TERMITES AND ECOSYSTEM FUNCTION

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Summary

The several ways termites interact with the plant-soil-litter system are outlined in a conceptual web of pathways to show how distinct actions of termites may impact ecosystem functioning, either positively or negatively. That is, because of their several modes of feeding and nesting, termites may act as agents of decomposition or pedogenesis, pests, competitors of grazing livestock, or as sources of greenhouse gases. In addition, these same feeding and nesting modes lead to the establishment of symbiotic interactions between termites and organisms ranging from microbes to invertebrates and vertebrates, and even plants. All this confers upon termites a role on ecosystem functioning that goes far beyond that of a mere link in the food web.

1. Introduction

The role of termites on ecosystem function has been motivating scientists for a long time. Unlike many other detritivores, termites play a key role in CO_2 release from dead organic matter in tropical soils. By feeding on the wide decomposing continuum from fresh litter to humus, termites can affect the entire dynamics of soil carbon, both directly, by digesting cellulose, and indirectly, by breaking down litter, thereby easing microbial action on otherwise unexposed surfaces of litter items. Such a complex action demands a full array of studies. As a consequence, the fast-accumulating knowledge produced to date expands the realm of entomology to encompass branches of science as diverse as biochemistry, soil science, microbiology, population and community ecology, and even global carbon budget studies. Aware that the rapid growth of this subject may attain unmanageable levels, researchers have engaged in producing many excellent reviews and breakthrough papers over the last years, either in the form of single articles or comprehensive compilations. Examples of such works are listed at the end of this chapter for reference. This chapter aims to contribute to such an effort, presenting a synthetic overview of the several ways termites interact with the plant-litter-soil system and the consequent effects this interaction would pose on ecosystem function on an ecological time scale. Rather than restricting our analysis only on termites inhabiting within the soil matrix, we will be including other species, such as the mound building or the arboreal nesting termites, as long as their action impacts the plant-litter-soil system in some way. We intend to review here not only the physical and chemical changes imposed by such organisms on the soil but also how such modifications would affect local biota. We will keep our framework within the ecological time scale in view of the complexity such a scale can pose on its own. Readers interested on a broader approach such as the effects of termites upon soils on the geological time scale might however profit from our outline, since it could be viewed as a snapshot within a full time series.

2. Overview of Termite Biology

Termites affect and are affected by the environment when inflicting physical and chemical changes in the plant-litter-soil system and they do so through their nesting, foraging, and feeding behavior. Therefore, to fully understand the interplay between termites and ecosystem function, we must first take into account key aspects of their biology. Throughout this section, we shall point out these aspects in a summarized way, aiming to clarify the discussion presented in subsequent sections. Readers interested on a full account on termite biology could start by checking some seminal works presented in the reference list at the end of this chapter.

2.1. Taxonomic Issues

Termites are typical tropical insects whose phylogenetic and nomenclatural status is currently controversial. Until recently, they were considered to form the Order Isoptera but a number of taxonomical studies have shown that termites are indeed a type of cockroach and, as such, they should be classified under the order Blattaria (also known as Blattodea). It has been proposed that Isoptera be retained as an unranked name within Blattaria (i.e. Blattaria: Isoptera), until cockroach phylogeny is better resolved and an appropriate ranking can be applied. Here, we follow such an approach while using the term Isoptera. In addition to that debate, termite families and subfamilies have been recently reviewed and discussed and the approximate current scenario is presented in Table 1 as compared with the old one for reference. According to this new proposition, extant termites are distributed among 8 families of which Mastotermitidae is confined to Australia and Serritermitidae is exclusive to the Neotropics. The Termitidae hold nearly 80% of the extant species. Termite taxonomical diversity is, in fact, moderate: there are now approximately 2600 species distributed among 280 genera.

Grassé (1986)		Engel et al. (2009)	
Mastotermitidae		Mastotermitidae	
Hodotermitidae		Hodotermitidae	
Termopsidae		*Termopsidae *sensu novum*	
	Termopsinae	**Archotermopsidae, new family	
	Stolotermitinae	Stolotermitidae	
	Porotermitinae		Stolotermitinae
			Porotermitinae
Kalotermitidae		Kalotermitidae	
Serritermitidae		Serritermitidae (*Serritermes* + *Glossotermes*)	
Rhinotermitidae		Rhinotermitidae	
	Coptotermitinae		Coptotermitinae
	Heterotermitinae		Heterotermitinae
	Prorhinotermitinae		Prorhinotermitinae
	Psammotermitinae		Psammotermitinae
	Termitogetoninae		Termitogetoninae
	Rhinotermitinae		Rhinotermitinae
	Stylotermitinae	Stylotermitidae	
Termitidae		Termitidae	
	Macrotermitinae		Macrotermitinae
			Sphaerotermitinae
	Apicotermitinae		Apicotermitinae
	Nasutitermitinae		Nasutitermitinae
			Syntermitinae
	Termitinae		Termitinae
			Foraminitermitinae

Table 1. Termite classification according to two propositions.
* Termopsidae *sensu novum* (comprises only *Termopsis*, a fossil genus);
** Included genera: *Archotermopsis, Zootermopsis, Hodotermopsis*

2.2. Life History

Termites are eussocial insects, that is, insects that live in colonies composed of individuals (i) from more than one generation (e.g., parents and offspring) (ii) presenting cooperative care of the young and (iii) showing reproductive division of labor. Termite colonies are normally composed of a reproductive pair (king and queen) and their offspring comprising thousands of non-reproductive individuals. Eventually, the reproductive pair originates reproductive offspring, which swarm out of the nest to establish a new colony. A termite colony, therefore, can be grouped into morphological 'castes', which can be reproductive (king, queen, and their reproductive offspring) or sterile (workers and soldiers). As with other biological systems, exceptions apply: Neotropical Apicotermitinae (Termitidae) termites do not possess soldiers, and Kalotermitidae and Termopsidae (traditional sense or Archotermopsidae in the new classification) do not possess true workers. Instead, their immature nymphs do most of the tasks of the colony. Such nymphs (called pseudergates) present very plastic development pathways, staying in this phase by stationary molts or differentiating either into soldiers or secondary reproductives (with wing buds).

As a general rule, workers perform most of the tasks that keep the colony running smoothly, including caring for the royal couple and nest mates, foraging, repairing the nest and defending the colony. Soldiers, in their turn, are more specialized in the colony's defence.

Some species (including all Kalotermitidae and Termopsidae, plus some Rhinotermitidae) live within wood. Others, among which include some Rhinotermitidae and some Termitidae, live inside the soil matrix in nests that are better described as diffuse gallery systems. Some (e.g., Termitidae *Procornitermes* spp.) build very architecturally complex nests, albeit completely subterranean. Others, while keeping intricate gallery systems inside the soil, still build mounds emerging from the soil surface. Among those, the Termitidae *Syntermes* spp. build loose earthen mounds whose major portion rests within the soil and no cemented walls are distinguishable above the soil surface. *Cornitermes* spp. and *Macrotermes* spp. (both Termitidae), in their turn, are well known examples of creating highly structured nests with hard walls built from a mixture of clay, saliva and feces, whose major portion is seen above the soil surface. Such buildings are normally called 'termitaria'. In addition to being their builders' colony, termitaria can also shelter other organisms or are important nutrient hotspots for plants and their associated fauna. Termitaria, therefore, have a potential ecological role that can not be disregarded as we shall see later.

Some very specialized termite species do not build their own nests but live exclusively inside other termites' buildings; well known examples being the *Serritermes serrifer* (Serritermitidae) and *Inquilinitermes* spp. (Termitidae). These are called 'inquilines', a term that also applies to those termite species that are able to build their own nests but are facultative termitaria invaders. Termite nests may also house microbes, plants, invertebrates and vertebrates, which are called 'termitophiles' or 'termitariophiles', depending respectively on whether they are associated to the host termites or to the termitaria itself.

Apart from those species that live inside wood or those that are strict inquilines, termites need to leave their nests in order to look for food. Most species do so within subterranean tunnels or mud galleries built on the surface but some species are able to forage above ground in the open (e.g., *Hospitalitermes* spp. and *Syntermes* spp. which are both Termitidae and a few others).

2.3. Food and Feeding Habits

Feeding habits of termites are distinctive in that species partition themselves along the decomposition continuum, feeding not only on wood, as dictated by current notion, but on items ranging from living plants and trees at one extreme to highly dispersed organic material in the soil at the other. Interestingly, termites do not restrict themselves to directly derived plant food but can also feed on animal products such as dung, mammalian hooves and even fresh mammalian carcasses. Therefore, when referring to litter feeding by termites, we do so in the broadest sense of the word 'litter': waste products from vegetal and animal origin.

Termite species can be classified into at least four 'feeding groups' or 'functional taxonomic groups', according to the portion of the humification gradient they feed on.

These groups are:

- **Wood and grass feeders, group I:** lower termites (i.e. non-Termitidae) feeding on dead wood and grass.

- **Litter feeders, group II:** Termitidae with a range of feeding habits including dead wood, grass, leaf litter, micro-epiphytes, fungus comb and conidia.

- **Soil-wood feeders, group III:** Termitidae feeding in the organic rich upper layers of the soil, presumably feeding on the soil-wood interface.

- **Soil feeders, group IV:** Termitidae, which are called 'true soil-feeders', ingesting apparently mineral soil to feed on organic matter usually found highly dispersed therein.

By feeding on such items, termites may act as both detritivores and decomposers because in addition to comminuting litter to smaller particles, they are also able to digest lignocellulose through a combination of enzymes produced by themselves and by their microbial gut symbionts. It must be noted that this ability to digest cellulose is not trivial among animals. Those feeding on cell wall frequently do not produce endogenous cellulolytic enzymes, having to rely on microbial endosymbionts to digest cellulose. Moreover, the ability to digest cellulose has environmental significance since it represents half of the biomass synthesized by plant such that its decomposition is prone to impact global carbon cycling.

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Biographical Sketches

Og DeSouza is a lecturer at The Federal University of Viçosa (UFV) in Minas Gerais State, Brazil, where he divides his time between teaching and research. His research interests include termite ecology and behavior. From 1986-1988, he carried out his masters degree at UFV, with field work at the Biological Dynamics of Forest Fragments Project in Manaus working on the effects of forest fragments on termite species richness. From 1989-1993 he carried out his doctoral research at Imperial College, Silwood Park, again on ecosystem fragmentation and termite communities, this time in Cerrado (Brazilian 'savanna'). In between, he has worked on self-organized tolerance to stress in termites, aiming to investigate basal mechanisms of social behavior. Currently, he is starting a project on the behavioral ecology of termite inquilinism.

Eliana M. Cancello is a taxonomist, curator of Isoptera and other othopteroid groups at Museu de Zoologia da Universidade de São Paulo (MZUSP) since 1986. Her main research interests are the taxonomy and systematics of the Neotropical termites and their biogeography. Since 2000, she has been working on the termites of The Atlantic Forest (Brazil) along with more general research projects on systematics of Dictyoptera.