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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 exclosure 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.

1. Introduction

Termites are ecosystem engineers that perform important functional roles in many ecosystems (Freymann 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 (Freymann 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; Freymann 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 (Freymann 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 (Freymann 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 (Freymann et al., 2008), further enriching the soil (Freymann 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; Freymann 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 km^2) for eight years, while access by other herbivores has been unhindered (see Lagendijk 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; Lagendijk 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 (Lagendijk 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 (Lagendijk 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; Lagendijk 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 km^2) were joined and indigenous game species reintroduced. Since then the reserve has expanded to its current 235 km^2. 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 (Lagendijk 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; Lagendijk, unpubl. data). Sand Forest can form a dense vegetation with closed canopy up to 15 m high. Characteristic tree species include *Balanites maughamii*, *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 (Lagendijk, 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