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Functional traits of trees on and off termite mounds: understanding the origin of biotically-driven heterogeneity in savannas

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Browser; Competition; Defence; Fire; Herbivory; Macrotermes; Polyphenols; Soil nutrients; Stress; Woody species

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Abstract

Questions: In African savannas, *Macrotermes* termites contribute to small-scale heterogeneity by constructing large mounds. Operating as islands of high nutrient and water availability and low fire frequency, these mounds support distinct, diverse communities of trees that have been shown to be highly attractive to browsers. However, the distinct traits of tree species on termite mounds have hardly been studied, even though this may help to understand processes determining (1) their characteristic community structure and (2) attractiveness for browsers. Here, we compare functional trait and browser preference values between tree species on and off termite mounds.

Location: Hluhluwe-iMfolozi Park, Kwazulu-Natal, South Africa.

Methods: We recorded tree community compositions for 16 large *Macrotermes natalensis* mounds and 16 control plots of 100 m^2 each in a paired design. For each observed tree species we measured 22 traits, related to water and nutrient use, fire tolerance, light competition and anti-herbivore defence, and compared average trait values between mound and control communities. Furthermore, we investigated the feeding preferences of ungulate browsers for the most common tree species and how this was linked to their associated traits.

Results: Termite mounds supported tree communities that were distinct from the surrounding savanna vegetation. Mounds hosted more evergreen and less leguminous tree species than control communities, and the dominant species were less mechanically defended, less nutritious, had larger leaves and lower wood density than the species dominating control plots. Browsers preferred leguminous tree species with high leaf N and P content, which were relatively rare on termite mounds.

Conclusions: Overall, we conclude that termite mounds in this savanna form small refuges for tree species that seem less adapted to fire (more evergreens), have low nutrient availability (less nitrogen fixers) and suffer from water stress (larger leaf sizes) than typical savanna trees. Surprisingly, despite their reputation as browsing hotspots, the tree species dominating mounds are less nutritious and less preferred by browsers than tree species of the surrounding savanna, which may be explained by the relatively nutrient-rich nature of this savanna or intraspecific trait differences.

Introduction

Savannas are among the most species-rich ecosystems on Earth (Mittermeier et al. 1998), in which their high spatial heterogeneity plays an important role (Scholes 1990). This heterogeneity is found at several spatial scales, with different abiotic and biotic processes creating heterogeneity at each scale (Scholes 1990; Gilson 2004; Cromsigt 2006). At large spatial scales, rainfall patterns can drive habitat heterogeneity (e.g. Sinclair et al. 2008). At intermediate scales, fire, geological and soil factors become more important (Scholes 1990; Higgins et al. 2000), while at the smallest

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scales, heterogeneity is mainly driven by biotic agents, such as mammalian herbivores (Cromsigt & Olff 2008; Waldram et al. 2008) or termites (Moe et al. 2009; Okullo & Moe 2012; Gosling et al. 2012). In small reserves, where large landscape-level gradients are often less important, the biotic drivers of local scale heterogeneity are essential in creating and maintaining high biodiversity (Cromsigt & Olff 2008).

Mound-building termites, such as *Macrotermes* spp., are key drivers of heterogeneity at local scales (Dangerfield et al. 1998; Sileshi et al. 2010). It has been shown that their mounds constitute only ca. 5% of the savanna landscape, but with high tree densities that strongly contribute to the small-scale variation in woody vegetation cover (Moe et al. 2009; Levick et al. 2010). In addition, the tree communities found on mounds are often very diverse, hosting many species that are not found elsewhere in the savanna (Traoré et al. 2008; Moe et al. 2009; Okullo & Moe 2012). These tree species supply popular food for herbivores, with megaherbivores preferentially browsing mound trees (Holdo & McDowell 2004; Loveridge & Moe 2004; Levick et al. 2010). However, the determinants of the altered tree community composition on termite mounds, such as modified nutrient, water and light availability and fire regimes, have remained poorly studied until now. Furthermore, we do not understand why the trees found on termite mounds are so attractive to ungulate browsers. Exploration of the functional traits of the dominant tree species may shed light on these determinants. Therefore, we investigated how traits related to stress tolerance, competition for light and plant mineral nutrition differ between dominant tree species on and off *Macrotermes natalensis* mounds in an African savanna. Furthermore, we investigated the relationships between these traits and attractiveness to browsers.

Several abiotic and biotic factors have been suggested to play important roles in the local community assembly of savanna trees: drought, fire, soil fertility and competition for light (Walter 1971; Frost et al. 1986; Scholes & Walker 1993; Bond & Wilgen 1996; Cramer et al. 2010). All of these factors can be locally modified by *Macrotermes* activity through the construction of their mounds (Dangerfield et al. 1998) and removal of nearby litter and plants. The soil used for construction of mounds often comes from deeper soil layers (Holt & Lepage 2000) and therefore has higher clay content and elevated concentrations of several cations, inorganic carbon and extractable nitrate and ammonia (Holt & Lepage 2000; Okullo & Moe 2012; Gosling et al. 2012). The finer soil texture creates a higher water potential in the mound soil (Konaté et al. 1999). In addition, the construction of subterranean feeding galleries and tunnels increases soil infiltration rates and improves soil water transmission properties in the vicinity of the mounds, thereby further increasing soil water availability (Holt & Lepage 2000). Also, termite mound vegetation is apparently less affected by fire than the surrounding savanna (Dangerfield et al. 1998; Moe et al. 2009). The higher tree densities that may result from higher water availability and less fire impact (Loveridge & Moe 2004; Traoré et al. 2008; Moe et al. 2009; Levick et al. 2010) may create stronger competition for light among these trees on the mounds.

The effects of *Macrotermes* on plant resource availability, competition and fire regimes are probably reflected in the traits of tree species that preferentially occur on mounds. These same traits can also be important in explaining why browsers preferentially feed on trees that dominate termite mounds: most browser species do not feed randomly, but prefer foliage with a high nutrient content and low chemical and mechanical defences (Cooper & Owen-Smith 1985, 1986; Owen-Smith & Cooper 1987; Emslie 1999).

Therefore, in this study, we use a trait-based approach (McGill et al. 2006) and asked two questions: (1) do *Macrotermes* affect the trait-based community assembly of trees by creating environments with reduced abiotic stress and increased light competition; and (2) can the resulting functional differences between tree species dominating mounds or the surrounding savanna explain why *Macrotermes* mounds act as browsing hotspots? For the first question, we compared values of several plant traits related to drought, fire and herbivory resistance and attractiveness, light competition and nutrient limitations between woody species dominating termite mounds and species dominating the surrounding savanna. We expected trees dominating mounds to be less stress tolerant (e.g. more often evergreen, lower wood density) and stronger light competitors (e.g. less legume species) than trees dominating the surrounding savanna. For the second question, we studied the feeding preferences of ungulate browsers and investigated how these preferences are related to plant species traits. We expected that trees dominating mounds are more nutritious (e.g. higher leaf N and P and lower polyphenol content) than trees dominating the surrounding savanna, and that trees with these traits will be favoured by browsers. Answering these questions may help to understand the unique ecological role of termite mounds as key determinants of savanna heterogeneity, specifically in forming browsing hotspots for large herbivores.

Methods

Study area

Fieldwork was carried out in Hluhluwe-iMfolozi Park (HiP), an 89 665-ha mesic savanna nature reserve in Kwazulu-Natal, South Africa (Appendix S1). Altitude ranges from 40 to 750 m a.s.l. Most areas in the park burn

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frequently, with a mean fire return period of 3.8 yr (Balfour & Howison 2002). Vegetation types vary from grasslands, savannas and broad-leaved thickets, to upland forest. Broad-leaved woodland communities are dominated by *Euclea divinorum* or *Spirostachys africana*, but more than half of HiP consists of savanna dominated by *Acacia* spp., with varying amounts of woody cover (Whateley & Porter 1983). HiP contains a rich assemblage of browsing ungulate species, with the more common ones, in decreasing order of body size, being: African elephant (*Loxodonta africana*), black rhino (*Dicerosbicornis minor*), giraffe (*Giraffa camelopardalis*), kudu (*Tragelaphus strepsiceros*), nyala (*Tragelaphus angasii*), bushbuck (*Tragelaphus strepsiceros*), impala (*Aepycero smelampus*) and grey duiker (*Silvicapra grimmia*).

Here we: (1) compared tree community composition and tree trait values between mound and control plots (hereafter: 'mound study'), and (2) studied the feeding preferences of different browser species (hereafter: 'browser preference study').

Mound study: plot selection

During November and December 2009, 16 sites were selected and stratified at random at different locations within HiP. Sites were within 500 m of a road (for safety reasons), at least 500 m from larger rivers and from drainage areas, and at least 600 m from each other, with the mean nearest neighbour distance being 3.4 km (Appendix S1). At each *a priori* selected site the nearest *Macrotermes* spp. mound was selected for study. A mature termite mound was recognized by its central dome-shaped structure surrounded by a cone-shaped erosion skirt. We defined a mound plot as the 10 m × 10 m area around the centre of the mound. Although most mounds were smaller than 10 m × 10 m, it is likely that within this area the vegetation has been highly altered by *Macrotermes* activity, since the influence of *Macrotermes* on plant communities extends well beyond their own mound, e.g. through subterranean foraging tunnels (Levick et al. 2010). By surveying 16 relatively small sites that were at relatively large distances from each other, we made sure that any statistical differences found between mound and control plots in our study represented patterns that could be generalized for our whole study area, rather than differences resulting from pseudoreplication.

The 16 control plots, also 10 m × 10 m, were selected by taking a random distance between 20 and 80 m from the centre of the termite mound at a random compass bearing (1–360°). Obvious landscape features, such as wallows, were avoided. Where another *Macrotermes* mound was closer to the control plot, a new random distance and direction was taken.

Mound study: plot sampling

Surface cover of grass, forbs and bare soil and average height of the vegetation were estimated for both mound and control plots. Then, all trees above 0.5 m in height in the plots were identified to species level using Pooley (1997), local experts and the herbarium collection of the HiP. Canopy height of individual trees was estimated using two classes: above and below 2 m in height. This 2-m cut-off has been shown to reflect a cut-off between high and low mortality from fires (Higgins et al. 2007) and, furthermore, has been shown that except for giraffes and elephants, browsers rarely feed on vegetation above 2 m (Du Toit 1990). Stem diameter at stump level of trees was estimated using seven classes: (1) 0–1 cm, (2); 1–3 cm, (3) 3–10 cm, (4); 10–20 cm, (5) 20–30 cm, (6) 30–40 cm and (7) 40–50 cm. Tree diameter was used to calculate the total surface area (TSA) of each species in a plot: $\mathrm{TSA} = \sum_{i=1}^{n} \pi r_i^2$, in which n is the number of individuals and r is the average radius from the diameter class the i-th individual belongs to (e.g. 0.25 cm for class 1). TSA was used as a proxy for the biomass of the given species in a plot.

Mound study: trait selection

At each site, 22 traits were measured for all tree species, representing functional adaptations to drought, fire, herbivory resistance and attractiveness, light competition and nutrient limitations. The traits examined were specific leaf area (SLA), leaf area (LA), leaf fractal dimension (FD), thorn length (TL) and density (TD), branch angle (BA), leaf trichome density (TrD), wood density (WD) and leaf polyphenol, carbon (C), nitrogen (N), phosphorus (P), sulphur (S), potassium (K), sodium (Na), calcium (Ca), magnesium (Mg), iron (Fe), manganese (Mn), zinc (Zn), boron (B) and copper (Cu) content. For the functional significance of these traits, see Cooper & Owen-Smith (1986); Brown & Lawton (1991); Yates & Peckol (1993); Marschner (1995); Olff et al. (1999); Weiher et al. (1999); Hacke et al. (2001); Westoby et al. (2002); Cornelissen et al. (2003).

Mound study: locations and sample size of trait measurements

Traits were measured for each species in each site where the species was found for SLA, LA, FD, TL, TD and BA (all five measurements per site), WD (three measurements per site), SLA (five to 30 leaves), LA (five to 30 leaves), FD (five to 30 leaves), leaf polyphenol, C and N content. TrD was measured for each species in one to 14 sites, and leaf P, Na, Ca, Mg, P, S, Fe, Mn, Zn, B and Cu concentrations were measured for each species in one to seven sites. Ideally, trait values would have been measured across

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different sites for all species, but for the rarer species this was impossible. With our approach, we calculated species average trait values with as many replicates as possible; consequently, replication was thus higher for more common species. As many traits as possible were sampled from the same set of individuals in each plot.

Whenever possible, we measured these trait values on trees found off termite mounds, so that trait value differences between species reflected intrinsic species differences, not differences caused by the environment. Only when within a site, a species was only found on a termite mound, did we measure traits of that particular species on individuals growing on the mound. By measuring almost all trait data on trees growing off mounds, our analysis focussed on characterizing the mean trait value of each species across different sites, not on within-species variation, i.e. between plots or between termite mounds and the surroundings. This is based on the assumption that intrinsic species differences are generally much larger than trait variations within species (Garnier et al. 2001). This assumption received some support from our data (Appendix S2).

Mound study: trait measurements

For LA, five to 30 leaves (depending on size and weight of leaves) from multiple individuals were taken in the field and photographed with a background reference scale. The software SigmaScanPro v 5.0 (Systat Software Inc., San Jose, CA) was used to measure LA and leaf FD (leaf perimeter/LA) on fresh leaves. Leaves were then dried at 50 °C for at least 48 h and weight was measured to 0.001 g precision. SLA was calculated by dividing the total LA by the dry weight of a leaf sample. TL was measured from at least five thorns of three individuals. TD was measured similarly (five branches, three individuals per site) over 20 cm at the top of a branch. Both traits were measured at a height of 1.0 m if possible, a height that most browser species can reach (Du Toit 1990). BA was measured for five individuals using a protractor. TrD was measured by counting the number of trichomes on a 50 mm × 50 mm leaf surface using an electron microscope. For WD, three branches of 20-cm long with a diameter between 2 and 13 mm were collected for each species per site and dried in an oven at 50 °C for at least 48 h. Then dry mass was measured and WD calculated as: $WD = \frac{\pi r^2 L}{M}$, where WD is wood density in $m^3 \cdot kg^{-1}$, r radius of the branch in m, L length of the branch in m and M dry weight of the branch in kg.

For chemical analyses, for each species in each site, bulk samples of leaf material were taken, dried at 50 °C for at least 48 h and ground with a ball mill. Polyphenol content, as a measure of generic chemical defence, was measured using the method described in Mole & Waterman (1987). Leaf C and N content was measured for each species in each site by taking 5 mg of finely ground leaf material (weighed to 1 μg precision) and measuring concentrations with a Carlo-Erba NA 1500 element analyser in duplicate (Carlo-Erba, Milan, Italy). The leaf content of K, Na, Ca, Mg, P, S, Fe, Mn, Zn, B and Cu was measured at the laboratory of BLGG AgroXpertus in Wageningen via ICP atomic emission spectrometry, conforming to NEN6966.

Mound study: calculating trait averages

For each species and each trait, values were usually measured in several sites. These different values were used to calculate an average species trait value (ASTV) (see Appendix S3 for values). When combining the community composition data with ASTV data, we could calculate unweighted (based on presence–absence data), abundance- and biomass-weighted average trait values. Abundance-weighted average trait values ($\overline{at}$) were calculated as: $\overline{at} = \sum_{i=1}^{n} a_i t_i / \sum_{i=1}^{n} a_i$, where n is the number of species found in a plot, a_i abundance of the i-th species and t_i the ASTV of the i-th species. Biomass-weighted average trait values ($\overline{bt}$) were calculated as: $\overline{bt} = \sum_{i=1}^{n} b_i t_i / \sum_{i=1}^{n} b_i$, where n is number of species found in the plot, b_i biomass of the i-th species and t_i the ASTV of the i-th species.

Browser preference study

In June and July 2003 and 2004, tree communities in a total of 219 plots of 50 m × 50 m, situated within all the different habitat types of HiP (Whateley & Porter 1983), except for grassland, were sampled. Distance between adjacent plots ranged from 100 to 3410 m (Appendix S1). Sampling effort for different habitat types was proportional to habitat contribution of the total area of HiP (Fig. S1c in Appendix S1).

In all plots, all trees between 0.51–2.0 m (a height mostly utilized by browsers) were recorded. Individual trees were identified using Pooley (1997), local experts and the herbarium collection of the HiP. Then, all entire individual trees were assessed for ungulate browser impact. Browser damage was identified as characteristic browser cropping or stripping of branch ends (Estes 1991). If at least one browsing mark was observed on a tree, it was considered as a browsed individual, otherwise as an unbrowsed individual. For each tree species that was also sampled in the 'mound study'and that occurred in at least 50 'browser preference study' plots, the preference index (PI) for each browser was calculated: PI = ((BMO − BME)/BME), in which BMO is number of individual trees of the given tree species on which browsing marks were observed, and BME is the number of individual trees of the given tree species on which browsing marks were

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expected, i.e. the relative abundance of the tree species multiplied by the total number of tree individuals on which bite marks were observed. PI could be calculated for 26 tree species, which accounted for 72.3% of the total number of individuals of the 'mound study' sites.

Data analysis

Non-metric multi-dimensional scaling (NMDS) analyses, based on the Bray–Curtis dissimilarity index (Bray & Curtis 1957), were performed to visualize differences in community composition of mound and control tree communities. Four NMDS dimensions were calculated, with 50 iterations. Furthermore, to investigate whether differences in species composition between mound and control sites were significant, a PERMANOVA, using the sites as random blocks, was performed, based on the Bray–Curtis dissimilarity index (Bray & Curtis 1957). To identify 'indicator species' for control and mound plots, the Dufrene & Legendre (1997) indicator value, using 100 000 randomizations, was calculated. To visualize relationships between traits, principal components analysis (PCA) was performed with all scaled trait values as active variables and browser PI as a passive variable. PCAs rely on data sets without missing values and therefore missing trait values were estimated using multiple imputations with chained equations (MICE). Simple linear regression analyses were used to investigate the relationships between browser PI and functional traits of tree species. Paired Wilcoxon signed-rank tests, using the sites as blocks, were used to study differences in species richness and abundance patterns, vegetation cover, vegetation height (unweighted, abundance-weighted and biomass-weighted), trait averages (of all species, but also focusing on legumes vs non-legumes) and (unweighted, abundance-weighted and biomass-weighted) average browser PI values between mound and control plots. Unpaired Wilcoxon signed-rank tests were used to compare the SATVs between species restricted to mound plots and species restricted to control plots. To reduce the chance of making type I errors, we performed false discovery rate analyses following the Simes (1986) procedure. All analyses were done using R-2.13.1 (R Development Core Team 2011; R Foundation for Statistical Computing, Vienna, AT).

Results

Tree community structure

In total, we found 67 tree species in our survey, of which 44 occurred in control plots and 59 occurred in mound plots (Appendix S3). Twenty-three tree species were unique to termite mounds, while only eight species were unique to control plots. Seven indicator species (Dufrene & Legendre 1997) were identified for termite mound plots: *Gymnosporia senegalensis*, *G. nemorosa*, *Berchemia zeyheri*, *Sideroxylon inerme*, *Coddia rudis*, *Pappea capensis* and *Schotia brachypetala*, while there were no significant indicator species for control plots. Mound and control tree communities differed significantly in composition (PERMANOVA, $F = 2.050$, $P = 0.010$; Fig. 1). Tree communities of termite mounds were more species-rich and had a higher Shannon–Wiener diversity than communities from the surrounding savanna, with on average 57% more species found in termite mound plots (Table 1; all $P < 0.05$). Overall abundance of trees did not differ between mound and control plots (Table 1; $P = 0.660$), although abundance of trees with a canopy height above 2 m was 4.5 times higher on mound plots than on control plots (Table 1; $P = 0.023$). Termite mounds had a higher proportion of bare soil than control plots, an equal proportion of forb cover as control plots and a lower proportion of grass cover than control plots (Table 1).

Relationships between functional traits

The PCA analyses revealed that quantitative traits of tree species were relatively weakly correlated, so that even the

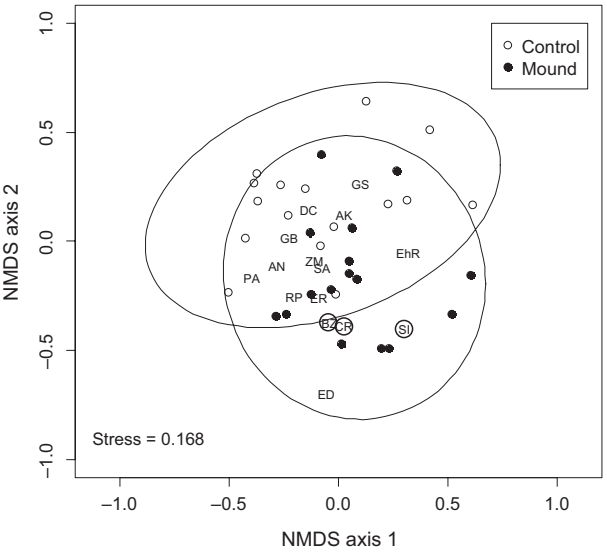


Fig. 1. Biplot of the first two NMDS axes. Control plots are given in white, mound plots in black. The ellipses around the dots represent the two-dimensional confidence intervals (±2 SD) of the average NMDS values of both mound and control plots. The 15 most dominant species found in this study are shown in NMDS space with their abbreviations: AK, *Acacia karroo*; AN, *A. nilotica*; BZ, *Berchemia zeyheri*; CR, *Coddia rudis*; DC, *Dichrostachys cinerea*; ED, *Euclea divinorum*; ER, *E. racemosa*; EhR, *Ehretia rigida*; GB, *Gymnosporia buxifolia*; GS, *G. senegalensis*; PA, *Plectroniella armata*; RP, *Rhus pentheri*; SA, *Spirostachys africana*; SI, *Sideroxylon inerme*; ZM, *Zizyphus mucronata*. The species that were identified as indicator species for mound plots are circled.

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Table 1. Species richness, abundances, diversity and evenness: comparison of averages between control and mound sites.

	Control	Mound	*V*	*P*
Species richness	7.500 (0.816)	11.81 (1.065)	121.5	0.004*
Abundance	127.8 (27.49)	135.2 (14.94)	77	0.623
Abundance > 2 m	2.875 (1.258)	12.94 (3.781)	59	0.023*
Diversity	1.208 (0.108)	1.807 (0.131)	125	0.002*
Evenness	0.622 (0.038)	0.740 (0.028)	109	0.034†
% Bare ground	28.18 (5.96)	45.09 (4.93)	120.5	0.007*
% Forb cover	9.44 (2.25)	9.59 (1.31)	56	0.850
% Grass cover	62.28 (5.36)	45.31 (4.93)	13	0.008*
Grass height (cm)	29.84 (4.14)	22.81 (4.27)	15	0.036†
Forb height (cm)	32.19 (5.16)	26.56 (3.61)	39	0.243

SE shown in parentheses. Abundance > 2 m indicates the abundance of trees with a canopy height over 2 m. Significance testing was done using a paired Shapiro–Wilks test, with *V* as the test statistic and an associated *P*-value. *P*-values below 0.05 that remained significant after false discovery rate testing are shown with an*, those that were not significant after false discovery rate testing are shown with a†.

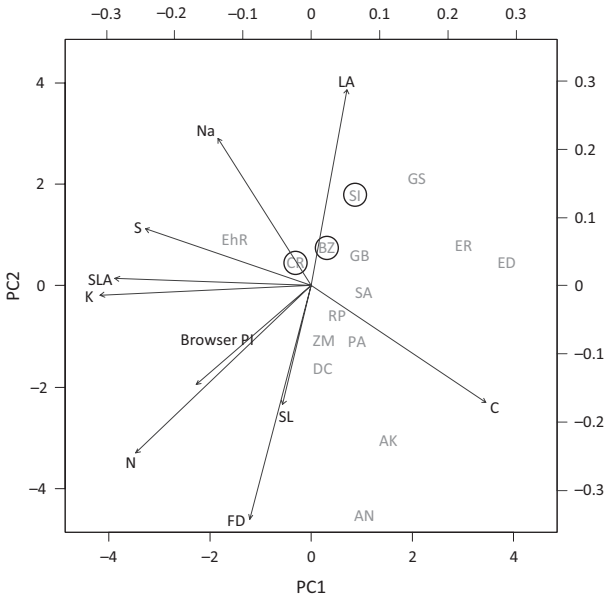


Fig. 2. Biplot with the first two dimensions from the PCA. All measured, continuous trait variables (scaled) were used as active variables and browser PIs as passive variables. For each dimension, the five trait variables that correlated most strongly with it are plotted, as well as the browser PIs. Furthermore, the 15 tree species that were most abundant in the mound study are plotted. Abbreviations, traits: LA, individual leaf area; C, leaf carbon content; SL, spine length; FD, leaf fractal dimension; N, leaf nitrogen content; K, leaf potassium content; SLA, specific leaf area; S, leaf sulphur content and Na, leaf sodium content. Abbreviations, PIs: ele., elephant PI; rhino, rhino PI; other, PI of 'other browsers' and 'all', all PI of all browsers combined. Abbreviations of tree species names: AK, *Acacia karroo*; AN, *A. nilotica*; BZ, *Berchemia zeyheri*; CR, *Coddia rudis*; DC, *Dichrostachys cinerea*; ED, *Euclea divinorum*; ER, *E. racemosa*; EhR, *Ehretia rigida*; GB, *Gymnosporia buxifolia*; GS, *G. senegalensis*; PA, *Plectroniella armata*; RP, *Rhus pentheri*; SA, *Spirostachys africana*; SI, *Sideroxylon inerme*; ZM, *Zizyphus mucronata*. The species that were identified as indicator species for mound plots are circled.

strongest components explained a relatively low amount of total trait variation: the first and second PC, respectively, explained 19.0% and 14.1% of total trait variance, and together 33.2% (Table S4A in Appendix S4). The first PC was positively correlated with leaf C content and negatively correlated with SLA, leaf N, P, K and S content, and therefore mostly related to variation in growth rate/resource use efficiency (Westoby et al. 2002). The second PC was mostly positively related to leaf FD, spine length and leaf N content, and negatively correlated to individual LA and leaf Na content; therefore, this second PC mostly represented a 'typical legume–non-legume axis' (Fig. 2, Table S4B in Appendix S4).

Differences in trait values between mound and control trees

When focusing on species presence–absence data (and thereby ignoring differences in species abundances between plots), tree communities on termite mounds had a lower average value of leaf FD (28.6% lower), SD (50.4% lower) and leaf polyphenol content (22.5% lower), and higher values of leaf B content (17.4% higher). Furthermore, mounds contained relatively less legume species (50.1% fewer) (Table 2, Table S4C in Appendix S4; all $P < 0.05$).

Tree communities on termite mounds contained species with a lower abundance-weighted average FD (35.2% lower), SD (61.6% lower), WD (4.5% lower) and leaf N (10.7% lower), P (11.9% lower) and Zn (17.0% lower) concentration than species from control plots (Table 2, Table S4F in Appendix S4; all $P < 0.05$). In contrast, LA (68.1% higher) and leaf Ca (19.1% higher) and Mg (19.1% higher) concentrations had a higher abundance-weighted average value on termite mounds (Table 2, Table S4F in Appendix S4; all $P < 0.05$). Furthermore, mound plots contained 149.8% more evergreen species and 72.0% fewer legume species than control plots (Table 2, Table S4F in Appendix S4; both $P < 0.05$).

Tree communities on termite mounds also contained species with a lower biomass-weighted average value of leaf FD (41.0% lower) and leaf N (13.0% lower) and Zn (27.2% lower) concentration than species from control plots (Table 2, Table S4I in Appendix S4; all $P < 0.05$). In contrast, LA had a 62.7% higher biomass-weighted average value on termite mounds (Table 2, Table S4I in Appendix S4; $P < 0.05$). Furthermore, mound plots contained 141.4% more biomass of evergreen species and 70.8% less biomass of legume species than control plots (Table 2, Table S4I in Appendix S4; both $P < 0.05$).

When studying differences in average trait values between mound and control communities, but focusing

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Table 2. Unweighted, abundance- and biomass-weighted trait averages: comparison between control and mound sites.

Trait	Unweighted trait average		Abundance-weighted trait average		Biomass-weighted trait average	
	V	*P*	*V*	*P*	*V*	*P*
Specific leaf area ($cm^2 \cdot g^{-1}$)	79	0.597	72	0.860	46	0.274
Individual leaf area (cm^2)	106	0.051	116	0.011*	131	<0.001*
Leaf fractal dimension ($cm^2 \cdot cm^{-1}$)	15	**0.004***	11	**0.002***	11	**0.002***
Spine length (mm)	28	**0.039**†	48	0.323	54	0.495
Spine density (no. spines)	6	**<0.001***	20	**0.011***	29	**0.044**†
Branch angle (°)	75	0.744	26	**0.029**†	69	0.980
Trichome density (trichomes mm^{-2})	74	0.782	72	0.860	48	0.323
Wood density ($kg \cdot L^{-1}$)	33	0.074	9	**0.001***	36	0.105
Polyphenol concentration ($g \cdot kg^{-1}$)	19	**0.009***	31	0.058	45	0.252
C concentration (% dry weight)	25	**0.025**†	27	**0.034**†	41	0.175
N concentration (% dry weight)	24	**0.021**†	15	**0.004***	1	**<0.001***
P concentration ($mmol \cdot kg^{-1}$)	26	**0.029**†	12	**0.002***	31	0.058
S concentration ($mmol \cdot kg^{-1}$)	86	0.375	61	0.744	61	0.744
K concentration ($mmol \cdot kg^{-1}$)	74	0.782	90	0.274	34	0.083
Na concentration ($mmol \cdot kg^{-1}$)	112	0.021†	99	0.117	102	0.083
Ca concentration ($mmol \cdot kg^{-1}$)	97	0.144	136	<0.001*	93	0.211
Mg concentration ($\mu mol \cdot kg^{-1}$)	110	0.029†	121	0.004*	104	0.065
Fe concentration ($\mu mol \cdot kg^{-1}$)	72	0.860	40	0.159	41	0.175
Mn concentration ($\mu mol \cdot kg^{-1}$)	69	0.980	101	0.093	65	0.900
Zn concentration ($\mu mol \cdot kg^{-1}$)	39	0.144	18	**0.008***	9	**0.001***
B concentration ($\mu mol \cdot kg^{-1}$)	124	0.002*	103	0.074	76	0.706
Cu concentration ($\mu mol \cdot kg^{-1}$)	57	0.597	31	0.058	33	0.074
Evergreen (no = 0; yes = 1)	94.5	0.053	127	0.001*	128	<0.001*
Leguminous (no = 0; yes = 1)	15	**0.004***	13	**0.003***	8	**<0.001***
Poisonous (no = 0; yes = 1)	6	0.107	20	0.834	11	0.363

Significance testing was done using a paired Shapiro–Wilks test, with *V* as the test statistic and an associated *P*-value. When the *P*-value was below 0.05 and the highest trait values were found in mound plots, the *P*-value is underlined. When the highest trait values were found in control plots, the *P*-value is bold. *P*-values below 0.05 that remained significant after false discovery rate testing are shown with a*, those that were not significant after false discovery rate testing are shown with a†.

on either legume or non-legume species, most of the trait differences between mound and control species found when studying all species simultaneously disappear (Appendix S4). When comparing trait differences between species that were found on either control termite or mound plots, hardly any significant differences were found (Table S4L in Appendix S4).

Relationships between browser PI, woody species trait values and habitat type

Although correlations were weak, browsers tended to prefer tree species with both low PC1 and PC2 scores (Fig. 2). Subsequent simple regression analyses revealed that browsers significantly preferred deciduous and leguminous trees ($T = 3.225$, $P = 0.004$, $R^2 = 0.302$ and $T = 2.081$, $P = 0.048$, $R^2 = 0.153$, respectively). Furthermore, browser PI correlated positively with tree species spine density ($T = 2.234$, $P = 0.035$, $R^2 = 0.172$), leaf P and N content ($T = 2.139$, $P = 0.043$, $R^2 = 0.160$ and $T = 2.769$, $P = 0.011$, $R^2 = 0.242$, respectively) and negatively with leaf Mg content ($T = -3.019$, $P = 0.005$, $R^2 = 0.287$). Consequently, tree communities on termite mounds had lower abundance- (control: -0.019 ± 0.026, mound: -0.092 ± 0.033, $V = 15$, $P = 0.004$) and biomass- (control: 0.049 ± 0.038, mound: -0.103 ± 0.040, $V = 6$, $P < 0.001$) weighted average ungulate browser PI values.

Discussion

In this study, we used a trait-based approach to gain more insight into (1) the processes determining the characteristic community structure of tree communities on *Macrotermes* mounds in African savannas, and (2) why the trees from these communities are so attractive to browsers.

Differences between mound and savanna tree communities

We found that termite mounds supported unique tree communities, which were more species-rich and had higher species diversity than tree communities in the

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surrounding savanna, in line with results of Moe et al. (2009) and Traoré et al. (2008). Surprisingly, we did not find differences in overall tree densities between *Macrotermes* mound communities and communities from other areas of the savanna. This is contrary to other studies (Loveridge & Moe 2004; Moe et al. 2009). However, when comparing the densities of trees with a canopy height above 2 m between termite mound and control plot communities, we found that termite mounds contained 4.5 times as many large trees. This suggests that canopy cover is also more closed at a height of 2 m and, therefore, that less light penetrates lower parts of on mounds than in the surrounding savanna, where light levels are much high (Fig. 3) and unlikely to limit tree growth. Reduced light penetration through mound vegetation could increase the importance of light competition and self-thinning.

Not only did the tree species composition differ between termite mounds and the surrounding savanna, also the composition of functional traits differed. In general, termite mounds contained more evergreen, broad-leaved species such as *Gymnosporia senegalensis*, *G. nemorosa*, *Berchemia zeyheri*, *Sideroxylon inerme*, *Coddi arudis*, *Pappea capensis* and *Schotia brachypetala*, while tree communities in the surrounding savanna were dominated by deciduous, fine-leaved and spiny species of the leguminous Mimosaceae family, such as *Acacia* spp., *Dichrostachys cinerea* and *Ormocarpum trichocarpum*. This difference was also reflected in differences of average values of quantitative traits between mound and control communities: trees species on mounds had lower thorn densities and larger leaves with lower leaf fractal dimensions. In addition, tree species dominating mounds had lower wood density and lower leaf N, P and Zn concentrations, but higher leaf Ca and Mg concentrations.



Fig. 3. Cover of tall, dense vegetation is higher than in the surroundings on this dome-shaped *Macrotermes* mound. Note that the woody species on the mound hardly have any leaves below a height of ~1.5 m, which is within reach of most browser species.

There are several explanations of why legume species are relatively more common in surrounding savanna than on termite mounds. The main differences between Mimosaceae trees dominating most of the savanna and tree species dominating mounds are that (1) most Mimosaceae species are N-fixing, (2) spiny, (3) deciduous, (4) fine-leaved and (5) poor light competitors (Vitousek & Howarth 1991). *Macrotermes* mounds form relatively resource-rich islands (Gosling et al. 2012), thereby reducing the need for trees to acquire extra N through N fixation or protect tissue from browsing with spines (Coley et al.1985; Bryant et al. 1989; Vitousek & Howarth 1991). Also, although the evergreen leaves of tree species found on mounds are more costly to produce than deciduous leaves, in the long term, their long life expectancy is advantageous if (i) there is no strong seasonal drought and (ii) there are no imposed disturbances (such as fire) that destroy leaves (Givnish 2002). Indeed, termite mounds are known as areas with high water availability (Holt & Lepage 2000) and our data show that the surface of *Macrotermes* mounds consists of a high proportion of bare ground. This suggests a relatively low fuel load on termite mounds, resulting in lower impacts of fires on mounds. Also, our findings that tree species dominating mounds had lower wood density and higher leaf area than species dominating the surrounding savanna, suggests that these mound tree species are less adapted to drought than tree species in the surrounding savanna. These traits reflect well known life-history trade-off strategies between high growth rates (for low wood density/large leaves) and high water use efficiency (for high wood density/small leaves) (Hacke et al. 2001; Westoby et al. 2002), implying that tree species with low wood densities and large leaves benefit from the higher nutrient and water availability on mounds. Finally, the finding that densities of tall trees are 4.5 times higher on termite mounds than in the surrounding savanna suggests that these mounds might be among the rare places in savannas where light competition plays an important role in the community assembly of trees. N fixation is an expensive, carbon consuming process (Vitousek & Howarth 1991); therefore, in the mound environment where competition for light is likely to be important, N fixation comes at a high cost, explaining the relatively low density of leguminous tree species.

It should be emphasized that these trait differences between tree species dominating termite mounds and surrounding savanna mainly reflect trait differences between species from the leguminous Mimosaceae family, which dominates most of the savanna, and other tree species. When comparing trait differences between mound and control trees, but taking either legume or non-legume

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species into account, or when looking only at presence–absence data, fewer differences in average trait values were found. Also, when comparing trait values of species unique to mound plots or control plots, hardly any differences were found. This suggests that the trait differences found between trees from mound and control plots mainly reflect differences in the relative abundance of legume species on and off mounds. This is surprising, since species in the Mimosaceae show high phylogenetic and functional relatedness. Therefore one would expect them to have overlapping niches, making their co-existence problematic. We suggest that due to the harsh conditions (drought, fires) that make the savanna hostile for most other tree species, different species from the Mimosaceae are not only able to co-occur in most of the savanna, but in relatively high numbers. Termite mounds are among the rare sites in the savanna with high abundance of other tree genera. These do not seem to have traits related to coping with severe drought and fires, but have traits that enable them to capture light more efficiently, making growth of legumes difficult. This is in line with the notion that reduced growth because of light competition might actually be more prevalent between functionally dissimilar species than between species that share several functional traits (Mayfield & Levine 2010).

For tree species growing on relatively nutrient-rich mound soils, it seems counter-intuitive that the leaves contain less N and P than leaves of tree species dominating the surrounding savanna. There are two possible explanations for these results: (1) water limitation generally promotes plant nutrient concentration (Olff et al. 2002) and (2) abundances of leguminous, N-fixing species on termite mounds are relatively low. This ability to fix N not only helps plant species to acquire N in nutrient-poor environments, but also acquire P (Houlton et al. 2008).

Tree traits and habitat and food preferences of browsers

For browsers, the above differences in leaf N and P content between tree species dominating control and mound plots are crucial. Browsers preferred to feed on deciduous and leguminous tree species with high N and P content. These results suggest that browsers should preferentially feed on tree species that do not dominate termite mounds. This was indeed the case: browser PI values were higher for tree species dominating typical savanna vegetation than tree species dominating *Macrotermes* mound vegetation. This is surprising, since other studies have shown termite mounds are browsing hotspots, where more tree branches are consumed than in the surrounding vegetation (Holdo & McDowell 2004; Loveridge & Moe 2004), browser densities are higher (Mobæk et al. 2005; Brody et al. 2010) and the vegetation is more affected by browsing (Levick et al. 2010). Of these studies, only Holdo & McDowell (2004) analysed some nutrients in the tree foliage. They found that leaves from termite mound trees contained more P, K, Mg and Ca and suggested that this might explain their finding that elephants prefer to feed on trees growing on termite mounds. Our data also show higher Ca and Mg content of tree species dominating termite mounds, but a negative relationship between Mg content and browser preference index, and lower P content of tree species dominating termite mounds. Given these results, we conclude that differences in tree community composition between termite mounds and the surrounding savanna do not explain the high browsing rates of mound vegetation found in other studies. The question thus remains why some termite mounds function as browser hotspots.

One answer could simply be that mounds are not actually always brower hotspots. To the best of our knowledge, all published studies that compared browser intensities (Mobæk et al. 2005; Brody et al. 2010), browser densities (Holdo & McDowell 2004; Loveridge & Moe 2004) and vegetation effects of browsers (Levick et al. 2010) on and off mounds, suggest that browsers prefer to feed on *Macrotermes* mounds. However, the mounds in our study site, which were dominated by non-preferred species, could be exceptional, in that browsers do not prefer and possibly even avoid, mound vegetation. The soils in HiP are relatively nutrient-rich when compared to soils in other savanna reserves, which might partly explain why the vegetation on mounds in our system does not have elevated nutrient levels when compared with the surrounding area. Another possible, more likely, explanation could be that, within species, tree individuals growing on termite mounds are more attractive to browsers than trees growing in the surrounding savanna. Soils on *Macrotermes* mounds in general (Holt & Lepage 2000) and also in our specific system (Gosling et al. 2012) are richer in many nutrients than the surrounding savanna. This could lead to similar nutritional differences between individuals of the same species growing on and off termite mounds, as found in Gosling et al. (2012). Other possibilities are that during the warmest periods of the day, browsers prefer to forage in areas with dense vegetation that provide shade, even if these same areas provide relatively low-quality food, or that browsers select areas with high quantities of food for their foraging activity.

Conclusions

In summary, tree species growing on termite mounds seem to be less adapted to nutrient deficiency, drought and fire and more to light competition than tree species dominant in the surrounding savanna. This is in line with other studies describing termite mound soils as nutrient-rich areas

with high water availability and low fire frequencies. Within a stressful environment, *Macrotermes* 'engineer' benign islands of trees with fast growth and dense canopies, thereby promoting local-scale heterogeneity in savannas and contributing to their biodiversity. Despite the nutrient-rich soils of mounds, the foliage of tree species growing there is relatively nutrient-poor and not preferred by ungulate browsers. Since *Macrotermes* mounds are known as 'browsing hotspots', this is a surprising finding, and more research on intraspecific trait differences between trees growing on and off mounds might shed more light on this.

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References

Balfour, D.A. & Howison, O.E. 2002. Spatial and temporal variation in a mesic savanna fire regime: responses to variation in annual rainfall. *African Journal of Range and Forage Science* 19: 45–53.

Bond, W.J. & Wilgen, B.W. 1996. *Fire and plants*. Chapman & Hall, London, UK.

Bray, J.R. & Curtis, J.T. 1957. An ordination of upland forest communities of southern Wisconsin. *Ecological Monographs* 27: 325–349.

Brody, A.K., Palmer, T.M., Fox-Dobbs, K. & Doak, D.F. 2010. Termites, vertebrate herbivores, and the fruiting success of *Acacia drepanolobium*. *Ecology* 91: 399–407.

Brown, V.K. & Lawton, J.H. 1991. Herbivory and the evolution of leaf size and shape. *Philosophical Transactions of the Royal Society: Biological Sciences* 333: 265–272.

Bryant, J.P., Kuropat, P.K., Cooper, S.M., Frisby, K. & Owen-Smith, N. 1989. Resource availability hypothesis of plant antiherbivorede fence tested in a South African savanna ecosystem. *Nature* 340: 227–229.

Coley, P.D., Bryant, J.P. & Chapin, F.S. 1985. Resource availability and plant antiherbivore defence. *Science* 230: 895–899.

Cooper, S.M. & Owen-Smith, N. 1985. Condensed tannins deter feeding by browsing ruminants in a South-African savanna. *Oecologia* 67: 142–146.

Cooper, S.M. & Owen-Smith, N. 1986. Effects of plant spinescence on large mammalian herbivores. *Oecologia* 68: 446–455.

Cornelissen, J.H.C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, D., Gurvich, D.E., Reich, P.B., ter Steege, H., Morgan, H.D., van der Heijden, M.G.A., Pausas, J.G. & Poorter, H. 2003. A handbook of protocols for standardized and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* 51: 335–380.

Cramer, M.D., van Cauter, A. & Bond, W.J. 2010. Growth of N_2-fixing African savanna *Acacia* species is constrained by below-ground competition with grass. *Journal of Ecology* 98: 156–167.

Cromsigt, J.P.G.M. 2006. The impact of resource heterogeneity on large grazer resource partitioning at different spatial scales: a synthesis. In: Cromsigt, J.P.G.M. (ed.) *Large herbivores in space. Resource partitioning among savanna grazers in a heterogeneous environment*, pp. 103–107. PhD thesis, University of Groningen, Groningen, NL.

Cromsigt, J.P.G.M. & Olff, H. 2008. Dynamics of grazing lawn formation: an experimental test of the role of scale-dependent processes. *Oikos* 117: 1444–1452.

Dangerfield, J.M., McCarthy, T.S. & Ellery, W.N. 1998. The mound-building termite *Macrotermes michaelseni* as an ecosystem engineer. *Journal of Tropical Ecology* 14: 507–520.

Du Toit, J.T. 1990. Feeding-height stratification among African browsing ruminants. *African Journal of Ecology* 28: 55–61.

Dufrene, M. & Legendre, R. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67: 345–366.

Emslie, R.H. 1999. The feeding ecology of the black rhinoceros (*Diceros bicornis minor*) in Hluhluwe-Umfolozi Park, with special reference to the probable causes of the Hluhluwe population crash. PhD thesis. Stellenbosch University, Stellenbosch, South Africa.

Estes, R.D. 1991. *The behaviour guide of African mammals, including hoofed mammals, carnivores, primates*. Russell Friedman Books CC, Johannesburg, ZA.

Frost, P., Median, E., Menaut, J.C., Solbrig, O., Swift, M. & Walker, B. 1986. *Response of savannas to stress and disturbance*. IUBS, Paris, FR.

Garnier, E., Laurent, G., Bellmann, A., Debain, S., Berthelier, P., Ducout, B., Roumet, C. & Lavas, M.L. 2001. Consistency of species ranking based on functional leaf traits. *New Phytologist* 152: 69–83.

Gilson, L. 2004. Evidence of hierarchical patch dynamics in an East African savanna? *Landscape Ecology* 19: 883–894.

Givnish, T.J. 2002. Adaptive significance of evergreen vs. deciduous leaves: solving the triple paradox. *Silva Fennica* 36: 703–743.

Gosling, C.M., Cromsigt, J.P.G.M., Mpandza, N. & Olff, H. 2012. Effects of erosion from mounds of different termite genera on distinct functional grassland types in an African savannah. *Ecosystems* 15: 128–139.

Hacke, U.G., Sperry, J.S., Pockman, W.T., Davis, S.D. & McCulloch, K.A. 2001. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia* 126: 457–461.

Higgins, S.I., Bond, W.J. & Trollope, W.S.W. 2000. Fire, resprouting and variability: a recipe for tree–grass coexistence in a savanna. *Journal of Ecology* 88: 213–229.

Doi: 10.1111/j.1654-1103.2012.01459.x © 2012 International Association for Vegetation Science

Higgins, S.I., Bond, W.J., February, E.C., Bronn, A., Euston-Brown, D.I.W., Enslin, B., Govender, N., Rademan, L., O'Regan, S., Potgieter, A.L.F., Scheiter, S., Sowry, S., Trollope, L. & Trollope, W.S.W. 2007. Effects of four decades of fire manipulation on woody vegetation structure in savanna. *Ecology* 88: 1119–1125.

Holdo, R.M. & McDowell, L.R. 2004. Termite mounds as nutrient-rich food patches for elephants. *Biotropica* 36: 231–239.

Holt, J.A. & Lepage, M. 2000. Termites and soil properties. In: Abe, T., Bignell, D.E. & Higashi, M. (eds.) *Termites: evolution, sociality, symbioses, ecology*, pp. 389–407. Kluwer Academic, Dordrecht, NL.

Houlton, B.Z., Wang, Y., Vitousek, P.M. & Field, C.B. 2008. A unifying framework for dinitrogen fixation in the terrestrial biosphere. *Nature* 454: 327–331.

Konaté, S., Le Roux, X., Tessier, D. & Lepage, M. 1999. Influence of large termitaria on soil characteristics, soil water regime, and tree leaf shedding pattern in a West African savanna. *Plant and Soil* 206: 47–60.

Levick, S.R., Asner, G.P., Kenney-Bowdoin, T. & Knapp, D.E. 2010. The spatial extent of termite influences on herbivore browsing in an African savanna. *Biological Conservation* 143: 2462–2467.

Loveridge, J.P. & Moe, S.R. 2004. Termitaria as browsing hotpots for African megaherbivores in miombo woodland. *Journal of Tropical Ecology* 20: 337–343.

Marschner, H. 1995. *Mineral nutrition of higher plants*, 2nd edn. Academic Press, London, UK.

Mayfield, M.M. & Levine, J.M. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters* 13: 1085–1093.

McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. 2006. Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution* 21: 178–185.

Mittermeier, R.A., Myers, N., Thomsen, J.B., Fonseca, G.A.B. & Olivieri, S. 1998. Biodiversity hotspots and major tropical wilderness areas: approaches to setting conservation priorities. *Conservation Biology* 12: 516–520.

Mobæk, R., Narmo, A.K. & Moe, S.R. 2005. Termitaria are focal feeding sites for large ungulates in Lake Mburo National Park, Uganda. *Journal of Zoology* 267: 97–102.

Moe, S.R., Mobaek, R. & Narmo, A.K. 2009. Mound-building termites contribute to savanna heterogeneity. *Plant Ecology* 12: 31–40.

Mole, S. & Waterman, P. 1987. A critical analysis of techniques for measuring tannins in ecological studies I. Techniques for chemically defining tannins. *Oecologia* 72: 137–147.

Okullo, P. & Moe, S.R. 2012. Termite activity, not grazing, is the main determinant of spatial variation in savanna herbaceous vegetation. *Journal of Ecology* 100: 232–241.

Olff, H., Vera, F.W.M., Bokdam, J., Bakker, E.S., Gleichman, J.M., deMaeyer, K. & Smit, R. 1999. Shifting mosaics in grazed woodlands driven by the alternation of plant facilitation and competition. *Plant Biology* 1: 127–137.

Olff, H., Ritchie, M.E. & Prins, H.H.T. 2002. Global environmental controls of diversity in large herbivores. *Nature* 415: 901–904.

Owen-Smith, N. & Cooper, S.M. 1987. Palatability of woody plants to browsing ruminants in a South African savanna. *Ecology* 68: 319–331.

Pooley, E. 1997. *The complete field guide to trees of Natal, Zululand and Transkei*, 3rd edn. Natal Flora Publications Trust, Durban, ZA.

Scholes, R.J. 1990. The influence of soil fertility on the ecology of Southern African dry savannas. *Journal of Biogeography* 17: 415–419.

Scholes, R.J. & Walker, B.H. 1993. *An African savanna: synthesis of the Nylsvley study*. Cambridge University Press, Cambridge, UK.

Sileshi, G.W., Arshad, M.A., Konaté, S. & Nkunika, P.O.Y. 2010. Termite-induced heterogeneity in African savanna vegetation: mechanisms and patterns. *Journal of Vegetation Science* 21: 923–937.

Simes, R.J. 1986. An improved Bonferroni procedure for multiple tests of significance. *Biometrika* 73: 751–754.

Sinclair, A.R.E., Hopcraft, J.G.C., Olff, H., Mduma, S.A.R., Galvin, K.A. & Sharam, G.J. 2008. Historical and future changes to the Serengeti ecosystem. In: Sinclair, A.R.E., Packer, C., Mduma, S.A.R. & Fryxell, J. (eds.) *Serengeti III. Human impacts on ecosystem dynamics*, pp. 7–46. University of Chicago Press, Chicago, IL, US.

Traoré, S., Nygard, R., Guinko, S. & Lepage, M.G. 2008. Impact of *Macrotermes* termitaria as a source of heterogeneity on tree diversity and structure in a Sudanian savannah under controlled grazing and annual prescribed fire (Burkina Faso). *Forest Ecology and Management* 255: 2337–2346.

Vitousek, P.M. & Howarth, R.W. 1991. Nitrogen limitation on land and in the sea – how can it occur? *Biochemisty* 13: 87–115.

Waldram, M., Bond, W.J. & Stock, W. 2008. Ecological engineering by a mega-grazer: white rhino impacts on a South African savanna. *Ecosystems* 11: 101–112.

Walter, H. 1971. *Ecology of tropical and subtropical vegetation*. Oliver & Boyd, Edinburgh, UK.

Weiher, E., van der Werf, A., Thompson, K., Roderick, M., Garnier, E. & Eriksson, O. 1999. Challenging Theophrastus: a common core list of plant traits for functional ecology. *Journal of Vegetation Science* 10: 609–620.

Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A. & Wright, I.J. 2002. Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics* 33: 125–159.

Whateley, A. & Porter, R.N. 1983. The woody vegetation communities of the Hluhluwe-Corridor-Umfolozi game reserve complex. *Bothalia* 14: 745–758.

Yates, J.L. & Peckol, P. 1993. Effects of nutrient availability and herbivory on polyphenolics in the seaweed *Fucus vesiculosus*. *Ecology* 74: 1757–1766.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Description of study site and sampling locations.

Appendix S2. Comparison of inter- and intraspecific variation in trait values.

Appendix S3. List of sampled species with their average values for each trait.

Appendix S4. Extra results.

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