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Review

Infestation of African savanna ecosystems by subterranean termites

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ABSTRACT

This review is an analysis of the dimensions of termite infestation in African savannas. The aim of this work is to draw the attention of ecologists, conservationists, policy makers and farmers to the current and future threats of subterranean termites to the functioning and sustainability of such ecosystem habitats. This study analyzes and describes termite problem (questionable changes in density and assemblage structure) in selected African savannah ecosystems, synthesizes information on the effects of various human induced habitat disturbance regimes on termites' assemblage structure, predators, nests and feed resources to generate hypotheses relating termite infestation with anthropogenic activities; it describes and critiques existing termite management practices. The review is suggestive that the infestation and resultant undesirable effects of subterranean termites in African savannahs are largely a consequence of the inappropriate savannah management practices (overgrazing, indiscriminate tree cutting and overhunting) undertaken by humans in pursuit of various livelihood options. Based on the evidence presented herein, we hypothesized that (1) human induced habitat disturbance in savanna ecosystems alters the feeding group composition of termites' assemblages, favoring grass harvesters and polyphagus termite feeders that forage on more abundant food items, paying little attention to rarer food items and (2) habitat disturbance through activities like heavy grazing and overhunting results in decline in the populations of both macro and microscopic termite predators, which eventually enhances the proliferation of termite populations, escalates the density of termite nests particularly epigeal mounds and intensifies consumption of herbaceous savannah vegetation. The review calls for dedicated efforts to develop ecological thresholds of savannah biotic and abiotic ecosystem components in which human induced disturbance regimes trigger the destructive behavior of termites. This would provide information that will act as a precautionary savannah habitat monitoring and decision support tool to prevent future infestation of savannah habitats with termites. Also, the review shows that majority of the termite control practices are ineffective, ecologically unsustainable and above all, do not address the root cause of termite infestation and thus merely provide temporary relief to the problem. As such, termite control methods that attempt to enhance proliferation of termite predators need to be studied, developed and emphasized. This review reveals that human induced habitat disturbance depletes termites' predator populations, leading to proliferation of termite populations particularly grass harvesters that intensify their consumption on grass biomass and eventually contribute to denudation of herbaceous vegetation cover in savannah ecosystems.

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1. Introduction

In many tropical savannah ecosystems, termites (Isoptera) are arguably the most important soil ecosystem engineers (Bignell, 2006). In dry savannas for example, where the short duration of the rainy season impedes litter and cattle-dung decomposition by flies, beetles and bacterial and fungal populations (Bignell and Eggleton, 2000; Schuurman, 2005), termites play a key role in nutrient recycling through consumption and mineralization of plant materials. Also, termites play a significant role in bioturbation and soil formation (Brossard et al., 2007; Jouquet et al., 2002), vegetation growth and diversity (Jouquet et al., 2002; Konaté et al., 1999); soil animal and microbial diversity (Anand et al., 2010; Jouquet et al., 2006; Villenave et al., 2009); and soil hydraulic properties (Elkins et al., 1986). Despite their undoubted importance, there is a growing concern over the deleterious effects of subterranean termites on the productivity of several savanna ecosystems in Africa. As such, most termite management practices are focused on total elimination of termite population rather than sustaining their population. In fact, in certain savannah ecosystems, the devastating effects of termites on savannah vegetation outweigh their beneficial role to the extent they have been labeled as the primary cause of ecosystem deterioration (Mugerwa et al., 2012; Wood, 1991). Construction of numerous and massive epigeal mounds (referred to little hills in South Africa) by mound building species (Lovegrove and Siegfreid, 1986, 1989) is associated with reduction of land area for production of herbaceous biomass (particularly grasses) for livestock nutrition. Depending on the density of epigeal mounds in an area, Mugerwa et al. (2011a, 2011b) reported that termite mounds can cover between 25% and 75% of the total habitat soil surface area at the expense of both herbaceous vegetation and livestock nutrition. The live termite mounds do not only occupy potential areas of herbaceous vegetation production but also suppress growth of vegetation on them. Also, termites have been noted to consume enormous amounts of herbaceous vegetation, contributing to the formation and/or expansion of bare surfaces that facilitate high rates of water runoff, erosion and silting of downstream water reservoirs in rangeland ecosystems (Mugerwa, 2011; Zziwa et al., 2012b).

Reports by Okwakol and Sekamatte (2007), Mugerwa (2011), Wood (1991) and Zziwa et al. (2012a) attributed termite problem to inappropriate savannah ecosystem management practices (such as overgrazing, indiscriminate tree cutting, inappropriate fire regimes and over hunting among others) but the actual mechanisms through such activities that trigger the negative effects of termites in savannah habitats remain elusive. Other studies merely relate termites' assemblage structural changes to varying regimes of human induced habitat disturbance through activities such as clearing of trees (Dawes, 2010; Okwakol, 2000; Vasconcellos et al., 2010), livestock grazing (Tracy et al., 1998) and burning (Tracy and Dawes-Gromadzki, 2007) but do not show how such changes may result in or escalate the current termite problem. This review covers previous studies undertaken in African (Fig. 1) and non-African savanna ecosystems to analyze and describe the termite problem in selected African savannah habitats (Section 2), synthesizes information on the effects of various human induced habitat disturbance regimes on termites' assemblage structure, predators, nests and feed resources to generate hypotheses relating termite infestation with anthropogenic activates (Section 3); describes and critiques existing termite management practices (Section 4) and finally concludes by suggesting areas for sustainable management of termites in African savannahs.

2. The termite problem in African savannas

Although termites are undoubtedly important organisms that play a key role in the functioning of many savanna ecosystems (Chapin et al., 2002; Holt and Lepage, 2000; Jouquet et al., 2011; Okullo and Moe, 2012), there are growing concerns over their negative effects in same ecosystems (Eriksson and Ehrlén, 1992; Fridley et al., 2007; Rogers et al., 1999). Many termite species especially *Macrotermes* species construct large epigeal mounds (Pearce, 1997; Traore et al., 2008) that occupy significant portions of the soil surface in many savanna ecosystems (Picker et al., 2007). Mugerwa et al. (2011b) reported that epigeal termite mounds occupied up to 75% of the total soil surface area in several savanna habitats in the grasslands of central Uganda. Picker et al. (2007) also reported that giant earth mounds formed by the Southern harvester termite *Microhodotermes viator* occupied enormous proportions of the land surface in the Succulent Karoo, Nama-Karoo and Fynbos biomes, with mound densities ranging from 143 to 704 km^{-2}. Lovegrove and Siegfreid (1986, 1989) reported that the "little hills" of the same species occupied 14–25% of the land surface in South-western parts of Southern Africa. In the Sudanian savanna ecosystem of Burkina Faso, Traore et al. (2008) noted that the basal area occupied by epigeal mounds constructed by *Cubitermes*, *Macrotermes* and *Trinervitermes* species ranged from 219 to 985 m^2 ha^{-1}. Although no information was accessed on the mean basal area covered by termite mounds in Ethiopia, Wood (1991) reported that the number of epigeal mounds constructed by *Macrotermes* species alone ranged from 2 to 5 epigeal mounds per hectare. Yet, several authors have provided evidence that mound density is remarkably escalating, suggesting that the current mound density in savanna ecosystems may even be much higher than what is reported in this paper. Supporting evidence to this comes from investigations by Mugerwa et al. (2011a) who reported that the number of epigeal mounds (525 mounds ha^{-1}) in the year 2011 in the grasslands of central Uganda was 192% higher than the value (180 ha^{-1}) reported previously by Okwakol and Sekamatte (2007) and is 28 times higher than the highest density (18.5 ha^{-1}) of epigeal mounds reported in Uganda by Pomeroy (1977). The immediate effect of the escalating density of termite mounds in savanna grasslands is a reduction in the area available for grazing, limiting livestock herbivory to relatively smaller areas which often translate into overgrazing. In the proceeding section (Section 3), we discuss how overgrazing further exacerbates the termite problem. Based on the fact that active termites' mounds are usually devoid of herbaceous vegetation (Rogers et al., 1999), termites'