# The role of microarthropods in emerging models of soil organic matter

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## 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. The contribution of microarthropods to litter and SOM decomposition rates, however, 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, inclusion of microarthropods in emerging models of SOM formation could reduce model uncertainties.

Key words: Carbon cycling; 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 has begun to shift from determining *rates* of decomposition toward tracking the *fate* and *transformation* of organic matter in the soil.

Soil organic matter 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) and protected from further biological attack. Adsorption and desorption of MAOM on clay particles, as well as 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 (i.e.

mites and springtails) 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), is a highly diverse and abundant group of organisms, ubiquitous in most ecosystem types (Nielsen et al., 2015). They influence SOM formation at all trophic levels of the soil food web, with feeding preferences ranging from primary decomposers and litter transformers, to saprotrophs, microbial grazers, and even predators of other soil fauna (Petersen and Luxton, 1982; Pollierer et al., 2009; Nielsen et al., 2015).. Microarthropods also redistribute organic matter and microbes in the soil matrix, creating hot spots of microbial activity and soil aggregation and turnover (Maaß et al., 2015). It has been estimated using chemical and litter bag exclusion studies that microarthropods increase litter decomposition rates (Seastedt, 1984; Garcia-Palacios et al., 2013), and more recent model-based inferences show that the effects of microarthropod suppression on SOM formation during litter decomposition may accumulate over time (Soong et al., 2016).

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). Microbes in the soil are generally more limited by C availability than by nutrients so the effects of nutrient mobilization on SOM formation are more likely to be by alleviating nutrient stress on plants. The release of nutrients by microarthropods could increase plant uptake and productivity with potential feedbacks to ecosystem productivity and organic matter inputs to the soil (Bardgett and Chan, 1999) (Soong et al., 2016). However, N mineralization could also lead to greater leaching and export of nutrients.

Microarthropods likely have a greater effect on the formation and turnover of oPOM than MAOM. Mineral associated organic matter derives mainly from adsorption reactions between clay surfaces and microbial products and other low molecular weight compounds (Grandy and Neff, 2008; Mambelli et al., 2011; Keiluweit et al., 2015). Therefore, microarthropods are most likely to influence MAOM through altering SOM chemistry and leachate, and through top-down controls on microbial abundance, turnover and composition. Alterations to MAOM complexes during passage through the microarthropod gut are also possible. However, microarthropods directly influence soil aggregation and oPOM through the deposition of organic matter in the form of fecal pellets, eggs residues, molting residues and necromass that can form a nucleus for soil aggregates and become oPOM (Maaß et al., 2015). Furthermore, their movement and feeding on organic matter may disrupt aggregates resulting in the release of oPOM (Maaß et al., 2015). Similarly, microbial grazing by microarthropods indirectly influences aggregate formation and stability, particularly by disrupting mycorrhizal fungi hyphae but also through selective feeding that can modify microbial community composition. Moreover, microarthropod feeding can contribute to the redistribution and dispersal of bacteria and fungi in the soil, which may in turn influence SOM dynamics (Maaß et al., 2015).

The direct and indirect effect of these microarthropod activities can now be incorporated into the evolving understanding 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 adsorb 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 control the balance between ecosystem C storage and productivity (Soong et al., 2016).

The contributions of microarthropods to SOM formation can and should therefore be considered in emerging models of SOM formation and transformation for more accurate model predictions. 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). However, data on the functional effects of these impacts on SOM formation processes described here must still be collected. Furthermore, the contribution of microarthropods to pyrogenic organic matter decomposition is largely unknown (Ameloot et al., 2013). 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 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). However, the main effects and side effects of any manipulation of the microarthropod community should be carefully quantified in order to accurately measure effects. Due to the direct and indirect role of microarthropods in SOM formation and dynamics presented here, as well as their variable yet ubiquitous presence in most ecosystems, we believe that the inclusion of microarthropods in emerging models of SOM dynamics is a viable and worthwhile effort that will help to shed light on unexplained variation in existing SOM models.

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References

Ameloot, N., Graber, E.R., Verheijen, F.G.A., De Neve, S., 2013. Interactions between biochar stability and soil organisms: review and research needs. European Journal of Soil Science 64, 379-390.

Anderson, J.M., Ineson, P., 1984. Interactions between microorganisms and soil invertegrates in nutrient flux pathways of forest ecosystems, In: Anderson, J.M., Raynor, A.D.M., Walton, D.W.H. (Eds.), Invertebrate Microbial Interactions. Cambridge University Press, Cmbridge, pp. 59-88.

Bardgett, R., Chan, K., 1999. Experimental evidence that soil fauna enhance nutrient mineralization and plant nutrient uptake in a montane grassland ecosystem. Soil Biology & Biochemistry 31, 1007-1014.

Berg, M., De Ruiter, P., Didden, W., Janssen, M., Schouten, T., Verhoef, H., 2001. Community food web, decomposition and nitrogen mineralisation in a stratified Scots pine forest soil. Oikos 94, 130-142.

Carrillo, Y., Ball, B.A., Bradford, M.A., Jordan, C.F., Molina, M., 2011. Soil fauna alter the effects of litter composition on nitrogen cycling in a mineral soil. Soil Biology and Biochemistry 43, 1440-1449.

Cotrufo, M.F., Soong, J.L., Horton, A.J., Campbell, E.E., Haddix, M.L., Wall, D.H., Parton, W.J., 2015. Soil organic matter formation from biochemical and physical pathways of litter mass loss. Nature Geoscience 8, 776-779.

Cotrufo, M.F., Soong, J.L., Vandegehuchte, M.L., Nguyen, T., Denef, K., Ashley Shaw, E., Sylvain, Z.A., de Tomasel, C.M., Nielsen, U.N., Wall, D.H., 2014. Naphthalene addition to soil surfaces: A feasible method to reduce soil micro-arthropods with negligible direct effects on soil C dynamics. Applied Soil Ecology 74, 21-29.

Garcia-Palacios, P., Maestre, F.T., Kattge, J., Wall, D.H., 2013. Climate and litter quality differently modulate the effects of soil fauna on litter decomposition across biomes. Ecology Letters 16, 1045-1053.

Grandy, A.S., Neff, J.C., 2008. Molecular C dynamics downstream: The biochemical decomposition sequence and its impact on soil organic matter structure and function. Science of the Total Environment 404, 297-307.

Hunt, H.W., Wall, D.H., 2002. Modelling the effects of loss of soil biodiversity on ecosystem function. Global Change Biology 8, 33-50.

Keiluweit, M., Bougoure, J.J., Nico, P.S., Pett-Ridge, J., Weber, P.K., Kleber, M., 2015. Mineral protection of soil carbon counteracted by root exudates. Nature Climate Change 5, 588-595.

Kleber, M., 2010. What is recalcitrant soil organic matter? Environmental Chemistry 7, 320-332.

Lehmann, J., Kleber, M., 2015. The contentious nature of soil organic matter. Nature advance online publication.

Maaß, S., Caruso, T., Rillig, M.C., 2015. Functional role of microarthropods in soil aggregation. Pedobiologia 58, 59-63.

Mambelli, S., Bird, J.A., Gleixner, G., Dawson, T.E., Torn, M.S., 2011. Relative contribution of foliar and fine root pine litter to the molecular composition of soil organic matter after in situ degradation. Organic Geochemistry 42, 1099-1108.

Nielsen, U.N., Wall, D.H., Six, J., 2015. Soil Biodiversity and the Environment. Annual Review of Environment and Resources 40, 63-90.

Petersen, H., Luxton, M., 1982. A Comparative Analysis of Soil Fauna Populations and Their Role in Decomposition Processes. Oikos 39, 288-388.
Pollierer, M.M., Langel, R., Scheu, S., Maraun, M., 2009. Compartmentalization of the soil animal food web as indicated by dual analysis of stable isotope ratios (15N/14N and 13C/12C). Soil Biology and Biochemistry 41, 1221-1226.
Schmidt, M.W.I., Torn, M.S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I.A., Kleber, M., Kogel-Knabner, I., Lehmann, J., Manning, D.A.C., Nannipieri, P., Rasse, D.P., Weiner, S., Trumbore, S.E., 2011. Persistence of soil organic matter as an ecosystem property. Nature 478, 49-56.
Seastedt, T.R., 1984. The Role of Microarthropods in Decomposition and Mineralization Processes. Annual Review of Entomology 29, 25-46.
Soong, J.L., Calderon, F.J., Betzen, J., Cotrufo, M.F., 2014. Quantification and FTIR characterization of dissolved organic carbon and total dissolved nitrogen leached from litter: a comparison of methods across litter types. Plant and Soil 385, 125-137.
Soong, J.L., Vandegehuchte, M.L., Horton, A.J., Nielsen, U.N., Denef, K., Shaw, E.A., De Tomasel, C.M., Parton, W.J., Wall, D.H., Cotrufo, M.F., 2016. Soil microarthropods support ecosystem productivity and soil C accrual: evidence from a litter decomposition study in the tallgrass prairie. Soil Biology & Biochemistry 92, 230-238.
Swift, M.J., Heal, O.W., Anderson, J.M., 1979. Decomposition in Terrestrial Ecosystems. University of California Press.
Teuben, A., Verhoef, H.A., 1992. Direct contribution by soil arthropods to nutrient availability through body and faecal nutrient content. Biology and Fertility of Soils 14, 71-75.
van Groenigen, J.W., Lubbers, I.M., Vos, H.M.J., Brown, G.G., De Deyn, G.B., van Groenigen, K.J., 2014. Earthworms increase plant production: a meta-analysis. Scientific Reports 4, 6365.
von Lutzow, M., Kogel-Knabner, I., Ekschmitt, K., Matzner, E., Guggenberger, G., Marschner, B., Flessa, H., 2006. Stabilization of organic matter in temperate soils: mechanisms and their relevance under different soil conditions - a review. European Journal of Soil Science 57, 426-445.
Wickings, K., Grandy, A.S., 2011. The oribatid mite Scheloribates moestus (Acari: Oribatida) alters litter chemistry and nutrient cycling during decomposition. Soil Biology & Biochemistry 43, 351-358.

Figure legend

**Figure 1.** A schematic representation of the main pathways of soil organic matter (SOM) formation highlighting 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 (free POM) is SOM unprotected by aggregates or mineral adsorption. Microarthropods may influence SOM formation in this context by, 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 exercises; 2) Fragmentation of litter by litter transforming springtails and mites, which increases free POM inputs to the soil while also increasing the surface area available for leaching of dissolved organic matter; 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 loss is dominated by leaching early in decomposition, with fragmentation becoming more important over time.