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No evidence for an elephant-termite feedback loop in Sand Forest, South Africa



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ABSTRACT

Termites and mammalian herbivores might derive mutual benefit from each other through positive feedback loops, but empirical evidence is lacking. One suggested positive feedback loop is between termites and elephant, both ecosystem engineers. Termites, as decomposer organisms, contribute to nutrient cycling and soil enrichment, creating hotspots with increased forage quality. Elephant are known to select these high quality vegetation patches, depositing woody debris when foraging, but it is unknown whether elephant presence might affect termites, and if a feedback loop between these two taxa exists. We tested this hypothesis by measuring termite diversity and activity over three months in the summer wet season, inside and outside a long-term (eight years) elephant enclosure experiment in Sand Forest at Phinda Private Game Reserve, South Africa. Termites were sampled using cellulose baits and woody debris was quantified using line transects. Termite activity was not affected by eight years of elephant absence, despite a greater volume of woody debris where elephant were present. Termite assemblages were similarly unaffected by elephant absence. Apart from *Schedorhinotermes*, all other termite genera were sampled in both treatments. Therefore, the postulated positive feedback loop between termites and elephant is not supported in Sand Forest. However, this does not contradict findings that areas with high termite activity positively influence herbivore foraging, only that elephant foraging does not affect termite activity. This suggests that elephant disturbance (and elephant management policies) has little to no effect on termites and the fundamental roles they play in ecosystems over at least the short-term.

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1. Introduction

Termites are ecosystem engineers that perform important functional roles in many ecosystems (Freyman et al., 2010; Jouquet et al., 2011; Sileshi et al., 2010). The significance of termites for ecosystem functioning is widely acknowledged and receives considerable attention from the scientific community, with much effort applied to disentangling their specific contributions to ecosystem functioning (Davies et al., 2014b; Lu et al., 2013; Okullo and Moe, 2012; Schuurman, 2005). Termites contribute to processes such as nutrient cycling and decomposition, modify soil hydrology and texture, and alter vegetation patterns, with cascading effects across multiple trophic levels (Freyman et al., 2010; Jouquet et al., 2011; Sileshi et al., 2010). Non-uniform patterns in termite activity across landscapes result in patchiness in the provision of these services, leading to spatial heterogeneity (Davies et al., 2014a;

Freyman et al., 2010). For example, seasonally variable hotspots of termite activity led to localised increases and heterogeneity in the abundance of herbivores and their predators in the Serengeti National Park, Tanzania (Freyman et al., 2010). Termite foraging activity has also recently been shown to mitigate against long-term herbivore-induced reductions of functional diversity of savanna woody plants (Joseph et al., 2015) and to increase the robustness of semi-arid ecosystems (Bonachela et al., 2015). Changes in termite assemblages (i.e. species richness, abundance or composition) can be anticipated to impact, and potentially jeopardise, ecosystem functioning and biodiversity.

Vegetation on termite mounds acts as nutrient-rich feeding patches (i.e. foraging hotspots) for herbivores in nutrient-poor, semi-arid environments (Davies et al., 2016; Levick et al., 2010; Mobæk et al., 2005, but see Van der Plas et al. (2013) and Muvengwi et al. (2013) for contrasting results in nutrient-rich landscapes). African Elephant (*Loxodonta africana*) have been recorded to preferentially browse on woody vegetation growing on termite mounds compared with trees growing in the savanna matrix (Holdo and McDowell, 2004; Loveridge and Moe, 2004). Because elephant are destructive feeders, dropping

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woody debris as they browse (Kerley et al., 2008), it has been proposed that a positive feedback loop might exist between (wood-feeding) termites and elephant (Holdo and McDowell, 2004). Termites enrich the soil with nutrients (Freyman et al., 2008; Sileshi et al., 2010), creating nutrient hotspots with increased foraging quality (Davies et al., 2016; Holdo and McDowell, 2004; Loveridge and Moe, 2004). Elephant then select these high quality vegetation patches and supply woody debris (through their destructive feeding behaviour) and dung to termites, which use these resources (Freyman et al., 2008), further enriching the soil (Freyman et al., 2008; Holdo and McDowell, 2004). While it is known that elephant select these termite-induced nutrient-rich patches in the landscape (Holdo and McDowell, 2004; Loveridge and Moe, 2004), it is unknown if, and how, elephant affect termites, and whether the putative positive feedback loop actually exists. Indeed, several such feedback loops have been suggested between termites and mammalian herbivores (Cromsigt and te Beest, 2014; Davies et al., 2012; Freyman et al., 2010; Levick et al., 2010), but aside from a recent study showing that 50 years of ungulate herbivory can modulate woody species assemblages formed by centuries of termite activity (Seymour et al., 2016), empirical testing is lacking.

Exclosure experiments can be useful for testing such proposed phenomena by examining effects on the presence and absence of certain species or groups. However, exclosure experiments are usually designed to exclude groups of species of similar size, and so do not facilitate the testing of single species effects in treatments (e.g. Asner et al., 2009; Goheen et al., 2007; Levick and Rogers, 2008; Riginos and Young, 2007; Siebert and Eckhardt, 2008). In contrast, the herbivore exclusion experiment in the Sand Forest of Phinda Private Game Reserve, South Africa, separates the effects of individual herbivore species, and provides an opportunity to elucidate species-specific influences. Here, elephants have been excluded from a large patch of Sand Forest (3.09 km²) for eight years, while access by other herbivores has been unhindered (see Legendijk et al., 2011, 2012), providing a unique opportunity to examine whether the putative positive feedback loop between elephants and termites exists.

The interaction between elephant and biodiversity receives much (negative) attention (Kerley et al., 2008), with lower biodiversity often reported where elephant are present (e.g. Cumming et al., 1997; Kerley et al., 2008; Legendijk et al., 2012). Some positive effects of elephant have been documented, such as an increase in lizard densities in elephant-impacted trees (Pringle, 2008), as well as (short-term) neutral effects on woody species assemblages (Legendijk et al., 2015). In light of the current elephant debate in southern Africa (i.e. what effect elephant numbers and impacts have on ecosystems), the effects of elephant on biodiversity require additional research, and the effect of elephant on termite diversity has as yet not been tested. In addition, little is known about termite diversity in Sand Forest, and our results further contribute to knowledge of the biodiversity value of this rare and relatively understudied forest type (Kirkwood and Midgley, 1999).

Sand (Licuáti) Forest is a critically endangered semi-deciduous dry forest-type restricted to very few and relatively small areas in eastern South Africa and southern Mozambique (Mucina and Rutherford, 2006). The forest-type occurs in small patches within a savanna matrix, which, together with its low seedling recruitment rate, makes it vulnerable to disturbances such as herbivory, fire and the harvesting of natural resources (Legendijk et al., 2012; Matthews et al., 2003; Mucina and Rutherford, 2006). However, Sand Forest is an important habitat that warrants conservation because of its high levels of diversity and endemism across the whole biota. Several studies have focused on floristics (see for example Gaugris and Van Rooyen, 2008; Kirkwood and Midgley, 1999; Legendijk et al., 2012), but studies on invertebrates are few (but see Botes et al. (2006) for dung beetles, and Haddad et al. (2010) for spiders).

There were, therefore, two objectives of this study. First, we measured termite diversity (i.e. species density, abundance and assemblage composition) and activity levels (i.e. frequency and intensity of attack at

cellulose baits) in Sand Forest, and secondly, we tested the postulated positive feedback loop between termites and elephants. Our primary focus was on wood-feeding termites because we expected this feeding group to be most affected by elephant foraging, which provisions abundant dead wood, important for termite species that feed on lignin and cellulose. We expected higher activity by wood-feeding termites where elephant were present compared to where they were excluded. In contrast, we expected soil-feeders, another major termite functional group, to negatively respond to elephant presence, in similar ways to how they respond to anthropogenic disturbance in other forested areas (Eggleton et al., 1996). Because elephant can reduce vegetation densities through their foraging activities (i.e. pulling out seedlings and pushing over trees; Kerley et al., 2008), and indirectly affect microclimatic conditions, we expected soil-feeders to respond negatively to elephant disturbance. The diversity of soil-feeders might therefore be reduced in areas where elephants are present.

2. Material and methods

2.1. Study area

The study was conducted in Phinda Private Game Reserve (Phinda hereafter; 27°92′–27°68′ S; 32°44′–32°20′ E), a privately-owned conservation area in north-eastern KwaZulu-Natal, South Africa. The climate is subtropical, with a distinct summer rainy season (November to April). Temperatures range from a minimum of 10 °C in winter to a maximum of 35 °C in summer, with mean annual rainfall of 815 mm (2004–2014; FetchClimate, Microsoft Research, <http://fetchclimate2.cloudapp.net>).

Phinda was established in 1991, when several private game farms (comprising 130 km²) were joined and indigenous game species reintroduced. Since then the reserve has expanded to its current 235 km². Elephant were reintroduced between 1992 and 1994, and densities increased from 0.34 km⁻² in 1994 to 0.39 km⁻² in 2013, which is relatively low compared with densities in other protected areas in South Africa (range: 0.01–1.88 km⁻²; Van Aarde et al., 2008). Other browsing ungulates in the reserve are giraffe (*Giraffa camelopardalis*; 0.51 km⁻²), kudu (*Tragelaphus strepsiceros*; 0.15 km⁻²), nyala (*Tragelaphus angasii*; 6.81 km⁻²), impala (*Aepyceros melampus*; 6.38 km⁻²), red duiker (*Cephalophus natalensis*; 0.06 km⁻²), common duiker (*Sylvicapra grimmia*; no count available) and suni (*Neotragus moschatus*; no count available). The numbers in parentheses represent approximate densities derived from helicopter game counts conducted in 2013. The only browsing herbivores that utilise the Sand Forest are elephant, nyala, red duiker and suni (Legendijk et al., 2011, 2012).

Several Sand Forest patches surrounded by a savanna matrix occur within the reserve on sandy, acidic soil (<10% clay and a pH between 3 and 4.1; Legendijk, unpubl. data). Sand Forest can form a dense vegetation with closed canopy up to 15 m high. Characteristic tree species include *Balanites maughanii*, *Cleistanthus schlechteri*, *Cola greenwayi*, *Croton pseudopulchellus*, *Dialium schlechteri*, *Drypetes arguta*, *Hymenocardia ulmoides*, *Newtonia hildebrandtii* and *Pteleopsis myrtifolia* (Moll, 1980; Kirkwood and Midgley, 1999; Matthews et al., 2003). A grass stratum is generally absent from the forest, but can appear after episodic high rainfall events (Legendijk, pers. obs.). Sand Forest is sensitive to fire and the vegetation does not recover if burnt (Matthews et al., 2003). Phinda management actively protects the Sand Forest patches from fire.

2.2. Experimental design and sampling

We made use of an existing long-term Sand Forest herbivore exclosure experiment. This experiment was set-up in November 2005 to exclude herbivores of different sizes (i.e. elephant, nyala, red duiker and suni). We used the control area (no exclosure) and the elephant exclosure for this study. The elephant exclosure fence consists of two

electrified (60 pulses of 7000 V/min) high tension galvanized wires (2.4 mm thick), approximately 1.8 m and 2 m above the ground, enclosing 3.09 km² of a 5.2 km² Sand Forest patch. Elephant had access to the control area, but were restricted from the elephant enclosure, as opposed to nyala, duiker and suni that had access to both areas. The control area consisted of the other 2.11 km² of Sand Forest that is open to the rest of the reserve. See Lagendijk et al. (2011) for a more detailed description of the experiment.

Termites were sampled at 16 sites consisting of eight control and eight elephant enclosure plots. Plots of different treatments (i.e. control vs. elephant enclosure) were set-up approximately 100 m either side of the elephant enclosure fence to avoid any potential edge effects (plots between treatments were at least 200 m apart). Our primary focus was on wood-feeding termites, for which cellulose baiting is an appropriate method (Davies et al., 2013). In November 2013, twenty cellulose baits in the form of toilet paper rolls (500 sheets single-ply, unscented) were buried in each plot (i.e. 16 plots) to a depth of ~3 cm, in a grid of 5 × 4 baits, each spaced 8 m apart.

Baits were checked and replaced approximately every 28 days for three months from December 2013 to February 2014 (wet season), coinciding with the time of highest termite activity in southern Africa (Davies et al., 2015). Rainfall during December, January and February was 65, 59 and 54 mm respectively (data from monitoring station approximately 9.5 km from the study site). A representative sample of termites present at the baits (i.e. soldiers and workers; ± 10 individuals for each species present) was collected from each bait, after which the bait was replaced with a new bait. We sampled across three consecutive months in order to account for any potential variation in termite activity over the sampling period. Both wood- and soil-feeding termites were found on the baits and sampled. Specimens were preserved in 80% ethanol for identification.

Baits were further monitored for signs of activity of wood-feeding termites. Intensity of attack was scored from 0–5 (0 = baits completely intact; 1 = 1–25% consumed; 2 = 26–50% consumed; 3 = 51–75% consumed; 4 = 76–99% consumed; 5 = 100% consumed; following Dawes-Gromadzki, 2003). Baits that were disturbed ($N = 31$) or removed ($N = 8$) by other animals, such as elephant or baboons (*Papio ursinus*), were excluded from analyses.

The volume of dead wood (i.e. woody debris lying on the forest floor without living roots) available to termites on the forest floor was estimated using the line intersection method (Berge et al., 2008; Warren and Olsen, 1964). Ten lines of 20 m were positioned randomly in each plot and used to sample large logs (≥ 19 cm diameter), medium wood (11–19 cm) and small wood (5–11 cm). A 2 m subsection of each line was systematically chosen to sample woody litter (0.5–5 cm). All measurements were made in situ, with no material removed from the field. Dead wood availability was quantified once, in January 2014, because we did not expect large changes to the availability of dead wood over the course of the study. January fell in the middle of the sampling period and so was considered to represent the average wood availability during sampling.

2.3. Termite identifications

Termite specimens were identified to species wherever possible, and to genus when taxonomic constraints prevented species level identification. Termites were identified by ABD (wood-feeders) and PE (soil-feeders). Voucher specimens are lodged in the National Collection of Insects at the Agricultural Research Council, South Africa.

2.4. Analyses

Termites were classified into four functional groups (FGs), based on their food preferences following Donovan et al. (2001): (I) the non-termitids, that feed on dead wood and grass, all with symbiotic flagellate protists in their gut; (II) termites that feed on a wide range of

relatively un-decomposed materials, such as dead wood, grass, and leaf litter; (III) humus-feeders, whose guts contents contain still-visible plant fragments; and (IV) true soil-feeders, whose gut contents contain soil without visible plant fragments. Functional groups II–IV contain only Termitidae (Donovan et al., 2001), and have no flagellate protists in their guts.

Termite data were analysed at the generic level due to challenges with the identification to species level for most genera. Termite generic density, abundance, assemblage composition and activity levels were compared between areas where elephant were present and absent across the different sampling months. Due to animal disturbance, the number of baits available for termite sampling differed per plot. The termite data were corrected for the number of baits per plot, by multiplying the mean generic density or abundance per bait per plot by 20 to obtain the generic density or abundance per 20 baits.

Generic density and abundance of all termites between treatments (i.e. elephant presence vs. absence), and across sampling months, were analysed using a linear model with a Gaussian error distribution. Assumptions of normality and homogeneity of variance in the data were assessed using a Shapiro-Wilk test (normality) and Levene's test (homogeneity of variance), as well as visually with histograms and boxplots, and found to be met. Generic density and abundance were also analysed separately for wood- (FGs I and II) and soil-feeding termites (FGs III and IV). Effects of elephant presence and sampling month on wood-feeding termites were assessed using a generalized linear model with a quasipoisson error distribution and log-link function (because assumptions of normality and homogeneity of variance were violated). For soil-feeding termites, effects of elephant presence and sampling month on generic density were analysed using a linear model with a Gaussian error distribution, whereas a generalized linear model with a quasipoisson error distribution and log-link function was used for the abundance of soil-feeding termites. Post hoc testing was conducted using Tukey contrasts.

Termite assemblages were compared between treatments and sampling months for all functional groups combined, as well as for wood- and soil-feeding termites separately. A PERMANOVA, based on 9,999 permutations, was used to test for differences in termite assemblages between areas where elephant were present and absent, and among sampling months, including interaction effects between these factors. Abundance values were square root-transformed prior to analysis to ensure that both common and rare genera influenced the calculation of the Bray-Curtis similarity index (Clarke and Warwick, 2001). We used the zero-adjusted Bray-Curtis coefficient, which adds a dummy genus to the assemblages, because many samples were relatively sparse in number of genera and abundance (Clarke and Gorley, 2006). A similarity percentage analysis (SIMPER) was performed to identify which genera contributed most to the differences between assemblages, which included both wood- and soil-feeding termites in the analyses. We also used the Bray-Curtis similarity index to construct two nMDS ordinations using 25 iterations to depict differences in the assemblages of wood- and soil-feeding termites separately. We chose to use nMDS over PCA or other ordination techniques because there are few (if any) assumptions about the data and relationships between samples associated with this technique (Clarke and Warwick, 2001). The stress value of the ordination represents the goodness of fit, with a 2D stress value < 0.05 representing an extremely good fit; < 0.1 a good fit; < 0.3 > 0.2 a reasonable fit with some caution applied to interpretation; and > 0.3 a poor fit (Clarke and Warwick, 2001).

Frequency of termite attack was calculated as the proportion of baits with evidence of termite foraging during each sampling month. The proportion of attack between areas with and without elephant, and across sampling months, was analysed using ANOVA, after square root-transformation of the data to meet assumptions of normality and homogeneity of variance.

Differences in intensity of attack between the two treatments (i.e. elephant presence vs. absence) were assessed using a generalized linear

model, fitted with a negative binomial error distribution and log-link function, as this provided a better fit than a Poisson distribution, which was overdispersed. *P*-values used for post hoc pairwise comparisons were adjusted using the Bonferroni method.

The volume of dead wood available on the forest floor was calculated using the following formula adapted from Berge et al. (2008):

$$V = nd^2\pi 10^4/8t,$$

where *V* is the total volume ($\text{m}^3 \text{ha}^{-1}$) of items of diameter class *d* (m), *n* is the number of intersections for items of diameter class *d* and *t* is the total length of the transect (m).

The volume of dead wood for each of the four categories (i.e. litter, small, medium and large wood), as well as all categories combined, were then compared between treatments using independent *t*-tests.

Multivariate species assemblage analyses were performed using PRIMER v. 6. All other analyses were performed in SPSS 22 (IBM SPSS Statistics) and R v. 3.1.2 (www.r-project.org). Significance levels were set at $P < 0.05$.

3. Results

We sampled termites from 11 genera, five subfamilies and two families (Tables 1, A1). Termite genera from all four functional groups were sampled. The most abundant wood-feeding termites sampled were from the genus *Odontotermes*, and the most abundant soil-feeding termite was the soldierless genus *Astalotermes*.

Eight years of elephant absence did not significantly affect generic density ($F_{1,42} = 1.196$, $P = 0.28$; Fig. 1a) or abundance ($F_{1,42} = 0.050$, $P = 0.82$; Fig. 1b). Generic density was affected by sampling month ($F_{2,42} = 3.775$, $P = 0.03$; Fig. 1a), with a greater generic density in February than in December ($P < 0.01$). In contrast, abundance was not affected by sampling month ($F_{2,42} = 0.524$, $P = 0.60$; Fig. 1b). No significant interaction effects between treatment and sampling month were found for generic density ($P = 0.36$) or abundance ($P = 0.61$).

When separating these results between wood- and soil-feeding termites, we found the generic density of both functional groups to be unaffected by elephant presence (wood-feeders: $LR \chi^2_1 = 1.717$, $P = 0.19$; soil-feeders: $F_{1,42} = 0.038$, $P = 0.85$; Fig. 2ab). Only generic density of wood-feeding termites was affected by sampling month ($LR \chi^2_2 = 7.726$, $P = 0.02$; soil-feeders: $F_{2,42} = 0.281$, $P = 0.97$), with greater generic density in February than in December ($P < 0.05$; Fig. 2a). The abundance of wood- and soil-feeding termites separately were also not affected by elephant presence (wood-feeders: $LR \chi^2_1 = 0.055$, $P =$

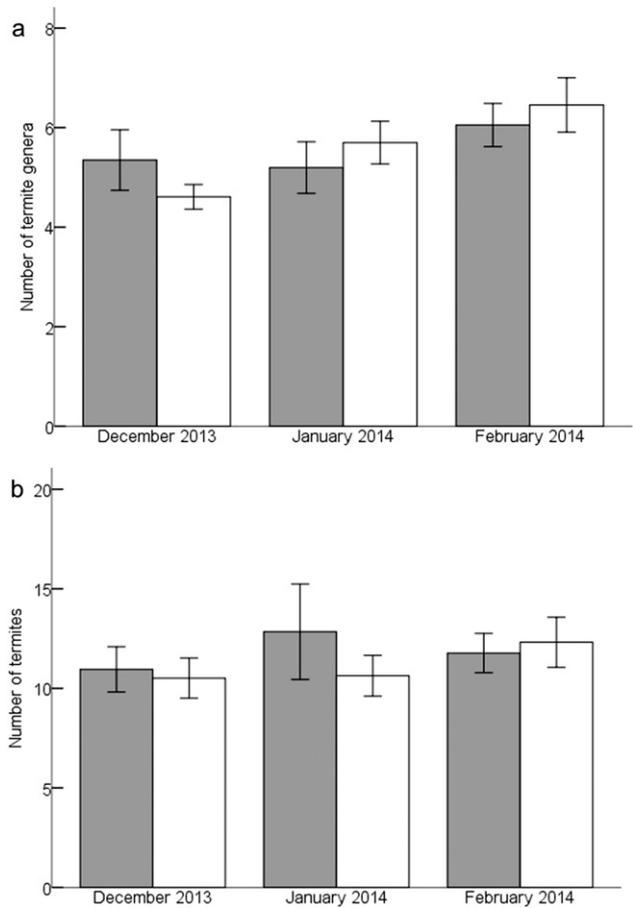


Fig. 1. Mean termite generic density (a) and mean abundance (b) in areas with (grey bars) and without elephant (open bars) in Sand Forest, South Africa. Error bars represent one standard error. $N = 8$ replicates per treatment (i.e. elephant present vs. elephant absent).

0.82; soil-feeders: $LR \chi^2_1 = 0.001$, $P = 0.97$; Fig. 2cd) or sampling month (wood-feeders: $LR \chi^2_2 = 1.275$, $P = 0.53$; soil-feeders: $LR \chi^2_2 = 0.685$, $P = 0.71$; Fig. 2cd). No significant interaction terms for treatment and sampling month were recorded for generic density ($P > 0.97$) or abundance ($P > 0.63$), for either wood or soil-feeding termites.

Table 1
Termite genera encountered in Sand Forest, South Africa

Family	Subfamily	Genus	Functional group*	Abundance (number of encounters** per plot per month; mean \pm SE)					
				December		January		February	
				Elephant present	Elephant absent	Elephant present	Elephant absent	Elephant present	Elephant absent
Termitidae	Apicotermittinae	<i>Adaioprotermes</i> sp.	III	0.63 \pm 0.26	0.90 \pm 0.31	0.92 \pm 0.35	0.26 \pm 0.17	0.38 \pm 0.19	0.40 \pm 0.29
		<i>Alyscotermes</i> sp.	III	0.89 \pm 0.23	0.50 \pm 0.27	1.86 \pm 0.56	1.52 \pm 0.27	1.35 \pm 0.47	0.55 \pm 0.21
		<i>Apicotermes</i> sp.	IV	0.38 \pm 0.26	Absent	1.09 \pm 0.64	0.76 \pm 0.42	0.64 \pm 0.33	0.84 \pm 0.27
	Cubitermittinae	<i>Astalotermes</i> spp.	III	2.04 \pm 0.61	1.94 \pm 0.32	4.18 \pm 0.61	3.29 \pm 0.89	3.63 \pm 0.81	3.48 \pm 1.01
		<i>Cubitermes</i> sp.	IV	2.03 \pm 0.63	2.43 \pm 0.56	1.82 \pm 0.85	1.14 \pm 0.35	1.05 \pm 0.35	1.10 \pm 0.29
	Termitinae	<i>Microcerotermes</i> spp.	II	0.51 \pm 0.27	Absent	0.13 \pm 0.13	0.76 \pm 0.25	0.26 \pm 0.17	0.84 \pm 0.28
		<i>Macrotermes</i> spp.	II	1.03 \pm 0.44	1.50 \pm 0.60	0.14 \pm 0.14	0.25 \pm 0.16	0.67 \pm 0.38	0.65 \pm 0.39
	Nasutitermittinae	<i>Microtermes</i> spp.	II	0.13 \pm 0.13	Absent	0.27 \pm 0.18	0.13 \pm 0.13	0.40 \pm 0.20	1.06 \pm 0.55
		<i>Odontotermes</i> spp.	II	2.77 \pm 0.14	2.84 \pm 1.05	1.00 \pm 0.73	1.53 \pm 0.50	0.86 \pm 0.32	1.07 \pm 0.46
		<i>Trinervitermes</i> sp.	II	Absent	Absent	Absent	Absent	Absent	0.14 \pm 0.14
Rhinotermitidae	<i>Schedorhinotermes</i> sp.	I	0.64 \pm 0.33	0.14 \pm 0.14	1.18 \pm 0.41	0.76 \pm 0.31	1.92 \pm 0.59	1.21 \pm 0.43	

* Termites were classified into four functional groups (FGs), based on their food preferences following Donovan et al. (2001): (I) the non-termitids, that feed on dead wood and grass, all with symbiotic flagellate protists in their gut; (II) termites that feed on a wide range of relatively un-decomposed materials, such as dead wood, grass, and leaf litter; (III) humus-feeders, whose guts contents contain still-visible plant fragments; and (IV) true soil-feeders, whose gut contents contain soil without visible plant fragments. Functional groups II–IV contain only Termitidae (Donovan et al., 2001), and have no flagellate protists in their guts.

** Encounters: the number of times a termite species is found on a bait in a plo

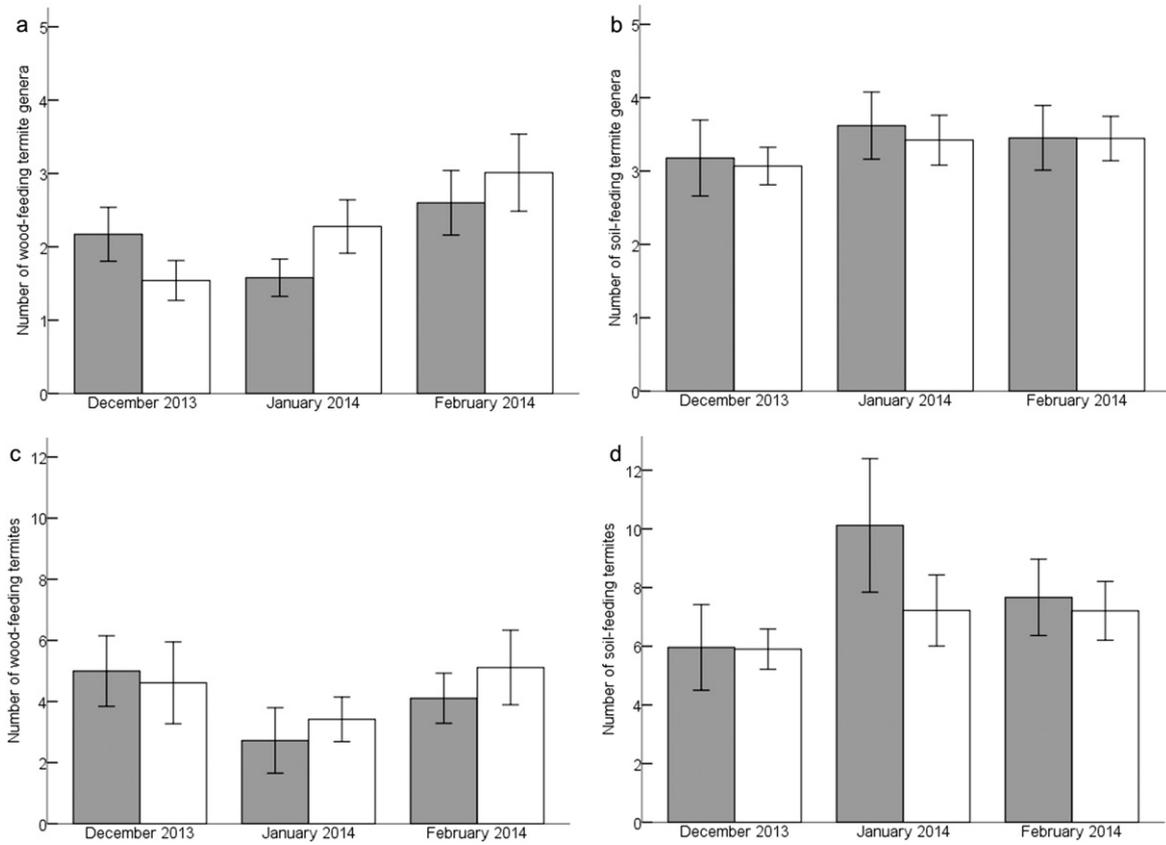


Fig. 2. Mean generic density of wood- (a) and soil-feeding termites (b), and mean abundance of wood- (c) and soil- (d) feeding termites in areas with (grey bars) and without elephant (open bars) in Sand Forest, South Africa. Error bars represent one standard error. $N = 8$ replicates per treatment (i.e. elephant present vs. elephant absent).

Termite assemblages including termites of all functional groups were not affected by elephant presence ($F_{1,42} = 0.717$, $P = 0.62$), but did differ among sampling months ($F_{2,42} = 3.148$, $P < 0.01$), with assemblages being different between December and January ($P < 0.01$) as well as between December and February ($P < 0.01$). The differences between the December and January assemblages were mostly driven by differences in abundances from termites from functional groups II and III, of which *Odontotermes* showed the greatest change (decline) in abundance of all termite genera between December and January (13.9%; Table A2). Differences between December and February could not be attributed to one specific functional group. However, the greatest change (decline) occurred with the genus *Cubitermes* (13.5%; Table A2). Assemblages including only wood-feeding termites were not affected by elephant presence ($F_{1,42} = 1.197$, $P = 0.33$; Fig. 3a). This was also clear from the nMDS ordination, although this needs to be interpreted with some caution as the 2D stress value of 0.23 indicates a reasonable, but imperfect fit. Assemblages of wood-feeding termites were only affected by sampling month ($F_{2,42} = 2.767$, $P = 0.02$), with assemblages differing between December and January ($P = 0.02$) and between December and February ($P = 0.01$). Assemblages of soil-feeding termites were not affected by elephant presence ($F_{1,47} = 0.554$, $P = 0.66$; Fig. 3b), but were affected by sampling month ($F_{2,42} = 2.889$, $P < 0.01$), with assemblages differing between December and January ($P < 0.01$) and December and February ($P < 0.01$). No significant interaction effects between treatment and sampling month were found for any of the assemblage comparisons ($P > 0.5$).

Activity levels of wood-feeding termites were not significantly affected by elephant presence (frequency: $F_{1,42} = 0.801$, $P = 0.38$; intensity: $\chi^2_1 = 2.547$, $P = 0.11$; Fig. 4). Frequency of attack was not affected by sampling month ($F_{2,42} = 1.043$, $P = 0.36$; Fig. 4a), but intensity of attack was ($\chi^2_2 = 20.025$, $P < 0.001$), with lower attack

intensity in December than in January or February ($P \leq 0.027$; Fig. 4b). No significant interaction effects between treatment and sampling month were found for frequency or intensity of attack by termites ($P \geq 0.649$).

Elephant presence had a significant effect on the total volume of woody debris (i.e. fallen dead wood ranging from litter to large branches and pushed over trees), with a greater volume of dead wood where elephant were present ($t_{612,236} = 3.793$, $P < 0.001$). Volumes of litter, small and medium-sized woody debris were also greater where elephant were present ($t_{158} = 3.220$, $P < 0.01$; $t_{149,285} = 4.882$, $P < 0.001$; $t_{156,326} = 2.335$, $P = 0.021$ respectively; Fig. 5). The volume of large woody debris did not differ between areas with and without elephant ($t_{152,627} = 1.393$, $P = 0.166$; Fig. 5).

4. Discussion

Despite the significantly greater volume of available woody debris where elephant were present, termite activity and assemblages did not differ between areas where elephant were present or absent, and we therefore found no evidence of a feedback loop between termites and elephant. Within ecological networks, trophic interactions may represent important feedback loops, with strong and weak linkages, as well as direct and indirect interactions (Worm and Duffy, 2003). Due to the many components within ecosystems, feedback loops are most often indirect. The absence of one component, be it a plant or herbivore species, can change environmental conditions, and subsequently affect ecosystem stability leading to the potential loss of other species, thereby affecting biodiversity levels and ecosystem functioning (Worm and Duffy, 2003). Specifically, the loss of a keystone species, such as elephant or termites, may lead to a loss of several other species (Walker, 1995).

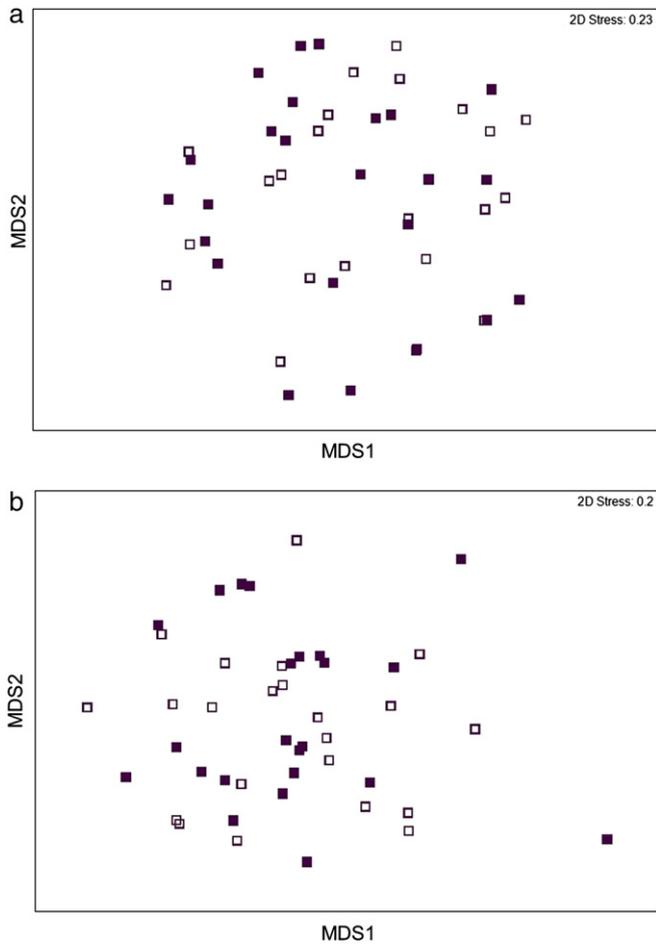


Fig. 3. nMDS ordinations showing no effect of elephant presence (filled squares) or absence (open squares) on assemblages of a) wood-feeding and b) soil-feeding termites in Sand Forest, South Africa.

Termites, particularly the functional group of wood-feeding termites, use woody debris, and might be expected to benefit from elephant disturbance. Generally, wood-feeding termites are positively associated with a moderate level of disturbance due to increased litter availability, whereas disturbance has a negative impact on soil-feeders (Eggleton et al., 2002). Wood-feeders are therefore generally more resilient to disturbance than soil-feeders. In our study, even though more woody debris was available for wood-feeding termites in disturbed areas (i.e. where elephants were present), no differences in diversity (measured as generic density, abundance and assemblage composition) or activity were found after eight years of elephant exclusion. In contrast, habitats in an old growth forest along a human disturbance gradient from primary forest to secondary, logged forest to crop plantations, showed a decline in termite densities, abundances (Luke et al., 2014) and richness (Jones et al., 2003). Since we did not detect a difference in wood-feeding termites between the two elephant treatments, this suggests that termites in Sand Forest are resilient to natural (elephant) disturbance, which may be less severe than human disturbance. This is further supported by studies that have found wood- and soil-feeding termites to be relatively resilient to fire, another natural disturbance (Avitabile et al., 2015; Davies et al., 2012; Neoh et al., 2015). Similarly, soil-feeding termites have been shown to be very sensitive to anthropogenic forest disturbance elsewhere (Eggleton et al., 1996), but were unaffected by elephant presence in our study, supporting the notion that elephant disturbance is less severe compared with human disturbance. Elephant could also increase soil compaction

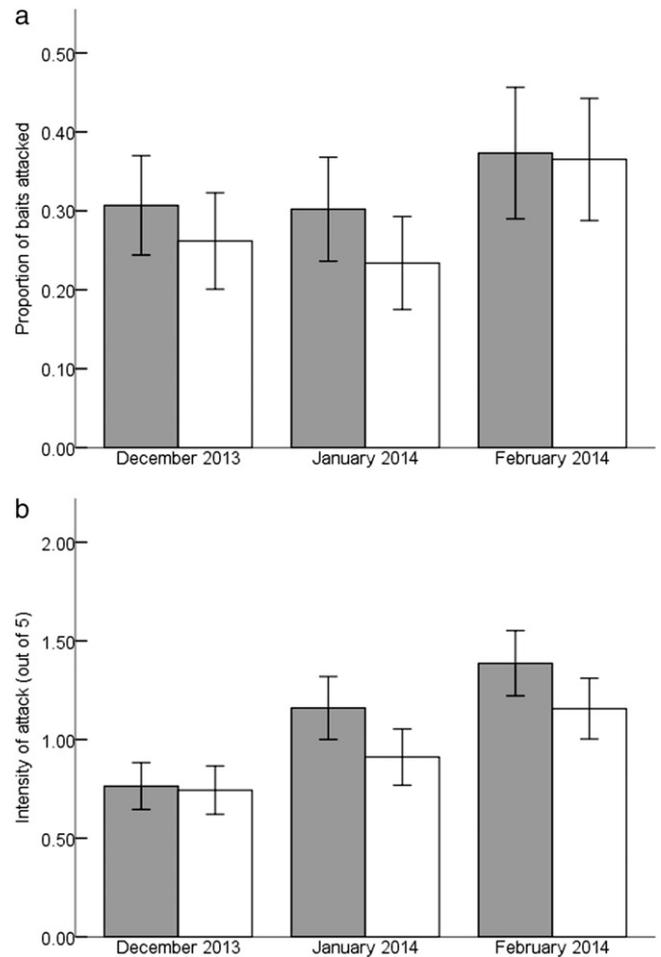


Fig. 4. Mean frequency (a) and mean intensity (b) of termite attack on cellulose baits in areas with (grey bars) and without elephant (open bars) in Sand Forest, South Africa. Error bars represent one standard error. $N = 8$ replicates per treatment (i.e. elephant present vs. elephant absent).

through trampling, and reduce soil moisture content by reducing tree densities and cover (Haynes, 2012; Scholes and Archer, 1997). These actions could also negatively affect soil-feeding termites, which are

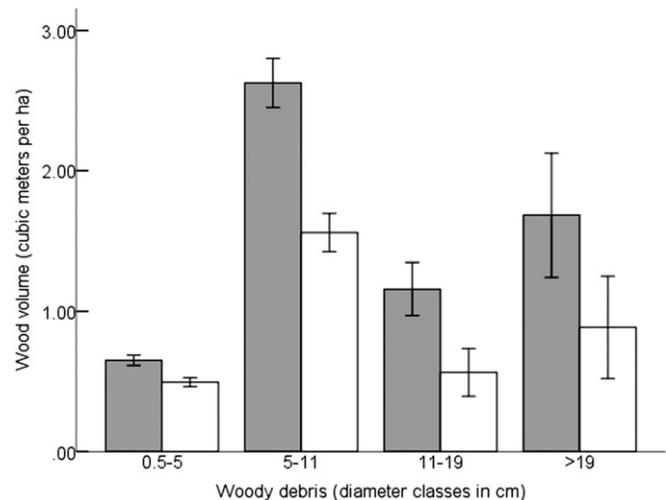


Fig. 5. Mean volume of woody debris ($\text{m}^3 \text{ha}^{-1}$) in various size classes in areas with (grey bars) and without elephant (open bars) in Sand Forest, South Africa. Error bars represent one standard error. $N = 8$ replicates per treatment (i.e. elephant present vs. elephant absent).

sensitive to soil conditions (Eggleton et al., 2002; Luke et al., 2014). However, we did not find any evidence of an (indirect) elephant effect on soil-feeding termites in Sand Forest. Other processes such as predation, competition and constraints on colonisation might be more important in determining termite diversity and activity here. In addition, termite colonies, particularly those of larger fungus-growing genera such as *Macrotermes* or *Odontotermes*, can be relatively long-lived (up to several decades; Jouquet et al., 2005; Keller, 1998) and might not be affected by the comparable short time-frame (eight years) of our elephant exclusion. Further monitoring or sampling in areas where elephant have been absent for longer periods will be necessary to confirm our findings. Similarly, studies in different ecosystems (e.g. savannas) will help to clarify the generality of our results. Nevertheless, eight years of elephant absence did significantly affect the volume of woody debris available to termites and such changes in resources would be expected to influence termite colonies. The lack of effect despite this resource change suggests instead that termite diversity is indeed unaffected by elephant presence.

Overall, we sampled eleven genera of termites, which is relatively few considering that termites are most diverse in tropical closed canopy forests (Attignon et al., 2005). However, our findings are in line with termite surveys from savannas and similar latitudinal bands (e.g. Davies et al. (2012): 7–16 genera, Dawes-Gromadzki (2003): 9 genera, and Carrijo et al. (2009): 16 genera), and termite diversity is known to decrease with latitude (Eggleton et al., 1994). Furthermore, Sand Forest occurs in relatively small forest fragments surrounded by savanna, and termite diversity may not be directly comparable to other (sub)tropical forests. Termites are likely to have colonised Sand Forest from the surrounding savanna, and so the termite diversity in Sand Forest might be expected to be more similar to the adjacent savanna than to closed canopy forest (although this was not tested in this study). In addition, the baiting method employed (using cellulose baits) was primarily aimed at sampling wood-feeding termites and not ideal for sampling soil-feeding termites, for which other methods such as active searching are more appropriate and effective (Davies et al., 2013; Jones and Eggleton, 2000). More soil-feeding termite genera might be present in Sand Forest, but were undetected by our sampling protocol. Nevertheless, we found relatively high species diversity and abundance of soil-feeding termites compared with wood-feeding termites. This was surprising given our sampling protocol and because Sand Forest soil is relatively sandy, containing < 10% clay (Lagendijk, unpubl. data), which is below the known clay content range preferred by soil-feeding termites (Donovan et al., 2001). Sand Forest soil contains a thick humus-layer that is often uniform and thick, particularly in the less disturbed areas (i.e. where elephant are absent; pers. obs. Lagendijk) and we sampled three humus-feeding genera (*Adaioprotermes*, *Alyscotermes* and *Astalotermes*) out of the five soil-feeding genera sampled. Furthermore, we suspect that soil-feeding termites, which are highly dependent on moisture, were attracted to the increased moisture levels in the cellulose baits as these were able to retain more moisture than the surrounding substrate. This is corroborated by our finding that there was no effect of sampling month on soil-feeding termite density and abundance. The November prior to the December sampling was relatively wet (88 mm) compared with the sampling months of January and February (Phinda Private Game Reserve, unpubl. data). Wood-feeding termite densities were lower in December compared with February, but soil-feeding termites were unaffected by this increase in moisture. We suspect that the baits were too moist to attract wood-feeding termites during December, and unattractive in part due to fungal infection, as suggested previously (Davies et al., 2013). This pattern was also reflected in the intensity of attack data, with lower attack intensity in December. Termite assemblages also displayed some temporal variation, with different assemblages present in December, the wettest month, compared with both January and February for both wood- and soil-feeders, as well as when the groups were combined. This could also possibly be attributed to differing rainfall amounts.

5. Conclusions

We found termite diversity to be relatively low in Sand Forest and activity levels of wood-feeding termites to be unaffected by eight years of elephant absence (despite increased woody debris where elephant were present). We conclude that the postulated positive feedback loop between termites and elephant does not hold, at least not over the short-term (eight years) in Sand Forest. However, these findings do not dispute that areas with high termite activity influence herbivore foraging (including elephant), but only suggest that elephant foraging does not affect termite activity. This indicates that natural disturbances such as elephant impact or fire, have little to no consequence on termites, and the fundamental roles they perform in ecosystems. This finding that elephant do not affect termite diversity is important for conservation management. Termites play a key role in many ecosystem processes (Jouquet et al., 2011), including within areas where elephant populations and their impacts are increasing and of great concern (Kerley et al., 2008). There is often a unidirectional bias of reporting negative effects of elephant in the literature (see Kerley et al., 2008), and it is of crucial importance that non-significant or positive results are also reported (see also Lagendijk et al., 2015). Here, we found that elephant management does not affect termites and the important ecosystem functions they perform, allowing managers to redirect efforts and concerns surrounding elephant management elsewhere.

Table A1

Termite genera and species encountered in Sand Forest, South Africa.

Family	Subfamily	Genus (species)	Functional group
Termitidae	Apicotermatinae	<i>Adaioprotermes</i> sp.	III
		<i>Alyscotermes</i> sp.	III
		<i>Apicotermes</i> sp.	IV
		<i>Astalotermes</i> sp. 1	III
		<i>Astalotermes</i> sp. 2	III
		<i>Astalotermes</i> sp. 3	III
	Termitinae	<i>Cubitermes</i> sp.	IV
		<i>Microcerotermes</i> sp. 1	II
		<i>Microcerotermes</i> sp. 2	II
	Macrotermatinae	<i>Macrotermes michaelsoni</i>	II
		<i>Macrotermes natalensis</i>	II
		<i>Microtermes</i> spp.	II
		<i>Odontotermes</i> sp. 1	II
		<i>Odontotermes</i> sp. 2	II
		<i>Odontotermes</i> sp. 3	II
Nasutitermitinae	<i>Trinervitermes</i> sp.	II	
	<i>Schedorhinotermes lamanianus</i>	I	

Table A2

SIMPER analyses of the termite assemblages per sampling month in Sand Forest, South Africa. Only the pairwise tests with significantly different termite assemblages are shown.

Sampling month	Genus	Average abundance	Average dissimilarity	Cumulative %	
December vs. January	<i>Odontotermes</i>	1.35	0.79	6.14	13.87
	<i>Astalotermes</i>	1.32	1.83	5.76	26.9
	<i>Macrotermes</i>	0.82	0.19	5.58	39.51
	<i>Alyscotermes</i>	0.62	1.17	5.26	51.41
	<i>Cubitermes</i>	1.37	1.05	5.13	63.02
	<i>Schedorhinotermes</i>	0.31	0.72	4.21	72.54
	<i>Adaioprotermes</i>	0.65	0.5	3.89	81.34
	<i>Microcerotermes</i>	0.22	0.4	3.56	89.39
	<i>Apicotermes</i>	0.15	0.57	2.78	95.67
	<i>Microtermes</i>	0.06	0.19	1.92	100
December vs. February	<i>Cubitermes</i>	1.37	0.92	6.27	13.45
	<i>Schedorhinotermes</i>	0.31	1.01	5.54	25.34
	<i>Macrotermes</i>	0.82	0.5	5.17	36.43
	<i>Astalotermes</i>	1.32	1.9	5.14	47.46
	<i>Odontotermes</i>	1.35	0.75	4.76	57.67
	<i>Adaioprotermes</i>	0.65	0.37	4.75	67.87
	<i>Alyscotermes</i>	0.62	0.77	4.06	76.58

(continued on next page)

Table A2 (continued)

Sampling month	Genus	Average abundance	Average dissimilarity	Cumulative %	
	<i>Microtermes</i>	0.06	0.51	3.74	84.61
	<i>Apicotermes</i>	0.15	0.65	3.66	92.46
	<i>Microcerotermes</i>	0.22	0.49	3.08	99.06
	<i>Trinervitermes</i>	0	0.07	0.44	100

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