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Termite species and functional diversity as determined by vegetation and edaphic characteristics in a savanna ecosystem

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Abstract

Background Savanna ecosystems support a diversity of biota and are influenced by vegetation and edaphic characteristics, shaping resident communities. This study was carried out at Mlawula nature reserve, a protected savanna ecosystem to determine impacts of vegetation and edaphic characteristics on termite species and functional diversity, as well as their activity. Termites were sampled from November 2017 to March 2018 in two habitat types, i.e. encroached and non-encroached by *Dichrostachys cinerea* over five months.

Results Twelve genera were collected over the study period, dominated by *Microtermes* sp. Termite species diversity and populations were significantly between habitat types, with higher numbers and species in non-encroached sites. Four functional groups (FG) were collected from both habitat types, with FGII being the most dominant group in both and no significant differences in FG diversity between the habitat types. Of the vegetational and edaphic variables measured, only canopy cover was significantly different between habitat types and was higher in encroached sites. Intensity and frequency of attack were significantly higher in non-encroached sites, indicating a decline in termite activity in encroached sites.

Conclusions Results indicated that, with the exception of canopy cover, vegetational and edaphic characteristics are not affected by increased woody vegetation invasion within the system assessed. However, due to reduction in termite diversity and activity, increased woody vegetation invasion is a threat to termites and associated ecosystem services they provide. The investigation provided information at both community and ecosystem level for the savanna assessed on the need for insect conservation both within protected areas and surrounding landscapes. Since the study suggested that termite populations and associated activity could be reduced due bush encroachment, monitoring of the impacts of increasing woody plant invasions is essential for insect conservation and maintenance of savanna ecosystem function and heterogeneity.

Keywords Ecosystem services, Termite activity, Functional diversity, Woody plant invasion, Encroachment

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Background

Plants are the dominant living biomass in terrestrial ecosystems thus the primary determinants of ecosystem structure and consequent biodiversity (Gillison 2003). Changes in vegetation diversity and structure as a result of various threats therefore have implications for resident biodiversity. In savannas, one of the major threats to biodiversity is habitat degradation due to invasion and thickening of aggressive undesired woody species cover, e.g. *Senegalia mellifera* (M. Vahl) Seigler &

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Ebinger, *Dichrostachys cinerea* Wight*, Terminalia sericea* Burch and *Acacia reficiens* Wawra*,* resulting in an imbalance of grass:bush ratio and alteration of vegetational diversity (De Klerk, 2004; O'Connor et al. 2014). Such encroachment has severe impacts on biodiversity, resulting in changes of habitat structure and complexity, with associated changes in community structure and species richness of resident biota, such as small mammals and vegetation (Hoffman & Zeller, 2005; Bussa and Shibu 2020). Additionally, edaphic and environmental conditions are principal factors determining the functioning and dynamics of these terrestrial ecosystems, e.g. rainfall, soil moisture balance and soil nutrients have an effect on vegetation structure, composition and productivity (de Klerk, 2004). These factors influence not only the species composition of resident communities but also their activity and functionality, making them an important resource for a number of ecosystem processes (Lavelle, 1996; Gosling et al., 2016; Nisa et al., 2021).

Many studies have focussed on the effects of bush encroachment and edaphic factors on vegetation composition and productivity as well as vertebrates while little is understood on how these processes affect invertebrate abundance, diversity and functional activity, particularly insects such as termites. As soil engineers, termites play a key role in the functioning of many natural ecosystems such as the African savannas. In these savannas, they influence the distribution of natural resources such as water and nutrients in the landscape and consequently the diversity of soil microbes, plants and animals (Muller et al., 1997; Jouqert et al. 2011; Davies et al., 2014; Davies et al., 2015). Termites respond to environmental conditions such as moisture, temperature levels, soils and nutrients (Davies et al., 2015) and can thus be used as biological indicator species to assess the health of habitats. As indicators, termites demonstrate the effects of anthropogenic disturbances on the biotic system (McGeoch, 1998; Jones & Eggleton, 2000; Gillison 2003).

In addition to species diversity, termite diversity has been studied with respect to the classification of species into functional groups based on the types, variety of food materials, nesting sites and resulting functional diversity, which is an important driver of the ecosystem function (Diaz and Cabido 2001; Eggleton & Tayasu, 2001; Villeger et al., 2008; Jouqert et al. 2011). Accordingly, there are four feeding habits supported by morphological and phylogenetic data (Grohmann, 2010). Different feeding groups have different impacts on the environment but provide similar ecosystem services (Jouquet et al, 2006). The aim of the study was to assess selected edaphic and vegetation characteristics within a nature reserve and their effects on termite species and functional diversity. It was hypothesised that species and functional diversity of termites is higher in the non-bush encroached sites at Mlawula nature reserve due to more heterogeneous vegetation structure and composition. Specific questions were proposed for the study, i.e. What are the edaphic and vegetational characteristics of bush encroachment at Mlawula nature reserve? How many termite species exist within the nature reserve and what are their functional groups? Is there a difference in termites species diversity between bush encroached and non-encroached sites? Which edaphic and vegetational factors determine termite diversity within the sampling sites? This would provide an understanding of invertebrate role in soil function and their interaction with abiotic components (Lavelle, 1996). Both biotic and abiotic factors are known to influence termite activity thus an understanding of these is important in understanding key determinants of savanna productivity and heterogeneity (Lehmann et al., 2011; Gosling et al. 2016).

Methods

Description of study area

This study was conducted at Mlawula nature reserve, situated in north eastern eSwatini, from November 2017 to March 2018. The reserve covers approximately 16,500 hectares and lies within the transitional zone between two biogeographic regions, i.e. the dry thorn savannas of the west and the moister thickets of the east. Mlawula Nature reserve is adjacent to other protected areas such as Mbuluzi Game reserve and Hlane Wildlife sanctuary. The average annual rainfall for Mlawula is estimated to be between 500 and 600 mm, although this varies within the reserve. Temperatures vary considerably between seasons and have high diurnal variation. Winter average minimum and maximum temperatures are 10 °C and 26 °C, respectively, and summer temperatures of 22 °C and 36 °C, respectively.

Mlawula's flora is notable for its great richness and diversity, comprising of about 1035 species including ironwood and endemic cycads. The reserve is noteworthy for its high diversity of fauna, with about 350 bird species, over 60 species of small and large mammals recorded in the reserve. While it is believed that there may be as many as 20,000 species of insects and 10,000 species of spiders, current check lists are limited to a few insect orders such as the beetles, butterflies and moths, with no list for termites.

Identification of sites

In this area, the primary woody species responsible for woody plant invasion is *D. cinerea*. Satellite images from Google Earth were used to identify two types of sampling sites, i.e. encroached and non-encroached sites. Coordinates of five of each type were randomly selected and

Geographic Position system (GPS) was used to locate points on the ground (Fig. 1).

Sampling procedure

Two sampling methods, i.e. active search and baiting were used to collect the termites.

Active searching

A standardised direct search sampling protocol based on searching different microhabitats for termites was followed (Dawes-Gromadzki, 2003). A 100 by 2 m belt transect, was laid out on each plot, with each sub-divided into twenty 5 by 2 m sections and each section searched for termites for 10 min. Searches were conducted beneath suitable termite habitat structures such as stones, logs, dung and soil and all samples encountered were collected. For each termite population encountered, representatives of the soldier caste were collected and preserved in 80% alcohol.

Baiting

In order to maximise species diversity sampled, unscented, white toilet paper rolls were used, since this has been found to be the most effective bait material (Davies et al, 2013). Thirty toilet paper rolls were buried 10 m apart in a 50 m × 40 m grid within each site. Baits were inspected for termites and termite attack once a month over the 5 months. Soldiers were collected and preserved in 80% alcohol for identification. Additionally, termite activity was determined using two parameters, i.e. frequency of attack and intensity of attack. The proportion of baits attacked at each census was recorded as a frequency of termite attack. Baits were also scored for the intensity of attack following Dawes-Gromadzki 2003; Davies et al., 2013; Felicitas et al., 2018 as: 0 = completely intact; 1 = 1–25% consumed; 2 = 26–50% consumed; 3 = 51–75% consumed; 4 = 76–99% consumed; 5 = 99–100% consumed.

Vegetation and soil sampling

The vegetation structure in all ten sites was determined to find the relationship between the vegetation and termite diversity and activity. This was estimated along a transect at every 20 m using a 1 m × 1 m quadrat and the following variables were measured as indicated:

i. Vegetation cover within the quadrat was determined by assessing overall vegetation cover (%) estimated then categorised into vegetation types, i.e. % vegetation cover, % grass, % shrubs and % forbs.
ii. Tree height, if present measured in metres (m)
iii. Canopy cover measured using a densiometer and expressed as a percentage (%)
iv. Area covered by rock and/or bare ground expressed as percentage (%)
v. Dominant species of grass within quadrat

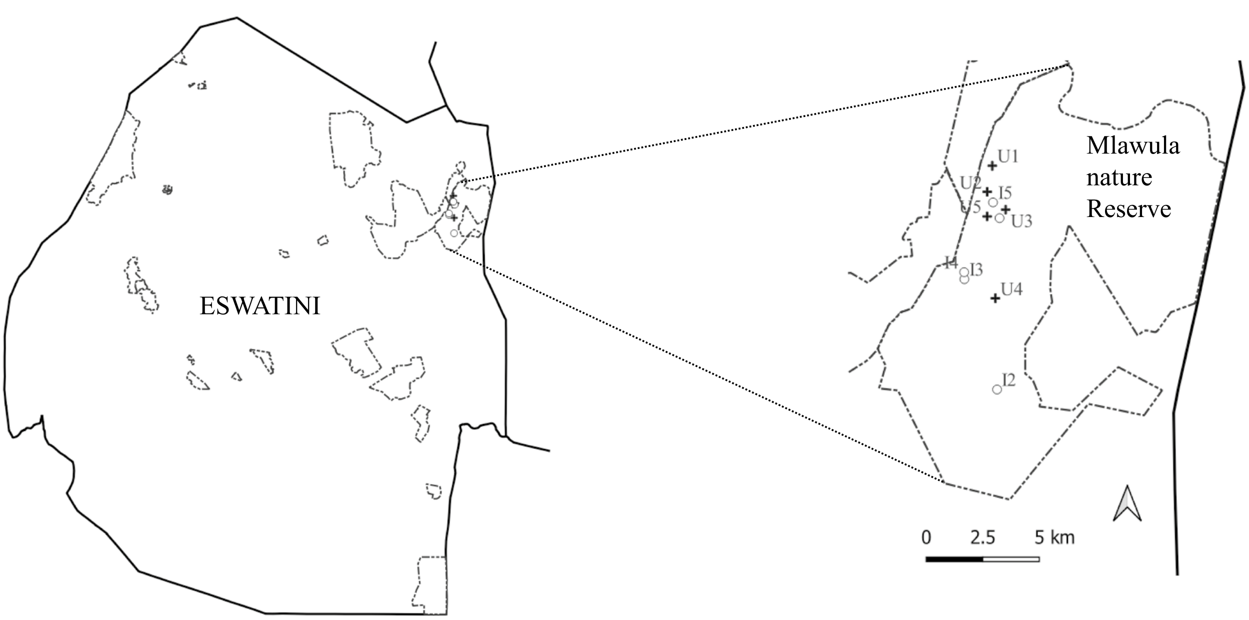

Fig. 1 Map showing the location Mlawula Nature reserve within the eastern part of Eswatini. Enlargement on the right shows the ten sampling sites at Mlawula Nature Reserve, U = Non-encroached, I = encroached by *D. cinerea*

Soil samples were collected once from each site during the study to quantify edaphic characteristics. Ten (10) samples were randomly collected from each site at a depth of 10 cm using a hand trowel. Samples from the same site were then mixed to create a homogenous average sample and 50 g from each site was then taken to the Ministry of Agriculture Soil Testing Unit at Malkerns Research Station for determination of % exchange acidity, pH, potassium, phosphorus, organic carbon and organic matter.

Sample processing.

(i) Initial identification of termites to the lowest possible taxonomic level (Genus) using their morphological characters was done based on keys and descriptions by Uys (2002). Genera were then separated into morphospecies if more than one species was collected, e.g. *Odontotermes*.
(ii) Species were also assigned to feeding and functional groups based on literature available on southern African termites and in situ observations. These were classified based on the classification which places termites into four groups depending on the state of humification of the feeding substrate, morphological and phylogenetic data (Donovan et al., 2001; Felicitas et al., 2018; Grohmann, 2010). The groups are: Group I which consists of lower level dead wood and grass feeding termites; Group II has termites with a wide feeding range including grass, dead wood, leaf litter and microphytes; Group III termites feed on the organic-rich upper soil/wood interface and Group IV contains true soil feeding termites which ingest mineral soil.

Data analysis

Data obtained were analysed in line with the questions posed for the study to determine the relationship between termite diversity and environmental variables measured. Statistical analyses were carried out in PRIMER-E to assess differences in species and functional diversity patterns between the sampling sites, sampling methods as well as their interaction with the vegetation and edaphic characteristics measured. Alpha and beta termite diversity indices were determined for within and between site comparisons of termites' species and functional diversity since the use of several biodiversity indices is necessary for efficient biodiversity assessment (Heino et al., 2005).

Community analyses were carried out in order to determine sampling efficiency and completeness. The module ANOSIM used to ascertain variation between habitat types, methods and months of sampling while SIMPER determined similarity between sites by identifying species responsible for this within the two habitat types. BEST analysis was carried out to determine which of the environmental variables measured explained the pattern of termite diversity observed within the sampling sites. For this, Spearman rank used as correlation method and Euclidean distance as a measure of resemblance.

Results

Termite species and functional diversity

A total of 1481 termites were collected, representing twelve species from eleven genera, during the period of sampling, with *Microtermes* sp., *Allodontotermes rhodesienses*, *Ancistrotermes latinosus* and *Odontotermes* sp.2 being the most abundant (Table 1, Fig. 2).

Comparatively, there were no significant differences in termite diversity and populations between sampling methods used, i.e. direct search and baiting ($R=0.008$; $p=0.311$) while these were significant between the habitat types ($R=0.1$; $p=0.001$) and month of sampling ($R=0.139$; $p=0.001$). Non-encroached sites had significantly higher numbers of termites and species collected compared to encroached sites. Over the months of sampling, November had the lowest termite numbers thus having a low similarity in termite populations compared to the other months, at 29.4% (Fig. 3).

Four functional groups (FGs) were collected from all sampling sites and there were no significant differences in functional group diversity between the two habitat types ($p>0.05$; Fig. 4), with FG II being the most dominant group in both types. FG 1, represented by *Trinervitermes* sp., had the least representation in non-encroached sites, while FG III (*Amitermes* sp.) was least in the encroached sites. Distribution of specific genera within each FG varied across sites, e.g., while the majority of genera within FGII occurred in all sampling sites, *Schedorhinotermes* sp. was restricted to only two sites. *Trinervitermes* sp. also occurred in only one non-encroached site and 2 encroached sites.

Vegetational and edaphic characteristics of encroached and non-encroached sites at Mlawula nature reserve.

Of the 15 vegetational and edaphic variables measured, i.e. % vegetation cover, % grass, % shrubs and % forbs, tree height, % canopy cover, % rock, % bare ground, dominant species of grass, % exchange acidity, pH, potassium, phosphorus, organic carbon and organic matter, there were no significant differences between encroached and non-encroached sites, with the exception of canopy cover ($p=0.024$), which was significantly lower in non-encroached sites (14.52 ± 1.32%) compared to encroached sites (18.998 ± 0.93%).

Results from BEST analysis indicated that optimal results to explain the relationship between termite diversity and environmental variables measured could

Table 1 Termite species encountered, their functional groups and feeding material where w = wood feeder, d-dung feeder, l = litter feeder, g = grass feeder and s = soil feeder (Uys, 2002; Dowes-Gromadzki and Spain 2003; Davies et al., 2015; Felicitas et al., 2018). U = non-encroached, I = encroached

Family	subFamily	Species	FG	U (no. of sites)	I (no. of sites)	Feeding material
Rhinotermitidae	Rhinotermitinae	*Schedorhinotermes* sp.	II?	2 (1)	7 (1)	w
Termitidae	Macrotermitinae	*Allodontermes rhodesiensis* (Sjöstedt 1914)	II	106 (5)	168 (5)	w, d
		Ancistrotermes latinosus (Holmgren, 1912)	II	148 (5)	88 (5)	w, d, l
		Macrotermes sp.	II	61 (4)	38 (4)	g, d, l, w
		Microtermes sp.	II	170 (5)	146 (5)	g, w
		Odontotermes sp.1	II	62 (5)	48 (5)	w
		Odontotermes sp.2	II	135 (5)	79 (4)	w
	Nasutitermitinae	*Rhadinotermes* sp.	II	5 (3)	5 (4)	w
		Trinervitermes sp.	I	1 (1)	7 (2)	g, l
	Termitinae	*Amitermes* sp.	III/IV	21 (4)	5 (2)	w, l
		Cubitermes sp.	IV	40 (5)	64 (5)	s
		Microcerotermes sp.	II	17 (4)	58 (5)	w
	Total no	*N*		768	713	
	Total species	*S*		12	12	
	Species richness	d		0.45	0.46	
	Pielou's evenness	J'		0.24	0.29	
	Shannon diversity	H'(loge)		0.34	0.40	
	Simpson's diversity	1-Lambda'		0.15	0.19	

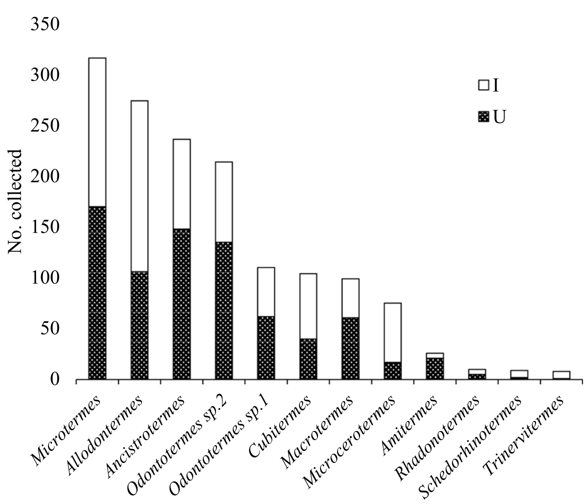

Fig. 2 Species diversity over sampling period. U = non-encroached, I = encroached

be obtained with seven of the variables measured, i.e. exchange acidity, soil potassium, % vegetation cover, % rocks, % shrubs, grass species and number of termites collected (Rho = 0.732, $p = 0.032$). These variables were subsequently used for PCA analysis in order to determine correlation. 99.8% of the variation was explained in the 2 PCA axes, with increasing potassium from non-encroached to encroached sites, explaining the first axis while PC2 was dominated by decreasing vegetation cover and number of species (Fig. 5).

Comparison of activity between a bush encroached and a non-bush encroached sites

With regard to termite activity, there were significant differences in frequency of attack and intensity of attack between types of sampling sites, with both parameters being higher in non-encroached sites compared to encroached sites (Figs. 6 and 7). Mean frequency of attack was 96.33 ± 3.23% in non-encroached sites compared to 78.50 ± 7.68% observed in encroached sites. Intensity of attack also illustrated a similar trend, with non-encroached sites having higher scores (4.30 ± 0.47) compared to encroached sites (3.75 ± 0.44).

Non-encroached sites had 55.09% similarity, dominated by *Microtermes* sp., *Ancistrotermes latinosus*and *Odontotermes* sp.2 while encroached sites had 47.53% similarity, dominated by *Allodontotermes rhodesiensis*, *Microtermes* sp. and *A. latinosuss*. Species contributing to dissimilarity (51.42%) between encroached and non-encroached sites were the most abundant species, i.e. *Odontotermes* sp.2, *A. rhodesiensis* and *A. latinosus*.

Discussion

According to Uys (2002), 54 genera comprising 165 species are described from southern Africa. Diversity and abundances obtained in this study area were comparable

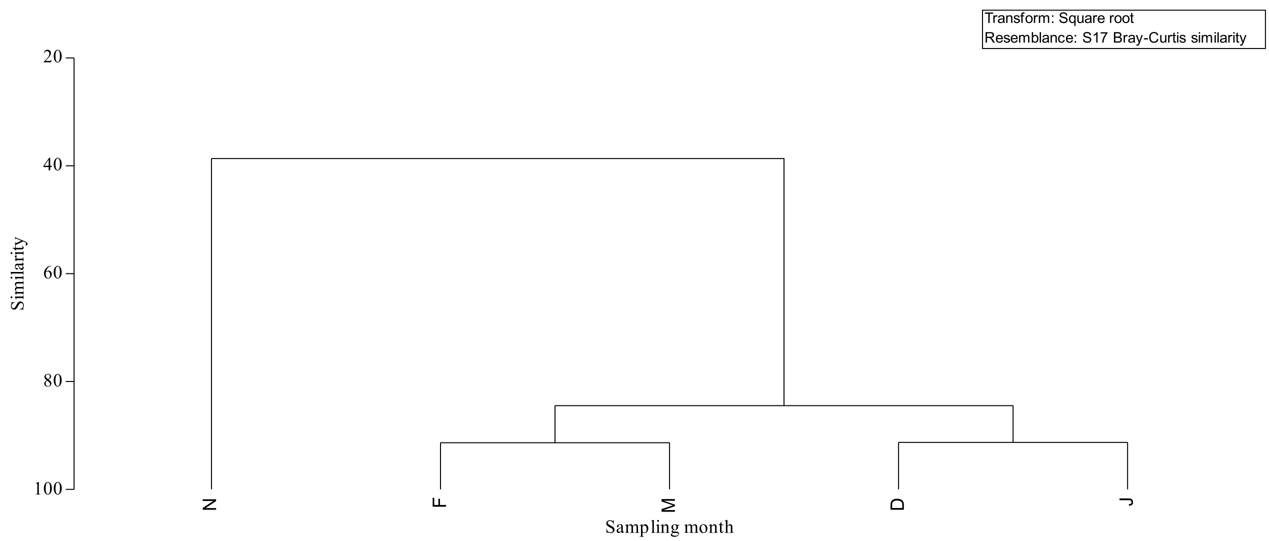

Fig. 3 Cluster for sampling months. Months of sampling abbreviated as *N* November, *D* December, *J* January, *F* February, *M* March

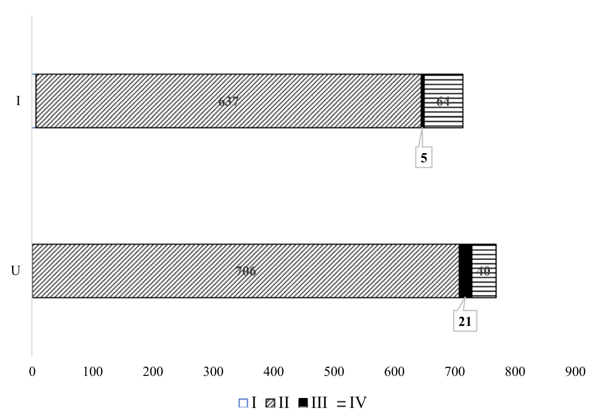

Fig. 4 Functional groups collected from habitat sampling types

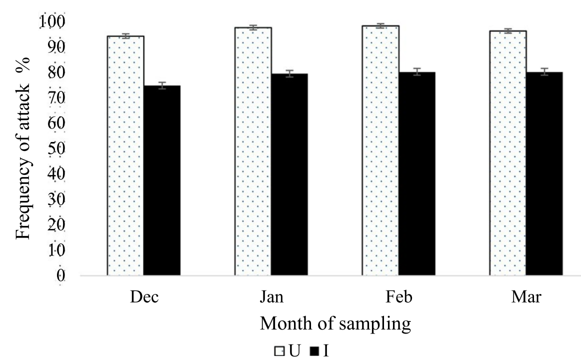

Fig. 6 Frequency of attack (proportion of baits attacked at each census)

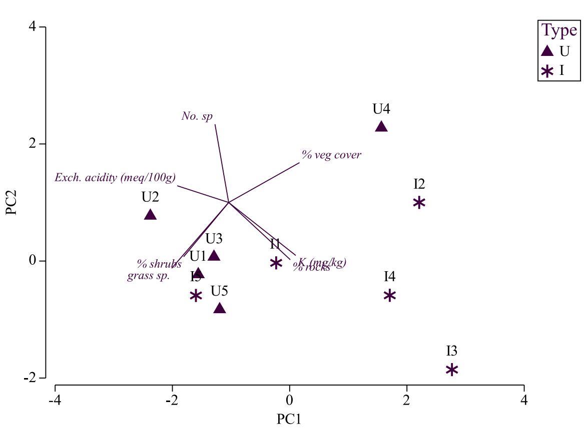

Fig. 5 PCA of best environmental variables. U = Non-encroached, I = Encroached sites

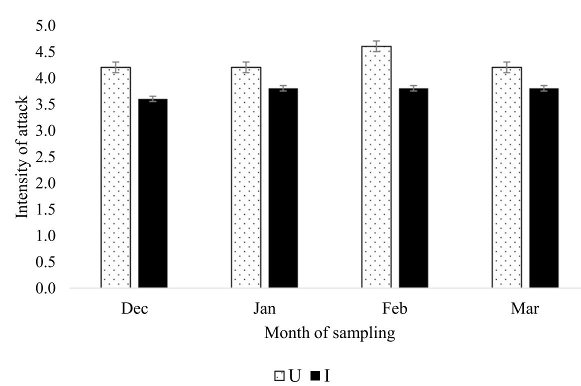

Fig. 7 Intensity of attack

to other studies within the savanna ecosystem in southern Africa (Leitner et al., 2018; Muvengwi et al., 2017). Since there were no significant differences between sampling methods, both methods used are sufficient for species diversity estimates and equally important in arid savanna (Davies et al., 2013). Effective sampling methods are critical for understanding termite diversity and impacts of land use and ecosystem function and their integration facilitates the detection of a wide range of species in an area (Dawes-Gromadzki & Spain, 2003).

Both termite population densities and species diversity seem to be affected by woody plant invasion since these were observed to be lower in encroached sites. Increased woody plant growth due to encroachment has an effect on other insect groups, e.g. ants which were observed to be lower in encroached areas, as observed for termites in this study. However, of the termite genera collected, functional group diversity was not significantly different between habitat types although some functional groups were specific to specific sites. FGII has the widest range of feeding material used and is resistant to environmental disturbances (Davies et al., 2013; Muvengwi et al., 2017) so this could explain the dominance by this group in this ecosystem. FGI members are grass and litter feeders and while litter was not measured in this study, grass cover was low in both habitat types (30.5% non-encroached 21.4% encroached) and absence of these resources will limit termite populations and could explain the low densities of this group within the study area. FGIII, i.e. soil/wood feeders, was notably higher in non-encroached sites. FGIV, i.e. soil feeders such as *Cubitermes* sp. are vulnerable to habitat disturbance due to their resource needs (Calderon and Constantino 2007) but were not significantly different between habitat types due to woody plant invasion. In this study, functional group diversity was similar between the two habitat types suggesting limited habitat degradation within areas sampled in relation to this parameter.

While there were no significant differences in the majority of edaphic and vegetation variables measured between encroached and non-encroached sites, canopy cover was significantly different between these sites. This was higher in encroached sites due to higher densities of *D. cinerea* and could have negative implications for termite populations since *D. cinerea* is known to be a poor food source for termites and resistant to termite attack (Leitner et al., 2018). Changes in canopy cover is a negative change in vegetation structure and could contribute to termite population reduction or extinction (Gillison 2003). Increased canopy cover in encroached sites was also observed at Kruger Park (Leitner et al., 2018). Non-significant differences in other environmental variables such as bare ground, forb cover, grass species were also observed by Leitner et al., 2018; implying other environmental factors not measured in both studies could be affected by encroachment and that structural complexity of closed plots is of little consequence (Dawes-Gromadzki & Spain, 2003). Long-term assessment on whether *D. cinerea* or any woody encroaching species impacts edaphic and vegetational characteristics would probably provide some insight as similar short-term studies have also observed no significant differences between encroached and non-encroached areas for these parameters (Leitner et al., 2018).

Measurement of a wide range of environmental variables enables the selection of the most appropriate variables which can be used to characterise a habitat and associated biota. In this study, seven variables proved to be sufficient to explain the termite diversity observed and included both edaphic and vegetational characteristics i.e. exchange acidity, soil potassium, % vegetation cover, % rocks, % shrubs, grass species and number of termites collected. Seemingly, vegetational and edaphic factors influencing resident biota varies and is dependent on the taxon under consideration, e.g. Phosphorus and Nitrogen have detrimental effect on nematodes; while soil moisture and herb layer were important for carabid beetle distribution and abundance (Baranová et al. 2018; Nisa et al., 2021) while different variables, as listed above, were determinants for termites in this study. Although the edaphic and vegetational variables measured were not significantly different between encroached and non-encroached sites, results suggested that termite populations and associated activity could be affected by bush encroachment, with these being reduced in encroached sites, as also observed in other savanna ecosystems within the region (Leitner et al., 2018).

Due to the ecosystem services provided by termites, implications of this are a conservation concern since bush encroachment was identified as increasing in the local savanna ecosystem (Leitner et al., 2018; Roques et al., 2001). Ecosystem resilience and resistance are strongly influenced by the traits of the dominant plant species (Diaz and Cabido 2001) thus the increase in woody plant invasions may have implications for savanna ecosystem function and heterogeneity, as observed for termite activity in this study. As a result, insect conservation efforts are needed on a broader scale, i.e. within conservation and production landscapes to ensure maintenance of ecosystem integrity since they are known to be useful as monitors of land-use changes (Muller et al., 1997).

Conclusions

With bush encroachment observed to be increasing in the study area, the impacts of bush encroachment on the biodiversity in this environment have not been fully explored. This study has provided insight on these effects on termite species and functional diversity while also providing an inventory of termite species and activity at within a savanna conservation area. The utilisation of both species and functional diversity provided information at both the community and ecosystem level. Conservation of insects such as termites is essential at all levels for maintenance of ecosystem integrity.

Abbreviations

PRIMER-E	Plymouth Routines in Multivariate Ecological Research
ANOSIM	Analysis of similarity test
BEST	BioEnv and stepwise test
PCA	Principal component analysis
FG	Functional group

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Author contributions
ZM: data curation, writing—review, project administration CNM: conceptualisation, methodology, supervision, writing original draft. Both authors read and approved the final manuscript.

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Availability of data and materials
All data generated or analysed during this study are included in this published article [and its supplementary information files].

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

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