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**A hierarchical framework for studying the role of biodiversity in
soil food web processes and ecosystem services**

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ABSTRACT

Soil food webs play a key role in the cycling of carbon and nutrients and in sustainably provisioning ecosystem services. Despite the tremendous diversity of organisms that soil food webs harbor, we still know surprisingly little about the role of biodiversity in influencing the processes and services provided by soil food webs. To guide future research in this area, we outline a conceptual framework linking hierarchical levels of soil biodiversity to ecosystem processes and services. Here, we distinguish among different hierarchical levels of diversity: trophic, functional, taxonomic and genetic diversity. We conclude that the levels of food web diversity that matter most vary with the processes or services considered, with functional trait diversity being the most universally influential level of diversity. Increased research emphasis on manipulating diversity across hierarchical levels of biodiversity organization, with an explicit focus on the functional role of the component species, is critical for enhancing our understanding of the role of soil food web diversity in driving ecosystem processes and services.

Keywords: Ecosystem functioning, Food web interactions, Functional traits, Soil biodiversity, Soil fauna, Soil microorganisms, Trophic levels

Soil food webs can be comprised of an immense organismal diversity, with site-specific patterns of diversity being influenced by long-term drivers such as climatic and edaphic factors, resource availability, and biogeographical influences on the species pool, as well as short-term drivers such as agricultural disturbances (Fig. 1). Ecological theory suggests positive relationships between biodiversity and ecosystem functioning (Balvanera et al. 2006), but whether or not this also applies to soil food web diversity remains poorly understood (de Graaff et al. 2015). It is

well-recognized that soil biota are important in driving ecosystem processes and in affecting the responses, resilience, and adaptability of ecosystems to environmental change (Bardgett and van der Putten, 2014; Nielsen et al., 2015; Tsiafouli et al., 2015). Recent progress has been made in unravelling the role of soil food web composition in driving the cycling of carbon and nutrients (De Vries et al. 2013). However, studies explicitly testing the effect of soil food web diversity are scarce (Nielsen et al. 2011; De Graaff et al. 2015).

Our limited understanding of the role of biodiversity in soil ecosystem processes can, at least in part, be attributed to the difficulty of identifying and functionally classifying soil organisms and the challenges of manipulating extremely small creatures in a cryptic habitat (Cortois and De Deyn 2012). Previous studies aiming to determine the effects of soil food web diversity on ecosystem functioning have manipulated diversity in various ways, often based on trophic, taxonomic or organismal body size categories. These categories have been based on theoretical and/or practical considerations, but coordinated approaches of linking hierarchical levels of soil food web diversity to specific ecosystem processes are lacking (De Graaff et al. 2015). Here, we provide a conceptual framework linking hierarchical levels of soil food web diversity to ecosystem processes (Fig. 1). The framework provides guidance for design of future studies in this rapidly developing area of research. We focus on the question: ‘what level of diversity matters most for different ecosystem processes’?

In soil food webs, diversity can be detected across hierarchical levels of organization (Fig. 1, left side). At an overarching level, soil food web biodiversity can be described in terms of energy channels, i.e., groups of organisms consuming biomass that originates from the same primary energy source (Moore and Hunt, 1988). The chemical composition of substrates consumed and the rates of energy flow differ among energy channels (Wardle et al. 2004). Thus, diversity at

this level affects rates of litter decomposition based on complementary use of resources (Fig. 1). At a lower level in the hierarchy, studies on the role of biodiversity in soil food web processes have often focused on trophic diversity, i.e., the presence and abundance of different trophic groups (e.g., Ladygina et al. 2010). Increases in trophic group diversity can positively affect process rates (e.g., Huhta et al. 1998), likely due to increased probability that trophic niches important to ecosystem processes are filled. However, increased trophic group diversity may inhibit process rates when top-down control by predators suppresses populations in lower trophic groups (Santos et al. 1981; Becker et al., 2012). In general, trophic group diversity may adequately predict rates of basic soil ecosystem processes such as decomposition, but this hierarchical level of diversity falls short in predicting rates of more specialized processes such as ammonification, nitrification, denitrification, and biological N fixation (Fig. 1).

Moving down a level in the hierarchy, soil organisms show high levels of functional diversity. Functional diversity can be defined as the grouping of organisms based on traits that influence ecosystem processes (Tilman, 2001). Work in plant communities suggests that functional trait diversity can strongly influence ecosystem processes (Diaz and Cabido, 2011). Thus, we predict that functional trait diversity will be the most universally influential level of diversity across a range of ecosystem processes and food web attributes (Fig. 1). More precisely, effects of biodiversity on ecosystem processes should be predictable based on the degree of functional dissimilarity among taxa, with increasing diversity enhancing niche partitioning (Heemsbergen et al. 2004; Coulis et al. 2015). Trait-based approaches have been used in predicting responses to shifts in environmental conditions of soil faunal communities, such as nematodes (Cesarz et al., 2015), mites (Lindo et al., 2012) and collembola (Makkonen et al., 2011; Widenfalk et al., 2015), but our understanding of how organism traits affect soil ecosystem processes (i.e., effect traits)

remains limited. In agriculture, however, it has been shown that greater functional diversity may translate into changes in soil food web services such as plant protection (Fig. 1). For example, diverse rhizosphere microbial communities may increase plant pathogen resistance and disease suppression (Jousset et al., 2014; Hol et al. 2015). Moreover, trait diversity of mycorrhizal fungi has been linked to plant productivity (van der Heijden and Scheublin, 2007) and soil aggregation (Rillig et al., 2015).

Considering the hierarchy of soil food web diversity, few studies have examined the ecosystem-level impacts of diversity at lower hierarchical levels such as taxonomic diversity (i.e., the diversity of taxa or operational taxonomic units) or phylogenetic diversity (the diversity of genotypes within taxa) (de Graaff et al. 2015). Certainly individual species in soil communities can influence ecosystem processes; a few species can dominate soil processes and have disproportionate impact on energy flow (see Thompson et al. 2012) and there is evidence that different soil microbial (e.g., Hanson et al., 2008) and faunal taxa (Bignell and Eggleton, 2000; Milcu et al., 2008; Heemsbergen et al., 2004) can have disparate influences on C cycling. We expect that taxonomic diversity will be more important for processes such as N fixation or the metabolism of methane and nitrous oxide that require specialized enzymes and abiotic conditions rather than more general processes such as the decomposition of simple substrates. For example, it is well recognized that microbial diversity is particularly important if the traits underlying the process are phylogenetically conserved and, hence, the process is carried out by taxonomically restricted groups of organisms (Schimel 1995; Webster et al. 2005). In this light, seemingly general processes might become ‘narrower’ if each organism requires taxon-specific environmental conditions to carry out the process (Schimel 1995). In agriculture, taxonomic diversity is of particular importance because of the often highly specialized and species-specific

interactions involved (Burdon et al. 2006). Based on studies to date, we expect that genetic diversity will, in most cases, have a fairly minor influence on ecosystem processes. An exception to this is nitrogen fixation, a highly specialized ecosystem process where high levels of genetic diversity exist and this diversity influences the symbiotic efficiency (Azarias Guimarães et al. 2012). Interestingly, in terms of soil food web services, increased genotypic diversity of bacterial mutualists has been shown to reduce plant protection (Becker et al. 2012).

Soil food web stability is important for the sustainable provisioning of ecosystem services, especially in light of anthropogenically-induced environmental perturbations that confer significant stress on soil organisms (e.g., de Vries et al., 2012). Here, one of the main structuring forces is the degree of trophic connectedness (Neutel et al. 2007). This has been suggested to strongly depend on omnivorous interactions and, hence, indicates an important role of trophic diversity in driving food web stability. However, from aboveground and aquatic food webs we know that species interactions can also impact food web stability both within and across trophic levels (Rooney and McCann, 2012). However, this has not yet been tested for soil food webs. In addition, longer-term soil food web responses to environmental changes may not only depend on taxonomic and functional shifts (Awasthi et al. 2014), and hence trait diversity, but should also depend on adaptive evolutionary responses, and hence genetic diversity (Lau and Lennon, 2012; Low-Décarie et al. 2015). Experimental examples of how evolutionary dynamics would drive soil food web response are, however, scarce (Fig. 1).

Advancing our understanding of soil food web diversity impacts on ecosystem processes will require an investment in manipulative studies. Our hierarchical framework suggests that functional trait biodiversity will be the biodiversity level that most often influences a wide array of ecosystem processes. Manipulation of functional diversity is most feasible for soil fauna. In

this context, body size has often been used as a surrogate for ‘function’ (e.g., Bradford et al., 2002; Wagg et al., 2014). While using body size groups is attractive because of its tractability, it requires caution because empirical support for correlations between size and function is weak for most soil fauna groups. However, important progress has recently been made for nematodes (George and Lindo, 2015). Alternatively, soil biodiversity can be manipulated at the trophic level (Mikola and Setälä, 1998). The benefit of this approach is that it is firmly grounded in trophic dynamic theory. However, allocating soil organisms to trophic levels is a daunting task because of our poor understanding of their feeding preferences and the high degree of omnivory (e.g., Digel et al., 2014). Soil biodiversity can also be manipulated by using a removal approach, for example by inoculation of sterilized soils with serial dilutions of soil organisms extracted from living soils (e.g., Wertz et al., 2006). Removal experiments may provide information on the consequences of losses of soil biodiversity under environmental change or in response to disturbance. A complication, however, is that most empirical removal experiments probably select for survival of specific taxa or functional groups, thereby confounding diversity treatments with shifts in community composition.

It should also be noted that both for soil fauna and microorganisms, studies to date generally use amounts of biodiversity that are much lower than typical field conditions (de Graaff et al., 2015; Nielsen et al., 2011; Nielsen et al., 2015). As a result, the often large positive responses to increases in biodiversity are not surprising. At lower diversity, increases in biodiversity lead to significant ecosystem process responses, as increases in taxonomic diversity will also increase functional diversity. However, functional redundancy in soil food webs is often high (Setälä, 2002; but, see Mori et al., 2016 for novel evidence on how functional redundancy in fungal communities may decrease when spatial variation is taken into account). A threshold of

functional redundancy may be reached especially quickly for more specialized processes such as ammonification and N fixation compared to more general processes like decomposition, for which the threshold of functional redundancy occurs at relatively high amounts of biodiversity. This hypothesis, however, remains untested. Manipulating amounts of diversity that are realistic to soil communities would yield particularly useful information and would allow for the assessment of thresholds for a variety of ecosystem processes, both specific and general. Here, the threshold of process responses to increases in biodiversity is likely to differ across sites that differ in terms of geological and climatic drivers as it has now become apparent that site factors predictably regulate soil communities (Fierer et al., 2012).

The large numbers of cryptic organisms and the different hierarchical levels of diversity in soil food webs present a major challenge for characterizing and understanding how soil organism biodiversity influences ecosystem processes. However, a hierarchical approach to understanding and assessing the role of biodiversity provides a structure for approaching this complex problem. Novel developments in the analyses of soil biodiversity promise to provide new insights into the enormous genetic and taxonomic diversity belowground and the divergent niches occupied by soil organisms (Taylor et al. 2014; Delgado-Querizo et al., 2016). However, large-scale molecular sequencing alone (e.g. Wu et al., 2011; Tedersoo et al., 2014) will not improve our understanding of the role of biodiversity in driving soil ecosystem processes. We advocate prioritizing enhancing our understanding of the functional roles of soil organisms (moving beyond body size groups), coupled with a mechanistic understanding that manipulates biodiversity at different hierarchical levels: within- and across energy channels, trophic groups, functional groups, taxa, and genetic differences.

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Figure legend

Fig. 1. Conceptual diagram depicting the hierarchical levels of soil food web diversity and the uncertainties of their differential influences on key soil ecosystem processes and soil food web services and attributes. Soil food web diversity can be considered at different hierarchical levels, depending on what metrics are used for diversity. Body size groups may span multiple levels of hierarchical organization. Similarly, energy levels integrate soil diversity across organizational levels and, as such, could be considered overarching. Body size of soil organisms may span the entire hierarchy. These levels of food web diversity are expected to differentially influence ecosystem processes and soil food web attributes and services, as denoted by the width of the gray and blue shapes. For example, decomposition rates are likely strongly influenced by the energy channels and trophic group diversity, with a lesser impact by lower levels of the hierarchy, such as species identity. The level of darkness of the shapes indicates the level of uncertainty with dark colors indicating relatively strong experimental evidence and light colors indicating weak experimental evidence. Note that shapes are relative estimates based on published literature and expert judgement, and hence, should be interpreted as guidance for future research. This diagram is not meant to be all-inclusive; other processes, attributes and services could be considered. OTU = Operational taxonomic unit