Functional role of microarthropods in soil aggregation

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Functional role of microarthropods in soil aggregation

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Soil aggregation has received a lot of attention in the last years; however, the focus was mostly on soil microorganismsor larger soil fauna, especially earthworms. The impact of the large group of microarthropods, e.g. Collembola and Acari, is nearly unknown and hence underrepresented in the literature. Here we propose and discuss potential direct and indirect mechanismsofhow microarthropods could influence this process with the focus on collembolans, which are in general a relatively well studied taxon.Indirect mechanisms are likely to have larger impacts on soil aggregation than direct effects. The variety of indirect mechanisms based on the provision of organic material like faecal pellets, molts and necromass as food source for microorganisms is high and given available evidence we propose that these mechanismsare the most influential. We highlight the need for overcoming the challenges of culturing and handling of these animals in order to be able to design small scale experiments and field studies which would enable us to understand the role of the different functional groups, their interaction with other soil faunaand the impact of land use practices on soil aggregation.

Key words: soil structure; microarthropods; Collembola; Acari

Introduction

Soil structure plays a critical ecosystemic role in biogeochemical processes (e.g. Jastrow, 1996), water infiltration, gas exchange efficacy, and resistance against erosional loss, and influences the performanceof soil biota, including roots (Hartge and Stewart, 1995; Miller and Jastrow, 1992; Oades, 1984; Rillig and Mummey, 2006). Soil structureis often referred to as the arrangement of different macro- and microaggregate size fractions (organic/mineral complexes of >250µm or <250µm, respectively) and the corresponding pore spaces (Hartge and Stewart, 1995; Rillig and Mummey, 2006). Inhierarchically structuredsoils, organic matter serves as the main binding agent to form and stabilize aggregates (Tisdall and Oades, 1982), but additionally, soil texture, soil microorganisms, roots, inorganic binding agents, the predominant environmental conditions, and the soil fauna are important for this process (Dexter and Horn, 1988; Rillig et al., 2015).

While soil fauna is generally acknowledged as being important for soil aggregation, direct empirical evidence is scarce for microarthropods, including mites and collembolans, the two most abundantand diverse groups. This is surprising given that these animals can occur at high densities,and given their role in the processing of organic matter via chemical, physical and biological mechanisms (Lee and Foster, 1991; Wolters, 2000). We are only aware of two studies that have experimentally quantified the impact of Collembola on soil structure (Siddiky et al., 2012a, b); these experimental data, however,revealed an effect size comparable to that of much more thoroughly studied soil biota, such as fungi. These experiments should be extended to the field as this might also be of agricultural interest.

Among the various groups of soil biota, especially the effects of mycorrhizal fungi, bacteria, earthworms, and termites have been studied intensely (e.g.; Lee and Foster, 1991; Oades and Waters, 1991; Bossuyt et al., 2005; Pulleman et al., 2005; Rillig and Mummey, 2006; Velasquez et al., 2007). It is known that the excretion of e.g. polysaccharides by bacteria and the physical enmeshment of soil particles by fungal mycelia have a positive effect (see e.g. Degens, 1997; Lynch and Bragg, 1985; Oades, 1993; Rillig and Mummey, 2006; Tisdall, 1994b). Larger soil animals like earthworms and termites directly affect soil structure by their burrowing activities and by the digestion and excretion of relatively large amounts of organic material and soil particles, which might also lead to increased soil aggregation (e.g. Lavelle, 1988; Lee, 1985; Lee and Foster, 1991; or see review by Six et al., 2004; Tisdall, 1994a, 1994b).

Given this striking asymmetry in our understanding of biotic contributions to soil aggregation, we here propose and discuss potential mechanisms forCollembola, which are also likely applicable to other soil microarthropods. We distinguish between direct and indirect effects (Fig. 1);however all the mechanisms we discuss would in reality take place simultaneously and in interaction with each other. As the collembolan *Folsomia candida* is very well studied, especially with regard to properties that might be involved in mechanisms of soil aggregation, we base our discussion mostly on this species, but we believe without much loss of generality.

[Fig. 1]

Direct mechanisms

Direct effects of collembolans on soil structure can be categorized in terms of input of organic material, which positively contributes to soil structure, and degradation of aggregates, which is a negative effect.

Organic matter inputs

Possible positive, direct effects of collembolans on soil structure include the production, modification and movement of organic matter, which can then serve as binding agents, nuclei or building blocks for aggregates. Assimilated nutrients can either be contained in animal tissue or be excreted as metabolic waste.Especially because microarthropods can occur in high numbers, they might produce a large amount of faecal pellets. It has to be assumed that many soils contain millions of faecal pellets per square meter (Hopkin, 2007). In this context,Kubiena (1953) reports about the so-called ‘alpine pitch rendzinas’ on limestone which are nearly completely composed of collembolan faeces forming a 15-20cm deep black humus layer.

Collembolan eggs are deposited in clutches and need a couple of days to weeks to develop (Hopkin, 2007). Eggs of the collembolan family Sminthuridaemight be covered by a mixture of soil and collembolan waste to protect them from mold and dehydration (Betsch-Pinot, 1976, 1977; Dallai et al., 2008). After hatching, the remaining egg integuments might serve as source of fresh organic material to microorganisms (which will be discussed in the paragraph about indirect mechanisms) or, due to the attached soil particles and organic material, as nuclei for microaggregate formation. Collembolans go through several instars, which might mean molting at fairly high rates. Most species molt throughout their whole life (up to 45 times). Specimens of *Folsomia candida* may live up to six months; however, for other species shorter or far longer (one year and longer) life-spanshave been reported (Hopkin, 2007), which means that their production of molts could be significant. Interestingly, some oribatid mites can even survive for up to three years (Capinera, 2008).Their molts are hard-bodied due to chitin and other components in the cuticle (see Weigmann, 2006) and hence their breakdown should be slower, and thus they could serve as more long-lived building blocks of aggregates. Finally, the production of necromassespecially in short-lived species besides faecalpellets, molts and eggs, can potentially influence soil aggregation. Unfortunately, there is no study dealing explicitly with the input of these types of organic material. Given the potentially high local abundances, this should clearly be a target of future research.

Degradationof soil aggregatesvia disturbance

Collembola and Oribatida usually consist of populations in the order of 10,000 to 100,000individuals per square meter (see Hopkin, 2007; Weigmann, 2006). Canthey therefore counteract the formation of aggregates by crawling around or feeding on e.g. microorganisms, plant remains or various excretory products? The impact of this disturbance on a *per capita* basis might be low, but data about the impact of locally high abundant microarthropods on soil aggregation are missing.

Indirect mechanisms

Several studies have investigated the soil food web, functional characteristics and feedbacks between the different organism groups also in relation to aboveground biota; however, there are few data on the impact of interacting taxa like fungi and microarthropods on soil aggregation (Salmon and Ponge, 2001, Siddiky et al., 2012a, 2012b). Fungi and bacteria are directly and indirectly contributing to the production and release of materials and compounds that contribute to soil structure dynamicswhile soil animals affect the translocation and provision of organic material for colonization, like faecal pellets, molts, eggs, and necromass,and the modification of the activity of microorganisms by grazing (Coleman et al., 2002). There are studies suggesting that Collembola could have a positive effect on mycorrhizal functioning as their fungal grazing might enhance fungal growth and respiration (Lussenhop, 1992). Other studies suggest that collembolans could also have no or negative effects (Fitter and Garbaye, 1994; Fitter and Sanders, 1992),which brought attention to collembolans as important regulators of the mycorrhizal symbiosisacting in a density-dependentfashion (Gange, 2000). If there were positive effectson fungal growth or branching patterns, these effects could enhance soilaggregation processes, while the reduction of fungal biomass could have either negative effects or change the composition of the soil microbial community with unclear functional consequences. It is also likely that the observed effects depend on the abundance of Collembola or other microarthropods, a hypothesis that should therefore be tested (for enchytraeids see Hedlund and Augustsson, 1995). It has also been shown that Collembola do feed on arbuscularmycorrhizal fungi (AMF), but, depending on the species, prefer non-AMF mycelia(e.g. Klironomos and Kendrick, 1996; Klironomos and Ursic, 1998; Moore et al., 1985; Thimm and Larink, 1995).Another important aspect of the interaction between the microbial community and microarthropods is the dispersal of spores (Klironomos and Moutoglis, 1999; Lussenhop, 1992). AMF spores can be far larger (20-500 µm)than non-AMF spores (Trappe, 1982) and it is more likely that spores are ingested by earthworms rather than by Collembola (Fitter and Sanders, 1992; Moore et al., 1985). Brown (1995)has shown that spores can survive the gut passageof earthworms with an increased germination rate afterwards (for more information about gut microbiota in various taxa see e.g. Pherson and Beattie, 1979; Ponge andCharpentie, 1981, König, 2006.). Still, collembolans are also able to act as vectors by transporting spores attached to their cuticle (Gormsen et al., 2004), which is also known for one oribatid group, the Damaeidae (Weigmann, 2006). Although this phenomenon might be restricted to only a few species it should be considered as important means of microbial transport which might have an impact on the composition of the microbial community.

As described in the paragraph about the provision of organic material, one major question is how the organic materials influence the colonization by and composition of microbial communities, which might lead to enhanced aggregate formation. There are several potential mechanisms which have been investigated only in part so far.

Foster et al. (1983) report that fresh faecal pellets can be recognized as round and smooth surfaces under the scanning electron microscope, whereas older pellets are mostly densely covered by fungal hyphae; this highlights the importance of microarthropodsinassisting microbial colonization of organic matter. It is also known that during the molting of collembolans the whole midgut epithelium is also excreted to dispose of the accumulated toxins (Fountain and Hopkin, 2001; Humbert, 1979). The total gut volume of *Folsomia candida* was estimated up to 10nl, faecal pellets had a volume of approx. 1nl (Thimm et al., 1998) and contained approx. 1.55×10^4 bacterial cells (identified by light microscopy) of which only less than 0.01% were dead. Taking into consideration that, under laboratory conditions, the reported period between the ingestion and the defecation of bacterial cells can be less than one hour (Czarnetzki and Tebbe, 2004), the amount of living microbial cells excreted per individuum during a life cycle is enormous. Some authors (e.g. Hanlon, 1981; Thimm et al., 1998) have already highlighted the importance of the constant local input of gut (but also other ingested) bacteria which might lead to an enhanced competition between already existing soil microorganisms, and this might affect soil aggregation depending on the ensuing species composition.The same might also be true for other organic material provided through oviposition or necromass.

Collembolans usually excrete urine via the labial nephridia, but can also release insoluble products via the midgut epithelium (Hopkin, 1997; Larsen, 2007). Most of the nitrogenous and phosphorus-containing waste products are released as ammonia (Sjursen and Holmstrup, 2004), uric acid and phosphate, depending on the species. In spite of the studies addressing these aspects(e.g. Cragg and Bardgett, 2001; Milcu et al., 2006; Verhoef et al., 1988) it is not clear how these different waste productsinfluence local environmental conditions and hence the microbial community.Some studies have also investigated partly species-specific characteristics of nitrogen and carbon release (Petersen, 1980; Sjursen and Holmstrup, 2004), the influence of the available resource quality (Chen et al., 1995) and the creation of nutrient sources for heterotrophic microbes and primary producers (Rusek, 1998). These processes should therefore be recognized as integral components of soil structure (Fjellberg, 1986; Rusek, 1985).

Indirect effects of microarthropods via the provision of organic material to microorganisms are not the only indirect mechanisms to be considered. The complex interactions with the larger components of the soil fauna have not yet been considered in detail in any study (but see Ponge 1988; Ponge, 1991;Salmon and Ponge, 2001). In our opinion, especially the interaction between different functional groups should be more closely investigated, as the biggest effect sizes are assumed to be found in this context rather than in studies dealing with direct effects.

Another important aspect is the impact of different agricultural practices on soil fauna and soil aggregation as abiotic factors. Once the biotic interactions between different faunal groups have become clearer, another focus should be on the impact of tillage, ploughing or compaction of soil on these interactions. It is known that different taxonomic groups respond differently to agricultural practices in different types of soils and depending on fertilizer additions etc. (see e.g. van Capelle et al., 2012, Roger-Estrade et al., 2010, for microarthropods see Ponge et al. 2013), however, closer investigation would be necessary in order to develop appropriate strategies to e.g. increase soil fertility and resistance towards erosional loss by increasing soil stability via soil fauna.

Conclusion

Despite their underrepresentation in the soil aggregation literature, we highlighted and discussed several potential mechanisms via whichmicroarthropods could influence soil aggregation.

Due to their relatively small body size and total biomass, which is lower than that of fungi, bacteria and other taxa such as nematodes and protozoa, microarthropods may rather indirectly than directly affect soil structure. However, in some cases the impact of the production of assumedly large amounts of organic material in form of necromass, eggs, etc. might play an important role as direct starting points for microaggregate formation. We propose to start studying soil aggregation formation with easy-to-handle species such as*Folsomiacandida*in experimental designs that allow assessing the direction and magnitude of the various possible mechanisms, especially direct vs indirect mechanisms.Difficulties with culturingmicroarthropodsforexperiments, but also withthe collection of direct observationshave hampered empirical studies to date. The usage ofhigh resolution filmingand photographing, which is nowadays very feasible given the remarkable advances in microscopy technologies, is necessary to observe how microarthropods act in the formation of soil aggregates. Coupling these technologies with small scale experimental designs will allow teasing apart the roles of various mechanisms that act simultaneously. An element of complexity and realisms will be given by studies addressing the impact of different taxa (e.g. Collembola and Acari) on soil structure in opposition to studies focusing onspecies-specific effects. In this context, a focus should in our opinion be on the interaction of functionally defined,trait-based groups across all soil biota.

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Figure captions

Fig. 1: Overview of potential mechanisms used by microarthropods for the formation of soil aggregates. Mechanisms are divided into direct and indirect processes and based on Collembola and oribatid mites as most abundant soil microarthropod representatives.