

The Importance of Coprophagous Macrodetritivores for the Maintenance of Vegetation Heterogeneity in an African Savannah

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ABSTRACT

Grazing ecosystems are often characterized by dynamic vegetation structure mosaics of short grazing lawns and tall grass vegetation that are important for the biodiversity and functioning of these ecosystems. Grazing-induced trampling, causing soil compaction and reduced water infiltration, has been shown to be an important mechanism for lawn grass formation. However, insights in reverse bioturbation mechanisms were mostly lacking, especially how tall vegetation persists under continuous grazing by herbivores. In this study, we explore if defecation by large herbivores in combination with different groups of coprophagous macrodetritivores can locally convert compacted grazing lawn patches back to tall bunch grasslands

with a more loose soil. Across a rainfall gradient in an African savannah, we separated the potential roles in this process between dung beetles versus earthworms and termites. We placed different mesh sizes under dung piles and studied the consequences for soil, vegetation, and hydrological properties. We found that soil water infiltration rate, soil organic matter content, electrical conductivity, bunch grass cover, and bunch grass biomass were significantly promoted by dung addition, irrespective of position along the rainfall gradient. In addition, the presence of tunneling dung beetles significantly increased water infiltration rate and biomass of bunch grasses, pointing at a new mechanism whereby macrodetritivores affect the structure and diversity of plant communities. We conclude that coprophagous macrodetritivores interact with large herbivores in contributing to the maintenance of structural heterogeneity in the vegetation of grazing ecosystems, with a special role played by soil-tunneling dung beetles.

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INTRODUCTION

Grazing ecosystems are often characterized by dynamic vegetation structure mosaics (Frank and others 1998; Schrama and others 2013) of short horizontally growing, stoloniferous lawn grasses (Hempson and others 2014), and tall tussock-forming bunch grasses (Anderson and others 2013), that are important in the biodiversity and functioning of these ecosystems (Knapp and others 1999; Pickett and others 2003; Cromsigt and Olf 2008). In migratory systems, the maintenance of heterogeneity in vegetation structure is attributed to seasonally intensive grazing alternating with rest periods, where herbivores concentrate grazing on preferred resources and move on through the landscape, leaving less preferred patches intact (McNaughton 1979; Knapp and others 1999). Moreover, resident grazing herds may promote structural heterogeneity when total grazing pressure is maintained at intermediate levels; thus, patchiness is maintained by the aggregation of herbivores on higher forage quality patches (Stuth and others 1997; Cromsigt and others 2009; Oom and others 2010). Expansive patchiness of tall grasses alternating with grazing lawns provides an essential buffer against high herbivore density oscillations, since tall vegetation may be used as a lower quality forage reserve (Owen-Smith 2004; Ruifrok and others 2015) as well as increasing habitat availability and potential for biodiversity (Hagenah and others 2009; van der Plas and others 2013a) which may be especially important in more confined natural areas (Chapin and others 2000).

The main mechanisms that have been put forward for grazing lawn formation are co-evolution of plants that tolerate or resist grazing (McNaughton 1984; Milchunas and others 1988) in the presence of large herbivores which optimize foraging strategies (Westoby 1974; McNaughton 1979) and positive nutrient feedbacks (Ruess and McNaughton 1987; Cromsigt and Olf 2008). In addition, the growing emphasis on the effects of global change has inspired additional explanations for vegetation patchiness. In particular, scale-dependent differences in water availability at the landscape scale, where water runs off from dry bare soil and seeps into the soil under perennially vegetated patches (Rietkerk and Van de Koppel 1997), resulting in an uneven distribution of water, thus promoting a patchy mosaic of dry bare patches alternating with moist vegetated patches. Although mosaics of tall and lawn grasses are frequently described as a typical feature of grazed ecosystems with an important role of large herbivores (Frank and

others 1998; Stock and others 2010), the maintenance of tall vegetation has traditionally been ascribed to a range of determinants of temporal patch avoidance, either through predation risk (Hopcraft and others 2010), avoidance of dung due to pathogen risk (Hart 1990; Cid and Brizuela 1998), or seasonal migration (Fryxell and Sinclair 1988; Fryxell 1991). However, recent work shows important differences in soil physical properties with significantly higher water infiltration rates and increased soil macroporosity in tall vegetated bunch patches compared to adjacent short vegetated lawn patches, within the same spatial context (Veldhuis and others 2014; Howison and others 2015; van Klink and others 2015). Coupled to this, we find higher abundance of soil macrodetritivores within the tall vegetation (Howison and others 2015). This suggests that mechanisms other than temporal patch avoidance, such as the bioturbating activities of soil macrodetritivores, may be important in creating differences in soil properties within tall vegetation (Howison and others 2015; Schrama and others 2015). In time (between 5 and 10 years), we observe spatial dynamics of tall and short patches converging into each other, that is, tall vegetation invades lawn or lawn invades tall vegetation. Therefore, we expect positive feedbacks generated by large grazing herbivores which promote lawn to alternate with positive feedbacks generated by soil bioturbation.

Soil macrodetritivores play a crucial role in soil formation processes (Wilkinson and others 2009). As far back as Darwin (1881) and more recently (Meysman and others 2006), scientists recognize the importance of bioturbation by soil organisms in long-term modifications in local soil conditions through nesting and foraging behavior, thereby often promoting their own resources and conditions (van Breemen 1993). Estimates for the magnitude of impact soil organisms have, through mounding, mixing, and burial range from 3 to 53 ton ha⁻¹ y⁻¹ of processed soil for the temperate regions and between 730 and 1100 ton ha⁻¹ y⁻¹ in the humid tropics (Wilkinson and others 2009). Predominantly in the agricultural literature, we find studies that quantify the benefits to natural soil processes by bioturbating soil macrodetritivores (Lal 1988; Stuth and others 1997) and consequences for aboveground biomass production (Curry and Boyle 1987; van Breemen 1993). However, to our knowledge, no clear linkages have been made between the bioturbating activities of soil biota and patch conversion from lawn to tall grass vegetation patches through soil amelioration, within grazing ecosystems literature.

In this study, we test the hypothesis that macrodetritivore aggregation in dung patches can cause compacted, dry lawn grass-dominated grazing lawns to revert to bioturbated, wetter, tall bunch grass-dominated patches (Figure 1). If this is true, this may explain why small-scale vegetation structural heterogeneity in grazing ecosystems can persist even under continuous grazing pressure throughout the growing season. For this, we experimentally tried to switch herbivore-compacted grazing lawns to macrodetritivore, bioturbation-dominated tall bunch grass patches by dung addition (Figure 1), with experimental separation of the importance of different groups of coprophagous macrodetritivores (that is, earthworms, termites, and dung beetles). The study was situated along a steep rainfall gradient to test for effects contingent on water availability. For understanding the mechanisms involved, we measured the importance of the incorporation of dung into the soil profile thus enhancing soil organic matter content and nutrient availability (Mittal 1993), and the promotion of water infiltration through tunneling, foraging, and nesting activities (Lal 1988), separating between dung beetle and earthworm/termite effects. We measured the consequences for aboveground biomass for tall bunch grasses, lawn grasses, forbs, leaf litter production, and bare ground cover to quantify the strength of patch conversion.

METHODS

Research Area

This research was performed at Hluhluwe-iMfolozi Park (HiP) between the coordinates 28°00" to 28°26"S and 31°41" to 32°09"E in northern KwaZulu Natal, South Africa. HiP is a highly heterogeneous but relatively small (900 km²) nature conservation area within the savannah biome of Southern Africa, situated in the transition zone between the foothills of the kwaHlabisa mountains and the coastal lowlands (Mucina and Rutherford 2006; Stock and others 2010). Elevation decreases from 500 to 40 m.a.s. in a northwest-southeast plane, which is strongly associated with a decreasing rainfall gradient from 920 to 490 mm y⁻¹, falling mostly between October and April. The areas host a high plant and animal diversity (including several endemics (Smith and others 2008) and high wildlife abundance (Cromsigt and others 2009; Stock and others 2010; Kleynhans and others 2011)). Air temperatures range from a mean minimum temperature of 13°C to a mean maximum temperature of 35°C (Balfour and Howison 2001). The vegetation comprises a patchy mosaic of tall bunch grasses (*Themeda triandra*, *Sporobolus pyramidalis*, *Eragrostis curvula*) and short lawn grasses (*Sporobolus nitens*, *Paspalum notatum*, *Digitaria longiflora*, *Cynodon dactylon*). The most commonly

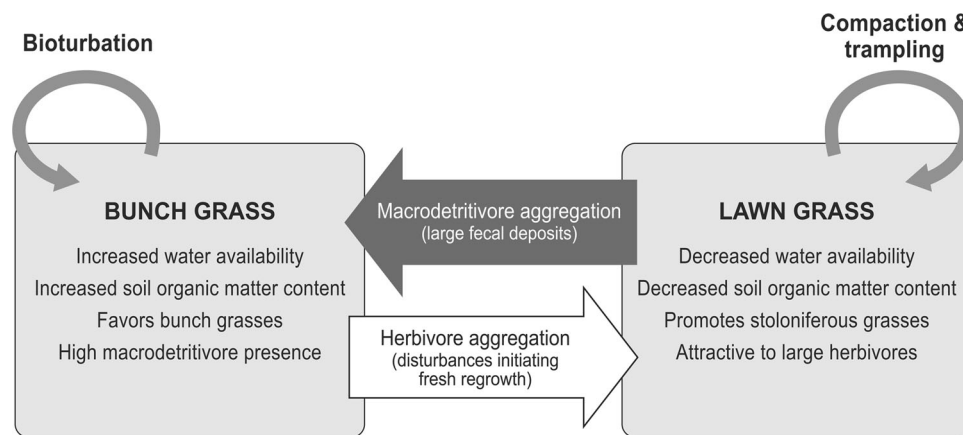


Figure 1. The positioning of subject of the current study (*black arrow*) in a schematic representation of main patch (or state) conversion mechanisms in grazing mosaics that can be viewed as multiple stable states, as each vegetation state enforces its own persistence. The *thin-lined arrow* represents mechanisms whereby herbivores aggregate at specific locations in a bunch grassland at such high densities that this converts that patch for a longer period to a grazing lawn. Causes of this aggregation can be, for example, the utilization of green-flush after a small fire, the emergence of a drinking point (water stagnation, for example, after a tree is uprooted), or the emergence of a rubbing post (for example, due to tree breaking off). The *black arrow* represents the central question of the present study: can macrodetritivore aggregation triggered by defecation “uncompact” lawn grass patches into bunch grass-dominated patches? Does this sufficiently ameliorate soil conditions through increased water and nutrient availability, promoting establishment and maintenance of tall bunch grass vegetation?

occurring large herbivore species are white rhinoceros (*Ceratotherium simum*), Cape buffalo (*Syncerus caffer*), impala (*Aepyceros melampus*), nyala (*Tragelaphus angasi*), Burchell's zebra (*Equus quagga*), waterbuck, warthog (*Phacochoerus africanus*) and wildebeest (*Connocheates taurinus*). Coprophagous macrodetritivores include different species of earthworms (Plisko 2012), termites (Freyman and others 2008), and dung beetles (Coleoptera: Scarabaeidae), which can be divided into paracoprids, which tunnel in soil beneath the dung pile; endocoprids, which reside and brood their young directly within the dung pile; and telecoprids, which famously roll their dung balls away from the dung pile and bury them at some distance (Stronkhorst and Stronkhorst 1997; Nichols and others 2008; Chao and others 2013).

Treatments

In a full factorial block design, we compared the changes that occurred in two dung addition treatments to a control site within every replicate, which would account for any changes that occurred due to external environmental factors (for example, seasonal progression). For the two dung addition treatments, we placed 20 kg dung piles

($1 \times 1 \times 0.25$ m, a typical defecation) on top of either a double sheet of fine metal mesh (0.1×0.1 cm—to prevent penetration of tunneling dung beetles and similar large macrodetritivores from the dung into the soil, or coarse mesh (2×2 cm—allowing the activity of all types of macrodetritivores (Figure 2A–F). This design allowed the separation between the effects of activities of macrodetritivores that arrive in the dung pile from belowground (termites and earthworms) and macrodetritivores arriving from aboveground (dung beetles). The dung was collected as fresh as possible in the early morning, that is, had to have been deposited by a white rhinoceros within the previous night and was mixed thoroughly in a large 80-L bin before placing on the mesh. All plots including that of the control sites were located in mixed bunch-lawn vegetation where the ratio ranged between 40:60 and 60:40 and no obvious signs of soil macrodetritivore activities were visible. This excluded (delays in) plant species colonization from the experimental design as a potential explanation for understanding vegetation responses. Vegetation plots were located directly adjacent to the dung addition plots, orientated along the main downslope gradient. Vegetation responses were

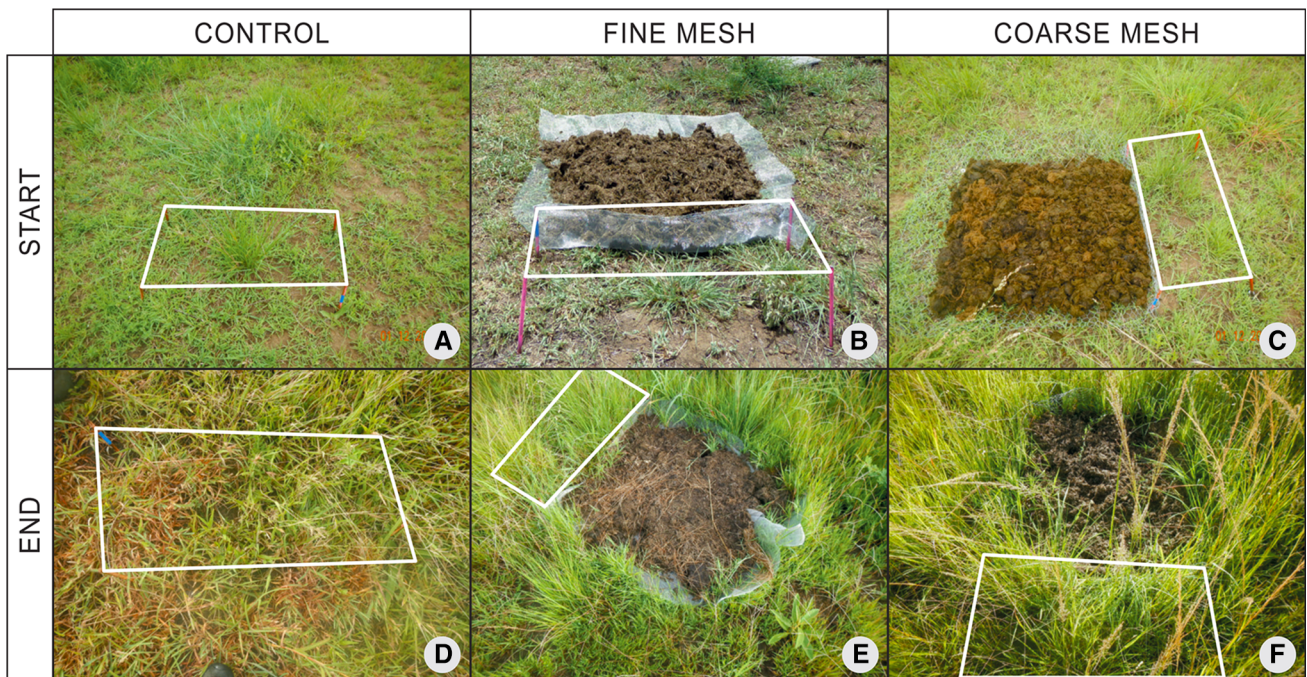


Figure 2. A full factorial design of 5 sites with 3 replicates per site. We placed 20-kg white rhinoceros (*Ceratotherium simum*) dung in **A** comparable plots of mixed bunch-lawn grass vegetation, **B** on top of a double layer of fine mesh (\varnothing 1 mm), and **C** a single layer of coarse mesh (\varnothing 2 cm). After 12 weeks, measures of vegetation cover, changes in vegetation biomass, and soil properties were recorded in the vegetation plots downslope adjacent to the dung piles (**D**, **E**, **F**). A substantial amount of dung mass (remaining coarse fragments) was still present on top of the ground at the experimental sites at the end of the experiment (**E**, **F**).

therefore not explained by the direct killing of vegetation by the shading of the dung, whereas any increased infiltration of water at the dung patch was expected to also extent to affect the undisturbed vegetation directly next to it, downhill. The experiment was done in a randomized block design at 5 sites of 3 replicates per treatment (control, coarse mesh, fine mesh), arranged in 3 blocks containing all 3 treatments. Spacing between blocks within a site was from 50 to 100 m. The 5 sites (maximally 30 km and minimally 2 km apart) were positioned across a rainfall gradient from 500 to 700 mm y^{-1} to allow for generality of the conclusions (that is, not contingent to a specific rainfall or set of local soil conditions). The experiment lasted for 12 weeks, in the period between December 2013 and March 2014. Figure 2 provides an overview of the layout of the different experimental treatments.

Macrodetritivore Distribution

Two plots of 40 × 40 cm per dung pile were used to score earthworm casts and termite sheeting, which are characteristic signs of their presence (Henrot and Brussaard 1997; Ndiaye and others 2004; Kihara and others 2014) and used as relative estimates for their activities between sites. The dung piles were carefully lifted and one plot was located central (maximum moisture) and one randomly at the edge (transitioning from wet to more dry). Plots were divided into 10 cm² subplots (4 × 4 subplots) and in each subplot the cover of termite, earthworm, or dung beetle holes was scored as 0 (not present), + (<25), 25–50, 51–75, 76–100% coverage. To quantify the abundance and distribution of dung beetles we also conducted a dung colonization study following the approach of Stronkhorst and Stronkhorst (1997). To not disturb the patch conversion experiment by macrodetritivore sampling, we collected additional dung and placed 3 × 10 kg dung piles on a sheet of coarse mesh within 20 m of each replicate. Dung was placed at 7 am in the morning and equal portions were removed and placed in a 10-L plastic basin and searched for beetles (dung-dwellers) after 3, 5, 8, and 26 h of dung incubation. All dung beetles encountered were counted, identified and the pronotum width measured to estimate body size. At 8 and 26 h of dung incubation, we applied a water flotation method (Edwards 1991) below the dung piles to sample soil-tunneling dung beetles. Body mass from pronotum width calibration curves per dung beetle species (≈10 individuals per species, dried for 200 h at 70°C) was used to estimate

the biomass of each individual, using linear regression.

Ground Cover and Vegetation Biomass Measurements

Permanent 40 × 80 cm vegetation monitoring plots were set up as controls and on the downslope side of the dung pile. Ground cover by vegetation was assessed by dividing the plot into 36 smaller 10 cm² subplots (4 × 8 subplots). Each subplot was subdivided into quarters and in each subplot the lawn vegetation (stolons and leaf cover), bunch grass vegetation (basal cover), forbs, litter, and bare soil were given a score of 0 (not present), + (<25), 25–50, 51–75, 76–100% soil cover. Vegetation height for lawn was estimated by dropping a small disk pasture meter (weighing 68.5 g, Ø 11.5 cm) sliding along a plastic pole (Ø 2 cm) from 50 cm height above the ground, repeated 3 times within the vegetation plot. For the bunch grass vegetation, we recorded the number of tussocks, and within each tussock counted the number of individual ramets and measured the length of the tallest leaf from 10 randomly selected ramets. These non-destructive measurements were used to calculate real vegetation biomass using a series of calibration plots. The vegetation cover and height were recorded in these plots the same way as in the vegetation plots. The vegetation of each plot was then clipped separately for the lawn and bunch grasses, dried at 70°C until constant weight (24 h), and weighed. Linear regressions were then fitted to calculate the dry biomass from estimated abundance for each group. Vegetation measures were conducted at the start and end of the experiment.

Soil Measurements

Soil water infiltration rate (mm s^{-1}) was measured using a double-ring infiltrometer (Bower 1986). Soil organic matter content (%) was estimated using the loss on ignition method by ashing the samples for 16 h at 420°C (Stock and others 2010). Soil electrical conductivity ($\mu S cm^{-3}$) was measured as a proxy for soil salinity (Mills and others 2009). Soil air porosity (%) was measured by maximally compressing 10 × 5 cm Ø soil cores using a technique following Jafarzadeh (2006). Lastly, we estimated soil moisture content (%) and bulk density (g cm^{-3}) using 100 cm³ volumetric samples dried at 105°C for 48 h (Terzaghi 1996). Soil measurements were conducted at the start and end of the experiment to control for environmental effects.

Dung Analysis

Dung electrical conductivity ($\mu\text{S cm}^{-3}$) was measured as a proxy for dissolved salts content (Mills and others 2009) by washing a mixed sub-sample (50 g) of fresh dung at the beginning and end of the experiment with 150 ml of demineralized water. A second set of dung samples (50 g) was weighted and dried at 70°C for 48 h (until constant weight). Differences in dung moisture content were calculated between the start and end of the experiment.

Data Analysis

We used redundancy analysis (RDA) as available in the vegan R package (Oksanen and others 2013) to reduce the dimensionality of the dataset, and explore the multivariate relationships between predictor and response variables. The RDA calculations were based on correlation instead of covariance matrices to standardize variables of varying scales and magnitudes. PERMANOVA (permutational multivariate ANOVA available from the vegan R package (Oksanen 2011), with 999 permutations) was used to test for treatment and rainfall effects for the combined response of vegetation cover

(bunch, lawn, forb) and soil properties (water infiltration, organic matter, electrical conductivity, air porosity, moisture, bulk density) to the experimental treatments. Dung colonization by different groups of coprophagous macrodetritivores along the rainfall gradient was analyzed using Linear Mixed Models (LMM) (Pinheiro and others 2013) with block as a random effect. Using general LMMs, we compared vegetation and ground cover measures (litter, bare ground), the change in bunch and lawn vegetation biomass (change = end BM—start BM), and soil properties in relation to the two dung addition treatments (placed on fine and coarse mesh), using rainfall and their interactions with block as a random effect. Because no interaction effects were found across the rainfall gradient for all response measures (Table 1), we further tested for differences between treatments by contrasting pairs of treatments (Bates and others 2014) with block nested within site as random effects. Response ratios were calculated following Hedges and others (1999). All statistical analyses were conducted using the statistical software R, version 3.1.1 (RCoreTeam 2015).

Table 1. The Effects of Dung Addition Treatments Along a Rainfall Gradient on Vegetation and Soil Properties, Allowing Separation of Impacts of Dung Beetles Versus Earthworms and Termites

Measure	Treatment F-value	Rainfall F-value	Interaction (treatment* Rainfall) F-value				Means			Effect size						
			Control	Fine mesh	Coarse mesh		Control	Fine mesh	Coarse mesh	Fine Mesh	SE	Coarse Mesh	SE			
Vegetation and ground cover	Bunch cover	8.65 **	7.04 *	0.94	n.s.	17.24	a	28.83	b	30.81	b	0.51	0.13	0.58	0.13	
	Lawn cover	1.64	n.s.	5.07 *	0.04	n.s.	33.18	a	29.64	a	26.51	a	-0.11	0.10	-0.22	0.10
	Non bunch cover (lawn + bare + forb)	3.59 *	6.98 **	1.74	n.s.		65.65	a	54.40	b	55.81	b	-0.19	0.05	-0.16	0.05
	bunch/non-bunch cover ratio	3.03 *	1.75	n.s.	0.87	n.s.	0.29	a	0.83	b	0.73	b	1.05	1.78	0.92	1.68
	Litter cover	0.38	n.s.	1.24	n.s.	1.19	n.s.	11.88	a	11.51	a	10.18	a	-0.03	0.19	-0.15
Shoot biomass	Change in biomass bunch	9.01 ***	8.74 **	0.10	n.s.	10.72	a	23.94	b	20.44	c	0.65	0.19	0.80	0.19	
	Change in biomass lawn	0.69	n.s.	1.38	n.s.	1.84	n.s.	12.07	a	19.85	a	9.35	a	-0.25	0.21	0.50
Soil properties	Water infiltration	10.08 ***	1.75	n.s.	1.41	n.s.	1.00	a	3.31	b	10.04	c	1.20	0.90	2.31	1.59
	Organic matter	8.33 **	47.36 ***	0.55	n.s.	4.65	a	5.20	b	5.71	b	0.11	0.16	0.21	0.14	
	Salinity	33.91 ***	13.26 ***	1.06	n.s.	54.25	a	121.87	b	143.65	b	0.81	0.06	0.97	0.07	
	Air porosity	1.56	n.s.	7.82 **	0.04	n.s.	11.47	a	14.33	a	14.47	a	0.22	0.16	0.23	0.15
	Soil moisture	0.89	n.s.	31.92 ***	0.36	n.s.	11.85	a	12.77	a	12.64	a	0.07	0.13	0.07	0.13
Bulk density	0.91	n.s.	1.37	n.s.	0.25	n.s.	1.34	a	1.30	a	1.26	a	-0.03	0.24	-0.06	0.24

Means with different letters are significantly different (using contrasted pairs of treatments (Bates and others 2014)). Effect sizes were calculated following Hedges and others (1999). Results with significant effects are shown in bold and variables significantly affected by the dung addition treatment are highlighted in grey. Asterisks denote significant F values (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

RESULTS

The RDA analysis revealed two main axes of variation within the data. Axis 1 mostly represents variation within the data along the rainfall gradient (55%, indicated as contours, Figure 3) and axis 2 represents the variation mostly due to the dung addition treatments in comparison to the control (40%, indicated as ellipses, Figure 3). The

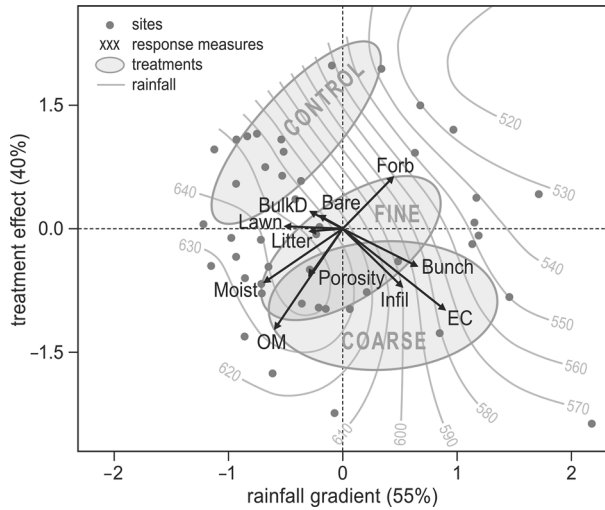


Figure 3. Biplot showing the RDA analysis of response measures (ground cover and soil properties), in relation to constrained treatments (shown as centroid ellipses: control, fine, and coarse mesh treatments) and unconstrained predictors (shown as contours: rainfall). Lawn, Bunch, Litter, Bare, Forb = ground cover scores; Infil = water infiltration; EC = electrical conductivity (as proxy for salinity); OM = soil organic matter content; Porosity = soil air porosity; Moist = soil moisture content; BulkD = soil bulk density.

PERMANOVA showed that the relationships between plant cover (bunch, lawn and forb) and soil properties (water infiltration rate, organic matter content, electrical conductivity, air porosity, soil moisture content, bulk density) for both rainfall (PERMANOVA: $F_{(1,44)} = 6.41, P < 0.01$) and dung addition treatments (PERMANOVA: $F_{(2,44)} = 14.86, P < 0.001$) were highly significant.

Macrodetritivore Distribution

The analysis of the variation in the colonization of the dung by coprophagous macrodetritivores revealed that earthworms increased in abundance with increasing rainfall (LMM: $F_{(2,57)} = 14.44, P < 0.001$), whereas termites instead decreased in abundance (LMM: $F_{(2,57)} = 5.81, P < 0.05$) (Figure 4a). The colonization by tunneling dung beetles instead was not related to the rainfall gradient (LMM: $F_{(1,13)} = 1.71, P = 0.21$), whereas dung-dwelling dung beetles increased significantly in abundance with increasing rainfall (LMM: $F_{(1,13)} = 7.64, P < 0.05$) (Figure 4b). The different mesh size treatments were successful in separating effects of dung beetles from that of earthworms and termites because only very few holes (average < 1, max = 3) indicative of soil-tunneling dung beetles were found beneath the double fine mesh layer compared to the coarse mesh (average = 22, max = 128), (Paired *t* test: $T_{(1,13)} = 2.41, P < 0.05$).

Ground Cover and Vegetation Biomass Measurements

Bunch grass cover was significantly higher in both of the dung addition treatments, which were not

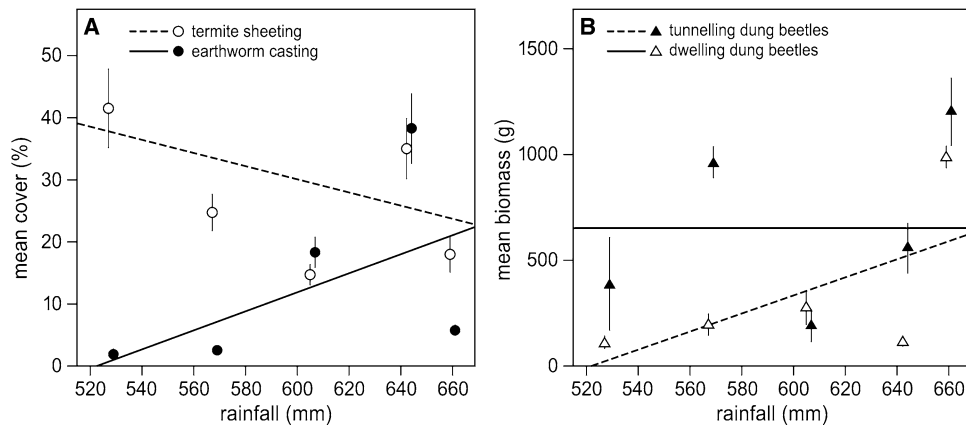


Figure 4. Changes in (proxies for) the abundance of different coprophagous macrodetritivores along the rainfall gradient in the dung colonization experiment. **A** Colonization of termites and earthworms, measured as % surface cover of their sheeting or casting beneath a dung pile. **B** The cumulative mean biomass (dry weight) of soil-tunneling versus dung-dwelling dung beetles (Coleoptera: Scarabaeidae). Points represent mean ± SE.

different from each other, whereas lawn grass was not affected by the dung addition treatments (Table 1). The dung addition treatments significantly favored the expansion of bunch grass at the cost of non-bunch cover (lawn + bare ground + forb cover), as indicated by the uniformly higher ratio of bunch to non-bunch cover (Table 1) across the rainfall gradient. The change in bunch grass shoot biomass between the start and end of the experiment was significantly higher for the dung addition treatments. In addition, bunch grass shoot biomass increased towards higher rainfall and a significant difference was detected between the different mesh treatments, where bunch grass next to the coarse mesh treatment was higher than next to the fine mesh (see differences in means and response ratios, Table 1). The change in lawn grass biomass was not different between the control and treatments and was uniform along the rainfall gradient (Table 1).

Soil Measurements

Water infiltration rate, soil organic matter content, and electrical conductivity were significantly positively affected by the dung addition treatments; a significant difference was detected between treatments where water infiltration in the coarse mesh treatment was highest. However, there were no significant differences between treatments for soil organic matter content and electrical conductivity (Table 1). Soil air porosity, soil moisture content, and bulk density were unaffected by the dung addition treatments. Soil organic matter content, air porosity, and soil moisture content were all significantly positively correlated and soil electrical conductivity negatively correlated to increasing rainfall, whereas water infiltration rate and bulk density were unrelated to the rainfall gradient (Table 1).

Dung Analysis

Electrical conductivity of the remaining dung at the end was significantly lower compared to the start of the experiment (Paired t test: $T_{(1,4)} = 11.67$, $P < 0.001$). Moisture content of the remaining dung was wetter at the end compared to the start of the experiment (Paired t test: $T_{(1,4)} = 7.33$, $P < 0.01$).

DISCUSSION

A remarkable first finding is that the effect of adding dung on vegetation and soil variables were equal in magnitude at all sites along the rainfall gradient in our study area. Specifically, the re-

sponses of the tall bunch grasses to the experimental manipulations were uniform across the rainfall gradient. In contrast, earthworms and termites replaced each other along the rainfall gradient, where earthworms were more prevalent towards higher mean annual rainfall and termites were more prevalent towards the drier regions, suggesting a functional complementarity at the landscape scale that is in agreement with other such studies (Lal 1988; Henrot and Brussaard 1997). Dung beetles are attracted by aromatic cues and, being mobile, opportunistically occupy dung piles within hours of its deposition (Stronkhorst and Stronkhorst 1997). Soil-tunneling dung beetles were equally spread along the rainfall gradient; however, dung-dwelling dung beetles increased in abundance towards higher rainfall.

We demonstrated that basal cover of tall bunch grasses in this savannah ecosystem can significantly increase within 12 weeks by attracting coprophagous soil biota which colonize the dung pile, either entering the dung pile from below (earthworms and termites) or from above (dung beetles). We showed that particularly the cover ratio of bunch:non-bunch and biomass of bunch grasses profit from important alterations to soil properties. Macrodetrivores had two main effects on soil properties as shown by our results. First, they increased soil organic matter content, which positively enhances nutrient availability (Ruess and McNaughton 1987) through incorporation of dung into the soil. Secondly, they increased water availability through the creation of more permeable soil, because we found significantly higher infiltration rates under the dung piles, which was due both to accessing the dung from below the pile and the burying of dung balls by soil-tunneling dung beetles. We did not find differences in soil moisture; however, our measure was a once-off instantaneous measure. In our interpretation of the results, we put higher emphasis on the differences in infiltration rate, as actual soil moisture differences are subject to much stronger temporal variability (for example, depending on rainfall the previous day). Increased soil permeability allows surface water, running off from adjacent compacted vegetation patches, to soak into these patches therefore improving growing conditions. Lawn cover and lawn dry mass were unaffected by the dung addition treatments, although we did not control for biomass removal by grazing herbivores, (caging the plots would have led to unwanted interactions). However, grazing by herbivores would lead to a reduction in both biomass and cover, as herbivores generally prefer the higher

quality lawn grasses. A more likely explanation is therefore that the better growing conditions (more water and nutrients) allowed the taller, thicker rooted bunch grasses (van der Plas and others 2013b) to expand in basal cover and aboveground biomass. Therefore, although bunch grasses were not able to displace lawn grasses in 12 weeks, bunch grasses were able to invade the available bare ground (faster than the lawn species) and displace herbaceous forb species.

A clear result was that soil electrical conductivity was significantly higher in the vicinity of the dung pile, likely caused from salts in the dung leaching into the ground. Higher electrical conductivity (as a proxy for salinity) is physiologically stressful to plants (Parida and Das 2005) as it can impair the water balance of the plant in ecosystems with a clear dry season. However, it has been shown that nutrient addition is generally far more important to plant production than salinity (Poorter and Nagel 2000). Soil bulk density and air filled porosity tended to increase in the presence of dung and soil macrodetritivores; however, the effect of treatment was not significant. The contrast between our findings and expectations from other studies could be because most studies test the decreasing effect of soil macrodetritivores on bulk density in the excavated soil (Joschko and others 1989; Mittal 1993). In this case, the soil remaining within the undisturbed soil profile remains at the same average density (in our case, per 10 cm³) albeit with increased water infiltration rate and organic matter content due to increased presence of millimeter-scale biovoids. Quantifying these effects would require more advanced quantification of 3D soil physical structure than we did in our study.

Previous studies have shown that increased nutrient addition as ureum or NH₄NO₃ in the presence of herbivores promotes lawn formation in savannahs (Ruess and McNaughton 1987), specifically above a certain threshold patch size (Cromsigt and Olf 2008). Such studies mostly mimic nutrient returns by herbivores as urine (Veldhuis and others 2014) or fecal deposits that comprise small pellets and are easily scattered. Our study suggests that large dung piles may have an opposite effect in grazing ecosystems. In this case, the residual plant material remains on top of the soil surface for an extended period of time. Very large herbivores such as buffalo, white rhino, and elephant (Hobbs 1996; Stronkhorst and Stronkhorst 1997) defecate in exponentially larger quantities compared to herbivores weighing less than 500 kg (Hobbs 1996). The social and territorial behavior in males of smaller grazers such as zebra, wildebeest,

and impala to defecate on the same pile, leading to middens can lead to similar effects. Territorial middens created by megaherbivores (>1000 kg) such as male white rhinoceros are surrounded by grazing lawns created by frequent use, intense grazing pressure, and increased nutrients (Owen-Smith 1988). On the other hand, female rhinoceros do not concentrate their dung in middens and defecate throughout the landscape (Estes 1991). Our observed natural effects of dung on termites and associated soil properties likely point to a similar mechanism known from African agro-ecosystems. Rural farmers in Niger have been shown to utilize termite activities to restore degraded and compacted soil by placing vegetative residue on the soil surface. This promotes feeding tunnel formation of termites and thus ameliorates soil conditions by improving water infiltration, incorporation of organic materials into the soil profile, and vegetation establishment (Lal 1988). Similarly, organic mulch (woody debris + straw) has been shown to work well in the Sahel in improving water infiltration in degraded (crusted) soils due to its stimulating effect on termites (Mando and Miedema 1997).

We conclude that our study supports the hypothesis that macrodetritivore aggregation in and under dung piles can lead to patch conversion from short lawn grass dominated to tall bunch grasses in small-scale grazing mosaics (Figure 1). Removal of the keystone species from African savannahs, such as the white rhinoceros (as now ongoing in our study area due to heavy poaching), which strongly interact with macrodetritivores could hence induce large ecological changes, with cascading impacts on local vegetation heterogeneity, biodiversity, and associated ecosystem functions and services (Coleman and Williams 2002). Across a wider range of ecosystems, similar types of interactions between macrodetritivores and soil are now even considered to be at least as important as the classical trophic interactions studies (Reise 2002; Meysman and others 2006).

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