**QUEEN'S
UNIVERSITY
BELFAST**

Functional role of microarthropods in soil aggregation

Maaß, S., Caruso, T., & Rillig, M. C. (2015). Functional role of microarthropods in soil aggregation. *Pedobiologia*, 58(2-3), 59-63. <https://doi.org/10.1016/j.pedobi.2015.03.001>

Published in:
Pedobiologia

Document Version:
Peer reviewed version

Queen's University Belfast - Research Portal:
[Link to publication record in Queen's University Belfast Research Portal](#)

Publisher rights

© 2015, Elsevier. Licensed under the Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International <http://creativecommons.org/licenses/by-nc-nd/4.0/> which permits distribution and reproduction for non-commercial purposes, provided the author and source are cited.

General rights

Copyright for the publications made accessible via the Queen's University Belfast Research Portal is retained by the author(s) and / or other copyright owners and it is a condition of accessing these publications that users recognise and abide by the legal requirements associated with these rights.

Take down policy

The Research Portal is Queen's institutional repository that provides access to Queen's research output. Every effort has been made to ensure that content in the Research Portal does not infringe any person's rights, or applicable UK laws. If you discover content in the Research Portal that you believe breaches copyright or violates any law, please contact openaccess@qub.ac.uk.

1 Type of contribution: *Idea paper*
2 Running title: Microarthropods and aggregation
3 Number of words: 2,483
4 Number of tables: 0
5 Number of figures: 1
6 Number of references: 72
7

8 **Functional role of microarthropods in soil aggregation**
9

10 Authors:

11 **Stefanie Maaß^{a,b}, Tancredi Caruso^c, Matthias C. Rillig^{a,b*}**

12 ^a Institut für Biologie, Plant Ecology, Freie Universität Berlin, Altensteinstraße 6, 14195
13 Berlin, Germany

14 ^b Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), 14195
15 Berlin, Germany

16 ^c School of Biological Sciences, Queen's University of Belfast, 97 Lisburn Road,
17 Belfast, BT9 7BL, Belfast, Northern Ireland

18 * Corresponding author: phone +49 (0)30 838 53165, fax: +49 (0)30838 453165;
19 email: rillig@zedat.fu-berlin.de
20

21 Stefanie Maaß : stefanie-maass@gmx.de

22 Tancredi Caruso: t.caruso@qub.ac.uk

23 Matthias C. Rillig: rillig@zedat.fu-berlin.de
24
25

Soil aggregation has received a lot of attention in the last years; however, the focus was mostly on soil microorganisms or 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 mechanisms of how 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 mechanisms are 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 fauna and 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 performance of soil biota, including roots (Hartge and Stewart, 1995; Miller and Jastrow, 1992; Oades, 1984; Rillig and Mummey, 2006). Soil structure is often referred to as the arrangement of different macro- and microaggregate

size fractions (organic/mineral complexes of $>250\mu\text{m}$ or $<250\mu\text{m}$, respectively) and the corresponding pore spaces (Hartge and Stewart, 1995; Rillig and Mummey, 2006). In hierarchically structured soils, 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 abundant and 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 for Collembola, 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 Sminthuridae might 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-spans have 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 necromasses especially in short-lived species besides faecal pellets, 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.

Degradation of soil aggregates via disturbance

Collembola and Oribatida usually consist of populations in the order of 10,000 to 100,000 individuals per square meter (see Hopkin, 2007; Weigmann, 2006). Can they 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 dynamics while 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 symbiosis acting in a density-dependent fashion (Gange, 2000). If there were positive effects on fungal growth or branching patterns, these

effects could enhance soil aggregation 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 arbuscular mycorrhizal 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 Moutoglou, 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 passage of earthworms with an increased germination rate afterwards (for more information about gut microbiota in various taxa see e.g. Pherson and Beattie, 1979; Ponge and Charpentier, 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 an 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 microarthropods in assisting 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 products influence local environmental conditions and hence the microbial community. Some studies have also investigated partly species-specific characteristics of nitrogen and carbon release (Petersen, 1980; Sjørsen 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 which microarthropods 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 *Folsomia candida* in experimental designs that allow assessing the direction and magnitude of the various possible mechanisms, especially direct vs indirect mechanisms. Difficulties with culturing microarthropods for experiments, but also with the collection of direct observations have hampered empirical studies to date. The usage of high resolution filming and 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 realism will be given by studies addressing the impact of different taxa (e.g. Collembola and Acari) on soil structure in opposition to studies focusing on species-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.

Acknowledgement

This paper was partly supported by the project SENSE (Structure and Ecological Niche in the Soil Environment; EC FP7 - 631399 - SENSE), which is an EU Marie Curie Career Integration Grant to T.C.. SM was supported by a doctoral scholarship from the Friedrich Naumann Foundation.

References

- Betsch-Pinot, M.C., 1976. Le comportement reproducteur de *Sminthurus viridis* (Collembola, Symphypleona). Z. Tierpsychol. 40, 427-439. doi: 10.1111/j.1439-0310.1976.tb00945.x.
- Betsch-Pinot, M.C., 1977. Les parades sexuelles primitives chez les Collemboles Symphypléones. Rev. Ecol. Biol. Sol14, 15-19. doi: 10.1080/11250000209356447.
- Bossuyt, H., Six, J., Hendrix, P.F., 2005. Protection of soil carbon by microaggregates within earthworm casts. Soil Biol. Biochem.37, 251-258. doi: 10.1016/j.soilbio.2004.07.035.
- Brown, G., 1995. How do earthworms affect microfloral and faunal community diversity? Plant Soil 170, 209-231. doi: 10.1007/BF02183068.
- Capinera, J., 2008. Encyclopedia of Entomology 2nd edition. Springer, New Delhi, India.
- Chen, B., Snider, R.J., Snider, R.M., 1995. Food preference and effects of food type on the life history of some soil Collembola. Pedobiologia 39, 496-505.

268 Coleman, D., Fu, S.L., Hendrix, P., Crossley, D., 2002. Soil foodwebs in
 269 agroecosystems: impacts of herbivory and tillage management. *Eur. J. Soil Biol.*
 270 38, 21-28. doi: 10.1016/s1164-5563(01)01118-9.

271 Cragg, R.G., Bardgett, R.D., 2001. How changes in soil faunal diversity and
 272 composition within a trophic group influence decomposition processes. *Soil Biol.*
 273 *Biochem.* 33, 2073-2081. doi: 10.1016/S0038-0717(01)00138-9.

274 Czarnetzki, A.B., Tebbe, C.C., 2004. Diversity of bacteria associated with Collembola
 275 – a cultivation-independent survey based on PCR-amplified 16S r RNA genes.
 276 *FEMS Microbiol. Ecol.* 49, 217-227. doi: 10.1016/j.femsec.2004.03.007.

277 Dallai, R., Zizzari, Z.V., Fanciulli, P.P., 2008. The ultrastructure of the spermathecae
 278 in the Collembola Symphypleona (Hexapoda). *J. Morphol.* 269, 1122-1133. doi:
 279 10.1002/jmor.10649.

280 Degens, B.P., 1997. Macro-aggregation of soils by biological bonding and binding
 281 mechanisms and the factors affecting these: a review. *Aust. J. Soi. Res.* 35, 431-
 282 459. doi: 10.1071/s96016.

283 Dexter, A.R., Horn, R., 1988. Effects of land-use and clay content on soil structure as
 284 measured by fracture surface-analysis. *Z. Pflanz. Bodenkunde* 151, 325-330.
 285 doi: 10.1002/jpln.19881510511.

286 Fitter, A.H., Garbaye, J., 1994. Interaction between mycorrhizal and other soil
 287 organisms. *Plant Soil* 159, 123-132. doi: 10.1007/BF00000101.

288 Fitter, A.H., Sanders, I.R. 1992. Interactions with the soil fauna. In M.F. Allen (Ed.),
 289 *Mycorrhizal Functioning: An Integrative Plant-Fungal Process*. Chapman & Hall,
 290 London, UK, pp. 333-354.

291 Fjellberg, A., 1986. Recent advances and future needs in the study of Collembola
 292 biology and systematics. *Quaest. Entomol.* 21, 559-570.

293 Foster, R.C., Rovira, A.D., Cock, T.W., 1983. Ultrastructure of the root soil interface.
 294 St Paul Minnesota: American Phytopathological Society.

295 Fountain, M.T., Hopkin, S.P., 2001. Continuous monitoring of *Folsomia candida*
 296 (Insecta: Collembola) in a metal exposure test. *Ecotox. Environ. Safe.* 48, 275-
 297 286. doi: 10.1006/eesa.2000.2007.

298 Gange, A., 2000. Arbuscular mycorrhizal fungi, Collembola and plant growth. *Trends*
 299 *Ecol. Evol.* 15, 369-372. doi:10.1016/S0169-5347(00)01940-6.

300 Gormsen, D., Olsson, P.I.A., Hedlund, K., 2004. The influence of collembolans and
 301 earthworms on AM fungal mycelium. *Appl. Soil Ecol.* 27, 211-
 302 220. doi:10.1016/j.apsoil.2004.06.001.

303 Hanlon, R.D.G., 1981. Some factors influencing microbial-growth on some animal
 304 faeces. II. Bacterial and fungal growth in soil animal faeces. *Pedobiologia* 21,
 305 264-270.

306 Hartge, K.H., Stewart, B.A., 1995. *Soil Structure: Its Development and Function*. CRC,
 307 Lewis Publishers, Boca Raton, USA.

308 Hedlund, K., Augustsson, A., 1995. Effects of enchytraeid grazing on fungal growth
 309 and respiration. *Soil Biol. Biochem.* 27, 905-909. doi:10.1016/0038-
 310 0717(95)00016-8.

311 Hopkin, S.P., 1997. *Biology of the Springtails (Insecta: Collembola)*. Oxford University
 312 Press.

313 Hopkin, S.P., 2007. *A key to the Collembola (Springtails) of Britain and Ireland*. Field
 314 Studies Council, Shrewsbury, UK.

315 Humbert, W., 1997. Midgut of *Tomocerus minor* Lubbock (Insecta, Collembola) –
 316 Ultrastructure, cytochemistry, aging and renewal during molting cycle. *Cell*
 317 *Tissue Res.* 196, 39-57. doi: 10.1007/BF00236347.

318 Jastrow, J.D., 1996. Soil aggregate formation and the accrual of particulate and
 319 mineral-associated organic matter. *Soil Biol. Biochem.* 28, 665-676. doi:
 320 10.1016/0038-0717(95)00159-x.

321 Klironomos, J.N., Kendrick, W.B., 1996. Palatability of microfungi to soil arthropods in
 322 relation to the functioning of arbuscular mycorrhizae. *Biol. Fert. Soils* 21, 43-52.
 323 doi: 10.1007/BF00335992.

324 Klironomos, J.N., Moutoglis, P., 1999. Colonization of nonmycorrhizal plants by
 325 mycorrhizal neighbours as influenced by the collembolan, *Folsomia candida*.
 326 *Biol.Fert. Soils* 29, 277-281. doi: 10.1007/s003740050553.

327 Klironomos, J.N., Ursic, M., 1998. Density-dependent grazing in the extraradical
 328 hyphal network of the arbuscular mycorrhizal fungus *Glomus intraradices* by the
 329 collembolan *Folsomia candida*. *Biol.Fert. Soils* 26, 250-253. doi:
 330 10.1007/s003740050375.

331 König, H., 2006. *Bacillus* species in the intestine of termites and other soil
 332 invertebrates. *J. Appl. Biol.* 101, 620–627. doi: 10.1111/j.1365-
 333 2672.2006.02914.x

334 Kubiena, W., 1953. *Bestimmungsbuch und Systematik der Böden Europas*. Enke,
 335 Stuttgart, Germany.

336 Larsen, T., 2007. *Unravelling Collembolan Life Belowground: Stoichiometry,*
 337 *Metabolism and Release of Carbon and Nitrogen*. PhD thesis, University of
 338 Copenhagen, Denmark.

339 Lavelle, P., 1998. Earthworm activities and the soil system. *Biol.Fert. Soils* 6, 237-251.
 340 doi: 10.1007/bf00260820.

341 Lee, K.E., 1985. *Earthworms, their Ecology and Relationships with Soils and Land*
 342 *Use*. Academic Press, Sydney, Australia.

343 Lee, K.E., Foster, R.C., 1991. Soil fauna and soil structure. *Aust. J. Soil Res.* 29, 745-
 344 775. doi: 10.1071/sr9910745.

345 Lussenhop, J., 1992. Mechanisms of microarthropod-microbial interactions in soil. *Adv.*
 346 *Ecol. Res.* 23, 1-33. doi:10.1016/S0065-2504(08)60145-2.

347 Lussenhop, J., Fogel, R., Pregitzer, K., 1991. A new dawn for soil biology: video
 348 analysis of root-soil-microbial-faunal interactions. *Agric. Ecosyst. Environ.* 34,
 349 235-249. doi:10.1016/0167-8809(91)90111-A.

350 Lynch, J.M., Bragg, E., 1985. Microorganisms and soil aggregate stability. *Adv. Soil*
 351 *Sci.* 2, 133-171. doi: 10.1007/978-1-4612-5088-3_3.

352 Milcu, A., Partsch, S., Langel, R., Scheu, S., 2006. The response of decomposers
 353 (earthworms, springtails and microorganisms) to variations in species and
 354 functional group diversity of plants. *Oikos* 112, 513-524. doi: 10.1111/j.0030-
 355 1299.2006.14292.x.

356 Miller, R.M., Jastrow, J.D., 1992. The role of mycorrhizal fungi in soil conservation. In
 357 Bethlenfalvay, G.J. & Linderman, R.G. (Eds.), *Mycorrhizae in Sustainable*
 358 *Agriculture*. American Society of Agronomy, Madison, WI.

359 Moore, J.C., John, T.V.S., Coleman, D.C., 1985. Ingestion of vesicular-arbuscular
 360 mycorrhizal hyphae and spores by soil microarthropods. *Ecology* 66, 1979-
 361 1981. doi: 10.2307/2937394.

362 Oades, J.M., 1984. Soil organic-matter and structural stability – mechanisms and
 363 implications for management. *Plant Soil* 76, 319-337. doi: 10.1007/bf02205590.

364 Oades, J.M., 1993. The role of biology in the formation, stabilization and degradation
 365 of soil structure. *Geoderma* 56, 377-400. doi: 10.1016/0016-7061(93)90123-3.

366 Oades, J.M., Water, A.G., 1991. Aggregate hierarchy in soils. *Aust. J. Soil Res.* 29,
 367 815-828. doi: 10.1071/sr9910815.

368 Petersen, H., 1980. Population dynamics and metabolic characterization of Collembola
 369 species in a beech forest ecosystem. Paper presented at the Proc. VII Int. Soil
 370 Zool. Colloq. of the I.S.S.S.
 371 Pherson, D.A., Beattie, A.J., 1979. Fungal loads of invertebrates in beech leaf litter.
 372 Rev. Ecol. Biol. Soil, 16, 325-335.
 373 Ponge, J.F., Charpentié, M.J., 1981. Etude des relations microflore-microfaune:
 374 expériences sur *Pseudosinella alba* (Packard), Collembole mycophage. Rev.
 375 Ecol. Biol. Soil, 18, 291-303.
 376 Ponge, J.F., 1988. Ecological study of a forest humus by observing a small volume. III.
 377 The F1 layer from a moder humus under *Pinussilvestris*. Pedobiologia, 31, 1-
 378 64.
 379 Ponge, J.F., 1991. Food resources and diets of soil animals in a small area of Scots
 380 pine litter. Geoderma, 49, 33-62.
 381 Ponge, J.F., Pérès, G., Guernion, M., Ruiz-Camacho, N., Cortet, J., Pernin, C.,
 382 Villenave, C., Chaussod, R., Martin-Laurent, F., Bispo, A., Cluzeau, D., 2013.
 383 The impact of agricultural practices on soil biota: A regional study. Soil Biol.
 384 Biochem. 67, 271-284.doi:10.1016/j.soilbio.2013.08.026.
 385 Pulleman, M.M., Six, J., Uyl, A., Marinissen, J.C.Y., Jongmans, A.G., 2005.
 386 Earthworms and management affect organic matter incorporation and
 387 microaggregate formation in agricultural soils. Appl. Soil Ecol. 29, 1-15. doi:
 388 10.1016/j.apsoil.2004.10.003.
 389 Rillig, M.C., Aguilar-Trigueros, C.A., Bergmann, J., Verbruggen, E., Veresoglou, S.D.,
 390 Lehman, A., in press. Plant root and mycorrhizal fungal traits for understanding
 391 soil aggregation. New Phytol. doi: 10.1111/nph.13045.
 392 Rillig, M.C., Mummey, D.L., 2006. Mycorrhizas and soil structure. New Phytol. 171, 41-
 393 53. doi: 10.1111/j.1469-8137.2006.01750.x.

394 Roger-Estrade, J., Anger, C., Bertrand, M., Richard, G., 2010. Tillage and soil ecology:
 395 Partner for sustainable agriculture. *Soil Till. Res.* 111, 33-40. doi:
 396 10.1016/j.still.2010.08.010.
 397 Rusek, J., 1985. Soil microstructures-contributions on specific soil organisms. *Quaest.*
 398 *Entomol.* 21, 497-514.
 399 Rusek, J., 1998. Biodiversity of Collembola and their functional role in the ecosystem.
 400 *Biodivers. Conserv.* 7, 1207-1219. doi: 10.1023/a:1008887817883.
 401 Salmon, S., Ponge, J.F., 2001. Earthworm excreta attract soil springtails: laboratory
 402 experiments on *Heteromurus nitidus* (Collembola: Entomobryidae). *Soil Biol.*
 403 *Biochem.* 33, 1959-1969. doi: 10.1016/s0038-0717(01)00129-8.
 404 Siddiky, M.R.K., Kohler, J., Cosme, M., Rillig, M.C., 2012a. Soil biota effects on soil
 405 structure: Interactions between arbuscular mycorrhizal fungal mycelium and
 406 collembola. *Soil Biol. Biochem.* 50, 33-39. doi: 10.1016/j.soilbio.2012.03.001.
 407 Siddiky, M.R.K., Schaller, J., Caruso, R., Rillig, M.C., 2012b. Arbuscular mycorrhizal
 408 fungi and collembola non-additively increase soil aggregation. *Soil Biol.*
 409 *Biochem.* 47, 93-99. doi: 10.1016/j.soilbio.2011.12.022.
 410 Six, J., Bossuyt, H., Degryze, S., Denef, K., 2004. A history of research on the link
 411 between (micro)aggregates, soil biota, and soil organic matter dynamics. *Soil*
 412 *Till. Res.* 79, 7-31. doi: 10.1016/j.still.2004.03.008.
 413 Sjursen, H., Holmstrup, M., 2004. Direct measurement of ammonium excretion in soil
 414 microarthropods. *Funct. Ecol.* 18, 612-615. doi: 10.1111/j.0269-
 415 8463.2004.00877.x.
 416 Thimm, T., Hoffmann, A., Borkott, H., Munch, J.C., Tebbe, C.C., 1998. The gut of the
 417 soil microarthropod *Folsomia candida* (Collembola) is a frequently changeable
 418 but selective habitat and a vector for microorganisms. *Appl. Environ. Microb.*
 419 64, 2660-2669.

420 Thimm, T., Larink, O., 1995. Grazing preferences of some Collembola for
 421 endomycorrhizal fungi. *Biol. Fert. Soils* 19, 266-268. doi: 10.1007/BF00336171.
 422 Tisdall, J.M., 1994a. Formation of soil aggregates and accumulation of soil organic
 423 matter. In Carter, M.R. & Stewart, B.A. (Eds.), *Structure and Organic Matter
 424 Storage in Agricultural Soils*. CRC Press, Boca Raton, Florida.
 425 Tisdall, J.M., 1994b. Possible role of soil-microorganisms in aggregation in soils. *Plants
 426 Soil* 159, 115-121. doi: 10.1007/BF00000100
 427 Tisdall, J.M., Oades, J.M., 1982. Organic-matter and water-stable aggregates in soils.
 428 *J. Soil Sci.* 33, 141-163. doi: 10.1111/j.1365-2389.1982.tb01755.x
 429 Trappe, J.M., 1982. Synoptic keys to the genera and species of zygomycetous
 430 mycorrhizal fungi. *Phytopathology* 72, 1102-1108.
 431 Van Cappelle, C., Schrader, S., Brunotte, J., 2012. Tillage-induced changes in the
 432 functional diversity of soil biota- A review with a focus on German data. *Eur. J.
 433 Soil Biol.* 50, 165-181. doi: 10.1016/j.ejsobi.2012.02.005.
 434 Velasquez, E., Pelosi, C., Brunet, D., Grimaldi, M., Martins, M., Rendeiro, A.C., Barrios,
 435 E., Lavelle, P., 2007. This ped is my ped: Visual separation and near infrared
 436 spectra allow determination of the origins of soil macroaggregates.
 437 *Pedobiologia* 51, 75-87. doi: 10.1016/j.pedobi.2007.01.002.
 438 Verhoef, H.A., Prast, J.E., Verweij, R.A., 1988. Relative importance of fungi and algae
 439 in the diet and nitrogen nutrition of *Orchesella cincta* (L.) and *Tomocerus minor*
 440 (Lubbock) (Collembola). *Funct. Ecol.* 2, 195-201. doi: 10.2307/2389695.
 441 Weigmann, G., 2006. Hornmilben (Oribatida). In Dahl 76. Goecke & Evers, Keltern,
 442 Germany.
 443 Wolters, V., 2000. Invertebrate control of soil organic matter stability. *Biol. Fert. Soils*
 444 31, 1-19. doi: 10.1007/s003740050618.
 445

446

447

448

449

450 Figure captions

451

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