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Why is the influence of soil macrofauna on soil structure only considered by soil ecologists?

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ABSTRACT

These last twenty years have seen the development of an abundant literature on the influence of soil macrofauna on soil structure. Amongst these organisms, earthworms, termites and ants are considered to play a key role in regulating the physical, chemical and microbiological properties of soils. Due to these influential impacts, soil ecologists consider these soil macro-invertebrates as 'soil engineers' and their diversity and abundance are nowadays considered as relevant bioindicators of soil quality by many scientists and policy makers. Despite this abundant literature, the soil engineering concept remains a 'preach to the choir' and bioturbation only perceived as important for soil ecologists.

We discussed in this article the main mechanisms by which soil engineers impact soil structure and proposed to classify soil engineers with respect to their capacity to produce biostructures and modify them. We underlined the lack of studies considering biostructure dynamics and presented recent techniques in this purpose. We discussed why soil engineering concept is mainly considered by soil ecologists and call for a better collaboration between soil ecologists and soil physicists. Finally, we summarized main challenges and questions that need to be answered to integrate soil engineers activities in soil structure studies.

1. Introduction

Soil structure regulates a large number of ecological functions, including those that control water infiltration, percolation and retention, gas exchanges, soil organic matter (SOM) and mineral nutrients dynamics, soil microbial biomass, diversity and activity and the susceptibility of soil to erosion. It is a highly dynamics property of soils (Kay, 1990) subject to a large number of variables that can be gathered into environmental (e.g., parent material, topography and climate responsible of shrinking/swelling and freezing/thawing processes), anthropic (e.g., land use management, mechanical disturbance of soil structure by tillage, passage of heavy machines, etc.) and biological (e.g., displacement of soil particles and/or stabilization of soil structure by macrofauna, plant roots and microbial activities) (Dexter, 1988; Kay, 1990; Oades, 1993).

Among soil macrofauna (i.e., soil invertebrates larger than 2 mm), earthworms, termites and ants are considered to play important roles in controlling soil structure dynamic as referred to recent reviews of Blouin et al. (2013a) for earthworms, Holt and Lepage (2000) and Jouquet et al. (2011) for termites, and Cammeraat and Risch (2008) for ants. They are commonly named soil engineers (*sensu* the ecosystem engineer concept defined by Jones et al., 1994, 1997) because of their large population and activities in temperate and tropical ecosystems (Lavelle, 1997; Jouquet et al., 2006). Their foraging and burrowing activities, as well as their ability, in the case of social insects, to create nest structures with specific soil properties in and on soil, largely influence the physical environment in which they live and consequently, soil structure dynamics and the corresponding regulation of soil ecological functions and ecosystem services (Lavelle et al., 2006; Birkhofer et al., 2008). Although less widespread, other soil macro-invertebrates can also play an important role in regulating ecosystem functions in some environments (e.g., beetles larvae (Nichols et al., 2008; Brown et al., 2010; Badorreck et al., 2012) and millipedes (Toyota et al., 2006; Fujimaki et al., 2010)). However, in comparison with

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earthworms, termites and ants, the effects of these organisms remain largely unexplored.

The main objectives of this review article are (i) to highlight the main mechanisms by which soil engineers influence soil structure and (ii) to discuss how their activity is perceived by soil scientists studying the dynamic of soil structure from a review of the existing scientific literature.

2. Influence of soil macrofauna on soil structure

2.1. Critical mechanisms

Soil engineers influence soil structure through the incorporation of litter in the soil. Some species feed on litter and organic residues on the soil surface. They incorporate these organic matters in the soil profile within soil aggregates or in coating their galleries. This is the case of anecic earthworms *sensu* Bouché (1977), and litter- and seed-feeder termites and ants (Yamada et al., 2005; Stadler et al., 2006; Wagner and Jones, 2006; Freymann et al., 2008; Benckiser, 2010). This incorporation of fresh organic matter in soil, which otherwise would have been degraded on soil surface, has large consequences for soil structure because SOM is one of the key factors controlling soil porosity and soil aggregate stability and dynamic (Tisdall and Oades, 1982).

The spheres of influence or volumes of soil influenced by soil engineers are commonly named drilosphere, termitosphere and myrmecosphere, respectively for earthworms, termites and ants (Lavelle, 1997). With respect to their capacity to produce galleries, to modify soil aggregates properties and mineral properties, three groups of soil engineers can be differentiated (Fig. 1):

(i) The bioturbator sensu stricto. This first group corresponds to organisms that influence soil structure through the production of galleries and the translocation of soil aggregates without changing their internal organization, at least at the short-term scale. Galleries are formed from the displacement of earthworms in soil or the burrowing activity of social insects. They can form large networks and occupy a significant volume of soil in some situations (Capowiez et al., 1998; Mando et al., 1999; Buhl et al., 2004; Perna et al., 2008). Obviously, these large macropores are of primary importance in the regulation of water infiltration, the diffusion of solutes (Ehlers, 1975; Nkem et al., 2000; Léonard and Rajot, 2001; Cammeraat et al., 2002; Dominguez et al., 2004; Zehe et al., 2010), gas exchanges and aeration through soil (Kretzschmar and Monestiez, 1992; Capowiez et al., 2006), and they are also expected to influence the spatial distribution of roots and plants (Springett and Gray, 1997; Traore et al., 2008). Some species primarily modify soil porosity but their effects on soil aggregation dynamics are indeed very limited. This group is typically represented by ants that only displace soil aggregates for the creation of their nest structure and subterranean galleries, and also includes burrowing dung beetles, scarabidae and millipede species (Nichols et al., 2008; Snyder et al., 2009).

(ii) The soil aggregate re-organizers. This second group is represented by species that are able to modify soil structure through both the construction of galleries and the consumption of soil aggregates, called biogenic aggregates (Lavelle, 2002). This group includes most of the termite and earthworm species (Jouquet et al., 2011; Blouin et al., 2013b) but it can also include some geophagous millipede species (Toyota et al., 2006; Fujimaki et al., 2010). This group is characterized by an ability to modify the internal organization of soil aggregates. While the quantity of soil aggregates that have been produced by soil engineers is difficult to estimate (Jouquet et al., 2009; Bottinelli et al., 2012, 2013), several studies showed that earthworm casts can make up the majority of soil aggregates in the soil surface or even a whole soil horizon in some situations. As an example, the earthworm species *Amynthas khami* accumulates a large quantity of water stable casts on the soil surface in some environments in Northern Vietnam (from 8 to 22 kg casts m^{-2}) that forms a typical granular horizon from 5 to 10 cm deep (Jouquet et al., 2008b). The same hypothesis has been

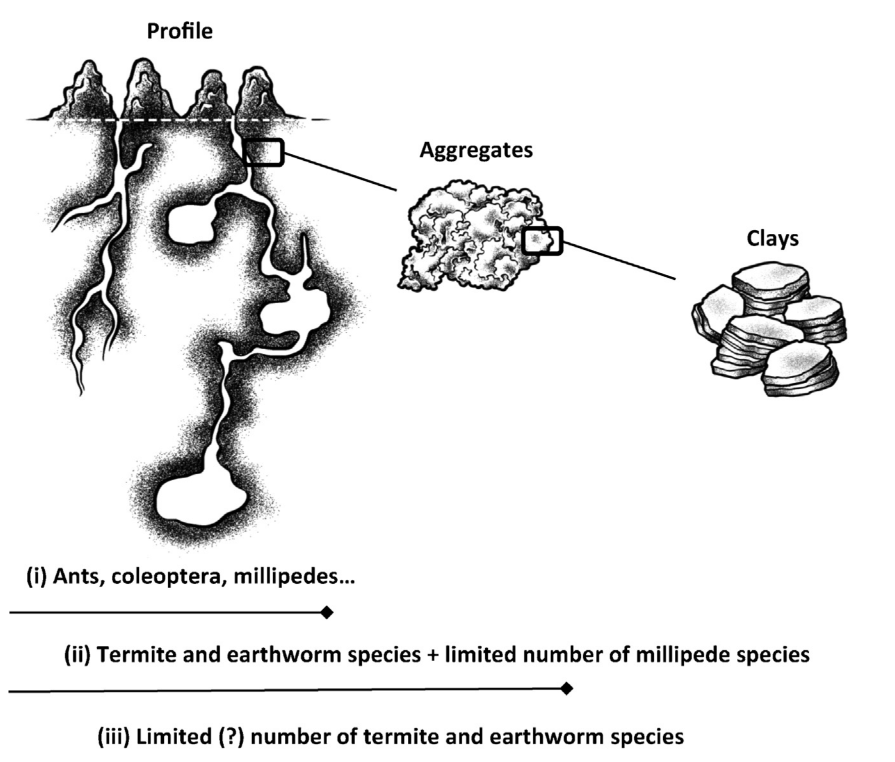

Fig. 1. How soil engineers influence soil structure is variable, with respect to their capacity to produce galleries, modify soil aggregates and mineral properties. Three groups can be differentiated: (i) the bioturbator sensu stricto, (ii) the soil aggregate re-organizers and (iii) the mineral weathering agents.