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Influence of termites on the soil seed bank in an African savannah

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Abstract

In savannah ecosystems, termites drive key ecosystem processes, such as primary production through creation of patchiness in soil nutrients availability around their nests. In this study, we evaluated the role of termites in altering the soil seed bank size, an important ecosystem component that has often been overlooked in previous work. Data on above ground vegetation and soil seed bank samples were collected from four microhabitats, that is, the wooded mound, unwooded mound, tree sub-canopy and the open grassland matrix in a protected game reserve in south-central Zimbabwe. The seedling emergence method was then used to identify species present in the soil samples. One-way analysis of variance followed by Tukey's multiple comparison tests was executed to test for significant differences in plant species richness among the four microhabitats. The results indicate that plant species richness was high on wooded termite mound but did not differ between the unwooded and the sub-canopy microhabitats. The open grassland microhabitat had the lowest plant species richness. The influence of termites on the soil seed bank composition was also life form specific. The herb and woody life forms had significantly ($\alpha = 0.05$) higher species richness in the soil seed bank at wooded and unwooded termite mounds when compared to the other two microhabitats. Overall, these results imply that termites alter the soil seed bank and the findings enhance our understanding of the significant role termites play in regulating processes in savannah ecosystems.

Résumé

Dans certains écosystèmes de savane, les termites entraînent des processus clés, telle la production primaire, par la création de taches autour de leurs nids où les nutriments du sol sont accessibles. Dans cette étude, nous avons évalué le rôle des termites dans la modification de la taille de la réserve de semences, une composante importante de l'écosystème qui fut souvent négligée dans les travaux antérieurs. Les données sur la végétation aérienne et des échantillons des stocks de graines dans le sol ont été collectés dans quatre micro-habitats, à savoir une termitière boisée, une autre non boisée, la sous-canopée des arbres et la matrice de prairie ouverte, dans une réserve de faune protégée au centre-sud du Zimbabwe. La méthode par émergence des semis a été utilisée pour identifier les espèces présentes dans les échantillons de sol. L'analyse de la variance à un facteur et des tests de comparaisons multiples de Tukey ont été pratiqués pour tester les différences significatives de la richesse en espèces de plantes entre les quatre micro-habitats. Les résultats montrent que la richesse en espèces végétales était élevée sur les termitières boisées mais ne différait pas entre les habitats situés dans la partie non boisée et sous la canopée. Le micro-habitat de prairie ouverte avait la plus faible richesse en espèces végétales. L'influence des termites sur la composition de la réserve de graines du sol était aussi spécifique de la forme de vie. Les formes de vie herbacées et ligneuses avaient une richesse en espèces significativement plus élevée (α = 0,05) dans les stocks de semences du sol sur les termitières, boisées ou pas, que dans les deux autres micro-habitats. En général, les résultats impliquent que les termites altèrent les stocks de semences du sol. Ils améliorent notre compréhension du rôle significatifs que jouent les termites dans les processus régulateurs d'un écosystème de savane.

KEYWORDS
microhabitats, niche, seed banks, seedling density, termite mounds

1 | INTRODUCTION

Seed demography is an important element in the regeneration niche of plants. Seeds are the basic demographic units of most ecosystems and they play an important role in the perpetuation of these ecosystems (Wilson et al., 1992). Many plant species recruit from seeds in the soil. Seed banks are continually replenished by fresh seed input and they are being depleted. Understanding the processes that alter the soil seed bank size and composition may shed insight about the persistence and fluctuations of plant populations (Thompson & Grime, 1979). In savannah ecosystems, many termites build above ground mounds in addition to regulating key ecosystem processes, such as nutrient cycling and primary production (Diaye, Dupponis, Brauman, & Lepage, 2003). Nests built by termites tend to have higher organic matter content than surrounding areas. This, in turn, creates islands of fertility in a landscape. A gradient of decreasing primary productivity with distance from termite mounds has been recorded across tropical savannahs (Scholes & Archer, 1997).

Increased productivity around mounds may lead to high seed production by plants established there and this may boost the soil seed bank. Because termites are elevated features, they may trap wind-dispersed seeds (Howe, 1977). Further, the high forage quality of mound vegetation tends to attract herbivores that may defecate or release seeds that are attached to their coats and fur while foraging. Therefore, hypothetically termites have the potential to increase the soil seed bank size and alter its diversity. Previous studies have focused mostly on how termites alter the nutrient content of savannah soils (Brossard, Lopez, Lepage, & Leprum, 2007; Lavelle et al., 2006; Semhi, Chaudhuri, Clauer, & Boealin, 2008). Another facet of seed bank studies has focused on using seed bank data for weed management in agricultural societies. However, little research has been done on how termites affect the soil seed bank in savannah ecosystems, yet the soil seed bank plays an important role in the dynamics of plant communities.

Understanding how termite activity influences the structure and dynamics of plant communities in savannah ecosystems is critical considering the significant role these ecosystems play in providing ecosystem goods and services. The savannah ecosystems harbour the largest diversity of mammal herbivores globally. For example, in Africa more than 50% of the total human population depends on savannahs for their sustenance.

Several factors may alter the soil seed bank size and composition. For example, Dostal (2004) found that in a mountain grassland ecosystem, three mound building ant species altered the soil seed bank. The soil seed bank size was lower in mound soils than on the surrounding open grassland plots. Wagner, Poschlod, and Setch (2003) also did a study on soil seed bank to investigate the composition and vertical distribution of soil seed banks on sites ranging from currently managed to long-term abandoned and the results form a restoration point of view. They found that the seed bank of unmanaged areas is greater than that of the managed areas. They implied that human interference in ecosystem management affected soil seeds recruitment. To the best of our knowledge, no study has evaluated whether termites alter the soil seed bank composition in savannah ecosystems.

Termites account for 40%–60% of the soil fauna biomass in tropical ecosystems (Woods & Sands, 1978). They also play an important role in the functioning of savannah ecosystems. It has been estimated that in savannah ecosystems termite biomass ranges from 70 to 110 kg/ha, thus termite biomass is comparable to the biomass of ungulates, 10–80 kg/ha (Ackerman, Texeira, Riha, & Fernandez, 2007). The effects of termites on soil morphology and processes are well known at scales ranging from the catena (Wielemaker, 1984) to entire landscapes. Two major processes of nest building that can be important for soil modification are bioturbation, which involves the mixing and accumulation of soil from different sources and horizons (Nkem, DeBruyn, Grant, & Hulugale, 2000), and the transportation of organic material from the surroundings into the nests as food. Moe, Mobaek, and Narmo (2009) found that in east African savannahs mound building termites contribute to savannah vegetation heterogeneity. They found that both woody and forbs richness were significantly higher on mounds, when compared to open savannah plots. This was attributed to the fact that mound soils are less leached and contain a higher concentration of soil nutrients than the surrounding soils. Similar results were reported in West African savannahs (Semhi et al., 2008).

This study therefore, tests the hypothesis that by creating above ground mounds and increasing soil fertility, plant growth and reproduction around these mounds, termites may trap wind-blown seeds and increase the accumulation of seeds in the seed bank. To refute this hypothesis, we specifically tested whether plant species richness is higher on termite mounds than the surrounding microhabitats and assessed the interaction effect of soil depth and micro habitat on the composition and size of the soil seed bank.

2 | MATERIALS AND METHODS

2.1 | Study sites

The study was conducted at Kyle game reserve. Kyle game reserve is located at latitude 20°11′00 E, longitude 31°01′00 S, in south-eastern Zimbabwe, near Masvingo (Figure 1). It covers about 44 km^2 of land. The climate is subtropical with a mean daily maximum temperature ranging from 21°C in June to 29°C in October. The long-term average rainfall is 365 mm (100-year period: 1906–2006, Masvingo weather station). The vegetation varies from deciduous Miombo bush land thickets to open grasslands (Masocha, 2009).

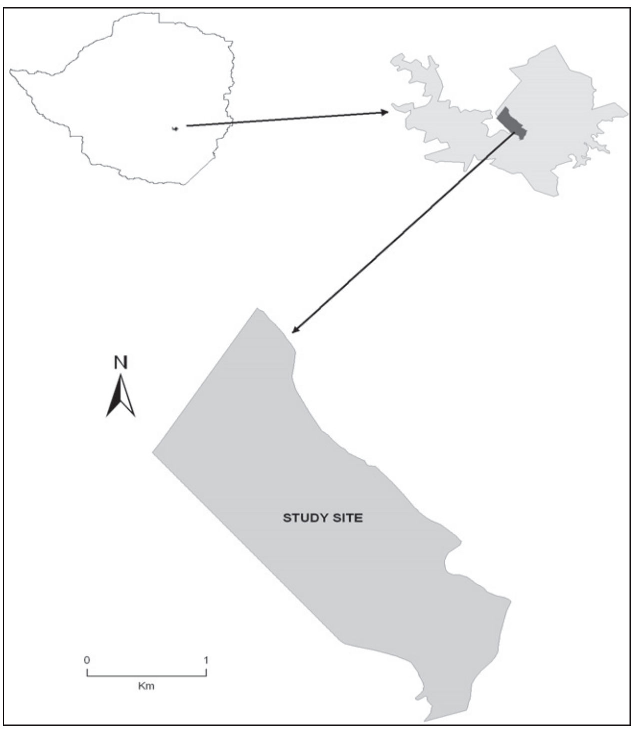

FIGURE 1 Map showing the location of the study site in Kyle Game Reserve, south-central Zimbabwe

2.2 | Vegetation sampling

Vegetation data were collected from four microhabitats located in the western part of the study site where termite activity is pronounced. The microhabitats sampled were (a) unwooded mounds, (b) isolated trees located adjacent to mounds, (c) wooded mounds and (d) open grasslands. To select these microhabitats all unwooded mounds were visited and their coordinates mapped with a hand-held global positioning system receiver. The coordinates were inputted into a computer. A sample of 15 mounds was selected randomly in a spreadsheet. For each unwooded mound selected, the three microhabitats described above were selected provided that they were located at least thirty metres from the unwooded mound and each other. At each microhabitat, above ground vegetation was sampled from circular plots (15 in total). The radius of the unwooded mound was used for all plots. In each plot, the numbers of woody species present and the number of individuals per species were recorded. The composition and density of herbaceous vegetation was recorded from 1-m × 1-m subplots located at the centre and each cardinal point in the larger plot.

2.3 | Soil seed bank sampling

In June 2010, soil seed samples were collected from the same plots after most seeds have been deposited. Soil samples were collected from all five 1-m^2 subplots from which herbaceous plots had been sampled. The samples were collected using an auger with a diameter of thirty centimetres and a depth of 7.5 centimetres. The soil samples were collected at 0-5 cm and 5.1- 20 cm depths, which represent the transient and persistent seeds, respectively. All samples were mixed according to depth and plot to form composite samples.

2.4 | Seedling emergence experiment

Seed bank samples were germinated in a glass house at the University of Zimbabwe and monitored. Germination trays with a diameter of 20 cm on the base, depth of 5 cm and a diameter of 30 cm on the top were used. Each tray was filled with a 2 cm layer of compost soil, followed by a 1 cm layer of river sand so as to separate the seed bank from the compost soil. The seed bank samples were spread in a 10 cm layer on top of river sand. Seed bank samples from the two depths (i.e. 0–5 cm and 5–20 cm) were prepared separately. Trays were placed randomly on benches in the glasshouse. The samples were watered every day with 500 ml of water for 4 weeks. To minimize positional effects, the samples were shuffled randomly every 2 weeks. The number of seedlings that emerged per tray was recorded for the 4 weeks that the experiment ran.

2.5 | Data analysis

One-way analysis of variance (ANOVA) was used to test the research hypothesis that species richness differs significantly among the four microhabitats versus the null hypothesis that the means were the same. Species richness data were log transformed to satisfy the assumption of normality. Where the conclusion from the One-way ANOVA test was that the means were significantly different. We performed post hoc analysis with Tukey's honestly significant difference test to establish which pairs were different. Data on plant species richness were also pooled by habitat and means compared with a paired *t* test. Species data for wooded and unwooded mounds were combined into one sample while data for the sub-canopy and open grassland plots were combined to form the second sample. The data were checked and confirmed to follow normality using Shapiro's Wilk test prior to executing the paired *t* test.

All plant species that emerged in the soil seed bank samples were classified according to life form into grass, sedge, herb and woody categories. Those that could not be identified at emergence were raised in a glasshouse until their life form identity could be confirmed by a senior botanist at the University of Zimbabwe. One-way ANOVA following normality tests was then executed to evaluate whether the influence of termite activity on soil seed bank was life form specific. The research hypothesis tested was that at least one of the means differ versus the null hypothesis was that the means were the same.

3 | RESULTS

3.1 | Variation in plant species richness among microhabitats

The error plots in Figure 2 show variation inplant species richness detected from the soil seed bank samples collected from four microhabitats. The four microhabitats evaluated for the soil seed bank

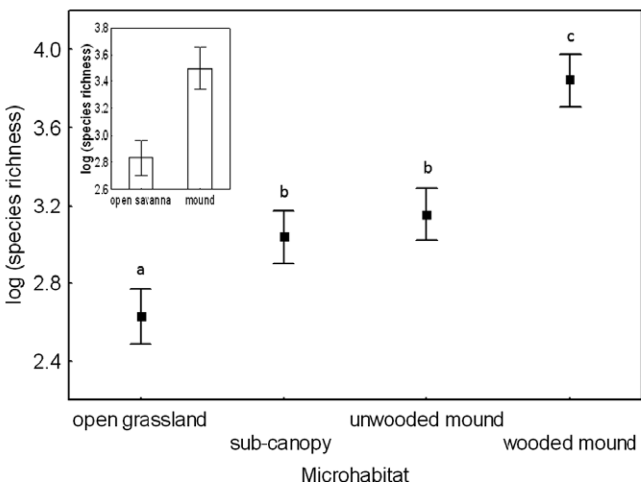

FIGURE 2 Error plots showing variation in mean plant species richness among the open grassland, sub-canopy of trees, unwooded and wooded termite mound r microhabitats in the Kyle Game Reserve of Zimbabwe. Black squares represent means and vertical bars denote 95% confidence intervals. Means with different letters differ significantly at $p < 0.05$ based on Tukey's HSD multiple comparison tests. The inset shows significantly higher plant species richness in soil seed bank samples collected from termite mounds compared to the surrounding open savannah habitats

composition were: wooded termite mounds, unwooded termite mounds, sub-canopy of isolated trees located adjacent to termite mounds, as well as the open grassland matrix. Results of the one-way ANOVA showed that mean plant species richness differed significantly across the four microhabitats ($F_{3,5}$ = 53.7, $p < 0.001$). Further pair-wise comparisons using Tukey's honestly significant difference (HSD) test indicated that plant species richness was highest on wooded termite mounds and lowest in the open grassland microhabitat as shown in Figure 2. However, the mean plant species richness did not differ significantly ($p > 0.05$) between the sub-canopy and unwooded termite mound microhabitats. The error plots in Figure 2 further indicate that while mean plant species richness in these two microhabitats was significantly higher than that of the open grassland microhabitat, it was significantly lower than that of wooded termite mound microhabitat.

When data on plant species richness identified in soil seed bank samples were pooled by habitat type and compared, the results of the paired *t* test showed that the mean plant species richness of termite mound habitats regardless of whether they were wooded or unwooded was significantly higher than that of the open savannah habitat type as depicted in the inset in.

3.2 | Influence of termite activity on species richness of different life forms

Table 1 shows life form specific differences and similarities in the mean plant species richness across the four microhabitats. The data in Table 1 indicate that mean grass species richness was significantly lower at wooded mounds compared to the other three microhabitats. However, results of the post hoc analysis indicated that mean grass species richness did not differ significantly among the open grassland, sub-canopy and unwooded microhabitats. With regard to herbs, data in Table 1 show that mean herb richness did not differ significantly among the wooded and unwooded termite mound microhabitats but was significantly higher at these microhabitats compared to the open grassland and sub-canopy microhabitats. Results of one-way ANOVA followed by post hoc multiple comparisons further revealed that sedge richness was significantly higher at wooded termite mounds but did not differ among the open grassland, unwooded mound and sub-canopy microhabitats. Differences in plant species richness in the soil seed bank were more pronounced when the woody life form was considered. Woody plant species richness was highest in the wooded microhabitat followed by the sub-canopy microhabitat. The open grassland and unwooded mound microhabitats had the lowest mean woody species richness as presented in Table 1.

4 | DISCUSSION

This study evaluated whether termite activity, in particular the building of dome-shaped nests (mounds) which creates spatial heterogeneity in a landscape, alters the soil seed bank composition in a southern African savannah. The results of our seed emergence

TABLE 1 Life form specific variation in mean plant species richness in the soil seed bank among four microhabitats. Data presented are *M* ± 1 *SE*

Life form	Open grassland	Sub-canopy	Unwooded mound	Wooded mound
Grass richness	7.1 ± 0.4[a]	6.8 ± 0.5[a]	7.5 ± 0.8[a]	4.9 ± 0.4[b]
Herb richness	4.5 ± 0.7[a]	5.5 ± 0.6[a]	14.3 ± 0.9[b]	14.9 ± 1.5[b]
Sedge richness	0.7 ± 0.2[a]	0.6 ± 0.2[a]	0.65 ± 0.2[a]	0.9 ± 0.2[b]
Woody richness	2.1 ± 0.5[a]	9.3 ± 1[b]	2.7 ± 0.5[a]	23.9 ± 1.6[c]

Note. Means with different small letters of the English alphabet as superscripts differ significantly at $p < 0.05$ based on Tukey's post hoc multiple comparison tests.

experiment indicate that the diversity of plant species was highest on wooded termite mounds compared to three other adjacent microhabitats, namely unwooded termite mounds, sub-canopy of isolated trees and the open grassland. In our study, the open grassland microhabitat had the lowest diversity of plant species whereas plant diversity did not differ between the unwooded termite mounds and the sub-canopy of scattered trees. Our results from a southern African savannah are in conflict with those of Ackerman et al. (2007) who in his seed bank experiment in the Central Amazonia secondary forests found that the number of seedlings that grew in the termite mound material was lower than the control soil. The lower number of seedlings in the Ackerman et al. (2007) study was attributed to poor conditions for germination in the termite material as well as increased seed predation from the surface of the termite mound. The discrepancy between the results in Ackerman et al. (2007) and the current study could be explained by the fact that the latter focused on seedlings whereas our study targeted viable seeds present in the soil.

While the ecological factors to account for the higher diversity of plant species in soil seed bank samples from termite mounds especially those colonized by woody species were not explored in this study, the higher diversity of plant species at termite microhabitats compared to other microhabitats reported is in line with several other previous results based on vegetation assessments that focused on standing vegetation (Loveridge & Moe, 2004; Spain & Mcivor, 1988). The role of birds in boosting the seed bank size at wooded termite mounds warrants further research for previous work has observed that in savannahs, birds in addition to using woody species as stop-over sites in their flights, often perch and roost in trees that establish on termite mounds (Scholes and Archer, 1997) and as they defecate, these birds likely increase seed input into termite mound material. The surface roughness created by the mound structure itself as well as the structure of woody species established on the mounds is also known to trap wind-dispersed seeds (Howe, 1977) thus overall increasing the diversity of soil seed bank at wooded termite mound microhabitats.

We interpret the result indicating the mean plant species richness of termite mound habitats regardless of whether they were wooded or unwooded was significantly higher than that of the open grassland matrix as additional evidence in support of the assertion that termite activity contributes to the high biodiversity of the soil seed bank. By focusing on viable seeds present in the soil, this study was able to underscore the important role termite mound building activity plays in the regeneration of plant communities through seeds, which is essential for the persistence of plant communities in the savannah ecosystems.

Another important aspect of the results is that the influence of termites on seed bank size is life form specific. The findings of this study clearly indicate that herbs and woody species benefit from termite influence. The mean species richness of sedges and woody species was at least twice as high at termite mounds microhabitat compared to those less impacted by termite activity. From this pattern, one may deduce that termite mounds may provide a refuge for these life form to escape grass competition as well as fire-induced mortality in the open grassland matrix and the sub-canopy habitats as hypothesized previously (Joseph et al., 2011).

5 | CONCLUSION

The aim of this study was to evaluate the influence of termites on the soil seed bank composition in a protected African savannah ecosystem. Based on the seedling emergence experiment conducted, it was found that the mean plant species richness of termite mound habitats–both wooded or unwooded–was significantly higher than that of the open grassland habitat. Two life forms, namely herbs and woody species appear to benefit from termite mound building activity as they were observed to be more diverse in soils of termite origin compared to that collected from open grassland sites. The conclusion that can be drawn from the present study is that termite activity significantly alters the soil seed composition in savannah landscapes.

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