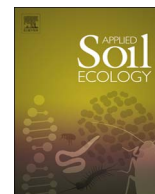




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Short communication

Methodological advances to study the diversity of soil protists and their functioning in soil food webs

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ABSTRACT

Soils host the most complex communities of organisms, which are still largely considered as an unknown ‘black box’. A key role in soil food webs is held by the highly abundant and diverse group of protists. Traditionally, soil protists are considered as the main consumers of bacteria in soils. However, recent insights obtained using new methodologies, provide clear evidence for the trophic diversity of microbial eukaryotes, showing that non-bacterivorous soil protists (fungivores, omnivores, predators of other protists and nematodes), photosynthetic taxa and plant-as well as animal parasites might be equally important.

Here we provide an overview of methodologies to study these important soil organisms. Major gaps of knowledge are highlighted, which can be addressed using a combination of now available methods. These studies will undeniably reveal an even higher functional diversity of protists and likely raise awareness of their ecological importance in soils.

1. Introduction

Disentangling the drivers of decomposition and the flow of energy through the soil food web remains one of the greatest challenges in soil biology (Scheu, 2002). Traditionally, soil organisms were extracted and visually identified leading to the widest knowledge on large organisms such as earthworms (Brown, 1995; Edwards and Bohlen, 1995; Lee, 1985). In line, prokaryotic bacteria and eukaryotic fungi at the base of the soil food web are comparably well studied, due to (1) their key functional roles for decomposition and the mineralisation of nutrients (de Ruiter et al., 1995; Hunt et al., 1987), (2) the availability of an immense repertoire of techniques to study them (Alef and Nannipieri, 1995; Frostegård et al., 1993; Martin-Laurent et al., 2001; Paul, 2014). Knowledge on the smallest primary consumers of bacteria and fungi is least, despite their suggested major roles in nutrient cycling and energy transfer to higher trophic levels in the soil food web (de Ruiter et al., 1995; Hunt et al., 1987). These groups are nematodes and, predominantly, protists (Hunt et al., 1987; Ingham et al., 1985).

2. Taxonomic and functional diversity of soil protists

While nematodes by virtue of their morphologically distinct feeding structures can immediately be grouped into different trophic guilds

(Ettema, 1998; Sohlenius, 1980; Yeates, 1979), soil protists have been mainly considered as bacterial feeders (Bezemer et al., 2010; de Ruiter et al., 1995; Hunt et al., 1987) and grouped according to their locomotion into the morphotypes of flagellates, ciliates and (naked and testate) amoebae (Darbyshire, 1994; Ekelund and Rønn, 1994). The full taxonomic diversity of protists (Adl et al., 2005, 2012), which are suggested to reach numbers between 10,000 and 100,000 individuals per gram of soil, is only gradually being acknowledged in soil biology. So far, concepts integrating this taxonomic diversity at the base of soil food webs is lacking (Geisen, 2016a; Geisen et al., 2016) (Fig. 1, grey boxes).

Developing techniques revolutionized not only our understanding on the species richness of prokaryotes and fungi (Fierer et al., 2007; Rousk et al., 2010; Urich et al., 2008), but also on protists. Potential parasites and pathogens of plants and animals were shown to be very common and abundant members of soil protist communities (Bass et al., 2016; Bates et al., 2013; Geisen et al., 2015c; Grossmann et al., 2016). Many protist taxa found in soil surveys seem to symbiotically inhabit other eukaryotes of the soil meso- and macrofauna, such as mites, collembolans, and especially earthworms (Field and Michiels, 2005, 2006; Geisen et al., 2015a; Pizl, 1986; Purrini, 1984; Velavan et al., 2009) (Fig. 1, red italicized). Purely phototrophic (algae) or mixotrophic protists are mainly associated with soil crusts and might

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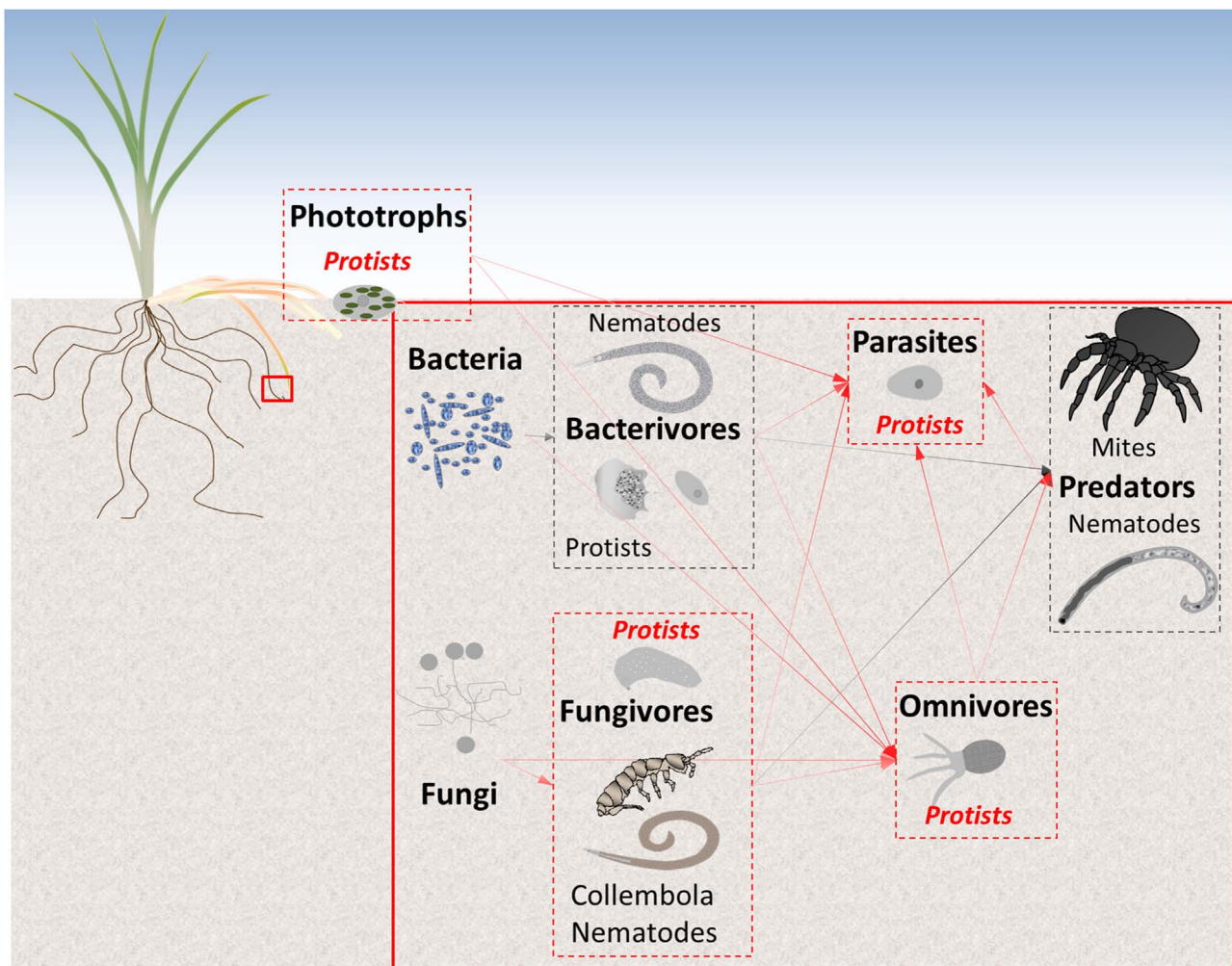


Fig. 1. The base of soil food webs with focus on the diversity of soil protists; red arrows connecting red boxes with italicized term *Protists*: previously non-considered nutrient flow from or to functional units of protists; grey: commonly used standard nutrient flow through the soil food web. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Note: Additional functional units of protists present in soils including mixotrophs and predators are not shown here; other groups of soil organisms (e.g. mites and collembolan) are also often more diverse than depicted in here; higher trophic levels omitted for simplification.

represent an important carbon input into soil systems that is only beginning to be appreciated (Jassey et al., 2015; Seppely et al., 2017). Non-surprisingly, classical cultivation based approaches have profoundly furthered our knowledge on soil protist functioning, showing that a taxonomically wide range of soil protist taxa are fungal feeders (Chakraborty and Old, 1982; Ekelund, 1998; Geisen et al., 2016; Heal, 1963; Petz et al., 1986), but their distribution in soil and functional importance are largely unknown (Fig. 1, red italicized). More recently, the discovery of omnivorous protists with a significant role as nematode predators (Bjørnlund and Rønn, 2008; Geisen et al., 2015b; Rønn et al., 2012), has dramatically changed our perception of microbial food webs and highlighted for the first time the importance of feedback loops in nutrient flows (Geisen, 2016a; Geisen et al., 2015b) (Fig. 1, red italicized).

3. Methodology to study soil protists

These examples focusing on protists illustrate the discrepancy in soil food web models that virtually have not changed since their introduction almost 30 years ago (Hunt et al., 1987); this is even more surprising taken into account the cumulative review article by Scheu (2002) proposing that methodological improvements should be implemented to study soil food webs 15 years ago. Biochemical methods, such as the analyses of phospholipid fatty acids (PLFA), have provided a

thorough understanding of abundances and a rough idea of the community composition of bacteria and fungi (Frostegård and Bååth, 1996; Frostegård et al., 1993). Despite commonly being applied, the usefulness of PLFAs to specifically study protists has been disproven as the 'protist markers', such as 20:2 ω 6c, 20:3 ω 6c, 20:4 ω 6c, are present in nematodes and other soil fauna (Ruess and Chamberlain, 2010).

Meanwhile, many methods have already been replaced by new approaches. Especially molecular tools now allow comparably non-expensive, user-friendly high-throughput analyses of soil organisms and have revolutionized our understanding of the abundances (qPCR approaches) and community structure (targeted amplicon high-throughput sequencing (AS)) of prokaryotic bacteria and archaea (Fierer et al., 2009; Leininger et al., 2006; Roesch et al., 2007) and fungi (Buée et al., 2009; Davison et al., 2015; Tedersoo et al., 2014). However protists, as the remaining third microbial group have received little attention (Bates et al., 2013; Lentendu et al., 2014), most prominently exemplified by the lack of molecular tools to reliably study abundances of the entity or even specific protist taxa. This is illustrated by the fact that even closely related protist species fundamentally differ in copy numbers of targeted barcode genes which makes copy-number to abundance information such as used in qPCR inapplicable at least to target a wider range of protists. More information is needed on the applicability of qPCR methods, but at present qPCR seems rather inapplicable to quantify most protist taxa if not rigorously tested with

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