# TERMITES AND ECOSYSTEM FUNCTION

**Og DeSouza**
*Federal University of Viosa, Viosa, MG, Brazil*

**Eliana Marques Cancello**
*Zoology Museum of Sao Paulo University, So Paulo, SP, Brazil*

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## Contents



## 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.

Table 1. Termite classification according to two propositions. Extinct termites are not included.

**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 colonys 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.

## 3. Termites as Elements of the Soil Food Web

Termites are not alone in impacting the soil environment. In fact, the soil biota is likely to be the most complex biological community, whose components belong to a wide range of functional groups (i.e. microsymbionts, decomposers, elemental transformers, soil ecosystem engineers, soil-borne pest and diseases, and microregulators), which deliver ecosystem services essential to life on earth. Such organisms encompass a wide range of taxa and are frequently grouped according to their body width as follows:

- **Microflora and microfauna:** Organisms smaller than 100 m such as Bacteria, Fungi, Nematoda, Protozoa, Rotifera and some Acari.

- **Mesofauna:** Organisms with body width in the range of 100 m2 mm such as most Acari, Collembola, Protura, Diplura, Symphyla, Enchytraeidae, Chelonethi and most Isoptera (termites) as well as some Chilopoda, Diplopoda, Megadrilli (earthworms), Coleoptera, Aranaeida, and Mollusca.

- **Macro and megafauna:** Organisms whose body width is larger than 20 mm including some Isoptera, Opiliones, Isopoda, and Amphipoda as well as most Chilopoda, Diplopoda, Megadrilli (earthworms), Coleoptera, Aranaeida, and Mollusca.

The interactions of these organisms among themselves and between the physicochemical-chemical features of the soil ultimately regulate the two main life-supporting processes on Planet Earth: production and decomposition. That is, when a plant or an animal dies, their bodies must be decomposed in order to release the nutrients which will be re-incorporated into the food web as biomass. Dead organic matter, however, only becomes new production after it is broken down (by soil macro and mesofauna) and then transformed from organic to mineral compounds (mostly by soil microflora and microfauna) to become available to plants, thereby re-entering the food web.

What seem remarkable about termites are the significance and diversity of the roles they play in soil biophysicochemical processes in the tropics. That is, due to their high abundance and biomass, termites take active roles in cellulose processing and soil bioturbation. In doing so, termites establish symbioses with both microbes in their guts and many other organisms in their mounds in such a way to significantly impact local biota. In summary, despite not being the only organisms capable of modifying the soil system, termites represent a complexity of biotic and abiotic interactions which entitle focused study. In the following sections, we will try to pinpoint such interactions and their interconnections, aiming to build a comprehensive picture of how termites affect ecosystem function through their actions on the soil system.

## 4. Ecosystem Impacts from Soil Engineering by Termites

The role of termites on the soil-litter system may be thought of as starting from two main actions: (i) feeding and (ii) soil excavation. Although such actions may begin independently, their pathways may merge, at least conceptually, thereby achieving a reasonable level of complexity. Therefore, in order to ease reasoning, readers are invited to follow this text tracing the corresponding pathways depicted in Fig. 1.

Figure 1. Pathways arising from the interactions between termites and the plant-soil-litter system

### 4.1. Feeding

Termites are major components of detritivore macro-fauna in tropical soils. It is estimated that they may comprise 75% of all insect biomass and 10% of all animal biomass in the tropics. Reported values of termite biomass average approximately 8.56 g $m^{-2}$ for primary or near-primary tropical forests worldwide and 4.14 g $m^{-2}$ for tropical savannas. Such values may attain impressive significance. In the Amazonia rain forest, for instance, total animal biomass is reported to be around 20 g $m^{-2}$, of which 11 g may be uniquely composed by termites. They are also numerically important: termite abundance in tropical forest systems are known to range from 19 to roughly 10,500 individuals $m^{-2}$ and from 49 to 4400 in tropical savannas. This combination of biomass and abundance confers high efficiency to food processing into greenhouse gases. It has been demonstrated that several termite individuals can transform food into 2.1 times more $CO_2$. few individuals amounting to the same total biomass. With such a biomass, they are able to consume a large part of litter produced in tropical systems in addition to live plant tissues. In an average savanna ecosystem, termite consumption achieves 20% net primary productivity, which is roughly the same as that of mammalian herbivores.

By breaking litter down into smaller particles (Fig. 1, box 1), termites can enhance microorganism action because such a fragmentation exposes litters inner surfaces otherwise unavailable for prompt attack by bacteria and fungi. Of course, this is not unidirectional as fungal preconditioning is known to attract decomposer animals (including termites) to, and ease their actions upon, woody materials. It is also not widespread since not all termites feed on fresh litter but species are known to partition themselves along decomposition gradients, each specializing in digesting at progressively more advanced stages of decomposition.

Termite feeding is therefore expected to have a large influence on the timing of litter decomposition and its consequent incorporation into soil as humic compounds or its counterpart, the efflux of carbon to atmosphere. That is, by feeding on the wide decomposing continuum from fresh litter to humus, termites can affect the entire dynamic of soil carbon, both directly, by digesting cellulose, and indirectly, by breaking down litter and easing microbial action. Wood-feeding termites and their microbiota, for instance, have been reported to oxidize approximately 99% of the carbon they consume, releasing it mainly as $CO_2$. Soil-feeding termites, meanwhile, are well known to feed on highly humified material and are even suspected of processing complex polyaromatic components of soil organic matter that have been previously modified by microorganisms. Depending on the ecological context, such processes may lead either to a positive or a negative impact on carbon release as $CO_2$ $CH_4$ atmosphere. It is being proposed that one of the reasons for the soil being brown in the tropics depends on the effects of top-down (i.e. predators) and bottom-up (i.e. food quality) forces upon termite foraging behavior. That is, such trophic controls upon the use of resources by neotropical termites may prevent them from processing all available litter and humus, the remaining material being left to form impervious dark-colored humic complexes in the soil. This seems in accordance with some evidence that forest clearance (or simplification) would increase termite-related $CH_4$, if one takes into consideration that anthropogenic disturbance may impact trophic relationships in ecosystems.

Further complexity is added to this scenario by the role of some termites as pests, a status mainly achieved by consuming (i) wood from buildings and furniture and (ii) living plant tissues. Despite being in low proportions (approximately 10% of termite species are considered pests), their economic impact is highly significant. We shall, however, keep our discussion on the ecological aspects of termite pest actions.

Pests feeding on wooden structures are, ecologically, the same as non-pests feeding on dead organic matter since in doing so xylophagous termites are performing their role as carbon cycling agents (as commented above). On the other hand, when a living plant is attacked by termites, its growth and reproduction are impaired. Termites crop pests, therefore, could delay carbon cycling. Whether or not these counteracting actions are relevant to global carbon budgets is still untested.

Contributions from termites to global $CO_2$ and $CH_4$ are nowadays shown to be negligible. Recent re-calculations estimate contributions within the range 0.2-2% of global totals from all sources of $CO_2$ and 2-4% from all sources of $CH_4$. Such values are still impressive considering that they come from a single taxon representing only 0.01% of the global terrestrial species richness. It must be stressed that this, by no means, implies that termites have no key roles in ecosystem processes as we shall see below.

In semi-arid low-input agricultural systems, for instance, soil fauna (termites) are believed to determine the rate of decomposition of organic resources, whereas the abundance of fungus-growing termites from the Okavango Delta (Botswana) determines almost all observed variation in decomposition rates of wood debris. Enhanced digestion of OM as a consequence of termite action leads to increased OM content in soil with consequent enhanced porosity and stability of aggregates. In fact, porosity and microaggregation of Ferralsols in the Brazilian savanna (Cerrado) is thought to be heavily dependent on the action of termites and earthworms. The improvements arising from such a scenario are obvious. OM decomposition in itself is an important step in energy fluxes since nutrients are thereby made available to plants. Termites, in fact, were shown to affect the whole nitrogen cycle in semi-arid ecosystems; their biogenic structures representing a rich soil compartment especially in inorganic nitrogen accessible to plants. In addition, aggregate stability helps to prevent erosion and enhanced porosity leads to better trade-off between water retention and drainage while promoting better aeration and bulk density. In fact, macropores made by termites are known to increase water infiltration by a mean factor 2-3, reducing runoff. Such improvements in soil inundation by a mean factor 2-3, reducing runoff. Such improvements in soil physical and chemical properties have been hypothesized to be the cause of improved plant growth in proximity to termite mounds. Moreover, positive impacts of termites on plant growth are now known to lead to benefits to biodiversity. That is, increased plant growth increases the animal carrying capacity of an environment since it implies more food for herbivores. The more the herbivores, the more food there is for higher order consumers (predators, parasites, and parasitoids; or carnivores in a broader sense). As the abundance of herbivores and carnivores increases, larger amounts of excrements and carcasses are made available to scavengers, detritivores, and ultimately, decomposers. That is, in the end, soil improvements promoted by termites are prone to affect the whole food web. Current evidence gives some support to such a speculation and we will examine this in more detail in the next section.

### 4.2. Soil Excavation

Conspicuous total biomass of termites also indicates pronounced perturbation to the soil matrix (a process called soil bioturbation). Soil turnover due to mound building by termites may surpass 10 tonnes $ha^{-1}$ a year. In addition, construction of surface galleries may exceed the contribution of mound construction and cause subsequent erosion to soil turnover. This is because surface galleries are constantly eroded and accidentally destroyed, being continuously re-built by termites.

Soil bioturbation by termites can be analyzed at two levels (Fig. 1, box 2). A finer grain level would be represented by the processes occurring at the soil-particle scale. On this scale, we are concerned about the manipulation and ingestion of soil particles by termites and their subsequent modifications on physicochemical and biological properties after gut transit. On a larger scale, termites biogenic structures (mounds, tunnels, galleries) can modify soil traits that ultimately affect availability of resources to other organisms.

While revolving soil, some termites can also ingest soil particles and process them in their gut. It must be noted that not all termites ingest mineral soil particles and certainly not all termites can digest soil organic matter. Others, such as Macrotermitinae workers, ingest minerals but have no digestive process for humic material. However, soil feeding species occur in at least 3 subfamilies (Termitinae, Nasutitermitinae and Apicotermitinae) and are reported to comprise 67% of all termite genera and 50% of all termite species. Taking an estimate of 281 genera and 2600 species worldwide, this makes about 188 genera and 1300 species that are soil-feeding. Among those, some partitioning also occurs: some feed on the organic rich layers of the soil while others ingest more mineral soil to feed on its highly dispersed organic content (see previous discussion on termite feeding groups).

Soil-feeding also occurs in other taxa, such as mites, enchytraeids, collebolans as well as juveniles of some hemipterans and dipterans. However, this habit has become ecological significant only in termites and endogeic earthworms.

Soil-feeding termites present a characteristic digestive tube, presumably associated with the needs of processing their highly specialized food. In fact, compared to wood-feeders and fungus growers, the guts of soil-feeders present greater relative length and number of chambers. This seems to imply that a physiological relength and number of chambers. This seems to imply that a physiological re-organization of the guts, in addition to new mutualisms with microbes, is needed for soil-feeding. This is supported by the observation that gut transit modifies several chemical traits of food ingested by soil-feeding termites. For instance, stability of the soil organic matter seems to increase through the formation of organomineral complexes with the mineral component of the food. Besides, feces of the soil-feeding *Thoracotermes macrothorax* are known to present higher total C and total N content than parent soil, with a large reduction (about 50%) in C/N ratio. In addition, fulvic acid is slightly increased and humic acid is depleted. Whether all this occurs because more recently formed organic matter is selected by termites, or because humic acid is depolymerized during gut transit, is still undetermined. Whatever the mechanism, however, these outputs have major environmental significance. Stability of organomineral complexes include putting soil C into long-turnover pools and this, along with depletion in the C/N ratio, has an overall benefit in the maintenance of fertility.

### 4.3. Termitogenic Structures

Termites also excavate soil aiming to build nesting and foraging structures. Nests, especially the epigeous ones, are the most conspicuous termite products and were the prime reason for the inclusion of termites in ecosystem engineering ranks. Nests may affect ecosystem function in at least three ways:

- Sequestrating nutrients and carbon which, otherwise, would be washed out into deeper soil or lost to the atmosphere;
- Increasing the absolute amount and impacting the quality of living space for other species;
- Increasing habitat patchiness and therefore affecting, on a broader scale, the enhancement of living space mentioned above.

In this respect termites, along with earthworms and ants, are considered to be ecosystem engineers because in causing changes to biotic or abiotic materials, they modify, maintain and/or create habitats.

An impressive range of species can be associated to epigeous nests, either cohabiting with the nest builder within the nest or using the nests walls. Such species are normally referred to as termitophiles (from Greek meaning termite friends) and can be as diverse as microorganisms, plants, insects, amphibians, reptiles, mammals among others. Fleming & Loveridge, when comparing *Macrotermes* mounds with surrounding woodland, have found 93 plant species and 27 vertebrate species associated with the nests. Of those, 20 plant and 6 vertebrate species always occurred on nests and not in surrounding woodland. Similarly, Redford found 27 different species of ants plus termites cohabiting *Cornitermes cumulans* mounds in a Brazilian Cerrado, among those 17 are termites from 14 different genera.

Termite species that live in other termites nests are normally referred to as inquilines to distinguish them from other termitophiles. Classical examples include *Inquilinitermes* spp., whose generic name says everything about their main nesting behavior (*Inquilinus* is Latin for lodger or tenant), and *Serritermes serrifer*, which nests within *Cornitermes cumulans* nests.

Another interesting association between termite nests and biodiversity arises from the use of mounds by plants and their dependent herbivores. Mounds originally built, but not necessarily occupied, by *Macrotermes* spp. are said to be browsing hotspots for African megaherbivores in nutrient-poor woodlands. It has been demonstrated that by supporting denser vegetation as moundless spots, termite mounds become important in sustaining populations of black rhino and elephants in these woodlands. It is assumed that these mounds function as eutrophic islands in such environment, which is in accordance with other findings on *Cubitermes nikoloensis* mounds. In these latter mounds, plant growth benefits from the high content of P and mineral nitrogen in the walls and from the high amount of symbiotic microbiota (mycorrhiza and rhizobia) in the soil in the immediate vicinity of mounds.

In fact, microorganisms may profit a lot from a termites building habit. Bacterial density of *Cubitermes niokoloensis* mounds can be significantly higher (1.5 to 3 times) than that of the surrounding soil. The mounds of such termites can be hotspots of mineral nitrogen (reported values attaining 100 times and 50 times) compared to the savanna soil. This high level of mineral nitrogen was associated with a higher density of denitrifying bacteria and increased denitrification and ammonification potentials (3 and 4 times respectively) in the mound compartments compared to the reference soil. Enhanced microorganism diversity, abundance, and activity on nests can enhance inorganic and organic processing, which in turn can enhance plant growth. This consequent increment in plant growth can proceed either through increased nutrient availability or via increased OM content, merging the pathways discussed earlier for soil ingestion and litter breakdown (Fig. 1).

Enhanced microorganism activity in nests (and other termitogenic structures) may also impact global carbon budget. $CH_4$ from termite mounds in secondary forest sites in Cameroon was found to be higher than that in nearby primary forest. $CH_4$ in soil (and hence, diminished emission to atmosphere) depends on the length of the oxidative paths, which are a function of soil properties such as porosity and bulk density. Because such traits are affected by termite action, it is plausible to suspect that termites might have enhanced oxidation rates in undisturbed sites by improving soil structure and by providing a supply of substrate for the methane-oxidizing community. That is, $CH_4$ by termites seems to be mitigated by their own tunnels, galleries and nests with the help of associated microorganisms.

Nests break physical and chemical habitat homogeneity, thereby creating new niches that sustain a biodiversity which is higher than that of areas lacking in mounds. Heterogeneity in soil fertility created by termite nests in Amazonia, for instance, is believed to promote plant diversity by allowing the coexistence of plants dependent on rich as well as plants specialized in living in poor soils. Such a concentration of nutrients, however, may also be thought deleterious to plants because (i) it causes depletion of nutrients in the surroundings of termite mounds and (ii) it means that nutrients would stay immobilized in a nests walls for some time until erosion returns them to the soil. The net outcome of such antagonistic forces remains yet to be tested in the field.

A similar effect might arise from the physical heterogeneity created by nests. At least theoretically, environments presenting higher physical diversity may impair least theoretically, environments presenting higher physical diversity may impair the efficiency of predator simply because preys profit more from hiding places. Records on fields presenting impressive densities of termites and hence high habitat heterogeneity are common in the literature. To our knowledge, however, it has not yet been shown whether or not such heterogeneity does impair predators efficiency. Therefore, we warn that it should be regarded simply as a plausible hypothesis.

Termites can also build hypogeous and arboreal nests, which are at least as architecturally complex and ecologically meaningful as the epigeous ones. The ecological significance paralleling epigeous and non-epigeous termite nests is shown, for instance, by the fact that these latter nest types are also able to house associated biodiversity. Nests of *Constrictotermes cyphergaster*, a typical arboreal nesting termite from Cerrado (Brazilian savanna), are well known to be cohabited by *Inquilinitermes* spp. Other arboreal termite nests, among which are some *Nasutitermes* spp., are used by birds as a nesting site.

Similar information on multiple-occupation is lacking for hypogeous nests although some species (e.g., most *Procornitermes* spp.) do build highly complex hypogeous nests. Such nests, being composed of a set of interconnected, superimposed chambers, would stand as suitable niches for inquilines. In addition, provided that termites build their hypogeous nests by selecting suitable particles from the soil, such nests would also be eutrophic islands within the soil matrix. Therefore, it is highly likely that termite nests, epigeous, arboreal, or hypogeous, exert similar impact on ecosystem function.

When building nests as well as tunnels and galleries, termites are known to utilize soil particles selectively, according to ecological, physiological, and behavioral needs. Some fungus-growers prefer surface soil to build their galleries and deeper soil to build their fungus-comb chambers. Other species build their mounds using selected particles of clays that have high cation exchange capacities (CEC). Soil particle selection, therefore, can turn mounds into important sites for nutrient exchange and this can be particularly true in systems that are generally low in soil organic matter.

## 5. Concluding Remarks

We conclude that the termites impacts on soil are neither restricted to soil ingestion nor to soil feeding species. Litter processing/digestion and building activities of all termites other than the true dry wood species (including that of arboreal nests) also promote modifications on a soils physical, chemical and biological traits. Such modifications may affect the environment; from soil physicochemical structure and dynamics to global carbon budgets through niche availability. Ultimately, soil engineering by the termites impacts diversity and abundance of microorganisms, plants, invertebrates and vertebrates as well as affecting global carbon flux. Whereas evidence points to positive impacts of termites on biodiversity, negative effects are also recognizable and quantitative studies are still lacking to evaluate relative strengths of both classes of effects.

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## Glossary

**Colony** : A group of interdependent individuals living together, normally inside natural cavities or in specially built sheltering structures.

**Epigeous** : Termitaria which have most of their physical structure above the soil surface. The word has Greek roots: epi (upon) + geo (earth).

**Foraging** : The act of searching for and gathering food.

**Hypogeous** : Underground termitaria. The word has Greek roots: hypo(below) + geo (earth, ground).

**Litter** : Dead plants and animals, or parts there from, normally found on/in the soil.

**Mounds** : Termitaria built on the soil surface made from soil particles mixed with termite saliva and assembled with termite feces. A termite mound also has an underground portion. Typical mound builders are *Cornitermes cumulans* from the Neotropics and *Macrotermes michaelseni* from Tropical Africa.

**Nest** : In the context of this chapter, nest is used as a synonym of termitaria.

**Termitaria** : The physical structures built by termites to house their colonies. Termitaria can be above ground, underground or attached to trees.

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**Biographical Sketches**

**Og DeSouza** is a lecturer at The Federal University of Viosa (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 So 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.

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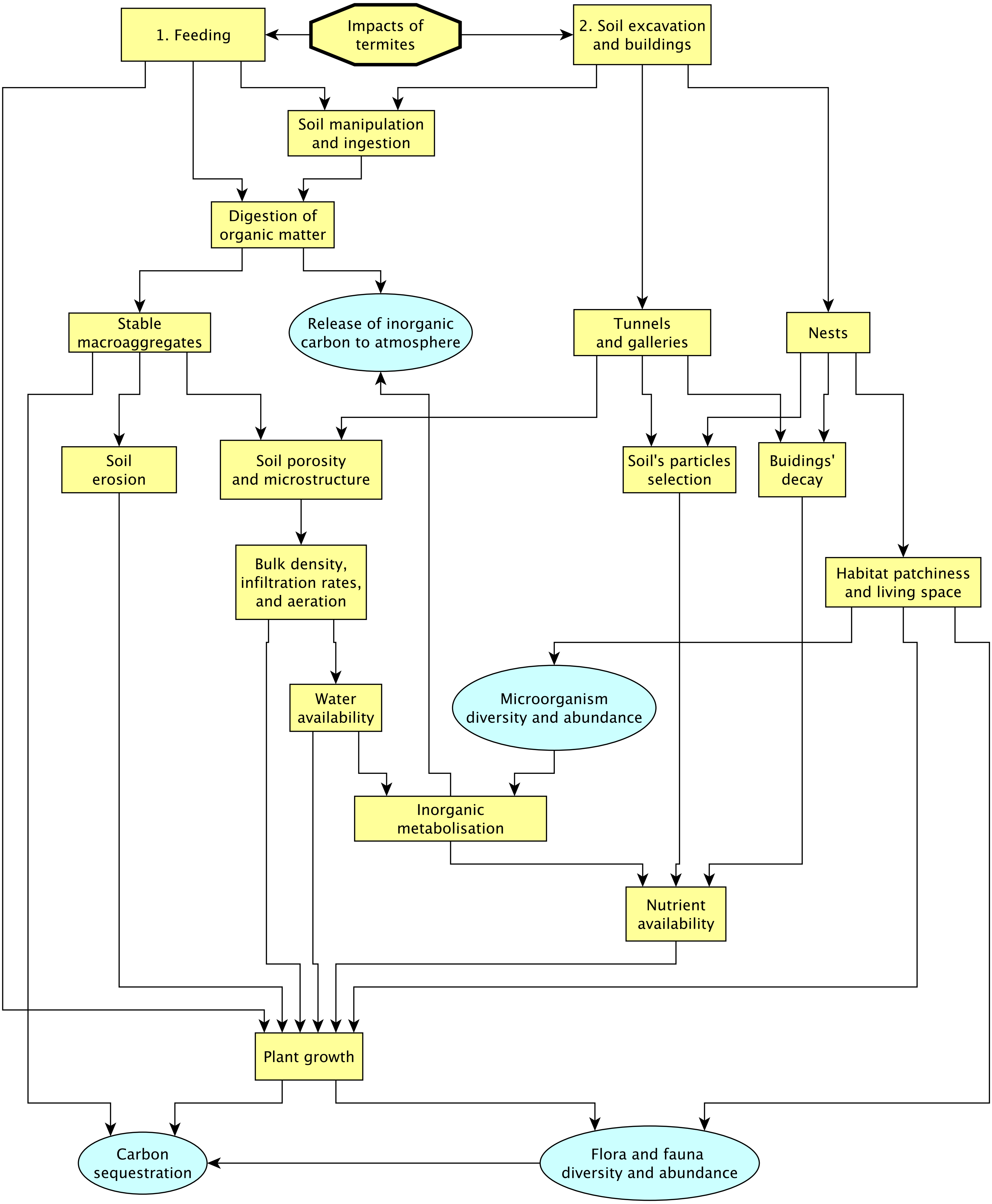

1. Feeding
Impacts of termites
2. Soil excavation and buildings
Soil manipulation and ingestion
Digestion of organic matter
Stable macroaggregates
Release of inorganic carbon to atmosphere
Tunnels and galleries
Nests
Soil erosion
Soil porosity and microstructure
Soil's particles selection
Buidings' decay
Bulk density, infiltration rates, and aeration
Habitat patchiness and living space
Water availability
Microorganism diversity and abundance
Inorganic metabolisation
Nutrient availability
Plant growth
Carbon sequestration
Flora and fauna diversity and abundance

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

| 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 |