

The bacterial-fungal energy channel concept challenged by enormous functional versatility of soil protists



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ABSTRACT

Protists (=protozoa) are commonly treated as bacterivores that control the bacterial energy channel in soil food webs. This ecologist's perspective is, however, challenged by taxonomic studies showing that a range of protists feed on fungi, other protists and even nematodes. Recently, it was revealed that obligate and facultative mycophagous protists are common soil inhabitants, while others are facultative nematophagous. Furthermore, protists act as parasites and pathogens of plants and animals. This neglected functional diversity of protists, that is similarly prevalent for other groups of soil organisms, reveals that current food web model models are oversimplified.

Facultative feeding of various protist taxa on bacteria and fungi, the source of both major energy channels, strongly implies that a clear split of the energy channels at lower trophic levels does not exist and that more complex energy flows prevail in soil food webs. Future efforts should therefore target ecological functioning of protists and other groups of soil organisms, on a species-specific level, to create more meaningful functional units that then need incorporation in modified soil food web models. Such efforts will help disentangling the structure, diversity and resulting functioning of complex soil systems, including energy flows through the soil food web.

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1. Introduction

Fungi, plants and animals are by far the most-intensely studied and best-known eukaryotes. In terms of diversity, however, these mostly multicellular groups represent only small monophyletic branches in the eukaryotic tree of life, while the vast majority are single-celled protists (Adl et al., 2012; Pawlowski, 2013). Despite this enormous diversity, soil protists are commonly termed protozoa due to their predominant heterotrophic lifestyle similar to animals and are placed into four morphogroups: naked and testate amoebae, flagellates and ciliates (Esteban et al., 2006; Adl et al., 2012). This grouping is, however, highly artificial as only ciliates are monophyletic and a huge diversity of often entirely unrelated taxa are lumped together into the other morphogroups. Similar to diversity, the abundance of protists is huge with numbers between 10,000 and 100,000 in a single gram of soil (Clarholm, 1981; Geisen et al., 2014a). This number based on classical cultivation based approaches is likely an underestimation as state-of-the-art molecular techniques revealed that thousands additional, often

unknown protist groups, inhabit the same soil volume (Bates et al., 2013; Geisen et al., 2015c; Dupont et al., 2016).

In terms of functioning, soil protists have been included in soil food web models merely as major bacterivores controlling the bacterial energy channel (Hunt et al., 1987; Moore and Hunt, 1988; de Ruiter et al., 1995). Many ecological studies have consequently only focused on bacterial feeding protists such as the model taxon *Acanthamoeba castellanii*, which enforced the notion to consider protists as bacterivores (e.g. (Bonkowski and Brandt, 2002; Andersen and Winding, 2004; Koller et al., 2013)). These studies revealed important insights into ecosystem services provided by protists, such as plant growth stimulation by protist grazing-induced nutrient provisioning, i.e. the microbial loop in soils (Clarholm, 1985) and stimulation of plant growth promoting rhizobacteria by selective feeding (Bonkowski, 2004; Jousset et al., 2006).

2. Deviations from the classical concept of protists being merely bacterivorous

Interestingly, taxonomists have described a range of protist taxa in soils that prey on organisms other than bacteria (Chakraborty et al., 1983; Coûteaux, 1985; Coûteaux and Darbyshire, 1998;

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Berney et al., 2015) and many protists can only be cultivated when supplied with other fungal or protist eukaryotes as prey (Smirnov and Brown, 2004; Berney et al., 2015). Targeted ecological studies investigating non-bacterivorous protists suggested that the biomass of mycophagous protists might equal that of classical bacterivorous protists (Ekelund, 1998). In addition, many “bacterivorous” protists are actually facultative mycophagous (Geisen et al., 2016) suggesting that (facultative) mycophagous protists are of similar importance to bacterivores in controlling the population and community structure of fungi (Fig. 1). Furthermore, deviations from the classical ‘protist-bacteria food webs’ were revealed by negative effects of protists on nematodes (Yeates and Foissner, 1995; Bjørnlund and Rønn, 2008); the small but common soil protist *Cryptodiffugia operculata* even benefits strongly in fitness when feeding on nematodes (Geisen et al., 2015b). This case of a reversed loop exemplifies how complex real soil food webs are and how much they differ from commonly applied soil food web models (Figs. 1 and 2).

Thanks to continuously improving molecular tools such as high-throughput sequencing (HTS), it is now evident that parasitic and pathogenic protist taxa are common in soils. Among those are oomycetes and plasmodiophorids, which, despite their morphological similarities with fungi, are protists that predominantly infect plants (Adl et al., 2012; Burki, 2014; Geisen et al., 2015c). Similarly, animal infecting taxa, such as apicomplexans, compose a significant fraction of protists in soils (Bates et al., 2013; Geisen et al., 2015a, 2015c; Dupont et al., 2016; Grossmann et al., 2016) (Fig. 1). While this enormous functional diversity of protists to nutrient flows in the soil food web is likely important, the extent

and relative importance of functions other than bacterivory await to be quantified.

3. So why are protists commonly considered as purely bacterivorous?

Most groups of soil protists, especially small, but numerically dominant (naked) amoebae and flagellates, are tightly attached to small soil particles and can only be studied using enrichment cultivation (Foissner, 1997). Enrichment of (clonal) protist cultures is mostly performed by cultivation on bacteria such as *Escherichia coli* or co-extracted bacteria in a bacterial growth medium (Smirnov and Brown, 2004), which inevitably selects against non-bacterivorous taxa. Furthermore, many small protists are suggested to be unable to engulf larger prey suggesting that small bacteria might be the only organisms those protists feed upon. However, counterevidence for this hypothesis is given by some small flagellates and amoebae that feed on larger fungi, nematodes and human cells by adopting different methods such as prey penetration or pack hunting (Geisen et al., 2014b, 2015b, 2016). Last, scientific fields, such as taxonomy and ecology, are typically separated resulting in a lack of interdisciplinary integration and therefore knowledge transfer such as on the functional diversity of soil protists.

4. Implications and future perspectives

Evidence of multiple examples of functionally diverse soil protists other than being merely bacterivorous strongly implies that there is a need to include those functional groups in existing food

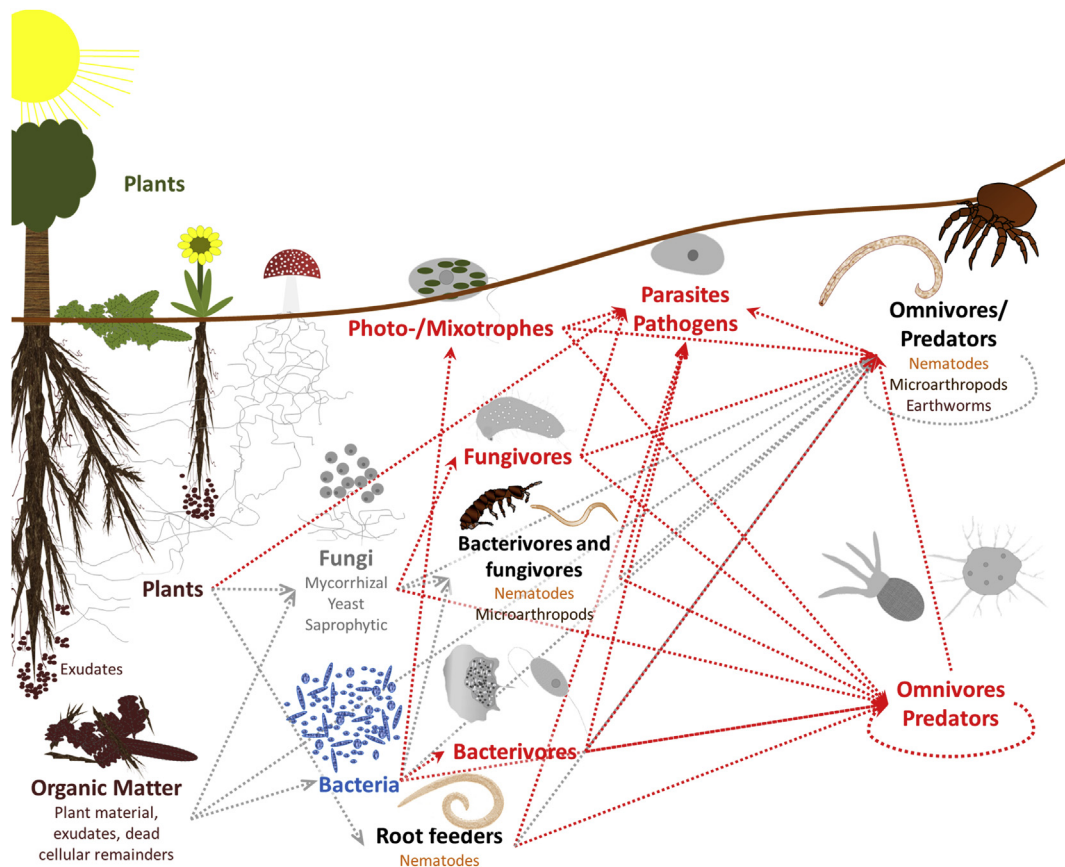


Fig. 1. Conceptual soil food web focusing on the neglected functional diversity of soil protists, directly showing that the bacterial and fungal energy channels merge already at the first higher trophic level. Direct interactions indicated with arrows (red: interactions of protists with other soil organisms, grey: interactions between non-protists); different organism groups encoded by different colours. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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