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Termitaria *vs.* mistletoe: Effects on soil properties and plant structure in a semi-arid savanna

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ABSTRACT

Termite mounds by creating patches of increased resource availability (e.g. water and nutrients) are a major source of spatial heterogeneity in savannas. Likewise, mistletoes via input of nutrient-rich litter alter nutrient and water availability increasing environmental heterogeneity in semi-arid savanna. Despite this recognition, the influence of termitaria and mistletoe on soil properties and plant community have not been investigated together. We established eight 100 m^2 plots each on termitaria, under mistletoe-infected trees and in the surrounding savanna and examined the soil properties and the structure of *Securinega virosa* (Euphorbiaceae) and *Euclea divinorum* (Ebenaceae) in semi-arid savanna, southwest Zimbabwe. Soil properties significantly differed among the sampling sites ($p = 0.001$) with soils of increasing clay, soil moisture, pH and phosphorus, calcium and ammonium concentrations occurring on termite mounds. Soils under mistletoe-infected trees were associated with silt, organic matter, sodium, potassium, magnesium and nitrate and the surrounding savanna was associated with soils of increasing sand content. Plant structure also differed significantly between sites with greater basal area of both *S. virosa* and *E. divinorum* on termitaria relative to mistletoe-infected trees and the surrounding savanna. However, the stem density of *S. virosa* was greater under mistletoe-infected trees than on termitaria and in the surrounding savanna. Plant structural variables of individuals of the same species were affected by different soil properties across treatments. The major patterns showed that plant structure was influenced positively by soil moisture and nitrate and negatively by phosphorus on termitaria; positively by clay, soil moisture and ammonium and negatively by potassium under mistletoe-infected trees; and by phosphorus and calcium in the surrounding savanna. These findings show that soil properties, plant structure and their relationships differ between termitaria, mistletoe-infected trees and surrounding savanna, and these differences are suggested to increase heterogeneity in soil resources availability and vegetation structure in semi-arid savanna.

1. Introduction

Ecosystem spatial heterogeneity is a key characteristic of African savanna landscapes (Scholes, 1990). One of the major sources of spatial heterogeneity in savannas are patches of increased resource availability (e.g. nutrients) such as those created by termites (Sileshi et al., 2010) and mistletoes (Ndagurwa, 2015). Termites through mound building activities redistribute and concentrate nutrients on termite mounds relative to the surrounding areas (Muvengwi et al., 2016). Likewise, mistletoes by depositing nutrient-rich litter over extended periods beneath parasitized trees also concentrate nutrients within their immediate vicinity (March and Watson, 2007, 2010; Ndagurwa et al., 2013, 2014a). Thus, the activity of termites and mistletoes could modify resource availability and spatial heterogeneity in savanna ecosystems, and to our knowledge, despite this recognition, the influence of these factors on soil properties and plant assemblages are yet to be investigated together. Here, we compare how termites and mistletoes affect soil properties and plant structure in a semi-arid savanna.

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Termite species of the Macrotermitinae family such as *Macrotermes falciger* Gerstacker construct the most conspicuous and largest mounds in African savannas. These termites process and redistribute soil particles, organic matter, and plant materials to construct their mounds. Using saliva secretions and excreta, the plant material and organic matter are incorporated intimately with mineral constituents, particularly clay in nest construction (Lee and Wood, 1971). As a result, termite nest structures have more clay and silt, organic matter and mineral elements such as carbon, nitrogen, phosphorus and exchangeable cations than in the surrounding soils (Holdo and McDowell, 2004; Konaté et al., 1999; Muvengwi et al., 2016; Seymour et al., 2014; Sileshi et al., 2010). Along with a high clay content, the nest architecture improves soil structure and porosity which increases infiltration, and thus soil water availability (Konaté et al., 1999). As a result, by modulating the availability of resources to other organisms, termites are regarded as ecosystem engineers (Dangerfield et al., 1998).

Likewise, mistletoes can impact soil nutrients and water availability via their effects on litter quality and quantity as well as host tree water use. Mistletoes are aerial hemiparasites which obtain water and nutrients from their host plants via a specialized vascular attachment called a haustorium (Kuijt, 1969; Ehleringer and Marshall, 1995). Although mistletoes may obtain up to 60% of their carbohydrates from the host, most mistletoe species photosynthesize hence they are termed hemiparasites (Hull and Leonard, 1964). Because of their growth form they are buffered against large-scale fluctuations in resource availability by the host plant (Ehleringer and Marshall, 1995). Mistletoes maintain high transpiration rates to enable the movement of solutes from the host xylem to the parasite (Ehleringer and Marshall, 1995), and in the process, they increase whole tree water use (Sala et al., 2001). Consequently, parasitized trees are associated with low soil water availability (Ndagurwa et al., 2014b, 2015). As the flow of nutrients is unidirectional i.e. from host to parasite, mistletoes accumulate mineral elements to much higher concentrations than their hosts (Ehleringer and Marshall, 1995). In addition, the litter remains enriched due to minimal withdrawal of elements prior to leaf abscission (Leonard and Hull, 1965), and such litter decomposes faster and may also stimulate the decomposition of recalcitrant litter of co-occurring species (Quested et al., 2002). Furthermore, due to elevated and more extended periods of litterfall than their hosts, mistletoes contribute large volumes of nutrient-rich litter beneath infected trees enhancing nutrient returns, decomposition and nutrient cycling (March and Watson, 2007; Ndagurwa et al., 2015). Indeed, numerous studies have demonstrated changes in soil properties after mistletoe establishment (e.g., March 2007; Mellado et al., 2016; Muvengwi et al., 2015; Ndagurwa, 2015; Ndagurwa et al., 2013, 2016; Watson, 2016).

Given the ability of both termites and mistletoes to modify soil properties, there is a strong potential for these savanna landscape features to alter the structure and function of the local plant community. Previous research work has shown termitaria to contain plant assemblages that differ from the surrounding areas, mainly enriched in woody plants (Muvengwi et al., 2016; Sileshi et al., 2010; Van der Plas et al., 2013). Similarly, mistletoe infection has also been associated with increase in local plant species composition and productivity relative to areas without mistletoe (March, 2007; March and Watson, 2007; Ndagurwa et al., 2016). However, it is unclear how nutrient enrichment and plant community structure may differ between termite mounds and mistletoe-infected trees. Termites and mistletoes markedly differ in the mechanisms with which they modify soil properties, and therefore they are also likely to assemble plant communities of varying composition and structure, which, to our knowledge, is yet to be examined. Moreover, the soil properties which structure plant communities on termitaria or under mistletoe-infected trees remains to be addressed.

Here, we focus on the soil physical and chemical properties and vegetation structure on termitaria, beneath mistletoe-infected trees and in the surrounding savanna. In this ecosystem, termite mounds and mistletoes are dominant features of the landscape. Therefore, the objectives of this study were to determine whether (a) mistletoes influence soil nutrient concentrations and plant structure like *Macrotermes falciger* mounds and (b) differences in soil physical and chemical properties are reflected in the structure of individuals of the same species growing on termitaria, beneath mistletoe-infected trees and in the surrounding savanna.

2. Materials and methods

2.1. Study area description

We studied soil nutrient concentrations and vegetation structure on termitaria, beneath mistletoe-infected trees and in the savanna matrix in 2016 at the 160 ha National University of Science and Technology Field Laboratory (20°08′S, 28°36′E, 1341 m a.s.l.) in the southern highveld of Zimbabwe. The study site experiences three climatic seasons: a hot wet period (November to April), a cool dry period (May to July) and a hot dry period (August to October). The mean annual rainfall ranges between 325 and 915 mm, with a mean annual rainfall of 600 mm. Mean annual temperatures is 23.7 °C (Mlambo et al., 2005). The study site is a semi-arid deciduous open woodland savanna with a tree crown cover of 30–40%. The overstory is dominated by *Colophospermum mopane* (Kirk ex Benth.) Kirk ex J. Leonard, *Acacia karroo* Hayne, *Acacia gerrardii* Benth., *Acacia nilotica* (L.) Willd. Ex Delile and *Dichrostachys cinerea* (L.) Wight & Arn. and a diverse herbaceous layer dominated by perennial grasses such as *Panicum maximum* Jacq., *Schmidtia pappophoroides* Steud., *Heteropogon contortus* L., *Bothriochloa radicans* (Letim.) A. Camus and *Enneapogon scoparius* Stapf and such as *Tragus berteronianus* Schult., *Aristida adscensionis* L., *Chloris virgata* Swartz, and *Dactyloctenium aegyptium* (L.) Willd. (Mlambo et al., 2007).

Mounds of *Macrotermes falciger* occur randomly across the reddish-brown chromic luvisols (FAO, 1988) of the study site. These termites construct subterranean nests essentially for shelter and cultivation of exosymbiotic *Termitomyces* fungi, which alters soil physical and chemical properties (Muvengwi et al., 2016). *Macrotermes* mounds have higher soil moisture, clay content and soil nutrient concentrations than the surrounding soils, with approximately twice the concentrations of soil nutrients (e.g., Muvengwi et al., 2014, 2016; Sileshi et al., 2010).

Aerial hemiparasites (hereafter mistletoes) occur in the study site, mainly on *Vachellia* spp. (formerly *Acacia*). The most common mistletoes in the study site are *Erianthemum ngamicum* (Sprague) Danser (Loranthaceae), *Plicosepalus kalachariensis* (Schinz) Danser (Loranthaceae) and *Viscum verrucosum* Harv. (Viscaceae) (Mapaura and Timberlake, 2004). Previous research work demonstrated, for four *Vachellia* spp. studied, that mistletoe infections were higher in large than small trees (Ndagurwa et al., 2012). Mistletoe-infected trees were also associated with higher litterfall, soil nutrient concentrations, soil microbial biomass and lower soil moisture than uninfected trees (Ndagurwa et al., 2013, 2014a,b, 2016). The consequence of these changes to the soil layer include shifts in the composition, abundance and productivity of understorey plant and animal communities (e.g. litter-dwelling arthropods Ndagurwa et al., 2014b; grasses, Ndagurwa et al., 2016).

2.2. Sampling design and data collection

For this study, we selected termite mounds (*Macrotermes falciger*), mistletoe-infected trees (*Vachellia karroo* Hayne.) and savanna woodland plots/control plots (hereafter surrounding savanna) ($n = 8$ for each category) (Fig. 1). Termite mounds with surface area of at least 100 m^2 and height ≥ 1 m were selected because they have a stable soil chemistry and contain a variety of plant assemblages (Joseph et al., 2012; Seymour et al., 2014). We measured the long and short diameter of each termite mound at right angles using a tape measure and calculated area approximating the mound as an ellipse (Muvengwi, 2017). The mean ± SE termite mound surface area was 112.4 ± 9.54 m^2 and