Termite-induced heterogeneity in African savanna vegetation: mechanisms and patterns

Gudeta W. Sileshi, M. A. Arshad, Souleymane Konaté & Philip O.Y. Nkunika

Abstract

Objectives: To (1) assess the strength of evidence for the role of termites in vegetation heterogeneity in African savannas, and (2) identify the mechanisms by which termites induce such heterogeneity.
Location: African savannas.
Methods: We conducted a review of the literature, a meta-analysis and qualitative systems analysis to identify mechanisms to explain the observed patterns.
Results: The review provided evidence for termite-induced heterogeneity in floristic composition and vegetation patterning in savannas across Africa. Termites induced vegetation heterogeneity directly or indirectly through their nest-building and foraging activities, associated nutrient cycling and their interaction with mammalian herbivores and fire. The literature reviewed indicated that termite mounds essentially act as islands of fertility, which are responsible for ecosystem-level spatial heterogeneity in savannas. This was supported by the meta-analysis, which demonstrated that mounds of *Ancistrotermes*, *Macrotermes*, *Odontotermes* (family Macrotermitinae), *Cubitermes* (family Termitinae) and *Trinervitermes* (Nasutitermitinae) are significantly enriched in clay (75%), carbon (16%), total nitrogen (42%), calcium (232%), potassium (306%) and magnesium (154%) compared to the surrounding savanna soil.
Conclusions: Termite activity is one of the major factors that induce vegetation patterning in African savannas. The implications of this are discussed and research questions for future studies and modelling efforts are indicated.

Keywords: Banded vegetation; Bush encroachment; Desertification; Fertility islands; Fire; Herbivory; Spotted vegetation.

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Introduction

Resource heterogeneity has been the driving force in the species richness, abundance and coexistence of animal and plant assemblages in savannas (du Toit et al. 2003). Therefore, understanding heterogeneity has recently become an important component of the research agenda in ecology, conservation and management of savannas. Besides climate and soil, which are important at large scales, disturbance regimes such as herbivory and fire and their interactions are cited as the major factors responsible for vegetation structure in savannas (Mourik et al. 2007; De Knegt et al. 2008; Sankaran et al. 2008).

Although termites are sometimes mentioned as disturbance agents in savannas (Cromsigt & Olff 2008), many of their well-known roles in the functioning of ecosystems (Wood & Sands 1978; Eldridge et al. 2001) have been ignored in general models of vegetation dynamics, as well as specific studies on pattern formation. Most of the studies that link vegetation patterns with termites have focused on mound-building species. Not all termites are mound-builders, and those that have subterranean nests could be easily overlooked or their role ignored by vegetation ecologists. Systematic studies and syntheses linking termite biology with vegetation dynamics are also lacking. Even where empirical studies exist, contradictory data often result from studies conducted on different species and in different environments. This has hindered progress in understanding the magnitude of termite effects on vegetation, and the mechanisms by which they induce patterns in African savannas. This review attempts to bring together information from various disciplines and provide an up-to-date synthesis to answer questions such as: are there documented examples of termite-induced patterns in savanna vegetation? If so, how do termites induce patterning?

What are the implications for savanna management and conservation efforts? The objectives of the study are to (1) assess the strength of evidence for the role of termites in vegetation heterogeneity in African savannas, and (2) identify the mechanisms by which termites induce such heterogeneity.

Methods

We conducted a review of the literature to examine the evidence for vegeation heterogeneity associated with termite activity and identify potential mechanisms by which termites induce patterning. The area of savannas was defined based on Underwood et al. (1999) and the distribution of African savanna plants (Bürger 2001). A literature search was conducted focusing on these areas. For savanna ecologists who have no specialist knowledge of termite biology, the role of termites in vegetation patterning may not be immediately clear. Therefore, this review starts with the biology and diversity of termite species in African savannas. This is followed by a synthesis of the literature on links between vegetation and termite activity, and the potential mechanisms that lead to pattern formation.

The review was complemented by a meta-analysis (Hedges et al. 1999) of termite mound properties, including soil texture, carbon, nitrogen, phosphorus, potassium, calcium, magnesium, sodium, pH and cation exchange capacity (CEC). This is required because some studies have reported increases of these variables in mounds while others have reported the opposite (Appendix S1; Jones 1990). Some studies also indicated that termite mounds have soil properties more favourable for preferential grass and tree establishment than the surrounding savanna soil. Therefore, the meta-analysis aimed at testing the strength of evidence for, and the generality of this observation across, study sites. All published studies that had a pair of mean values for results of soil chemical or physical analysis from a termite mound (TMS) and the corresponding value for the surrounding savanna soil (SS) were included in the anlysis. In total 32 peer-reviewed publications were found (Appendix S1) with mound soil analysis for the genera *Macrotermes* (26 publications), *Odontotermes* (eight publications), *Trinervitermes* (four publications), *Ancistrotermes* (three publications) and *Cubitermes* (three publications). All analyses were based on the chemical properties of the top 30 cm of soil, in which 90% of grass roots are known to be concentrated. We used the logarithm of the response ratio, (RR = TMS/SS) as the effect size metric for anlysis (Hedges et al. 1999). The advantage of this approach is that it puts the results of all studies on a common scale so that they can be readily combined, compared and interpreted irrespective of the time, place and method of data collection and soil analysis. Statistical inference was based on the robust (trimmed and Winsorized) estimates of the log(RR) and 95% confidence intervals (95%CI). Robust estimators were used because they give unbiased estimates of the population mean (Wu & Zou 2009). The advantage of trimming and Winsorization is that when outliers are present in the data, these methods help reduce the effects of extreme values. The 95%CI of RR quantifies both the direction and magnitude of change in the termite mound with respect to the surrounding soil. If termites do not have any effect, soil texture and concentrations of chemicals in the mound and adjacent unmodified soil will be the same (i.e. RR = 1.0 or logRR = 0.0), and the 95%CI of RR will include 1.0.

Based on the results of the literature review and the supplementary meta-analysis, we conducted a qualitative systems analysis (Fig. 1), integrating the complex interactions and the potential feedback loops between and within the biological and physical components.

Termite Biology and Diversity in African Savannas

There are over 660 known species of termite in Africa (Kambhampati & Eggleton 2000) but species diversity varies within and between regions. Due to the xeric conditions in northern Africa, species diversity is low (< 15 species) compared to the eastern, southern and western regions of the continent. Over 177 species were recorded in East Africa (i.e. Uganda, Kenya and Tanzania) alone. Out of these, 143 species belong to the East African fauna, which is also continuous with that of Somalia, Ethiopia and the Sudan to the north, and Malawi, Zimbabwe and Mozambique to the south (Wanyonyi et al. 1984). Some 165 species have been recorded from the southern Africa region, including South Africa, Zimbabwe, Mozambique, Botswana, Swaziland, Lesotho and Namibia (Uys 2002). The approximate numbers of species in the major genera and their feeding and nesting habits are given in the appendix (Appendix S2). However, the numbers are likely to be underestimated because the taxonomy of Africa termites is notoriously difficult, and many new species are yet to be described (Uys 2002). The list (Appendix S2) is also limited to genera that have their main distribution in the savanna. To reduce clutter, those genera that strictly feed on soil/humus

Fig. 1. Systems analysis of the feedback between termite-induced resource heterogeneity and vegetation in African savannas. Termite-induced processes are represented by one-way solid arrows, while one-way broken arrows indicate other processes. Two-way interactions are represented by solid double arrows. Plus (+) signs indicate positive feedback processes that lead to tree establishment and recruitment, while negative (–) signs indicate the opposite.

and also do not build epigeal nests have been excluded from the list.

Termites are usually divided into lower and higher termites. The lower termites of Africa belong to the families Kalotermitidae, Termopsidae, Rhinotermitidae and Hodotermitidae. Members of the family Kalotermitidae feed mainly on dry wood, do not construct definite nests and live in small colonies in sound or dead wood. The family Termopsidae is represented by two species (Kambhampati & Eggleton 2000), which feed on and nest within damp and decaying wood. The family Rhinotermitidae consists of mainly subterranean, wood-eating termites.

The family Hodotermitidae consists of the so-called harvester termites, which are among the most notorious pests of pasture, crops and structural timber (Uys 2002). This family is represented by the genus *Hodotermes* in East Africa and *Hodotermes* and *Microhodotermes* in southern African. *Hodotermes* species are dry savanna specialists represented by *Hodotermes erythreensis* in Eritrea and Somalia, and *H. mossambicus* ranging from Ethiopia to South Africa (Uys 2002). Both species build subterranean nests and feed on grass.

The higher termites all belong to the family Termitidae, which is the most divergent group,

showing considerable variation in feeding and nesting habits and social organization. Unlike the lower termites, Termitidae typically lack eukaryotic flagellate protista. Their feeding is also not limited to wood; some feed exclusively on soil, while others "cultivate" and consume cellulolytic fungi. In Africa the Termitidae are represented by over 600 species (>90% of all known species) (Kambhampati & Eggleton 2000) in four subfamilies (Apicotermitinae, Termitinae, Macrotermitinae and Nasutitermitinae). The subfamily Apicotermitinae currently consists of 70 African species (Kambhampati & Eggleton 2000). However, the number is likely to increase when description of the large number of unidentified species is completed (Uys 2002). The subfamily Termitinae consists of about 272 African species (Kambhampati & Eggleton 2000). Although most Termitinae are forest species, some are common in the savannas (Appendix S2). The subfamily Nasutitermitinae consists of 56 species, which mainly feed on grass, leaf litter and wood (e.g. logs, stumps and standing dead trees). Grass-eating has been developed as a specialized habit in the genus *Trinervitermes*, which makes it a serious pest of pasture and rangeland. *Trinervitermes* species build conspicuous dome-shaped mounds, which are a common sight in African savannas (Uys 2002).

The last subfamily is the Macrotermitinae (fungus-growing termites), consisting of over 165 African species (Kambhampati & Eggleton 2000), and arguably the most destructive wood-feeding insect. Although the Macrotermitinae originated in the rainforests of Africa (Aanen & Eggleton 2005), there are more species in savannas (94 species) compared with rainforests (44 species). The main genera include *Odontotermes*, *Macrotermes*, *Pseudacantotermes*, *Microtermes*, *Ancistrotermes* and *Allodontotermes* (Appendix S2). With over 44 savanna species in Africa, *Odontotermes* is the most numerous genus (Aanen & Eggleton 2005). *Odontotermes* species consume a variety of plant material, and are notorious pests of crops, trees and wood. Some species build massive and tall mounds, others build low, flattened mounds, while others do not build mounds at all. *Macrotermes* species dominate the termite fauna in arid environments (Turner et al. 2006), and build the most massive mounds that are characteristic of African savannas (Appendix S2, 3). While many *Macrotermes* species have a narrow range, some such *Macrotermes bellicosus*, *M. falciger*, *M. michaelensis* and *M. subhyalinus* occur throughout most of the African savanna. *Macrotermes bellicosus* occurs from Eritrea in the north to South Africa in the south, from sea level to 1800 m, under most conditions other than tropical rainforest

and desert sand. The genus *Pseudacanthotermes* consists of three savanna species, occurring mainly in woodland savanna (Aanen & Eggleton 2005). These species exhibit a wide range of feeding and nesting habits (Appendix S2). The remaining genera (i.e. *Microtermes*, *Allodontotermes*, *Ancistrotermes* and *Synacanthotermes*) build subterranean nests without any surface structure indicating the presence of a colony in the soil. They feed mainly on wood, litter, dung and occasionally damage trees and crops. Of these, the most numerous and economically important genus is *Microtermes*, which consists of serious pests of trees, wood, crop plants and lawns.

Mechanisms and Vegetation Patterns

The review provided evidence for termite-induced heterogeneity in floristic composition and vegetation patterning in savannas across Africa. In the following sections, we identify potential mechanisms by which termites induce resource heterogeneity, and discuss these in relation to the observed vegetation patterns.

Nest-building

Nest-building is one of the major mechanisms by which termites induce heterogeneity in floristic composition and pattern formation (i.e. spotted and banded vegetation patterns). According to the literature, perused mounds (epigeal nests) have a unique floristic composition. For example, out of 59 plant species recorded on the Loita plains in Kenya, six species appeared exclusively around *Odontotermes* mounds. Each mound also supported a micro-association within a larger vegetation type (Glover et al. 1964). Out of 40 woody species observed in Lake Mburo National Park in Uganda, 11 were unique to *Macrotermes* mounds (Moe et al. 2009). *Macrotermes* mounds also had a floristic composition distinct from the surrounding savannas in the Kagera Plains of Tanzania, Rwanda and Uganda, (Bloesch 2008). In the woodland savannas (*miombo*) of Zimbabwe, out of the six floristic subtypes, the *Albizia* sub-type was restricted to *Macrotermes* mounds (Campbell et al. 1988). Mounds (probably *Macrotermes*) also had twice the density of trees and three times the woody basal cover of the adjacent *miombo* woodland in Zimbabwe (Loveridge & Moe 2004). In the Marakele National Park in South Africa, *Macrotermes* mounds had a floristic composition with affinities to both savannas and forests (Van Staden & Bredenkamp 2006). Some plant species were found to prefer termite mounds more than the savanna. According to

Dossou-Yovo et al. (2009), members of the family Caparaceae are restricted to termite mounds in Benin. This indicates that termite mounds favour some tree species more than others.

Heterogeneity in floristic composition could be related to the influence of mounds on the density and distribution of woody species (Abbadie et al. 1992; Brouwer et al. 1992; Eldridge et al. 2001; Groen et al. 2008; Traoré et al. 2008a, b; Dossou-Yovo et al. 2009) and grasses (Arshad 1982; Belsky 1983; Steinke & Nell 1989; Smith & Yeaton 1998; Barot et al. 1999; Jouquet et al. 2004, 2005; Moe et al. 2009). For example, in the humid savannas of West Africa, the density of woody species was two to three times higher on *Macrotermes* mounds than in inter-mound areas (Abbadie et al. 1992). On a savanna site in northern Burkina Faso, the density of trees and shrubs was five times higher ($2859\,\mathrm{ha}^{-1}$) on *Macrotermes* mounds compared with the inter-mound area ($527\,\mathrm{ha}^{-1}$). Although the mound soil covered only 2.7% of the area, it supported 8.2% of the trees on that site (Eldridge et al. 2001). This is probably because of the positive effect of mounds on woody plant establishment and recruitment. For example, on savanna sites in Burkina Faso, Traoré et al. (2008a, b) found more abundant seedling regeneration on *Macrotermes* mounds than in adjacent areas. *Acacia* spp. survived better around the mounds than in the inte-rmound area at two sites Kenya (Cox & Gakahu 1985). In a South African savanna, termite mounds had a positive effect on tree growth (Groen et al. 2008). In the Sahel, the tallest *Faidherbia albida* trees in a field were usually associated with the proximity to termite mounds (Brouwer et al. 1992).

Certain grass species are also associated with termite mounds. For instance, in Lake Mburo National Park, *Setaria homonyma* and *Pycreeus nitidus* occurred exclusively on *Macrotermes* mounds (Moe et al. 2009). A striking feature of areas close to the mounds is the dominance of *Cynodon dactylon* and rarity of the dominant savanna grass *Themeda triandra* (Arshad 1982; Steinke & Nell 1989; Moe et al. 2009). In a semi-arid savanna in Kenya, grass standing crop and biomass were highest within the first 5 m from the base of *Macrotermes* mounds (Arshad 1982). Similarly, in the Eastern Cape of South Africa, plant biomass and grass growth were significantly higher around mounds compared with the open savanna (Steinke & Nell 1989). According to Smith & Yeaton (1998), the pioneer grass *Tragus koelerioides* and the climax grass *Themeda triandra* dominated around active nests. As the nests become inactive and erode away, these two grass species

were replaced by the subclimax grass *Eragrostis lehmanniana* (Smith & Yeaton 1998). The palms *Hyphaene crinita* in Zimbabwe (Boughey 1963) and *Borassus aethiopum* in West Africa (Barot et al. 1999; Barot & Gignoux 2003) are often clustered around termite mounds. This is because the termite mounds and tree clumps growing on them positively influence seedlings and juveniles of *B. aethiopum* (Barot & Gignoux 2003). Not only the mounds, but also subterranean nests could influence grass distribution. For example, in the Guinean savannas of Côte d'Ivoire, subterranean nests of *Odontotermes* strongly influenced distribution of some grass species (Jouquet et al. 2004). *Imperata cylindrica* was more dominant on *Odontotermes pauperans* nests than elsewhere, while the reverse was true for *Hyparrhenia diplandra* and *Andropogon schirensis* (Jouquet et al. 2004).

Several researchers have also implicated termite mounds in the formation of spotted and banded vegetation patterns in arid areas. Typical examples of spotted vegetation include termitaria-peppering in Somalia (Macfadyen 1950) and thicket clumps in Rwanda, Tanzania, Uganda (Bloesch 2008; Moe et al. 2009), Zambia (Cole 1963), South Africa (Van Staden & Bredenkamp 2006; Mourik et al. 2007) and Ghana (Okali et al. 1973). Banded vegetation patterns such as "tiger bush" have also been associated with termite mounds in different regions of Africa (Glover et al. 1964; Eldridge et al. 2001). The most elaborate patterns of this type were reported from the Loita Plains in Kenya (Glover et al. 1964) and northern Burkina Faso (Eldridge et al. 2001). The various tree and grass patterns described above could potentially emerge from resource heterogeneity created by nest-building in at least four different ways. These are briefly discussed below.

Microtopography and drainage

Termites have been reported to modify microtopography by building mounds (McFarlane & Darlington 1989; Midgley & Musil 1990; McCarthy et al. 1998) and bands (Sattaur 1991). The main builders of the large mounds are members of the subfamily Macrotermitinae (mainly *Odontotermes*, *Macrotermes* and *Pseudacanthotermes* spp.). The Termitinae (mainly *Cubitermes* spp) and Nasutitermitinae (mainly *Trinervitermes* spp.) build smaller mounds, which occur at higher densities than the Macrotermitinae (Appendix S3). Mounds occupy on up to 9% of the area, for example, in the humid savannas of West Africa (Abbadie et al. 1992). In the Laikipia savanna of Kenya, the area influenced by mounds can account for up to 21% of

the habitat (Palmer 2003). *Macrotermes* mounds alone were reported to occupy 5% of the area in Lake Mburo National Park in Uganda (Moe et al. 2009). Unlike mounds, bands consist of alternating ridges and troughs, each ridge about 2-m high and up to 1-km long. The troughs act as drainage channels for water if rainfall is high enough. This banding is seen all over southern Africa, and termites of the genus *Odontotermes* are thought to be the main builders (Sattaur 1991). Banded vegetation patterns could develop on such sites, or even through the coalescing of spotted vegetation on mounds (e.g. Eldridge et al. 2001). Studies in parts of Rwanda, Tanzania and Uganda (Bloesch 2008), Malawi and Zimbabwe (McFarlane & Darlington 1989), Zambia (Cole 1963) and Botswana (McCarthy et al. 1998) suggest that creation of termite-built topography above the flood level is critical to persistence of the thicket clumps. Microtopography could also play a significant role in nutrient availability and water economy of semi-arid savannas (Harris et al. 1994).

Soil texture and bulk density

The studies reviewed indicate that termites can modify soil texture and bulk density through various mechanisms. First, termites translocate large quantities of soil through their foraging (e.g. soil sheeting) and nest-building activities, which involve tunneling and translocating several cubic meters of soil from deep horizons to the surface (Turner et al. 2006). Above-ground nests are continually being eroded and reconstructed, thus redistributings soil over the surface. As termites preferentially move fine and medium-sized particles, they also contribute to stoneline formation. Geological studies in Malawi (Crossley 1986) show that *Macrotermes falciger* transports sediment from beneath and deposits homogeneous red clayey sand sheets of up to 5-m thick on the surface. These activities may change the soil bulk density, porosity and other physical properties.

Some of the studies reviewed provided quantitative data on these changes, most of which focused on termite mounds (Appendix S1). Meta-analysis of these data supported claims made in the literature. The mound soil was 75% more enriched in clay and 27% more enriched in silt content than the adjacent savanna soil (Fig. 2a). The most striking feature of this relationship was that clay enrichment was highest on sites with low (< 20%) clay content than those with higher clay content (Fig. 2b). Soil clay content (from Konaté et al. 1999) showed a
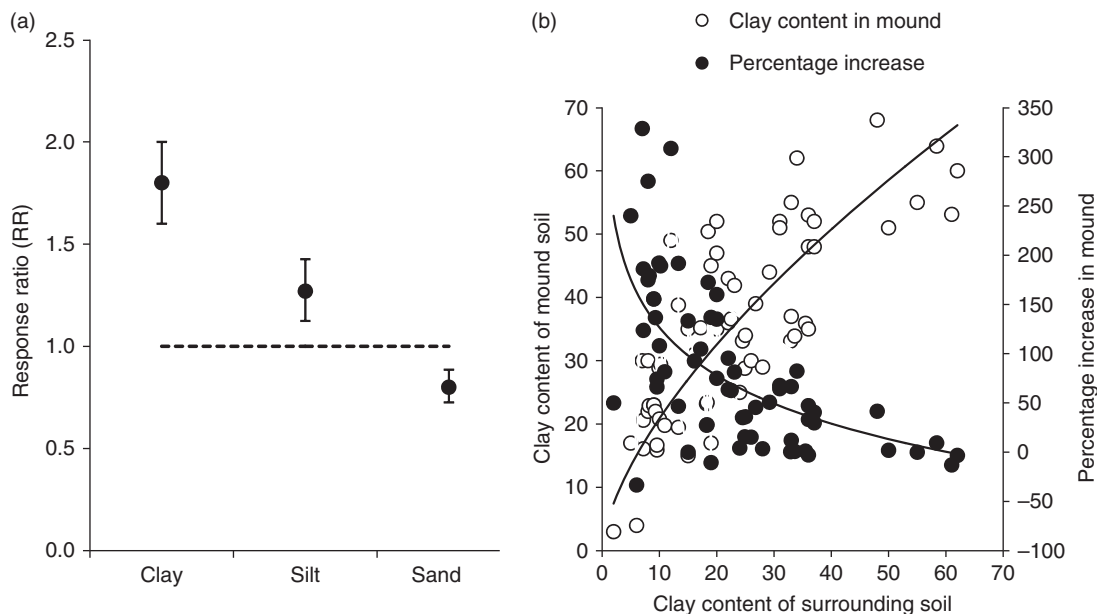

Fig. 2. Results of meta-analysis of soil clay, silt and sand content (a) and the relationship between the clay content of the mound and the surrounding soil (b). Circles in (a) represent Winsorized mean response ratios (RR). In Fig. 2a, the mean values are presented in the original (i.e. back-transformed) scale. For each soil variable, RR > 1.0 indicates significant enrichment in the mound soil relatve to the reference savanna soil, while RR < 1.0 shows reduction in the mound soil. The dotted horizontal line (RR = 1.0) represents a situation where the soil clay, silt or sand content in the mound and adjacent soil are the same. Error bars represent 95% confidence intervals. Solid line in (b) represents trend in the relation between clay content of the mound soil and the reference soil. Termite mound soil and the reference soil do not significantly differ when the 95% confidence interval includes 1.0. The solid circles and thin line represents trends in clay content of the mound relative to the reference soil.
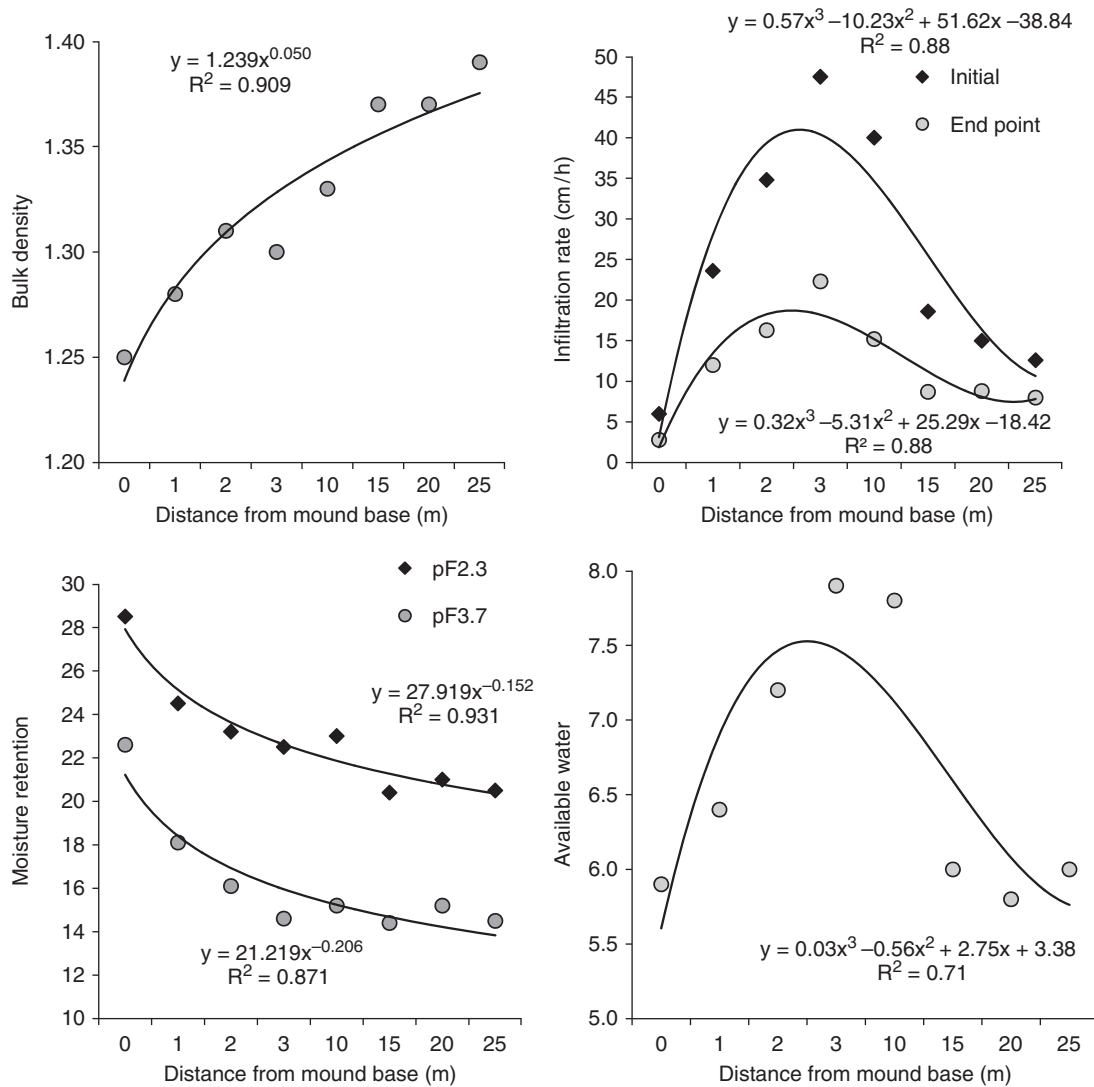
Fig. 3. Variation in bulk density $(g\,cm^{-3})$, infiltration rate $(g \cdot cm \cdot hr^{-1})$, moisture retention (pF2.3-pF3.7), and soil available water with distance from the base of a *Macrotermes michaelseni* mound (0). Regression models were fitted to data from Arshad (1982).

significant nonlinear decline with distance from the top of *Odontotermes* mounds ($R^2 > 0.90$; $P < 0.001$). Detailed measurement of variations in bulk density with distance from mounds of *Macrotermes michaelseni* were made by Arshad (1982) in a semi-arid savanna in Kenya. We re-analysed these data and found nonlinear variations in soil bulk density with distance from the base of the mound (Fig. 3). The mound proper normally has higher bulk density than the adjacent soil, probably because termites re-pack soil to form hard protective layers for the mounds (Arshad 1982). The picture completely changes with distance from the mound base (Fig. 3), where bulk density increases nonlinearly ($P < 0.0001$). Such

changes are likely to affect the availability of nutrients and water to savanna plants.

Water dynamics

The literature from various regions of Africa indicates that termites can bring about spatial heterogeneity in soil moisture and water dynamics (Arshad 1982; Belsky 1983; Konaté et al. 1998; Léonard & Rajot 2001; Turner et al. 2006). For example, Belsky (1983) found termite modification of water infiltration was one factor causing mosaic vegetation patterns in Serengeti National Park. In the semi-arid savannas of Namibia, the *Macrotermes* colony acted as a "water-gathering system"

that draws water from a broad expanse of soil towards the nest (Turner 2006). The colony also acted as a vertical conveyor of soil and water. Colonies in open habitats moved four times more soil water than colonies in wooded habitats (Turner et al. 2006). In the Lamto savanna of the Ivory Coast, mound soil in the 0-60-cm depth range contained 33% more available water in the dry season than control soil (Konaté et al. 1999). Water infiltration was also found to be higher in plots with termites compared with those where termites were controlled in Burkina Faso (Mando et al. 1999). In Niger, macro-pores made by termites intercepted runoff and increased infiltration in a crusted soil (Léonard & Rajot 2001).

Detailed measurements of variations in soil water with distance from mounds were made in a semi-arid savanna in East Africa (Arshad 1982). We re-analysed these data and found nonlinear changes in soil water with distance from the base of the mound (Fig. 3). Infiltration increased with distance from the mound base up to 10 m and then declined steadily thereafter (Fig. 3). Moisture retention declined exponentially, while availabe water increased within 2-10 m of the mound base and then declined (Fig. 3). However, the permeability of the mound itself was very low, probably due to its high bulk density (Arshad 1982).

The spatial heterogeneity in soil water created by termite activity has implications for growth and survival of trees (Konaté et al. 1999; Turner 2006) and grasses (Arshad 1982; Steinke & Nell 1989). With higher water availability around termite mounds, seedlings could establish more easily near mother trees. Increased leaf retention by trees on termite mounds during the dry season has also been noted in the drier savannas of southern and western Africa (Konaté et al. 1999; Turner 2006). This probably shows that termite colonies provide a local source of water that sustains the trees well into the dry season (Turner et al. 2006). Increased growth of grass was also reported around the mound due to accumulation of runoff water at the base of the mound (Steinke & Nell 1989).

Nutrient availability

The large mounds of the Macrotermitinae are often cited as one cause of spatial heterogeneity in soil nutrients. The few studies available on the relatively small mounds of other termites (e.g. *Cubitermes*, *Trinervitermes*) also indicate that these modify soil properties (Brossard et al. 2007). For example, the mounds of *Cubitermes niokoloensis* had five times more carbon and seven to 15 times more nitrogen (N) than the surrounding soil (Sall et al. 2002). Subterranean nests of *Odontotermes* spp. were also shown to influence soil nutrients significantly (Jouquet et al. 2005).

The literature provides conflicting information on the effect of termite mounds on soil organic matter and nutrients. However, meta-analysis of the published data (Appendix S1) showed that mounds of the Termitinae have a significantly higher carbon content (16% more) than the adjacent soil (Fig. 4). Total N was also significantly higher in the mound soil (42% more) compared with the surrounding soil (Fig. 4). Although the phosphorus content of the mound soil was 20% higher, it did not significantly differ from that of surrounding savanna soil (Fig. 4). Termite mounds were significantly enriched in exchangeable calcium (232% more), potassium (306% more), magnesium (154% more) and sodium (78% more) than the surrounding soil (Fig. 4b). Termite mound soils were 85% more enriched in cations than the surrounding soil (Fig. 4). This is probably because termites transport cation-rich clay from the subsoil for construction of the mound. Soil pH also increased by 8% in the termite mounds compared with the adjacent soil (Fig. 4). The nutrients in mounds are slowly released as the mound is eroded, thus creating spatial mosaics of relatively more productive areas or "fertility islands" (Smith & Yeaton 1998; Eldridge et al. 2001; Masanori & Tooru 2004). The presence of mounds is likely to increase the range of environmental conditions over the small scale, thus allowing more plant species with contrasting niches to co-exist. Soil texture, water and nutrients all differ on and off mounds, but the relative importance of each of these factors to vegetation patterns could not be established here. Whether termites promote soil fertility only by concentrating clay or also by providing a nutrient subsidy to the mound soils is also not yet clear, and this is an area open to future research.

Herbivory

Apart from soil-feeding species, most termites (Appendix S2) can potentially induce vegetation heterogeneity through their feeding on trees (Gould et al. 1993), grasses (Wood & Sands 1978; Mitchell 2002) and litter (Lepage 1981). This can occur on either the nest site or by foraging in the open savannas. Harvester termites often cause denudation of grass cover around their nest (Sands 1965). The combined effects of nesting and foraging by some termites species can also create bare spots, such as the so-called "fairy circles" (Becker 2007). In the dry savannas of Namibia, fairy circles of 5-10 m in diameter occur in a regular array at densities of
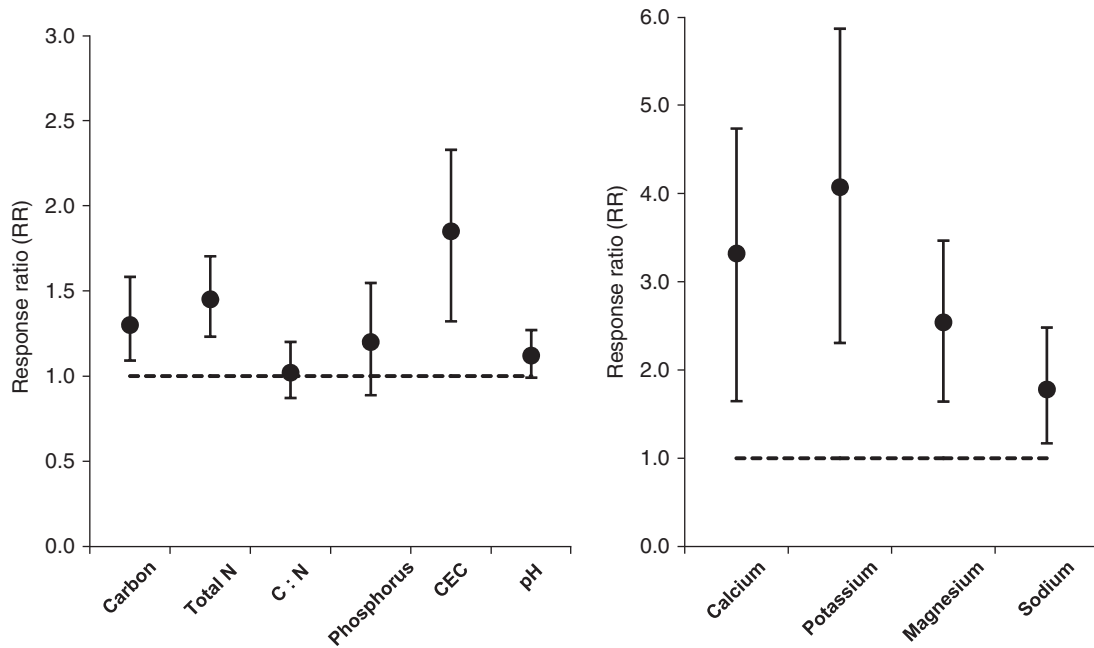
Fig. 4. Results of meta-analysis of soil chemical properties. Circles represent Winsorized mean response ratios (RR). The mean values are presented in the original (i.e. back-transformed) scale. For each soil variable, $RR > 1.0$ indicates significant enrichment in the mound relative to the reference savanna soil, while $RR < 1.0$ shows reduction in the variable under study. Termite mounds and reference soils do not significantly differ when the 95% confidence interval (error bars) includes 1.0. The dotted horizontal line ($RR = 1.0$) represents a situation where chemical content in the mound and adjacent soil is the same.

36–47 ha^{-1} (Becker 2007). Although several hypotheses have been invoked to explain this phenomenon (van Rooyen et al. 2004), recent evidence demonstrates that harvester termites (*Hodotermes mossambicus*) and ants are the prime causal agents for fairy circles in Namibia (Becker 2007). Those species that build arena nests (e.g. *Odontotermes* spp.) could lead to lasting denudation of vegetation on the nest site (Darlington 2007). For example, arena nests of *Odontotermes fulleri* measuring up to 10 m in diameter are often bare, and the circular spots observed in Somalia (Macfadyen 1950) probably represent arena nests (Darlington 2007).

In the open savanna, selective killing of seedlings, saplings and mature trees by the Macrotermitinae could play a role in the tree species composition of savannas. For example, tree species that are vulnerabe to termite attack were unable to flourish in woodlands in Tanzania (Gould et al. 1993). Grass-feeding species often remove large quantities of grass. For example, *Hodotermes mossambicus* alone removes up to 3 t ha^{-1} of forage (about 60% of the standing grass biomass) in South Africa (Mitchell 2002). In Namibia the same species removes 25% of the grass in years of average rainfall, and two to three times as much in years of drought (Becker 2007). In West African savannas, termites remove 20–25% of the grass standing crop

(Wood et al. 1983). Although termite biomass in African savannas (70–110 kg ha^{-1}) is comparable with the biomass of ungulates (10–80 kg ha^{-1}) and megaherbivores (<110 kg ha^{-1}), termites consume more plant material than all the herbivores put together (Pomeroy et al. 1991; Moe et al. 2009). This suggests that herbivory by termites could contribute to spatial heterogeneity in vegetation, probably as much as that reported for mammalian herbivores.

Nutrient cycling and transfer

There are different ways by which termites can influence nutrient cycling and hence plant communities. Jones (1990) reviewed the key role that termites play in carbon and nutrient fluxes in large areas of Africa. Here, we will briefly describe some of the mechanisms based on information in the more recent literature. Termites that feed on dead wood, litter and grass could accelerate formation of humus and the cycling of mineral elements. It is well known that termites accumulate, protect and slowly leak mineralized N into the system (Masanori & Tooru 2004). A large number of termite species also feed on herbivore dung (Appendix S2). On average, about one-third of the dung deposited in savannas is removed by termites within 1 month, thus recycling

nutrients rapidly (Freymann et al. 2008). Soil-feeding termites also process large quantities of humus, and play a significant role in the cycling of organic matter and mobilization of N (Ji et al. 2000). This reallocation of organic matter and its availability for mineralization may play a major role in nutrient cycling in savannas.

The large amounts of soil translocated by termites may also play a role in nutrient transfer. In a South African savanna, *Hodotermes mossambicus* brings to the surface up to $0.70 \, t \, ha^{-1}$ of soil annually as soil dumps, which contain about five times as much N as the surrounding soil (Hewitt et al. 1990). In an arid area of northern Kenya, *Odontotermes* species translocate up to $1.1 \, t \, ha^{-1}$ of soil sheeting annually (Bagine 1984). In Senegal, *Macrotermes subhyalanus* and *Odontotermes nilensis* bring to the surface $0.70–0.95 \, t \, ha^{-1}$ of soil sheeting annually (Ndiaye et al. 2004). The soil sheeting has higher organic carbon and mineral N than the unmodified soil (Ndiaye et al. 2004). The nutrients contained in soil sheeting are recycled quickly (Bagine 1984; Mora et al. 2003) and hence can create spatial heterogeneity in soil nutrients.

Termites can also exert strong spatial controls on landscape-scale N dynamics. For example, wood-feeding termites are known to fix atmospheric N through their gut flora (Lilburn et al. 2001). Recent studies in East African savannas show that termite mounds influence biological N-fixation (BNF) rates by the trees (Fox-Dobbs et al. 2010). The percentage of N derived from BNF in *Acacia drepanolobium* trees was higher (55–80%) away from mounds than near mounds (40–50%). This indicates that *A. drepanolobium* trees preferentially utilize soil-based N sources in lieu of fixed N when these sources are readily available near termite mounds (Fox-Dobbs et al. 2010). The spatial extent of these effects, combined with the spacing of termite mounds, creates highly regular patterning in N fixation rates, resulting in marked habitat heterogeneity in an otherwise uniform landscape (Fox-Dobbs et al. 2010). Vigorous research is needed to establish the amount of N fixed by termites, the effect of mounds on N-fixation by legumes and the wider implications for savanna vegetation.

Another often-ignored aspect is the recycling of nutrients accumulated in the termite biomass. According to Hewitt et al. (1990), 63% of the N ingested by *Hodotermes mossambicus* is converted to termite biomass. Although the amount of nutrients returned to the soil upon death of the termites is not quantified, it obviously contributes to the nutrients captured by plants. For example, the release of nutrients accumulated in the biomass of sub-terranean termites coincided with productivity "pulses" of shallow-rooted plants in the Chihuahuan Desert (Schaefer & Whitford 1981). This aspect has not been studied in African savannas, and its role in vegetation heterogeneity remains unclear.

Interaction with mammalian herbivores

The interaction between termites and herbivores can either be competitive or complementary (Fig. 1) in causing vegetation heterogeneity. The removal of large quantities of grass by *Hodotermes*, *Trinervitermes*, *Macrotermes* and *Odontotermes* spp can deplete forage, thus directly competing with grazing ungulates. The competition often becomes intense when drought and over-grazing occur together (Pomeroy et al. 1991). Where grass cover is reduced by over-grazing or drought below a certain critical level, harvester termites are able to exploit the increased availability of nesting sites, and cause complete denudation of grass cover (Sands 1965). This can potentially modify tree–grass competition. Mammalian herbivores are often attracted to termite mounds because the vegetation is more productive and enriched with nutrients. Mounds of Macrotermitinae have been shown to act as browsing/grazing "hotspots" in various savannas (Loveridge & Moe 2004; Mobæk et al. 2005). In turn, herbivores may import nutrients through dung and urine (Brody et al. 2010), thus increasing the nutrient status of these intensively grazed/browsed sites. Establishment of woody species may also be facilitated by seed deposited in dung. On the other hand, damage to plants may be higher on such sites due to the increasd browsing.

Modification of fire regimes

The literature from various savannas indicates that interactions between termites and fire can also lead to vegetation heterogeneity (Trapnell et al. 1976; Benzie 1986; Fig. 1). While fire may have negative impacts on termites (Sileshi & Mafongoya 2006), termites-induced heterogeneity in resources can also modify fire regimes. In savannas with a high fire frequency, fire may almost completely suppress tree establishment. In such systems, termite mounds can form a buffering mechanism against the total suppression of trees.

The severity of fire is often determined by the fuel load, which is mostly grass and litter. But termite foraging and nest-building can introduce spatial patchiness in the fuel load as termites consume large quantities ($1.5–4 \, t \, ha^{-1}$) of litter annually (Lepage 1981; Pomeroy et al. 1991). In the

Tsavo National Park in Kenya, 90% of dead wood decomposition is mediated by termites (Buxton 1981). In West African savannas, termites remove 60% of annual woodfall, 3% of tree leaf litter (Collins 1981) and 60% of grass litter (Ohiagu & Wood 1979). Termites process 8% of the annual litter production in semi-arid savannas of Senegal and process 28% in humid savannas of the Cote d'Ivoire (Lepage et al. 1993). By comparison, bush fires remove only 0.2% of the annual woodfall (Collins 1981) and about 36% of all plant production (Wood & Sands 1978).

The concentration of trees on termite mounds may also supress grass biomass, thus modifying fire intensity (Barot et al. 1999; Bloesch 2008). For example, thicket clumps on termite mounds are resistant to fire (Bloesch 2008). This is probably because the trees on mounds are out of reach of fire as they are usually very tall (Loveridge & Moe 2004; Van Staden & Bredenkamp 2006). Damage and top-kill by fire is also minimal around thicket clumps (Mourik et al. 2007; Groen et al. 2008). This is because fire skirts around the edges of tree clumps due to the elevation above grass fires and the frequently bare soil at the foot-slope of mounds (Cole 1963; Mourik et al. 2007; Bloesch 2008; Groen et al. 2008). Hence, fire-sensitive species are able to survive better in tree clusters (Groen et al. 2008; Moe et al. 2009).

Implications and Research Questions

In the literature perused, most of the vegetation pattern was attributed to termite mounds. This ignores the role of those species that do not build mounds, which are actually the majority of termite species. Although, the original builder of a mound could be one species, each mound may be inhabited and modified by several species through time, so that it is often difficult to determine which one first established the mound. In Zambia, Coaton (1962) found species of not less than 20 different genera in the mounds of *Macrotermes*. In Nigeria, Collins (1981) found that 37% of the mounds of *Cubitermes fungifaber* were occupied by a total of 31 termite species. Termite mounds also have long life spans, measured in centuries (Coaton 1962; Watson 1967). Until recently, the origin of the vegetated mounds (*heuweltjies*) in South Africa and Namibia has been controversial (Midgley & Musil 1990; Picker et al. 2006). Potts et al. (2009) presented evidence showing that termites had built the *heuweltjies* before the last glacial period. This indicates that the current vegetation on mounds is not necessarily associated with the work of contemporary species, rather with generations of termites over the centuries.

The review and meta-analyses have provided evidence for a network of termite-induced feedbacks leading to resource heterogeneity and, consequently, vegetation patterning in savannas (Fig. 1). The potential for termites to induce spatial heterogeneity in resources has both theoretical and practical importance. Its theoretical significance stems from our increasing appreciation of the influence of pattern on process. Pattern influences the spread of disturbance, the movement and persistence of organisms, and the redistribution of matter and nutrients. Obviously, resource heterogeneity will have impacts on the ratio between tree and grass biomass, which will, in turn, affect animal production, shape species assemblages and determine carbon sequestration capacities. Patchiness may play a critical role in maintaining ecosystem productivity by concentrating limiting resources, especially in semi-arid ecosystems. If termites alter the spatial structure of an ecosystem, it will have potentially important consequences for a wide variety of ecosystem functions. For example, vegetated bands can act as natural bench structures that limit soil erosion. From a practical perspective, an important issue is the relationship between spatial heterogeneity and biodiversity. Changes in spatial heterogeneity caused by termites imply changes in habitat diversity, and influence the diversity of plants and consumers, ranging from insects to birds and mammals (Palmer 2003; Brody et al. 2010). Once trees are established, positive feedback mechanisms (Fig. 1), including nurse effects, nutrient accumulation and reduction of fire instensity, may result in expansion of tree clumps. The trees may improve overall quality of grasses by enhancing growth and nutrient uptake during the wet season, and by delaying grass wilting in the dry season (Treydte et al. 2008). This may attract grazing herbivores, which further add to the nutrient status of the patches (Fig. 1). Empirical studies and modelling efforts on savanna dynamics have ignored these feedbacks that may be intiated by termite activity. Future efforts could provide more insight into savanna dynamics if they could relate these local-level patterns with their landscape-scale significance.

The findings of this study also have significant implications for savanna management, including the threat of bush encroachment and invasion by alien species. Bush encroachment is the suppression of palatable grasses and herbs by unpalatable woody species, which eventually reduce the extent of high-quality rangeland and carrying capacity for livestock (Wiegand et al. 2005). According to Wiegand et al. (2005), bush encroachment is part of a cyclical succes-

sion between open savanna and woody dominance, which can be explained in terms of patch dynamics. In that sense, termite-induced spatial patchiness in resources may trigger bush encroachment. Cole (1963) argued that bush encroachment is a natural phenomenon in the southern African savannas, where termite nests function as vehicles carrying evergreen forest tree species or mopani clumps into the grasslands. Therefore, the management of bush encroachment cannot be achieved without adequate understanding of termite interaction with fire and herbivores. Alien invasive species could also establish more easily around termite mounds (Masocha et al. 2008). For example, the alien invasive plants *Lantana camara* and *Duranta erecta* show clumped distribution around *Macrotermes* mounds (Masocha et al. 2008). This highlights the need for concerted research efforts on the role of termite mounds in bush encroachment and invadibility of savannas by alien species.

The findings also have implications for the regeneration of degraded land and desertification control. In the Sahel, manipulation of termite density and activity has been shown to increase woody plant regeneration and speed the restoration of degraded areas (Mando et al. 1999). For example, tree species such as *Faidherbia albida* used in traditional agroforestry, desertification control (Kirmse & Noton 1984) and re-greening of the Sahel (Coghlan 2006) regenerate faster around termite mounds (Vandenbeldt & Geiger 1991; Brouwer et al. 1992). The potential role of termites in the dynamics of soil water and nutrients (Mando et al. 1999; Léonard & Rajot 2001; Masanori & Tooru 2004), initiation of spotted and banded vegetation patterns in semi-arid areas (Glover et al. 1964; Eldridge et al. 2001) and the link between these patterns and desertification (von Hardenberg et al. 2001) highlights the need to take termite ecology more seriously in restoration ecology and desertification control.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Peer-reviewed publications used for the meta-analysis of effect of termite mounds on soil properties

Appendix S2. Approximate number of termite species (NSP)∗ with known distribution in African savannas, feeding and nesting[§] habit (E = Epigeal mound, S = subterranean, W = wood, A = arboreal, M = within the matrix of living mounds as inquilines or derelict mounds of other termite species).

Appendix S3. Estimated mean nest density (number per ha) of eppigeal mounds of common termite species in African savannas

Appendix S4. Reference cited in Appendix S1-S3
Photo S1. Mound-centred vegetation

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