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Effect of vegetation encroachment on *Macrotermes subhyalinus* (Rambur) activity and associated mound vegetation, in Lake Mburo National Park, Uganda

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ABSTRACT

Termites play a key-role in the savanna ecosystem. As primary producers and decomposers, they transport soil nutrients vertically and horizontally, creating a more heterogeneous landscape. Increased canopy cover will shade termite mounds and potentially disrupt the fine-tuned thermo-regulated central parts of the termite nests. In this study, I assessed the effect of woody encroachment in Lake Mburo National Park, Uganda on *Macrotermes subhyalinus* (Rambur) termites. I tested if mound activity and density, and if woody vegetation on termite mounds differed between the vegetation communities; natural, woody encroached and cleared (previously woody) savanna. Data was collected from 105 randomly located mounds (sites) in 15 areas. On each mound tree species, tree height, basal diameter (0.3 m), and diameter at breast height (1.3 m) was recorded. In addition to the random mounds, the five closest surrounding mounds were also checked for activity, giving a total of 612 surveyed mounds. All the mounds within a 40 m radius were counted for density measures, 967 mounds was recorded at the 105 sites. In total, I recorded 47 species comprising 1721 individual trees. Woody encroached and cleared areas had significantly lower proportions of active mounds than natural savanna areas, although, regardless of vegetation community, the abundance of *M. subhyalinus* was extremely low, with only 26 active mounds. The density of mounds (ha^{-1}) was higher in the woody encroached areas (22.52 ± 6.6 SD) than in natural savanna (14.95 ± 7.37 SD) and cleared areas (16.47 ± 6.37 SD). The richness of woody vegetation on mounds was significantly higher in the natural savanna (9.4 ± 4.01 SD), than in woody encroached (6.8 ± 3.98 SD) and cleared areas (5.4 ± 2.96 SD). The evenness and diversity of woody vegetation on mounds was highest in natural savanna areas, but not significantly higher than in woody encroached and cleared areas. Mounds in cleared areas had more trees lower than 1.3 m in height than both mounds in woody encroached and natural savanna areas, while mounds in woody encroached areas had higher abundance of trees above 1.3 m in height, than mounds in cleared and natural savanna areas. Woody encroached and cleared areas had species abundance curves levelling around 30 species, while natural savanna areas had a species accumulation curve that did not level. Due to the overall low abundance of active mounds, regardless of woody vegetation cover, I concluded that other factors might cause the substantial overall decline of active termite mounds in Lake Mburo National Park.

SAMMENDRAG

Termitter har en nøkkelrolle i et savanne-økosystem, der de er primærprodusenter og nedbrytere. De transporterer næringen i jorden og lager dermed et mer heterogent landskap. Fortetting av vegetasjonen vil gi økt skygge på termittuene og potensielt forstyrre de sensitive thermo-regulerte delene inne i tuene. Denne oppgaven ser på hvilke effekter fortetting av vegetasjonen i Lake Mburo National Park i Uganda har på andel av aktive tuer, og tettheten av tuer fra arten *Macrotermes subhyalinus* (Rambur). Jeg testet om aktiviteten, tettheten og tredekke på termitt-tuer var forskjellige i tre forskjellige vegetasjonstyper; naturlig savanne, gjengrodd savanne og ryddet (tidligere gjengrodd) savanne. I alt ble det samlet inn data fra 105 tilfeldig valgte tuer (sites), i 15 områder. På hver tue ble hvilken art, høyden på treet, bakkediameter (0.3 m) og diameter i bryst høyde (1.3 m) registrert. I tillegg til den tilfeldige tuen, ble de fem nærmeste tuene også sjekket for aktivitet. Totalt ble 612 tuer sjekket. Alle tuer innenfor en 40 m radius rundt den tilfeldige tuen ble telt for å se tettheten av tuer. 967 tuer ble telt i de 105 sitene. Totalt ble 1721 trær registret, fordelt på 47 arter. Gjengrodd og ryddet savanne hadde signifikant lavere andel aktive tuer enn naturlig savanne områder. Likevel var den totale andelen aktive *M. subhyalinus* tuer, uavhengig av vegetasjonstypen, ekstremt lav, med kun 26 registrerte aktive tuer. Tettheten av tuer per ha^{-1} var høyere i gjengrodd savanne (22.52 ± 6.6 SD) enn i naturlig (14.95 ± 7.37 SD) og ryddet savanne (16.47 ± 6.37 SD). Variasjonen av trær var signifikant høyere på den naturlige savannen (9.4 ± 4.01 SD), enn i gjengrodd (6.8 ± 3.98 SD) og ryddet savanne (5.4 ± 2.96 SD). Jevnheten og diversiteten av trær var høyest på den naturlige savannen, men ikke signifikant høyere enn i gjengrodd og ryddet savanne. Flere trær lavere enn 1.3 m ble funnet på tuer i ryddet savanne enn på tuer i både naturlig og gjengrodd savanne, mens tuer i gjengrodd savanne hadde høyere forekomst av trær over 1.3 m enn tuer i naturlig og ryddet savanne. Antall arter funnet i alle vegetasjonstypene var rundt 30, men en artsrikhets-kurve viste at antall arter observert på den naturlige savannen fortsatt var stigende. På grunn av den lave andelen av aktive termitt-tuer, uavhengig av vegetasjonstype, konkluderte jeg med at andre faktorer i tillegg til økt vegetasjonsdekke er grunnen til nedgangen i aktive termitt-tuer i Lake Mburo National Park.

CONTENTS

INTRODUCTION

Termites are the most important decomposers in tropical ecosystems, and responsible for up to 80 % of the decomposition in dry tropical landscapes (Mando & Brussaard 1999), like the grassland savanna. The termite genera *Macrotermes* (family *Termitidae*; subfamily *Macrotermitinae*) are ecosystem-engineers in the African savanna, as they construct mounds that contribute to savanna heterogeneity, with several microhabitats, like habitats for birds and rodents (Joseph et al. 2011; Okullo et al. 2013; Sileshi et al. 2010). They also play a major role in nutrient flow and decomposition of organic matter in the soil (Jouquet et al. 2011; Weir 1973), meaning they restructure the soil, which in turn influences soil infiltration and run-off (Jouquet et al. 2011)

A study conducted by Mando and Brussaard (1999) showed that plant cover was higher in savanna areas with termites. Moe et al. (2009) found that the number of woody species on *Macrotermes* mounds was four times higher than savanna areas, and in addition, the plant density was greater on the mounds. The *Macrotermes* do not thrive as well in forest or woodland as they do in the open savanna (Korb & Linsenmair 2001). A study from Mabira Forest Reserve, Uganda, showed that *Macrotermitinae* increased their abundance nine-fold after the forest was cleared (Okwakol 2000). Different species of termites are affected differently by clearing, and Okwakol (2000) found that both *Apicotermitinae, Termitinae and Macrotermitinae* increased their abundance after forest clearing, while *Nasutittermitinae* decreased. When clearing areas, some species, particularly those that are dependent on dead or live wood for food, like species within the subfamily *Macrotermitinae*, will be directly affected by the disturbance (Okwakol 2000). Korb and Linsenmair (1999) found *Macrotermes bellicosus* living in forest areas in the Ivory Coast had a lower fitness than termites in open areas. This may indicate that termites relocate if their current nest becomes shaded by dense vegetation. Pomeroy (2005) found that when termite-colonies relocate the survival rate after two years when building a new mound was 63%, while colonies that occupy an old mound had a survival rate of 92% after two years.

Trees commonly invade grassland savanna, turning it into woodlands (Parr et al. 2012). The main reasons is the change in CO_2-concentrations in the atmosphere and reduced fire frequency. Most tropical grasses have C_4-photosynesis, while most tropical trees have C_3-photosyntesis. High temperature and low CO_2-levels favour C_4- grasses, while high temperature and high CO_2-consentrations favour C_3-grasses and trees (Higgins & Scheiter 2012; Parr et al.

2014). When the change from savanna grassland to woodland has begun, it will escalade as the reduction of C4-grasses decrease the flammability of the area, which in turn favours the C_3-plants (Hoffmann et al. 2012; Parr et al. 2012). Termites are resilient to both seasonal and frequency fires, and woody species on termite mounds are far less damaged by fire compared to woody species off mounds (Davies et al. 2012; Joseph et al. 2013). However, woody encroachment will affect the ground temperature and thereby the temperature inside the mounds. *Macrotermes* spp. cultivates a fungus of the genus *Termitomyce* inside their nest, this fungus act as an important food-source (Heim 1941; Korb & Linsenmair 1999b). However, changes in temperature and CO_2-consentrationas will lower the metabolism of the fungi (Korb & Linsenmair 1999b). The problem of woody encroachment of savanna areas has been observed in Lake Mburo National Park, in Uganda.

The overall goal of this study was to assess effects of increased woody vegetation on *Macrotermes subhyalinus* (Rambur) density and to study if the woody vegetation on termite mounds differed between open, densely wooded and cleared (previously densely wooded) savanna. The specific objectives were to: 1) relate the status (active/inactive) of mounds with the tree density on mounds, 2) assess the relationship between woody vegetation density and termite mound density, and 3) study effects of increased woody cover on richness, evenness and diversity of trees on termite mounds.

As guiding hypotheses I predicted that; 1) the proportion of active mounds would be highest in natural savanna areas followed by cleared and woody encroached areas, as an earlier study by Korb and Linsenmair (1998) showed that open areas with high temperature on the ground are more suitable for the *M. bellicosus* species; 2) the proportion of mounds would be highest in natural savanna areas, followed by cleared and woody encroached areas, because dry and sun exposed areas are optimal habitats for *Macrotermes* species (Korb & Linsenmair 2001); and 3) that the species richness, evenness and diversity of trees on mounds would be highest in the natural savanna areas, followed by the woody encroached and the cleared areas.

METHODS

Study area

The study area is located in Lake Mburo National Park, in southwest Uganda (0^{0} 36’ 0”S, 30^{0} 57’ 0”). The park is ~260 km^{2}, and a part of the Akagera ecosystem, that stretches from Rwanda and Tanzania in the south to the Katonga River in Uganda. It lies in the rain shadow between Lake Victoria Basin and the Rwenzori Mountains, and with two distinct rainy seasons it receives 750-800 mm of rain annually (Blösch 2008). October and February are wet, while July and August are dry. The day temperature varies from 21.5 to 34^{o}C, with an average temperature of 27.5^{o}C (Blösch 2002). The park has an elevation between 1220 and 1450 m a.s.l. Soil types found in the park are Ferralsol, Histosol, Vertisol, and Leptosol (Blösch 2002).

Lake Mburo National Park consist of natural savanna areas with thickets, grassland and woodland (Blösch 2008; Langdale Brown et al. 1964). Some savanna areas are now turning into woodland areas, dominated by *Acacia hockii*. Several factors may have contributed to the increased densities of trees. Before the national park was established, pastoral people lived in the park and used it for domestic cattle grazing (Emerton 1999). Reduced grazing pressure together with long-time absence of megaherbivores such as elephants can also be part of the reason. Change in climatic conditions might also be a factor. To open the dense *A. hockii* vegetation, the park staff are clearing some of these woody encroached areas by cutting and/or burning vegetation. The cleared areas are around 300 m wide and 700-1000 m long, primarily along park roads (Patrick Rubagyema, Warden of research and monitoring in Lake Mburo National Park, Pers. comm. July 2015).

The dominating woody species on the termitaria is *Grewia* sp., *Maytenus heterophylla* and *Rhus natalensis* (Moe et al. 2009). Dominating graminoides on termitaria are *Sporobolus pyramidalis* and *Themeda triandra,* and dominating forbs are *Psilotricbum axilliflorum,* and *Commelina* sp. In savanna areas dominating woody species are *Dichrostachys cinerea, Acacia sieberiana, Solanum incanum* and *Acacia gerrardii.* Dominating graminiodes are *Temeda triandra* and *Sporobolus staphianus*, and dominating forbs are *Ocimum gratissimum, Bidens grantii* and *Asparagus flagellaris* (Moe et al. 2009).

The *Macrotermes* collect organic components from outside the mound, process the components and deposit it on the fungus comb (Badertscher et al. 1983; Heim 1941). The fungi decompose the material, making the fungal tissue rich in nitrogen, phosphorus and potassium, the termites then feeds on this tissue (Jones et al. 1994). This is a mutualistic relationship, as *Macrotermes* cannot break down cellulose, and the fungi depend on the termites to bring the components from the surface (Rouland-Lefevre et al. 2002; Schuurman 2005). For the metabolism of the fungi to be optimal the temperature inside the mound has to be stable at 30ºC, the *Macrotermes* therefore has complex thermoregulatory mechanisms in their mound (Korb & Linsenmair 1999b; Weir 1973). The species studied in this thesis is *M. subhyalinus* (David Bignell, pers. comm. March 2016). Previously the species has been identified as *Macrotermes herus* (Bakuneeta 1989). Termite systematics has not been revised since the 1970s, and because *M. herus* and *M. subhyalinus* are similar, it may be that they should be classified as one species (D. Bignell, pers. comm.).

In the park more than 300 species of birds and 68 mammals (Averbeck 2002) have been recorded. The most common herbivore is the impala (*Aepyceros melampus*), and Lake Mburo is the only locality where impala is found in Uganda. Other common herbivores are Burchell's zebra (*Equus burchelli*), waterbuck (*Kobus ellipsiprymnus*), warthog (*Phacochoerus africanus*), African buffalo (*Syncerus caffer*), eland (*Taurotragus oryx*) and bushbuck (*Tragelaphus scriptus*). The herbivore biomass in the park has been estimated to be 89 kg ha^{-1} (Rannestad et al. 2006)

Data collection

Data was collected from June to September 2015. Mounds were recorded in 15 different areas. Three different vegetation communities were studied (natural savanna, woody encroached and cleared areas). The cleared areas had been cut and burned within the last 3-5 years. Six woody encroached areas, six cleared areas, and three natural savanna areas was used in the study. In each area, vegetation was recorded on seven random mounds (i.e. on 105 mounds). To locate the random mounds I selected a random distance (between 90 and 150 m) and walked in a random direction for the given distance, the closest mound to the end point was selected. The random mounds had to meet some size criteria, to ensure the *M. subhyalinus* created the mound and that the mound had tree vegetation. The mounds size criteria was set to be minimum 0.5 m tall, and two meter in diameter. Data recorded for each mound was diameter (maximum distance across the mound), height and GPS-coordinates. On all the randomly chosen mounds, trees within one meter from where the mound levelled was recorded. Variables recorded for each tree was species, tree height, basal diameter (0.3 m) and diameter on breast height (1.3 m).

Trees below 0.3 m was recorded only as present cover. In total, I recorded 47 species comprising 1721 individual trees. All the randomly chosen mounds were checked for activity by drilling a 50 cm deep hole into the mound. The mounds were marked, and re-located and checked after six days. If the hole was covered by new constructions, it was set as active. If the hole was still present, the mound was recorded as inactive. Mounds were drilled even if it had visible new constructions, to control the method worked. On all mounds with visible new constructions, the hole was always covered when checked after six days. In addition to the random mounds, all mounds within a circle with 40 m radius (termed site) around the randomly chosen mound were counted and surveyed for activity. In total 976 mounds were counted in 105 sites. Relascope measures, 15 m from the random mound was recorded. Four measures (south, north, west and east) at each mound.

Statistical analysis

The statistical analysis was conducted using the program R version 3.2.3 for Windows. Since only a few of the recorded mounds were active I used a Fisher-Exact test to test for differences between active mounds in the three community types (natural savanna, woody encroached, and cleared). For the density data a general linear regression model (GLM) was fitted with the function “allEffects” from the R package “effects” (Fox 2003), with family “poisson”, and I used a model with number of mounds as response variable and the vegetation communities as explanatory variables.

Shannon diversity index (Whittaker 1977) was used to estimate the species diversity of each site, and Pielou evenness index (Pielou 1966) was used to estimate evenness. Using a GLM, with vegetation community as explanatory variable, with natural savanna as reference, diversity, richness and evenness indexes were tested. To test the differences within each of these indexes I used a GLM for each, with richness, diversity and evenness as response variables, and stems per mound, volume (m^3), cover type, relascope measures, and two-way interactions as explanatory variables. I used a backwards elimination to select the most parsimonious model. The model for richness was made with the family “poisson”. I used a Spearman Correlation test to test for correlations between the indexes and stems per mound and volume (m^3), within each of the vegetation communities.

For each vegetation community two species abundance curves was made, to see the recruitment of trees (below 1.3 m) growing on mounds, separated from bigger individuals (above 1.3 m).

Using the functions “betadisperser” and “betadriver” in the R package “vegan” (Oksanen *et.al*. 2015), the beta diversity for each of the tree community types was calculated. A Tukey Honest Significant Differences test (Tukey HSD-test) was used to test differences in beta-diversity between the type of vegetation community. The function “fitspecaccum” and a “Lomolino model” in R package “vegan” (Oksanen *et.al*. 2015), was used to create species accumulation curves. I used a Kruskal Wallis H-test and a Dunn’s test as a post hoc test to check for differences in relascope measures between the vegetation communities, and differences in mound sizes (given in m^3) between the vegetation communities (Dunn 1964; Kruskal & Wallis 1952).

RESULTS

Only 26 of the 612 surveyed mounds were active. The mean sizes (m^3) of mounds in natural savanna areas were largest with 96.05 m^3 (± 72.56 SD), cleared areas had 58.60 m^3 (± 88.97 SD), while woody encroached areas had a mean mound size of 25.16 m^3 (± 24.68 SD) (natural savanna vs cleared areas; $P = 0.06$, vs woody encroached areas; $P = 0.002$, Dunn's test). Relascope measures from the vegetation communities showed that woody encroached areas had the highest density of trees with 5.59 $m^2\ ha^{-1}$ (± 1.79 SD), cleared areas had 3.15 $m^2\ ha^{-1}$ (± 1.8 SD) and natural savanna areas 1.97 $m^2\ ha^{-1}$ (± 1.12 SD) (woody encroached areas vs cleared areas; $P < 0.0001$, vs natural areas; $P < 0.0001$, Dunn's test). Mounds in woody encroached areas had high numbers of tall woody stems (above 1.3 m), while natural savanna had the most new seedlings (below 0.3 m). While the number of short trees was similar in all three communities (Table 1).

Table 1: Total number of woody individuals recorded on mounds, divided into height-categories; below 0.3 m**,** between 0.3 m and 1.29 m, and above 1.3 m, within each of the vegetation communities (natural savanna, woody encroached and cleared areas).

Vegetation community	Below 0.3 m	Between 0.3 m and 1.29 m	Above 1.3 m
Natural savanna	146	183	279
Woody encroached	76	185	356
Cleared	112	186	198

Mound activity

Woody encroached and cleared areas had significantly lower proportions of active mounds than natural savanna areas (woody encroached areas; vs natural savanna; $P < 0.0001$, vs cleared areas; $P = 0.004$, Fisher-Exact tests) (Table 2). Combined, woody encroached and cleared areas had a significantly lower proportion of active mounds than natural savanna areas ($P < 0.0001$, Fisher-Exact tests). The proportion of active mounds between woody encroached and cleared areas was not significantly different ($P = 0.38$, Fisher-Exact tests) (Table 2).

Table 2: Differences in proportions of active mounds in natural savanna (14 of 126 active) and woody encroached areas (4 of 252 active), and in cleared areas (8 of 252 active), by Fisher-Exact tests.

Vegetation community	Active/Inactive mounds	*P*- values
Natural savanna ~ woody encroached	14/126 ~ 4/252	$P < 0.0001$
Natural savanna ~ cleared	14/126 ~ 8/252	$P = 0.004$
Natural savanna ~ cleared + woody encroached	14/126 ~ 12/504	$P < 0.0001$
Cleared ~ woody encroached	8/252 ~ 4/252	$P = 0.38$

Mound density

The mean density of termite mounds (ha^{-1}) was higher in woody encroached areas (22.52 ± 6.6 SD) than compared with natural savanna (14.95 ± 7.37 SD) and cleared areas (16.47 ± 6.37 SD) (woody encroached areas; vs natural savanna; $P < 0.0001$, vs cleared areas; $P < 0.0001$, GLM) (Fig. 1, Table 3). Cleared areas were not significantly different from natural savanna areas ($P = 0.15$, GLM) (Fig. 1, Table 3).

Table 3: Estimates of mound density in the different vegetation communities. In model 1 woody encroached is the reference, and natural savanna and cleared explanatory variables. In model 2 natural savanna is the reference, and woody encroached and cleared explanatory variable. H is the mean value of densities (GLM).

Fixed effects	H	Estimate β	SE	*z*	*P*-value
Model 1					
Intercept	-	3.11	0.03	95.8	$P < 0.001$
Natural savanna (vs woody encroached)	14.95	-0.41	0.06	- 6.29	$P < 0.001$
Cleared (vs woody encroached)	16.47	-0.31	0.05	- 6.25	$P < 0.001$
Model 2					
Intercept	-	2.70	0.06	47.93	$P < 0.001$
Woody encroached (vs. natural savanna)	22.52	0.41	0.06	6.29	$P < 0.001$
Cleared (vs natural savanna)	16.47	0.097	0.07	1.43	$P = 0.15$

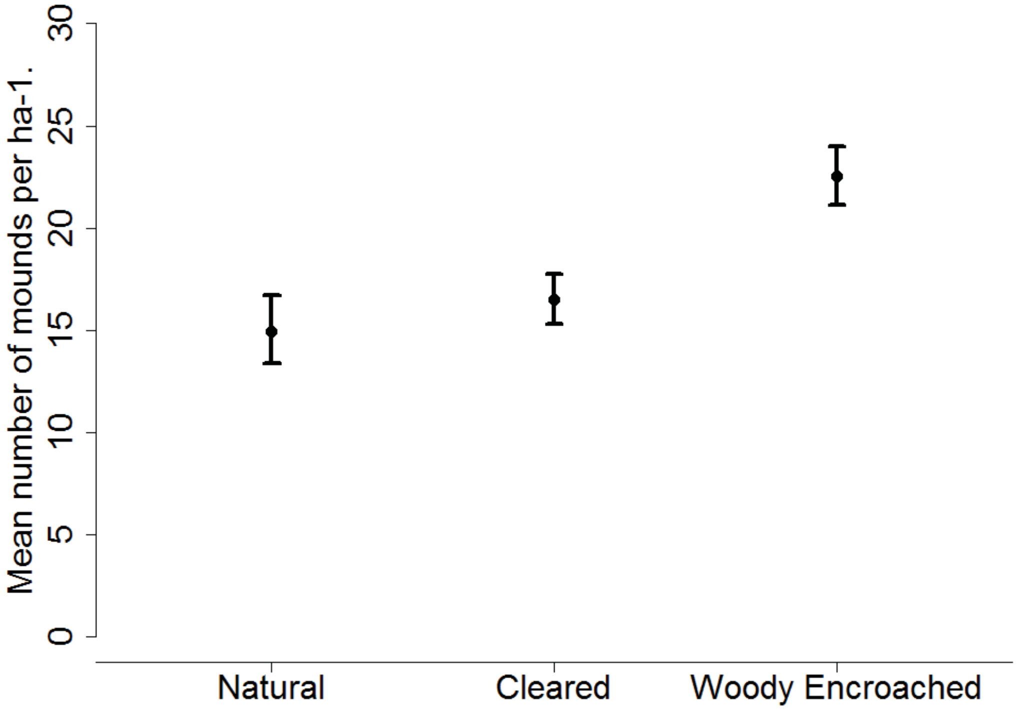

Figure 1: Mean number of mounds per ha^{-1}, in natural savanna (n=157 mounds), cleared savanna (n=346 mounds) and in woody encroached savanna (n=473 mounds). The bars give the 95% CI.

Differences in tree diversity

In total 1721 individual trees and 47 species were recorded. The average species richness per mound in cleared (5.4 ± 2.96 SD) and woody encroached areas (6.8 ± 3.98 SD) was significantly lower than natural savanna areas (9.4 ± 4.01 SD) (natural vs cleared; $P < 0.001$, vs woody encroached; $P = 0.01$, GLM) (Table 4). Natural savanna areas (0.89 ± 0.05 SD) did not have a significantly higher Pielou evenness index than cleared (0.85 ± 0.21 SD) or woody encroached areas (0.83 ± 0.25 SD) (natural vs cleared; $P = 0.51$, vs woody encroached; $P = 0.83$, GLM). The Shannon diversity index was significantly lower in both cleared (1.36 ± 0.54 SD) and woody encroached areas (1.56 ± 0.69 SD), than in natural savanna areas (1.9 ± 0.37 SD) (natural vs cleared; $P < 0.001$, vs woody encroached; $P= 0.03$, GLM) (Table 4).

Table 4: Estimates of Shannon diversity index, richness and Pielou evenness index in the different vegetation communities. In the model, natural savanna is the reference, and cleared and woody encroached explanatory variables. H is the mean values of the indices (GLM).

Fixed effects	H	Estimate β	SE	*t*	*P*-value
Richness					
Intercept	-	9.38	0.79	11.91	< 0.001
Cleared (vs. Nat. sav.)	5.42	-3.95	0.96	-3.096	< 0.001
Woody Encroached (vs. Nat. sav.)	6.83	-2.55	0.96	-2.641	0.0096
Evenness					
Intercept	-	0.89	0.027	32.19	< 0.001
Cleared (vs. Nat. sav.)	0.85	0.02	0.034	-0.66	0.5109
Woody Encroached (vs. Nat. sav.)	0.83	0.007	0.034	0.21	0.8315
Diversity					
Intercept	-	1.90	0.13	15.13	< 0.001
Cleared (vs. Nat. sav.)	1.36	-0.54	0.15	-3.49	< 0.001
Woody Encroached (vs. Nat. sav.)	1.56	-0.35	0.15	-0.24	0.0269

There was a positive correlation between stems per mound and the species richness and diversity in all vegetation communities, while stems per mound did not correlate with evenness in any of the vegetation communities (Fig. 2, Table 5). The correlations between mound volume (m^3) and the species richness and diversity was positive in woody encroached and cleared areas, but not in natural savanna areas. Evenness did not correlate with mound volume (m^3) in any of the vegetation communities (Fig 3, Table 5).

Table 5: Correlation coefficients of richness, Pielou evenness index and Shannon diversity index in the different vegetation communities, with "stems per mound" and "volume (m^3)" as explanatory variables, by Spearman correlation test.

	Stems per mound			Volume (m^3)		
	Natural savanna	Cleared	Woody encroached	Natural savanna	Cleared	Woody encroached
Richness	0.95***	0.86***	0.92***	0.17	0.66***	0.48**
Evenness	- 0.53*	0.07	0.32*	- 0.26	-0.0004	0.29
Diversity	0.82***	0.64***	0.76***	0.06	0.42**	0.51***

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

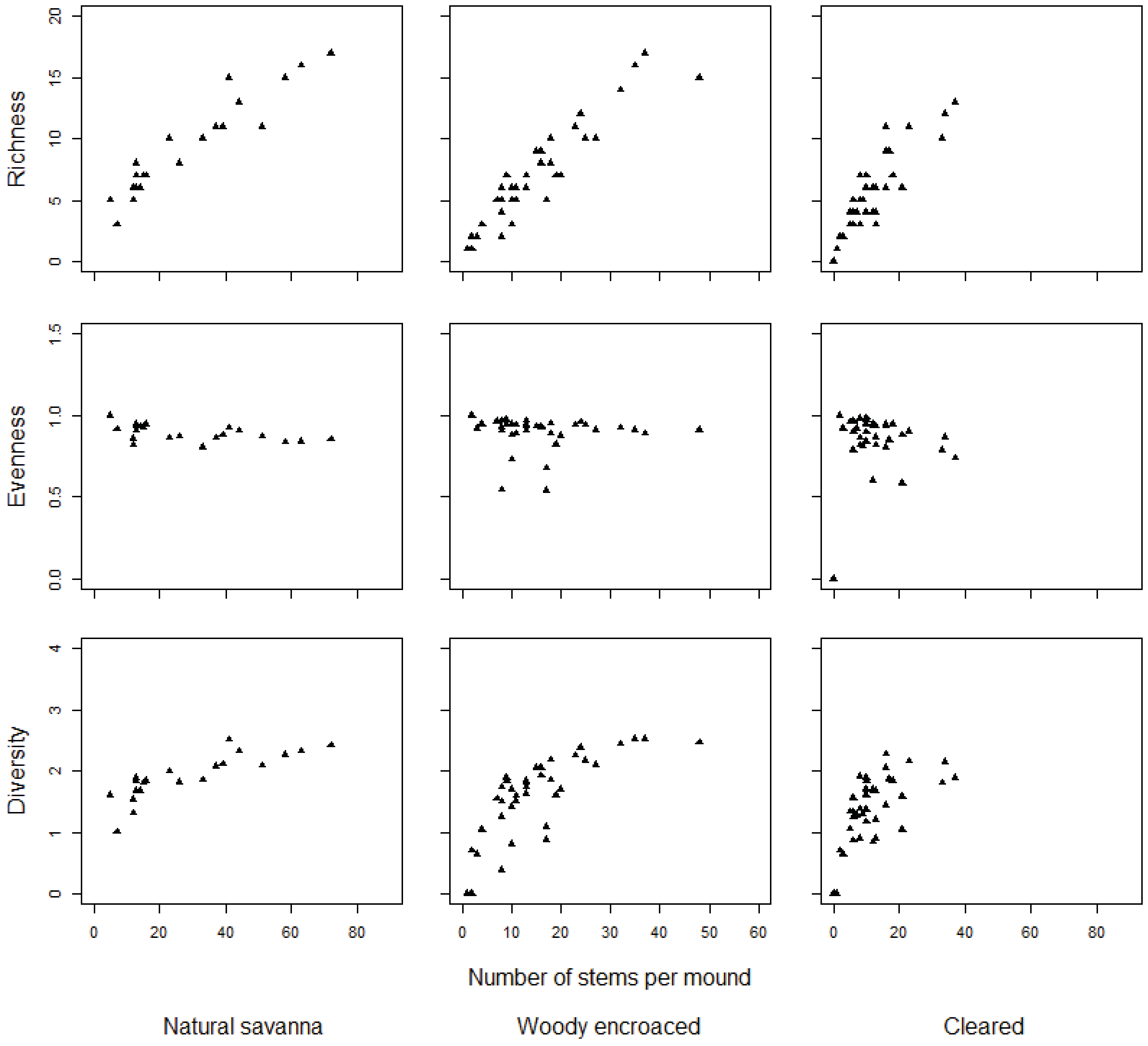

Figure 2: Relationship between species richness, Pielou evenness and Shannon diversity and number of trees recorded on each mound, for each of the three vegetation communities. Natural savanna has 21 sites, woody encroached has 42 and cleared areas has 42 sites.

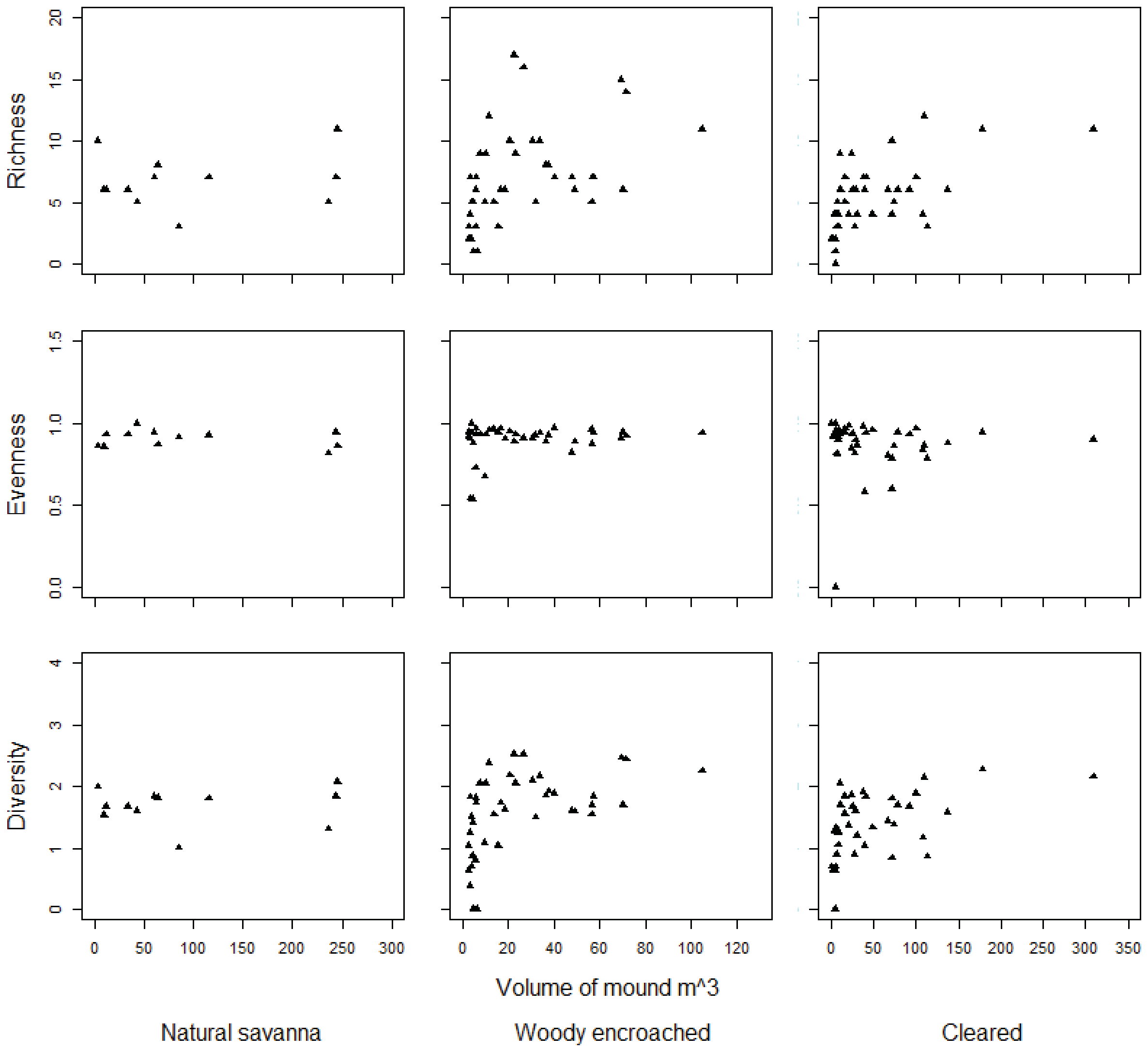

Figure 3: Relationship between species richness, Pielou evenness and Shannon diversity and mound volume (m^3), for each of the three vegetation communities. Natural savanna has 21 sites, woody encroached has 42 and cleared areas has 42 sites.

The accumulation of species levels out at around 30 species on the mounds in woody encroached and cleared areas (Fig. 4). The accumulation of species on mounds was still increasing after the 21 mounds recorded with vegetation in natural savanna areas. The number of different species recorded below 1.3 m on mounds in cleared, woody encroached and natural savanna areas was 20, 29 and 27, respectively. The most frequent species in cleared areas were *A. hockii*, *A. gerrardii* and *M. heterophylla* (Fig. 5a). In woody encroached areas *M. heterophylla*, *Olea Africana* and *R. natalensis* (Fig. 5b) were most frequent, while in natural savanna areas *R. natalensis* and *Scutia myrtina* were most frequent (Fig. 5c). The number of different species recorded above 1.3 m on mounds in cleared, woody encroached and natural savanna areas was 31, 28, and 27, respectively. The most frequent species in cleared areas was *R. natalensis* (Fig. 6a). In woody encroached areas, *M. heterophylla*, *Grewia bicolor*, *R. natalensis* and *Grewia similis* were most frequent (Fig. 6b). In natural savanna areas *S. myrtina*, *G. similis* and *R. natalensis* were the most frequent (Fig. 6c).

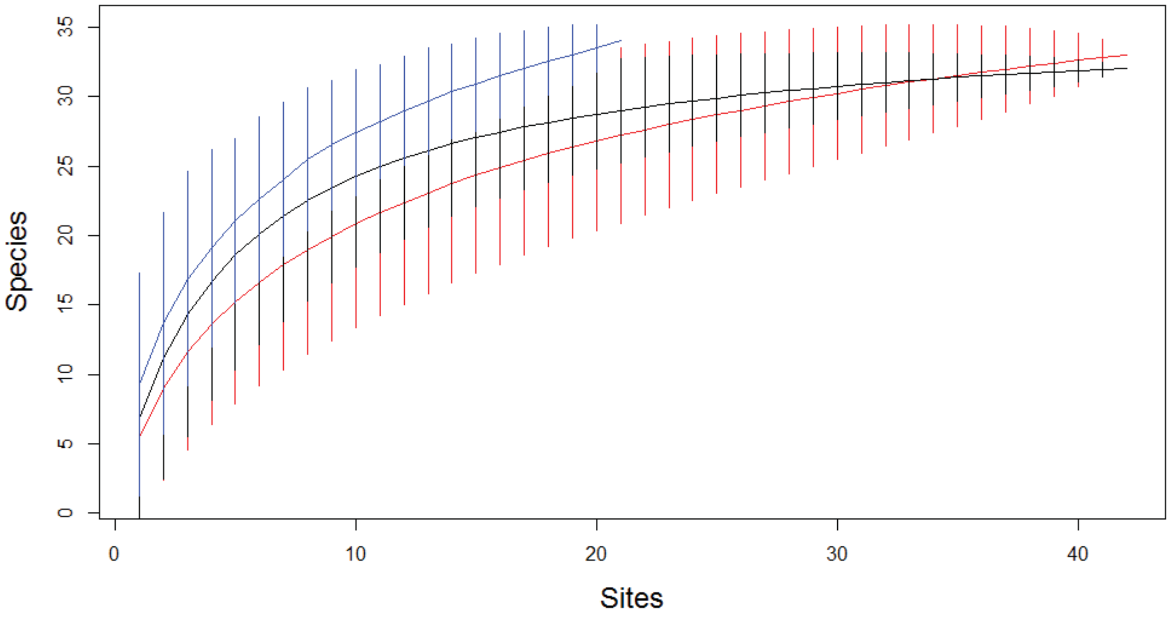

Figure 4: Species accumulation curve for mounds in the vegetation communities. Blue is natural savanna areas (± SE), red is woody encroached areas (± SE), and black is cleared areas (± SE).

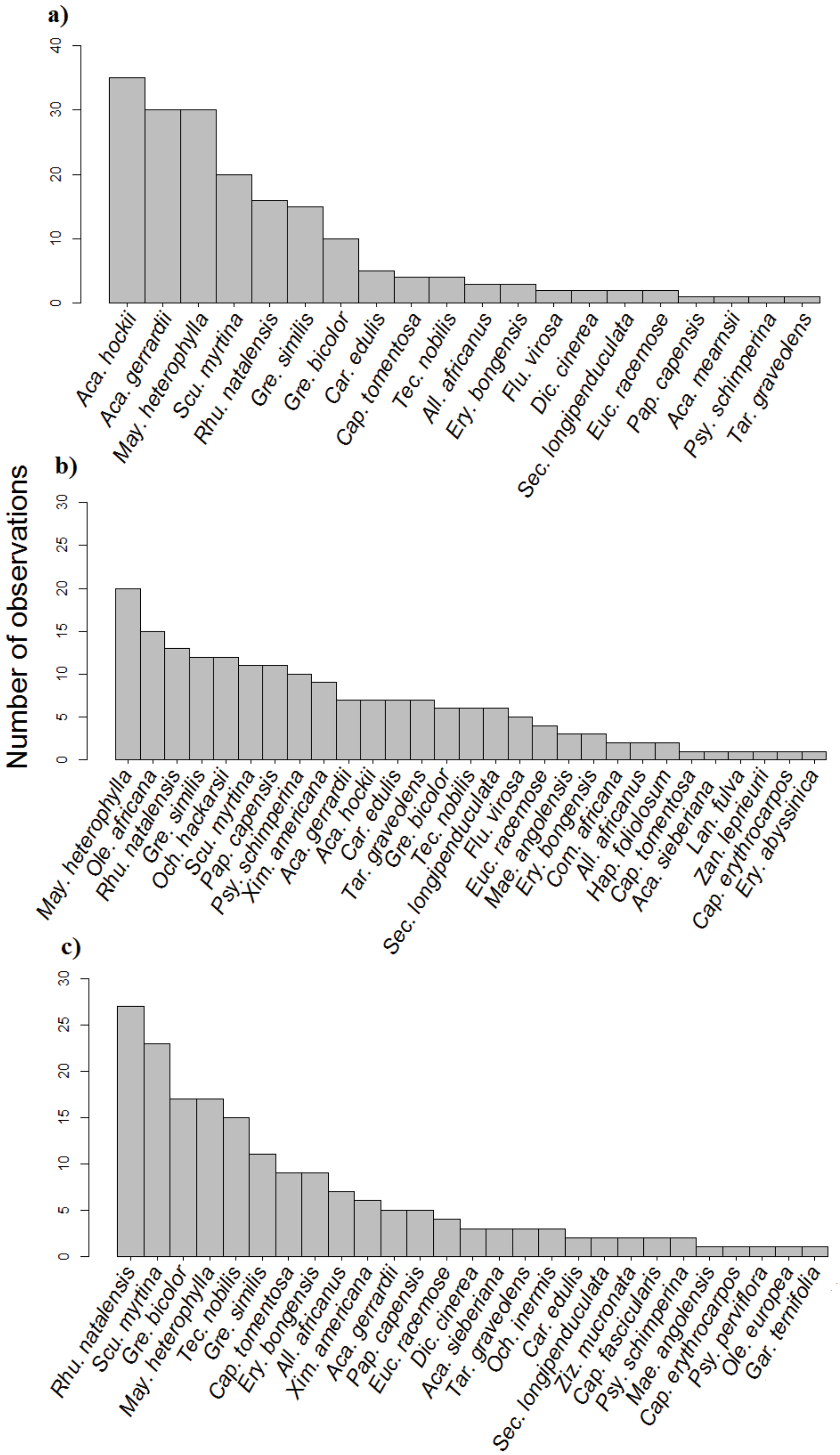

Figure 5: Total number of species recorded on mounds with height below 1.3 m, in the different types of vegetation community (cleared areas (**a**), woody encroached areas (**b**) and natural savanna areas(**c**)).

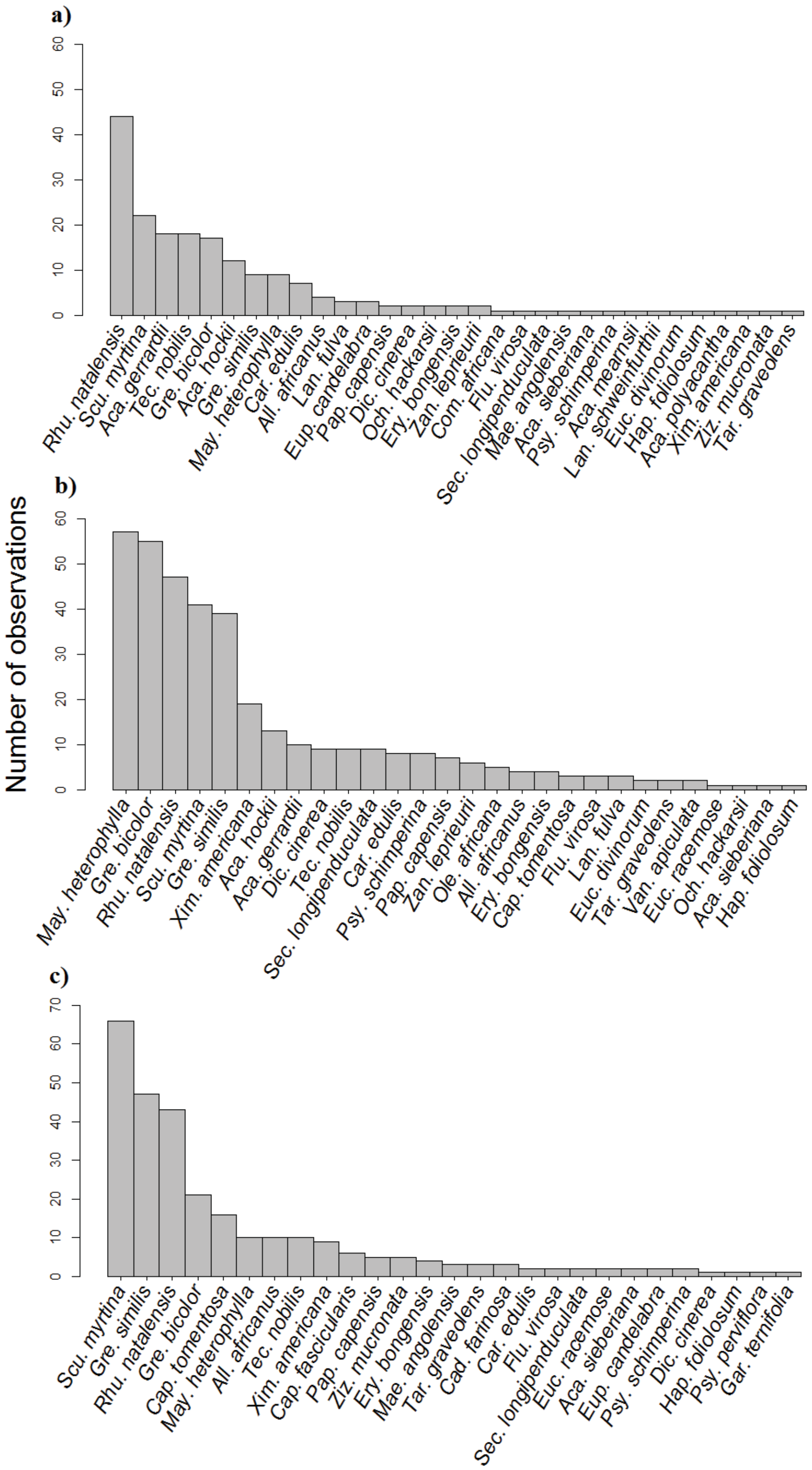

Figure 6: Total number of species recorded on mounds with height above 1.3 m, in the different types of vegetation community (cleared areas (**a**), woody encroached areas (**b**) and natural savanna areas(**c**)).

There were no differences in beta diversity between the mounds in the three vegetation communities (natural savanna vs cleared; *P* = 0.87, vs woody encroached areas; *P* = 0.11, cleared vs woody encroached areas *P* = 0.15, Tukey HSD-tests) (Fig. 7).

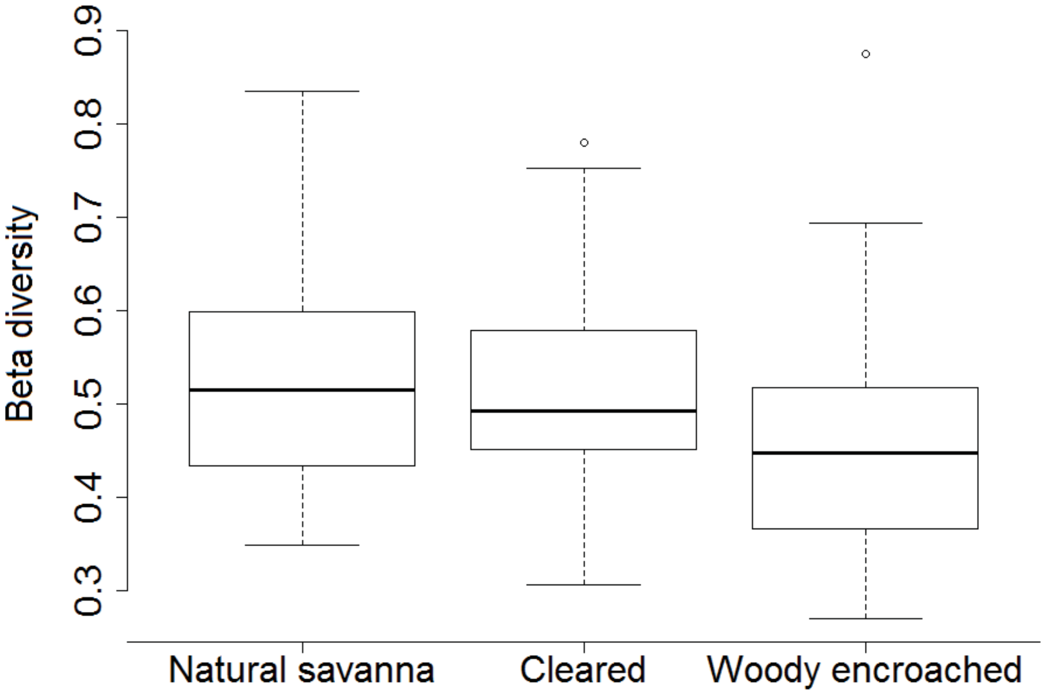

Figure 7: Mean beta-diversity on mounds in natural savanna areas (0.53 ± 0.12 SD), cleared areas (0.51 ± 0.12 SD) and woody encroached areas (0.46 ± 0.13 SD).

DISCUSSION

Regardless of the vegetation communities, very few mounds in this study were active, 14 in natural savanna areas, 4 in woody encroached areas and 8 in cleared areas, meaning only 26 out of 612 mounds were active. The overall density of mounds was significantly higher in woody encroached areas than in both natural savanna and cleared areas. The species richness was higher in the woody encroached areas, than in natural savanna and cleared areas. The species abundance distribution showed that the cleared areas had few species with high dominance, while the natural savanna and woody encroached areas had more species with high abundance. Mounds in the natural savanna and woody encroached areas also had more trees taller than 1.3 m.

As predicted natural savanna areas had most active mounds, followed by cleared and woody encroached areas. Increased woody cover would create less favourable habitats, as woody cover decreases temperature inside the mounds (Korb & Linsenmair 1998). Clearing of woody areas would thus improve the habitats, and give a higher abundance of active termite mounds. Some studies have found that active termite mounds lacked vegetation cover (Pomeroy 2005; Rogers et al. 1999), while Moe et al. (2009) had large and vegetated active mounds in their study. Of all active mounds that was recorded in my study, all but one, had vegetation cover, consisting with what Moe et al. (2009) found. Pomeroy (1977) did a large-scale study covering areas throughout Uganda, and found that 96 of 122 of *M. subhyalinus* mounds was active, and a previous study from Lake Mburo National Park (Glosli 2008) found that close to 50% of mounds examined were active (in natural savanna areas). Several studies have found dramatic declines in termite abundances, Lepage (1984) found that the abundance of *M. bellicosu* had a decrease in active mounds from 14.3 to 0.8 ha^{-1} in just a few years. They found that the decline started with increased aardvark (*Orycteropus afer*) attacks, but escalated over a two-year period (1979-1981) because of attacks from doryline ants. Severe drought and burning of plant material after cutting of fields, and aardvarks was found to be the cause of *M. subhyalinus* declines in Senegal and Kenya (Pomeroy 2005b; Roy-noël 1971). In my study the natural savanna areas had the highest proportion of active mounds, although compared to Glosli's study (2008), who found that 145 out of 310 mounds were active, the proportion of active termite mounds was extremely low. Suggesting other factors then vegetation community are influencing the abundance of active termites, therefor it is not possible to determine if clearing of woody encroached areas are affecting the termite abundance in Lake Mburo

National Park. Suggestions to why termite abundance changes are increased ant attacks and climatic conditions, such as change in precipitation, temperature, CO_2-consentrations and fire (Davies et al. 2014; Korb & Linsenmair 1998; Lepage 1984).

In contrast to the prediction that the proportion of mounds would be highest in natural savanna areas, followed by cleared and woody encroached areas, the result of this study show that woody encroached areas had significantly higher densities, than natural savanna and cleared areas. The density of termite mounds ranged from 14.92 ha^{-1} in savanna areas to 22.52 ha^{-1} in woody encroached areas. Pomeroy (1977) found mound densities of *M. subhyalinus* and *M. bellicosus* in Uganda ranged from 1-4 ha^{-1} and in Kruger National Park in South Africa, a comprehensive study found *Macrotermes* densities of mounds to be 0.46 ha^{-1} (Davies et al. 2014). While one study in the Ivory Coast densities of *M. bellicosus* was measured ranging from 4.0 – 41.7 ha^{-1} (Lepage 1984), another study from the Ivory coast found densities ranging from 11.2 ha^{-1} to as high as 83.3 ha^{-1} (Korb & Linsenmair 1998). These differences in density are caused by a combination of several abiotic factors; underlying geological differences, mean annual precipitation and variation in temperature (Davies et al. 2014; Korb & Linsenmair 1998). Seemingly, mound densities are lower in southern parts of Africa, compared to East and West Africa. Davies et al. (2014) found that termites in open savanna areas had bigger colonies, and therefore had larger distances between mounds, whereas woody areas were sub-optimal, and had shorter distances between mounds, and the mounds themselves were smaller. The mounds I recorded in natural savanna areas were bigger than in woody encroached and cleared areas. However, the density of mounds was lower in natural savanna and cleared areas, compared to woody encroached areas. The high density, but small mounds in the woody encroached areas implies that the termites have a small territory and presumably, their colony is small. Whereas the large but fewer number of mounds in natural savanna indicates a larger territory and colony. Furthermore, it might be that the mounds in natural savanna areas are older, and therefor bigger, than in the two other vegetation communities. The results of my study support Davies et al. (2012) findings, stating that conditions in natural savanna areas are optimal for termites, whereas woody encroached areas are sub-optimal. As termite mounds are abandoned and re-colonised, it is probable to assume that mounds in optimal habitats are re-colonised more often than in sub-optimal habitats.

As predicted, the species richness and diversity was higher in the natural savanna, than in woody encroached and cleared areas. The evenness, however, did not differ between the vegetation communities. Species richness had a strong positive correlation with number of stems per mound and mound volume (m^3) in all vegetation communities. The Shannon diversity index was also highest on mounds in natural savanna areas and had a positive correlation with number of stems per mound and mound volume (m^3) in all vegetation communities. The natural savanna mounds were the most species rich and diverse, followed by the mounds in the woody encroached areas. However, the beta-diversity on mound was not significantly different between any of the vegetation communities. The Pielou evenness index was highest in natural savanna areas, although, it was not significantly higher from either woody encroached and cleared areas. Several studies have found a positive effect of *Macrotermes* on vegetation growth in savanna landscapes (Joseph et al. 2014; Moe et al. 2009; Okullo & Moe 2012b; Støen et al. 2013) and in woodland and forest areas (Axelsson & Andersson 2012; Belyaeva & Tiunov 2010; Korb & Linsenmair 1999; Traoré et al. 2008). The overall species richness is greater in woodland areas than in grassland (Kiyingi et al. 2010). However, when only considering vegetation growing on termite mounds, far more species have been recorded for mounds located in savanna areas compared to mounds in woodlands (Moe et al. 2009; Traoré et al. 2008). In other words, termite mounds in savanna areas have a higher species richness than mounds in woodland areas, even though overall species richness is higher in woodland areas (Moe et al. 2009; Traoré et al. 2008). Overall grazed nutrient-rich areas have higher species richness than areas without grazing (Proulx & Mazumder 1998), this is also found on mounds (Okullo & Moe 2012b). It might be explained by the fact that ungulates prefer to feed on thickets in the savanna (Loveridge & Moe 2004; Mobæk et al. 2005), and assumedly also deposit lots seeds on or close to the mounds. A previous study has found that several ungulates (most of which is observed in Lake Mburo National Park) prefer to stay open areas, or areas with some light vegetation, and avoid areas with denser vegetation (Hirst 1975). It is then reasonable to think that most ungulates in Lake Mburo National Park prefer to stay in natural savanna and cleared areas rather than woody encroached areas, and by feeding on vegetation and deposit seeds on the mounds, contributing to species richness and diversity.

Mounds in woody encroached areas had a high number of trees above 1.3 m, compared to natural savanna and cleared areas. Mounds in cleared areas had a higher amount of seedlings than woody encroached, whereas the highest amount of seedlings was on mounds in natural savanna areas. The total number of species recorded in natural savanna areas did not differ from woody encroached and cleared areas (34, 34 and 33, respectively). However, the species accumulation curve revealed that the curve of natural savanna never levelled, showing that there were still new species recorded at each site. The sample-size of natural savanna areas was half the size of woody encroached and cleared areas. This means that if the sample-size had been the same in all three vegetation communities, I would expect species richness, Pielou evenness and Shannon diversity to be even higher in natural savanna areas, compared to woody encroached and cleared areas.

On mounds in cleared areas *A. hockii, A. gerrardii* and *M. heterophylla* was the most abundant recruitment species below 1.3 m, while *R. natalensis* was the single most dominating species on mounds above 1.3 m, with almost twice as many individuals recorded as the second most dominating. There were few *A. hockii* individuals recorded above 1.3 m, indicating that the species was outcompeted by other species on the mounds. *M. heterophylla* was the most dominating recruitment species on mounds in woody encroached areas. *O. africana* and *Ochna hackarsii* were also frequently recorded as recruitment species in woody encroached areas, but only a few individuals above 1.3 m were recorded. Both species were only recorded in woody encroached areas. *M. heterophylla, G. bicolor, R. natalensis, S. myrtina* and *G. similis* were most dominant among trees above 1.3 m on mounds in woody encroached areas. *G. bicolor* had poor recruitment with few recordings below 1.3 m in the woody encroached areas. In natural savanna areas *R. natalensis, S. myrtina, G. bicolor, M. heterophylla, Teclea nobilis* and *G. similis* were the most dominant species below 1.3 m, while *S. myrtina, G. similis* and *R. natalensis* were most dominating above 1.3 m. *Capparis tomentosa* was recorded frequently as both recruitment and above 1.3 m on mounds in natural savanna areas, while in woody encroached and cleared areas few individuals were recorded and were all below 1.3 m. *R. natalensis* was the overall dominant species on mounds in all vegetation communities and in all sizes. This can be explained by a previous study that found *R. natalensis* to be important in creation, as well as the expansion of thickets (Blösch 2008). Moe et al. (2009) found that the most dominating species on termite mounds in savanna areas in Lake Mburo National Park was *Grewia mollis, G. similis, M. heterophylla* and *R. natalensis*. This mostly consist with my findings, except for *G. mollis*. *Grewia* spp are considered to be a common species with pioneer characteristics (Blösch 2002). Several other *Grewia* spp were found in this study, but *G. mollis* was not found on any sites and seems to have disappeared from the area.

CONCLUSION

Woody encroached areas had a less active mounds then both natural savanna and cleared areas. Although, due to the dramatic decline in abundance of *M. subhyalinus* in Lake Mburo National Park, regardless of the vegetation community, I concluded that other factors than woody cover might affect the disappearance of termites. Termite mounds in woody encroached areas were smaller in volume (m^3), but higher in abundance, compared to natural savanna and cleared areas. This result supports the theory that dense woody vegetation cover makes a sub-optimal habitat for *M. subhyalinus*. The vegetation richness and Shannon diversity index was highest in the natural savanna areas, thus, increase of woody cover leads to a decrease in woody species richness and Shannon diversity index in the savanna.

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