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Soil protistology rebooted: 30 fundamental questions to start with

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ABSTRACT

Protists are the most diverse eukaryotes. These microbes are keystone organisms of soil ecosystems and regulate essential processes of soil fertility such as nutrient cycling and plant growth. Despite this, protists have received little scientific attention, especially compared to bacteria, fungi and nematodes in soil studies. Recent methodological advances, particularly in molecular biology techniques, have made the study of soil protists more accessible, and have created a resurgence of interest in soil protistology. This ongoing revolution now enables comprehensive investigations of the structure and functioning of soil protist communities, paving the way to a new era in soil biology. Instead of providing an exhaustive review, we provide a synthesis of research gaps that should be prioritized in future studies of soil protistology to guide this rapidly developing research area. Based on a synthesis of expert opinion we propose 30 key questions covering a broad range of topics including evolution, phylogenetics, functional ecology, macroecology, paleoecology, and methodologies. These questions highlight a diversity of topics that will establish soil protistology as a hub discipline connecting different fundamental and applied fields such as ecology, biogeography, evolution, plant-microbe interactions, agronomy, and conservation biology. We are convinced that soil protistology has the potential to be one of the most exciting frontiers in biology.

1. Introduction

Protists are everywhere, in aquatic and terrestrial ecosystems, free-living, and as symbionts (including parasites) of many organisms including humans. These usually single-celled or colonial microorganisms are by far the most diverse eukaryotes (Adl et al., 2012) and their species-numbers might easily exceed 10 million (Global Soil Biodiversity Atlas; www.globalsoilbiodiversity.org). Since the term 'protista' was introduced (Haeckel, 1866), profound taxonomic re-orderings have taken place. The vast majority of eukaryotic lineages has been shown to be protists, with the exception of the derived monophyletic multicellular lineages: animals, plants, and some fungi (Burki, 2014). Electron microscopy and molecular phylogenies have revealed that both algal and protozoan lineages are intermingled throughout the eukaryote phylogenies (Delwiche, 1999; Burki, 2014), and hence it is less confusing to use Haeckel's broader category of 'protist'. Similarly, the classical protozoan morphological categories: flagellates, testate and naked amoebae – but not ciliates - are not monophyletic but distributed across the eukaryotic tree of life (Adl et al., 2012). A snapshot of the immense morphological and phylogenetic diversity of soil protists is visualized in Fig. 1. We therefore recommend to use 'protist' as a term for all single celled phototrophic, mixotrophic and heterotrophic eukaryotes, with the exception of fungi.

The huge diversity of protist species has only recently become evident as many morphospecies recognizable under the microscope were shown to hide many cryptic species (Boenigk et al., 2012). This 'dark matter of biodiversity' suggests that protist taxon richness has been considerably underestimated. A recent study of environmental eukaryotic diversity based on state-of-the-art high-throughput sequencing (HTS) showed that protists are considerably more diverse than plants and animals in the sunlit zone of oceans (de Vargas et al., 2015). HTS studies of soil protists have shown a wide diversity of non-phagotrophic protists and the diversity of protists in soils is at least as diverse as that in aquatic systems e.g. (Bates et al., 2013; Geisen et al., 2015c). Nevertheless, soil protists are much less well studied than their aquatic counterparts and this gap is increasing (Fig. 2a).

Soil protists have received relatively little attention mainly due to methodological challenges, especially their isolation from the opaque soil matrix. These, however, do not entirely explain why soil protists are relatively less studied than other soil organisms, especially bacteria, fungi and nematodes (Fig. 2b). The volume of work on microbial bacteria and fungi far outweighs protist studies, possibly because of their direct role as primary decomposers, and they represent monophyletic groups that can more easily be studied with various targeted methodological approaches (Foissner, 1987; Mitchell, 2015). Even soil viruses have been subject to more studies than soil protists, despite being extremely challenging to study (Fierer et al., 2007) and their uncertain functional importance in soils. The under-studied nature of soil protists is exemplified by a comparison between research on protists and on soil archaea, a domain erected in 1990 and reported to be functionally important in soil only decade ago (Leininger et al., 2006; Bates et al., 2011). Historically studies mentioning soil protists in the title were eight times more abundant than those including archaea (Fig. 2b, Supplementary Table 2). However, in the last 15 years, this pattern entirely changed; studies on soil protists decreased by 15% while those on other common soil organisms