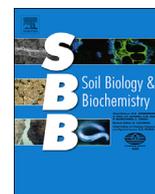




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## Editorial

## Re-visioning soil food webs



Classical soil food web theory identifies distinct energy channels through which resources flow belowground (Hunt et al., 1987; Moore and Hunt, 1988; de Ruiter et al., 1993). Channels are initially divided based on their basal resource, either roots or detrital inputs. The latter channel is then further sub-divided into bacterial- and fungal-based compartments. These compartments are considered to differ markedly in their substrate use, community composition and response to disturbance, with their relative dominance determining carbon and nutrient cycling rates and storage (van der Heijden et al., 2008; Bardgett and Wardle, 2010; Strickland and Rousk, 2010). Recent evidence, however, blurs these distinctions and their functional significance (Strickland and Rousk, 2010; Pollierer et al., 2012). Instead, labile root inputs such as exudates are suggested to fuel more than half of the activity of belowground food webs (van Hees et al., 2005; Pollierer et al., 2007; Gilbert et al., 2014), with these carbon compounds flowing directly through the root to the detrital channel. Root exudates are thus increasingly considered to be a major basal resource flow to all energy channels within soils (Bardgett et al., 2014). Emerging conceptualizations of soil organic matter (SOM) stabilization pinpoint these exudates as dominant precursors of SOM formation, because fungi and bacteria grow efficiently on them and convert them to secondary products and biomass that are stabilized on soil minerals and in soil aggregates (Bradford et al., 2013; Cotrufo et al., 2013; Lehmann and Kleber, 2015).

In a series of 14 *Perspectives*, the likely dominance of root exudates as a food source for symbiotic and free-living bacteria and fungi – in addition to our changing understanding of how organisms interact with one another belowground – is used to argue for a re-evaluation of how soil food webs are structured and operate. The papers present new perspectives on trophic relationships and resource flows, the importance of how communication and behavior shape organism physiology and resulting biogeochemical process rates, and highlight a range of understudied and recently discovered interactions. They make the case that these perspectives must be examined to generate a richer, more comprehensive understanding of soil biology, and its impact on soil properties and processes.

The first three *Perspectives* present different facets of the argument that the importance of root exudates as a resource for soil organisms necessitates a reconceptualization of how soil food webs are structured. Franciska de Vries was originally invited to conclude the Special Issue with a defense of the classic energy channel concept, given her prominent papers linking the relative dominance of fungal versus bacterial compartments to land

management and climate change impacts on soil biogeochemical processes (de Vries et al., 2012, 2013). Instead, her paper with Caruso challenges that concept and leads off the Special Issue and hence the charge for a new conceptual framework. They argue that the prevalence of both bacterial and fungal feeding on labile root exudates unites the three classic channels (root, bacterial and fungal). The unification then temporally and spatially couples aboveground and belowground dynamics much more closely because factors that affect exudation rates and patterns (i.e. living plant physiological responses), have immediate consequences for energy flow to the base of the food web of nearly all soil organisms (de Vries and Caruso, 2016). The authors conclude with the point that to validate their proposed revisions, a variety of advanced methodological approaches need to be employed, which passes the baton neatly onto Morriën (2016). She summarizes the range of techniques, including isotopic tracers, sequencing, gut content analyses, biomarkers and network analyses, increasingly available and cost effective that can be employed to resolve pathways of elemental movement through soils. If you like, how we go about quantifying and connecting historically unobservable interactions.

Ballhausen and de Boer (2016) build on the theme of root exudate flows, arguing that much of the labile carbon exuded by roots is first consumed not by mycorrhiza and bacteria, but rather saprotrophic fungi. They provide evidence that these saprotrophs have their own equivalent of rhizosphere bacteria, necessitating an expansion of the rhizosphere concept to consider the saprotrophic niche, where bacteria function as primary consumers around roots and secondary consumers around fungal hyphae. If each trophic transfer incurs a net loss of energy from the system, then this new pathway may result in less carbon retained in soils when labile exudates flow through fungal saprotrophs and not directly to rhizosphere bacteria.

Wolkovich (2016) takes a different perspective on unification of the energy channels, viewing it from the top-down versus bottom-up. She builds the case that multi-channel omnivory, where a consumer feeds across multiple energy channels, is widespread in most food webs. The classic energy channel concept does include multi-channel feeding but only at high trophic levels, whereas Wolkovich makes the case that empirical evidence increasingly suggests that multi-channel feeding occurs at the lowest trophic level, primary consumers. Given that the majority of consumers appear to multi-channel feed, the existence of distinct energy channels is brought into question. And consequently so are our constructs of the processes influencing soil food web stability and trophic dynamics.

If Wolkovich's *Perspective* is the architectural drawings, Geisen's is the bricks and mortar through which the concepts are realized. He focuses on the soil protists, which play a central role in classical soil food webs as the primary bacterivores. He details their broader functional roles and that they are key multi-channel feeders, uniting the bacterial and fungal energy channels through bacterivory combined with obligate and facultative mycophagy. Perhaps the greatest revelation in his *Perspective* is that protists have now been shown to feed on nematodes, which previously were thought to be their primary predators. This novel trophic interaction reverses classical conceptions of energy and matter flows in soil food webs (Geisen, 2016), and highlights how much more there might be to learn about the organization of belowground communities.

Non-consumptive "trophic" interactions are now a dominant empirical and theoretical feature of aboveground and aquatic food webs (Schmitz, 2010), and the *Perspectives* by Hawlena and Zaguri (2016), and Buchkowski (2016), extend this thinking to the belowground. The former show the potential for fear (of predation) to change the behavior and phenotypes of soil microbes and animals, altering the fluxes of trace gases from the soil to atmosphere, decomposition rates and even soil nitrogen stocks. Buchkowski equally builds the case for a shift from the bottom-up or resource control of soil food webs, detailing how density- and trait-mediated effects may overwhelm the presumed dampening by omnivory of top-down control. Using empirical examples, he makes the case for a move away from our fidelity to a few linear soil food web models to adopt approaches for representing the complexity of top-down controls. Importantly, he suggests a hierarchical approach to the aggregation of feeding guilds so that they might be disassociated to investigate taxon-specific effects when empirical evidence reveals their importance (as in the case of consumers of basidiomycete fungi, Crowther et al., 2012). Buchkowski's *Perspective* is perhaps best read in partnership with Kardol et al. (2016), where they lay out a framework for organizing the hierarchical levels of soil food webs to understand how soil biodiversity affects food web properties and ecosystem process rates. In doing so they provide a tractable and measurable way to approach the challenge of linking pattern in soil biodiversity to process. They highlight the need for manipulative studies to tease out causation and consider the methodological challenges we face in such endeavors.

Despite many decades of soil food web models, both Soong and Nielsen (2016), and Grandy et al. (2016), highlight that soil animals are absent from both traditional (Parton et al., 1987; Jenkinson, 1990) and the rapidly proliferating (Allison et al., 2010; Hagerty et al., 2014; Sulman et al., 2014; Wieder et al., 2014; Tang and Riley, 2015) microbial-explicit SOM models. The explicit inclusion of feedbacks between soil microbes and abiotic factors in the latter models commonly improves biogeochemical predictions and alters our expectations of climate change impacts on SOM stocks (Wieder et al., 2013). The authors make the point, however, that it may be too early to represent microbe-fauna interactions in global carbon models, given glaring gaps in our understanding of these interactions. Yet both *Perspectives* make a compelling case that representation of faunal processes in more conceptual models is likely to lead to rapid advances in our understanding of how animals shape soil processes, mirroring similar gains achieved through the representation of microbial physiology and interactions. Rousk's (2016) *Perspective* is then particularly timely, highlighting that most soil food webs are parameterized using standing biomass estimates of organisms. He makes the argument that food webs and their parameters should instead be populated on the basis of organism growth rates, given that growth relates most strongly to the biogeochemical process rates food web models are often used to predict.

The Special Issue concludes with three *Perspectives* that reflect the incompleteness of our understanding of soil food webs, made strikingly apparent in the preceding contributions. Risk-benefit analyses feature prominently in the *Perspective* by DeAngelis (2016), which conjures up a powerful auditory 'image' through the opening sentence, "If we could hear signaling in soils, it would be loud." DeAngelis introduces to us the idea that many of the interactions in soils, within and among microbes, animals and plants, are mediated at least to some extent through chemical communication. This communication modulates myriad processes in soil food webs, including predation and decomposition. Next, Averill's (2016) *Perspective* emphasizes the potential importance of non-trophic interactions in regulating soil processes and determining organic matter stocks. He builds the increasingly compelling case that recalcitrant plant tissue chemistry is not a dominant driver of elevated soil carbon stocks in forests dominated by tree species forming symbioses with ectomycorrhizae. Instead, he promotes the idea that ectomycorrhizal fungi can outcompete saprotrophs for detrital nitrogen sources, either through exploitative competition or direct antagonistic interactions (i.e. interference competition). His essay reminds us that food web models need to consider the broad range of ecological interactions, beyond trophic interactions, if they are to inform us about soil food web process and structure.

King (2016) completes the Special Issue, with a focus on animals that, in contrast to protists, have largely been left out of soil food web models. Soil samples to quantify belowground communities are usually taken randomly, meaning that data on the density of eusocial insects (e.g. ants and termites) are rarely gathered (Fierer et al., 2009) because the bulk of their biomass is non-randomly distributed in colonies. When colonies are specifically collected, biomass of these insects can be greater than that of all other litter macroinvertebrates, a fact known for tropical systems but now apparent even in the temperate zone (King et al., 2013). King makes the point that termites are competitors with many other detritivores and saprotrophic fungi for organic inputs, and have strong engineering effects. Equally, ants play a prominent role in soil engineering and are ubiquitous omnivores. Consequently social insects have a wide range of direct and indirect interactions with most other organisms in soil food webs. Not only then do we need new measurements of established players in soil food webs (Morriën, 2016; Rousk, 2016), we also need measures of players and processes that have received little attention.

When the classic conceptions of energy channels within soil food webs were formalized, I am sure that those scientists that drew together these powerful and far-reaching ideas never intended or considered that the story would end there. The contributions to this Special Issue highlight the need to revise the narrative. In doing so, the field will have to reconcile why bacterial to fungal ratios appear to correlate so strongly with soil properties (Bardgett and McAlister, 1999; Waring et al., 2013), because the mechanistic explanations for these associations now seem unsatisfactory. As we develop new conceptual frameworks, we should also look beyond academia. The classic linear, energy channel conceptualization of soil food webs is used to communicate soil biology to the general public and practitioners, through such portals as the U.S. Department of Agriculture's soil health webpage (<http://www.nrcs.usda.gov/wps/portal/nrcs/main/soils/health/biology>). We need to ensure that the best available science is synthesized for communication to these audiences, to help efforts that seek to protect the most fundamental natural resource that soil represents. The *Perspectives* in this Special Issue suggest that we should pull down the temple where fungal: bacterial dominance is synonymous with detrital-based food webs, and construct in its place a labyrinth connected via root inputs and root-zone interactions as

dominant factors shaping soil communities and associated ecosystem dynamics.

## References

- Allison, S.D., Wallenstein, M.D., Bradford, M.A., 2010. Soil-carbon response to warming dependent on microbial physiology. *Nature Geoscience* 3, 336–340.
- Averill, C., 2016. Slowed decomposition in ectomycorrhizal ecosystems is independent of plant chemistry. *Soil Biology & Biochemistry* 102, 52–54.
- Ballhausen, M.-B., de Boer, W., 2016. The sapro-rhizosphere: carbon flow from saprotrophic fungi into fungus-feeding bacteria. *Soil Biology & Biochemistry* 102, 14–17. <http://dx.doi.org/10.1016/j.soilbio.2016.06.014>.
- Bardgett, R.D., McAlister, E., 1999. The measurement of soil fungal:bacterial biomass ratios as an indicator of ecosystem self-regulation in temperate meadow grasslands. *Biology and Fertility of Soils* 29, 282–290.
- Bardgett, R.D., Mommer, L., de Vries, F.T., 2014. Going underground: root traits as drivers of ecosystem processes. *Trends in Ecology & Evolution* 29, 692–699.
- Bardgett, R.D., Wardle, D.A., 2010. Aboveground-belowground Linkages: Biotic Interactions, Ecosystem Processes, and Global Change. Oxford Univ. Press, Oxford, UK.
- Bradford, M.A., Keiser, A.D., Davies, C.A., Mersmann, C.A., Strickland, M.S., 2013. Empirical evidence that soil carbon formation from plant inputs is positively related to microbial growth. *Biogeochemistry* 113, 271–281.
- Buchkowski, R.W., 2016. Top-down consumptive and trait-mediated control do affect soil food webs: it's time for a new model. *Soil Biology & Biochemistry* 102, 29–32. <http://dx.doi.org/10.1016/j.soilbio.2016.06.033>.
- Cotrufo, M.F., Wallenstein, M.D., Boot, C.M., Deneff, K., Paul, E., 2013. The Microbial Efficiency-Matrix Stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: do labile plant inputs form stable soil organic matter? *Global Change Biology* 19, 988–995.
- Crowther, T.W., Boddy, L., Jones, T.H., 2012. Functional and ecological consequences of saprotrophic fungus–grazer interactions. *The ISME Journal* 6, 1992–2001.
- de Ruiter, P.C., Moore, J.C., Zwart, K.B., Bouwman, L.A., Hassink, J., Bloem, J., Devos, J.A., Marinissen, J.C.Y., Didden, W.A.M., Lebbink, G., Brussaard, L., 1993. Simulation of nitrogen mineralization in the belowground food webs of 2 winter-wheat fields. *Journal of Applied Ecology* 30, 95–106.
- de Vries, F.T., Caruso, T., 2016. Eating from the same plate? Revisiting the role of labile carbon inputs in the soil food web. *Soil Biology & Biochemistry* 102, 4–9. <http://dx.doi.org/10.1016/j.soilbio.2016.06.023>.
- de Vries, F.T., Liiri, M.E., Bjørnlund, L., Bowker, M.A., Christensen, S., Setälä, H.M., Bardgett, R.D., 2012. Land use alters the resistance and resilience of soil food webs to drought. *Nature Climate Change* 2, 276–280.
- de Vries, F.T., Thebault, E., Liiri, M., Birkhofer, K., Tsiafouli, M.A., Bjørnlund, L., Jørgensen, H.B., Brady, M.V., Christensen, S., de Ruiter, P.C., d'Hertefeldt, T., Frouz, J., Hedlund, K., Hemerik, L., Hol, W.H.G., Hotes, S., Mortimer, S.R., Setälä, H., Sgardelis, S.P., Uteseny, K., van der Putten, W.H., Wolters, V., Bardgett, R.D., 2013. Soil food web properties explain ecosystem services across European land use systems. *Proceedings of the National Academy of Sciences of the United States of America* 110, 14296–14301.
- DeAngelis, K.M., 2016. Chemical communication connects soil food webs. *Soil Biology & Biochemistry* 102, 48–51. <http://dx.doi.org/10.1016/j.soilbio.2016.06.024>.
- Fierer, N., Strickland, M.S., Liptzin, D., Bradford, M.A., Cleveland, C.C., 2009. Global patterns in belowground communities. *Ecology Letters* 12, 1238–1249.
- Geisen, S., 2016. The bacterial-fungal energy channel concept challenged by enormous functional versatility of soil protists. *Soil Biology & Biochemistry* 102, 22–25. <http://dx.doi.org/10.1016/j.soilbio.2016.06.013>.
- Gilbert, K.J., Fahey, T.J., Maerz, J.C., Sherman, R.E., Bohlen, P., Dombroskie, J.J., Groffman, P.M., Yavitt, J.B., 2014. Exploring carbon flow through the root channel in a temperate forest soil food web. *Soil Biology & Biochemistry* 76, 45–52.
- Grandy, S.A., Wieder, W.R., Wickings, K., Kyker-Snowman, E., 2016. Beyond microbes: are fauna the next frontier in soil biogeochemical models? *Soil Biology & Biochemistry* 102, 40–44.
- Hagerty, S.B., van Groenigen, K.J., Allison, S.D., Hungate, B.A., Schwartz, E., Koch, G.W., Kolka, R.K., Dijkstra, P., 2014. Accelerated microbial turnover but constant growth efficiency with warming in soil. *Nature Climate Change* 4, 903–906.
- Hawlena, D., Zaguri, M., 2016. Fear and below-ground food-webs. *Soil Biology & Biochemistry* 102, 26–28. <http://dx.doi.org/10.1016/j.soilbio.2016.06.019>.
- Hunt, H.W., Coleman, D.C., Ingham, E.R., Ingham, R.E., Elliott, E.T., Moore, J.C., Rose, S.L., Reid, C.P.P., Morley, C.R., 1987. The detrital food web in a shortgrass prairie. *Biology and Fertility of Soils* 3, 57–68.
- Jenkinson, D.S., 1990. The turnover of organic carbon and nitrogen in soil. *Philosophical Transactions of the Royal Society London B* 329, 361–368.
- Kardol, P., Throop, H.L., Adkins, J., de Graaff, M.-A., 2016. A hierarchical framework for studying the role of biodiversity in soil food web processes and ecosystem services. *Soil Biology & Biochemistry* 102, 33–36. <http://dx.doi.org/10.1016/j.soilbio.2016.05.002>.
- King, J.R., 2016. Where do eusocial insects fit into soil food webs? *Soil Biology & Biochemistry* 102, 55–62. <http://dx.doi.org/10.1016/j.soilbio.2016.07.019>.
- King, J.R., Warren II, R.J., Bradford, M.A., 2013. Social insects dominate eastern US temperate hardwood forest macroinvertebrate communities in warmer regions. *PLoS One* 8, e75843.
- Lehmann, J., Kleber, M., 2015. The contentious nature of soil organic matter. *Nature* 528, 60–68.
- Moore, J.C., Hunt, H.W., 1988. Resource compartmentation and the stability of real ecosystems. *Nature* 333, 261–263.
- Morriën, E., 2016. Understanding soil food web dynamics, how close do we get? *Soil Biology & Biochemistry* 102, 10–13. <http://dx.doi.org/10.1016/j.soilbio.2016.06.022>.
- Parton, W.J., Schimel, D.S., Cole, C.V., Ojima, D.S., 1987. Analysis of factors controlling soil organic matter levels in Great Plains grasslands. *Soil Science Society of America Journal* 51, 1173–1179.
- Pollierer, M.M., Dyckmans, J., Scheu, S., Haubert, D., 2012. Carbon flux through fungi and bacteria into the forest soil animal food web as indicated by compound-specific <sup>13</sup>C fatty acid analysis. *Functional Ecology* 26, 978–990.
- Pollierer, M.M., Langel, R., Körner, C., Maraun, M., Scheu, S., 2007. The underestimated importance of belowground carbon input for forest soil animal food webs. *Ecology Letters* 10, 729–736.
- Rousk, J., 2016. Biomass or growth? How to measure soil food webs to understand structure and function. *Soil Biology & Biochemistry* 102, 45–47. <http://dx.doi.org/10.1016/j.soilbio.2016.07.001>.
- Schmitz, O.J., 2010. Resolving Ecosystem Complexity. Princeton Univ. Press, Princeton.
- Soong, J.L., Nielsen, U.N., 2016. The role of microarthropods in emerging models of soil organic matter. *Soil Biology & Biochemistry* 102, 37–39. <http://dx.doi.org/10.1016/j.soilbio.2016.06.020>.
- Strickland, M.S., Rousk, J., 2010. Considering fungal:bacterial dominance in soils – methods, controls, and ecosystem implications. *Soil Biology & Biochemistry* 42, 1385–1395.
- Sulman, B.N., Phillips, R.P., Oishi, A.C., Shevliakova, E., Pacala, S.W., 2014. Microbe-driven turnover offsets mineral-mediated storage of soil carbon under elevated CO<sub>2</sub>. *Nature Climate Change* 4, 1099–1102.
- Tang, J., Riley, W.J., 2015. Weaker soil carbon–climate feedbacks resulting from microbial and abiotic interactions. *Nature Climate Change* 5, 56–60.
- van der Heijden, M.G.A., Bardgett, R.D., van Straalen, N.M., 2008. The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. *Ecology Letters* 11, 296–310.
- van Hees, P.A.W., Jones, D.L., Finlay, R., Godbold, D.L., Lundström, U.S., 2005. The carbon we do not see—the impact of low molecular weight compounds on carbon dynamics and respiration in forest soils: a review. *Soil Biology & Biochemistry* 37, 1–13.
- Waring, B.G., Averill, C., Hawkes, C.V., 2013. Differences in fungal and bacterial physiology alter soil carbon and nitrogen cycling: insights from meta-analysis and theoretical models. *Ecology Letters* 16, 887–894.
- Wieder, W.R., Bonan, G.B., Allison, S.D., 2013. Global soil carbon projections are improved by modelling microbial processes. *Nature Climate Change* 3, 909–912.
- Wieder, W.R., Grandy, A.S., Kallenbach, C.M., Bonan, G.B., 2014. Integrating microbial physiology and physio-chemical principles in soils with the Microbial-Mineral Carbon Stabilization (MIMICS) model. *Biogeosciences* 11, 1147–1185.
- Wolkovich, E.M., 2016. Reticulated channels in soil food webs. *Soil Biology & Biochemistry* 102, 18–21. <http://dx.doi.org/10.1016/j.soilbio.2016.06.021>.

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Available online 31 August 2016