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Sustainable use of termite activity in agro-ecosystems with reference to earthworms. A review

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Abstract

Sustainable agriculture and agro-ecology justify the need to study and understand the role played by ecological processes, and soil biodiversity in particular, in agro-ecosystem functioning. A large number of studies have focused on earthworms in temperate and humid tropical ecosystems and have demonstrated their importance for improving soil biological, physical, and chemical properties in agro-ecosystems. Their “success” is so essential that earthworms are widely considered key species and relevant indicators of soil health in temperate ecosystems. In arid and sub-arid ecosystems, the role of “soil engineer” is usually attributed to termites, and especially fungus-growing termites in Africa and Asia. However, despite this recognition, significant effort is spent eradicating them in plantations because of their pest status. In this review, we discuss the status of termites (“pests” vs. “soil engineers”) and question whether termites play similar roles to earthworms in arid- and sub-arid agroecosystems, with a focus on their influence on nutrient cycling and water dynamics. We argue that the dream of controlling natural interactions and ridding plantations of termites remains a costly legacy of the green revolution. We review the agricultural practices that have been used to reduce termite damage in plantations by restoring refuges to predators or by reorienting termite foraging activity towards organic amendments. Then, we show that the stimulation of termite activity can be used to improve key ecological functions in agro-ecosystems, such as increasing water availability to plants or producing fertility hot-spots. Finally, we suggest that more research on how termites can be used for improving ecosystem services, as is actually done with earthworms in temperate and humid tropical countries, could lead to a paradigm shift in our understanding of the impact of termites in tropical agro-ecosystems.

Keywords Agro-ecology · Sustainability · Dryland · Heterogeneity · Pests · Ecosystem services · Ecosystem disservices

Contents

1. Introduction

2. Termites as pests

2.1. Damage resulting from termite activity

2.2 Why do termites become pests?

3. Termites as key decomposers and engineers in agro-ecosystems

3.1 Influence of termites on C and nutrient cycling

3.2 Influence of termites on soil water dynamics

3.3 Influence of termites on ecosystem complexity

4. Towards the sustainable application of termite activity in agro-ecosystems

4.1. Less intensive agricultural practices providing litter, predators, and pathogens

4.2. Considering agro-ecosystems as heterogeneous and complex environments

5. Conclusion and implications

Acknowledgments

References

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1 Introduction

The green revolution in the 1940s and blue revolution in the 2000s, which led to the intensive use of fertilizers, pesticides, irrigation, and high-yield crop varieties, have undoubtedly increased crop production and reduced the number of chronically undernourished people. Unfortunately, these gains in production have come at high environmental costs with the degradation and over-exploitation of terrestrial and aquatic ecosystems, hence threatening their sustainability and the services they provide to society (Tilman et al. 2002). It is in this context that the concepts of sustainable agriculture and agro-ecology have emerged as paradigm shifts, justifying the need to study and understand the roles played by ecological processes, and soil biodiversity in particular, in (agro)ecosystem functioning (Altieri 1995, 2002; Tilman et al. 2002; Wezel et al. 2009; Wilkinson et al. 2009).

Regarding their importance in soil functioning as key decomposers and soil bioturbators, a large number of studies have demonstrated the positive impacts of earthworms on numerous soil biological, physical, and chemical properties in agro-ecosystems (Lavelle 1997; Brown et al. 1999; Laossi et al. 2010; Jouquet et al. 2014; Bertrand et al. 2015; Kanianska et al. 2016). Their “success” is understood to be so important that earthworms are commonly considered emblems, key species, ecosystem engineers, and relevant indicators of soil health in temperate and humid tropical ecosystems (e.g., Lavelle 1997; Rochfort et al. 2009; Bertrand et al. 2015). In tropical arid and sub-arid ecosystems, soils are usually fragile, highly susceptible to erosion and compaction, and characterized by low clay and nutrient contents, low water infiltration rates, and low water holding capacities. In these environments, litter decomposition and soil bioturbation are mainly carried out by termites, which are therefore considered the “soil engineers” or “ecosystem services providers” of dry tropical soils (e.g., Smeathman 1781; Harris 1956; Lee and Wood 1971; Black and Okwakol 1997; Lavelle 1997; Bignell and Eggleton, 2000; Holt and Lepage 2000; Jouquet et al. 2011, 2016; Bottinelli et al. 2015). The influence of termites on ecosystem functioning can be considered across a range of spatial scales, from the modification of local soil properties and water infiltration rates to the creation of patches that influence the distribution of nutrients, water dynamics, plant growth, and diversity at the landscape scale (Collins 1983; Dangerfield et al. 1998; Yamada et al. 2005a, b; Pringle et al. 2010; Bonachela et al. 2015; Bottinelli et al. 2015; Jouquet et al. 2016) (Fig. 1).

Theoretically, biodiversity contributes to enhanced ecosystems services (Balvanera et al. 2006; Lavelle et al. 2006; Barrios 2007), such as ecosystem stability and productivity, and improved nutrition and human health (Baidu-Forson et al. 2012; Wall et al. 2015). However, soil organisms can also perform “disservices” (Dunn 2010). For instance, although

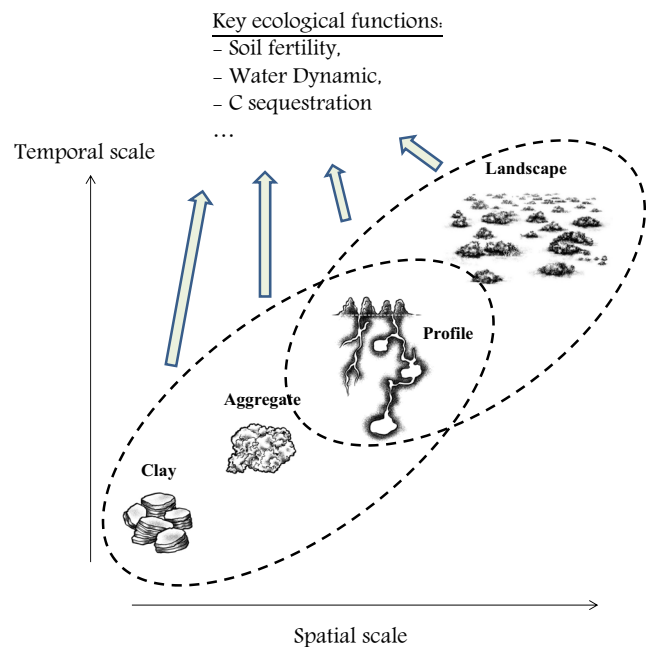


Fig. 1 Impact of termites on ecosystem functioning at different spatial and temporal scales. At the smallest scale, termites influence clay mineralogy and soil aggregation. The production of tunnels in soil and the construction of below- and aboveground nests are important at the soil profile scale. The concentrations of C and nutrients within termite nests maintain heterogeneity at the landscape scale. At these different scales of observation, termites influence several key ecological functions in agrosystems such as C sequestration, soil fertility, water dynamics, and nutrient distribution. Figure modified from Jouquet et al. (2016)

termites are excellent decomposers and have a positive impact on numerous ecological functions, they become serious issues when they attack crops and constructions. Consequently, the positive roles played by termites are often overshadowed by their status as pests threatening agriculture in the tropics where billions of US\$ are annually spent on their prevention and extermination (Su and Scheffrahn 2000; Verma et al. 2009; Tilahun et al. 2012; Shanbhag and Sundararaj 2013). A rapid and non-exhaustive survey assessing the number of articles on termites as either pests or ecosystem engineers (key words = “termites” and either “pest” and “control” or “ecosystem engineers”) reveals very clear differences, with approximately 2077 versus 154 articles for termites as “pests” and “ecosystem engineers,” respectively (source: Web of Science, carried out in March 2017) (Figs. 2 and 3). This clearly shows that more effort has been spent on eradicating termites than on understanding their environmental impacts, and/or how to use their impacts for improving specific ecological functions in agro-ecosystems. Hence, it appears that the role of termites, as ecosystem service providers (*sensu* Lavelle et al. 2006; Jouquet et al. 2011), is clearly under-appreciated and that more research is needed to better evaluate the importance of termite activity and diversity in tropical agro-ecosystems.

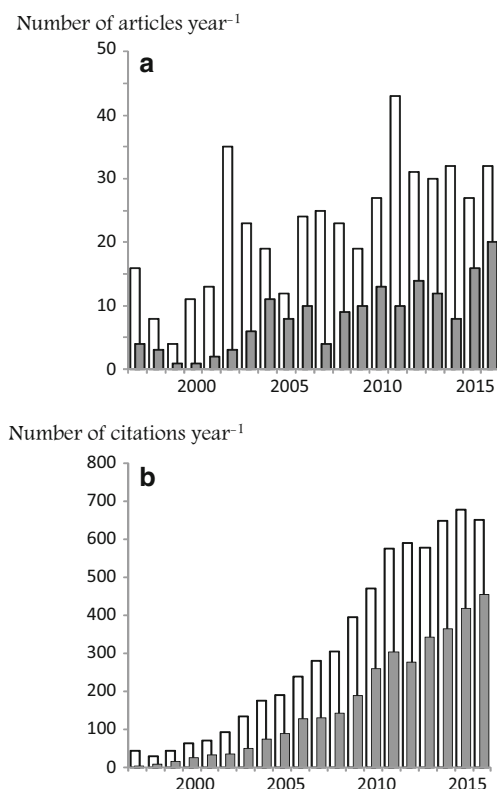


Fig. 2 Number of articles (a) and citations (b) referenced since 1997 in the Web of Science. Keywords are “termites” and either “pests” (in white) or “engineers” (in gray). This figure highlights that termites are perceived more through their negative than positive effects as “pests” and “engineers,” respectively

The aim of this article is to review the value of termites (“pests” vs. “key decomposers and soil engineers”) in the context of sustainable development and agro-ecology concepts. We discuss the use of termite bioturbation to improve agro-ecosystem services, as is actually done with earthworms, and thus “ask whether termites have the right” to request a similar status to that of earthworms in arid and sub-arid tropical ecosystems.

2 Termites as pests

2.1 Damage resulting from termite activity

To date, between 2300 and 3000 termite species have been identified (Kambhampati and Eggleton 2000; Engel et al. 2009). Among them, between 180 and 300 termite species are pests in homes and crops (Verma et al. 2009). All of these species belong to the wood-feeding and litter harvester groups. The fungus-growing Macrotermitinae species (Termitidae, especially from the genera *Macrotermes*, *Odontotermes*, *Ancistrotermes*, and *Microtermes*) and the Rhinotermitidae species (especially *Reticulitermes* spp. and *Coptotermes* spp.) contain most of the pest species (Pearce 1997). For example, fungus-growing termites are responsible

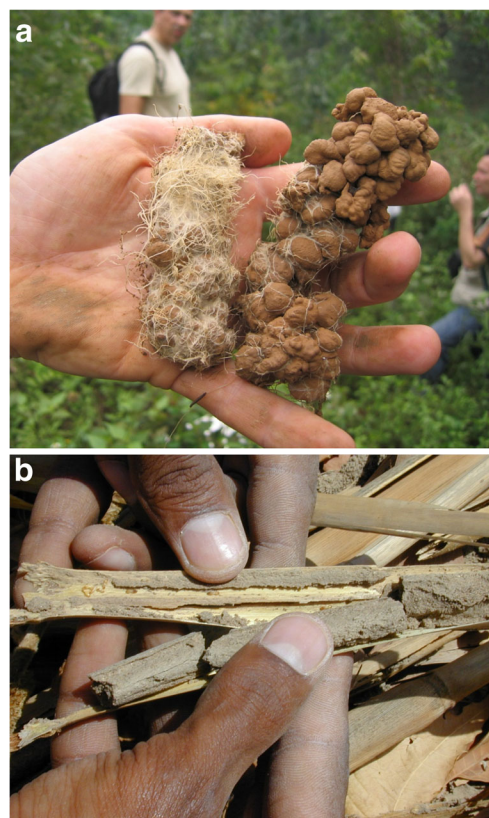


Fig. 3 Earthworms are generally considered to have a positive impact on plant growth and soil fertility. As an example, a shows a proliferation of roots within earthworm casts in Northern Vietnam (photograph by P. Jouquet). In contrast, termites are seen as pests in agro-ecosystems. A proliferation of termites and soil sheetings within plant stems is shown in b (photograph by C. Rouland-Lefevre)

for the majority of crop damage and 90% of tree mortality in South African forests (Mitchell 2002). In India, the total number of species drops to approximately 300 and only 35 have been reported to damage agricultural crops and wood constructions (Chhotani 1980; Verma et al. 2009; Shanbhag and Sundararaj 2013). In this country, the annual loss caused by termites has been estimated to reach several hundred million rupees (> 1.5 million US\$) (Potineni 1986). In the USA, termites are the most important structural pests and about 2–5 billion US\$ are spent annually on their prevention and extermination (Jeffery et al. 2010; Suiter et al. 2012). Termites can cause damage to crops, human constructions, pastures and forestry as well as to non-cellulosic materials such as electrical cables (Su and Scheffrahn 2000; Rouland-Lefèvre 2000; Mugerwa et al. 2011c; Mugerwa 2015a, b). The impact of termites is, however, highly variable. For instance, records on crop yield losses vary from 3 to 100% in Africa and Asia (Umeh and Ivbijaro 1999; Mitchell 2002; Sekamatte et al. 2003; Joshi et al. 2005; Verma et al. 2009). In a sub-humid tropical environment, Paul et al. (2015) found that a reduction in termite abundance was associated with a 22% increase in crop yield. Termite activity can also affect crop quality. For

example, the scarification of crop tubers by termites can reduce their market value and may increase the toxin contents in groundnuts (Black and Okwakol 1997). However, termite attack may not necessarily result in yield loss and their attacks are usually more significant in weak plants suffering from drought or inappropriate soil properties (Potineni 1986). Indeed, in a rainforest in central Amazonia, Apolinário and Martius (2004) found that around 15% of living trees contained termites whereas 70% of trees with rotten cores contained the wood-feeder *Coptotermes* spp. termites. In this specific environment, the existence of termites in internal cavities of living trees did not have a negative impact on the trees, although it could constitute a serious issue for the wood industry. Finally, aboveground termite mounds can also interfere with plowing and grazing and reduce the surface of land used by farmers to grow cash crops (Choosai 2010; Mugerwa 2015a, b). Mugerwa et al. (2011a, b) reported that termite mounds can cover between 25 and 75% of the total soil surface area in African savannas. For instance, the giant earth mounds formed by the Southern harvester termite *Microhodotermes viator* occupy 14 to 25% of the land surface in South-western parts of Southern Africa (Lovegrove and Siegfried 1986, 1989; Picker et al. 2007). In this case, the area occupied by termite mounds is a non-exploitable environment for the production of fodder and thus reduces the amount of food available for livestock. When termite mounds are bare of vegetation, these structures also facilitate high rates of water runoff and soil erosion in rangeland ecosystems (Janeau and Valentin 1987; Zziwa et al. 2012) (Fig. 4).

2.2 Why do termites become pests?

Termites have been considered as our “enemies” for decades, if not centuries (Snyder 1935). Energy and significant budgets have been spent to identify and improve methods for controlling or eradicating termite populations in human-impacted



Fig. 4 This photo shows a mound produced by *Odontotermes obesus* (Macrotermitinae) in a pasture in Southern India. The degradation of termite mounds by the rain or predators leads to an accumulation of soil in the vicinity of the mounds. The erosion of particles then forms a soil crust that impedes plant growth (Photograph by P. Jouquet)

environments (i.e., cities and agro-ecosystems). The control of termite pests relies mainly on chemical insecticides, although the use of biological control methods (e.g., based on the utilization of the entomo-pathogenic fungus *Metarhizium anisopliae*, or through the stimulation of ant predators) has also been reported (Cowie et al. 1989; Logan et al. 1990; Maniania et al. 2001; Sekamatte et al. 2001; Verma et al. 2009; Mugerwa 2015a, b). These methods are mostly ineffective and often not environmentally friendly (Cowie et al. 1989). As highlighted by Mugerwa (2015a, b), such methods do not address the root cause of termite infestation and thus only provide temporary relief to the problem. More research is therefore needed to understand why termites are still considered our “enemies” in agro-ecosystems even though it is recognized that they perform important services in cultivated and non-cultivated ecosystems. The main factors which lead to termites becoming pests are summarized in Table 1. Farmers usually rank overgrazing and deforestation among the most important factors leading to destructive behavior by termites (Mugerwa et al. 2011a, b). Sharma et al. (2004) studied the influence of termites on rice and wheat yields for 2 years in India and concluded that an approximate inverse relationship exists between termite incidence and rainfall or wet soil conditions, with a higher incidence of termites attributed to dry conditions. Overhunting activities can also lead to destructive behavior (Mugerwa 2015a, b). Finally, a shift in biodiversity can result in the predominance of pests in agro-ecosystems due to the disappearance and/or reduction of certain feeding groups from the ecosystems which often give way to other feeding groups that increase in abundance (Dawes 2010).

3 Termites as key decomposers and engineers in agro-ecosystems

Statements from soil ecologists such as “although termites pose potentially negative effects, their positive effects may be the overriding factors” are common (Lamoureux and

Table 1 Agricultural practices that lead to termites becoming pests in agro-ecosystems

Agricultural practice	Mechanism leading to termites gaining pest status
Deforestation and overgrazing	Reduction in food (less litter, lower diversity) leading to a reduction in termite diversity, lower inter-specific competition, and proliferation of resistant or invasive species
Ecosystem simplification and hunting	Less predators (arthropods, mainly ants, and mega-fauna such as bears, aardvark, pangolins, chimpanzees) leading to a lower control of termite populations
Drought	Plants are less resistant

O’Kane 2012). Hence, an abundant literature presents termites as ecosystem services providers. In agro-ecosystems, termites have an impact on three major ecological functions: (i) litter decomposition and nutrient recycling, (ii) water dynamics in soil, and (iii) ecosystem complexity and the distribution of nutrients at the landscape scale.

3.1 Influence of termites on C and nutrient cycling

In agro-ecosystems, termites can feed on plant material and/or soil humus and they are of the greatest importance in recycling C and nutrients from wood, other plant materials, and herbivore dung (e.g., Yamada et al. 2005a, b; Freymann et al. 2008; Noble et al. 2009; Veldhuis et al. 2017). If their impact on litter decomposition can be considered positive in fire-prone ecosystems where C and nutrients can be lost by fire (Konaté et al. 2003), termite foraging activity appears as a drawback when C and nutrients from the litter could have participated in the formation of humus without the action of termites (Potineni 1986). This is typically observed in dry tropical forests where most of the aboveground litter can be consumed by termites before it enters the soil layer (Yamada et al. 2005a). This is also true in agro-ecosystems where organic amendments (e.g., mulch, farmyard manure, or compost) are consumed by litter-feeder termites before being incorporated into the soil. In this case, nutrients become temporarily immobilized in the termite biomass and their symbiotic fungus (in the case of the fungus-growing termite species), thus limiting the positive outcomes of conservation farming practices in terms of soil chemical fertility and C sequestration (Potineni 1986). Organic matter can also be temporarily incorporated in termite sheetings and mounds. However, the low stability of termite-worked soil aggregates (Jouquet et al. 2004b, 2015a) suggests a rapid mineralization of this soil organic matter pool but a non-significant impact on nitrate and phosphate contents in soil (Harit et al. 2017). Since termites prefer some organic substrates to others, low palatable organic matter (e.g., compost) can be preferred to fresh residues (e.g., manure or straw) if the aims are to reduce the exportation of C from the field by termites and to increase the C content of soils. Finally, although less abundant in agro-ecosystems, the impact of soil-feeding termites on C sequestration and nutrient dynamics can also be considered as a drawback when they consume the C stock and nutrients from soil, thus hampering C sequestration in soils (Dahlsjö et al. 2014) (e.g., the 4p1000 initiative, see: <http://4p1000.org/> and Minasny et al. 2017).

3.2 Influence of termites on soil water dynamics

The beneficial impact of termites on water dynamics in soil appears to be more important than their impact on nutrient cycling at the field scale (Kaiser et al. 2017). Indeed, termite foraging activity is often associated with the production of

belowground galleries which increase soil macroporosity, create “preferential flow paths” and increase water infiltration in soil (Elkins et al. 1986; Mando et al. 1996, 1999; Mando and Miedema 1997; Léonard et al. 2001, 2004; Evans et al. 2011; Kaiser et al. 2017). The influence of termites on water infiltration is obviously influenced by the number of tunnels, their depths, size, etc. On average, it is considered that termites increase water infiltration above the natural rate by a factor of 1 to 4, depending on termite activity, soil type, and rainfall intensity (Lamoureux and O’Kane 2012; Kaiser et al. 2017). However, this effect is only significant in soils with low hydraulic conductivity. In the Chihuahuan desert, USA, termite foraging activity increases water infiltration from 51.3 to 88.4 mm h⁻¹ (Elkins et al. 1986). However, to be significant at the plot scale, a large number of foraging holes is sometimes needed (e.g., > 30 m⁻² in Sub-Saharan ecosystems, Léonard and Rajot 2001). Termite foraging activity can be associated with the production of large amounts of sheetings which are usually enriched in clay, silt, and organic matter compared to the surrounding top-soil (Harit et al. 2017). Especially in compacted and gravelly soils in semi-arid regions, sheetings can locally improve soil physical and chemical properties. On the other hand, in sloping land in a humid tropical climate, Jouquet et al. (2012) observed that sheeting degradation might also be related to crust formation, higher water runoff, and soil detachment.

3.3 Influence of termites on ecosystem complexity

At the landscape scale, termites also act as heterogeneity drivers when they produce aboveground mounds that appear like nutrient “hot-spots” or “fertility islands” in which primary productivity is locally increased and water flow improved. Although termite mounds usually represent a small proportion of the landscape, they might constitute a mosaic of comparatively more productive areas in an ecosystem (e.g., Lamoureux and O’Kane 2012). In contrast to the surrounding savanna soil, these constructions are usually enriched in cations (magnesium, potassium, calcium...) and clay (Arshad 1981; Coventry et al. 1988; Mills et al. 2009; Jouquet et al. 2004a, 2015b; Brossard et al. 2007; Lopez-Hernandez et al. 2004; Sileshi et al. 2010; Seymour et al. 2014). Depending on the feeding group (e.g., soil feeding termites vs. fungus-growers) and the pedoclimatic properties of the environment, these mounds can also have higher C and N contents compared to the surrounding soil. The higher clay content along with the higher proportion of swelling clay in termite mounds also explain their higher water retention (Konaté et al. 1999). As shown in African savanna ecosystems, these aboveground constructions also provide refuges for plants and soil biodiversity, offer a better resistance of plants to fire, represent foraging hot-spots for herbivores, and increase the robustness of dryland ecosystems to climatic change (Mobaek et al. 2005;

Traoré et al. 2008, 2015; Choosai et al. 2009; Moe et al. 2009; Brody et al. 2010; Erpenbach et al. 2013, Erpenbach et al. 2017; Davies et al. 2014, 2016; Seymour et al. 2014; Tobella et al. 2014; Bonachela et al. 2015).

4 Towards the sustainable application of termite activity in agro-ecosystems

Two main types of agricultural practices have been proposed for improving the services termites provide in agro-ecosystems while reducing their negative impacts. The first focuses on the provision of refuges for predators, which control termite populations, and of food for stimulating termite foraging activity and improving soil properties. The second relies on taking advantage of the heterogeneity created by termites at the landscape scale.

4.1 Less intensive agricultural practices providing litter, predators, and pathogens

Reduced food availability (litter) and the loss of termites' natural predators (e.g., ants, bears, armadillo, pangolins), parasites, and pathogens (e.g., nematodes, fungi) are reported to be among the major factors explaining why termites are destructive in grasslands and for crops (Snyder 1929; Mugerwa 2015a, b). Hence, one promising strategy is the development of practices that provide other food besides crops for termites and which stimulate predators and/or entomopathogens for controlling termite populations. For example, studies carried out in Africa and Asia showed that termite infestation and crop damage could be reduced by inter-cropping with legumes, mulching in crop plantations, or by keeping leaf litter on the ground in tree plantations (Pong 1974; Sands 1977; Shivashankar et al. 1991; Sekamatte et al. 2001, 2003; Girma et al. 2009; Kihara et al. 2015). Less damage to crops and tree attacks result from ants nesting and feeding on termites (e.g., *Leptogenys processionalis* in India, which live in temporary nests and always forage under low-intensity sunlight conditions (Rajagopal and Ali 1984); or *Pheidole megacephala* and *Megaponera foetens* in Africa (Sheppe 1970; Longhurst et al. 1978; Lepage 1981)), as well as the fact that termites prefer feeding on mulch and litter, a more palatable food resource for termites than crops and trees (Shivashankar et al. 1991; Mugerwa 2015a, b). The above examples are important because they show that termite attacks on crops and trees can be reduced to a level acceptable for farmers if termite populations are limited (but not eradicated) by stimulating predators or entomopathogens, such as fungi, ants, spiders, beetles and lizards, and/or if more palatable food is given to them (mulch and litter in these cases). Interestingly, several studies also showed that the application of mulch or different organic amendments (e.g., cattle or goat dung, urine,

or a mixture) increases termite foraging activity which in turn enhances soil porosity, water infiltration, and water holding capacity in soil (Mando et al. 1996, 1999; Roose et al. 1999; Léonard and Rajot 2001; Dawes 2010; Kaiser et al. 2017), while reducing termite damage on crops (Mugerwa 2015a, b), and increasing plant growth and yield. For example, in the case of the agricultural and forestry Zai systems, the application of organic matter into the soil triggers termite activity which then create burrows through the crusted soil surface, thus improving the productivity of the ecosystems from 0.5 to 5.3 tons ha⁻¹ for straw and from 0.15 to 1.7 tons ha⁻¹ for *Sorghum* (Roose et al. 1999). The main obstacle to the widespread uptake of this technique is, however, that it is labor intensive (300 h ha⁻¹ of work), requires a huge amount of organic substrates (3 tons ha⁻¹), and is limited to semi-arid environments receiving between 300 and 800 mm water (Roose et al. 1999). These results are also likely to be context dependent, and perhaps species dependent. Indeed, no significant influence on soil aggregate stability and C content was measured in sub-humid tropical ecosystems by Paul et al. (2015), who even measured an increase in crop yield (+ 34% for maize and 22% for soybean) after the eradication of termites in the field.

Tillage has a negative impact on termites and ants (Sanabria et al. 2016). The influence of zero or low tillage on termites has also been investigated in wheat and maize plantations in India (Reddy et al. 1994; Sharma et al. 2004). These practices were associated with lower termite damage compared to rotary and conventional tillage, probably because of the higher soil moisture that could favor pathogenic fungi (e.g., *Metarhizium anisopliae*, Grace 1997; Wright et al. 2005) or predators (e.g., ants) throughout the crop growth period. However, it is worth mentioning that zero and low tillage were also associated with weed development, potentially more herbicides for their control, and lower yield (Reddy et al. 1994; Sharma et al. 2004), thereby highlighting the limits of this approach.

4.2 Considering agro-ecosystems as heterogeneous and complex environments.

Aboveground termite mounds, especially those built by fungus-growing termites, create hot-spots of nutrients in ecosystems (Sileshi et al. 2010; Jouquet et al. 2016). Termite mounds are usually enriched in clay, exchangeable cations, and macronutrients compared with the surrounding top-soil layers (Holt and Lepage 2000; Jouquet et al. 2011). Their positive influence on plant growth and diversity, hydrology, and ecosystem resistance to drought was mainly found in non-cultivated environments (Collins 1983; Dangerfield et al. 1998; Yamada et al. 2005a; Pringle et al. 2010; Bonachela et al. 2015; Bottinelli et al. 2015; Jouquet et al. 2016). However, studies carried out in Africa highlight that these

structures can also help farmers to reduce the risks of crop failure (Brouwer et al. 1993; Harris et al. 1994, cited by Tilahun et al. 2012). Subsistence farmers in Africa and Asia commonly destroy and spread termite mound soils in their fields to improve soil fertility (Fairhead and Scoones 2005; Verlinden et al. 2006). Termite mounds can also be associated with fruit trees, as shown in Namibia by Verlinden et al. (2006). They provide numerous ecosystem services in paddy fields in Thailand such as shade for cattle and for growing vegetables, proteins from insects, mushrooms, medicines from the diversity of trees growing on mounds, or even refuges for predators such as ants (Choosai et al. 2009; Choosai 2010). In Africa, traditional soil classification is also based on the abundance of termite mounds (Adamou et al. 2007, Tilahun et al. 2012). Fairhead and Scoones (2005) mentioned that traditional farming practices in Africa consist in selecting lands with many large termite mounds, which can be used for gardening. These authors also report direct and indirect methods for triggering termite activity in the fields, for example through the maintenance of trees that offer a beneficial environment to termites (Fairhead and Scoones 2005).

5 Conclusion and implications

The relationship between termites and humans can be seen as another example of the numerous conflicts between humans and wildlife, such as those that exist between men and elephants, leopards, or tigers in India. As we learn to share our environment with large herbivores and predators, a new challenge for agronomists is to develop agricultural practices that get the best from termites (e.g., their abilities to improve water dynamics in soil and to improve soil fertility close to their nests) while making their negative impacts on plant growth and yield acceptable to farmers.

The green revolution led to a simplification and homogenization of agro-ecosystems and to an overuse of chemicals, thereby precluding termites from our cultivated lands. In retrospect, we know that the utilization of these chemicals is of concern as they create problems for our health and the environment. The dream of ridding termites from plantations thus appears today as a costly legacy from the green revolution. In contrast, the development in agroecology highlights the importance of considering the soil as a living system (e.g., Okwakol and Sekamatte 2007; Gobat et al. 2010), and of the enhanced use of biodiversity as an essential element of agro-ecological approaches (Altieri 1995). New, environmentally friendly and more ecological approaches have also to emerge to give termites a status similar to that of earthworms in arid and sub-arid ecosystems. It is stated in the Biodiversity Atlas (Jeffery et al. 2010) that “termites and ants appear to have a similar role to earthworms and enchytraeids in more temperate and tropical organic soils (...)”. This review highlights that

termites are obviously not playing the same roles as earthworms in arid- and sub-arid cultivated ecosystems, and that they provide both ecosystem services and disservices. However, the examples given in this article emphasize that (i) not all termite species are harmful in plantations and that a first step towards a more sustainable use of biodiversity is perhaps to teach farmers to recognize the different species and/or functional groups that occupy their lands and to adapt their management accordingly, (ii) termite damage can be reduced by restoring refuges to predators or by reorienting termite foraging activity towards organic amendments (litter and dung or compost materials), and (iii) the stimulation of termite activity improves key ecological functions in agro-ecosystems (water availability to plants and the creation of fertility hot-spots in the examples given above). This review also stresses the need for a better understanding of the services that termite mounds can provide in agro-ecosystems. We believe that one of the challenges for sustainable agriculture is to consider drylands as complex and heterogeneous systems where termite mounds can provide numerous services and contribute to ensure food security and improve the resistance to environmental change.

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