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Effects of soil macro- and mesofauna on litter decomposition and soil organic matter stabilization

Jan Frouz

Institute of Soil Biology & SoWa RI Biology Centre, Czech Academy of Sciences, Na Sádkách 7, CZ-37005 České Budějovice, Czech Republic
Institute for Environmental Studies, Faculty of Science, Charles University in Prague, Benátská 2, CZ-12800 Prague, Czech Republic
Environment Centre, Charles University in Prague, José Martího 2, CZ-16200 Prague, Czech Republic

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ABSTRACT

Soil fauna consumes substantial amounts of litter and can even consume the entire annual litterfall in some ecosystems. The assimilation efficiency of fauna may reach 50% but is usually much smaller. Soil fauna may affect soil organic matter (SOM) dynamics not only by assimilating litter but also by modifying the soil environment at many spatiotemporal scales. Litter processing by fauna usually results in a short-term increase in microbial activity in feces; this activity than decreases such that feces over the long term may decompose more slowly than the original litter. During passage through the guts of litter-feeding fauna, litter modifications include fragmentation, consumption of associated microorganisms, pH and redox changes, removal of easily decomposed polysaccharides, increase in the proportion of lignin, and decrease in soluble polyphenols and carbon:nitrogen (C:N) ratios. The coating of litter with clay during passage through earthworms reduces microbial access to the litter as well as conditions for microbial activity by reducing the diffusion of nutrients and oxygen. At a larger scale, soil fauna affects leaching and the release of particulate organic matter (POM), which in turn affect microbial activity in soil. Fauna also affects the distribution of organic matter in the soil profile and determine whether litter decomposes on the soil surface or as POM bound to soil particles, which substantially affects the microbial community and the rate of decomposition. Fauna affects the amount of organic matter entering different SOM pools, and this effect depends on litter quality and the degree of soil C saturation. At an even larger scale, fauna can change the soil profile, soil properties, and the plant community, which may in turn affect microbial activity and the decomposition rate. The effect of soil fauna on litter decomposition and soil C storage can be positive or negative. Faunal effects tend to be greatest in ecosystems under transition, e.g. ecosystem developing after some disturbance during primary or secondary succession.

1. Introduction

Soils contain three-times more carbon (C) than the atmosphere and play an important role in the C cycle, which is crucial for supporting ecosystem services (Schmidt et al., 2011). Litter represents a major source of soil organic matter (SOM). > 50% of net primary production is returned to the soil via decomposition of plant litter (García-Palacios et al., 2013; Wardle et al., 2004). Consequently, litter decomposition is a crucial step in the C cycle (Schmidt et al., 2011). By its effect on SOM, litter decomposition and SOM stabilization may affect other soil properties such as sorption, nutrient availability, pH, water holding capacity, etc. (Brady and Weil, 2008). All those are important supporting ecosystem services which directly or indirectly support many essential production and regulation services such as provisioning of food and fiber from plant production, provisioning of clean water, flood protection or climate regulation (Dominati et al., 2010).

The generally accepted major drivers of litter decomposition are climate and litter quality (Hättenschwiler et al., 2005; Lavelle et al., 1997; Meier and Bowman, 2008; McCay et al., 2013; Wardle et al., 2004). The products of litter decomposition usually become less available for future decomposition and help stabilize SOM. The mechanisms that contribute to the stabilization of SOM are highly variable and include selective preservation due to the recalcitrance of SOM; spatial inaccessibility of SOM to decomposer organisms; and interactions with mineral surfaces (von Lützow et al., 2006).

Litter decomposition and SOM stabilization can be affected by the identities of the soil organisms that perform decomposition. Although most of the decomposition of organic matter is conducted by soil microorganisms (Anderson and Ineson, 1984; Lavelle et al., 1997), many studies have recognized that soil fauna significantly affects decomposition rates, mostly as a consequence of affecting microbial activity (Anderson and Ineson, 1984; Aubert et al., 2010; Frouz et al., 2009;

E-mail address: frouz@natur.cuni.cz.

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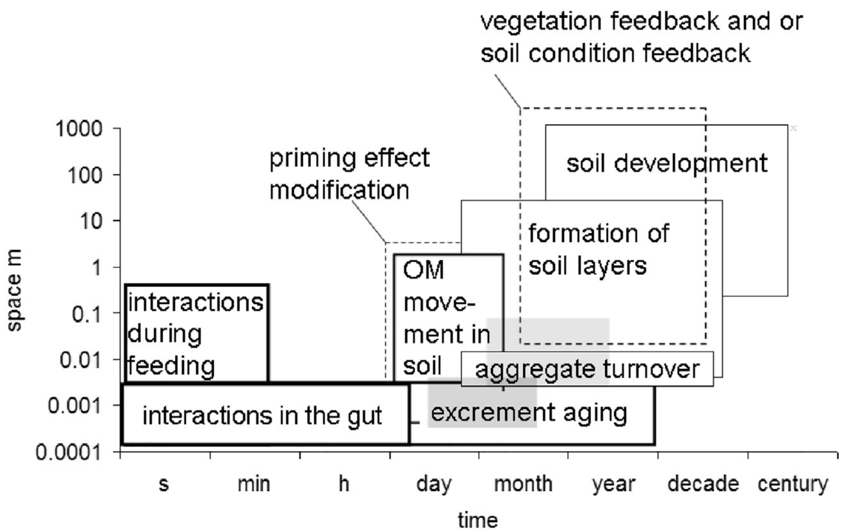

Fig. 1. Approximate spatiotemporal dimensions of the major processes affected by soil macro- and mesofauna. Processes in boxes with thicker lines are directly affected by soil fauna while those with thinner lines are processes that are indirectly affected by soil fauna. The grey-shaded rectangles indicate the ranges in lifespan and body size for soil macro- and mesofauna.

Hättenschwiler et al., 2005; Lavelle et al., 1997). The effect of soil fauna on litter decomposition is complex, i.e., it may include various interactions at various spatiotemporal scales. Soil fauna in its broader sense includes organisms of various sizes with various feeding modes; however in this article, I focus on macrofauna and mesofauna which feed on leaf litter. Feeding on litter, assimilating nutrients, and producing feces occur over time scales of hours to days and over spatial scales of millimeters to centimeters (Fig. 1). At similar spatiotemporal scale, fauna affects microflora in the uneaten leftovers of consumed litter. Faunal excrements (feces) contain microorganisms whose activities vary greatly depending on excrement age (Frouz and Šimek, 2009; Lavelle and Martin, 1992). In addition to modifying microbial activity, soil fauna may affect decomposition by mediating movement of organic matter in the soil profile via bioturbation, leaching, and other mechanisms (Kaneda et al., 2013). Moreover, fauna may create long-lasting structures that accumulate in the soil profile and affect soil profile development, see extensive review by Lavelle et al. (1997). As demonstrated by the invasion of North American forests by earthworms, these changes in soil may alter plant communities and the functioning of entire ecosystems (Bohlen et al., 2004). These changes may then affect rate of decomposition.

The effects of fauna on decomposition may differ substantially between undeveloped soils, which have not been previously affected by soil fauna, and soils that have been transformed by soil fauna for some time (Frouz et al., 2015). The complexity of these phenomena suggests that there is no simple, universal answer to the question "Does soil fauna increase or decrease the rate of litter decomposition?" The aims of this review are to describe the major patterns of how soil fauna affects litter decomposition and SOM stabilization at various spatiotemporal scales (Fig. 1), to explore the underlying mechanisms, and to highlight important interactions that occur at different spatiotemporal scales.

2. How much litter is eaten and assimilated by soil fauna?

The extensive manipulation experiment of Wall et al. (2008), which used litter bags that were accessible or inaccessible to soil fauna (in the latter case, fauna were excluded by naphthalene), indicated that fauna significantly increases litter mass loss in most biomes. Similarly, a meta-analysis of litter bag experiments in which fauna were excluded or not excluded by mesh size indicated that fauna promote mass loss in many biomes; the effect was strongest, however, in broadleaf temperate forests (Frouz et al., 2015). Kampichler and Bruckner (2009) indicated similar effect in studies that restricted mesofauna access by litter bag mesh size or insecticide use. However as pointed by Kampichler and Bruckner (2009), there is also a direct effect of insecticide or litter bag mesh size on decomposition which is seldom controlled for.

To determine the quantity of litter consumed by individual species of soil fauna, authors usually combine field estimates of faunal population density with laboratory estimates of faunal consumption or production efficiency. In this way, litter consumption can be assessed for individual species and for the whole community by summing the estimates for the dominant species. Using this approach, Frouz et al. (2015) estimated that larvae of the bibionid *Penthetria holosericea* consume about 40% of the annual litterfall in temperate alder forest. Karpachevsky et al. (1968) and Szabó (1974) estimated that bibionid larvae from genus *Bibio* could consume the entire annual litterfall in a broadleaf temperate forest. Knollenberg et al. (1985) found that a population of the earthworm *Lumbricus terrestris* in a floodplain forest could consume 94% of the annual litterfall in only 4 weeks. Millipedes have been estimated to consume from 10 to 40% of the annual litterfall (Bocock, 1963; Cárcamo et al., 2000; Dangerfield and Milner, 1996; David, 1987; Lawrence and Samways, 2003). Based on estimates of faunal density and consumption, Schaefer (1990) inferred that all annual litterfall is processed by soil fauna in a beech forest. These values can clearly vary even at the same sites depending on abiotic and biotic factors. Although the available data are insufficient to reliably quantify the effect of soil fauna on litter mass loss across all biomes, faunal distribution data (Petersen and Luxton, 1982) and the previously described global litter bag experiment (Wall et al., 2008) suggest that the fauna consumes most of the litterfall in temperate broadleaf forests and may significantly affect litter mass loss in other biomes except in deserts, semi-deserts, and Arctic areas.

The fact that fauna consumes substantial amount of litterfall brings us to the question of whether fauna competes for litter and if the amount of litter is a limiting factor for soil fauna. Litter removal by soil macrofauna has been often reported to reduce densities of soil mesofauna (Sayer, 2005). Studies investigating competition between macrofauna species are rare. However, Snyder et al. (2009) showed that with invasive earthworms are likely to compete for litter with native millipedes in Appalachian Mountains in southeastern North America. However, during the short-term experiment mortality nor growth of millipedes was not significantly affected by the presence of earthworms (Snyder et al., 2009). Soil fauna is very sensitive to litter removal; litter addition on the other hand often results in no or little increase in fauna density which is usually interpreted in a way that litter is not the limiting resource (Sayer, 2005). However, litter manipulations affect not only food availability but also microhabitat conditions (Sayer, 2005). This may explain the dramatic effect of litter removal as moisture, temperature, and shelter availability change substantially after removal