing). This notion is substantiated by a trend of increased grazing on the southern and eastern sides of mounds at the wettest site (Pretoriuskop) during the dry season when herbivores are more nutritionally stressed and mound vegetation experiences higher levels of herbivory.

The mechanisms by which termite mounds affect ecosystems could also depend on directional effects. Decomposition of organic matter, for example, is higher on mounds than off them (Acanakwo et al., 2019), and it is likely that decomposition rates vary with aspect (Jasińska et al., 2019), as well as with interactions with soil nutrients and herbivores (Wardle et al., 2002). Differences in aspect, soil nutrients, plant communities, and mammalian grazing with direction around termite mounds could change the way in which mounds interact with such processes to shape ecosystems. Additional quantification of intra-mound differences on ecosystem functions will further uncover the roles in which these structures, and the termites that build them, shape savanna landscapes.

AUTHOR CONTRIBUTIONS

All authors conceived the study. Andrew B. Davies collected and analyzed the data, and wrote the manuscript. All authors contributed to revisions.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Davies, 2024) are available from Figshare: <https://doi.org/10.6084/m9.figshare.26340679>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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