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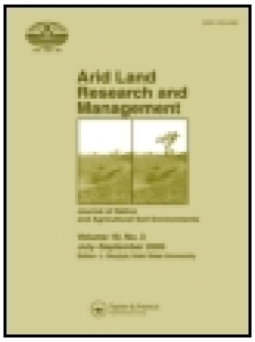

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Termite effects on soils and plants are generally consistent along a gradient in livestock grazing

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ABSTRACT

Livestock grazing is a major driver of ecosystem functions in drylands and would be expected to influence soil biota such as termites. We examined changes in soil chemistry and plant community composition on mounds constructed by the subterranean termite *Anacanthotermes ahngerianus* along a gradient in grazing intensity in an arid steppe in north-eastern Iran. The grazing gradient was represented by increasing distance from an area used by resting livestock, and plant and soil attributes measured within three adjacent microsites (termite mounds, non-mound controls, intervening annular zone surrounding the mounds). Values of soil EC; pH; exchangeable Ca, Mg, and Na; and total nitrogen and organic carbon were greatest in mound soils and declined from mounds to control microsites. Mounds were completely devoid of plants. Annular zones had three-times less cover than the control sites, but there were no differences in diversity or evenness. Electrical conductivity values were ten-times greater on mounds than controls close to resting sites, but the difference diminished rapidly with distance from resting sites. For all other soil and plant variables, differences between microsites were consistent across the grazing gradient. Increased grazing intensity was associated with increasing soil pH, EC and sand content, and reduced plant cover. Overall our study shows that the effects of termites on soil chemistry and plant cover varied little across the grazing gradient. Our results suggest that termite mounds may sustain their role as sites of enhanced soil nutrients under even high levels of grazing.

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Degradation; disturbance; rangelands; sheep; soil chemistry; soil organic matter

Introduction

Livestock grazing is a major disturbance in drylands (arid, semi-arid and dry subhumid environments), which occupy almost 40% of Earth's land surface and support a similar percentage of its human population. Globally, livestock grazing provides many cultures with meat, milk, and transport, yet overgrazing has resulted in extreme poverty and hardship and substantial negative effects on ecosystems (Steinfeld et al. 2006). In drylands the effects of grazing are most strongly felt around watering points and resting areas where livestock congregate and where their densities are greatest (Jankju Borzelabad 2008). Gradients in grazing become apparent where livestock move from watering points

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and resting areas to graze distant pastures. The grazing effect emanating from water is termed the piosphere effect (Lange 1969), and studies along piospheres indicate sharp reductions in livestock utilization with increasing distance from water (Landsberg et al. 2003). A similar phenomenon occurs in areas where livestock are corralled (Reid and Ellis 1995).

High levels of livestock grazing have been shown to influence soil physical and chemical properties. Specifically, increases in livestock intensity are known to reduce plant composition (Milchunas and Lauenroth 1993) and have marked effects on soil cations and anions and soil fertility (Eldridge et al. 2016). Perhaps the greatest effect of livestock grazing is herbivory, the removal and consumption of plant biomass (Eldridge et al. 2016). However, herbivory by invertebrates may also be substantial. Termites, for example, consume substantial quantities of plant material and are considered one of the most important insect taxa in drylands because they are both herbivores and detritivores (Coventry, Holt, and Sinclair 1988). Although termites could be seen as competing directly with livestock for plant biomass, they could also indirectly enhance plant growth for vertebrate herbivores through their positive effects on surface soils (Brody et al. 2010). Termites have been shown to have profound positive impacts on ecosystem structure, composition, and function. They enhance soil physical and chemical properties (Holt 1987; Holt and Lepage 2000), increase soil porosity and therefore infiltration by constructing large macropores in the soil (James et al. 2008), influence soil organic matter and nutrient cycling (Whitford and Eldridge 2013), and are important prey items for reptiles small mammals (Redford and Dorea 1984). Dramatic effects of livestock on vegetation and soil, particularly close to water or livestock resting sites, would also be expected to influence other herbivores such as termites.

We examined the effects of subterranean termites along a gradient in livestock grazing intensity to ask whether termite effects on plants and soils differ across gradients in livestock grazing. We used distance from livestock resting points as our surrogate for grazing intensity, examining plants and soils on and off the mounds of subterranean termites at increasing distance from resting points in an arid steppe rangeland in north-eastern Iran that is under intense livestock grazing pressure. This rangeland is extensively colonized by the subterranean termite *Anacanthotermes ahngerianus* Jacobson (Isoptera: Hodotermitidae), which builds large surface pavements up to 3 m in diameter that generally support less vegetation than the surrounding areas. The presence of these relatively large vegetation-free patches suggests that termites are contributing to large-scale degradation through their effects on surface soils. Our aim was twofold: to determine (1) the effects of termite mounds on plants and soils and (2) whether these effects changed in relation to increasing grazing pressure. This is important because livestock and termites are assumed to be the main causes of land degradation and desertification in the Shorlogh rangelands, yet the combined effects of livestock and termites on plants and soils have rarely been considered.

Methods

The study area

This research was conducted in the Shorlogh rangelands in northeastern Iran (36.32°N, 60.65E) about 578 m above sea level. The climate is cold arid and dry, the average annual temperature is 14.4°C, and average annual rainfall 202 mm (Ghayorifar and Khalily 2005). The vegetation is dominated by ephemeral species such as *Poa bulbosa* L. and *Bromus tectorum* L. during late winter and early spring. These species are replaced by perennial forbs such as *Diarthron vesiculosum* Jaub. and Spach., *Peganum harmala* L., *Alhagi maurorum* Medic. and *Sophora secundiflora* (Ortega) DC) during summer. Soils are classified as aridisols, with their texture being sandy clay loam. Soil depth varies from 80 to 120 cm and is limited by a calcareous hardpan (Beheshti 2015).

Soil, vegetation and termite sampling

At one livestock resting point we established three transects extending up to 720 m in north-south, west-east, and northeast-northwesterly directions. All mounds constructed by the subterranean termite *Anacanthotermes ahngerianus* within 5 m of each transect were identified, and ten in each transect randomly selected for detailed plant and soil measurements. At each of these thirty termite mounds we collected soil from the top 10 cm of the profile within three microsites: (1) termite mounds (hereafter 'mound'), (2) the zone immediately surrounding the mounds (hereafter "annular zone") and (3) a control, non-mound area that was located about 2–5 m from the edge of the mound away from any influence of termites (hereafter "control"). The annular zone is the area immediately surrounding the mound, which has been shown to have higher levels of soil nutrients and infiltration than the non-mound control areas (Eldridge 1994). Soil texture was measured using the hydrometer method (Gee and Bauder 1985), and Na, Mg, Ca, P, and K assessed using atomic absorption spectrophotometry. Total nitrogen (N) and carbon (C) were measured using the Kjeldahl and Walkley-Black methods. Electrical conductivity (EC) and pH were measured on a 1:5 soil:water extract with an electrical conductivity meter.

In June 2014 we sampled plants within 2 m × 1.5 m quadrats at a total of ten positions on the three transects (3–4 mounds per transect) at distances ranging from 300 m to 720 m from the livestock resting point. At each position, one quadrat was sampled in the annular zone and the other in the control, resulting in a total of twenty quadrats. Sampling was carried out when the dominant perennial plants (e.g., *Diarthron vesiculosum, Peganum harmala* and *Sophora secundiflora* were at the flowering stage. We assessed total vegetation cover and density of each plant species. We then calculated plant diversity (Shannon's Diversity Index), plant richness (Menhinick Index) and plant evenness (Smith and Wilson Index; Ejtehadi, Sepehri, and Akkafi 2009).

Statistical analyses

One-way ANOVA was used to examine potential differences in exchangeable Na, K, Mg, Ca, P, total N, electrical conductivity (EC), pH, and organic carbon (OC) among the three microsites (mound, annular zone, control) and plant attributes between the annular zone and control, and Tukey *post-hoc* tests used to determine which microsite differed significantly. We then used regression analyses to test for the effects of livestock grazing intensity on EC, pH, sand, silt, clay content, vegetation cover, plant richness, diversity, and evenness using distance from livestock resting point as a proxy for grazing intensity. Analyses were conducted for annular zone and control microsites only. To test for potential interactions between grazing intensity and microsite, for annular zone and control microsites, differences in slopes and intercepts for mound and control microsites were compared using *F* statistics.

Results

Effects of termite activity on soil and vegetation

Values of soil EC, pH, Ca, Mg, Na, and total N and OC were greatest in mound soils and declined with distance from the mounds, i.e., from termite mound out to the control microsites (Table 1, $P < 0.05$). Termite mounds had finer textures (more silt and clay) than the other two microsites but there were no changes in soil P ($P > 0.05$). Termite mounds were always completely bare. Plant cover was three-times greater on the control microsites than the annular zone around the mounds ($P < 0.001$) and richness greater on the control microsites ($P = 0.05$; Table 1). There were no differences, however, in diversity or evenness ($P > 0.09$).

Effects of livestock grazing intensity on soil and vegetation

Soil pH declined along the gradient at both the annular zones and control microsites (Figure 1a). However, this decline was significant only on the control microsites ($P = 0.045$, Table 2). Livestock grazing intensity had the greatest impact on soil EC, for both annular zone and control microsites ($P < 0.001$; Figure 1b, Table 2). Values of EC were 10-times greater on termite mounds (4.98 dS m^{-1}) than the controls (0.47 dS m^{-1}), but this difference rapidly diminished rapidly with declining grazing intensity, i.e., with increasing distance from livestock resting points (Microsite x Distance interaction: $P < 0.001$; Figure 1b). For the control microsites, however, EC remained relatively low but did increase significantly with declining grazing intensity ($P < 0.001$).

Table 1. Mean (±SE) values of soil physical and chemical properties, and plant community structure within three microsites associated with termite mounds. Within a row, different letters indicate a significant difference at $P < 0.05$; mounds were always devoid of plant cover.

	Termite mound		Annual zone		Control	
Attribute	Mean	SE	Mean	SE	Mean	SE
EC (dS m^{-1})	6.2^a	0.039	2.7^b	0.006	0.96^c	0.005
pH	8.12^a	0.028	7.83^b	0.028	7.39^c	0.027
Ca (ppm)	859.4^a	9.80	792.5^b	2.55	494.4^c	9.46
Mg (ppm)	120.6^a	9.80	97.1^b	1.09	91.6^b	0.79
Na (ppm)	21.1^a	0.46	8.3^b	0.053	2.4^c	0.31
K (ppm)	16.5^a	0.24	12.4^b	0.32	10.6^b	1.92
N (ppm)	0.12^a	0.002	0.09^b	0.002	0.04^c	0.002
P (ppm)	4.5^a	0.07	4.6^a	0.0	4.4^a	0.105
OC (%)	1.2^a	0.04	0.70^b	0.39	0.90^c	0.21
Sand (%)	53.7^a	1.02	66.8^b	1.25	73.1^c	0.76
Silt (%)	19.0^a	0.17	11.0^b	3.33	8.9^c	1.10
Clay (%)	27.3^a	1.45	23.0^b	1.19	17.1^c	1.19
Plant cover (%)	0	0	20.2^a	3.54	57.6^b	5.16
Richness	0	0	0.37^a	0.04	0.54^b	0.07
Diversity	0	0	0.59^a	0.12	0.84^a	0.07
Evenness	0	0	0.62^a	0.14	0.93^a	0.12

Note: Data indicated by different alphabetic letters (a, b, c) are statistically significant at $p < 0.05$.

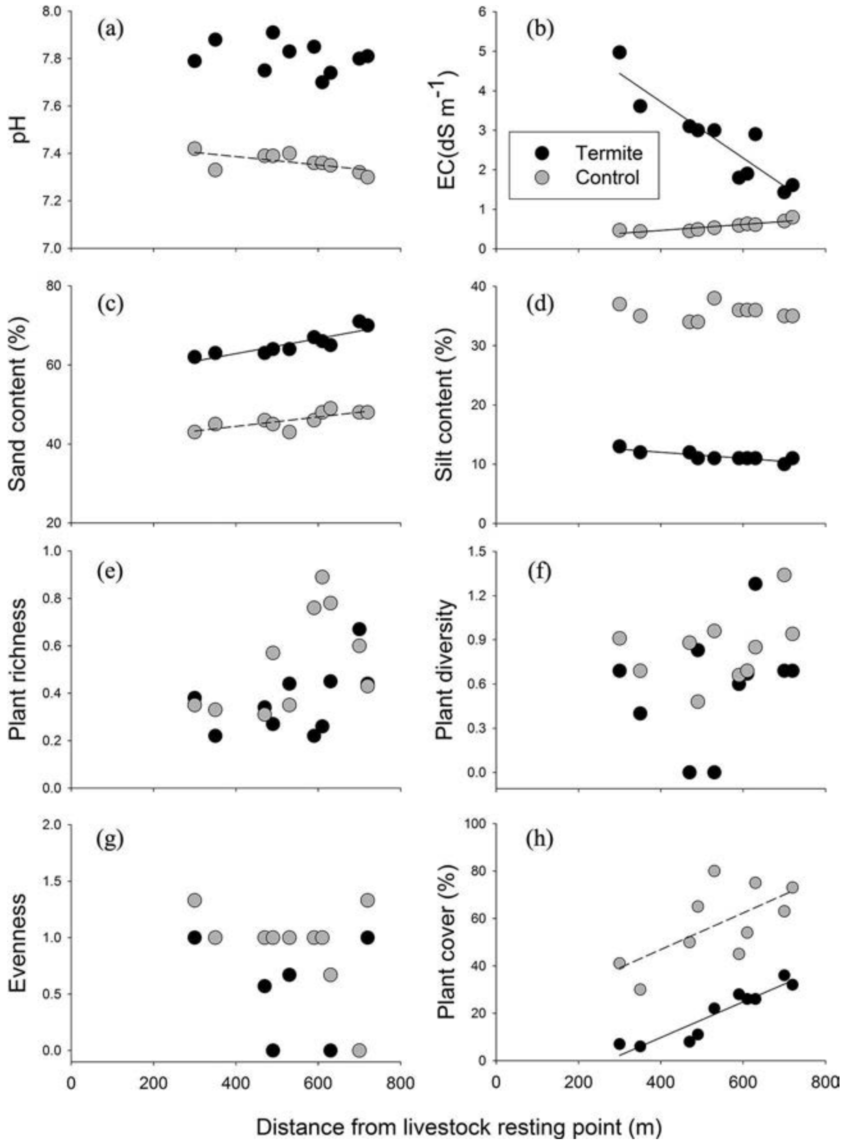

Figure 1. Trends in soil pH, electrical conductivity (EC), sand and silt contents, and plant richness, diversity, evenness and cover on the annular zone of termite mounds and the control microsites in relation to distance from livestock watering points. Linear models are presented for significant relationships only.

The percentage of sand declined (Figure 1c), and clay increased, with increasing grazing intensity, for both annular zone and control microsites (Table 2). Silt content increased with increasing grazing intensity, but only on the annular zones ($P < 0.001$; Figure 1d; Table 2). Plant cover increased with declining grazing intensity (increasing distance from resting points) for both annular zone ($P < 0.001$) and control ($P = 0.03$) microsites (Figure 1h, Table 2) and this effect was strongest in the annular zone ($R^2 = 0.89$) than control sites ($R^2 = 0.47$). There were no effects of increasing grazing intensity on plant richness, diversity or evenness ($P > 0.10$).

Table 2. Regression relationships for the effects of increasing grazing intensity (proximity to livestock resting points) on soil chemical and physical properties, and vegetation. For each parameter, the relationship was tested for Annular and Control microsites separately. Slopes and intercepts were compared between the regression lines. R^2 values are presented only for significant effects.

Parameter	Source	DF	*F*	*P*-value	R^2
EC	Control	1	33.26	<0.001	0.81
	Annular	1	41.33	<0.001	0.84
	Slope	1	49.90	<0.001	
	Intercept	1	55.34	<0.001	
pH	Control	1	5.61	0.045	0.41
	Annular	1	0.71	0.425	
	Slope	1	0.06	0.810	
	Intercept	1	392.62	<0.001	
Sand	Control	1	27.05	<0.001	0.77
	Annular	1	12.31	0.008	60.6
	Slope	1	2.06	0.170	
	Intercept	1	811.07	<0.001	
Silt	Control	1	0.10	0.763	
	Annular	1	24.66	0.001	0.76
	Slope	1	1.52	0.235	
	Intercept	1	2915.25	<0.001	
Clay	Control	1	9.17	0.016	0.53
	Annular	1	13.91	0.006	0.64
	Slope	1	0.77	0.393	
	Intercept	1	75.37	<0.001	
Plant cover	Control	1	6.89	0.030	0.47
	Annular	1	64.55	<0.001	0.89
	Slopes	1	0.00	0.946	
	Intercept	1	87.29	<0.001	
Plant richness	Control	1	3.53	0.100	
	Annular	1	2.50	0.153	
	Slopes	1	0.44	0.520	
	Intercept	1	5.56	0.031	
Plant diversity	Control	1	1.19	0.310	
	Annular	1	0.87	0.378	
	Slopes	1	0.06	0.820	
	Intercept	1	3.44	0.081	
Plant evenness	Control	1	1.97	0.198	
	Annular	1	0.78	0.400	
	Slopes	1	0.03	0.800	
	Intercept	1	2.95	0.104	

Discussion

In our study termites had marked effects on soil physical and chemical properties. Mounds created by termites had greater levels of soil properties than soils in the annular zone surrounding the nests, or the non-mound (control) interspaces. Specifically, termite mound soils had greater pH and EC, lower levels of exchangeable cations and anions, finer surface textures, and higher concentrations of soil organic carbon than the non-mound control surfaces. These values were also frequently greater than the annular zone surrounding the mounds. Apart from electrical conductivity, where values for mound and control converged at long distances from livestock resting areas, the effects were generally consistent across the grazing gradient.

Termite mounds are higher in fine material and organic matter

In our study we found higher levels of fine soil particles (silt and clay) on the mounds, consistent with the literature (e.g., Rajagopal 1983; Whitford and Eldridge 2013). This is attributed to the fact that termites use fine particles (clay) and saliva to form the structure of their nests (Lee and Wood 1971; Lal 1987; Hulugalle and Ndi 1993; Sarcinelli et al. 2009). The proportion of silt and clay in the mounds may depend on the ability of worker termites to transport specific-sized soil particles (Lee and Wood 1971). Termites then use their salivary secretions to bind transported organic matter and clay materials.

As central place foragers, the greatest effect of termites is to collect organic material from the area surrounding the mounds, increasing mound soil organic matter content (Whitford and Eldridge 2013). Levels of organic matter in some termite mounds have been shown to be five-times greater than those on adjacent nonmound soils (Decaëns, Galvis, and Amézquita 2001). In arid, semi-arid and some tropical ecosystems, more than half of the potential inputs to the soil organic pool are consumed by termites (Whitford, Ludwig, and Noble 1992). Nitrogen is highly associated with carbon, so it was not unexpected that our mounds also contained high levels of total nitrogen, consistent with global studies (Brossard et al. 2007; Abdus-Salam and Itiola 2012). Higher soil temperature and moisture in the mounds may also enhance the mineralization of N from stored organic matter (San Jose et al. 1989).

We found higher levels of soil pH and exchangeable cations and anions in mound soils than in the control soils. Greater levels of fine sediments and soil organic matter in termite mounds (Whitford and Eldridge 2013) also enhance soluble and exchangeable cations that are adsorbed onto these clay-rich particles (Rajagopal 1983; Mermut, Arshad, and St Arnaud 1984; Sarcinelli et al. 2009; Abdus-Salam and Itiola 2012). This effect has been widely reported from a range of environments (e.g., de Bruyn and Conacher 1990). Greater levels of soil Ca in termite mounds has been attributed to the breakdown of carotenes in plant tissue by termites (Lee and Wood 1971), leading to higher mound pH levels. Similarly, greater levels of P and exchangeable Mg on the mounds can be attributed to the digestion and degradation of plant tissues by termites (López-Hernández et al. 1989). The foraging behavior of termites can also lead to increasing mound concentrations of soil P (López-Hernández 2001), due to exposure of P-rich subsoil. In our study, however, exchangeable P did not differ significantly among the three microsites. This may be due to the patchy distribution of P and its lower mobility through the profile, which makes it highly dependent upon depth and location of soil sampling (López-Hernández et al. 1989).

Termite effects are largely consistent across a grazing gradient

Apart from changes in EC, the effects of termites were consistent across a grazing gradient, i.e., we observed similar trends for mound and control microsites with increasing distance from livestock resting points (Figure 1). This suggests to us that termites are largely insensitive to changes in livestock intensity, consistent with observations that mounds of the subterranean termite *Drepanotermes tamminensis* (Hill) were more abundant in grazed than ungrazed plots in semi-arid rangelands in Australia (Abensperg-Traun 1992). Of particular interest was the observation that EC values were extremely high close to, but declined markedly with increasing distance away from, livestock resting points, with values converging at 720 m from the resting areas (Figure 1b). Finer and more compacted soil surfaces under high intensity grazing could reduce soil moisture and consequently increase soil EC (Eskandari 1995). Conversely, greater cover of vegetation under low grazing intensity (Figure 1h) could reduce soil evapotranspiration and hence soil EC (Kashizenoozi, Saadat, and Namdar 2011).

We recorded greater vegetation cover under lower grazing intensity, i.e., with increasing distance from livestock resting points, and the trends were consistent for both the annular and control microsites. There were, however, no differences in diversity or richness. Reductions in plant cover with increasing grazing intensity are widely reported in the literature, but there have been few studies of potential interactions between termites and grazing (though see Abensperg-Traun 1992). Suppression of vegetation on the mounds by termites is known from drylands, where termite removal resulted in increased total plant canopy cover up to 20% (Bodine and Ueckert 1975). Lower levels of plant cover due to high grazing levels would be expected to reduce potential resources for grass harvesting termites; thus, the strong alignment between the models for plant cover on mounds and control sites (Figure 1h).

Concluding remarks

Our observations of greater organic matter, fine sediments on termite mounds is consistent with the notion that mounds act as fertile islands, and that this fertile island effect persists under even high levels of grazing i.e., close to livestock resting points. The degree to which mounds might act as fertile islands, however, is probably highly termite species-specific, and this would likely relate to mound structure (Hulugalle and Ndi 1993) i.e., whether they shed or retain water and nutrients (convex *cf.* concave surfaces; see Eldridge 1994). Studies from temperate areas have demonstrated greater vegetation cover and richness on mounds (Levick et al. 2010), but in arid and semiarid areas, vegetation is often suppressed on the mounds themselves but enhanced in the annular zone immediately surrounding the mound. Active removal of plants from the surface of the mounds by termites would reinforce this shedding of water to the area around the mounds, potentially leading to zones of fertile soil around the mounds. Overall therefore, the effect of termite activity was to concentrate resources around their mounds, leading to an increase in spatial heterogeneity, which is important for the functioning of arid systems. We showed that this effect was generally consistent across our grazing gradient. Predicted increases in aridity during the next century would likely result in greater livestock induced-degradation in drylands. The extent to which the positive effect of termites might be offset by high levels of grazing with increased levels of aridity is largely unknown.

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