

Woody encroachment slows decomposition and termite activity in an African savanna

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Abstract

Woody encroachment can lead to a complete switch from open habitats to dense thickets, and has the potential to greatly alter the biodiversity and ecological functioning of grassy ecosystems across the globe. Plant litter decomposition is a critical ecosystem process fundamental to nutrient cycling and global carbon dynamics, yet little is known about how woody encroachment might alter this process. We compared grass decay rates of heavily encroached areas with adjacent non-encroached open areas in a semi-arid South African savanna using litterbags that allowed or excluded invertebrates. We also assessed the effect of woody encroachment on termite activity, dominant decomposer organisms in savanna systems. We found a significant reduction in decomposition rates within encroached areas, with litter taking twice as long to decay compared with open savanna areas. Moreover, invertebrates were more influential on grass decomposition in open areas and termite activity was substantially lower in encroached areas, particularly during the dry season when activity levels were reduced to almost zero. Our results suggest that woody encroachment created an unfavourable environment for invertebrates, and termites in particular, leading to decreased decomposition rates in these areas. We provide the first quantification of woody encroachment altering the functioning of African savanna ecosystems through the slowing of aboveground plant decomposition. Woody encroachment is intensifying across the globe, and our results suggest that substantial changes to the carbon balance and biodiversity of grassy biomes could occur.

Introduction

Woody plant cover is increasing in grassy systems around the world, converting once open areas into dense thickets (Asner *et al.*, 2004; Parr *et al.*, 2012; Stevens *et al.*, 2017). African savannas, which cover approximately 13.5 million square kilometres (Riggio *et al.*, 2013), are no exception to this woody encroachment (also known as woody thickening) that has been documented since the early 20th century (Bews, 1917), but has become increasingly prevalent

over the last several decades (Archer *et al.*, 2000; Wigley *et al.*, 2010; O'Connor *et al.*, 2014). While poor land management (e.g. overstocking), changes in land use practices and changes in fire regimes can promote woody encroachment, global drivers such as increased atmospheric concentration of carbon dioxide that favours the growth of C3 woody plants over C4 grasses are also likely to be influential (Archer *et al.*, 1995; Wigley *et al.*, 2010; Stevens *et al.*, 2016).

Initially viewed as a threat to agriculture, woody encroachment occurs across multiple land uses, and in some instances protected areas have had the highest rates of encroachment (Wigley *et al.*, 2010; O'Connor *et al.*, 2014; Stevens *et al.*, 2017). A shift from grass- to woody-dominance in savannas reduces grazing capacity for herbivores, and results in cascading ecosystem effects (Sirami *et al.*, 2009; Eldridge *et al.*, 2011; Parr *et al.*, 2012). The induced ecosystem changes are often highly variable, with effects largely dependent on the species of encroaching woody plant (Eldridge *et al.*, 2011). Nonetheless, woody encroachment affects grassy biomes across the globe, and its prevalence is predicted to intensify in the coming decades (Moncrieff *et al.*, 2014; Stevens *et al.*, 2017). Potential changes to ecosystem function from woody encroachment therefore warrant research attention and understanding, especially given the antiquity, high biodiversity value and carbon sequestration potential of grassy systems (Grace *et al.*, 2006; Bond & Parr, 2010; Parr *et al.*, 2014).

Plant litter decomposition is a major ecological process linked to nutrient cycling and carbon dynamics (Raich & Schlesinger, 1992). Rates of decay are controlled by various agents, such as biotic activity (e.g. termites and fungi) and UV radiation, and drivers that regulate the influence of these agents (e.g. climate and litter quality) (Hobbie, 1992; Wardle *et al.*, 2004; García-Palacios *et al.*, 2013). To-date, only a handful of studies, all restricted to North American drylands, have assessed how woody encroachment might affect decomposition (Throop & Archer, 2007; Hewins *et al.*, 2017; Throop *et al.*, 2017), with differences in decomposition rates largely attributed to alterations in abiotic controls, such as soil-litter

mixing and solar radiation. However, the influence of woody encroachment on the decomposer community and their effects on decomposition remains unknown. Moreover, understanding of the effects of woody encroachment on decomposition in other systems is required before broad consensus can be reached.

Here, we investigate plant litter decomposition in a semi-arid African savanna with high levels of encroachment by an indigenous woody plant, *Dichrostachys cinerea* ((L.) Wight & Arn), which occurs over large areas of southern Africa (Bester, 1999; Roques *et al.*, 2001; O'Connor *et al.*, 2014). We examine: (1) the effects of woody encroachment on the rate of aboveground grass decomposition, (2) the contribution of invertebrates to plant litter decomposition in open and encroached areas, and (3) the effect of encroachment on the diversity and activity of fungus-growing termites, highly influential decomposers in African savannas (Buxton, 1981; Collins, 1981; Freymann *et al.*, 2008). We predicted that decomposition would be slower in encroached areas because the increased dominance of a single woody plant species at the expense of herbaceous undergrowth would reduce the activity of decomposer organisms through reduced food diversity and altered microclimatic conditions. Additionally, the increased shade (canopy cover) resulting from woody encroachment was anticipated to reduce UV radiation, thereby decreasing photodegradation and slowing decomposition (Austin & Vivanco, 2006; Austin, 2011).

Materials and methods

Study site

The study was conducted in Madikwe Game Reserve, South Africa (24° 47'S; 26° 10'E), a semi-arid savanna that receives approximately 540 mm of rain per year, typically falling between October and March. Substantial encroachment, often at the expense of grasses, has been documented in this system (Symeonakis & Higginbottom, 2014), with a 30 % increase in

woody cover (predominantly by *D. cinerea*) recorded in Madikwe between 1955 and 1996 (Hudak & Wessman, 2001).

We established 20 experimental replicates (50 x 50 m plots, spaced > 100 m apart to ensure independence) in encroached areas in the south of the park, and 20 replicates in open savanna areas in close proximity. The encroached areas consisted of patches of woody encroachment set within a matrix of non-encroached, open savanna. Ten of the open savanna replicates were placed in an adjacent area, up to 3 km from the encroached sites, and another ten were placed further away, up to 18 km from the encroached sites, within a fenced area due to concerns that wildlife would damage litterbags in the exposed, open savanna sites over the 12 month experimental period (See Table S1 in Supplemental material for additional study site information). The dominant historical land use across the study area, including the experimental replicate sites, was cattle grazing, with < 5 % of the area used for cropping (Hudak & Wessman, 2001). We made use of historical aerial photographs (dating back to 1955) to confirm that the selected sites (encroached and open) did not differ in their historical land use (e.g. agriculture vs. cattle ranching). To quantify any other potential differences in local environmental variables between the open and encroached areas, we measured the following attributes within each replicate: (a) percentage cover of bare ground, grass, forbs, dead wood and woody plant canopy; (b) grass species composition; (c) soil depth and (d) soil texture. Percentage cover of each attribute in (a) was estimated in nine 1 x 1 m quadrats per experimental replicate, each spaced 10 m apart, using a five-point scoring system (1 = < 5 %, 2 = 5 - 25 %, 3 = 26 - 50 %, 4 = 51 - 75 %, 5 = 76 - 100 %) and estimating the total percentage cover with the following equation:

$$\text{Total percentage cover} = \sum \frac{\text{midpoint \% for a score value} \times \text{no. quadrats with that score value}}{\text{total no. quadrats}}$$

[Equation 1]

Annual temperature and precipitation data for each replicate were obtained from

WorldClim – Global Climate Data (Fick & Hijmans, 2017) online resource at a 30 second spatial resolution (<http://worldclim.org/bioclimate>). Grass species were identified at 50 points, spaced 1 m apart, diagonally across each replicate following the step-point method (Evans & Love, 1957). Soil depth was measured using a 300 mm peg that was hammered into the ground at four points spaced > 25 m apart in each replicate. This relatively shallow maximum soil depth (300 mm) was chosen because it was considered the most critical for termite activity, with most termites foraging within the first 250 mm of soil (Wood *et al.*, 1982; Wood, 1988). A soil sample was also collected at each of these four points with a soil auger to a standardised depth of 20 cm. Soil samples were pooled per plot and a 50 g subsample was used to determine soil texture (sand, silt and clay content) with a particle size analysis using the pipette method (Briggs, 1977). We buried iButtons® (Thermochron, Maxim/Dallas Semiconductor Corporation, Dallas, Texas, USA) 2 cm below the soil surface in three replicates in each area (open and encroached) to measure hourly soil temperature for the duration of the study.

Decomposition experiment

We filled aluminium gauze litterbags with 9 g of *Themeda triandra* (Forssk.), oven dried at 70° C for 48 hours. *Themeda triandra* was chosen because it is a common, widespread local grass species with relatively high palatability (Van Oudtshoorn, 1999) and has been used previously in savanna decomposition experiments (e.g. Davies *et al.*, 2013a) where it decomposed at a rate that was expected to yield differences in mass loss between treatments over the course of our one year experiment. The litterbags measured 15 x 15 cm and consisted of 2 x 2 mm mesh (following Davies *et al.*, 2013a), allowing access by most small- to medium-sized invertebrates, including termites.

Each experimental replicate had two sets of litterbags, spaced 10 m apart: a treatment that suppressed invertebrates and a control (no invertebrate suppression). Naphthalene, an

arthropod repellent, was used to suppress invertebrates and was chosen to avoid the problems of altered microclimates associated with litterbags of different mesh sizes (Bradford *et al.*, 2002). Naphthalene is commonly used in decomposition studies (Austin & Vivanco, 2006; Wall *et al.*, 2008; Powers *et al.*, 2009) and provides a conservative estimate of the faunal contribution to litter decomposition (Blair *et al.*, 1989). Two naphthalene balls (approximately 8 g each) were placed underneath each treatment litterbag and replaced every two months to ensure sustained invertebrate suppression. In July 2013, six litterbags were nailed directly onto the substrate at each treatment and control set. One litterbag was collected from each litterbag set every two months for one year, starting in September 2013 (2 months in the field) and ending in July 2014 (12 months in the field). A total of 480 litterbags were used in the experiment: 2 savanna habitats (open and encroached) x 20 replicates each x 2 treatment sets each (control and invertebrate suppression) x 6 sampling periods. After collection, litterbags were oven dried at 70 °C for 48 hours. Litter was then hand-sorted to remove any soil and weighed to determine proportional mass loss (grass mass remaining was subtracted from the initial mass of each bag).

Termite activity

Cellulose baits (single ply, unscented toilet rolls) were used to measure termite activity within the open and encroached areas during two four-monthly periods, roughly spanning the wet (November 2013 - March 2014) and dry (March 2014 - July 2014) seasons. Nine baits were placed at each replicate, arranged in a 3 x 3 grid with 10 m spacing, with the first line of baits positioned 10 m from the decomposition experiment. We used two measures of termite activity: i) the amount of bait consumed, and ii) the frequency with which baits were attacked. Bait consumption was visually estimated after 2 and 4 months in each season according to the percentage consumed, following Davies *et al.* (2013b): 0 = 0 %; 1 = 1 - 25 %, 2 = 26 - 50 %, 3 = 51 - 75 %, 4 = 76 - 100 %.

3 = 51 – 75 %, 4 = 76 – 99 %, 5 = 100 %. For consistency, bait consumption was scored by the same observer throughout the study. Baits that had a consumption score of ≥ 2 after 2 months were replaced with new ones to ensure continuous bait availability. A cumulative score for each season (wet and dry) was calculated by either summing the two scores for the season if a bait had been replaced (i.e. maximum score = 10), or using the score after four months if a bait had not been replaced (i.e. maximum score = 5). Therefore, the cumulative consumption score for each season ranged from 0 (0 % of the baits consumed) to 10 (100 % of the baits consumed). Since termites have the potential to consume more bait than was provided, consumption scores of 10 (100 % of both baits consumed over the 2-month period) could be considered as a conservative estimate of termite activity levels. However, this possibility does not apply to our specific study because full consumption of both baits did not occur in any replicate (see Results). The frequency of termite attack at baits, measured as the proportion of baits per grid ($n = 9$) that showed signs of termite consumption, was also recorded every two months.

The experiment was reset after the wet season to measure termite activity during the dry season. To avoid spatial autocorrelation, a new grid of fresh baits was placed on the opposite side of the litterbags, 30 m away from the original grid, and the same scoring procedure followed. Termites present at baits were collected and stored in 70 % ethanol for later identification, using the soldier caste and following Uys (2002). The number of baits per replicate within which a particular termite species was encountered served as a measure of relative abundance (Davies *et al.*, 2013b). As an additional measure of termite activity in open and encroached areas, we recorded the number of termites present in litterbags collected in January, the peak of the summer wet season when savanna termites are most active (Davies *et al.*, 2015).

Data Analysis

We constructed multiple generalized linear mixed effects models with binomial error distributions to assess the effect of habitat (encroached or open), treatment (control or invertebrate suppression), sampling period (month) and aggregated termite activity (bait consumption across seasons) on the proportional mass loss (hereafter, mass loss) from litterbags. Analysis of litterbag mass loss after 12 months between the open sites that were close to the woody encroached areas and those that were further away revealed no significant differences (Mann Whitney-U test, $W = 31$, $p = 0.15$). We therefore did not distinguish between these different sites in subsequent analyses. The experimental replicate was set as a random effect in all models to account for each litterbag set within a replicate being repeatedly sampled over the six collection events. Candidate models, consisting of all combinations of fixed effects and their first and second order interactions, were compared using sample-size-corrected Akaike's Information Criterion (AICc), with the model with the lowest AICc value (hereafter, best model) used for further analysis using a Type II Analysis of Deviance test (Wald Chi-square test) to assess effect size and significance of each predictor variable and interaction term present in the model (Crawley, 2007). The performance of the best model was assessed for goodness of fit, homogeneity of variance and normality of residuals. Analyses were performed using the *lme4* package in R software, version 3.3.3 (R Core Team, 2016).

Litterbags collected after 12 months were used to estimate the decomposition constant (k), for each habitat (encroached or open) and treatment (control or invertebrate suppression), using the negative exponential single-pool decomposition model (Olson, 1963):

$$W_t = W_0 e^{-kt} \quad \text{[Equation 2]},$$

where W_0 is the initial litter mass (time = 0 years) and W_t is the litter mass after collection (time = 1 year).

Although k only describes average decomposition rates over one year and is likely to change over time, it is useful for comparison between habitats and treatments. The constant k (year^{-1})

was then used to estimate the half-life of grass material following (Olson, 1963):

$$T_{0.5} = \frac{0.693}{k} \quad [\text{Equation 3}],$$

where T is litter half-life and k is the decomposition constant calculated from equation 2.

Mann Whitney-U tests were applied to the percentage cover and soil depth data to compare environmental variables between habitats, as well as termite activity between habitats and seasons. Soil texture was compared between habitats using Student's t-tests (percentage sand, silt and clay content). Soil texture data were first arcsine transformed to meet the assumptions of normality. Mean monthly minimum and maximum soil temperatures were analysed using a linear mixed effects model, with experimental replicate set as the random effect (repeated measure) to account for measurements being recorded continuously from the same locations over the experimental year.

To assess whether there was a relationship between litterbag mass loss and termite activity (bait consumption as well as frequency of attack), linear regressions were performed for each habitat using the mass lost from control litterbags collected after 12 months and the average yearly termite activity scores (calculated from the wet and dry season bait consumption and frequency of attack per replicate). In addition, we regressed termite bait consumption scores against the frequency of termite occurrence at each habitat to assess how termite bait consumption was related to termite presence. Finally, an analysis of similarity (ANOSIM) was performed using PRIMER software v.5.0 (Clarke & Warwick, 2001) to assess whether the termite and grass communities differed between habitats.

Results

Open savanna areas had more grass cover than encroached areas, which in turn had more dead wood and greater woody plant canopy cover (Table 1). Although mean soil depth was greater in open areas (Table 1), there was a considerable overlap in soil depth values in the encroached

Table 1. Environmental variables measured at open and encroached savanna areas in Madikwe Game Reserve, South Africa. Total percentage cover (calculated using Equation 1, see Methods) are presented for variables scored according to their percentage cover in nine quadrats in each of 20 experimental replicates per habitat (open and encroached). Mean values are presented for the other variables. Test statistics are from Mann Whitney-U tests^a, Student t-tests^b or are the β coefficients from a linear mixed effects model^c. Significant ($P < 0.05$) differences between treatments are denoted with an asterisk

	Environmental variable	Open savanna	Woody encroached	Test statistic		p-value	
Total percentage cover	Bare ground	65.69	64.79	65670.00	a	0.77	
	Grass	17.59	11.56	105.00	a	< 0.05	*
	Forbs	3.62	3.61	149.50	a	0.13	
	Dead wood	3.522	6.07	312.00	a	< 0.01	*
	Canopy cover	5.61	14.76	266.00	a	< 0.05	*
Mean values	Soil depth (mm)	229.38	167.96	4424.00	a	< 0.01	*
	Sand (%)	83.85	81.7	- 1.31	b	0.20	
	Coarse silt (%)	13.10	15.7	1.60	b	0.12	
	Medium/fine silt (%)	2.30	1.55	- 1.30	b	0.20	
	Clay (%)	0.75	1.05	1.44	b	0.16	
	Soil temperature (°C)	23.23	22.13	2.36	c	< 0.05	*

sites (Fig. S2 and S3, Supplemental material). Bare ground, forb cover and soil texture (sand, silt and clay content) did not differ between open and encroached areas (Table 1), and there were no significant differences between grass assemblages in encroached and open sites (Global $R = 0.11$, $p = 0.06$). Monthly soil temperatures were higher in open savannas (Table 1), largely due to significantly higher maximum temperatures than encroached areas (Fig. S1, Supplemental material). Additionally, the open savanna had more extreme soil temperatures, with the lowest and highest recorded temperatures ($-2.5\text{ }^{\circ}\text{C}$ and $69\text{ }^{\circ}\text{C}$, respectively) exceeding those of encroached areas ($1.5\text{ }^{\circ}\text{C}$ and $58\text{ }^{\circ}\text{C}$, respectively). Open and encroached sites showed little difference in annual air temperature (mean \pm standard error, open savanna: $20.30 \pm 0.06\text{ }^{\circ}\text{C}$; encroached: $20.41 \pm 0.01\text{ }^{\circ}\text{C}$) and annual precipitation (mean \pm standard error, open savanna: $537.10 \pm 2.51\text{ mm}$; encroached: $538.25 \pm 1.28\text{ mm}$) (see also Table S1, Supplemental material).

Decomposition rates

Grass litter in the open savanna decomposed twice as fast (half-life ($T_{0.5}$) of control litterbags = 1.23 ± 0.37 years) as that in encroached areas ($T_{0.5} = 2.49 \pm 0.26$ years) (Fig.1). Differences in litterbag mass loss over time varied between open and encroached areas (there was a significant interaction between habitat and sampling period, Table S2 and S3, Supplemental material), with similar losses observed during the first six months (the dry season), but mass loss being faster in the open savanna in the second six months, corresponding with the wet season months (Fig. 1).

Invertebrates increased decomposition rate in both open and encroached areas, with control litterbags losing more mass than those that excluded invertebrates (Fig. 1). However, invertebrates were more influential in the open savanna where their suppression resulted in a greater decrease in decomposition rates relative to their suppression in the encroached areas

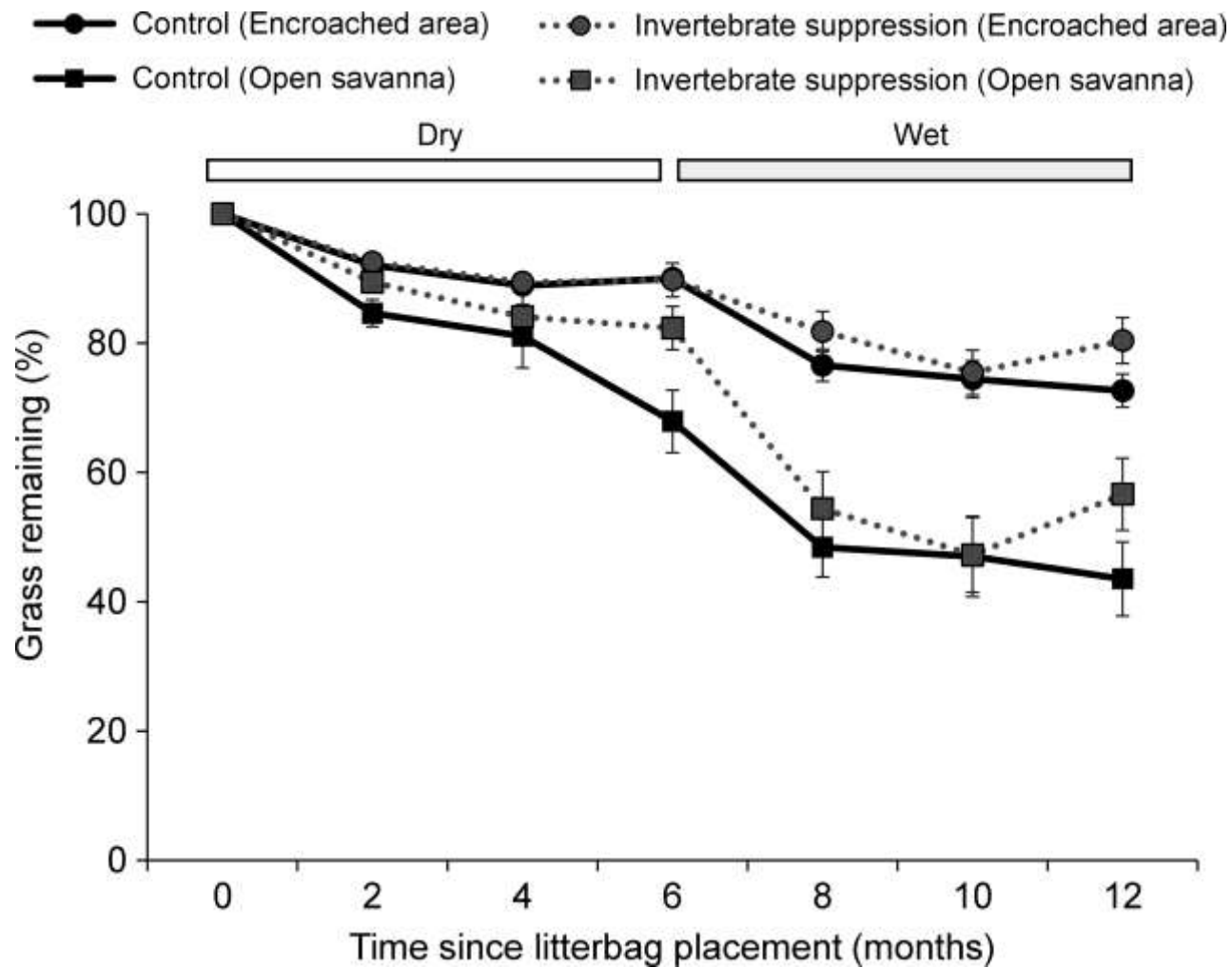


Figure 1. Mean (\pm standard error) percentage grass mass remaining in litterbags collected over 12 months in open and encroached savanna areas in Madikwe Game Reserve, South Africa. Litterbags either allowed (control) or suppressed invertebrates (treatment). Wet and dry season months are indicated above the figure

Table 2. Decomposition constants ($k \cdot \text{yr}^{-1}$) for litterbag treatments that allowed invertebrates (controls, denoted as + Invert) or suppressed invertebrate activity (treatment, denoted as - Invert) in open and encroached savanna areas in Madikwe Game Reserve, South Africa.

Habitat	+ Invert	- Invert	Δk
Open savanna	0.95	0.65	0.30
Woody encroached	0.33	0.23	0.10

(Table 2).

Termite activity influenced litterbag mass loss across habitats and seasons (Table S1, Supplemental material), but was more influential in open savannas during the wet season, as indicated by the significant two-way interactions between termite activity and habitat, as well as termite activity and sampling period (Fig. 2a; Table S2, Supplemental material). The increase in litter mass at the final collection event (Fig. 1) could either be an artefact of individual variation in litterbag decomposition rates (a common occurrence in sacrificial litterbag sampling protocols) or be due to tightly adhered soil particles and/or microbial biomass collected over time

Termite activity and species composition

Termite activity was significantly greater in open savannas (frequency of attack = 86 %; median intensity of attack = 2.61) compared with encroached areas (frequency of attack = 60 %; median intensity of attack = 1.81, $p < 0.01$), and was higher during the wet season at both open and encroached areas (Fig. 3). There was a significant relationship between bait consumption (across seasons) and litterbag mass loss after 12 months in encroached areas (Fig. 2a), but not in the open savanna. In contrast, there was a significant relationship between the frequency of termite occurrence and litterbag mass loss (Fig. 2b), as well as between bait consumption and frequency of termite occurrence in the open savanna, but not in the encroached areas (Fig. 2b and c).

We sampled termites from more baits in the open savanna ($n = 100$) than the encroached areas ($n = 41$). In addition, termites were only found in litterbags sampled in the open savanna ($n = 12$ litterbags) during the wet season, with control litterbags containing more termites ($n = 70$) than naphthalene treated litterbags ($n = 33$). Six termite genera were sampled, with their relative abundances differing between habitats and seasons, being generally higher in the open

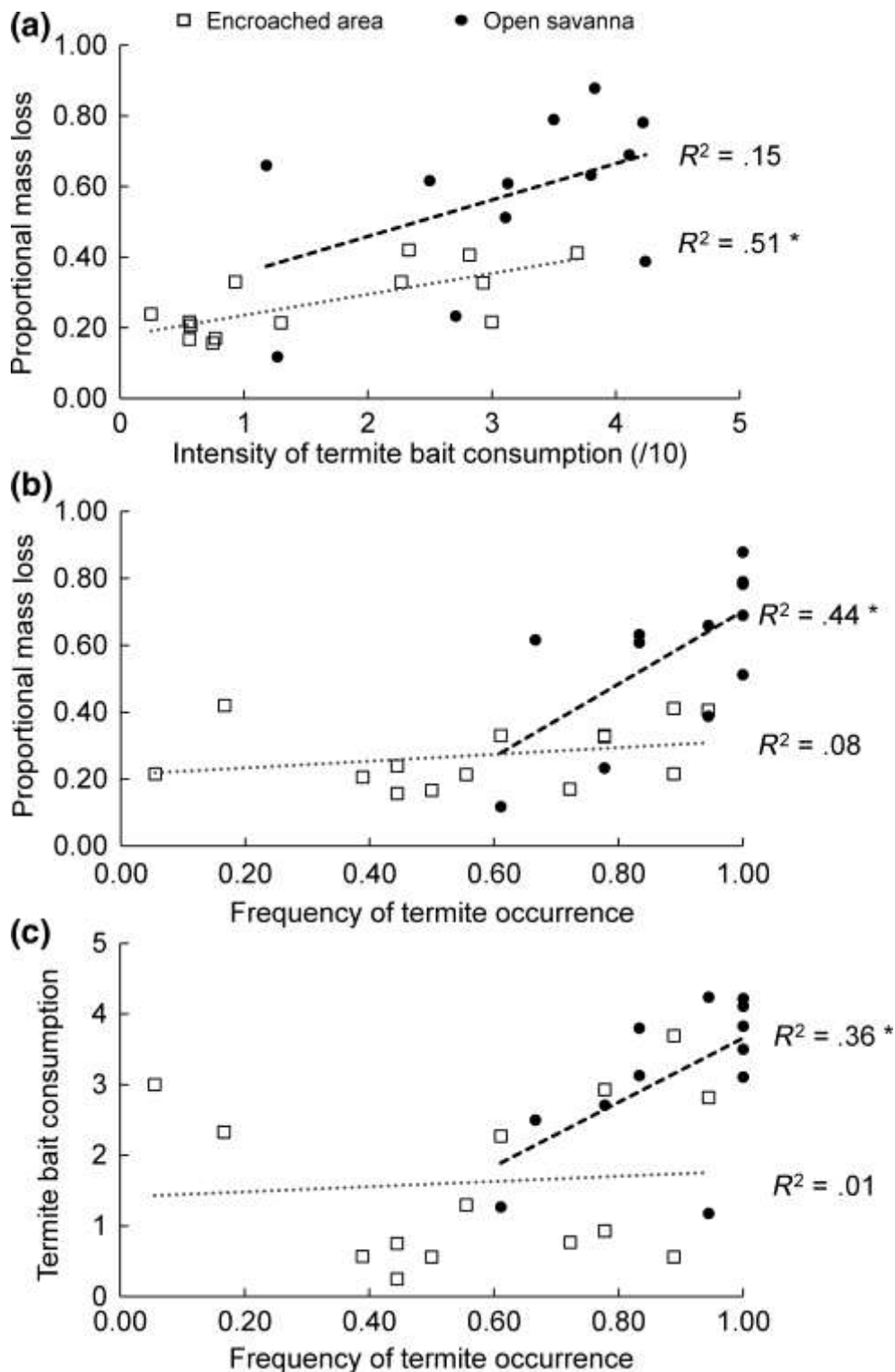


Figure 2. Proportional mass loss measured from control litterbags (invertebrates not suppressed) in relation to termite bait consumption (a), frequency of termite attack at baits (b), and bait consumption (c) by termites in relation to the frequency of termite occurrence 12 months after litterbag placement in encroached and open savanna areas in Madikwe Game Reserve, South Africa. Linear regression lines for the best fitting model are added (encroached area: black; open savanna: grey). Significant regressions are indicated with an asterisk. Termite consumption was scored from cellulose baits on a scale of 0 (no bait consumption) to 10 (total bait consumption). Frequency of attack was measured as the proportion of baits per experimental replicate that showed signs of termite activity

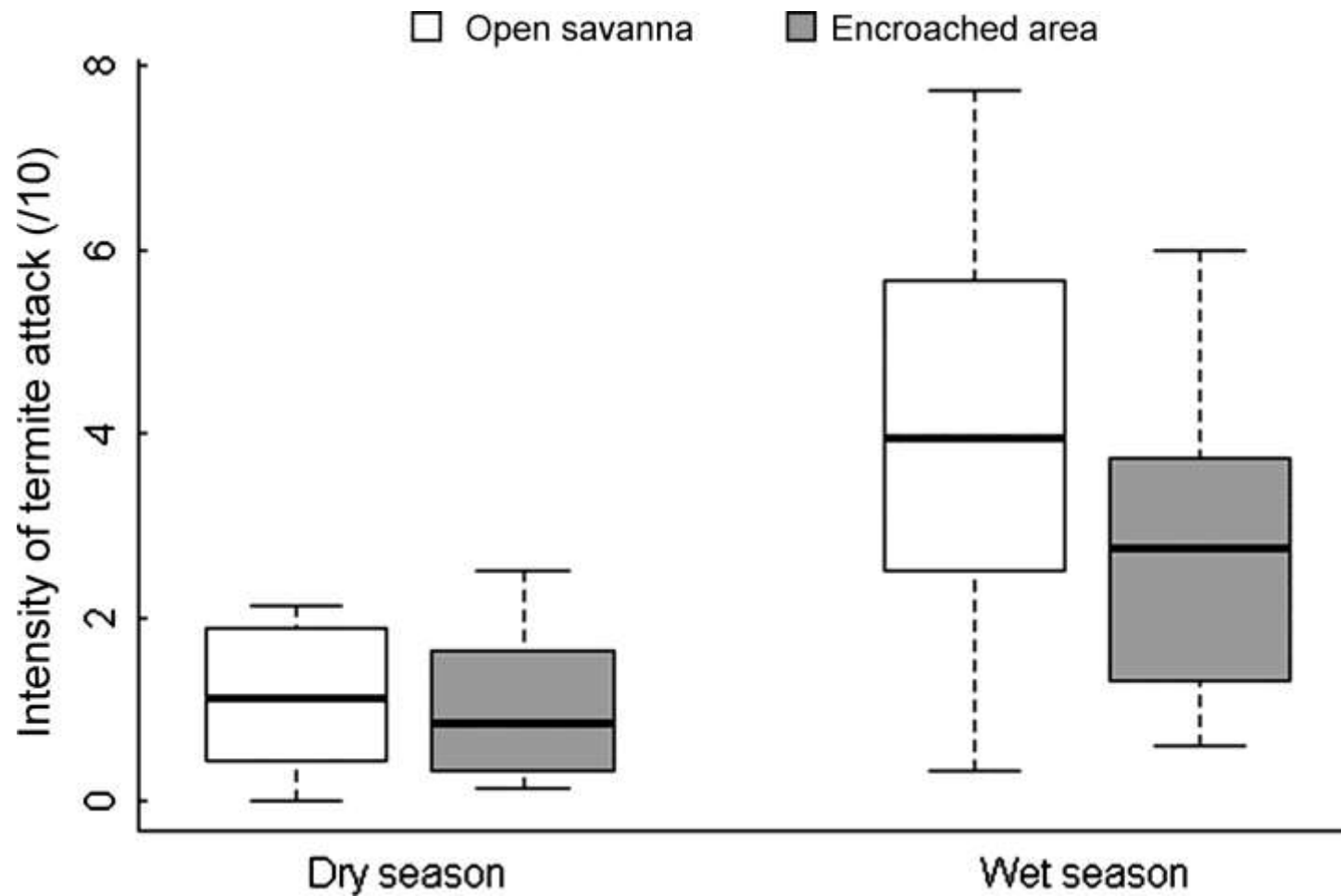


Figure 3. Boxplots indicating median (central line within box), interquartile range (box) and extreme (whiskers) termite activity scores (measured as the intensity of termite attack at cellulose baits) in open and encroached savanna areas in Madikwe Game Reserve, South Africa. Cellulose baits were scored according to the percentage of bait consumed by termites on a scale from 0 (no consumption) to 10 (total consumption) during the dry and wet season

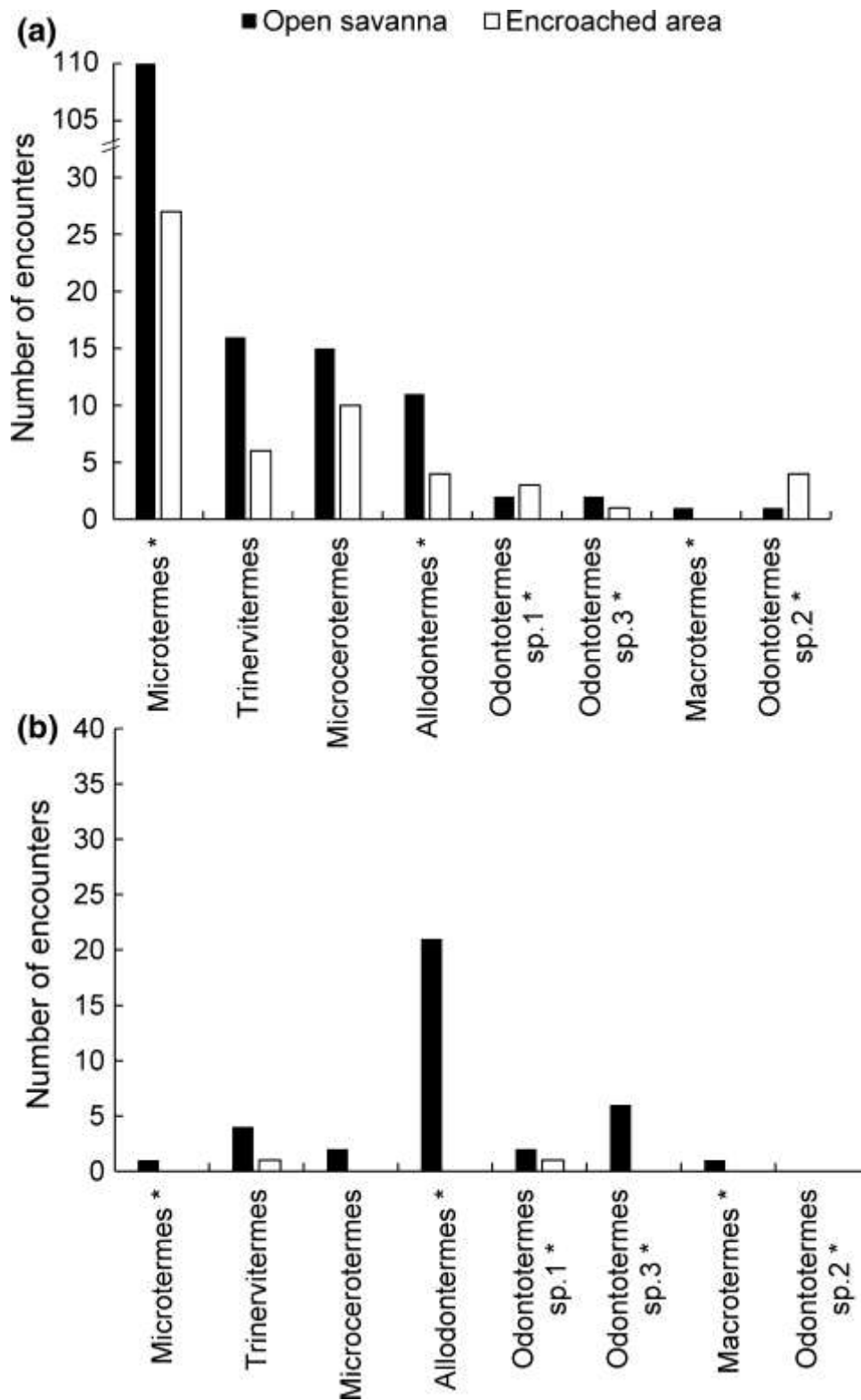


Figure 4. Number of encounters of each termite genus (and morphospecies in the case of *Odontotermes*) sampled from cellulose baits during the wet (a) and dry (b) season in Madikwe Game Reserve, South Africa. *Odontotermes* were separated into three morphospecies due to clear morphological differences in the soldier caste. Termite genera/morphospecies are ranked according to their abundance in open savanna areas during the wet season. Fungus-growing termite genera are denoted with an asterisk.

savanna and during the wet season (Fig. 4). Due to clear morphological differences in the *Odontotermes* soldier caste, we were able to separate this genus into 3 distinct morphospecies. This was not possible for other genera. However, differences in termite assemblages between open and encroached areas were small (ANOSIM, Global R = 0.13, $p < 0.01$), and no species turnover was observed: genera were simply sampled at lower abundances in encroached areas (Fig. 4). *Allodotermes* and *Odontotermes* were the only genera that were more abundant during the dry season, and this was only true for the open savanna (Fig. 4).

Discussion

Our results reveal substantial differences in aboveground litter decomposition rates and termite activity between open and encroached savanna areas, suggesting that woody encroachment can affect the functioning of savanna ecosystems. Encroached areas had significantly slower rates of decomposition, and we suggest that the decline in fungus-growing termite activity in these areas was likely a key determinant of this pattern. That changes in the termite community are a strong driver of changes in decomposition rate is supported by both the reduced number of termites sampled in encroached areas, and by the slower decomposition rates when invertebrates were suppressed. Slower decomposition in encroached areas has important implications for the global carbon budget, given the importance of decomposition to global carbon fluxes (Raich & Schlesinger, 1992), as well as for nutrient cycling in these systems. The reduction in termite activity in encroached areas also has important implications for multiple other ecosystem processes since termites are keystone organisms that influence several attributes of savanna ecosystems, including soil properties, hydrology, vegetation communities and patterns and impacts of herbivory (Sileshi *et al.*, 2010; Joseph *et al.*, 2015; Davies *et al.*, 2016).

Slower decomposition under woody encroachment corroborates previous findings from

a North American dryland (Throop & Archer, 2007), and suggests that this phenomenon is more widespread, extending to African savannas. Slower decomposition under woody encroachment also supports the notion that encroachment will likely lead to substantial changes in the functioning of grassy ecosystems (Scholes & Archer, 1997; Parr *et al.*, 2014), especially since woody encroachment is predicted to intensify in the future (Grace *et al.*, 2006; Moncrieff *et al.*, 2014). These changes have implications for future carbon dynamics since carbon will remain on the surface longer where decomposition is slower. However, slower decomposition may not necessarily lead to greater carbon storage in encroached areas because the inhibition of the grass-layer and associated fine-root biomass can decrease local carbon storage potential (Hudak *et al.*, 2003; Coetsee *et al.*, 2013).

Throop and Archer (2007) suggested that decreases in decomposition rates under woody encroachment were due to a reduction of soil-litter mixing because of increased grass cover under woody shrubs (although the mechanism for this is unclear). In contrast, we found less grass cover in the encroached areas, suggesting that increased woody plant density reduces, rather than increases, herbaceous undergrowth in African savannas (Scholes & Archer, 1997; Parr *et al.*, 2012; Symeonakis & Higginbottom, 2014). An alternative mechanism is therefore likely driving differences in decomposition under encroachment in our system, and we suggest that the reduced activity of fungus-growing termites in encroached areas is a key driver.

While encroached areas might be expected to provide favourable habitat for termites due to increased canopy cover and woody plant abundance that provides increased UV protection and buffering of extreme soil temperatures (Fig. S1, Supplemental material), as well as an increase in the availability of dead wood, which serves as a food source for termites (Eggleton *et al.*, 1996; Jones *et al.*, 2003; Muvengwi *et al.*, 2017), termite abundance was lower in encroached areas. Termite abundance in the encroached areas could be lower because the encroaching woody species, *D. cinerea*, is suggested to be a poor food source for termites: it is

frequently used in house construction and for fence posts due to its resistance to termite attack (Brokensha *et al.*, 1980; Arbonnier, 2004). The traits of woody encroaching species (e.g. their palatability to decomposers) have been emphasised previously (Eldridge *et al.*, 2011), and could affect the nature and degree of the impact of encroachment on ecosystems.

While it is also possible that the generally shallower soils in the encroached areas represent sub-optimal habitat for fungus-growing termites, savanna termites generally forage close to the soil surface (top 25 cm; Wood, 1988). In addition, deeper soils were not consistently associated with higher termite activity (Fig. S2, Supplemental material), and it is unlikely that soil depth was the primary cause of differences in decomposition rates between open and encroached areas, although our limited number of depth measurements means this finding should be treated with some caution.

Decomposition rates in both habitats also varied temporally, increasing substantially after six months of field placement, which coincided with the onset of the summer rains. Furthermore, termite activity affected decomposition rates through its interactions with both season and habitat, being most influential in the open savanna during the wet season. This is not surprising given the role of climate in influencing decomposition rates (Lavelle *et al.*, 1993), and because savanna termites are more active during the wet season (Davies *et al.*, 2015). Seasonal effects therefore warrant consideration in decomposition studies, as opposed to only considering annual variation in climate, particularly in seasonally varied environments such as savannas.

A greater frequency of termite encounters was a significant predictor of enhanced litter mass loss and bait consumption in open savanna (Fig. 2b-c). However, in encroached areas, high frequency of termite attack did not translate into greater bait consumption (Fig. 2c). This finding is likely due to the low number of encounters (relative abundance) of fungus-growing termite species in encroached areas (Fig. 4). Although we were unable to quantify this fully,

fewer individuals may have consumed each bait in encroached areas (explaining the low intensity of attack values) even when the frequency of baits attacked per replicate was high. These results show that in order to predict decomposition rates, it is not enough to simply know how frequently termites attack baits (as was the case for the open savanna), but also to quantify the amount of bait consumed.

However, the non-significant relationship between litterbag mass loss and termite consumption rates in the open savanna (Fig. 2a) suggests that termites are not the sole drivers of decomposition in this system. Photodegradation is an important agent of decomposition in arid environments (Austin & Vivanco, 2006; Austin, 2011), and has been shown to enhance plant litter decomposition in our study site (Leitner, 2015). It is therefore likely that in addition to direct negative effects on termites, woody encroachment also reduces the amount of photodegradation due to increased canopy cover, further contributing to slower decomposition rates. Further testing of the relative roles of invertebrates and photodegradation in African savannas, including in savannas undergoing woody encroachment, are needed before the contribution of each driver is fully understood. Similarly, while we observed woody encroachment to slow rates of grass litter decomposition, the potential effects of encroachment on wood decomposition remain to be investigated (but see Leitner, 2015), particularly as wood becomes the dominant litter type in encroached areas, and is likely to have even greater implications for the carbon budgets of these areas.

Nevertheless, our results suggest that woody encroachment has the potential to substantially alter aboveground litter decomposition and termite activity in African savannas. These findings have important and broadly applicable implications for ecosystem functioning given the vast expanse of savannas across Africa (> 13 million square kilometres (Riggio *et al.*, 2013), the importance of decomposition for biogeochemical cycling and the global carbon budget (Raich & Schlesinger, 1992), as well as termites being a keystone taxon increasing soil

productivity and landscape heterogeneity (Jouquet *et al.*, 2005; Sileshi *et al.*, 2010). Such changes to ecosystem processes and biodiversity resulting from current levels of woody encroachment should be adequately considered in predictions of global change impacts because they could challenge our understanding of how grassy systems function.

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Data accessibility

Data used in this manuscript have been archived in Figshare <https://figshare.com/s/ba48395035371ccde16b>

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SUPPLEMENTAL MATERIAL

Table S1. Coordinates and abiotic environmental variables for woody encroached (labelled as ‘Encroached’ under the replicate column) and open savanna (labelled as ‘Open’ under replicate) study sites in Madikwe Game Reserve, South Africa. Coordinates and elevations were obtained from a hand-held GPS unit in the field, and annual air temperature and annual precipitation data were extracted from Worldclim 2 at 30 seconds resolution (Fick SE, Hijmans RJ (2017) Worldclim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, **37**, 4302–4315).

Replicate	Longitude	Latitude	Elevation	Annual air temperature (°C)	Annual precipitation (mm)
Encroached1	26.38646	-24.8216	1009.743	20.48	546
Encroached2	26.38565	-24.8208	1015.751	20.48	546
Encroached3	26.38463	-24.8211	1016.953	20.48	546
Encroached4	26.38343	-24.8213	1019.837	20.48	546
Encroached5	26.38211	-24.8191	1021.038	20.44	541
Encroached6	26.38078	-24.8191	1023.442	20.44	541
Encroached7	26.37971	-24.8188	1026.325	20.44	541
Encroached8	26.37801	-24.8187	1027.046	20.44	541
Encroached9	26.37899	-24.8173	1031.372	20.44	541
Encroached10	26.37743	-24.8171	1033.054	20.44	541
Encroached11	26.37626	-24.8167	1035.938	20.44	541
Encroached12	26.37523	-24.8160	1037.380	20.38	539
Encroached13	26.37410	-24.8127	1045.312	20.35	532
Encroached14	26.37282	-24.8124	1046.994	20.35	532
Encroached15	26.37153	-24.8120	1050.599	20.35	532
Encroached16	26.37022	-24.8120	1051.320	20.35	532
Encroached17	26.36853	-24.8112	1060.212	20.35	532
Encroached18	26.36774	-24.8120	1054.204	20.35	532
Encroached19	26.36669	-24.8121	1051.800	20.35	532
Encroached20	26.36515	-24.8121	1052.761	20.30	531
Open1	26.40396	-24.8251	1003.494	20.53	549
Open2	26.40378	-24.8236	1005.417	20.57	547
Open3	26.40251	-24.8235	1007.820	20.57	547
Open4	26.40079	-24.8231	1009.743	20.57	547
Open5	26.39961	-24.8230	1011.425	20.53	548
Open6	26.39679	-24.8225	1015.271	20.53	548
Open7	26.39563	-24.8222	1018.875	20.53	548

Open8	26.39576	-24.8239	1020.798	20.53	548
Open9	26.41424	-24.8286	1000.851	20.57	549
Open10	26.41453	-24.8295	997.726	20.57	549
Open11	26.18227	-24.8376	1104.672	20.05	526
Open12	26.18358	-24.8376	1103.711	20.07	527
Open13	26.18353	-24.8385	1105.393	20.07	527
Open14	26.18208	-24.8386	1108.518	20.05	526
Open15	26.18189	-24.8395	1108.037	20.05	526
Open16	26.18323	-24.8397	1111.161	20.05	526
Open17	26.18283	-24.8407	1108.518	20.05	526
Open18	26.18139	-24.8403	1107.556	20.05	526
Open19	26.18083	-24.8411	1102.269	20.05	526
Open20	26.18221	-24.8413	1103.230	20.05	526

Table S2. Summary of the top five generalized mixed effects models for grass litter decomposition. Interaction terms are denoted by fixed effects separated by “:”.

Rank	Form of GLMM	Parameters	AICc	Δ_i	w_i
1	site + collection + treatment + termite activity + site : collection + site : termite activity + termite activity : collection + site : collection : termite activity	9	1130.50	0.00	0.50
2	site + collection + treatment + termite activity + site : collection + site : treatment + site : termite activity + termite activity : collection + site : collection : termite activity	10	1132.50	2.00	0.18
3	site + collection + treatment + termite activity + site : collection + site : termite activity + termite activity : collection + treatment : termite activity + site : collection : termite activity	10	1132.90	2.43	0.11
4	site + collection + termite activity + site : collection + site : termite activity + termite activity : collection + site : collection : termite activity	8	1133.50	3.07	0.03
5	site + collection + treatment + termite activity + site : collection + site : treatment + site : termite activity + termite activity : collection + treatment : termite activity + site : collection : termite activity	11	1135.90	5.42	0.01

Table S3. Results of the Type 2 Analysis of Variance test for all factors considered in the best Generalized Linear Model (GLM) for litterbag mass loss. Wald Chi-square test statistics (z) and p-values are reported.

Factor	z	p-value
Site	22.33	< 0.01
Treatment	5.93	< 0.01
Sampling period	209.09	< 0.01
Termite bait consumption	22.55	< 0.01
Sampling period x Site	11.36	< 0.05
Termite bait consumption x Sampling period	17.27	< 0.01
Termite bait consumption x Site	5.17	< 0.05
Termite bait consumption x Sampling period x Site	3.67	0.60

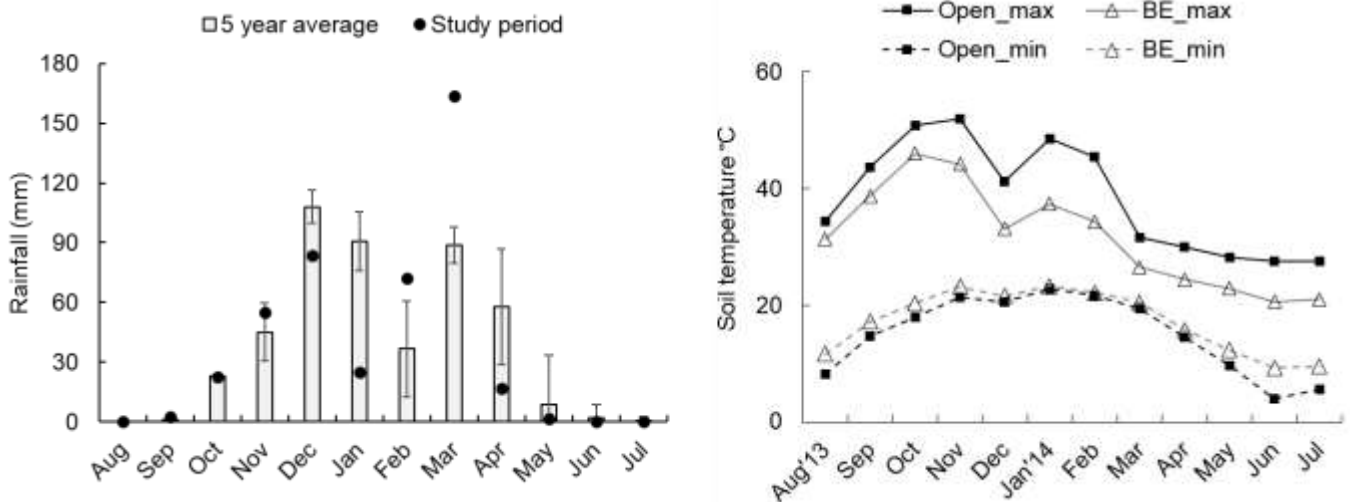


Figure S1. Monthly rainfall for Madikwe Game Reserve, South Africa from August 2013 to July 2014 compared to the five-year average prior to the study (left). Average monthly maximum and minimum soil temperatures as measured by Thermochron iButtons®, for open and woody encroached (BE) sites (right).

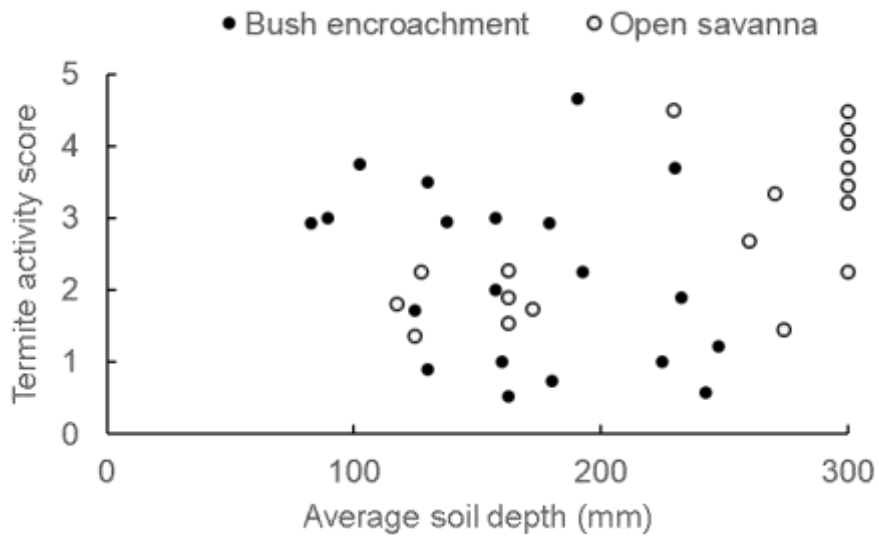


Figure S2. Soil depth measurements for open savanna and woody encroached sites measured to a maximum of 300 mm.

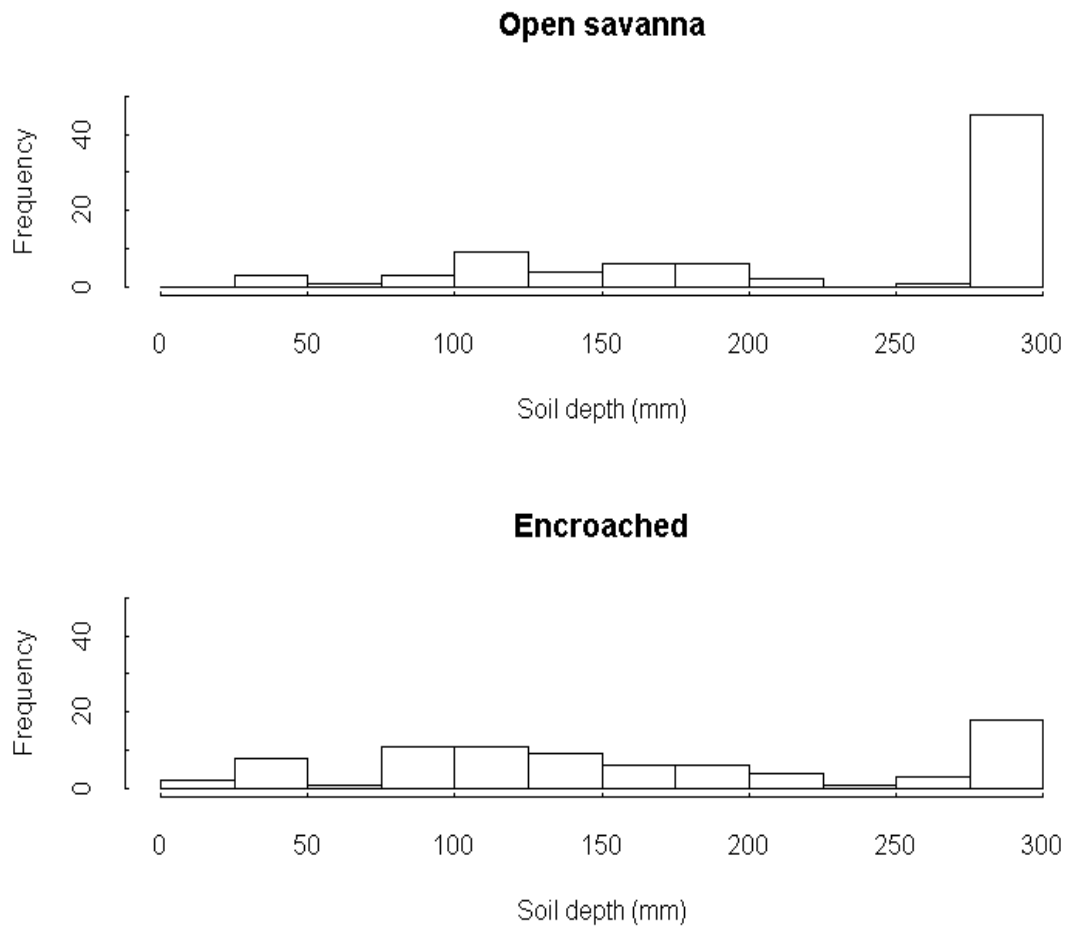


Figure S3. Termite activity score against soil depth for woody encroached and open savanna replicates in Madikwe Game Reserve, South Africa. Spearman’s ranked correlation results across sites indicate no notable trend between soil depth and termite activity ($\rho = 0.27$, $p > 0.05$).