

The influence of termite-induced heterogeneity on savanna vegetation along a climatic gradient in West Africa

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Abstract: Termites are renowned ecosystem engineers. Their mounds have been described as an important element of savanna vegetation dynamics, but little is known about their large-scale impact on vegetation composition. To investigate the influence of termite-induced heterogeneity in savannas along a climatic gradient in West Africa termite mound vegetation was compared with adjacent savanna vegetation using 256 paired plots (size of the termite mound and a corresponding savanna area) in five protected areas from northern Burkina Faso to northern Benin. On each plot vegetation and soil sampling was performed. Additionally bioclimatic variables from the WORLDCLIM database were used. The vegetation on the mounds and the surrounding savanna differed within all study sites (DCA length of gradient 3.85 SD) and showed complete turnover along the climatic gradient (DCA length of gradient 5.99 SD). Differences between mounds and savanna were significantly related to termite-induced changes in soil parameters, specifically clay enrichment and increased cation concentrations (base saturation). On a local scale, termite-induced differences in soil conditions were found to be the most important factor affecting mound vegetation, while on a regional scale, annual precipitation showed the strongest significant correlations. However, with increasing precipitation, differences between mounds and the surrounding matrix became more pronounced, and the contribution of mounds to local phytodiversity increased. Eleven plant species were identified as characteristic termite mound species. In the more humid parts of the gradient, more characteristic plant species were found that may benefit from favourable soil conditions, good water availability, and a low fire impact in the mound microhabitat.

Key Words: ecosystem engineers, habitat heterogeneity, *Macrotermes*, microhabitat

INTRODUCTION

Savanna structure and composition are thought to be mainly subject to the influence of fire and herbivory (Solbrig *et al.* 1996). However, recent studies suggest that termite activity plays an integral part in generating savanna vegetation patterns and dynamics (Okullo & Moe 2012a, Sileshi *et al.* 2010), while large herbivores maintain and amplify patterns and processes (Okullo & Moe 2012b). Termites influence patterns of savanna vegetation directly through foraging and indirectly

through reallocation of soil, water and nutrients (Sileshi *et al.* 2010, Wood & Sands 1978). Several species of termite construct above-ground earthmounds that incorporate the colony's nest. Termites, particularly those of the fungus-cultivating genus *Macrotermes*, have been described as ecosystem engineers (Dangerfield *et al.* 1998, Jouquet *et al.* 2011) influencing abiotic and biotic properties of savannas. Several authors have outlined similar influences of termite mound building on soils and, hence, on savanna vegetation, proposing that the creation of nutrient hot-spots leads to more heterogeneous ecosystems (Levick *et al.* 2010, Pringle *et al.* 2010).

It has been reported that mounds support a greater diversity of plants compared with surrounding areas (Moe *et al.* 2009, Okullo & Moe 2012a, Traoré *et al.* 2008a). In

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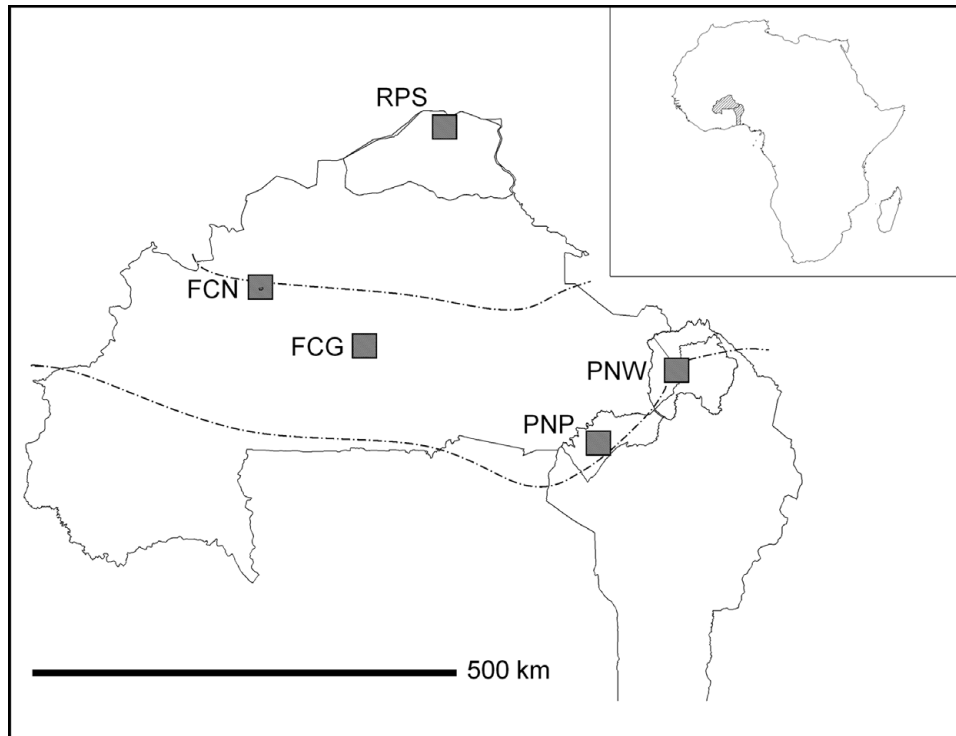


Figure 1. Study sites in protected areas along a climatic gradient in West Africa (Burkina Faso and northern Benin). Rectangles indicate approximate location of study sites. Sites from north to south: Sahel Partial Reserve (RPS, 360 mm MAP), Niouma Classified Forest (FCN, 670 mm), Gonsé Classified Forest (FCG, 760 mm), W National Park (PNW, 840 mm), and Pendjari National Park (PNP, 950 mm). Broken lines indicate approximate limits of Sahelian and Northern Sudanian vegetation zones.

particular, a greater diversity of woody plant species has been noted on mounds compared with the surrounding savanna. Mounds have been discussed in this context as focal points for tree regeneration within savannas (Cole 1963, Moe *et al.* 2009, Traoré *et al.* 2008a).

However, most studies have focused on the local impact of termite mounds on vegetation and have mainly been conducted at a single site. The overarching importance of mounds for savanna vegetation and their dynamics across savanna types and vegetation zones are still unclear. The aim of this study was to investigate differences between termite-mound vegetation and adjacent savanna vegetation both on a local scale and along a regional climatic gradient. We expected the phytodiversity on mounds to be higher than in the surrounding savanna along a climatic gradient, particularly with regard to woody plants. We further hypothesized that the phytodiversity of savanna vegetation and mound vegetation would increase along a climatic gradient from drier to more humid areas. Compared with the surrounding savannas, enrichment of clay and related soil parameters (i.e. increased field moisture capacity and nutrient concentrations) was expected to occur on mounds in similar magnitude along the climatic gradient. Finally, we aimed to reveal whether there were plant species characteristic of termite mounds

to improve ecological understanding of the role of termite mounds in creating vegetation heterogeneity.

METHODS

Study sites

This study was conducted in five protected areas (PA) in Burkina Faso and Benin, representing a climatic gradient from the Sahel zone to the limit of the southern Sudanian vegetation zone (Figure 1). Annual precipitation ranges from less than 400 mm in the Sahel to approximately 1000 mm in the Sudanian zone, with a distinct unimodal dry season of 5–7 mo occurring throughout the study area. The study sites were located in the Sahel Partial Reserve (Réserve Sylvo-Pastorale et Partielle de Faune du Sahel, abbreviated as RPS; 14°48'N, 0°42'W), Niouma Classified Forest (Forêt Classée de Niouma, FCN; 12°55'N, 2°41'W), Gonsé Classified Forest (Forêt Classée de Gonsé, FCG; 12°23'N, 1°18'E), W Transborder Park (Parc National du W, PNW; 11°48'N, 2°10'E) and Pendjari National Park (Parc National de la Pendjari, PNP; 11°22'N, 1°33'E). At each study site, we sampled the most abundant savanna types, excluding temporarily waterlogged or seasonally inundated localities, as these

represent ecologically extreme situations. Savanna types were identified based on surveys we performed and on vegetation classifications for the respective sites. Appendix 1 presents an overview of the sampled savanna types and mean annual precipitation (MAP) at our study sites.

In West Africa, conspicuous thicket clumps can be found on termite mounds, which are usually delimited by a distinct boundary from the adjacent savanna vegetation. Due to erosion, this boundary may be situated several metres from the actual mound slope. This pediment may also consist of areas bare of vegetation, emphasizing the contrast between the mound thicket and savanna. For brevity, we will refer to termite-mound vegetation as mounds.

Survey design

In a paired design, we sampled the vegetation of 128 mounds built by *Macrotermes* colonies and adjacent savanna plots. Within our study area, two *Macrotermes* species build the type of mounds that we studied with respect to architecture and size: *M. subhyalinus* (Rambur) and *M. bellicosus* (Smeathman). Species identification was confirmed by field work carried out in association with termite specialists (J. Korb & collaborators). The two *Macrotermes* species in our study area occur sympatrically, with the northern limit of *M. bellicosus* occurring within our study area (Ruelle 1970). Unfortunately, no detailed data on the distribution of *M. bellicosus* and *M. subhyalinus* in this region are currently available. Mounds containing living colonies of these two species may be identified based on architectural attributes (Korb 2011). In general, eroded and vegetated mounds in our study area do not contain living colonies, but re-colonization, mainly by *Microtermes* and *Ancistrotermes* spp., may occur (J. Korb, pers. comm.). We did not sample mounds where there was visible colonization. Because abandoned, eroded *M. bellicosus* mounds can be confounded with eroded *M. subhyalinus* mounds, we cannot report which *Macrotermes* species built the mounds. However, all of the studied termite mounds were comparable with respect to their structure and were distinguished from mounds built by other Macrotermitinae (e.g. *Odontotermes* spp.).

The topography of the selected savannas is almost flat. When selecting termite mounds, we avoided shallow depressions (bas-fonds) and hillsides. After identifying localities where mounds occur, we randomly selected mounds for vegetation sampling and determined their surface area as the longest diameter of the mound multiplied by its perpendicular diameter. A squared plot of corresponding size was established 15 m north of the limit of the mound to investigate the vegetation of the surrounding savanna. If additional mounds occurred within

15 m of the savanna plot, we rotated the direction from the corresponding mound anticlockwise in steps of 15°.

To avoid interpersonal differences in phytosociological cover estimations, all sampling was done by the first author. Estimations were performed separately for the tree layer (woody plants > 5 m), the shrub layer (woody and partially ligneous plants from 0.5 to 5 m), and the herbaceous layer (all plants up to 0.5 m in height). Vegetation was recorded twice, at the beginning (May–July) and the end of the rainy season (September–November), to account for variation in phenology. For the analysis, we used the maximum cover of each species (expressed in %) from the two samplings. The plant species nomenclature followed the African Plants Database (<http://www.ville-ge.ch/musinfo/bd/cjb/africa>).

Environmental data

We collected samples of 10 cm³ from the upper topsoil horizon of mounds and savannas, pooling samples from four directions in each case. Mound soil was collected from the slope of the mound. Savanna soil was sampled at a distance of 15 m from the edge of the mound, and all samples were subsequently sieved and air dried. For each mound and savanna plot, several descriptive soil parameters were used. We determined pH in aqueous suspension and 0.1 M KCl solution. Concentrations of plant-available phosphorus and potassium were determined spectroscopically using the calcium acetate lactate method. Nitrogen was determined using the Kjeldahl method. Organic and inorganic carbon were determined spectroscopically by wet and dry combustion, respectively (DIN ISO 10694), after volumetric determination of carbonates (DIN ISO 10693 1997-05).

Additionally, we selected at least three plot pairs in every savanna type at random, and determined cation exchange capacity (CEC), together with individual ion concentrations of sodium, potassium, calcium and magnesium (DIN ISO 13536:1997-04). For these samples, particle size distribution (PSD) also was determined, using the Köhn pipette method in seven grain size fractions.

Moreover, we used a set of 18 bioclimatic variables (Table 1) from the WORLDCLIM database with a spatial resolution of 30 arc seconds, i.e. approximately 1 km² (Hijmans *et al.* 2005). We added potential evapotranspiration (PET) and the Global Aridity Index (AI) to this dataset (Zomer *et al.* 2008), which also takes the radiation budget into account.

Statistical analysis

Prior to analyses, vegetation data were arcsine-square-root-transformed. Environmental data were standardized

Table 1. Spearman's rank correlation coefficients considering climatic variables and measured soil variables, correlated with DCA axes scores for 256 termite mounds and adjacent savanna plots along a climatic transect in West Africa. Climatic data were extracted from the WORLDCLIM database and the Global Aridity and PET database on a resolution of 30 arc seconds for each mound- and savanna-plot geolocation. Spearman's ρ is given for the correlation between the DCA scores of the first two axes with environmental variables; P-value for rank correlation test.

Environmental variable	Correlations for DCA Axis 1		Correlations for DCA Axis 2	
	ρ	P-value	ρ	P-value
Mean annual temperature	-0.53	< 0.01	0.20	< 0.01
Mean diurnal temperature range	-0.36	< 0.01	0.23	< 0.01
Isothermality	0.71	< 0.01	-0.21	< 0.01
Temperature seasonality	-0.61	< 0.01	0.13	0.03
Max. temperature of warmest month	-0.67	< 0.01	0.29	< 0.01
Min. temperature of coldest month	0.67	< 0.01	-0.20	< 0.01
Annual temperature range	-0.69	< 0.01	0.18	< 0.01
Mean temperature of wettest quarter	-0.79	< 0.01	0.36	< 0.01
Mean temperature of driest quarter	0.67	< 0.01	-0.20	< 0.01
Mean temperature of warmest quarter	-0.74	< 0.01	0.34	< 0.01
Mean temperature of coldest quarter	0.34	< 0.01	-0.03	0.60
Annual precipitation	0.81	< 0.01	-0.41	< 0.01
Precipitation of wettest month	0.79	< 0.01	-0.40	< 0.01
Precipitation of driest month	-0.79	< 0.01	0.42	< 0.01
Precipitation seasonality	0.81	< 0.01	-0.41	< 0.01
Precipitation of wettest quarter	0.60	< 0.01	-0.12	0.06
Precipitation of driest quarter	0.77	< 0.01	-0.26	< 0.01
Precipitation of warmest quarter	0.77	< 0.01	-0.26	< 0.01
Potential evapotranspiration (PET)	-0.40	< 0.01	0.22	< 0.01
Aridity index (AI)	0.81	< 0.01	-0.41	< 0.01
pH	-0.13	0.04	0.73	< 0.01
P ₂ O ₅	-0.05	0.39	-0.59	< 0.01
K ₂ O	-0.30	< 0.01	-0.65	< 0.01
Carbon	0.47	< 0.01	-0.48	< 0.01
Nitrogen	0.09	0.14	-0.57	< 0.01
C/N ratio	0.57	< 0.01	0.02	0.72
Carbonates	-0.09	0.17	-0.40	< 0.01
Organic substance	0.13	0.23	-0.57	< 0.01
Sand	-0.31	< 0.01	0.44	< 0.01
Silt	0.54	< 0.01	-0.15	0.17
Clay	-0.31	< 0.01	-0.57	< 0.01
Na	-0.18	0.10	-0.29	0.01
K	-0.25	0.03	-0.55	< 0.01
Ca	-0.03	0.78	-0.80	< 0.01
Mg	-0.03	0.82	-0.71	< 0.01
CEC (potential)	0.00	0.97	-0.72	< 0.01
CEC S-value	-0.06	0.57	-0.81	< 0.01
CEC V-value	-0.19	0.09	-0.77	< 0.01

to zero mean unit variance (pH values were previously antilogged). We used detrended correspondence analysis (DCA) to reveal differences in vegetation composition, as this technique provides eigenvalues that allow estimation of gradient length as a measure of variation between samples (Eilertsen *et al.* 1990, Hill & Gauch 1980). Downweighting of rare species was carried out because 57% of the species in our dataset were recorded in fewer than five sampling plots. We investigated the influence of climate and soil on vegetation differentiation by calculating Spearman's rank correlation coefficients between environmental data and the DCA scores of the first two axes. We calculated species richness, inverse

Simpson's Index of Diversity, and the evenness index E_{var} (Smith & Wilson 1996) separately for the three plant layers. Inverse Simpson's Index is a measure of diversity giving less weight to rare species (Tuomisto 2010). Separate treatment of herbaceous and woody layers is advisable due to their relative phytosociological independence in West African savannas (Hahn-Hadjali 1998), which was especially pronounced in our datasets. To examine species-sampling relations, we calculated species-accumulation curves by permuted random sample addition, with the x axis scaled by plot sampling area. As a net measure of differences in diversity between equal-sized paired mound and savanna plots,

we chose the logarithmic response ratio, calculated as the natural logarithm of the quotient of mound and comparison-plot values (Hedges *et al.* 1999). A positive ratio indicates greater diversity in mound plots, whereas a negative ratio indicates greater diversity in savanna plots. For the woody plant layers, we removed pairs where no woody cover occurred in one of the paired plots. Statistical significance of differences between mounds and adjacent savannas were tested using Welch's two-sample t-test.

We calculated indicator values for each species using the IndVal method (Dufrene & Legendre 1997), where 0 denotes no indication and 100% denotes perfect indication. We conducted 1000 iterations for each research site independently, using the groups of mound plots and savanna plots set a priori. We used the IndVal procedure to identify species that typically occur on termite mounds. Identification of characteristic species promotes understanding of savanna diversity. This method has the advantage of being based on field data rather than on expert knowledge, which is only partially available via floristic works. Species with significant indicator values greater than 60% (McGeoch *et al.* 2002) were considered to be characteristic termite-mound species.

All data analyses were performed using R 2.11.1 with the packages *vegan* 1.17–6 and *labdsv* 1.4–1.

RESULTS

Gradient analysis

DCA produced eigenvalues of 0.60 and 0.44, and gradient lengths of 5.99 and 3.85 for the first two axes, respectively. The first axis of the DCA showed plots in the latitudinal order of the five research sites from north to south. While the mound and savanna plots followed the first axis in parallel and approximately to the same extent, the second axis showed clear separation between mound and savanna plots (Figure 2).

The variation in vegetation composition depicted by the first axis was strongly correlated with bioclimatic variables (Table 1). Mean annual precipitation (MAP) and the Global Aridity Index (AI) correlated strongly with the axis scores (MAP: $\rho^2 = 0.66$, AI: $\rho^2 = 0.65$). The second axis was strongly correlated with soil variables, with the highest correlation occurring with the sum of base concentrations (S-value; $\rho^2 = 0.66$). Other CEC-related variables, such as clay content and the concentrations of K^+ , Ca^{2+} and Mg^{2+} ions as well as potential CEC and base saturation (V-value), were also correlated significantly with this axis. Among the set of soil variables available for all plots, pH ($\rho^2 = 0.54$) and potassium concentration ($\rho^2 = 0.43$) showed the strongest correlations.

Diversity analysis

Analysis of the mounds' impact on diversity indicated complex patterns. We detected a total of 561 species in our plots, 323 (57.6%) of which occurred in fewer than five plots. The lowest numbers of species on termite mounds were recorded in the Sahel (RPS, MAP 360 mm), and the highest were recorded in the central part of the north Sudanian vegetation zone (FCG, MAP 760 mm). Considering 30×30 -m woody-layer savanna plots only, species-accumulation curves exhibited similar patterns with strongly overlapping confidence intervals for all research sites except the Sahel (Figure 3). Also, curves for woody savanna vegetation showed the strongest notion of saturation. Termite-mound plots showed an overlapping pattern for two groups, with Pendjari National Park (PNP) and RPS both showing low overall species richness compared with the other sites. For adjacent savannas, PNP and RPS also showed congruence, but the species-accumulation curves for the other sites showed distinct differences and little overlap of confidence intervals (Figure 3). It should be noted that mound size (and, therefore, paired comparison site area) vary strongly between research sites, with smaller mounds in the Sahel. The overall mean species richness did not differ between termite mounds (25.6 ± 11.9) and the adjacent savanna (25.5 ± 15.3 , $P = 0.84$, t -value = 0.19, $df = 127$). When we partitioned our dataset by research sites (Figure 4), sites PNW (MAP 840 mm) and PNP (MAP 950 mm) in the south were observed to exhibit significantly higher species richness (SpR) on mounds (PNW SpR: 29.9 ± 5.76 , PNP SpR 19.0 ± 5.22) than in savanna plots (PNW SpR: 25.0 ± 4.71 , PNP SpR: 13.3 ± 4.98). No significant differences were found in the northern parts of the transect (RPS, MAP 360 mm; FCN, MAP 670 mm). Remarkably, the savanna vegetation at the central north Sudanian site (FCG, MAP 760 mm, SpR in savannas: 43.7 ± 9.12) was found to be significantly more diverse than the mound vegetation (FCG SpR on mounds: 36.2 ± 8.4). This also held true for the inverse Simpson's Index of Diversity (SI), which showed a greater diversity corrected for rare species at FCG (SI in savannas: 13.8 ± 6.35 , on mounds: 8.56 ± 4.46), whereas there were no significant differences found for the other research sites.

When woody layers were analysed alone, both southern sites showed significantly higher diversities on mounds for both species richness (PNW SpR on mounds: 12.5 ± 4.11 , in savannas: 7.54 ± 3.3 ; PNP SpR on mounds: 9.92 ± 2.98 , in savannas: 6.05 ± 2.86) and inverse Simpson's Index (PNW SI on mounds 12.1 ± 3.93 , in savannas: 7.25 ± 3.22 ; PNP SI on mounds: 9.39 ± 2.73 , in savannas: 5.93 ± 2.76), whereas no significant difference was detected at any other site.

With respect to the herbaceous layer, we found a significantly higher species richness on mounds only at

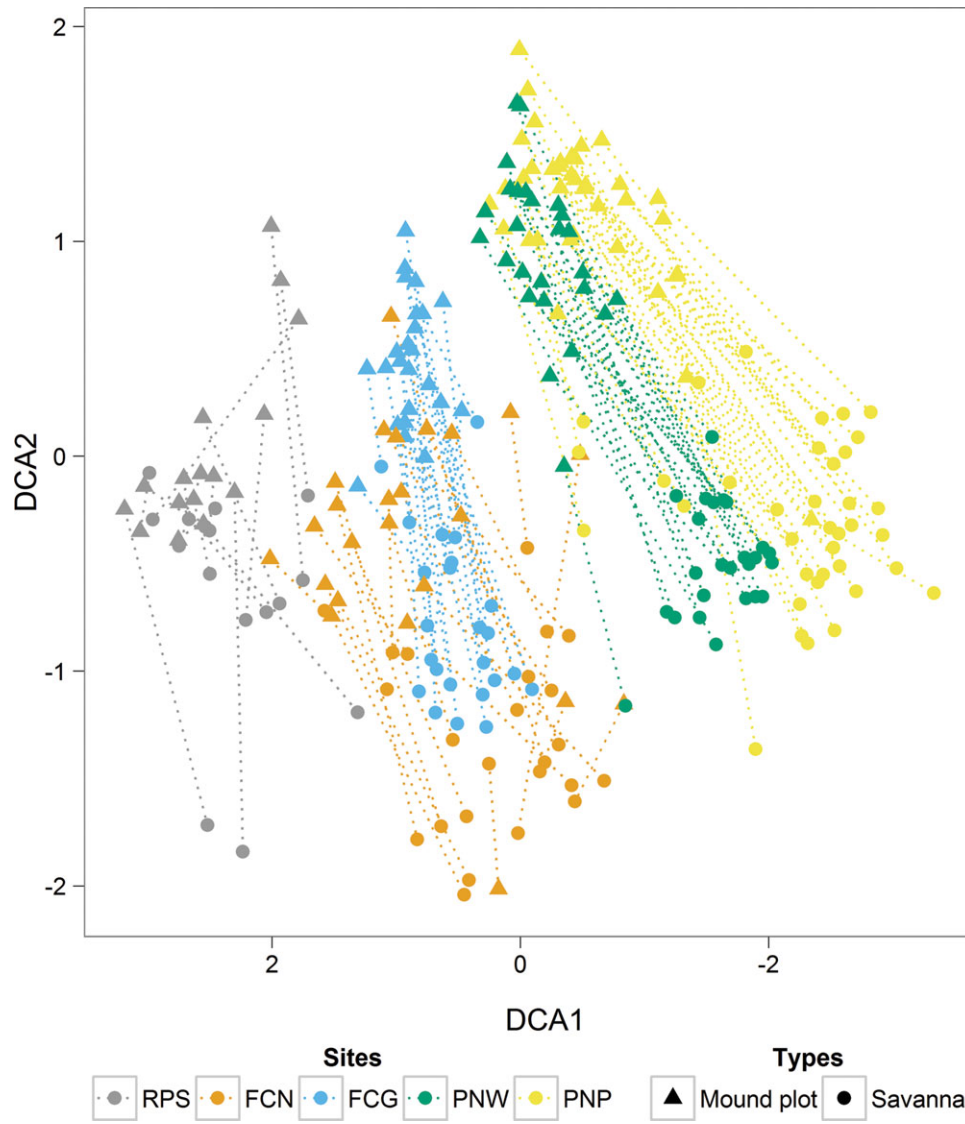


Figure 2. DCA plot of 128 sample pairs (mounds and adjacent savanna plots) and 561 species along a climatic gradient in West Africa. DCA produced eigenvalues of 0.60 and 0.44, and gradient lengths of 5.99 and 3.85 for the first two axes, respectively. Paired samples are connected by lines. Length of first axis: 6.5 SD units. Symbols indicate the plot type (mound or savanna), colours indicate research sites: Sahel Partial Reserve (RPS), Niouma Classified Forest (FCN), Gonsé Classified Forest (FCG), W National Park (PNW), Pendjari National Park (PNP).

PNP (SpR on mounds: 12.2 ± 5.09 , in savannas: 9.26 ± 4.51), whereas savanna herb layers exhibited greater species numbers than mounds at FCG (SpR in savannas: 40 ± 8.71 , on mounds: 34.0 ± 8.23). Inverse Simpson's Index for herbaceous layers presented significantly higher values on mounds both at the north (RPS, SI on mounds: 5.04 ± 1.4 , in savannas: 3.53 ± 1.85) and the south of the transect (PNW SI on mounds: 12.08 ± 3.93 , in savannas: 7.25 ± 3.22 ; PNP SI on mounds: 9.39 ± 2.73 , in savannas: 5.93 ± 2.76), though this was not the case for the central sites on the transect.

The evenness (E_{var}) of all species was significantly higher on mounds only at FCN (E_{var} on mounds: 0.27 ± 0.05 , in savannas: 0.22 ± 0.05). Herbaceous evenness

was also significantly higher on mounds only at FCN (E_{var} on mounds: 0.32 ± 0.06 , in savannas: 0.28 ± 0.04), while evenness for woody species was significantly lower on mounds than in savannas for RPS (E_{var} in savannas: 0.9 ± 0.17 , on mounds: 0.7 ± 0.21), FCN (E_{var} in savannas: 0.74 ± 0.22 , on mounds: 0.58 ± 0.21), and PNP (E_{var} in savannas: 0.75 ± 0.23 , on mounds: 0.61 ± 0.22).

Indicator species analysis

We found a total of 11 species that were characteristic of termite mounds (Table 2). More characteristic termite-mound species were found at study sites with higher

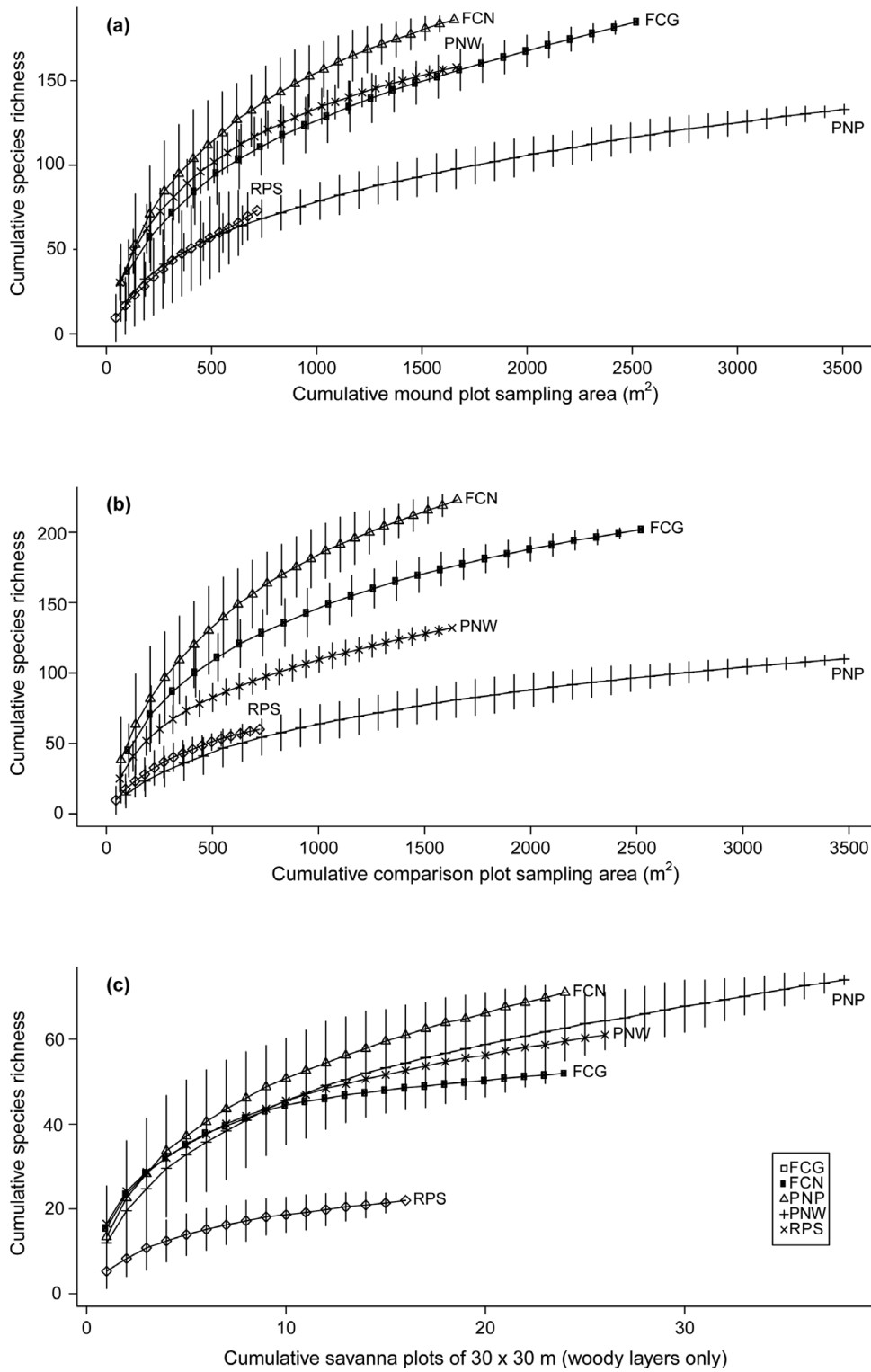


Figure 3. Plant species-accumulation curves for termite mounds (a), paired adjacent savanna plots (b) and 30 × 30-m woody-plant savanna plots (c) along a climatic gradient in West Africa. Vertical bars indicate confidence intervals after 100 permutations of randomly adding sites. For (a) and (b), x-axes are scaled by sampling plot area. Sites from north to south: Sahel Partial Reserve (RPS), Niouma Classified Forest (FCN), Gonsé Classified Forest (FCG), W National Park (PNW), and Pendjari National Park (PNP).

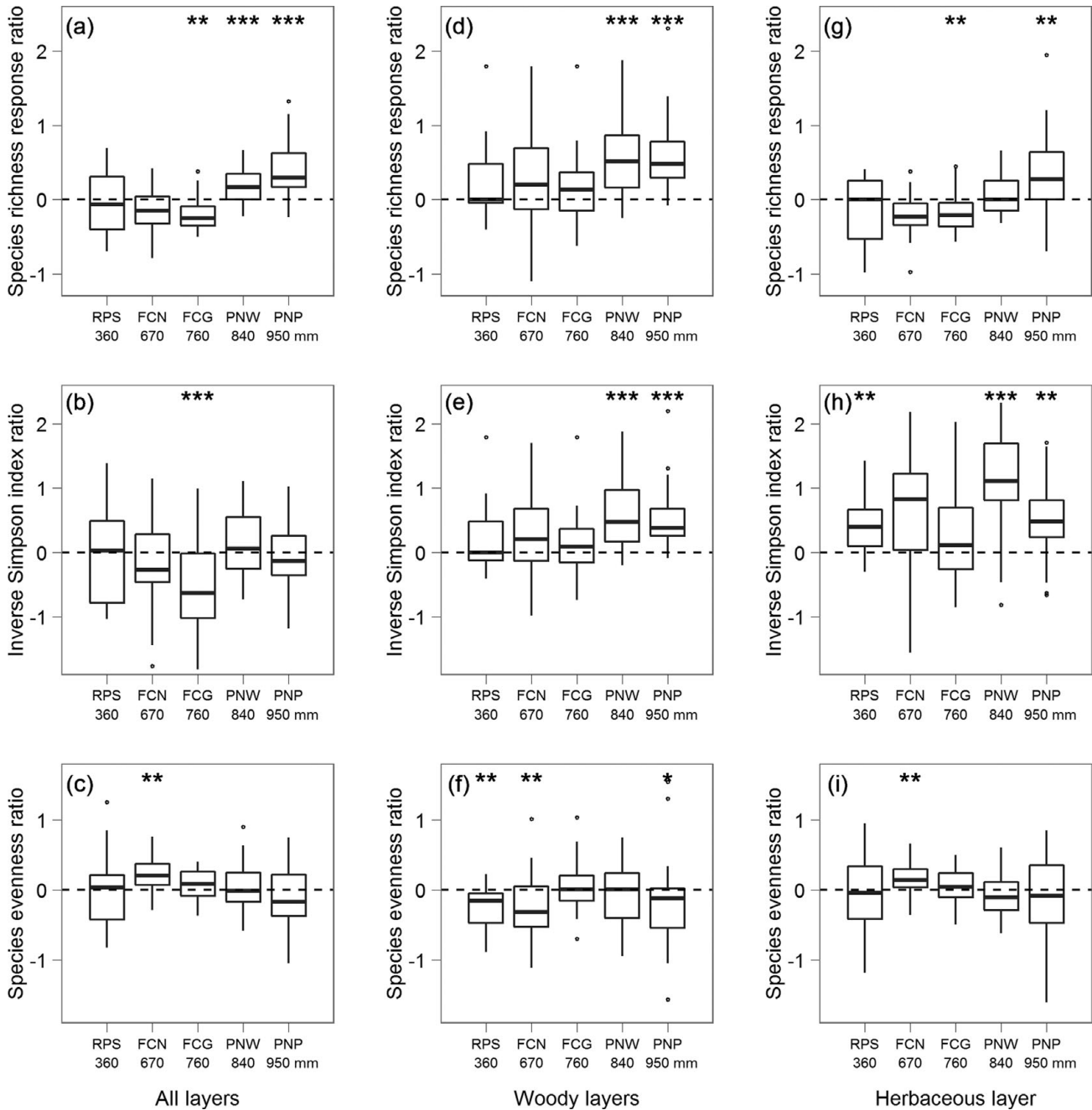


Figure 4. Log response ratio of plot pairs as measure of net diversity differences between termite-mound microhabitat and adjacent savannas. Boxplots (boxes represent the area between the first and third quartile, the whiskers extend to the most extreme data point which is no more than 1.5 times the length of the box away from the nearest end of the box) for each research site from north to south (RPS: Sahel Partial Reserve, FCN: Niouma Classified Forest, FCG: Gonsé Classified Forest, PNW: W National Park, PNP: Pendjari National Park, each given with MAP). Columns for boxplots of all layers (a–c), woody plant layers (d–f) and herbaceous layers (g–i) are shown separately. Response ratios above the broken line indicate higher values on mounds, while those below the line indicate higher values in corresponding savanna plots. Significant values are indicated by asterisks (*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$).

precipitation. At the driest, Sahelic site (RPS, MAP 360 mm), we detected no characteristic termite-mound species (only *Boscia angustifolia* presented a significant indicator value, which was 31.3% and therefore below the set threshold). At FCN (MAP 670 mm), several species

exhibited significant indicator values, but none exceeded the chosen cut-off value. Among the characteristic species, *Capparis sepiaria* and *Feretia apodanthera* had indicator values higher than 80% and were characteristic mound species for three sites (FCG, PNW and PNP).

Table 2. Characteristic species for 128 termite mounds separated by research sites along a climatic gradient in West Africa derived by the IndVal method. Sites from north to south: Sahel Partial Reserve (RPS, no characteristic species), Niouma Classified Forest (FCN, no characteristic species), Gonsé Classified Forest (FCG, five characteristic species), W National Park (PNW, six characteristic species), and Pendjari National Park (PNP, eight characteristic species). Significant indicator values between 60% and 100% are shown (100%: perfect indicator, $P \leq 0.05$, 1000 iterations). *, significant indicator, < 60% IndVal; n.s., present, but not significant; –, absent.

Sites: MAP (mm):	RPS 360	FCN 670	FCG 760	PNW 840	PNP 950
<i>Feretia apodanthera</i>	–	*	84.3	92.3	86.1
<i>Capparis sepiaria</i>	–	*	98.1	80.8	63.0
<i>Cadaba farinosa</i>	–	*	64.9	80.8	*
<i>Wissadula amplissima</i>	–	*	71.3	61.5	*
<i>Grewia bicolor</i>	n.s.	*	88.1	*	–
<i>Grewia lasiodiscus</i>	–	n.s.	–	65.4	65.4
<i>Maerua oblongifolia</i>	–	–	–	76.9	60.5
<i>Ampelocissus multistriata</i>	–	n.s.	–	*	78.9
<i>Grewia mollis</i>	n.s.	–	n.s.	*	60.7
<i>Asparagus flagellaris</i>	n.s.	*	n.s.	*	62.0
<i>Combretum aculeatum</i>	n.s.	n.s.	n.s.	*	60.5

The characteristic termite-mound species consist of nine shrubs and three ligneous forbs (*Ampelocissus multistriata*, *Asparagus flagellaris* and *Wissadula amplissima*). The last three species and both *Combretum aculeatum* and *Capparis sepiaria* exhibit a scrambling or climbing habit. Notably, at the family level, three Capparaceae were found to be characteristic of mounds (*Capparis sepiaria*, *Cadaba farinosa* and *Maerua oblongifolia*).

DISCUSSION

This study provides quantitative evidence of differences between termite-mound vegetation and adjacent savanna vegetation as well as of similar variability between termite-mound vegetation and adjacent savanna vegetation along a climatic gradient. However, mound vegetation was not shown to be more diverse at all of our sites, which we attribute partly to certain traits of the indicator plant species on the termite mounds addressed in this study.

Gradient analysis

We found that the mound and savanna plots formed separate groups along the second DCA axis: mound vegetation differed considerably from the surrounding savanna along the entire climatic gradient. This finding is in accord with those of a wide range of studies reporting mound vegetation to be distinct from savanna vegetation (Fanshawe 1968, Malaisse 1976, Schmitz 1963).

The higher cation concentrations of mound soils compared with the surroundings can be considered an explanation for pronounced differences between

mound and savanna vegetation. Nutrient levels and exchangeable cation concentrations have already been described as higher in termite mounds than in surrounding soils (Holt & Lepage 2000, Jouquet *et al.* 2011). We hypothesize that biopedoturbation, particularly the selection and transport of base-rich soil of the silt and clay fraction from deeper layers to the surface, as described by other authors (Abe *et al.* 2009, Arshad 1982, Mujinya *et al.* 2010), is crucial for the specific vegetation on termite mounds and represents a driving factor of general small-scale heterogeneity in African savannas. On a local scale, various studies report lower infiltration rates, but higher water availability on mounds (Dangerfield *et al.* 1998, Sileshi *et al.* 2010). It has been suggested that the existence of mounds allows colonization of a savanna by forest species and that the termite-mound vegetation in a particular vegetation zone is adapted to the conditions of a more humid vegetation zone (Bloesch 2008, Cole 1963). However, our regional analysis showed that vegetation differentiation can be attributed mainly to differences in MAP along a climatic gradient. Moreover, the observed changes on mounds were as pronounced as in the savanna matrix.

Diversity analysis

Overall species richness did not differ between termite mounds and the adjacent savanna vegetation. However, we found differences in the shape of the species-accumulation curves considering woody species and the vegetation including herbaceous species. High local heterogeneity in herbaceous vegetation of the paired mound and savanna plots leads to lower slopes for these plots. The surprisingly low species richness of the sampling in Pendjari National Park (PNP) might be considered a sampling artefact, as the majority of sites in PNP could not be visited during the wet season due to flooding. Also, local outcompeting of other species by herbaceous plants with higher productivity could be an explanation, which is supported by the species accumulation curve for 30 × 30-m woody-plant savanna plots. However, (also temporally) paired sampling allows for a direct comparison of net compositional differences between mounds and savannas, quite irrespective of differences in sampling time, or differences in the size of different plot-pairs. Net differences of species richness expressed as log response ratio showed no correlation with plot area. In this study, species richness was not found to be significantly higher on mounds when the whole dataset was considered, but even significantly lower on mounds in Gonsé Classified Forest (FCG). Higher plant diversity on mounds than in the surrounding savanna has been reported in several studies, especially for woody plants (Moe *et al.* 2009, Traoré *et al.* 2008a). Considering woody layers alone, mound richness in FCG

was no longer significantly lower, while both species richness and inverse Simpson's Index were still higher on mounds at W Transborder Park (PNW) and Pendjari National Park. FCG and FCN are considerably smaller than PNP and PNW, and are classified as forest reserves under higher anthropogenic pressure. FCG in particular, which is situated close to the Burkina Faso metropolis of Ouagadougou, is subject to a moderate but ongoing disturbance regime. As synanthropic herbaceous species contributed to the species richness at this site, disturbance might also explain why the overall species richness peaked here, in accordance with the intermediate disturbance hypothesis (Connell 1978, Huston 1979).

The increase in precipitation from north to south leads to an increasing share of phanerophytic life forms in the local flora (Schmidt *et al.* 2005). Enhanced woody plant establishment rates on mounds (Fleming & Loveridge 2003, Traoré *et al.* 2008b) could explain the considerably higher species richness and inverse Simpson's Index of Diversity on mounds at higher precipitation. Furthermore, separate treatment of vegetation layers is important, not only due to their phytosociological independence (Hahn-Hadjali 1998), but also because of the influence of canopy density. Shading by species with a long foliage period as well as a pronounced occurrence of climbers characterizes mound communities. A single specimen can often present a high cover value on a mound. In our dataset, for instance, single adult tamarind trees exhibited cover values of up to 90% per plot, shading out the herbaceous layer and thus lowering overall diversity.

However, diversity patterns may also be influenced by taxon-specific differences in mound architecture. Within the research area, *Macrotermes subhyalinus* is better able to cope with drier environmental conditions than *M. bellicosus*. Both species are subject to the same environmental constraint regarding homeostasis of their obligate fungi symbionts, but their mound architecture is different (Korb 2011). Different architecture might fundamentally influence the ability of plants to become established on mounds. The locations and concentrations of nutrients in mounds differ between species and genera of termites (Wood 1988, Wood & Sands 1978), and we can expect that further differences between the two *Macrotermes* species will be detected. However, we could not test this assumption because severely eroded *Macrotermes* mounds could not be attributed to a particular species.

Indicator species analysis

The identified indicator plant species exhibited different functional traits that might be related to their frequent and abundant occurrence on mounds. All species reaching significant indicator values >60%

are ligneous or subligneous perennials. A large proportion presents scrambling or climbing habits, i.e. *Capparis sepiaria*, *Wissadula amplissima*, *Grewia bicolor*, *Ampelocissus multistriata*, *Asparagus flagellaris* and *Combretum aculeatum*. The preference of indicator species for termite-mound microhabitats might be due to several benefits associated with the mounds, e.g. favourable soil conditions, accessible ground water and a certain degree of protection from fire. The higher number of characteristic mound plant species in areas with greater precipitation may be related to increases in overall woody species richness (Schmidt *et al.* 2005).

Termite mounds have often been recognized as refuges for woody plants within seasonally burned savannas (Fanshawe 1968, Joseph *et al.* 2011, Traoré *et al.* 2008b, Troll 1936). Specifically, plants with evergreen leaves (as the Capparaceae indicator species) are sensitive to burning. A previous study (Colonval-Elenkov & Malaisse 1975) specifically described the xerophytic features of termite mound vegetation in a Miombo savanna woodland.

However, the sclerophyllous *Capparis sepiaria* exhibited the deepest roots in a study of termite-mound-thicket root distribution in Ghana (Okali *et al.* 1973), and showed high rates of transpiration in a study of mound microclimate (Lawson & Jenik 1967). We assume that the characteristic Capparaceae species included in our study develop deep roots as well. Dependency on continuous access to ground water can also be assumed for *Feretia apodanthera* (also found in gallery forests and transient watercourses).

Shading and vertical structure provided by woody vegetation could favour lianescent species as well as mesophytic species in the understorey. Lianas are a life-form that is especially adapted to compete for light, and because these plants depend on available water, they develop deep roots (DeWalt *et al.* 2009). In several instances in the present study, a single shade-tolerant species, such as *Wissadula amplissima*, comprised the herbaceous cover as a result of forming monotypic stands. The mound microhabitats provide a wide range of benefits for other groups of organisms, such as birds (Joseph *et al.* 2011), large herbivores (Levick *et al.* 2010, Okullo & Moe 2012b), small vertebrates (Fleming & Loveridge 2003), insects and other invertebrates, and their predators (De Visser *et al.* 2008, Pringle *et al.* 2010). The identification of characteristic plant species associated with mounds gives a starting point for subsequent studies of their functional traits and biology, also addressing their role as resources for both the human population and for wildlife in West African savannas. Only recently, a first study from a single reserve in South Africa reported differences in functional traits of plants on and off mounds (van der Plas *et al.* 2012, in press). Our account of some functional characteristics can be a precursor to similar analyses in West Africa.

Unfortunately, processes of succession in these de novo microhabitats as well as their role in the long-term

dynamics of savanna ecosystems remain unclear, as long-term studies are lacking.

Additionally, the population dynamics of mound vegetation in landscapes undergoing rapid land-use changes, as are occurring in West African savannas (Reij *et al.* 2005, Tappan *et al.* 2004, Vincke *et al.* 2010), remain unaddressed. It is likely that the termite abundance, thus the termite-mound abundance outside of protected areas, will further decline. We would like to specifically encourage ongoing research on and the protection of viable mound-building termite populations and vegetation on mounds to elucidate the degree of interdependence of mounds and plants.

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Appendix 1. Research sites, mean annual precipitation (MAP) and number of mound/savanna plot pairs for each site per sampled savanna type. Vegetation zones according to White (1983). Tiger bush is a vegetation type composed of alternating, densely vegetated bands and bare areas parallel to the contour.

Vegetation zone	Site	MAP (mm)	Savanna types	Plot pairs
Sahel Zone	RPS	360	Tiger bush dominated by <i>Pterocarpus lucens</i> and <i>Acacia</i> spp.	16
Sudanian Zone	FCN	670	Tiger bush dominated by <i>Combretum micranthum</i> and <i>Pterocarpus lucens</i>	12
			Shrub savanna dominated by <i>Combretum nigricans</i> with subdominant <i>Sclerocarya birrea</i>	12
Sudanian Zone	FCG	760	Shrub savanna dominated by <i>Combretum micranthum</i> and <i>Guiera senegalensis</i>	12
			Shrub savanna dominated by <i>Terminalia</i> spp., <i>Ziziphus mauritania</i> and subdominant <i>Sclerocarya birrea</i>	12
Sudanian Zone	PNW	840	Woodland savanna dominated by <i>Isberlinia doka</i> and <i>Azelia africana</i>	13
			Woodland savanna dominated by <i>Terminalia avicennioides</i> and <i>Burkea africana</i>	13
Sudanian Zone	PNP	950	Shrub savanna dominated by <i>Crossopteryx febrifuga</i>	18
			Shrub savanna dominated by <i>Detarium microcarpum</i>	16
			Tree savanna dominated by <i>Terminalia avicennioides</i> and <i>Burkea africana</i>	4