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

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A B S T R A C T

As soil engineers, termites play a key role in the functioning of many tropical and subtropical ecosystems. This reviews 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 ecosystems 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.

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 macro-invertebrates 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

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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,