



Influence of termites on ecosystem functioning. Ecosystem services provided by termites

Pascal Jouquet^{a,b,*}, Saran Traoré^c, Chutinan Choosai^d, Christian Hartmann^a, David Bignell^e

^aIRD, UMR 211 BIOEMCO, Equipe Transferts, Centre IRD Bondy, 32 Avenue H. Varagnat, 93143 Bondy Cedex, France

^bIRD-SFRI, Dong Ngac, Tu Liem, Hanoi, Viet Nam

^cISNV/UPB, 01 BP 1091, Bobo-Dioulasso, Burkina Faso

^dDepartment of Plant Science and Agricultural Resources, Faculty of Agriculture, Khon Kaen University, Thailand

^eSchool of Biological and Chemical Sciences, Queen Mary University of London, Mile End Road, London E1 4NS, UK

ARTICLE INFO

Article history:

Received 9 February 2011

Received in revised form

18 May 2011

Accepted 24 May 2011

Available online 12 June 2011

Handling editor: Stefan Schrader

Keywords:

Termites

Soil functions

Soil engineers

Ecosystem services

ABSTRACT

As soil engineers, termites play a key role in the functioning of many tropical and subtropical ecosystems. This review assesses advances in our knowledge of the beneficial influences of termites on ecosystem functioning and services. Termites are amongst the main macroinvertebrate decomposers in arid and semi-arid environments, and exert additional impacts through the creation of biostructures (mounds, galleries, sheetings, etc...) with different soil physical and chemical properties. They influence the distribution of natural resources such as water and nutrients in the landscape and consequently the diversity of soil microbes, plants and animals. Surprisingly, considering the wide range of ecosystem services provided by termites, few researches have been reported on the utilization of termite activity for the management of soil fertility or for the rehabilitation of degraded soils. In our final section, we discuss the main obstacles hampering the development of such approaches and we suggest that ecosystem services provided by termites are not sufficiently appreciated, especially in the context of long-term processes and possible biotechnologies derived from a detailed knowledge of their biology.

© 2011 Elsevier Masson SAS. All rights reserved.

1. Introduction

With the intensification of agriculture over recent decades and the social and environmental imperative to develop sustainable agricultural practices, there is now a sharp focus on the influence of cultural systems on soil biodiversity and the role of soil biodiversity in mediating the main ecological functions of the system [80,107]. Amongst the below-ground biota, soil ecosystem engineers play a key role by regulating the fluxes of energy and materials across different spatial and temporal scales [69,71,77,79]. The primary concept in this engineering process is the ability of a key subset of the organisms to create soil biogenic structures with biological, physical and chemical properties different from those of the surrounding soil system [69,77].

In the tropics, termites (Isoptera) are arguably the most important soil ecosystem engineers [16]. Their functional domain (physical sphere of influence at the point scale) is designated the termitosphere [34,69,77,78]. In most lowland tropical habitats, where termites are

especially abundant, the termitosphere comprises a large part of the soil column, challenged only by the functional domain of earthworms (the drilosphere). Termites have the abilities to forage over long distances (metres to tens of metres) and to partially control their own living environments through the creation of nest structures where the humidity and temperature remain constant throughout all seasons. This gives them a striking ability to remain active in harsh environments, or during severe seasons, where most other soil macroinvertebrates are diminished or eliminated. For instance in arid and semi-arid tropical savannas, during the dry season termites remain virtually the only active group of invertebrate detritivores and bioturbators, consequently dominating the decomposition processes [31,131] and the provision of essential ecosystem services [80]. Subjective assessments of the importance of termites, based on observations of their very high population densities are now supported by a number of thorough studies which suggest they may represent 40–65% of the overall soil macrofaunal biomass in some biotopes [131]. Live biomass densities have been estimated to be from 70 to 110 kg ha⁻¹ and from 510 to 1150 g of live weight in the largest nests [12,131]. Abundances (all genera) can reach up to 15,000 ind m⁻² (rarely, but densities between 2000 and 7000 ind m⁻² are quite commonly reported), and individual nests can contain anything from

* Corresponding author. IRD, UMR 211 BIOEMCO, Equipe Transferts, Centre IRD Bondy, 32 avenue H. Varagnat, 93143 Bondy cedex, France.

E-mail address: pascal.jouquet@ird.fr (P. Jouquet).

a handful of individuals to many millions ([14,61] and references therein). These values are comparable to the biomass of ungulates and megaherbivores in African savannas [11,88] and thus strongly justify both discussion of the importance of termites in the functioning of tropical ecosystems and their inclusion in all models of processes.

To demonstrate the several impacts of termites, it is instructive to consider the functional-group classification based on the types and the variety of food materials used and the locations of their nesting and feeding sites. In soil, and at a first approximation, two main feeding groups of termites can be recognized: the soil- and litter feeders (including grass foragers). Across all environments inhabited by termites (the savannas being much greater in extent than the remaining humid forests), the litter-feeders can be proposed as the most important ecologically because of their consistent presence and (commonly but not exclusively) their numerical preponderance in terms of both species and individuals. Natural or lightly disturbed semi-natural humid forests, however, support a high diversity of soil-feeding forms, often with predominant biomass [14]. Soil-feeding may comprise more than one digestive strategy and process, with several evolutions or divergent clades [38,85]. Soil- and litter-feeding termites consume organic matter (humus, ingested with variable amounts of mineral material, standing or lying dead wood, woody litter or dead dry standing litter and grasses) and many build their nests and/or line their galleries with soil particles glued together with faecal matter [131]. Although belonging to the litter-feeding group, the fungus-growing termite species (Macrotermitinae) behave somewhat differently. They are usually litter-foragers (this can include small woody items) and characterized by an exosymbiosis with a fungus (*Termitomyces* sp.), which completes the degradation of the litter on which they feed [31]. Conversely to the other species, they do not incorporate faeces into their nests but enrich their constructions with saliva, which contains easily degradable carbon compounds as binding agents for silts and clays [56].

Several landmarks syntheses have been published in the last 40 years on the role of termites in soil systems [18,81,86,131], one of the most recent being the work of Holt and Lepage in 2000 [56]. However, a significant number of new articles have been published in the last decade and a contemporary dedicated review demonstrating the influence of termites on soil ecosystem functioning and updating the growing literature is now appropriate. In this paper we first review advances in our knowledge of how termites influence the soil system, plant growth and species diversity in tropical ecosystems. We then give examples of the utilization of termite activity for the promotion of ecosystem services in agricultural lands and identify four obstacles hampering further research on this topic. Finally, faced with accelerating land-use changes in the tropics, we briefly consider whether the active manipulation of termite activity can save or promote ecosystem services in the future.

2. Influence of termites on ecosystem functioning

2.1. Litter decomposition

In purely metabolic terms and in a global context, the decomposition of plant material is carried out primarily by free-living fungi and bacteria, but in many tropical habitats termites also contribute to the consumption and mineralization of a significant part of litter by processing large quantities of plant material [14,50,132]. This impact is especially large in more arid regions such as deserts and dry savannas where the short duration of the rainy season impedes litter and cattle-dung degradation by flies, beetles and bacterial and fungal populations [14,119]. This ecological niche is therefore occupied by termites, which are able to maintain a humid atmosphere in their own colony centres, and can therefore forage for and process large amounts of litter independently of ambient climate

[30,31,54,129]. A wide range of termite species typically feed on dead plant material such as wood, bark and straw, being able to digest woody fibres with the assistance of the gut microbiota, supplementing endogenous enzymes [17]. Even animal products, such as mammalian hooves and dungs, can also be consumed though spatially and temporally variable [47–50,104]. Like shredder organisms, termites can mechanically chop up plant material with their mandibles and grind it with their gizzard, thereby increasing the surface area accessible to soil microorganisms, as well as their own intestinal symbionts and speeding up net decay by protist, bacterial and fungal agents. One consequence of such termite activity is a return of organic matter into the soil, via faeces, the biomass of termite bodies and within their biogenic structures, which would otherwise be lost to the periodic fires characteristic of drier savannas and scrublands.

2.2. Bioturbation and soil formation

One of the major effects of termites in ecosystems is their role in soil loosening (reduction of bulk density) and both vertical and horizontal transport through bioturbation, and subsequent erosions of their constructions. Large amounts of soil are translocated from various depths of the profile to the soil surface during mound-, gallery- and sheeting constructions. This is especially true with termites of the subfamily Macrotermitinae [56] although it has also been assessed and documented in the genus *Trinervitermes* [25]. Using rare earth element and trace element concentrations, Sako et al. [117] confirmed that the nests of *Macrotermes* sp. are produced through the accumulation of highly weathered soil originating from deeper layers. The magnitude and route of soil translocation resulting from termite activity is directly related to their specific dietary habits and the properties of the soil they use [5,25,62]. The mounds of humivorous termites are built with materials coming mainly from the surface horizon and recycled at this level by erosion. By contrast, the fungus-growing Macrotermitinae can retrieve their material (wet soil particles) very deep in the profile, even down to the water table (which might be as low as 50 m in places such as the Sahel zone of Senegal) [56]. Over time these effects of termites on soil translocation will have strong consequences on the profile, making termites agents of pedogenesis as well as responsible for the distribution of resources in the ecosystem [22,42,71].

Soil transported by termites generally contains higher proportions of finer sized particles, and therefore typically demonstrates different clay mineral compositions than those predominating at the original surface [4,20,21,39,40,66,90–92]. In addition, termites have also been considered as weathering agents due to their ability to transform minerals chemically [62,117]. This process might be indirect, through the exposure of clays from deeper soil layers to the atmosphere and the weathering action of rain water, or direct through soil rehandling by termites. Using laboratory experiments, Jouquet et al. [62] showed that such rehandling can lead to an increase of the expandable layers of the silicate clay minerals. However, the effect depends on the handling intensity required (or available) for individual constructions [62,63,70]. The exact mechanisms by which termites influence clay mineralogical properties are unknown, however, it can be proposed that the grinding of soil particles by termite mandibles in the saliva-rich environment of the buccal cavity increases the surface area exposed to the surrounding solution, and then a release of interlayer K and the adsorption of hydrated or polar ions between the layers. If proven to apply in large areas of the world's savannas, this cumulated action over decades and centuries could be an ultimate determinant of soil fertility in environments dominated by low activity clays, such as kaolinite. Such a role could be expected across the subfamily Macrotermitinae,

but Boyer [20,21] suggested neof ormation is less common in the soil-feeding termites.

2.3. Soil organic matter and nutrient cycling

Termite nests and biomass have been characterized as “sinks” as they withdraw large quantities of litter and soil organic matter (SOM) from the “normal” decomposition pathways [129]. The consumption of organic matter by termites is used in the production of termite biomass and in the building of nest-structures. The return input of organic matter and mineral nutrients to the soil environment occurs via faeces, salivary secretions, corpses and predators. Mortality, particularly from ant predation, and mound erosion are important contributors to the turnover and redistribution of the organic matter and mineral nutrients in the ecosystem.

Except in the case of fungus-growing termites, the SOM content is usually higher in termite mounds and in the surrounding soil than in the soil unaffected by termites (considered as a control) [5,23,56]. The level of this enrichment is directly related to the specific dietary habits of termites and to the building materials used for nest making [25]. Enrichment becomes significant in poor sandy soils, such as those of savanna ecosystems, whereas smaller enrichments or none at all take place in more clayey soils and in organic rich humid forest soils [23,25]. In the nest structures of fungus-growing termite species, the quantity and quality of SOM are very variable depending on the species concerned and on the soil properties. The SOM content in fungus-growing termite-built structures can be similar [42], higher [1,8,64], or lower [9,23,33,43,51,66] than the surrounding control soil, depending on the initial soil properties.

Termite mound soils have higher levels of total N, greater cationic exchange capacity and more mineral nutrients (Ca^{2+} , Mg^{2+} , K^{+}) than surrounding soils [56,100], due to both the concentration in, and subsequent decomposition of, organic matter within the mounds and to the creation of stable biogenic aggregates which protect SOM from microbial decomposition for long periods, provided the structures are maintained [3,34]. Several studies have shown that the mineral N levels in termite-structures (galleries, sheetings, fungus-comb chambers and mounds) are much higher than those of the nearby soils, even without visible activity of termites [101,102]. This may be explained by the higher SOM mineralization in the biostructures [1], the higher retention of nutrients or protection of SOM in the soil aggregates [43,52], the fixation of atmospheric N by symbiotic hindgut bacteria of termites [31,133] or by the inhibition of nitrification [101]. Denitrification can also be higher in termitaria than in the surrounding soil [2]. Fewer studies have been done on the effect of termites on soil P, although this nutrient is often deficient in tropical soils, and contradictory results can be found in the literature. The influence of termites on the total and available P fractions seem to vary according to the functional group, the part of the termite nest sampled and also probably to the initial pedological properties. For instance, nests of soil and litter feeders display greater amounts of available P while fungus-growing termites tend to increase P sorption [87,92,115].

Unlike other termite feeding-guilds, which mineralise the OM ingested at high efficiency (up to 90% for cellulose and hemicellulose), it is suggested that the primary contribution of the soil-feeding termites is a positive influence on the overall OM dynamics. They mediate an intense humification process which begins during the gut transit, where a re-organization and re-integration of SOM with the mineral soil fraction occurs. This process leads to the formation of stable clay–humic complexes which are further incorporated as micro-aggregates in termite-structures, protecting the SOM from mineralisation [22]. More recently, it has emerged that in the *Cubitermes* clade (*sensu* [85]) of soil-feeding Termitinae, the digestive process first releases and then degrades peptide components of SOM,

while polyaromatic substances remain less significantly changed [27]. The significance of this process in the overall scheme of humification is unclear, but an immediate consequence is the mineralization of organic N as ammonia [59] and the emission of CH_4 and N_2O [26,103]. Model humic peptides labelled with ^{14}C were about 30% mineralized as CO_2 on passage through the soil-feeder gut [26,103].

At the landscape scale, termite activity plays a primary role in the distribution of resources. By feeding on organic litter and SOM in areas surrounding colony centres, termites reduce the inputs that would otherwise flow to the soil from other organisms. By contrast, the accumulation of resources in the termite nests lead to the creation of nutrient patches which contrast with the highly weathered tropical soils between them. The longest lasting of the mounds, which persist as inhabited and eroded biogenic structures, remains on scales of years to decades for some species. These structures seem likely the main factor generating the patch mosaics that characterize the soils and vegetation of many tropical landscapes, but more especially savannas [69,71].

2.4. Hydraulic properties and soil erosion

The role of termites in water infiltration and runoff is closely related to the importance, structure and arrangement of their subterranean biogenic structures, which comprise foraging and storage galleries, feeding chambers and communication channels, in addition to chambered colony centres (in wholly underground species) and the foundations of epigeal mounds. Quantitative information on the effects of termites on water infiltration into the soil is sparse. Many observations and a number of exclusion experiments demonstrate that the harvesting activity of termites creates a dense network of underground galleries that are connected to the soil surface by foraging holes through which water can penetrate and which constitute preferential flow paths [41,55,82,83,125]. Termite biostructures act therefore as a network of horizontal and vertical macropores influencing bulk density, aeration, water infiltration and runoff, then capturing overland flow and (potentially) determining the hydrological characteristics of watersheds [35,41,128]. The sizes, types of wall construction, depth distributions and extent of termite gallery systems differ markedly, depending on the ecological strategies of the species involved and the characteristics of the soil present [76]. Termite mounds can also influence water infiltration and nutrient leaching, although this effect is likely to depend on the age and whether the mounds are inhabited by termites or abandoned. For instance, in Brazil Rückamp et al. [114] found leaching from mounds built and inhabited by *Cornitermes silvestrii* was not different than from soil, but higher losses of nitrate and lower leaching of dissolved organic carbon occurred when mounds built by *C. silvestrii* were subsequently occupied by inquiline species. When colonies are present (especially the constructors), epigeal mound surfaces are hardened, leading to rainsplash and channelled runoff, but little erosion [56].

Termites sequester SOM and plant nutrients for considerable periods in their nests, mounds, galleries and other structures. The breakdown and erosion of nest structures, whether occupied or not, through the agencies of other organisms (i.e., termitophilous vertebrates, also cattle), rainfall and perhaps wind, continuously return their incorporated organic matter and nutrients to the soil. Also, the roots of surrounding plants frequently take up nutrients from the often-concentrated stores held in the bases of termite mounds and within decomposing organic materials in back-filled subterranean voids. The life span of termite-generated structures, generally measured from days and months to years or even decades, depends on the investment of time, energy and resources at the time of their construction and subsequently allocated for maintenance, their mechanical stability, on the intensity of individual rainfall events, and

whether these structures are re-colonized by other termite species or colonies. Processes of nutrient redistribution can be very fast, on the scale of a few days in the case of the erosion and redistribution of nutrients within galleries or sheetings but longer in the case of the redistribution of nutrients contained in mounds [32]. Termites use different construction strategies depending on whether the structure to be built is a lasting (a mound-nest) or a temporary one (sheetings, runways). Temporary structures built by Macrotermitinae (notably the rough sheetings placed over the surface of the ground and potential food items) can be created from the immediately adjacent soil and relatively little organic matter is supplied as a binding agent, whereas in the case of nests termites gather components deeper in soil and incorporate more organic matter [62,64].

As observed with *Trinervitermes* sp., fine-textured dispersive material can be deposited close to the mounds to form surface seals that may continue to modify local infiltration and drainage patterns until disrupted through the activity of soil fauna or plants [58]. On sloping surfaces, downhill transport and sorting of materials can be hastened by the actions of termites. Where prevalent, termites therefore may contribute materially to the formation of catenas [130]. Lepage [84] estimated that an 8 m³ *Macrotermes bellicosus* mound would take 20–25 years to erode. Erosion is very rapid in the first years after abandonment but the rate then subsides gradually until it is more or less negligible due to the stabilization effect of vegetation growth on the remains of the structure. Temporal scale is important: some termite mounds persist in the landscape for periods of a decade or more, and their individual influence on soil profile development during that time may be negligible. However, over 100s or 1000s of years, the importance of termites in the turnovers of both mineral materials and organic matter in the landscape and in the whole soil profiles may be much greater, such that long-term pedogenesis is mediated by their activity [29,58,130].

2.5. Vegetation growth and diversity

The concentration of SOM and nutrients in termite nest structures exaggerates resource patchiness and the structures can be considered as “fertile islands” or “sinks for nutrients” [5,46,57,60,69,71], which are beneficial resources for plants. There are also some evidences that termite nests serve as foci for nutrient redistribution in some landscapes and lateral flows have been shown to occur from these islands to the surrounding environments [29,56,71,105]. In modifying the soil structure, and especially in increasing the content of clay, termites may also have strong impacts on the availability of soil water for plants, added to the accumulation of available nutrients around the nests from erosion. As a consequence, plant growth on or in the vicinity of termite mounds is increased [68,75,121,122,124,129] with an attendant higher capacity to tolerate herbivory [24]. Most studies show that large mounds built by fungus-growing termites support different vegetations than the surrounding landscape, with some species exclusive to the mound sites [65,120,124], and therefore both generate diversity and affect the overall productivity of the plant community. Vegetated mounds also enhance spatial heterogeneity in the landscape [124], and as elevated sites, the larger termite-built structures may also give plants protection from fire and from land flooding [29], as well as improved drainage, greater soil depth, higher soil moisture and improved fertility status [75]. The weathering of termite mounds and the resulting enhancement of nutrients in their immediate vicinity may be partially exploited by the roots of adjacent plants and their associated mycorrhizal fungi [40,121]. Thus the perimeter zones may be preferential areas for the recruitment of tree seedlings and may therefore be qualified as ecosystem regeneration hot spots [124]. However, the hardness and imperviousness of living

termitaria can also discourage and impede the growth of plants [5,53,81].

2.6. Soil animal and microbial biodiversity

The heterogeneity created in soils by the demarcation of the termite functional domain is a major generator and regulator of soil biodiversity and promotes ecological stability [6]. As ecosystem engineers, termites modulate the availability of resources for other species, such as soil macro- and microfauna and microorganisms, and create habitats that can be used by a remarkable number of organisms for nesting, roosting or accommodating stages of their life cycles [69,127].

Many studies suggest that termite mounds and sheetings could constitute sites of microbial diversity, with a different assemblage structure from the parent soil [13,17,23,37,44,45,67,109]. At the same time, increasing evidences prove that termites are able to control microorganism numbers and probably diversity in selected parts of their mounds [111], such that the higher substrate availability, nutrient content, and moisture levels available promote the growth of a selected and possibly specialised community of commensal bacteria and fungi [1,66,118,122].

In addition to constituting a food resource for a wide range of animals, termite mound nests serve as refuge for a wide range of animals (inquilines), from other termite species and soil macrofauna [5,28,108] to small animals, such as birds, reptiles and mammals during unfavourable times, which species might otherwise face local extinction in unproductive environments [34,54,108,123]. The greater vegetation production and quality on and around the termite mounds therefore provides a template for distribution of prey and predator communities [108] and also contributes to increased grazing pressure by ungulate mammals and megaherbivores [54,98,99]. Earth-eating from termite mounds may also represent important nutritional resources for a variety of mammals, such as chimpanzees [72,90,91], elephants [116] and humans [57,89,128]. This behaviour has been explained by mineral deficiencies in mammal diets, and by the consequences of a temporary lack of fibre which leads to a rumen acidosis in herbivore ungulates. In such cases, termite-mound soils are nutritional supplements acting as a detoxifier due to their high content of clay and associated exchangeable cations [74].

3. Utilization of termites for the promotion of ecosystem services in agro-ecosystems

Although their regulatory role in natural habitats is widely recognized, few studies have been made to test whether termite activity can be manipulated for the promotion of ecosystem processes and therefore the provision of goods and services in agro-ecosystems. Certainly, the higher nutrient content in termite mounds has led to their use as soil amendments in many traditional agricultural practices, resulting in better crop yields [19]. Moreover, termite mounds can foster the development of mycorrhizal fungi [40] and even assist in the control of crop pests, such as *Striga hermonthica*, an obligate root hemiparasite which causes serious yield losses in cereals in Africa [7]. However, these interventions are small on the scale of the crises that face contemporary tropical agro-ecosystems [73,107]. Further, the exploitation of termite mound soils is limited by the slow rate of nest population renewal, and has only limited sustainability [25].

The ability of termites to develop in harsh environments and to promote water infiltration in crusted soils as a part of soil rehabilitation and vegetation cover regeneration has been strikingly demonstrated in Africa and Asia [93,94,106,108]. In these studies, the application of mulch or organic matter on or into the soil, as in the case of the agricultural and forestry “zai” systems [110], triggered the activity of termites which then created burrows opened

through the sealed surface of the soil. This results in an increase of soil hydraulic conductivity and water retention, and a reduction of the bulk soil density. The change of soil characteristics due to termite activity is enough to create the conditions necessary for natural vegetation development and then crop production on previously degraded bare soils.

Compared with the many studies linking earthworm engineering activity and ecosystem services and consequent experimental manipulations of earthworm populations, the utilization of termite activity for the promotion of ecosystem services is clearly underexplored. However, the proposition faces several obstacles, and research has therefore been limited. First, termites are obligate social insects: in many cases their breeding in culture (or on a semi-industrial scale) is therefore difficult, slow or impossible (notably with soil-feeders and the larger mound-building Macrotermitinae). It is also problematic to bring them directly to the field (as it can be done much more easily with earthworms) in sufficient numbers to be effective and with the colony structure and any associated symbiotic relationships intact. It is also likely that translocated termites would be extremely vulnerable to predation by ants while they were establishing their foraging galleries and defenses. Secondly, the development of indigenous termite activity in degraded land, mainly targeted as fungus-growing species, can only be achieved by the drilling of organic residues into the soil column (i.e., the *zai* system in Burkina Faso) or placement on the soil surface as mulch [95–97,112]. There is therefore a significant capital and labour cost before any advantageous result can be expected, and there may be the additional task of overcoming the farmers' perceptions that all termites are pests. Nevertheless, some pilot work with termites has been reported, for example the transplantation of soil monoliths from fertile to degraded (especially compacted) plots [10], and many observations link the preservation of termite communities in agricultural soils to the choice of cover and forage crops [36,47]. Third, termite activities affect the distribution of resources in ecosystems through the concentration of nutrients into their nest structures [71]. This influence of termites on the resource patchiness increases the complexity of land management. Finally, the utilization of termite activity for the promotion of ecosystem services also competes with less sustainable but more immediately attractive approaches. For instance, the utilization of chemical fertilizers and pesticides in agro-ecosystems, when affordable, are widely used by farmers with large and immediate marginal gains of crop yield, despite concomitant reductions in termite activity and diversity. This can be illustrated anecdotally: in North-East Thailand, the average abundance of termite mounds has dropped from 9 to 2 mounds ha⁻¹ in less than 20 years [29]. This decreasing density is mainly explained by the destruction of termite mounds by farmers who do not see any reason to preserve termites in their fields, yet the mounds provided several ecosystem services including maintaining a reservoir of animal and plant diversity which was usable as food, medicine or natural pesticides [28,29]. Vegetables (shallot, garlic, chili, tobacco...) were also cultivated on the fringes of termite mounds [113] and soil from the termite mounds was used as natural fertilizer, as still observed in Cambodia (Jouquet, pers. obs.). However such services, once self-generated in diverse agro-ecosystems, are nowadays in effect provided by affordable inputs as farmers gain access to chemical fertilizers, hospitals and markets.

4. Conclusion

Increasing knowledge about the importance of termites for the maintenance of the integrity and functioning of ecosystems has not prevented them being seen only as pests of crops, trees and wood. As a consequence, environmentally unfriendly methods to eliminate pest species are often damaging to beneficial ones. Of approximately 2800 described species, only 185 are proven pests

[126]. Thus, the main global impact of termites, outweighing their pest status, is clearly to provide the ecosystem services listed above. This role is however under-appreciated and more research is needed to better evaluate the importance of termite activity and diversity in tropical ecosystems. For instance, more studies must be performed on the impact of termite diversity on clay properties and nutrient cycling, and on the distribution and availability of these resources in the ecosystems. These researches, together with those dealing with the effect of termites on biodiversity (above- and below-ground organisms), are important to favour the development of field management schemes which will promote the recovery or enhancement of termite-mediated ecosystem services, especially in ecosystems subject to disturbance, degradation or agricultural intensification. For instance, in North-East Thailand, if the destruction of termite mounds is economically justifiable in the short term, the strategy is not necessarily sensible further into the future, and the adoption of cultural practices consistent with the preservation of natural termite communities may still be the best bet for the long-term preservation of ecosystem services (reviewed in [15]). In a changing world with a depletion of global petroleum resources and an increasing demand for less chemical inputs into agricultural ecosystems, external inputs may eventually become both uneconomic and unsustainable. In this scenario it is more likely that the self-renewing ecosystem services provided by termites will re-emerge as a relevant option in tropical agro-ecosystems.

Acknowledgment

We thank Michel Lepage for the inspiration provided by his work on termites and soil, for the field experience he has passed to his younger colleagues and for his excellence as a supervisor. This research was supported by IRD (Institut de Recherche pour le Développement, UMR 211 BIOEMCO).

References

- [1] L. Abbadie, M. Lepage, The role of subterranean fungus-comb chambers (Isoptera, Macrotermitinae) in soil nitrogen cycling in a preforest savanna (Côte d'Ivoire), *Soil Biol. Biochem.* 21 (1989) 1067–1071.
- [2] L. Abbadie, R. Lensi, Carbon and nitrogen mineralization and denitrification in a humid savanna of West Africa (Lamto, Côte d'Ivoire), *Acta Oecol.* 11 (1990) 717–728.
- [3] L. Abbadie, M. Lepage, X. Le Roux, Soil fauna at the forest-savanna boundary: role of termite mounds in ecosystem heterogeneity and nutrient cycling. in: J. Proctor (Ed.), *Nature and Dynamics of Forest-Savanna Boundaries*. Unwin, London, 1992, pp. 473–484.
- [4] S.S. Abe, T. Wakatsuki, Possible influence of termites (*Macrotermes bellicosus*) on forms and composition of free sesquioxides in tropical soils, *Pedobiologia* 53 (2010) 301–306.
- [5] I.L. Ackerman, W.G. Teixeira, S.J. Riha, J. Lehmann, E.C.M. Fernandes, The impact of mound-building termites on surface soil properties in a secondary forest of Central Amazonia, *Appl. Soil Ecol.* 37 (2007) 267–276.
- [6] M. Anand, A. Gonzalez, F. Guichard, J. Kolasa, L. Parrott, Ecological systems as complex systems: challenges for an emerging science, *Diversity* 2 (2010) 395–410.
- [7] Z. Andrianjaka, R. Bally, M. Lepage, J. Thioulouse, G. Comte, M. Kisa, R. Duponnois, Biological control of *Striga hermonthica* by *Cubitermes* termite mound powder amendment in sorghum culture, *Appl. Soil Ecol.* 37 (2007) 175–183.
- [8] M.A. Arshad, Physical and chemical properties of termite mounds of two species of *Macrotermes* (Isoptera, Macrotermitinae) and the surrounding soils of the semiarid savanna of Kenya, *Soil Sci.* 132 (1981) 161–174.
- [9] M.A. Arshad, M. Schnitzer, C.M. Preston, Characterization of humic acids from termite mounds and surrounding soils, Kenya, *Geoderma* 42 (1988) 213–225.
- [10] E. Barros, P. Curmi, V. Hailaire, A. Chauvel, P. Lavelle, The role of macrofauna in the transformation and reversibility of soil structure of an oxisol in the process of forest to pasture conversion, *Geoderma* 100 (2001) 193–213.
- [11] R.H.V. Bell, The effect of soil nutrient availability on community structure in African ecosystems. in: B.J. Huntley, B.H. Walker (Eds.), *Ecology of Tropical Savannas*. Springer-Verlag, Berlin, 1983, pp. 192–216.

- [12] N.V. Belyaeva, A.V. Tiunov, Termites (Isoptera) in forest ecosystems of Cat Tien National Park (Southern Vietnam), *Biol. Bull.* 37 (2010) 374–381.
- [13] D.E. Bignell, J.M. Anderson, R. Crosse, Isolation of facultatively aerobic actinomycetes from the gut, parent soil and mound materials of the termites *Procutitermes aburiensis* and *Cubitermes severus*, *FEMS Microbiol. Ecol.* 85 (1991) 151–160.
- [14] D.E. Bignell, P. Eggleton, Termites in Ecosystems. in: T. Abe, D.E. Bignell, M. Higashi (Eds.), *Termites: Evolution, Sociality, Symbioses, Ecology*. Kluwer Academic Publishers, Dordrecht, 2000, pp. 363–387.
- [15] D.E. Bignell, J. Tondoh, L. Dibog, S.P. Huang, F. Moreira, D. Nwaga, B. Pashanasi, F.-X. Susilo, M. Swift, Belowground biodiversity assessment: developing a key functional group approach in best-bet alternatives to Slash-and-Burn. in: C.A. Palm, S.A. Vosti, P.A. Sanchez, P.J. Erickson (Eds.), *Slash-and-Burn Agriculture: The Search for Alternatives*. Columbia University Press, New York, 2005, pp. 119–142.
- [16] D.E. Bignell, Termites as soil engineers and soil processors. in: H. König, A. Varma (Eds.), *Intestinal Microorganisms of Soil Invertebrates*. Springer, Berlin, 2006, pp. 183–220.
- [17] D.E. Bignell, Morphology, physiology, biochemistry and functional design of the termite gut: an evolutionary Wonderland. in: D.E. Bignell, Y. Roisin, N. Lo (Eds.), *Biology of Termites: A Modern Synthesis*. Springer, Dordrecht, 2011, pp. 375–412.
- [18] H.I.J. Black, M.J.N. Okwakol, Agricultural intensification, soil biodiversity and agrosystem function in the tropics; the role of termites, *Appl. Soil Ecol.* 6 (1997) 37–53.
- [19] J.P. Boga, P. Kouassi, A. Yapi, A. Tahiri, Y. Tano, Modification des propriétés des sols par les termites et impact des sols de termitières sur la production de maïs et de riz en savane de Côte d'Ivoire, *Sci. Tech.* 24 (2000) 54–66.
- [20] P. Boyer, Action de certains termites constructeurs sur l'évolution des sols tropicaux. 1^e partie; les termites et le sol, *Ann. Sci. Nat. Zool.* 15 (1973) 329–498.
- [21] P. Boyer, Quelques aspects de l'action des termites du sol sur les argiles, *Clay Miner.* 17 (1982) 453–462.
- [22] A. Brauman, Effect of gut transit and mound deposit on soil organic matter transformations in a soil-feeding termite: a review, *Eur. J. Soil Biol.* 36 (2000) 117–125.
- [23] A. Brauman, D.E. Bignell, I. Tayasu, Soil-feeding termites: biology, microbial associations and digestive mechanisms. in: T. Abe, D.E. Bignell, M. Higashi (Eds.), *Termites: Evolution, Sociality, Symbioses, Ecology*. Kluwer Academic Publishers, Dordrecht, 2000, pp. 233–259.
- [24] A.K. Brody, T.M. Palmer, K. Fox-Dobbs, D.F. Doak, Termites, vertebrate herbivores, and the fruiting success of *Acacia drepanolobium*, *Ecology* 91 (2010) 399–407.
- [25] M. Brossard, D. Lopez-Hernandez, M. Lepage, J.C. Leprun, Nutrient storage in soils and nests of mound-building *Trinervitermes* termites in Central Burkina Faso: consequences for soil fertility, *Biol. Fert. Soils* 43 (2007) 437–447.
- [26] C. Brümmer, H. Papen, R. Wassmann, N. Bruggemann, Fluxes of CH₄ and CO₂ from soil and termite mounds in south Sudanian savanna of Burkina Faso (West Africa), *Global Biogeochem. Cy.* 23 (2009) L09814.
- [27] A. Brune, M. Ohkuma, Role of the termite gut microbiota in symbiotic digestion. in: D.E. Bignell, Y. Roisin, N. Lo (Eds.), *Biology of Termites: A Modern Synthesis*. Springer, Dordrecht, 2011, pp. 439–475.
- [28] C. Choosai, J. Mathieu, Y. Hanboonsong, P. Jouquet, Termite mounds and dykes are biodiversity refuges in paddy fields in north-eastern Thailand, *Environ. Conserv.* 36 (2009) 71–79.
- [29] C. Choosai, Biological activity in paddy fields. The role of soil engineers in ecosystem functioning, PhD Thesis, Paris VI University, 2010.
- [30] N.M. Collins, The role of termites in the decomposition of wood and leaf litter in the southern Guinea savanna of Nigeria, *Oecologia* 51 (1981) 389–399.
- [31] N.M. Collins, The utilization of nitrogen resources by termites (Isoptera). in: J.A. Lee, S. McNeill, I.H. Rorison (Eds.), *Nitrogen as an Ecological Factor*. Blackwell Scientific Publications, Oxford, 1983, pp. 381–412.
- [32] R.A. Congdon, J.A. Holt, W.S. Hicks, The role of mound-building termites in the nitrogen economy of semi-arid ecosystems, *Proc. 6th Australasia Conf. Grassland Invertebrates Ecology*, Hamilton, New Zealand, 1993.
- [33] D. Contour-Ansel, E. Garnier-Sillam, M. Lachaux, V. Croci, High performance liquid chromatography studies on the polysaccharides in the walls of the mounds of two species of termite in Senegal, *Cubitermes oculatus* and *Macrotermes subhyalinus*: their origin and contribution to structural stability, *Biol. Fert. Soils* 31 (2000) 508–516.
- [34] J.M. Dangerfield, T.S. McCarthy, W.M. Ellery, The mound-building termite *Macrotermes michaelseni* as an ecosystem engineer, *J. Trop. Ecol.* 14 (1988) 507–520.
- [35] J.P.E.C. Darlington, The underground passages and storage pits used in foraging by a nest of the termite *Macrotermes michaelseni* in Kajiado, Kenya, *J. Zool. London* 198 (1982) 237–247.
- [36] T. Decaëns, J.H. Galvin, E. Amezcuita, Propriétés des structures produites par les ingénieurs écologiques à la surface du sol d'une savane colombienne, *C.R. Acad. Sci. Life Sci.* 324 (2001) 465–478.
- [37] M. Diouf, E. Miambi, P. Mora, S. Delgarde, C. Rouland, The impact of termite sheetings age on their fungal communities, *Eur. J. Soil Biol.* 42 (2006) 85–91.
- [38] S.E. Donovan, P. Eggleton, D.E. Bignell, Gut content analysis and a new feeding group classification of termites (Isoptera), *Ecol. Entomol.* 26 (2001) 356–366.
- [39] S.E. Donovan, P. Eggleton, W.E. Dubbin, M. Batchelder, L. Dibog, The effect of a soil-feeding termite, *Cubitermes fungifaber* (Isoptera: Termitidae) on soil properties: termites may be an important source of soil microhabitat heterogeneity in tropical forests, *Pedobiologia* 45 (2001) 1–11.
- [40] R. Duponnois, M. Paugy, J. Thioulouse, D. Masse, M. Lepage, Functional diversity of soil microbial community, rock phosphate dissolution and growth of *Acacia seyal* as influenced by grass-, litter- and soil-feeding termite nest structure amendments, *Geoderma* 124 (2005) 349–361.
- [41] N. Elkins, G. Babol, T. Ward, W. Whitford, The influence of subterranean termites on the hydrological characteristics of a Chihuahuan desert ecosystem, *Oecologia* 68 (1986) 521–528.
- [42] V. Eschenbrenner, Contribution des termites à la micro-agrégation des sols tropicaux, *Cah. ORSTOM, sér. Pédol.* 4 (1986) 397–408.
- [43] S. Fall, A. Brauman, J.L. Chotte, 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*, *Appl. Soil Ecol.* 17 (2001) 131–140.
- [44] S. Fall, S. Nazaret, J.L. Chotte, A. Brauman, Bacterial density and community structure associated with aggregate size fractions of soil-feeding termite mounds, *Microb. Ecol.* 48 (2004) 191–199.
- [45] S. Fall, J. Hamelin, F. Ndiaye, K. Assigbetse, M. Aragno, J.L. Chotte, A. Brauman, Differences between bacterial communities in the gut of a soil-feeding termite (*Cubitermes niokoloensis*) and its mounds, *Appl. Env. Sci.* 73 (2007) 5199–5208.
- [46] K. Fox-Dobbs, D.F. Doak, A.K. Brody, T.M. Palmer, Termites create spatial structure and govern ecosystem function by affecting N-2 fixation in an East African savanna, *Ecology* 91 (2010) 1296–1307.
- [47] A. Freijoo, E.B. Knapp, P. Lavelle, A.G. Moreno, Quantifying soil macrofauna in a Colombian watershed. in: J.J. Jiménez, R.J. Thomas (Eds.), *Nature's Plough: Soil Macroinvertebrate Communities in the Neotropical Savannas of Colombia*. CIAT, Cali, Columbia, 2001.
- [48] B.P. Freymann, S.N. de Visser, E.P. Mayemba, H. Olf, Termites of the genus *Odontotermes* are optionally keratophagous, *Ecotropica* 13 (2007) 143–147.
- [49] B.P. Freymann, R. Buitenwerf, O. Desouza, H. Olf, The importance of termites (Isoptera) for the recycling of herbivore dung in tropical ecosystems: a review, *Eur. J. Entomol.* 105 (2008) 165–173.
- [50] B.P. Freymann, S.N. de Visser, H. Olf, Spatial and temporal hotspots of termite-driven decomposition in the Serengeti, *Ecography* 33 (2010) 443–450.
- [51] E. Garnier-Sillam, E. Braudeau, D. Tessier, Rôle des termites sur le spectre poral des sols forestiers tropicaux. Cas de *Thoracotermes macrothorax* Sjöstedt (Termitinae) et de *Macrotermes mülleri* (Sjöstedt) (Macrotermitinae), *Insect. Soc.* 38 (1991) 397–412.
- [52] E. Garnier-Sillam, M. Harry, Distribution of humic compounds in mounds of some soil-feeding termite species of tropical rainforests: its influence on soil structure stability, *Insect. Soc.* 42 (1995) 167–185.
- [53] P.E. Glover, E.C. Trump, L.E.D. Wateridge, Termitaria and vegetation patterns on the Loita Plains of Kenya, *J. Ecol.* 52 (1964) 367–375.
- [54] C.C. Grant, M.C. Scholes, The importance of nutrient hot-spots in the conservation and management of large wild mammalian herbivores in semi-arid savanna, *Biol. Conserv.* 130 (2006) 426–437.
- [55] J.A. Holt, Mound-building termites and soil microbial biomass: an interaction influencing termite abundance, *Insect. Soc.* 43 (1996) 427–434.
- [56] J.A. Holt, M. Lepage, Termites and soil properties. in: T. Abe, D.E. Bignell, M. Higashi (Eds.), *Termites: Evolution, Sociality, Symbioses, Ecology*. Kluwer Academic Publishers, Dordrecht, 2000, pp. 389–407.
- [57] J.M. Hunter, *Macrotermes* geophagy and pregnancy clays in Southern Africa, *J. Cult. Geogr.* 14 (1993) 69–92.
- [58] J.L. Janeau, C. Valentin, Relations entre les termitières de *Trinervitermes* sp. et la surface du sol: réorganisations, ruissellement et érosion, *Rev. Ecol. Biol. Sol.* 24 (1987) 637–647.
- [59] R. Ji, A. Brune, Nitrogen mineralization, ammonia accumulation and emission of gaseous NH₃ by soil-feeding termites, *Biogeochemistry* 78 (2006) 267–283.
- [60] J.J. Jiménez, T. Decaëns, Chemical variations in the biostructures produced by soil ecosystem engineers. Examples from the neotropical savannas, *Eur. J. Soil Biol.* 42 (2006) 92–102.
- [61] J.A. Jones, Termites, soil fertility and carbon cycling in dry tropical Africa: a hypothesis, *J. Trop. Ecol.* 6 (1990) 291–305.
- [62] P. Jouquet, M. Lepage, B. Velde, Termite soil preferences and particle selection: strategies related to ecological requirements, *Insect. Soc.* 49 (2002) 1–7.
- [63] P. Jouquet, L. Mamou, M. Lepage, B. Velde, Effect of termites on clay minerals in tropical soils: fungus-growing termites as weathering agents, *Eur. J. Soil Sci.* 53 (2002) 521–527.
- [64] P. Jouquet, T. Mery, C. Rouland, M. Lepage, Modulated effect of the termite *Ancistrotermes cavithorax* (Isoptera, Macrotermitinae) on soil properties according to the internal mound structures, *Sociobiology* 42 (2003) 403–412.
- [65] P. Jouquet, N. Boulain, J. Gignoux, M. Lepage, Association between subterranean termites and grasses in a West African savanna: spatial pattern analysis shows a significant role for *Odontotermes n. pauperans*, *Appl. Soil Ecol.* 27 (2004) 99–107.
- [66] P. Jouquet, P. Barré, M. Lepage, B. Velde, Impact of subterranean fungus-growing termites (Isoptera, Macrotermitinae) on soil properties in a West African savanna, *Biol. Fert. Soils* 41 (2005) 365–370.
- [67] P. Jouquet, L. Ranjard, M. Lepage, J.C. Lata, Incidence of fungus-growing termites (Isoptera, Macrotermitinae) on the structure of soil microbial communities, *Soil Biol. Biochem.* 37 (2005) 1852–1859.

- [68] P. Jouquet, V. Tavernier, L. Rugolino, L. Abbadie, M. Lepage, Nests of subterranean fungus-growing termites (Isoptera, Macrotermitinae) as nutrient patches in savannah ecosystems, *Afr. J. Ecol.* 43 (2005) 191–196.
- [69] P. Jouquet, J. Dauber, J. Lagerlof, P. Lavelle, M. Lepage, Soil invertebrates as ecosystem engineers: intended and accidental effects on soil and feedback loops, *Appl. Soil Ecol.* 32 (2006) 153–164.
- [70] P. Jouquet, N. Bottinelli, J.C. Lata, P. Mora, S. Caqueneau, Role of the fungus-growing termite *Pseudacanthotermes spiniger* (Isoptera, Macrotermitinae) in the dynamic of clay and soil organic matter content, an experimental analysis, *Geoderma* 139 (2007) 127–133.
- [71] P. Jouquet, J. Mathieu, C. Choosai, S. Barot, Soil engineers as ecosystem heterogeneity drivers. in: S.I. Munoz (Ed.), *Ecology Research Progress*. Nova Science Publishing, Hauppauge, NY, 2007, pp. 187–199.
- [72] L.A. Ketch, D. Malloch, W.C. Mahaney, M.A. Huffman, Comparative microbial analysis and clay mineralogy of soils eaten by chimpanzees (*Pan troglodytes schweinfurthii*) in Tanzania, *Soil Biol. Biochem.* 33 (2001) 199–203.
- [73] M.G. Kibblewhite, K. Ritz, M.J. Swift, Soil health in agricultural systems, *Phil. Trans. R. Soc. Lond. Ser. B* 363 (2008) 685–701.
- [74] G. Klaus, B. Schmid, Geophagy at natural licks and mammal ecology: a review, *Mammalia* 62 (1998) 481–497.
- [75] S. Konaté, X. Le Roux, D. Tessier, M. Lepage, Influence of large termitaria on soil characteristics, soil water regime, tree leaf shedding pattern in a West African savanna, *Plant Soil* 206 (1999) 47–60.
- [76] C. Kooyman, R.F.M. Onck, The Interactions between Termite Activity, Agricultural Practices and Soil Characteristics in Kisii District, Kenya. Agricultural University Wageningen Papers, 1987, pp. 1–120.
- [77] P. Lavelle, D.E. Bignell, M. Lepage, V. Wolters, P. Roger, P. Ineson, O.W. Heal, S. Dhillon, Soil function in a changing world: the role of invertebrate ecosystem engineers, *Eur. J. Soil Biol.* 33 (1997) 159–193.
- [78] P. Lavelle, Functional domains in soils, *Ecol. Res.* 17 (2002) 441–450.
- [79] P. Lavelle, D. Bignell, M. Austen, V.K. Brown, V. Behan-Pelletier, J. Garey, P. Giller, S.J. Hawkins, G.G. Brown, M. St. John, B. Hunt, E. Paul, Connecting soil and sediment biodiversity: the role of scale and implications for management. in: D.H. Wall (Ed.), *Sustaining Biodiversity and Ecosystem Services in Soils and Sediments*. SCOPE Series, vol. 64. Island Press, Washington, DC, 2004, pp. 193–224.
- [80] P. Lavelle, T. Decaëns, M. Aubert, S. Barot, M. Blouin, F. Bureau, P. Margerie, P. Mora, J.-P. Rossi, Soil invertebrates and ecosystem services, *Eur. J. Soil Biol.* vol. 42 (Suppl. 1) (2006) S3–S15 ICSS-Soil Animals and Ecosystems Services, Proceedings of the XIVth International Colloquium on Soil Biology.
- [81] K.E. Lee, T.G. Wood, *Termites and Soils*. Academic Press, London, 1971.
- [82] J. Léonard, J. Rajot, Influence of termites on runoff and infiltration: quantification and analysis, *Geoderma* 104 (2001) 17–40.
- [83] J. Léonard, E. Perrier, J.L. Rajot, Biological macropores effect on runoff and infiltration: a combined experimental and modelling approach, *Agr. Ecosyst. Environ.* 104 (2004) 277–285.
- [84] M. Lepage, Distribution, density and evolution of *Macrotermes bellicosus* nests (Isoptera: Macrotermitinae) in the north-east of Ivory Coast, *J. Anim. Ecol.* 53 (1984) 107–117.
- [85] N. Lo, P. Eggleton, Termite phylogenetics and co-cladogenesis with symbionts. in: D.E. Bignell, Y. Roisin, N. Lo (Eds.), *Biology of Termites: A Modern Synthesis*. Springer, Dordrecht, 2011, pp. 27–50.
- [86] L. Lobry de Bruyn, A.J. Conacher, The role of termites and ants in soil modification: a review, *Aust. J. Soil Res.* 28 (1990) 55–93.
- [87] D. Lopez-Hernandez, M. Brossard, J.-C. Fardeau, M. Lepage, Effect of different termite feeding groups on P sorption and P availability in African and South American savannas, *Biol. Fert. Soils* 42 (2006) 207–214.
- [88] J.P. Loveridge, S.R. Moe, Termitaria as browsing hotspots for African mega-herbivores in Miombo woodland, *J. Trop. Ecol.* 20 (2004) 337–343.
- [89] A.I. Luoba, P.W. Geissler, B. Estambale, J.H. Ouma, P. Magnusson, D. Alusala, R. Ayah, D. Mwanaki, H. Friis, Geophagy among pregnant and lactating women in Bondo District, western Kenya, *Trans. R. Soc. Trop. Med. Hyg.* 98 (2004) 734–741.
- [90] W.C. Mahaney, R.G.V. Hancock, S. Aufreiter, M.A. Huffman, Geochemistry and clay mineralogy of termite mound soil and the role of geophagy in chimpanzees of the Mahale mountains, Tanzania, *Primates* 37 (1996) 121–134.
- [91] W.C. Mahaney, J. Zippin, M.W. Milner, K. Sanmugadas, R.G.V. Hancock, S. Aufreiter, S. Campbell, M.A. Huffman, M. Wink, D. Malloch, V. Kalm, Chemistry, mineralogy and microbiology of termite mound soil eaten by the chimpanzees of the Mahale mountains, Tanzania, *J. Trop. Ecol.* 15 (1999) 565–588.
- [92] M. Mamo, C. Wortmann, Phosphorus sorption as affected by soil properties and termite activity in eastern and southern Africa, *Soil Sci. Soc. Am. J.* 73 (2009) 2170–2176.
- [93] A. Mando, L. Stroosnijder, L. Brussaard, Effects of termites on infiltration into crusted soil, *Geoderma* 74 (1996) 107–113.
- [94] A. Mando, R. Miedema, Termite-induced change in soil structure after mulching degraded (crusted) soil in the Sahel, *Appl. Soil Ecol.* 6 (1997) 241–249.
- [95] A. Mando, L. Brussaard, Contribution of termites to the breakdown of straw under Sahelian conditions, *Biol. Fert. Soils* 29 (1999) 332–334.
- [96] A. Mando, L. Stroosnijder, The biological and physical role of mulch in the rehabilitation of crusted soil in the Sahel, *Soil Use Manage.* 15 (1999) 123–127.
- [97] A. Mando, L. Brussaard, L. Stroosnijder, Termite- and mulch-mediated rehabilitation of vegetation on crusted soil in West Africa, *Restoration Ecol.* 7 (1999) 33–41.
- [98] T.S. McCarthy, W.N. Ellery, J.M. Dangerfield, The role of biota in the initiation and growth of islands on the floodplain of the Okavango alluvial fan, Botswana, *Earth Surf. Proc. Landf.* 23 (1998) 291–316.
- [99] R. Mobaek, A.K. Narmo, S.R. Moe, Termitaria are focal feeding sites for large ungulates in Lake Mburo National Park, Uganda, *J. Zool. Lond.* 267 (2005) 97–102.
- [100] B.B. Mujinya, E. Van Ranst, A. Verdoodt, G. Baert, L.M. Ngongo, Termite bioturbation effects on electro-chemical properties of Ferralsols in the Upper Katanga (DR Congo), *Geoderma* 158 (2010) 233–241.
- [101] D. Ndiaye, R. Duponnois, A. Brauman, M. Lepage, Impact of a soil-feeding termite, *Cubitermes niokoloensis* on the symbiotic microflora associated with a fallow leguminous plant *Crotalaria ochroleuca*, *Biol. Fert. Soil* 37 (2003) 313–318.
- [102] D. Ndiaye, R. Lensi, M. Lepage, A. Brauman, The effect of the soil feeding termite *Cubitermes niokoloensis* on soil microbial activity in a semi-arid savanna in West Africa, *Plant Soil* 259 (2004) 277–284.
- [103] D.K. Ngugi, R. Ji, A. Brune, Nitrogen mineralization, denitrification, and nitrate ammonification by soil-feeding termites: a N-15-based approach, *Biogeochemistry* 103 (2011) 355–369.
- [104] J.C. Noble, W.J. Müller, W.G. Whitford, G.H. Pfitzner, The significance of termites as decomposers in contrasting grassland communities of semi-arid eastern Australia, *J. Arid Environ.* 73 (2009) 113–119.
- [105] J.C. Obi, A.O. Ogunkunle, Influence of termite infestation on the spatial variability of soil properties in the Guinea savanna region of Nigeria, *Geoderma* 148 (2009) 357–363.
- [106] M. Pardeshi, B.A. Kumar Prusty, Termites as ecosystem engineers and potentials for soil restoration, *Curr. Sci. India* 99 (2010) 11.
- [107] J. Pretty, W.J. Sutherland, J. Ashby, J. Auburn, D. Baulcombe, M. Bell, J. Bentley, S. Bickersteth, K. Brown, J. Burke, H. Campbell, K. Chen, E. Crowley, I. Crute, D. Dobbelaere, G. Edwards-Jones, F. Funes-Monzote, H.C.J. Godfray, M. Griffon, P. Gypmantisiri, L. Haddad, S. Halavatau, H. Herren, M. Holderness, A.M. Izac, M. Jones, P. Koohafkan, R. Lal, T. Lang, J. McNeely, A. Mueller, N. Nisbett, A. Noble, P. Pingali, Y. Pinto, R. Rabbinge, N.H. Ravindranath, A. Rola, N. Rosing, C. Sage, W. Settle, J.M. Sha, L. Shiming, T. Simons, P. Smith, K. Strzepeck, H. Swaine, E. Terry, T.P. Tomich, C. Toulmin, E. Trigo, S. Twomlow, J.K. Vis, J. Wilson, S. Pilgrim, The top 100 questions of importance to the future of global agriculture, *Int. J. Agr. Sustain.* 8 (2010) 219–236.
- [108] R.M. Pringle, D.F. Doak, A.K. Brody, R. Jocque, T.M. Palmer, Spatial pattern enhances ecosystem functioning in an African savanna, *PLoS Biol.* 8 (5) (2010) e1000377.
- [109] C. Roose-Amsaleg, Y. Brygoo, M. Harry, Ascomycete diversity in soil-feeding termite nests and soils from a tropical rainforest, *Environ. Microbiol.* 6 (2004) 462–469.
- [110] E. Roose, V. Kabore, C. Guenat, Zai practice: a west African traditional rehabilitation system for semiarid degraded lands, a case study in Burkina Faso, *Arid Soil Res. Rehab.* 13 (1999) 343–355.
- [111] R.B. Rosengaus, J.F.A. Traniello, M.S. Bulmer, Ecology, behavior and evolution of disease resistance in termites. in: D.E. Bignell, Y. Roisin, N. Lo (Eds.), *Biology of Termites: A Modern Synthesis*. Springer, Dordrecht, 2011, pp. 165–191.
- [112] C. Rouland, M. Lepage, J.L. Chotte, M. Diouf, D. Ndiaye, S. Ndiaye, C. Seuge, A. Brauman, Experimental manipulation of termites (Isoptera, Macrotermitinae) foraging patterns in a Sahelo-Sudanese savanna: effect of litter quality, *Insect. Soc.* 50 (2003) 309–316.
- [113] S. Ruaysoongnern, P. Prakongsri, Termite Mound in Agricultural System of Northeast Thailand, Farming System Project. Khon Kaen University, Khon Kaen, Thailand, 1988.
- [114] D. Rückamp, W. Amelung, L.D. Borma, L.P. Naval, C. Martius, Carbon and nutrient leaching from termite mounds inhabited by primary and secondary termites, *Appl. Soil Ecol.* 43 (2009) 159–162.
- [115] D. Rückamp, W. Amelung, N. Theisz, A.G. Bandeira, C. Martius, Phosphorus forms in Brazilian termite nests and soils: relevance of feeding guild and ecosystems, *Geoderma* 155 (2010) 269–279.
- [116] R.G. Ruggiero, J.M. Fay, Utilization of termitarium soils by elephants and its ecological implications, *Afr. J. Ecol.* 32 (1994) 222–232.
- [117] A. Sako, A.J. Mills, A.N. Roychoudhury, Rare earth and trace element geochemistry of termite mounds in central and northeastern Namibia: mechanisms for micro-nutrient accumulation, *Geoderma* 153 (2009) 1–2.
- [118] W.A. Sands, The association of termites and fungi. in: K. Krishna, F. Weesner (Eds.), *Biology of Termites*, vol. 1. Academic Press, New York, 1969, pp. 495–524.
- [119] G. Schuurman, Decomposition rates and termite assemblage composition in semiarid Africa, *Ecology* 86 (2005) 1236–1249.
- [120] G.W. Sileshi, M.A. Arshad, S. Konaté, P.O.Y. Nkunika, Termite-induced heterogeneity in African savanna vegetation: mechanisms and patterns, *J. Veg. Sci.* 21 (2010) 923–937.
- [121] A.V. Spain, J.G. McIvor, The nature and distribution of vegetation associated with the termitaria of some grass- and litter-feeding termites from north-eastern Australia, *J. Ecol.* 76 (1988) 181–191.
- [122] A.V. Spain, V. Gordon, P. Reddell, R. Correll, Ectomycorrhizal fungal spores in the mounds of tropical Australian termites (Isoptera), *Eur. J. Soil Biol.* 40 (2004) 9–14.
- [123] D.J. Tongway, J.A. Ludwig, W.G. Whitford, Mulga log mounds: fertile patches in the semi-arid woodlands of eastern Australia, *Aust. J. Ecol.* 14 (1989) 263–268.
- [124] S. Traoré, M. Tigabu, S.J. Ouedraogo, J.L. Boussim, S. Guinko, M. Lepage, *Macrotermes* mounds as sites for tree regeneration in a Sudanian woodland (Burkina Faso), *Plant Ecol.* 198 (2008) 285–295.
- [125] J.S. Turner, Termites as mediators of the water economy of arid savanna ecosystems. in: A. P.D'Odorico Porporato (Ed.), *Dryland Ecohydrology*. Springer, 2006, pp. 303–313 (Chapter 17).

- [126] M. Verma, S. Sharma, R. Prasad, Biological alternatives for termite control: a review, *Int. Biodeter. Biodegr.* 63 (2009) 959–972.
- [127] C. Villenave, D. Djigal, A. Brauman, C. Rouland-Lefevre, Nematodes, indicators of the origin of the soil used by termites to construct biostructures, *Pedobiologia* 52 (2009) 301–307.
- [128] A.R.P. Walker, B.F. Walker, F.L. Sookaria, R.J. Cannan, Pica. *J. Roy. Soc. Health* 117 (1997) 280–284.
- [129] W.G. Whitford, J.A. Ludwig, J.C. Noble, The importance of subterranean termites in semi-arid ecosystems in south-eastern Australia, *J. Arid Environ.* 22 (1992) 87–91.
- [130] W.G. Wielemaker, Soil formation by termites, a study in the Kisii area, Kenya. Doctoral Thesis, Agricultural University, Wageningen, 1984.
- [131] T.G. Wood, W.A. Sands, The role of termites in ecosystems. in: M.V. Brian (Ed.), *Production Ecology of Ants and Termites*. Cambridge University Press, Cambridge, 1978, pp. 245–292.
- [132] A. Yamada, A.T. Inoue, D. Wiwatwitaya, M. Ohkuma, T. Kudo, T. Abe, A. Sugimoto, Carbon mineralization by termites in tropical forests, with emphasis on fungus combs, *Ecol. Res.* 20 (2005) 453–460.
- [133] A. Yamada, T. Inoue, D. Wiwatwitaya, M. Ohkuma, T. Kudo, A. Sugimoto, Nitrogen fixation by termites in tropical forests, Thailand, *Ecosystems* 8 (2005) 1–9.