# Chapter 10 Ecological Impacts of Termites



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**Abstract** Macroinvertebrates play an important role in the maintenance of soil structural stability and fertility in many natural and man-modified habitats. Termites, as dominant invertebrates in tropical soils, have a major influence on soil chemical and physical structure. A diverse range of species processes a variety of plant organic matter at all stages of decomposition contributing to the efficient return of nutrients to the vegetation. Soil restoration and sustainable agricultural practices can be achieved through utilization of the ecosystem services of these organisms. The exploitation of termites for agroecosystem management and soil restoration remains, however, largely unexplored. Only few researches have been reported on the utilization of termite activity for the management of soil fertility or for the rehabilitation of degraded soils. The present chapter highlights the potentials of termites

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as detritivores, soil builders, restorers of degraded land, and producers of some greenhouse gases, in the light of available literature.

Keywords Termite • Detritivore • Soil • Mound • Degraded land

# 10.1 Introduction

Ecosystem engineers directly or indirectly modulate the availability of resources (other than themselves) to other species, by causing physical changes in biotic or abiotic materials. In so doing, they modify, maintain, and/or build habitats (Jones et al. 1994). A wide range of different soil macrofauna provides several key ecosystem services. In the tropics, termites are arguably the most influential soil-dwelling ecosystem engineers (Bignell 2006) whose biogenic structures (nests, soil sheetings, foraging holes, etc.) modify the availability of resources for other organisms. Through bioturbation they incorporate plant litter and crop residues into the soil, thereby modifying biological, chemical, and physical soil processes that affect the flow of energy and material (Fig. 10.1). They hence modify the habitat of other soil biota (Jones et al. 1994; Lavelle et al. 1997b; Pulleman et al. 2012).

Termites form an essential component of soil ecology having successfully coevolved for millions of years (French 1988). They are dominant invertebrates in tropical soils (Bignell and Eggleton 2000) and represent as much as 10% of all animal biomass and up to 95% of soil insect biomass (Jones and Eggleton 2000). By

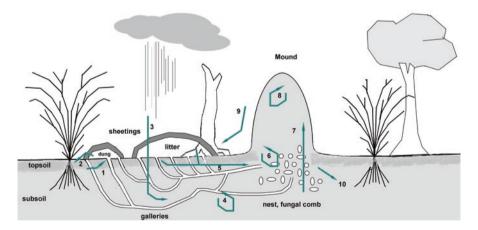


Fig. 10.1 Constructions built by *Macrotermes* spp. and mediated processes (arrows). (1) Soil turbation via construction of sheetings, (2) nutrient uptake from plant sheetings, (3) increased infiltration rates, (4) soil aeration, (5) organic matter relocation, (6) decomposition, (7) soil turbation via mound construction with subsoil, (8) mineralization and nutrient enrichment, (9) erosion and redistribution of mound material, (10) nutrient uptake from mound material by plants (Adapted and redrawn from Grohmann 2010)

virtue of microbial symbionts in their gut, they play a key role in processes such as carbon and nitrogen mineralization (Bignell and Eggleton 2000; Jouquet et al. 2011). Their role in ecosystems has been reviewed by several authors (e.g., Lobry de Bruyn and Conacher 1990; Bignell and Eggleton 2000; Jouquet et al. 2011).

Termites live in complex environments, and their functional domain (physical sphere of influence at the point scale) is designated as the termitosphere (Dangerfield et al. 1998; Lavelle 2002; Jouquet et al. 2006). They construct intricate networks of underground tunnels and soil-covered tubes to access resources as well as protect themselves from predators and harsh environmental conditions while foraging (Lee and Wood 1971; Lee and Su 2010). These soil insects also have the abilities to partially control their own living environments, where the humidity and temperature remain constant throughout all seasons. This gives them a striking ability to remain active during severe seasons, where most other soil macroinvertebrates are diminished or eliminated. Environmental factors along with availability of food and water resources, interactions with other predators and pathogens, and other genetic behaviors affect their population dynamics and behaviors of nesting and foraging, spatially or temporally, separately or in combination (Campora and Grace 2004; Cornelius and Osbrink 2010).

Being one of the most abundant biological compounds on the planet, cellulose is most commonly found in wood, providing an enormous resource for those organisms able to digest it (Norkrans 1963; Dixon et al. 1994). Termites are among the few organisms able to digest cellulose, contributing to their evolutionary and ecological success (Watanabe et al. 1998; Nakashima et al. 2002). Depending on the food source, the termites may be classified into three principal feeding guilds, mainly (1) wood feeders (xylophagous termites); (2) soil feeders, consuming organic residues in the soil (humivorous termites); and (3) termites feeding on both wood and organic residues (soil/wood-interface feeders Bignell and Eggleton (2000)). Besides, there are niche feeders like *Constrictotermes cavifrons*, which have been shown to feed on microepiphytes (Araujo 1970; Martius et al. 2000). They have considerable influence on soil organic matter turnover, nutrient cycling, and soil structure formation (Lavelle et al. 1997b; Brussaard 2012), strongly affecting animal and plant distribution (Holt and Lepage 2000).

Termites transport water from moist areas to relatively drier substrates and improve the microclimate by creating and maintaining a humid environment while softening their food material for easy consumption (Su and Puche 2003; Arab and Costa-Leonardo 2005; Wong and Lee 2010). Studies suggested that termites have a positive effect on soil structure and nutrient richness (Jouquet et al. 2011, 2014). Through their mound-building activities and impact on plant growth, termites enhance the heterogeneity of their ecosystems. Sileshi et al. (2010) reported that increased soil fertility and moisture found near termite mounds can have pronounced effects on vegetation communities and their productivity. Previous studies also found that woody vegetations growing on termite mounds were characterized by an increase of density (Moe et al. 2009), tree height (Levick et al. 2010), species richness (Traore et al. 2008), functional diversity (Joseph et al. 2014), and reproductive output (Brody et al. 2010).

Barrios (2007) concluded that soil organisms are essential for the functioning of natural and managed ecosystems and the productivity of land. Termites, by creating refugia for plants and nuclei for revegetation, can enhance dryland resistance to and recovery from drought (Bonachela et al. 2015). The exploitation of termites for agroecosystem management and soil restoration remains largely unexplored (Evans et al. 2011; Jouquet et al. 2014). This chapter reflects the present state of knowledge concerning ecological impacts of termites.

### 10.2 Detritivores

Termites are the dominant arthropod detritivores in many tropical soils, with highest diversity in lowland equatorial forests (Eggleton et al. 1996; Eggleton 2000). Their activities and interactions with soil result in significant temporal and spatial changes, through formations or modifications of soil, vegetation, and landscape (Ali et al. 2013). A diverse range of termite species processes a variety of plant organic matter at all stages of decomposition, from leaf litter to rotten wood and soil humus. Across all environments inhabited by termites, the litter feeders can be proposed as the most ecologically important, because of their consistent presence and their numerical preponderance in terms of both species and individuals (Jouquet et al. 2011). Overall, tropical termites may consume up to half of the annual litter production (Brauman 2000) and up to 90% of dead wood (Bezerra-Gusmão et al. 2011). Tropical rainforest is often associated with low-fertility soils (Jordan 1985), and termite cycling of organic matter efficiently contributes to the return of nutrients to the vegetation.

Termite associations with symbionts play a significant role in the digestion and decomposition of organic matter as well as moderating nutrient dynamics or global cycling, through the ingestion and redistribution of minerals (Bignell et al. 1978; Holt and Coventry 1990). Via foraging activities, large amounts of organic matter are relocated and taken to the termite nest. The primary food source of *Macrotermes* species consists of dead wood, grass litter, and dung (Dangerfield and Schuurman 2000). This food rapidly passes through the gut of the termites, and the material is then expelled as so-called primary feces onto the fungus combs, which consist of more or less degraded plant material pervaded by the basidiomycete fungus of the genus *Termitomyces* (Westhuizen and Eicker 1991; Osiemo et al. 2010). Fungus combs degrade plant structural compounds. Further decomposition occurs as the termites ingest the old parts from the bottom of the fungus combs (Rouland-Lefèvre 2000).

Termites are also the main agents for primary breakdown of surface mulches under conservation agriculture. They also perforate soil surfaces resulting in increased water infiltration rates (Mando and Miedema 1997). Dung deposited on the soil surface by mammalian herbivores needs to be broken down and eventually incorporated into the soil layer, as part of the nutrient cycling. Freymann et al. (2008) reported a diversity of termite taxa feeding on a wide range of mammalian dung. They can quickly remove large amounts of mammalian dung, especially in the dry season, when on average about 1/3 of the dung deposited in a given habitat is removed by termites within 1 month (with the highest rates observed in savannas) (Freymann et al. 2008). These authors also address issues like to what extent and which species of termites consume mammalian dung and whether termites might fulfill a similar ecosystem role as dung beetles.

## **10.3 Soil-Building Properties**

Macroinvertebrates have an important role in the maintenance of soil structural stability and fertility in many natural and man-modified habitats. The potential beneficial effects of soil macrofauna on soil physical characteristics in general, and on soil aggregations in particular, are well recognized (Kooistra and van Noordwijk 1996; Mando and Miediema 1997). Termites, in particular, have a very strong impact on the soil environment and are therefore called "ecosystem engineers." It was suggested some time ago (e.g., Adamson 1943) that they have an important role in maintaining the fertility of tropical soils and the productivity of ecosystems. These insects are often overlooked as important drivers of habitat quality. Yet the effects of termites on soil character and quality may rival or exceed that of vertebrate herbivores, being one of the most important biological agents for reworking the soils. Their behavior in selecting, transporting, and manipulating soil particles and cementing them together with saliva brings some immediate changes in soil structure and properties (Lobry de Bruyn and Conacher 1990; Wood 1996; Mando 1997). During their feeding and nesting activities, termites improve soil aeration, enhance water absorption and storage in soils, and facilitate carbon fluxes and storage. These processes are crucial for long-term soil fertility, plant growth, and soil formation (Jouquet et al. 2014).

It has been shown that termite activity increases the content of organic matter in the soils that they use for the construction of nests and also modifies the clay mineral composition of these soil materials (Jouquet et al. 2002b; Roose-Amsaleg et al. 2004). Tunneling by termites creates channels in soil through which water preferentially flows (Leonard and Rajot 2001; Turner 2006). Also, their incorporation of feces and saliva is known to affect soil microorganisms (Jouquet et al. 2011), generating higher microbial abundances, activities, and diversity in nests, compared to surrounding soils (Gupta et al. 1981; Holt and Lepage 2000; Chouvenc et al. 2011). Abundant literature is also available in relation to the effects of termites on the mobility of a number of elements. Semhi et al. (2008) reported that termite activities increase the contents of most major and some trace elements in their mounds.

Soil restoration and sustainable agricultural practices can be achieved through utilization of their ecosystem service capability (Crain and Bertness 2006; Brussaard et al. 2007). Termites provide self-renewing services, which might be a relevant option for sustaining soil productivity and rehabilitating degraded soils in tropical agroecosystems (Jouquet et al. 2011). Kaiser et al. (2017) provided evidence about the effectiveness of some termite species in restoring barren soil and maintaining

long-term soil productivity, thereby facilitating sustainable agriculture in sub-Saharan West Africa. They reported that the impact of termites is dependent on the particular species and their ecological requirements. Soil-feeding termites have a positive impact on the overall organic matter cycling in the tropics. This impact on the soil organic matter humification process is due to the most important feeding habit in terms of species diversity and soil-feeding species (Brauman 2000). Unlike other termites, their diet is not based on lignocellulosic plant degradation but on the consumption of the mineral-containing soil horizons, for acquisition of nutrients. During gut transit, the soil organic matter is then strongly modified, in terms of nature and organization.

Wood (1988) categorizes the main ways in which soil is modified by termites as physical disturbance of soil profiles, changes in texture, changes in nature and distribution of organic matter, changes in distribution of plant nutrients, and hence changes in soil fertility with, finally, construction of subterranean galleries. A number of studies focused on natural savanna ecosystems and reported beneficial effect of termites on soil porosity, water infiltration, nutrient uptake, and plant cover or biomass, demonstrating their capacity to rehabilitate degraded and crusted soils (Sarr et al. 2001; Dawes 2010).

Pedological influence of termites includes the production of biogenic aggregates, with physical and chemical properties different from the surrounding environment (Jouquet et al. 2016). Termites can mold up to 1300 kg ha<sup>-1</sup> of soil annually (Kooyman and Onck 1987a), and it has been suggested that their biogenic structures constitute microsites that protect organic carbon against rapid mineralization (Mora et al. 2003). Sarcinelli et al. (2013) investigated the alterations in soil chemical and physical properties promoted by pedobioturbation, during mound building. These authors reported that the concentrations of nutrients, organic carbon, and clay-size particles were significantly higher in mounds than in surface soils. On a weight basis, termite mounds had up to 32 times more nutrients, 12 times more organic carbon, and 5 times more clay than surrounding soils. They mentioned that termites greatly improve soil properties, representing truly ecosystem engineers in sandy soils, with an average soil turnover by mound-building activity reaching 10.5 m<sup>3</sup> ha<sup>-1</sup>. Studies have shown idiosyncratic effect of termites on pH, depending on the species and soil type. Nutting et al. (1987) found that subterranean termites in Sonoran Desert grassland, Heterotermes aureus and Gnathamitermes perplexus, slightly increased the soil pH by bringing clay-rich soil from deep layers to the surface.

There is strong evidence in the literature that ecosystem properties greatly depend on the diversity, distribution, and abundance of organisms (Hooper et al. 2005). The interactions among species, both above- and belowground, can have profound impacts on plant performance. In many arid ecosystems, however, termite nests impart substrate heterogeneity by altering soil properties, thereby enhancing plant growth (Bonachela et al. 2015). Jouquet et al. (2002a) showed that the sheetings of *Odontotermes* contain more nutrients, particularly carbon and exchangeable cations, than the underlying soil. Additionally, soil sheetings of *Macrotermes* and *Odontotermes* species contain large amounts of inorganic nitro-

gen (Ndiaye et al. 2004). Thus, sheetings might enhance the growth of plant root at sites with high termite activities. Termite interactions with soil depend on soil type, moisture, and organic matter content in different seasons and climatic regions. Other key factors affecting this interaction include termite species, size range, and morphological characteristics within a colony (Ali et al. 2013). It is well known that termite-induced changes in soil moisture, carbon availability, pH, and microbial biomass may have subsequent effects on soil carbon storage, plant community composition, and nutrient and water cycling. Yet it is virtually unknown as to how such changes in soil inputs and structure translate to changes in soil microbial biomass, carbon availability, pH, and moisture (Maynard et al. 2015).

#### **10.4 Mound Properties**

Several termite species build mounds or termitaria that provide a buffered environment against extreme temperature and humidity, as well as protection from predators. Termite mounds shape many environmental properties. Analogous structures built by ants and burrowing mammals are similarly influential worldwide (Alba-Lynn and Detling 2008). These mounds often differ from their parent soils in physical, chemical, and biological properties (Holt and Lepage 2000).

Termite mounds are often considered as "patches" or "hotspots" in ecosystems, which increase the spatial and temporal heterogeneity of ecological processes (Bottinelli et al. 2015). Thus termites are often referred to as "major bioturbators," "soil engineers," or even "master builders" (Lavelle et al. 1997a; Jouquet et al. 2006; Oberst et al. 2016). The materials needed for the construction of the nests are taken from the close environment, generally limited to a few meters surrounding the nested area. Termites mix soil materials with wood and excrements for the construction of their nests (Noirot 1970; Jungerius et al. 1999). The specific properties of mound soils are usually explained by the ability of termites to collect soil from deep layers. They specifically select fine-size particles such as clays and oxides (Watson 1962; Fall et al. 2001; Abe et al. 2009) and/or modify the mineralogical properties of clays while building their mounds (Jouquet et al. 2002b, 2007). Thus, termite mound soils are usually enriched in clay, compared to the surrounding soil environment.

These "biogenic" structures have a large impact on the regulation of major biogeochemical processes in most tropical ecosystems (Kaschuk et al. 2006; Robert et al. 2007). Normally a mound grows as the colony grows (Lee and Wood 1971), as a result of additions of soil particles to the mound structure. Termite mounds may persist in the landscape for more than two decades (Lobry de Bruyn and Conacher 1990). With time and abandonment, these mounds are eroded, and their material is redistributed on the soil surface, potentially creating a soil environment more favorable to plant establishment and development (Dangerfield et al. 1998; Konate et al. 1999).

Termite mounds form small islands of enhanced water and soil nutrient availability on otherwise dry and nutrient-poor hill crests, which can have important impacts on the community of plants (Davies et al. 2016). Rather, mound-field landscapes are more robust toward aridity, suggesting that termites may help stabilize ecosystems under global change (Bonachela et al. 2015).

Long-term enclosure of ungulate herbivores is known to decrease functional diversity of woody plant species, but this effect may be mitigated by termitaria. Joseph et al. (2015) reported that at regional scales, mounds can enhance functional diversity of woody plant despite the impacts of herbivory. Petipas and Brody (2014) tested how termites and vertebrate herbivores affect a common plant endosymbiont, arbuscular mycorrhizal fungi (AMF) and reported strong suppressive effect of termites on AMF communities. Mound soils provide a more hospitable environment for plant growth because of their higher levels of phosphorus, nitrogen, and micronutrients (Table 10.1) and enhanced water-holding capacities (Jouquet et al. 2011), thus reducing plant reliance on AMF for nutrient acquisition.

It is documented that termite mounds are rich in different plant nutrients (Semhi et al. 2008; Seymour et al. 2014) and can be safely used for different purposes like use in growing rice paddy cultivation, vegetable beds, and charcoal kilns (Miyagawa et al. 2011). Moreover, due to their higher density, mounds can be used as a bulking agent to speed up composting of agricultural waste as well as to enhance density of the matured compost. Karak et al. (2014) reported the suitability of termite mounds as a bulking agent for composting with crop residues and cow dung in pit method. These authors mentioned that use of 50 kg termite mound with the crop residues (stover of ground nut, 361.65 kg; soybean, 354.59 kg; potato, 357.67 kg; and mustard, 373.19 kg)

	Fenced		Open		F	
	Off	On	Off	On	value	P value
рН	6.17 (0.27)	7.36 (0.11)	6.31 (0.13)	7.50 (0.16)	135.11	<0.0001 ON
Р	1.19 (0.08)	4.26 (2.61)	1.41 (0.15)	2.31 (0.20)	6.86	0.0307 ON
Mg	982.83 (53.08)	614.00 (10.33)	968.50 (19.87)	699.17 (224.16)	22.81	0.0014 OFF
Са	4365.50 (554.32)	8256.67 (781.54)	4207.17 (236.08)	7860.0 (1798.77)	40.56	0.0002 ON
В	0.25 (0.04)	0.85 (0.19)	0.28 (0.03)	0.81 (0.17)	56.20	<0.0001 ON
Mn	73.28 (23.04)	45.83 (14.70)	70.75 (13.11)	34.93 (7.81)	12.25	0.00810FF
ECEC	33.68 (3.02)	49.42 (4.48)	32.97 (0.85)	48.96 (5.43)	13.88	<0.0001 ON
$NO_{3}^{-}$	1.33 (0.59)	17.97 (4.18)	1.0 (0.06)	14.67 (19.76)	6.81	0.0311ON

 Table 10.1
 Nutrient conditions from soils collected in fenced and open areas, on termite mounds, and in corresponding off-mound areas

Source: Petipas and Brody (2014)

*Note: ECEC* effective cation exchange capacity. Effective cation exchange capacity was estimated as the sum of exchangeable cations: Ca, K, Mg, and Na. Available phosphorus was extracted by Modified Morgan P (MM-P) method and measured colorimetrically. Means and standard deviations  $(\pm)$  are presented. *P* values are listed in the last column along with the higher main effect

and cow dung (84.90 kg) formed a good-quality compost within 70 days of composting, having nitrogen, phosphorus, and potassium as 20.19, 3.78, and 32.77 g kg<sup>-1</sup>, respectively, with a bulk density of 0.85 g cm<sup>-3</sup>. Shanbhag et al. (2017) studied the abundance and properties of mounds built by *Odontotermes obesus* in relation to rainfall and parent soil properties in southern Indian forests. They analyzed carbon and clay contents in soil samples collected from mounds and the surrounding topsoil. These authors reported that mound numerical density was positively correlated with mound height and that rainfall had a negative relationship with the abundance. The carbon content in mound walls depends mainly on how much clay the termites used, and the amount of clay in the surrounding topsoil determines mound soil properties. Finally, the use of mound material may present an opportunity to resource-poor farmers, provided that the application of mound materials is optimized and that any adverse effect on soil physical properties can be mitigated (Adhikary et al. 2016).

#### 10.5 Termite Diversity and Degraded Land

Soil feeders help create and maintain soil conditions favorable to plant growth. As many other organisms, also termite communities are affected by the degradation of the habitat. Termite diversity also decreases under long-term cultivation (Kooyman and Onck 1987b). Some studies focusing on termites in deforested/degraded landscapes showed that this group is a good bioindicator of perturbation and restoration processes (Attignon et al. 2005; e.g. Donovan et al. 2007; Vasconcellos et al. 2010; Bhavana et al. 2015). To promote macrofauna abundance and taxonomic richness in soils, integrated conservation soil management practices, with attention to the particular needs and preferences of termites and earthworms, are needed (Zida et al. 2011). According to de Paula et al. (2016), reforestation is a valuable strategy in restoring termite diversity, aiming at recovering the ecosystem services they provide. Only few researches have been reported on the utilization of termites for the management of soil fertility or for the rehabilitation of degraded soils. Jouquet et al. (2011) discussed the main obstacles hampering the development of such approaches. These authors suggested that the ecosystem services provided by termites are not sufficiently appreciated, especially in the context of long-term processes and of the possible biotechnologies derivable from a detailed knowledge of their biology.

#### **10.6** Production of Gases

In the tropics, termites are major players in the mineralization of organic matter, leading to the production of greenhouse gases. They may emit large quantities of methane (CH<sub>4</sub>), carbon dioxide (CO<sub>2</sub>), and nitrous oxide (N<sub>2</sub>O) into the atmosphere. The emission rate of gases by termites is highly variable from species to species. Soil-feeding termites emit more methane than wood-feeding termites (Brauman

et al. 1992; Bignell et al. 1997). Nitrous oxide production rates were higher in termites feeding on substrates with higher N content, such as soil and fungi, compared to those feeding on N-poor wood (Brauman et al. 2015).

Methane production by termites was first reported by Cook (1932) who observed the evolution of a gas from *Zootermopsis nevadensis* described as hydrogen and/or methane. Intensive studies during the following years have shown that methane is actually produced in the termite digestive tract by symbiotic microorganisms (Lee and Wood 1971). The flux of gases from termite nests into the atmosphere has been measured. The first quantitative figures for methane production by wood-feeding lower termites were reported by Breznak (1975). According to Zimmerman et al. (1982), global annual emissions calculated from laboratory measurements could reach  $1.5 \times 10^{14}$  g of CH<sub>4</sub> and  $5 \times 10^{16}$  g of CO<sub>2</sub>. The largest emissions should occur in tropical areas disturbed by human activities. Rasmussen and Khalil (1983) verified the role of termites in the global methane cycle and reported that termites are indeed a potentially significant source of atmospheric CH<sub>4</sub> with an estimated global production of about  $50 \times 10^{12}$  g year<sup>-1</sup>. Ho et al. (2013) reported that termites are a natural methane source contributing 3–4% to the total CH<sub>4</sub> budget, globally.

Termite production of gases is species specific and varies depending on the soil environment and their food quality (Brümmer et al. 2009; Jamali et al. 2013; Brauman et al. 2015). There are several important factors controlling the methane flux from a termite nest. The amount of  $CH_4$  produced in a colony depends on the emission rate by termites and the population in the colony (Sugimoto and Inoue 1998). The mound material showed higher methanotrophic activity. Termites are not known to harbor methane-oxidizing microorganisms (methanotrophs). However, a considerable fraction of the methane produced can be consumed by methanotrophs that inhabit the mound material (Ho et al. 2013).

The contribution of termite mounds to the overall carbon balance has been shown to be negligible in tropical savannas (e.g., Jamali et al. 2013). However, De Gerenyu et al. (2015) estimated that  $CO_2$  emissions from termite mounds constituted up to 10% of the total  $CO_2$  emission in a tropical forest, in southern Vietnam. Ohashi et al. (2017) determined the carbon dioxide emission from nests of termites and ants in a tropical rainforest in Malaysia. They noticed that  $CO_2$  emission from termite and ant nests was significantly higher than that from the bulk surrounding soils, suggesting that termite and ant nests are hotspots of  $CO_2$  emission from soil.

#### 10.7 Conclusion

Soil organisms are essential for the functioning of natural and managed ecosystems and the productivity of land. They maintain soil conditions favorable to plant growth. Termites, in particular, are ecosystem engineers, altering soil composition and hydrology. Their associations with symbionts play a significant role in the digestion and decomposition of organic matter. Overall, tropical termites may consume up to half of the annual litter production. A diversity of taxa also feed on a wide range of mammalian dung. Termite mounds are rich in different plant nutrients and shape many environmental properties. Rather, mound-field landscapes are more robust toward the impact of aridity, suggesting that termites may help stabilizing ecosystems, under global change.

Termites are a good bioindicator of perturbation and restoration processes. They can modify degraded environments and their biogenic structures, modifying the availability of resources for other organisms. During their feeding and nesting activities, termites improve soil aeration, enhance absorption and storage of water in soils, and facilitate carbon fluxes and storage. These processes are crucial for longterm soil fertility, plant growth, and soil formation. These insects may also emit large quantities of greenhouse gases like methane, carbon dioxide, and nitrous oxide into the atmosphere. Production of gases is, however, species specific and varies, depending on the soil environment and food quality.

### References

- Abe, S. S., Yamamoto, S., & Wakatsuki, T. (2009). Soil-particle selection by the mound building termite *Macrotermes bellicosus* on a sandy loam soil catena in a Nigerian tropical savanna. *Journal of Tropical Ecology*, 25, 449–452.
- Adamson, A. M. (1943). Termites and the fertility of soils. Tropical Agriculture, 20, 107-112.
- Adhikary, N., Erens, H., Weemaels, L., Deweer, E., Mees, F., Mujinya, B. B., Baert, G., Boeckx, P., & Ev, R. (2016). Effects of spreading out termite mound material on ferralsol fertility, Katanga, D.R. Congo. *Communications in Soil Science and Plant Analysis*, 47, 1089–1100.
- Alba-Lynn, C., & Detling, J. K. (2008). Interactive disturbance effects of two disparate ecosystem engineers in North American shortgrass steppe. *Oecologia*, 157, 269.
- Ali, I. G., Sheridan, G., French, J. R. J., & Ahmed, B. M. S. (2013). Ecological benefits of termite soil interaction and microbial symbiosis in the soil ecosystem. *Journal of Earth Sciences and Geotechnical Engineering*, 3, 63–85.
- Arab, A., & Costa-Leonardo, A. M. (2005). Effect of biotic and abiotic factors on the tunneling behavior of *Coptotermes gestroi* and *Heterotermes tenuis* (Isoptera: Rhinotermitidae). *Behavioural Processes*, 70, 32–40.
- Araujo, R. L. (1970). Termites of the neotropical region. In K. Krishna & F. M. Weesner (Eds.), Biology of termites (pp. 527–576). London: Academic.
- Attignon, S. E., Lachat, T., Sinsin, B., Nagel, P., & Peveling, R. (2005). Termite assemblages in a West-African semi-deciduous forest and teak plantations. *Agriculture, Ecosystems and Environment, 110*, 318–326.
- Barrios, E. (2007). Soil biota, ecosystem services and land productivity. *Ecological Economics*, 64, 269–285.
- Bezerra-Gusmão, M. A., Barbosa, J. R. C., Barbosa MR de, V., Bandeira, A. G., & Sampaio, E. V. S. B. (2011). Are nests of *Constrictotermes cyphergaster* (Isoptera, Termitidae) important in the C cycle in the driest area of semiarid caatinga in northeast Brazil? *Applied Soil Ecology*, 47, 1–5.
- Bhavana, K. V., Poovoli, A., & Rajmohana, K. (2015). A comparison on termite assemblages in coffee & teak plantations and semievergreen forest—A case study in North Wayanad, Kerala, India. *Tropical Agricultural Research*, 26, 456–467.
- Bignell, D. E. (2006). Termites as soil engineers and soil processors. In H. König & A. Varma (Eds.), *Intestinal microorganisms of soil invertebrates* (pp. 183–220). Berlin: Springer.
- Bignell, D. E., & Eggleton, P. (2000). Termites in ecosystems. In T. Abe, D. E. Bignell, & M. Higashi (Eds.), *Termites: Evolution, sociality, symbiosis, ecology* (pp. 363–387). Dordrecht: Kluwer Academic Publisher.

- Bignell, D. E., Oskarsson, H., & Anderson, J. M. (1978). Association of Actinomycete-like bacteria with soil-feeding termites (Termitidae, Termitinae). *Applied and Environmental Microbiology*, 37, 339–342.
- Bignell, D. E., Eggleton, P., Nunes, L., & Thomas, K. L. (1997). Termites as mediators of carbon fluxes in tropical forest: Budgets for carbon dioxide and methane emissions. In A. D. Watt, N. E. Stork, & M. D. Hunter (Eds.), *Forests and insects* (pp. 109–134). London: Chapman & Hall.
- Bonachela, J. A., Pringle, R. M., Sheffer, E., Coverdale, T. C., Guyton, J. A., Caylor, K. K., Levin, S. A., & Ce, T. (2015). Termite mounds can increase the robustness of dryland ecosystems to climatic change. *Science*, 347, 651–655.
- Bottinelli, N., Jouquet, P., Podwojewski, P., Grimaldi, M., & Peng, X. (2015). Why is the influence of soil macrofauna on soil structure only considered by soil ecologists? *Soil and Tillage Research*, *146*, 118–124.
- Brauman, A. (2000). Effect of gut transit and mound deposit on soil organic matter transformations in the soil feeding termite: A review. *European Journal of Soil Biology*, 36, 117–125.
- Brauman, A., Kane, M. D., Labat, M., & Breznak, J. A. (1992). Genesis of acetate and methane by gut bacteria of nutritionally divers termites. *Science*, 257, 1384–1387.
- Brauman, A., Majeed, M. Z., Buatois, B., Robert, A., Pablo, A. L., & Miambi, E. (2015). Nitrous oxide (N<sub>2</sub>O) emissions by termites: Does the feeding guild matte? *PLoS One*, 10, e0144340.
- Breznak, J. A. (1975). Symbiotic relationships between termites and their intestinal microbiota. Symbiosis (pp. 559–580). London: Cambridge University Press.
- Brody, A. K., Palmer, T. M., Fox-Dobbs, K., & Doak, D. F. (2010). Termites, vertebrate herbivores, and the fruiting success of *Acacia drepanolobium*. *Ecology*, 91, 399–407.
- Brümmer, C., Papen, H., Wassmann, R., & Brüggemann, N. (2009). Fluxes of CH<sub>4</sub> and CO<sub>2</sub> from soil and termite mounds in south Sudanian savanna of Burkina Faso (West Africa). *Global Biogeochem Cycles*, 23, GB1001.
- Brussaard, L. (2012). Ecosystem services provided by soil biota. In D. H. Wall (Ed.), Oxford handbook of soil ecology and ecosystem services. Oxford: Oxford University Press.
- Brussaard, L., de Ruiter, P. C., & Brown, G. G. (2007). Soil biodiversity for agricultural sustainability. Agriculture, Ecosystems and Environment, 121, 233–244.
- Campora, C. E., & Grace, J. K. (2004). Effect of average worker size on tunneling behavior of Formosan subterranean termite colonies. *Journal of Insect Behavior*, 17, 777–791.
- Chouvenc, T., Elliott, M. L., & Su, N. (2011). Rich microbial community associated with the nest material of *Reticulitermes flavipes* (Isoptera: Rhinotermitidae). *Florida Entomologist*, 94, 115–116.
- Cook, S. F. (1932). The respiratory gas exchange in *Termopsis nevadensis*. *The Biological Bulletin*, 63, 246–257.
- Cornelius, M. L., & Osbrink, W. L. A. (2010). Effect of soil type and moisture availability on the foraging behavior of the Formosan subterranean termite (Isoptera: Rhinotermitidae). *Journal* of Economic Entomology, 103, 799–807.
- Crain, C. M., & Bertness, M. D. (2006). Ecosystem engineering across environmental gradients: Implications for conservation and management. *BioScience*, 56, 211–218.
- Dangerfield, J. M., & Schuurman, G. (2000). Foraging by fungus-growing termites (Isoptera: Termitidae, Macrotermitinae) in the Okavango Delta, Botswana. *Journal of Tropical Ecology*, 16, 717–731.
- Dangerfield, J. M., Mccarthy, T. S., & Ellery, W. N. (1998). The mound-building termite Macrotermes michaelseni as an ecosystem engineer. Journal of Tropical Ecology, 14, 507–520.
- Davies, A. B., Baldeck, C. A., & Asner, G. P. (2016). Termite mounds alter the spatial distribution of African savanna tree species. *Journal of Biogeography*, 43, 301–313.
- Dawes, T. Z. (2010). Reestablishment of ecological functioning by mulching and termite invasion in a degraded soil in an Australian savanna. Soil Biology and Biochemistry, 42, 1825–1834.
- De Gerenyu, V. L., Anichkin, A., Avilov, V., Kuznetsov, A., & Kurganova, I. (2015). Termites as a factor of spatial differentiation of CO<sub>2</sub> fluxes from the soils of monsoon tropical forests in southern Vietnam. *Eurasian Soil Science*, 48, 208–217.

- de Paula, R. C., Silveira, R. M. L., da Rocha, M. M., & Izzo, T. J. (2016). The restoration of termite diversity in different reforestated forests. *Agroforestry Systems*, 90, 395–404.
- Dixon, R. K., Solomon, A. M., Brown, S., Houghton, R. A., Trexier, M. C., & Wisniewski, J. (1994). Carbon pools and flux of global forest ecosystems. *Science*, 263, 185–190.
- Donovan, S. E., Griffiths, G. J. K., Homathevi, R., & Winder, L. (2007). The spatial pattern of soildwelling termites in primary and logged forest in Sabah, Malaysia. *Ecological Entomology*, 32, 1–10.
- Eggleton, P. (2000). Global patterns of termite diversity. In T. Abe, D. E. Bignell, & M. Higashi (Eds.), *Termites: Evolution, sociality, symbioses, ecology* (pp. 25–51). Dordrecht: Kluwer Academic Publishers.
- Eggleton, P., Bignell, D. E., Sands, W. A., Mawdsley, N. A., Lawton, J. H., Wood, T. G., & Bignell, N. C. (1996). The diversity, abundance and biomass of termites under differing levels of disturbance in the Mbalmayo Forest reserve, Southern Cameroon. *Philosophical Transactions of the Royal Society of London, Series B*, 351, 51–68.
- Evans, T. A., Dawes, T. Z., Ward, P. R., & Lo, N. (2011). Ants and termites increase crop yield in a dry climate. *Nature Communications*, 2, 262.
- Fall, S., Brauman, A., & Chotte, J. L. (2001). Comparative distribution of organic matter in particle and aggregate size fractions in the mounds of termites with different feeding habits in Senegal: *Cubitermes niokoloensis* and *Macrotermes bellicosus*. *Applied Soil Ecology*, 17, 131–140.
- French, J. R. J. (1988). A case for ecosystem-level experimentation in termite research. Socio-Economic Planning Sciences, 14, 269–280.
- Freymann, B. P., Buitenwerf, R., Desouza, O., & Olff, H. (2008). The importance of termites (Isoptera) for the recycling of herbivore dung in tropical ecosystems: A review. *European Journal of Entomology*, 105, 165–173.
- Grohmann, C. (2010). Termite mediated heterogeneity of soil and vegetation patterns in a semiarid savanna ecosystem in Namibia. PhD thesis, Julius-Maximilians-Universität Würzburg (D), 119 pp.
- Gupta, S. R., Rajvanshi, R., & Singh, J. S. (1981). The role of the termite Odontotermes gurdaspurensis (Isoptera: Termitidae) in plant decomposition in a tropical grassland. *Pedobiologia*, 22, 254–261.
- HO, A., Erens, H., Mujinya, B. B., Boeckx, P., Baert, G., Schneider, B., Frenzel, P., Boon, N., & Van Ranst, E. (2013). Termites facilitate methane oxidation and shape the methanotrophic community. *Applied and Environmental Microbiology*, 79, 7234–7240.
- Holt, J. A., & Coventry, R. J. (1990). Nutrient cycling in Australian savannas. Journal of Biogeography, 17, 427–432.
- Holt, A. J., & Lepage, M. (2000). Termites and soil properties. In T. Abe, D. E. Bignell, & M. Higashi (Eds.), *Termites: Evolution, sociality, symbioses, ecology* (pp. 389–407). Dordrecht: Kluwer Academic Publishers.
- Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H., Lodge, D. M., Loreau, M., Naeem, S., Schmid, B., Setala, H., Symstad, A. J., Vandermeer, J., & Da, W. (2005). Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs*, 75, 3–35.
- Jamali, H., Livesley, S. J., Hutley, L. B., Fest, B., & Arndt, S. K. (2013). The relationships between termite mound CH<sub>4</sub>/CO<sub>2</sub> emissions and internal concentration ratios are species specific. *Biogeosciences*, 10, 2229–2240.
- Jones, D. T., & Eggleton, P. (2000). Sampling termite assemblages in tropical forests: Testing a rapid biodiversity assessment protocol. *Journal of Applied Ecology*, 37, 191–203.
- Jones, C. G., Lawton, J. H., & Shachak, M. (1994). Organisms as ecosystem engineers. *Oikos*, 69, 373–386.
- Jordan, C. F. (1985). Nutrient cycling in tropical forest ecosystems: Principles and their application in management and conservation. Chichester: Wiley.
- Joseph, G. S., Seymour, C., Cumming, G., Cumming, D. M., & Mahlangu, Z. (2014). Termite mounds increase functional diversity of woody plants in African savannas. *Ecosystems*, 17, 808–819.

- Joseph, G. S., Makumbe, M., Seymour, C. L., Cumming, G. S., Mahlangu, Z., & Cumming, D. H. M. (2015). Termite mounds mitigate against 50 years of herbivore induced reduction of functional diversity of savanna woody plants. *Landscape Ecology*, 30, 2161–2174.
- Jouquet, P., Lepage, M., & Velde, B. (2002a). Termite soil preferences and particle selections: Strategies related to ecological requirements. *Insectes Sociaux*, 49, 1–7.
- Jouquet, P., Mamou, L., Lepage, M., & Velde, B. (2002b). Effect of termites on clay minerals in tropical soils; fungus-growing termites as weathering agents. *European Journal of Soil Science*, 53, 521–527.
- Jouquet, P., Dauber, J., Lagerlof, J., Lavelle, P., & Lepage, M. (2006). Soil invertebrates as ecosystem engineers, intended and accidental effects on soil and feedback loops. *Applied Soil Ecology*, 32, 153–164.
- Jouquet, P., Bottinelli, N., Lata, J. C., Mora, P., & Caquineau, S. (2007). Role of the fungusgrowing termite *Pseudacanthotermes spiniger* (Isoptera: Macrotermitinae) in the dynamic of clay and soil organic matter content. An experimental analysis. *Geoderma*, 139, 127–133.
- Jouquet, P., Traore, S., Choosai, C., Hartmann, C., & Bignell, D. (2011). Influence of termites on ecosystem functioning. Ecosystem services provided by termites. *European Journal of Soil Biology*, 47, 215–222.
- Jouquet, P., Blanchart, E., & Capowiezc, Y. (2014). Utilization of earthworms and termites for the restoration of ecosystem functioning. *Applied Soil Ecology*, 73, 34–40.
- Jouquet, P., Chintakunta, S., Bottinelli, N., Subramanian, S., & Caner, L. (2016). The influence of fungus-growing termites on soil macro and micro-aggregates stability varies with soil type. *Applied Soil Ecology*, 101, 117–123.
- Jungerius, P. D., van den Ancker, J. A. M., & Mücher, H. J. (1999). The contribution of termites to the micro-granular structure of soils on the Uasin Gishu Plateau, Kenya. *Catena*, 34, 349–363.
- Kaiser, D., Lepage, M., Konaté, S., & Linsenmair, K. E. (2017). Ecosystem services of termites (Blattoidea: Termitoidae) in the traditional soil restoration and cropping system Zaï in Northern Burkina Faso (West Africa). Agriculture, Ecosystems and Environment, 236, 198–211.
- Karak, T., Sonar, I., Paul, R. K., Das, S., Boruah, R. K., Dutta, A. K., & Das, D. K. (2014). Composting of cow dung and crop residues using termite mounds as bulking agent. *Bioresource Technology*, 169, 731–741.
- Kaschuk, G., Cesar, J. P. S., Almeida, J. A., Sinhorati, D. C., & Berton, J. F. J. (2006). Termite activity in relation to natural grassland soil attributes. *Scientia Agricola (Piracicaba Braz)*, 63, 583–588.
- Konate, S., Leroux, X., Tessier, D., & Lepage, M. (1999). Influence of large termitaria on soil characteristics, soil water regime, and tree leaf shedding pattern in a West African savanna. *Plant and Soil*, 206, 47–60.
- Kooistra, M. J., & van Noordwijk, M. (1996). Soil architecture and distribution of organic matter. In M. R. Carter & B. A. Stewart (Eds.), *Structure and organic matter storage in agricultural soils*, *Advance in soil science* (pp. 15–57). Boca Raton: CRC Press.
- Kooyman, C., & Onck, R. F. M. (1987a). Distribution of termite (Isoptera) species in southwestern Kenya in relation to land use and the morphology of their galleries. *Biology and Fertility of Soils*, *3*, 69–73.
- Kooyman, C., & Onck, R. F. M. (1987b). The interaction between termite activity, agricultural practices and soil characteristics in Kisii district, Kenya (p. 120). Wageningen: Agricultural University Papers. 87–3.
- Lavelle, P. (2002). Functional domains in soils. Ecological Research, 17, 441-450.
- Lavelle, P., Bignell, D., Lepage, M., Wolters, V., Roger, P., Ineson, P., Heal, O. W., & Dhillion, S. (1997a). Soil function in a changing world: The role of invertebrate ecosystem engineers. *European Journal of Soil Biology*, 33, 159–193.
- Lavelle, P., Begon, M., & Fitter, A. H. (1997b). Faunal activities and soil processes: Adaptive strategies that determine ecosystem function. *Advances in Ecological Research*, 27, 93–132.
- Lee, S., & Su, N. Y. (2010). A novel approach to characterize branching network: Application to termite tunnel patterns. *Journal of Asia-Pacific Entomology*, 13, 117–120.
- Lee, K. E., & Wood, T. G. (1971). Termites and soils. London/New York: Academic.

- Leonard, J., & Rajot, J. L. (2001). Influence of termites on runoff and infiltration: Quantification and analysis. *Geoderma*, 104, 17–40.
- Levick, S. R., Asner, G. P., Kennedy-Bowdoin, T., & Knapp, D. E. (2010). The spatial extent of termite influences on herbivore browsing in an African savanna. *Biological Conservation*, 143, 2462–2467.
- Lobry de Bruyn, L. A., & Conacher, A. J. (1990). The role of termites and ants in soil modification: A review. *Australian Journal of Soil Research*, 28, 55–93.
- Mando, A. (1997). The role of termites and mulch in rehabilitation of crusted Sahelian soils (p. 101). Wageningen: Wageningen University.
- Mando, A., & Miedema, R. (1997). Termite induced change in soil structure after mulching degraded (crusted) soil in the Sahel. *Applied Soil Ecology*, 6, 241–249.
- Martius, C., Amelung, W., & Garcia, M. V. B. (2000). The Amazonian forest termites Constrictotermes cavifrons feeds on microepiphytes. Sociobiology, 35, 379–383.
- Maynard, D. S., Crowther, T. W., King, J. R., Warren, R. J., & Bradford, M. A. (2015). Temperate forest termites: Ecology, biogeography, and ecosystem impacts. *Ecological Entomology*, 40, 199–210.
- Miyagawa, S., Koyama, Y., Kokubo, M., Matsushita, Y., Adachi, Y., Sivilay, S., Kawakubo, N., & Oba, S. (2011). Indigenous utilization of termite mounds and their sustainability in a rice growing village of the central plain of Laos. *Journal of Ethnobiology and Ethnomedicine*, 7, 24.
- Moe, S. R., Mobaek, R., & Narmo, A. K. (2009). Mound building termites contribute to savanna vegetation heterogeneity. *Plant Ecology*, 202, 31–40.
- Mora, P., Seugé, C., Chotte, J. L., & Rouland, C. (2003). Physico-chemical typology of the biogenic structures of termites and earthworms: A comparative analysis. *Biology and Fertility of Soils*, 37, 245–249.
- Nakashima, K., Watanabe, H., Saitoh, H., Tokuda, G., & Azuma, J. I. (2002). Dual cellulosedigesting system of the wood-feeding termite, *Coptotermes formosanus* Shiraki. *Insect Biochemistry and Molecular Biology*, 32, 777–784.
- Ndiaye, D., Lepage, M., Sall, C. E., & Brauman, A. (2004). Nitrogen transformations associated with termite biogenic structures in a dry savanna ecosystem. *Plant and Soil*, 265, 189–196.
- Noirot, C. (1970). The nest of termites. In K. Krishna & F. M. Weesner (Eds.), Biology of termites (Vol. 2, pp. 73–125). New York: Academic.
- Norkrans, B. (1963). Degradation of cellulose. Annual Review of Phytopathology, 1, 325–350.
- Nutting, W. L., Haverty, M. I., & LaFage, J. P. (1987). Physical and chemical alteration of soil by two subterranean termite species in Sonoran Desert grassland. *Journal of Arid Environments*, 12, 233–239.
- Oberst, S., Lai Joseph, C. S., & Evans, T. A. (2016). Termites utilize clay to build structural supports and so increase foraging resources. *Scientific Reports*, *6*, 20990.
- Ohashi, M., Maekawa, Y., Hashimoto, Y., Takematsu, Y., Hasin, S., & Yamane, S. (2017). CO<sub>2</sub> emission from subterranean nests of ants and termites in a tropical rain forest in Sarawak, Malaysia. *Applied Soil Ecology*, 117–118, 147–155.
- Osiemo, Z., Marten, A., Kaib, M., Gitonga, L., Boga, H., & Brandl, R. (2010). Open relationships in the castles of clay: High diversity and low host specificity of *Termitomyces* fungi associated with fungus-growing termites in Africa. *Insectes Sociaux*, 57, 351–363.
- Petipas, R. H., & Brody, A. K. (2014). Termites and ungulates affect arbuscular mycorrhizal richness and infectivity in a semiarid savanna. *Botany*, 92, 233–240.
- Pulleman, M. M., Creamer, R., Hamer, U., Helder, J., Pelosi, C., Peres, G., & Rutgers, M. (2012). Soil biodiversity, biological indicators and soil ecosystem services-an overview of European approaches. *Current Opinion in Environment Sustainability*, *4*, 529–538.
- Rasmussen, R. A., & Khalil, M. A. K. (1983). Global production of methane by termites. *Nature*, 301, 700–702.
- Robert, O. E., Frank, U. O., & Agbonsalo, O. U. (2007). Influence of activities of termites on some physical and chemical properties of soils under different land use patterns. A review. *International Journal of Soil Science*, 2, 1–14.

- Roose-Amsaleg, C., Brygoo, Y., & Harry, M. (2004). Ascomycete diversity in soil-feeding termite nests and soils from a tropical rainforest. *Environmental Microbiology*, 6, 462–469.
- Rouland-Lefèvre, C. (2000). Symbiosis with fungi. In M. V. Brian (Ed.), Production ecology of ants and termites (pp. 289–306). Cambridge: Cambridge University Press.
- Sarcinelli, T. S., Schaefer, C. E. G. R., Filho, E. I. F., Mafia, R. G., & Neri, A. V. (2013). Soil modification by termites in a sandy-soil vegetation in the Brazilian Atlantic rain forest. *Journal* of Tropical Ecology, 29, 439–448.
- Sarr, M., Agbogba, C., Russell-Smith, A., & Masse, D. (2001). Effects of soil faunal activity and woody shrubs on water infiltration rates in a semi-arid fallow of Senegal. *Applied Soil Ecology*, 16, 283–290.
- Semhi, K., Chaudhuri, S., Clauer, N., & Boeglin, J. L. (2008). Impact of termite activity on soil environment: A perspective from their soluble chemical components. *International journal of Environmental Science and Technology*, 5, 431–444.
- Seymour, C. L., Milewski, A. V., Mills, A. J., Joseph, G. S., Cumming, G. S., Cumming, D. H. M., & Mahlangu, Z. (2014). Do the large termite mounds of *Macrotermes* concentrate micronutrients in addition to macronutrients in nutrient-poor African savannas? *Soil Biology and Biochemistry*, 68, 95–105.
- Shanbhag, R. R., Kabbaj, M., Sundararaj, R., & Jouquet, P. (2017). Rainfall and soil properties influence termite mound abundance and height: A case study with *Odontotermes obesus* (Macrotermitinae) mounds in the Indian Western Ghats forests. *Applied Soil Ecology*, 111, 33–38.
- Sileshi, G. W., Arshad, M. A., Konaté, S., & Nkunika, P. O. Y. (2010). Termite-induced heterogeneity in African savanna vegetation: Mechanisms and patterns. *Journal of Vegetation Science*, 21, 923–937.
- Su, N. Y., & Puche, H. (2003). Tunneling activity of subterranean termites (Isoptera: Rhinotermitidae) in sand with moisture gradients. *Journal of Economic Entomology*, 96, 88–93.
- Sugimoto, A., & Inoue, T. (1998). Methane oxidation by termite mounds estimated by the carbon isotopic composition of methane. *Global Biogeochem Cycles*, *12*, 595–605.
- Traore, S., Nygard, R., Guinko, S., & Lepage, M. (2008). Impact of *Macrotermes* termitaria as a source of heterogeneity on tree diversity and structure in a Sudanian savanna under controlled grazing and annual prescribed fire (Burkina Faso). *Forest Ecology and Management*, 255, 2337–2346.
- Turner, J. S. (2006). Termites as mediators of the water economy of arid savanna ecosystems. In P. D'Odorico & A. Porporato (Eds.), *Dryland ecohydrology* (pp. 303–313). Dordrecht: Springer.
- Vasconcellos, A., Bandeira, A. G., Moura, F. M. S., Araujo, V. F. P., Gusmao, M. A. B., & Constantino, R. (2010). Termite assemblages in three habitats under different disturbance regimes in the semi-arid Caatinga of NE Brazil. *Journal of Arid Environments*, 74, 298–302.
- Watanabe, H., Noda, H., Tokuda, G., & Lo, N. (1998). A cellulase gene of termite origin. *Nature*, 394, 330–331.
- Watson, J. P. (1962). The soil below a termite mound. Journal of Soil Science, 13, 46–51.
- Westhuizen, G. C. A., & Eicker, A. (1991). The 'Omajowa' or 'Termitenpilz', *Termitomyces* sp. (Agaricales) of Namibia. *South African Journal of Botany*, 57, 67–70.
- Wong, N., & Lee, C. Y. (2010). Influence of different substrate moistures on wood consumption and movement patterns of *Microcerotermes crassus* and *Coptotermes gestroi* (Blattodea: Termitidae, Rhinotermitidae). *Journal of Economic Entomology*, 103, 437–442.
- Wood, T. G. (1988). Termites and the soil environment. Biology and Fertility of Soils, 6, 228–236.
- Wood, T. G. (1996). The agricultural importance of termites in the tropics. Agricultural Zoology Reviews, 7, 117–155.
- Zida, Z., Ouédraogo, E., Mando, A., & Stroosnijder, L. (2011). Termite and earthworm abundance and taxonomic richness under long-term conservation soil management in Saria, Burkina Faso, West Africa. *Applied Soil Ecology*, 51, 122–129.
- Zimmerman, P. R., Greenberg, J. P., Wandiga, S. O., & Crutzen, P. J. (1982). Termites: A potentially large source of atmospheric methane, carbon dioxide, and molecular hydrogen. *Science*, 218, 563–565.