Title: The role of microarthropods in emerging models of soil organic matter

Jennifer L. Soong[a*]; Uffe N. Nielsen[b]

[a] Department of Biology, University of Antwerp, 2610 Wilrijk, Belgium, Email: Jennifer.soong@uantwerpen.be

[b] Hawkesbury Institute for the Environment, Western Sydney University, Locked Bag 1797, Penrith, NSW 2571, Australia. Email: u.nielsen@westernsydney.edu.au

[*] Corresponding author: Jennifer L. Soong

Abstract

A new understanding of soil organic matter (SOM) formation and stabilization has emerged over the past decade, highlighting the importance of microbial activity, mineral association of organic matter and aggregate occlusion of organic matter to SOM persistence. To date, the contribution of microarthropods to litter decomposition and SOM formation processes has not received due consideration and theoretical and empirical models should be modified to include how these organisms impact SOM protection. Here, we highlight the biological, chemical and physical mechanisms by which microarthropods influence SOM formation both directly and indirectly. Although more data is needed to quantify the impacts of different microarthropods on SOM dynamics, we highlight areas where inclusion of microarthropods in emerging models of SOM formation could reduce model uncertainties.

Key words: Carbon cycling; Food web interactions; Litter decomposition; Microarthropods; Nutrient cycling; Soil organic matter

Over the past decade a new understanding of soil organic matter (SOM) formation has emerged (Cotrufo et al., 2015; Lehmann and Kleber, 2015). Advances in molecular and analytical techniques have revealed the importance of organo-mineral interactions and soil aggregation, rather than simply biochemical recalcitrance, as key factors in organic matter persistence in the soil (von Lutzow et al., 2006; Kleber, 2010; Schmidt et al., 2011). Thus, the focus of litter decomposition and SOM formation studies is shifting from determining solely the *rates* of decomposition toward tracking the *fate* and *transformation pathways* of organic matter in the soil.

SOM is derived mainly from plant inputs. Low molecular weight compounds may leach into the soil and be metabolized by soil microbes, leach down through the soil profile or adsorb to mineral surfaces (mineral associated organic matter, MAOM). Fragments of particulate organic matter can be mixed into the soil as free particulate organic matter (fPOM) or become occluded in aggregates (oPOM), protected from further biological attack.
Adsorption/desorption of MAOM on mineral particles and disruption and reformation of soil aggregates creates dynamics of SOM governed by soil properties, environmental conditions and biological activity. Soil microbes are the primary decomposers of plant litter and SOM (Swift et al., 1979); however, the role of soil organisms at higher trophic levels has long been recognized (Petersen and Luxton, 1982; Seastedt, 1984). The importance of macroinvertebrates such as earthworms and termites on soil processes is relatively well quantified (e.g., van Groenigen et al., 2014). In contrast, the impact of other faunal groups such as microarthropods is less well understood and their contribution to SOM dynamics are rarely considered in models (but see Hunt and Wall, 2002; Soong et al., 2016).

Microarthropods, dominated by Acari and Collembola (i.e. mites and springtails), are a highly diverse and abundant group of organisms, ubiquitous in most ecosystem types (Nielsen et al., 2015). Their diverse feeding preferences range from primary decomposers and litter transformers, to saprotrophs, microbial grazers, and predators of other soil fauna (Petersen and Luxton, 1982; Pollierer et al., 2009; Nielsen et al., 2015), thus their impact on SOM formation spans all trophic levels of the soil food web. Microarthropods redistribute organic matter and microbes in the soil matrix, creating hot spots of microbial activity and soil aggregation (Maaß et al., 2015). It has been estimated using chemical and litterbag exclusion studies that microarthropods increase litter decomposition rates (Santos and Whitford, 1981; Seastedt, 1984; Garcia-Palacios et al., 2013), and more recent model-based inferences show that the negative effects of microarthropod suppression on SOM formation during litter decomposition may accumulate over time (Soong et al., 2016). The impact of microarthropod suppressions is most pronounced in temperate and wet tropical regions, indicating that microarthropod disturbances due to land use and climate change might have particularly large impacts on SOM dynamics in these ecosystems (Wall et al., 2008 ; Garcia-Palacios et al., 2013).

One of the most widely recognized roles of microarthropods in SOM dynamics is through the release of nitrogen (N) and phosphorus (P) during litter decomposition (Anderson and Ineson, 1984; Carrillo et al., 2011), generally increasing NO_3^- availability and altering SOM stoichiometry (Teuben and Verhoef, 1992; Wickings and Grandy, 2011). The release of nutrients by microarthropods could increase plant productivity and alter microbial responses to plant inputs with potential feedbacks to ecosystem productivity and SOM decomposition (Bardgett and Chan, 1999; Dijkstra et al., 2013; Soong et al., 2016). Altered nutrient availability impacts microbial substrate use efficiency (Sinsabaugh et al., 2013), but increased N mineralization can also lead to greater leaching and export of nutrients.

Microarthropods affect oPOM and MAOM formation directly and indirectly and the net effect of these interactive processes in different ecosystems and conditions is uncertain. MAOM derives mainly from adsorption reactions between clay surfaces and microbial products or other low molecular weight compounds (Grandy and Neff, 2008; Mambelli et al., 2011; Keiluweit et al., 2015). Microarthropods are most likely to influence MAOM indirectly through altering SOM chemistry and leachate, and through top-down controls on microbial abundance, turnover and composition. Direct alterations to MAOM complexes during passage through the microarthropod gut are also possible. Microarthropods directly influence soil aggregation and oPOM through the deposition of organic matter in the form of fecal pellets, eggs and molting residues, and necromass that can form a nucleus for soil aggregates and become oPOM (Maaß et al., 2015). In contrast, their movement and feeding on organic matter and fungal hyphae may disrupt aggregates resulting in the release of oPOM (Maaß et al., 2015). More data on the extent of microarthropod influence on these processes would greatly help to integrate microarthropods into SOM models.

The direct and indirect effect of microarthropod activities can and should now be incorporated into the evolving concepts of SOM formation (Fig. 1). With the evolution of our understanding from inherent resistance to degradation of organic matter toward MAOM and oPOM mechanisms of protection of SOM in the soil, our concepts of the impact of microarthropods beyond litter mass loss must also be revisited. For example, litter-transforming microarthropods may increase the input of litter fragments into the soil as fPOM or eventually oPOM (Fig. 1). Fragmentation also leads to more surface area for leaching of water-soluble litter components into the soil that may subsequently be utilized by microbes, lost through leaching or adsorbed to mineral surfaces (Soong et al., 2014). Although soil fauna themselves are not thought to contribute significantly to soil respiration during decomposition (Berg et al., 2001), microbial grazers stimulate microbial turnover, control microbial biomass and influence community composition (Maaß et al., 2015), which in turn will influence SOM decomposition. Finally, the influence of microarthropods on SOM stoichiometry due to their stimulation of nutrient mineralization over C mineralization may be an important control of the balance between ecosystem C storage and productivity (Soong et al., 2016).

Our conceptual framework (Fig. 1) illustrates some of the key pathways through which microarthropods impact SOM formation, but how these can be included in SOM models is a question ripe for exploration. Experiments across various ecosystem types that quantify the effects of microarthropods on SOM formation through such pathways are still needed to parameterize new models. These experiments would benefit from focusing on broad functional groups or traits to allow results to be generalizable. For example, the contribution of microarthropods to pyrogenic organic matter decomposition is largely unknown (Ameloot et al., 2013). This is particularly relevant given that land use practices and global change affect microarthropod abundances and activities, with cascading effects on ecosystem functioning (Nielsen et al., 2015). The challenges lie mainly in disentangling the direct and indirect impacts of microarthropods from other aspects of the soil food web. Physical exclusion of microarthropods using litterbags inhibits fragmentation and the input of fPOM to the soil, but litterbag-free isotopic tracing combined with direct soil community manipulations or chemical exclusion using naphthalene may be a promising way forward (Cotrufo et al., 2014). The main effects and side effects of any manipulation of the microarthropod community should be carefully quantified and reported in order to accurately measure effects. Based on the known impacts of microarthropods on SOM formation and dynamics, as well as their variable yet ubiquitous presence in most ecosystems, we believe that the inclusion of microarthropods in emerging mechanistic models of SOM dynamics is a viable and worthwhile effort that will help to advance the next generation of SOM models.

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Figure legend

Figure 1. Schematic representation of the main pathways of soil organic matter (SOM) formation and dynamics where microarthropods have measurable impacts. Mineral associated organic matter (MAOM), and aggregate occluded particulate organic matter (oPOM) summarize the main stabilizing mechanisms in emerging models of SOM, while free particulate organic matter (fPOM) is SOM unprotected by aggregates or mineral adsorption. Microarthropods may influence SOM formation in this context through 1) Influencing the turnover of microbial biomass and the release of dissolved nutrients via grazing, which is possible to quantify using measures of impacts on microbial activity and turnover rates and stable isotope labelling; 2) Fragmentation of litter by litter transforming springtails and mites, which increases fPOM inputs to the soil while also increasing the surface area available for leaching of dissolved organic matter and is possible to quantify using microarthropod suppression and isotope labelling techniques; 3) All microarthropods will contribute to the transfer of nutrients and carbon from MAOM to oPOM, and vice versa, through their role in aggregate formation and turnover. Litter mass inputs to the soil are dominated by leaching early in decomposition, with fragmentation becoming more important over time.