

Dynamics of juvenile woody plant communities on termite mounds in a West African savanna landscape

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Summary: Termites are keystone species in savanna ecology, and their mounds are thought to be an important source of habitat heterogeneity and structural complexity of the savanna. *Macrotermes termitaria* have been shown to allow woody plant colonisation of landscapes otherwise dominated by C4 grasses. In this study, we assess how resource-rich *Macrotermes* mounds affect juvenile woody plant and non-woody plant species diversity, community composition, biomass and population dynamics. We repeatedly sampled paired termite mound and savanna plots in Pendjari National Park (Sudanian vegetation zone, North Benin, West Africa) over the course of two years. Despite considerable overlap in their species pools, plant communities of mound and savanna plots were clearly separated in ordinations. Species richness and diversity of juvenile woody plants was consistently higher on termite mounds, while no differences could be detected for non-woody plants. Evenness of juvenile woody plants was generally lower on mounds, whereas density and basal area were higher on mounds. In contrast, we did not detect any influence of the mound microhabitat on colonisation, mortality and turnover of woody juveniles. Therefore, we suggest that differences in the communities on and off mounds should be strongly influenced by directed diaspore dispersal through zoochory.

Key words: β -diversity, biodiversity, bush encroachment, colonisation, habitat heterogeneity, *Macrotermes*, mortality, Pendjari National Park, termitaria

DYNAMIQUE DES PLANTES LIGNEUSES JUVENILES SUR TERMITIÈRES DANS UN PAYSAGE DE SAVANE OUEST-AFRICAIN

Résumé: Les termites sont des espèces clés en écologie des savanes, et leurs termitières pourraient être une importante source d'hétérogénéité de l'habitat et de complexité structurelle dans la savane. Il a été démontré que les termitières de *Macrotermes* permettent aux plantes ligneuses la colonisation de paysages dominés par des graminées C4. Dans cette étude, nous évaluons comment des termitières de *Macrotermes* riches en ressources affectent la diversité des plantes ligneuses juvéniles et des plantes non-ligneuses, ainsi que la composition de la communauté, la biomasse et la dynamique de leurs populations. Nous avons échantillonné des couples de termitières et de parcelles de savane à plusieurs reprises dans le Parc National de la Pendjari (savane soudanienne, Nord du Bénin, Afrique de l'Ouest) au cours de deux années. Malgré des compositions d'espèces similaires, les communautés végétales des termitières et des parcelles de savane étaient clairement séparées par des ordinations. La richesse en espèces et la diversité des plantes ligneuses juvéniles étaient constamment plus élevées sur les termitières, alors qu'aucune différence n'a pu être détectée pour les plantes non ligneuses. L'équitabilité des plantes ligneuses juvéniles était généralement plus faible sur les termitières, alors que la densité et la surface basale étaient plus élevées sur les termitières. En revanche, nous n'avons détecté aucune influence du micro-habitat des termitières sur la colonisation, la mortalité et le renouvellement des juvéniles ligneuses, nous suggérons donc que les différences dans les communautés sur et hors termitières devraient être fortement influencées par la dispersion de diaspores par zoochorie.

Mots clés: biodiversité, colonisation, diversité bêta, embroussaillage, hétérogénéité de l'habitat, *Macrotermes*, mortalité, Parc Nationale de la Pendjari, termitières

DYNAMIK JUVENILER GEHÖLZGESELLSCHAFTEN AUF TERMITENHÜGELN IN EINER WESTAFRIKANISCHEN SAVANNENLANDSCHAFT

Zusammenfassung: Termiten sind Schlüsselarten der Savannenökologie. Ihre Hügel werden als wichtige Ursache der Habitatheterogenität und Strukturkomplexität der Savannen angesehen. Für die Hügel von *Macrotermes* wurde gezeigt, dass sie Gehölzen die Besiedlung von Landschaften ermöglichen, die ansonsten von C4-Gräsern dominiert sind. In der vorliegenden Arbeit analysieren wir, wie Artendiversität, Artengemeinschaft und Populationsdynamik von juvenilen Gehölzen und krautigen Pflanzen durch ressourcenreiche *Macrotermes*-Hügel beeinflusst wird. Hierzu untersuchten wir wiederholt im Verlauf von zwei Jahren verbundene Stichproben von Termitenhügeln und benachbarten Savannenflächen des Pendjari-Parks (Sudanzone, Nordbenin, Westafrika). Trotz beträchtlicher Überschneidung des Artenpools der beiden Habitattypen ergaben Ordinationen eine klare Trennung der Pflanzengesellschaften. Artenreichtum und Diversität der juvenilen Gehölzarten waren auf den Termitenhügeln durchgängig höher als in ihrer Nachbarschaft. Für krautige Arten konnte dagegen kein Unterschied festgestellt werden. Die Evenness der jungen Gehölzpflanzen war auf den Hügeln niedriger, Dichte und Basalfläche höher als in der Nachbarschaft. Unterschiede in der Besiedlung, Sterblichkeit und im Turnover der jungen Gehölzpflanzen waren nicht feststellbar. Unserer Meinung nach könnten Unterschiede zwischen der Vegetation der Hügel und der ihrer Umgebung stark durch gerichtete Zoochorie beeinflusst sein.

Schlagworte: β -Diversität, Biodiversität, Verbuschung, Besiedlung, Habitatdiversität, Habitatheterogenität, *Macrotermes*, Mortalität, Pendjari Nationalpark, Termitenhügel

1 INTRODUCTION

Savanna systems occupy a large proportion of the global landmass (SANKARAN et al. 2005). They are thought to be shaped by competition of woody plants and grasses for limiting resources, such as water and nutrients (SCHOLLES & ARCHER 1997, SANKARAN et al. 2005). Further factors affecting the dynamics of savanna vegetation include an interplay of climate, fire, and large herbivores (BOND 2008, SANKARAN et al. 2008, STAVER et al. 2011, LEHMANN et al. 2014). It has long been suggested that termite mounds are key elements of woody plant establishment in savanna habitats (TROLL 1936, COLE 1963), and thus contribute to defining the character of the savanna landscape. However, few studies so far have addressed recruitment and dynamics of juvenile woody plants on termite mounds as compared to the surrounding savanna. Recently, emphasis has been renewed that further studies are needed to understand the role of termite mounds in the process of woody plant establishment in savannas (SILESHI et al. 2010). New insights in this regard could also be beneficial to a better understanding of bush encroachment, which can be observed in many open savanna habitats worldwide (SILESHI et al. 2010).

Available evidence suggests that woody plants establish preferably on termite mounds (COLE 1963, BLÖSCH 2008), and that their communities are shaped by fire and wildstock grazing. For instance, a recent study from East Africa showed higher densities of juvenile woody plants on termite mounds (STØEN et al. 2013). Higher seedling densities on mounds have also been reported for West Africa (TRAORÉ et al. 2008b), where at the same time strong temporal and seasonal variation of juvenile mortality was observed. Although a few studies on juvenile mound vegetation thus exist, the establishment, growth and mortality of juvenile woody plants on mounds compared to the surrounding savanna is overall poorly understood.

The aim of this study was to collect more data on vegetation dynamics on termite mounds, with a strong focus on juvenile woody plants. We contrasted data of juvenile woody plants against non-woody plants (including graminoids, geophytes, hemicryptophytes, and also semi-woody forbs and subshrubs) as their direct competitors. Our analysis was guided by several hypotheses related to differences in community composition and population dynamics between mounds and savannas. We expected (1) that plant communities on mounds are more diverse, and specifically show a higher within-group β -diversity than the surrounding savanna; and (2) that due to differences in mortality, colonisation, and diameter gain juvenile woody plants feature higher overall abundance, density, and biomass on termite mounds than in the surrounding savanna. All these factors should lead to a difference in woody plant species composition between mounds and savannas, as reported in many studies (JACKSON & GARTLAN 1965, MOE et al. 2009, SILESHI et al. 2010, JOSEPH et al. 2013a, VAN DER PLAS et al. 2013, JOSEPH et al. 2014). We furthermore expected that soil characteristics would differ between mounds and savannas and could be used to explain the results regarding the hypotheses on diversity, abundance, biomass, and mortality. Moreover, we assumed that dispersal mode should affect woody plant establishment on mounds. Within the communities of juvenile

plants, we expected animal-dispersed plants and plants with a mixed dispersal mode to be overrepresented on mounds compared to the surrounding savanna.

2 MATERIAL AND METHODS

2.1 Study area

We conducted our study in Pendjari National Park (PNP), North Benin (10° 30'–11° 30'N, 0° 50'–2° 00'E), in the vicinity of a permanent plot of the BIOTA West Africa project. PNP is situated at the limit of the North Sudanian Vegetation Zone (WHITE 1983). In a paired plot design, we sampled twelve termite mounds and twelve corresponding savanna plots. The sampling sites were situated in an alluvial landscape on skeletal soil based on tillites. The area is dominated by *Terminalia avicennioides* and *Burkea africana* in the tree layer. The park area is under an annual early burning regime prescribed by its conservation authorities.

2.2 Sampling

For our sampling, we chose mound plots randomly and approximated their size by multiplying the longest diameter of each termite mound with its perpendicular axis diameter. Corresponding savanna plots of the same size as the paired mound plots were placed 15 m north of the mound plots, to minimize influence of termite activity (LEVICK et al. 2010, OKULLO & MOE 2012a, 2012b). Mound size varied between 5.5 m² and 37.7 m² (mean: 22.3 m² \pm 8.0 SD). The average height of termite mounds was 1.5 m \pm 0.5 SD. Vegetation data were recorded in four subsequent sampling periods in 2008 and 2009 at the beginning (end of May) and the end of the rainy season (end of October), respectively. Using these four samplings, we aimed at following individual plants over time to investigate juvenile dynamics. Nomenclature followed the African Plants Database (2014; <http://www.ville-ge.ch/musinfo/bd/cjb/africa/>).

We considered woody plants with basal diameters < 5 cm as juveniles. We calculated diversity indices for each plot, including species richness for non-woody plants, and species richness, inverse Simpson index and evenness E_{var} after SMITH & WILSON (1996) for juvenile woody plants. Furthermore, we estimated plant cover for all species present and recorded abundances and basal diameters of juvenile woody plants. We used the basal area for each individual as a proxy measure for juvenile biomass. Many individuals consisted of multiple stems, and while the identity of stems could not be ensured between two samplings, great care was taken to attribute stems to a particular individual. We measured colonisation as the number of plantlets emerging in a sampling that had not been present in the previous census. Mortality rate was calculated as the proportion of individuals that disappeared between two samplings, after excluding newly recruited individuals. Colonisation and mortality combined were treated as overall turnover between samplings. In addition to our field measurements, we compiled information on life form and dispersal type for each species present from the literature (GUINKO 1984, HOVESTADT 1997, HOVESTADT et al. 1999, AKÉ ASSI 2001). We sampled soil of both mounds and the surrounding savanna. Mound soil was

sampled on the mound slope 1 m inwards of the mound's pediment limit (perceived as the outer limit of any visible alluvial fan). Savanna soil was sampled in 15 m distance to the mound's limit. To account for micro-scale heterogeneity, we pooled four topsoil subsamples of 10 cm³ for each plot. Soil samples were air-dried and sieved to < 2 mm prior to analysis. Concentrations of plant-available phosphorous (P₂O_{5av}), plant-available potassium (K₂O_{av}), organic and inorganic carbon, nitrogen, as well as pH and conductivity were determined. Additionally, we determined potential cation exchange capacity (CEC_{pot}, with ion concentrations of sodium, potassium, calcium, and magnesium) and particle size distribution (PSD, as percentage of the sand, silt, and clay fractions).

2.3 Statistical analysis

We calculated species accumulation curves to ascertain if our sample was representative for the local species pool. Differences in species richness, diversity, and evenness between plot types (mound/savanna) and samplings (1-4) were analysed using Wilcoxon matched-pairs signed-rank tests. Further Wilcoxon matched-pairs signed-rank tests were used to assess differences in basal area, number of individuals and stems, mortality, colonisation and turnover rates, and dispersal modes of juvenile woody plant species between mounds and savannas. Differences in soil composition were analysed using paired Wilcoxon rank sum tests. When multiple tests were performed, we corrected probability values with Benjamini & Hochberg correction (BENJAMINI & HOCHBERG 1995) to account for the higher probability of Type I errors.

To examine β -diversity on plot community level, we used constrained distance-based analysis of principal coordinates (CAP, or constrained db-RDA). CAP allows linear and metrical analysis, while non-Euclidian distance metrics can be applied for the ordination (ANDERSON & WILLIS 2003). Using abundance data for juvenile woody plants, we calculated Bray-Curtis distances among all plots as a basis for further analysis. To account for pseudoreplication, we used repeated samplings as a conditioning factor. When analysing non-woody communities, we used Whittaker's β_w on presence/absence data as a distance measure among plots. Whittaker's β_w is equivalent to Bray-Curtis distances for presence/absence data, and a dissimilarity analogon to Sørensen similarities. Blocked multiple response permutation procedure (MRPP) with permutations restricted by samplings was used to test for differences in mean β -diversity between plot types (MIELKE & BERRY 2001, MCCUNE & GRACE 2002). MRPP calculates the overall weighted mean of group mean distances δ for the original data set, and for permuted data. The expected delta $E\delta$ is the mean of original dissimilarities (assuming no structure in groups). MRPP does not require normal distribution and is sensitive to both location and spread of the groups. All statistical analyses were performed with R 3.1.1 (R Development Core Team 2014), using the package vegan 2.0.10 (OKSANEN et al. 2013).

3 RESULTS

In our 24 plots, we recorded a total of 227 plant species from 55 families. On mounds, we found 173 species, and in the paired savanna plots we recorded 162 species. Mounds and savannas had 108 (48%) species in common, while 65 species were exclusively found on mounds (29%, from

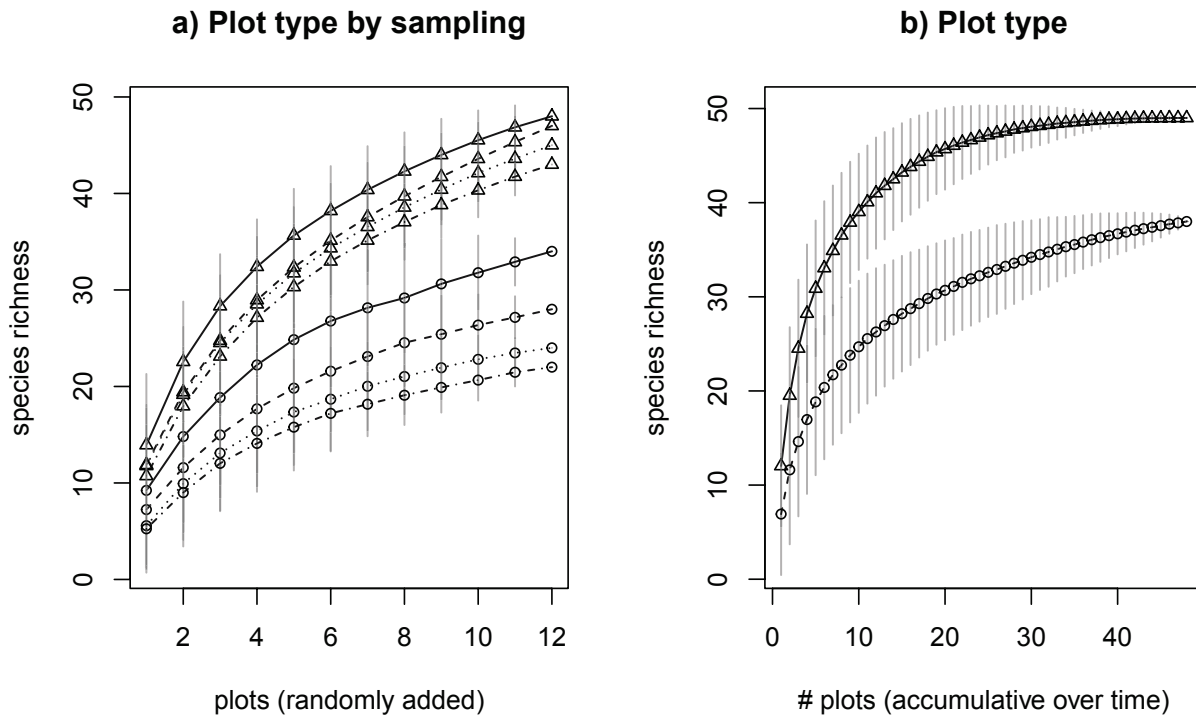


Fig. 1: Species accumulation curves (SAC) for mound and savanna plots. a) SAC per sampling for each plot type; b) SAC for each plot type, accumulative samples over time. Δ : mounds, \circ : savannas, vertical lines represent 95% confidence interval for each SAC / Courbes d'accumulation des espèces (SAC) pour relevés sur termitières et savanes. a) SAC par période d'échantillonnage pour chaque type de relevé; b) SAC pour chaque type de relevé, cumulée au fil de temps. Δ : termitières, \circ : savanes, des lignes verticales représentent des intervalles de confiance à 95 % pour chaque SAC.

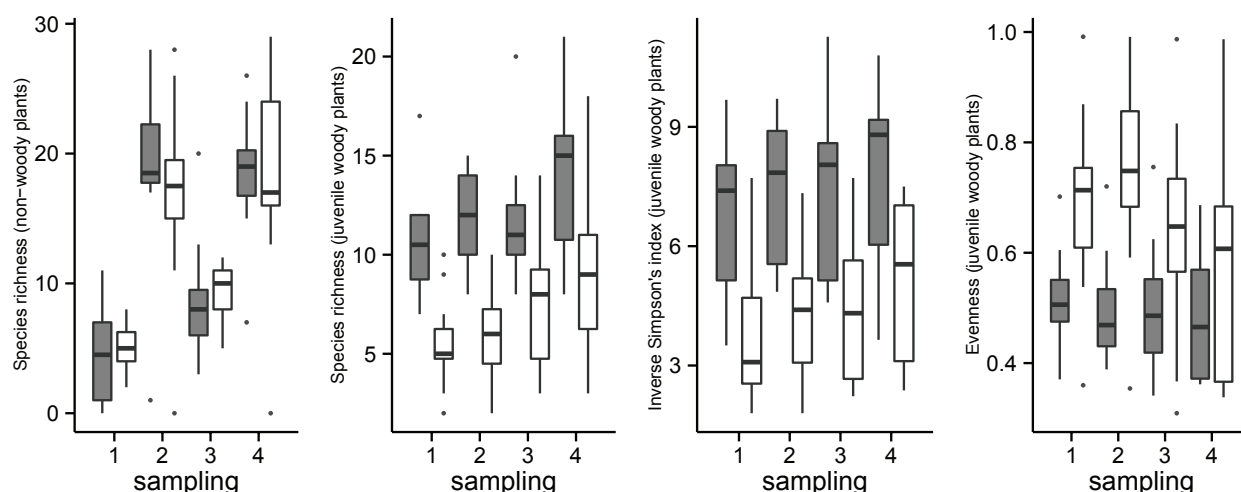


Fig. 2: Diversity of non-woody and juvenile woody plants on termite mounds ($n = 12$, dark grey boxes) and savanna plots ($n = 12$, white boxes) by sampling. For woody juveniles, differences between mounds and savannas are significant ($P < 0.05$), except for evenness in the third and fourth sampling period (Wilcoxon matched-pairs signed-rank test) / Diversité des non-ligneuses et plantes ligneuses juvéniles sur les termitières ($n = 12$, cadrat gris) et les parcelles de savane ($n = 12$, cadrat blanches) par échantillonnage. Pour les juvéniles ligneuses, les différences entre les termitières et les savanes sont significatives ($P < 0.05$), sauf pour l'équitabilité dans la troisième et la quatrième période d'échantillonnage (Wilcoxon matched-pairs signed rank test).

Table 1: Species richness of non-woody plants (herbaceous plants including graminoids, geophytes, hemicryptophytes, forbs and subshrubs) and species richness, inverse Simpson index and evenness of juvenile woody plants on mound and savanna plots. Given are mean and standard deviation across plots for each of the four sampling times. Statistical values Z and P are derived from Wilcoxon matched-pairs signed-rank tests with Benjamini & Hochberg adjustment / La richesse des espèces de plantes non ligneuses (plantes herbacées, y compris géophytes, hémicryptophytes, graminées et sous-arbrisseaux) et la richesse en espèces, l'indice inverse de Simpson et l'équitabilité des plantes ligneuses juvéniles sur termitières et relevés de savane. Étant donné sont moyenne arithmétique et l'écart-type sur relevés pour chacune des quatre périodes d'échantillonnage. Valeurs statistiques Z et P sont dérivées de Wilcoxon matched-pairs signed rank test avec l'ajustement de Benjamini & Hochberg.

			Mound		Savanna			
Sampling			Mean	SD	Mean	SD	Z	P-value
non-woody plants	species richness	1	4.42	3.63	4.92	1.88	-0.56	0.577
		2	18.83	6.53	17.17	7.13	1.12	0.262
		3	8.83	4.37	9.17	2.17	-0.88	0.381
		4	18.50	4.80	18.25	7.51	0.30	0.760
woody plants	species richness	1	10.58	2.71	5.58	2.27	3.05	0.004
		2	11.83	2.25	5.75	2.34	3.19	0.004
		3	11.75	3.17	7.58	3.29	2.94	0.004
		4	13.92	3.75	8.92	4.19	2.68	0.007
	inverse Simpson index	1	6.73	1.92	3.89	1.89	2.88	0.005
		2	7.41	1.81	4.23	1.56	2.98	0.005
		3	7.23	2.16	4.46	1.92	3.05	0.005
		4	7.76	2.40	5.07	2.11	2.73	0.006
	evenness	1	0.51	0.09	0.69	0.16	-2.95	0.007
		2	0.49	0.10	0.75	0.18	-2.91	0.007
		3	0.49	0.12	0.64	0.19	-2.12	0.045
		4	0.47	0.11	0.59	0.22	-1.19	0.232

31 families), and 54 species (24%, from 17 families) were only found in the adjacent savanna. Considering juvenile woody plants only, we found 57 species from 24 families in our plots (Appendix Table S1), with 49 species on mounds, and 38 species in the paired savanna plots. Mounds and Savannas had 30 species of juvenile woody plants in common (53%). We found 19 juvenile woody species from 14 families which were exclusive to mounds, while only eight of

the juvenile woody species (from six families) were exclusive to the savanna plots. Species accumulation curves (Fig. 1) indicated sufficient sampling per plot type, and over time. In all four samplings, species richness and diversity were significantly higher on termite mounds than in the surrounding savannas (Wilcoxon rank sum test: $P < 0.05$, Fig. 2, Table 1). Evenness was significantly higher in savannas than on mounds in the first two samplings.

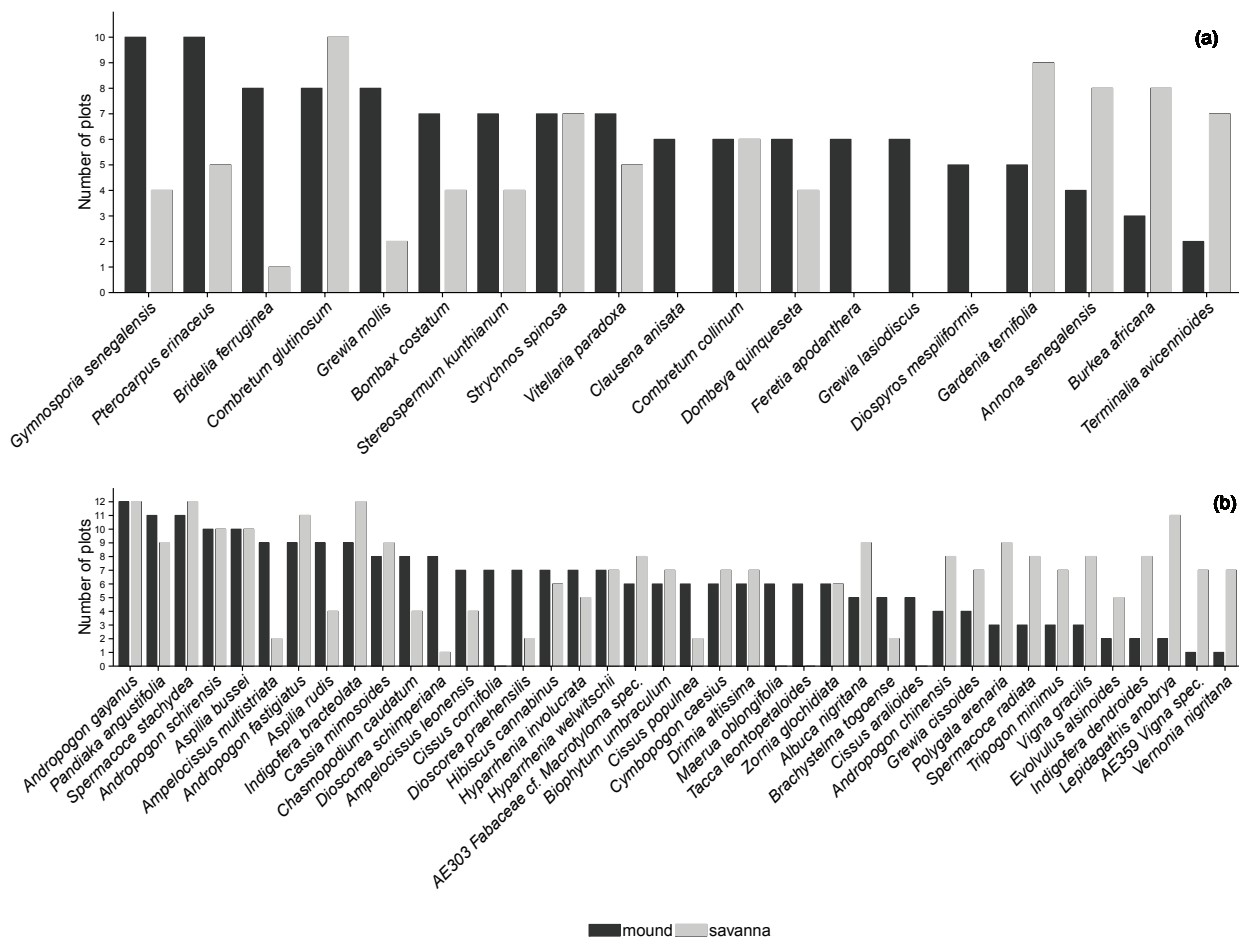


Fig. 3: Frequency of plant species, i.e. number of plots where a species was recorded on termite mounds (n=12) and savanna plots (n=12). (a) woody species, (b) non-woody species (herbaceous plants including graminoids, geophytes, hemicryptophytes, forbs and sub-shrubs). Only species present at more than four plots are included / Fréquence des espèces de plantes, ce est à dire le nombre de relevés où une espèce a été enregistrée sur les termitières (n = 12) et des relevés de savane (n = 12). (a) des espèces ligneuses, (b) des espèces non ligneuses (plantes herbacées, y compris graminées, géophytes, hémicryptophytes, et sous-arbrisseaux). Seules les espèces présentes à plus de quatre parcelles sont inclus.

Table 2: Basal area (cm²), number of individuals and number of stems of juvenile woody plants on mound and savanna plots. Given are mean and standard deviation across plots for each of the four sampling times. Statistical values Z and P are derived from Wilcoxon matched-pairs signed-rank tests with Benjamini & Hochberg adjustment / La surface basale (cm²), nombre d'individus et le nombre de tiges de plantes ligneuses juvéniles sur termitière et relevés de savane. Étant donné sont moyenne arithmétique et l'écart-type sur relevés pour chacune des quatre périodes d'échantillonnage. Valeurs statistiques Z et P sont dérivées de Wilcoxon matched-pairs signed rank test avec l'ajustement de Benjamini & Hochberg.

	Sampling	Mound		Savanna		Z	P-value
		Mean	SD	Mean	SD		
basal area	1	41.31	22.68	24.12	26.65	2.98	0.01
	2	59.52	32.16	28.49	26.52	2.94	0.01
	3	44.55	27.02	26.83	32.35	2.49	0.03
	4	87.79	43.89	41.52	38.11	2.40	0.03
number of individuals	1	22.17	9.52	12.50	5.99	2.98	0.01
	2	27.50	11.83	12.42	6.22	2.94	0.01
	3	28.08	12.92	19.42	11.33	2.49	0.03
	4	35.50	15.75	24.67	16.71	2.40	0.03
number of stems	1	93.83	77.58	27.00	15.77	2.98	0.01
	2	133.50	132.49	37.92	17.72	2.94	0.01
	3	138.42	121.45	56.08	33.44	2.49	0.03
	4	222.33	283.97	72.75	45.77	2.40	0.03

Table 3: Mortality rate, colonisation rate and turnover rate of juvenile woody plants on mound and savanna plots. Given are mean and standard deviation across plots for each of the four sampling times. Statistical values Z and P are derived from Wilcoxon matched-pairs signed-rank tests with Benjamini & Hochberg adjustment / Taux de mortalité, taux de colonisation et taux de roulement des plantes ligneuses juvéniles sur termitières et relevés de savane. Étant donné sont moyenne arithmétique et l'écart-type sur relevés pour chacune des quatre périodes d'échantillonnage. Valeurs statistiques Z et P sont dérivées de Wilcoxon matched-pairs signed rank test avec l'ajustement de Benjamini & Hochberg.

	Sampling	Mound		Savanna		Z	P-value
		Mean	SD	Mean	SD		
mortality	1-2	0.07	0.14	0.18	0.34	-0.29	0.77
	2-3	0.08	0.09	0.28	0.22	-2.07	0.10
	3-4	0.06	0.07	0.02	0.05	1.98	0.10
	1-4	0.05	0.09	0.16	0.27	-1.06	0.38
colonisation	1-2	0.20	0.16	0.30	0.34	0.07	0.94
	2-3	0.14	0.12	0.29	0.29	-0.88	0.92
	3-4	0.21	0.14	0.24	0.19	-0.40	0.92
	1-4	0.35	0.21	0.43	0.34	-0.68	0.92
turnover	1-2	0.16	0.11	0.26	0.33	0.14	0.89
	2-3	0.11	0.10	0.32	0.21	-2.17	0.12
	3-4	0.15	0.10	0.15	0.13	0.47	0.85
	1-4	0.25	0.15	0.36	0.28	-0.78	0.85

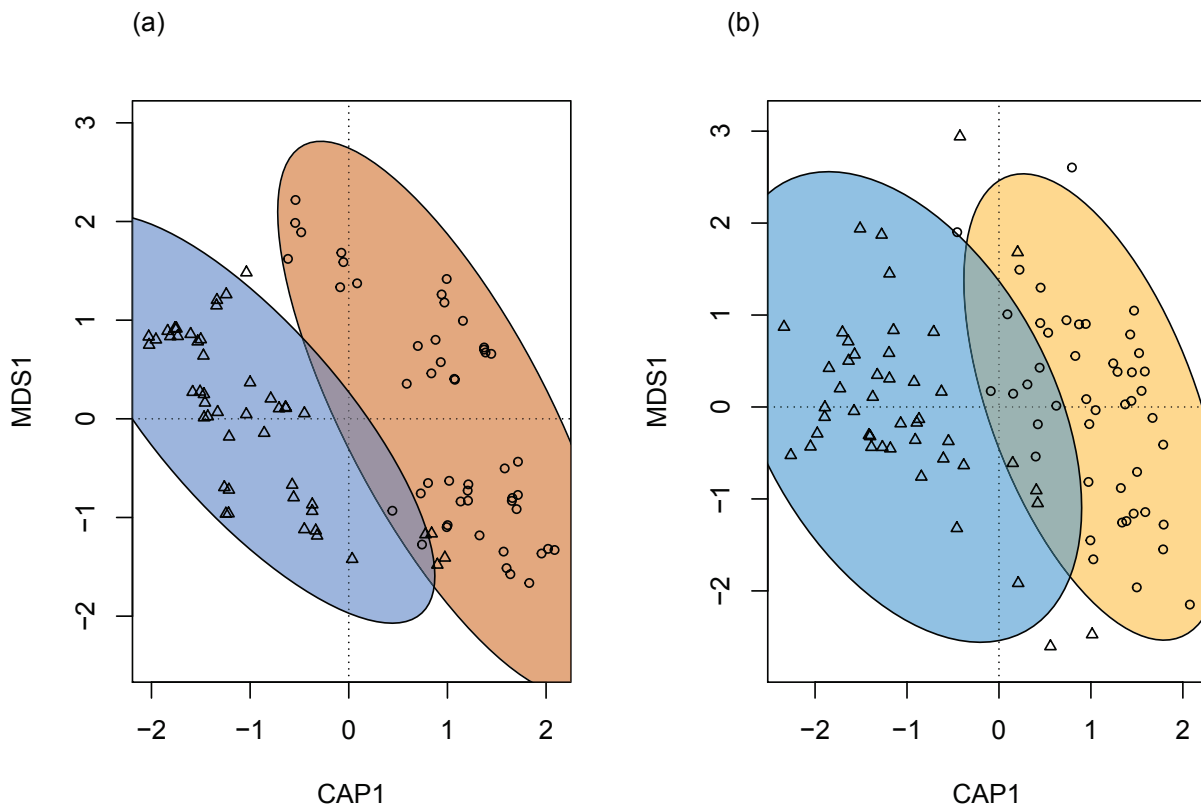


Fig. 4: Distance-based principal coordinate analysis for communities, constrained by plot type, (a) using Bray-Curtis distances on juvenile woody plants abundance data; (b) using Whittaker's β_w on non-woody species presence/absence data. Δ : mounds, \circ : savannas, ellipses mark the 95% confidence interval for each group / Analyse en coordonnées principales pour les communautés végétales à la base des distances, contrainte par type de relevé, (a) en utilisant des distances Bray-Curtis sur des données de l'abondance des plantes ligneuses juvéniles; (b) en utilisant le β_w de Whittaker sur des données de présence / absence des espèces non-ligneuses. Δ : termitière, \circ : savanes, ellipses marquent l'intervalle de confiance à 95% pour chaque groupe.

Overall, very few species occurred frequently, i.e. on many plots. Among both woody plantlets and non-woody plants, the most frequently found species occurred in either plot type (Fig. 3). In contrast, species restricted to one particular plot type were particularly infrequent. Of the species exclusive to mounds, only four non-woody and four woody species were found to be present at more than four of the sampled termite mounds over the whole sampling period. No species exclusive to the savanna was recorded in more than three of the savanna plots. The most frequent juvenile woody species exclusive to mounds (*Clausena anisata*, *Feretia apodanthera*, *Grewia lasiodiscus*) occurred on six of the mounds each, the most frequent juvenile woody species exclusive to savannas (*Pteleopsis suberosa*) was found only in three savanna plots.

During our four sampling periods, we measured the basal area of 859 plant individuals on and off mounds. As most individuals showed more than one stem, we collected a total

of 9382 stem measurements over time. Over the whole sampling period, the total number of individuals as well as the total number of stems and total basal area of juvenile woody plants was constantly and significantly higher on mounds than in the savanna plots between plot pairs (Table 2). With one minor exception, all figures increased over time. Only the number of individuals in savanna plots at the second sampling was one individual less than at the previous sampling. Mortality was not significantly different between mound and savanna plot pairs, and neither between samplings or over the whole sampling period. Colonisation, and therefore also overall turnover, were also not significantly different between plot pairs (Table 3).

Community composition of juvenile woody plants differed between mounds and surrounding savanna plots, as indicated by CAP (Fig. 4a). Although the first axis for all plant species covered only 7.38% of the total variability of the juveniles dataset, groups were clearly separated. This was un-

Table 4: Differences in dispersal mode among juvenile woody plant communities of mound and savanna plots. Given are mean number of species and standard deviation across plots for each of the four sampling times. Statistical values Z and P are derived from Wilcoxon matched-pairs signed-rank tests with Benjamini & Hochberg adjustment / Différences entre les modes de dispersion entre les communautés juvéniles de plantes ligneuses de termitière et relevés de savane. Étant donné sont moyenne arithmétique et l'écart-type sur relevés pour chacune des quatre périodes d'échantillonnage. Valeurs statistiques Z et P sont dérivées de Wilcoxon matched-pairs signed rank test avec l'ajustement de Benjamini & Hochberg.

Dispersal	Sampling	Mound		Savanna		Z	P-value
		Mean	SD	Mean	SD		
animals	1	6.58	1.51	2.73	1.85	3.51	<0.001
animals	2	7.42	1.73	2.42	1.68	4.11	<0.001
animals	3	7.33	1.78	4.00	2.37	3.02	0.005
animals	4	8.67	2.67	4.00	2.24	3.29	0.002
mixed	1	1.14	0.38	1.50	0.71	-1.01	0.714
mixed	2	1.12	0.35	1.50	1.00	-0.65	0.938
mixed	3	1.12	0.83	1.00	0.00	0.00	1.000
mixed	4	1.56	0.73	1.40	0.55	0.30	0.938
wind	1	3.33	1.50	2.83	0.94	0.76	0.724
wind	2	3.67	0.98	2.83	0.72	2.18	0.070
wind	3	3.67	1.50	3.67	1.07	-0.27	0.938
wind	4	4.08	1.62	4.67	1.72	-0.99	0.680

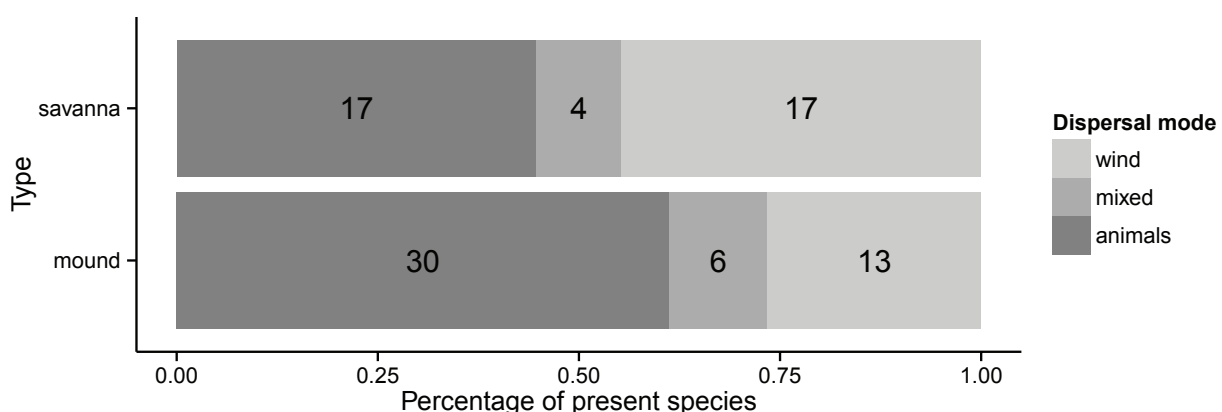


Fig. 5: Distribution of dispersal modes of juvenile woody plants on mound and savanna plots over all samplings. Numbers in the graph indicate the species count per dispersal mode according to the legend / Distribution de modes de dispersion des plantes ligneuses juvéniles sur termitières et relevés de savane plus de tous les échantillonnages. Chiffres indiquent des nombre d'espèces par mode de dispersion.

Table 5: Mean physical and chemical soil properties of all twelve termite mounds and twelve paired adjacent savanna plots in Pendjari National Park. Values are in mmol/kg unless otherwise indicated. Statistical values V and P are derived from Wilcoxon matched-pairs signed-rank tests with Benjamini & Hochberg adjustment / Moyenne des propriétés physiques et chimiques du sol de tous les douze paires de termitières et relevés de savane adjacentes du parc national de la Pendjari. Les valeurs sont en mmol/kg, sauf spécification contraire. Valeurs statistiques V et P sont dérivées de Wilcoxon matched-pairs signed rank test avec l'ajustement de Benjamini & Hochberg.

	Mound		Savanna		V	P-value
	Mean	SD	Mean	SD		
pH	6.81	0.66	5.68	0.38	76.0	0.004
P ₂ O _{5av}	1.12	1.18	0.45	0.14	44.5	0.092
K ₂ O _{av}	22.78	13.75	8.55	4.73	77.0	0.003
C	1.01	0.48	1.13	0.45	29.0	0.456
N	0.11	0.04	0.10	0.03	54.0	0.255
C:N ratio	8.81	1.26	11.82	2.63	1.0	0.003
Carbonates [%]	0.12	0.33	0.00	0.00	3.0	0.371
Organic substance [%]	1.03	1.33	1.34	1.34	11.0	0.673
CEC _{pot}	97.60	37.82	78.64	20.37	61.0	0.092
Base concentration	86.37	39.31	53.03	19.63	69.0	0.021
Base saturation [%]	86.60	12.01	67.42	12.04	73.0	0.009
K ⁺	6.24	5.36	1.37	1.53	77.0	0.003
Na ⁺	0.50	0.35	0.29	0.28	49.0	0.168
Ca ²⁺	62.85	28.25	40.15	14.64	65.0	0.045
Mg ²⁺	16.77	7.24	11.22	3.91	66.0	0.038
Sand [%]	45.14	7.50	58.38	7.18	2.0	0.004
Silt [%]	37.00	4.15	33.14	6.48	61.5	0.084
Clay [%]	17.86	6.83	8.48	2.48	76.0	0.004

derlined by the MRPP analysis, which showed a significant, albeit small difference between the groups with a slightly lower mean β -diversity for termite mounds (effect size $A = 0.06$, $\delta = 0.75$, $E\delta = 0.8$, $p = 0.001$, permutations = 999). CAP of presence-absence data for non-woody plants also showed mound and savanna groups (Fig. 4b). The first axis covered 4.41% of the total variability of the dataset. MRPP showed a significant difference in β -diversity for the groups with a slightly higher mean for termite mounds (effect size $A = 0.03$, $\delta = 0.79$, $E\delta = 0.81$, $p = 0.001$, permutations = 999).

A comparison of dispersal modes between the communities showed significantly more animal-dispersed species on mounds (Fig. 5, Wilcoxon matched pairs signed rank test, adjusted $p < 0.05$ for each sampling, Table 4), while both mixed dispersal mode and wind dispersal showed no significant differences between mound and savanna plots.

With respect to soil composition, termite mounds showed significant differences from the surrounding savannas (Fig. 6, Table 5). Physico-chemical analysis revealed that mound topsoil contained more plant-available potassium than savanna topsoil, and was enriched in clay. While the content of carbon and nitrogen did not differ significantly between mounds and savanna, the C:N ratio was significantly higher in savannas. Base saturation and base concentration were also significantly higher on mounds. Carbonates were absent in savanna soils, but present in mounds where they

could in some cases already be detected visually as small carbonate-rich nodules.

4 DISCUSSION

In this study, we used a repeated number of censuses and diameter measurements to gain more insight into patterns and processes within the community of juvenile woody plants and non-woody plants on and off termite mounds. While several of our hypotheses were confirmed, others had to be rejected or could not be adequately tested.

4.1 Biodiversity patterns

As expected, overall plant species richness and family richness were distinctly higher on mounds. Higher species richness on mounds was already reported in several studies from our study region (TRAORÉ et al. 2008a, KIRCHMAIR et al. 2012, ERPENBACH et al. 2013). Comparing paired plots, we detected higher species richness and diversity of juvenile woody plants on mounds than on the adjacent savanna plots (Figs.1 & 2, Table 1). Higher plant species richness and diversity on mounds could be explained by several factors. First, termite mounds offer a more favourable environment for plants by providing higher nutrient and moisture availability in an otherwise deficient ecosystem (ADAMSON 1943, KONATÉ et al. 1999, JOUQUET et al. 2006, SILESHI et al. 2010), which was also confirmed by our soil analysis. Second, mounds offer some degree of shelter and protec-

Shepard Sediment Classification Diagram

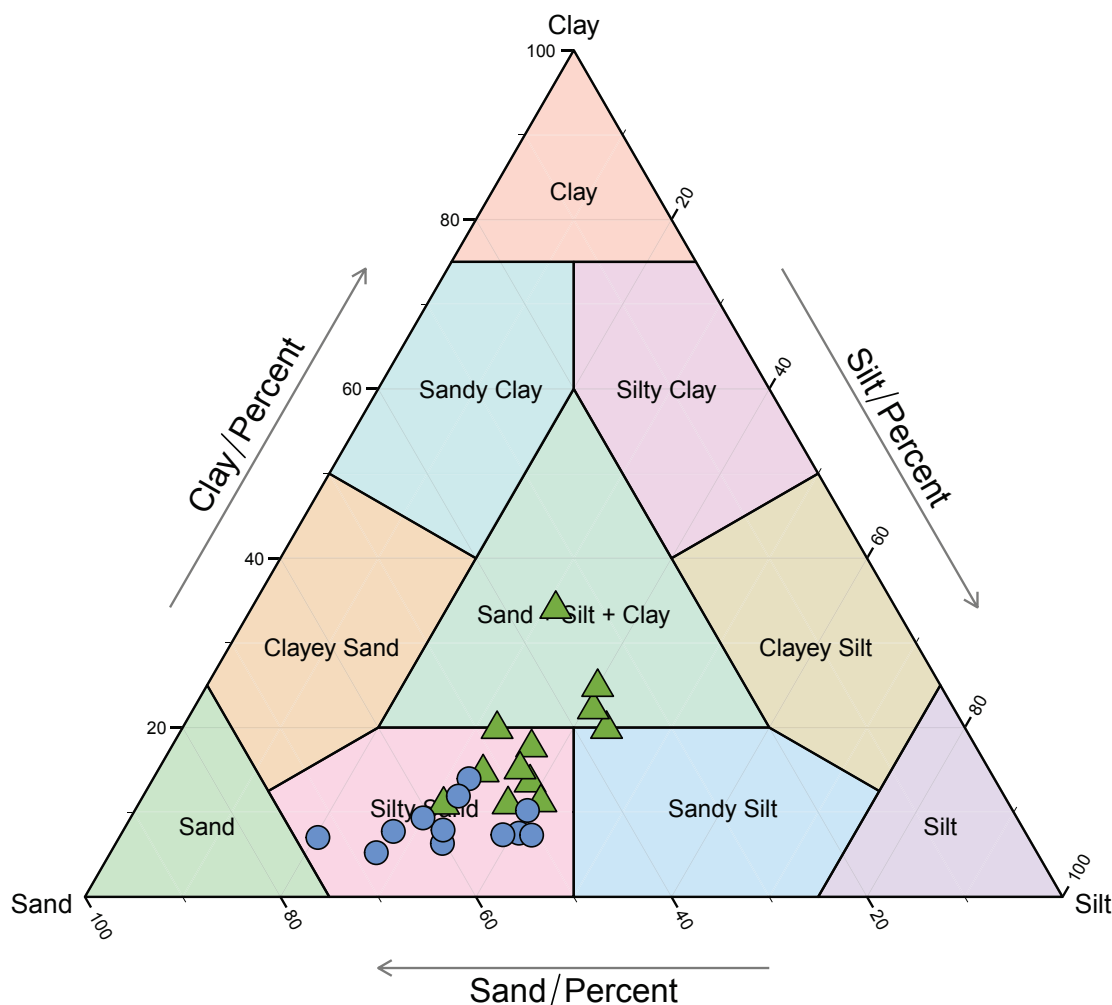


Fig. 6: Shepard diagram of termite mound and savanna plot soil samples. Mounds were characterized by higher clay content than the surrounding savanna plots. Δ : mounds, \circ : savannas / Shepard schéma des échantillons de sol de termitières et de savanes. Termitières ont été caractérisées par la teneur plus élevée en argile que les relevés de savane environnantes. Δ : termitières, \circ : savanes.

tion from disturbance such as fire and flooding (LAWSON & JENIK 1967, MCCARTHY et al. 1998, DEAN et al. 1999, BLÖSCH 2008, JOSEPH et al. 2013b), which on one hand can be a direct effect of termite activity due to slight elevation above the surrounding surface and a sparsely vegetated pediment around the mound base. On the other hand, it can also be an indirect effect due to less available fuel, i.e. less dry herbaceous, and more lush woody biomass, on mounds. Third, higher small-scale heterogeneity in soil and microclimatic conditions on mounds should promote the coexistence of plant species with different habitat requirements (compare, e.g., MOE et al. 2009, SILESHI & ARSHAD 2012, and also more generally STEIN et al. 2014 and MOESLUND et al. 2013). All these conditions enable the occurrence of species on mounds that may otherwise be discriminated against in the savanna by environmental stressors and competition.

Contrary to our findings (Fig. 2, Table 1), we had expected higher evenness on mound than savanna plots based on previous studies (MOE et al. 2009, OKULLO & MOE 2012a). However, the latter study only included herbaceous plants, for which evenness could not be investigated in the current ana-

lysis. VAN DER PLAS et al. (2013) also reported higher evenness on mounds, which was however not statistically significant when accounting for false discovery rate. In contrast, several studies also reported significantly lower evenness of mound vegetation, including woody and non-woody plants (LOVERIDGE & MOE 2004, KIRCHMAIR et al. 2012, STØEN et al. 2013). The lower evenness on mounds that we found in our study was likely caused by frequent and abundant species, like *Gymnosporia senegalensis*, and furthermore by species which were found infrequently, but in high abundance on mounds. For example, *Pseudocedrealia kotschy* and *Afzelia africana* occurred on only a single mound each, but with a maximum of 14 and 11 individuals, respectively, for a given sampling period.

With respect to community composition, the ordinations showed a clear separation of mound and savanna communities for both woody juvenile and non-woody plants (Fig. 4). However, the community differences were less strongly pronounced as expected, which we attribute to the high number of shared frequent species (Fig. 3). Surprisingly, our hypothesis of higher β -diversity on mounds compared with

savanna plots was only confirmed for non-woody plants, but not for woody plants. Accordingly, the higher overall woody plant species richness we found on mounds should be influenced mainly by higher α -diversity and not, as expected, by joint contributions of α - and β -diversity. The lower β -diversity of woody plant species on mounds compared to savanna plots implies a more frequent reoccurrence of characteristic woody plant species on mounds. This makes sense considering that the three most-frequent woody plant species exclusive to mounds occurred on six mounds each, whereas the single most-frequent species exclusive to the savanna occurred only on three plots. Moreover, this trend towards a slightly more uniform typical "termite-mound vegetation" within juvenile woody plant communities is in accordance with findings from a related study that identified mainly woody plant species as characteristic mound species across multiple sites in West Africa (ERPENBACH et al. 2013). Unsurprisingly, β -diversity between mound and savanna plots was consistently higher than among-group β -diversity for both woody and non-woody plants. This goes in line with our findings of 65 exclusive mound species and 54 exclusive savanna species, including both woody and non-woody species (also compare Fig. 3).

4.2 Population dynamics

In accordance with our hypothesis, basal area of juvenile woody plants was constantly and significantly higher on mound than on savanna plots in all samplings (Table 2). This goes in line with the higher number of individuals and higher number of stems that we found on mounds. Basal area of woody plants is often used as a proxy for biomass and productivity (CATCHPOLE & WHEELER 1992, VANCLAY 1992). We expected higher productivity on mounds, as a large number of studies has reported higher soil nutrient levels on mounds (JOUQUET et al. 2006, SILESHI & ARSHAD 2012). Also our own soil analysis revealed a better supply with potassium and other bases, and a more favourable (i.e., in this circumstance, smaller) C:N ratio on mounds than in the savanna. More fertile soil as well as higher water storage capacity due to higher clay content should thus promote productivity on mounds, similarly to the already mentioned promotion of plant diversity. These favourable conditions could also play a role in reducing mortality on mounds, as was suggested by MOE et al. (2009). Lower mortality, higher colonisation rates or a combination of both should be responsible for the higher abundance that we found on mounds. Mean mortality was generally lower on mounds than on savanna plots, even though the difference was not statistically significant (Table 3). Surprisingly, we neither found any significant differences in colonisation and turnover rates between mound and savanna; however, more studies with increased statistical power are needed to confirm or reject these results and understand mortality and colonisation dynamics better. We would therefore suggest to focus on a selected set of frequent and abundant species in future analyses. This would make it possible to extend the scope of further analysis to species level, and to distinguish between effects of biotic interaction among plants (e.g., density-dependent mortality, inter- and intraspecific competition) and of other influential environmental factors (e.g., fire, water availability, herbivory) on juvenile woody plants

on mounds. It is likely that intraspecific density affects several species on mounds, as density-dependent mortality has already been shown for *Acacia erythrocalyx* (TRAORÉ et al. 2008b). Moreover, not only mortality, but also species-specific biomass gain should be influenced by density as well as other mound-mediated factors. Unfortunately, in our dataset, the analysis of basal area gain as a biomass proxy was impeded. Continuous diameter measurements could only be conducted for one third of the 859 sampled individuals, due to high turnover rates and die-back of juveniles. Only four woody species were present both at more than four plots and at all four samplings, but not necessarily with the same individuals. In combination with low overall frequency and abundance of each species, this hampered an adequate testing of our hypothesis. Currently available experimental research indicates that differences in soil nutrients between mound and savanna influence neither the number of seedlings nor the growth rates of selected species (MULLER & WARD 2013). However, the experiment was performed under greenhouse conditions, and soil handling might have influenced the outcome. An experimental study of two herbaceous model species found that in situ biomass gain was higher on mounds than in the surrounding savanna, while biomass gain was higher on potted savanna soil than handled mound soil, presumably due to soil handling (GROHMANN 2010). However, experimental research in situ is highly challenging: in an experimental approach run simultaneously to our survey presented in this study, less than 1 % of all germinated seedlings ($N = 1000$) in a random block design with in situ and ex situ replicates survived long enough to obtain biomass measurements. As population dynamics on mounds and their impact on plant growth and survival of seedlings and saplings remain poorly understood, further research focussing on juvenile plants is desperately needed.

Regarding dispersal modes, we found that animal-dispersed species were overrepresented in the communities of juvenile woody plants on mounds, as predicted (Fig. 5, Table 4). In contrast, we did not detect differences in the proportion of wind-dispersed species and species with a mixed dispersal mode. It has been shown that protection from fire can lead to a prevalence of animal-dispersed colonisers in a savanna landscape (SWAINE et al. 1992), and the importance of termite mounds as refugia from severe fire has recently been emphasised (TRAORÉ et al. 2008a, JOSEPH et al. 2013b). Based on these findings, we would, however, expect a stronger effect of mounds as more fire-protected habitats on seedling mortality than was found in our study. We therefore suggest that directed dispersal by animals is a driving force behind the higher number of individuals and species, and also lower evenness on mounds. Due to the high structural complexity of mounds, they are attractive to animals already in an unvegetated stage. After establishment of woody plants, attractiveness should be increased through the high structural complexity of mound vegetation, which has been shown to harbour a large proportion of species with a climbing and scrambling habitus, and higher vegetation density (MOE et al. 2009, ERPENBACH et al. 2013). Such structural complexity can provide shelter, thermoregulation, roosting and nesting sites, and more heterogeneous food resources (LAWTON 1983). The resulting high attractiveness of mounds has

been shown for various taxa (FLEMING & LOVERIDGE 2003, MOE et al. 2009, BRODY et al. 2010, GARDEN et al. 2010, JOSEPH et al. 2011; but see also van der PLAS et al. 2013). Thus, structural complexity of mounds and mound vegetation can potentially lead to higher input of animal-dispersed diaspores, leading to higher dominance of some well-dispersed species and higher individual density, but also to higher species richness than in the surrounding savanna. Animal-dispersed species are often thought to have better long-distance dispersal ability than wind-dispersed species (HOVESTADT et al. 1999, HOVESTADT et al. 2005). Considering that some species often found on mounds, e.g. *Diospyros mespiliformis*, also typically occur in gallery forests and forest islands within the savanna habitat (HOVESTADT et al. 1999), the mound microhabitat could be considered an important stepping stone for populations of these otherwise spatially disconnected habitats.

Further long-term studies are needed to understand population dynamics on mounds and surrounding savanna habitats in more detail. Still, the outcomes of our study and of previous research emphasize that termite mounds represent crucial habitats for both plant and animal species and provide essential contributions to spatial structure and complexity in savanna systems.

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APPENDIX

Appendix Table S1: List of juvenile woody species found on mounds and savannas over the whole sampling period.

Family	Species	mound	savanna
Anacardiaceae	<i>Lannea acida</i>	+	+
Anacardiaceae	<i>Ozoroa insignis</i>	+	
Annonaceae	<i>Annona senegalensis</i>	+	+
Bignoniaceae	<i>Stereospermum kunthianum</i>	+	+
Bombacaceae	<i>Bombax costatum</i>	+	+
Caesalpiniaceae	<i>Afzelia africana</i>	+	
Caesalpiniaceae	<i>Burkea africana</i>	+	+
Caesalpiniaceae	<i>Cassia sieberiana</i>	+	
Caesalpiniaceae	<i>Detarium microcarpum</i>	+	+
Caesalpiniaceae	<i>Piliostigma thonningii</i>	+	+
Caesalpiniaceae	<i>Tamarindus indica</i>	+	
Celastraceae	<i>Gymnosporia senegalensis</i>	+	+
Combretaceae	<i>Anogeissus leiocarpa</i>	+	
Combretaceae	<i>Combretum adenogonium</i>	+	+
Combretaceae	<i>Combretum collinum</i>	+	+
Combretaceae	<i>Combretum glutinosum</i>	+	+
Combretaceae	<i>Combretum molle</i>	+	+
Combretaceae	<i>Combretum nigricans</i>	+	+
Combretaceae	<i>Guiera senegalensis</i>		+
Combretaceae	<i>Pteleopsis suberosa</i>		+
Combretaceae	<i>Terminalia avicennioides</i>	+	+
Combretaceae	<i>Terminalia laxiflora</i>		+
Ebenaceae	<i>Diospyros mespiliformis</i>	+	
Euphorbiaceae	<i>Bridelia ferruginea</i>	+	+
Euphorbiaceae	<i>Flueggea virosa</i>	+	
Fabaceae	<i>Pericopsis laxiflora</i>	+	
Fabaceae	<i>Philenoptera laxiflora</i>	+	+
Fabaceae	<i>Pterocarpus erinaceus</i>	+	+
Fabaceae	<i>Xeroderris stuhlmannii</i>		+
Loganiaceae	<i>Strychnos innocua</i>		+
Loganiaceae	<i>Strychnos spinosa</i>	+	+
Malvaceae	<i>Cienfuegosia heteroclada</i>	+	
Meliaceae	<i>Pseudocedrela kotschy</i>	+	+
Meliaceae	<i>Trichilia emetica</i>	+	+
Mimosaceae	<i>Acacia dudgeonii</i>	+	
Mimosaceae	<i>Acacia gourmaensis</i>	+	+

Family	Species	mound	savanna
Mimosaceae	<i>Acacia hockii</i>	+	+
Mimosaceae	<i>Dichrostachys cinerea</i>	+	
Mimosaceae	<i>Prosopis africana</i>		+
Moraceae	<i>Ficus sur</i>	+	
Olacaceae	<i>Ximenia americana</i>	+	+
Polygalaceae	<i>Securidaca longepedunculata</i>		+
Rubiaceae	<i>Crossopteryx febrifuga</i>	+	+
Rubiaceae	<i>Fadogia cienkowskii</i>		+
Rubiaceae	<i>Feretia apodanthera</i>	+	
Rubiaceae	<i>Gardenia aqualla</i>	+	
Rubiaceae	<i>Gardenia erubescens</i>	+	+
Rubiaceae	<i>Gardenia ternifolia</i>	+	+
Rutaceae	<i>Clausena anisata</i>	+	
Rutaceae	<i>Zanthoxylum zanthoxyloides</i>	+	
Sapotaceae	<i>Vitellaria paradoxa</i>	+	+
Simaroubaceae	<i>Quassia undulata</i>	+	
Sterculiaceae	<i>Dombeya quinqueseta</i>	+	+
Sterculiaceae	<i>Sterculia setigera</i>	+	
Tiliaceae	<i>Grewia lasiodiscus</i>	+	
Tiliaceae	<i>Grewia mollis</i>	+	+
Verbenaceae	<i>Vitex madiensis</i>	+	
Zygophyllaceae	<i>Balanites aegyptiaca</i>	+	+