



Protist diversity on a nature reserve in NW England—With particular reference to their role in soil biogenic silicon pools



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ARTICLE INFO

Article history:

Received 3 December 2015

Received in revised form 2 February 2016

Accepted 3 February 2016

Keywords:

Protist

Population size

Diversity

Testate amoebae

Diatoms

Biogenic silicon

ABSTRACT

Soil protists play fundamental roles in many earth system processes, yet we are only beginning to understand the true diversity of the organisms involved. In this study we used conventional (microscopy-based) methods to characterise the diversity and estimate protist population sizes in soils from a variety of distinct habitats within Mere Sands Wood nature reserve in NW England. We produced population size data for over ninety soil protists belonging to two major eukaryotic functional groups: testate amoebae (TA) and diatoms, adding substantial 'cryptic diversity' to the nature reserves recorded biota. From these population size data we estimated relative contributions of TA and diatoms to soil biogenic silicon (BSi) pools and found significant correlations between taxon richness and the TA and diatom Si pool. This could indicate that protist functional diversity can influence terrestrial BSi pools, especially in early successional plant communities where TA and diatoms can potentially increase Si mineralisation and/or create Si 'hot spots' and hence, the biological availability of this element for subsequent plant uptake. TA were particularly abundant in mor humus type soils further supporting the idea that they could be important players in nutrient cycling in such soils. Overall, we demonstrate this is a useful approach in order to start to attempt to estimate the role of protists in the Si cycle and other ecological processes.

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1. Introduction

Over the last 40 years there has been a profound shift in the way in which many scientists view the role of life in the context of the whole Earth—from life being viewed as just inhabiting the planet, to it playing major roles in the workings of the Earth System. This systems view of the Earth mainly developed during the 1980s and 90s and was influenced by several sources; including the extra-planetary perspective that came from NASA's Apollo Missions and the Gaia hypothesis developed by James Lovelock and Lynn Margulis in the early 1970s (Hamilton and Grinevald, 2015). From the start what was to become Earth Systems science—especially as envisaged by the Gaia hypothesis put a strong emphasis on the role of microorganisms in the Earth system (Margulis and Lovelock, 1974). Lovelock (1993) also argued that soils made an interesting model for the planet as a whole, because life plays a major role in

constructing soils rather than merely adapting to abiotic soil conditions. Indeed the development of soils and the associated vegetation cover may have played significant roles in Earth history through the climatic effects of the weathering of soil minerals on the global climate (Schwartzman and Volk, 1989; Lenton et al., 2012). However, while clearly of crucial importance, the ecology of soils in general, and soil microbes in particular, was until recently somewhat understudied. As one of us wrote a few years ago: 'The soil is largely "out of sight" to an ecologist without a spade and, for much of the 20th century, this has meant that it was also 'out of mind' to most ecologists. At best, it tended to be treated as a black box, with the behaviour of its inhabitants lumped together under simple labels such as decomposers or nitrogen fixers' (Wilkinson, 2008). Even within microbial ecology soil protists have been far less studied than bacteria or fungi—although there are some signs that this is starting to change (Wilkinson et al., 2012). In some recent studies both traditional approaches (Finlay and Fenchel, 2001; Domonell et al., 2013; Geisen et al., 2014; Andriuzzi et al., 2016) and modern (Geisen et al., 2015; Lara et al., 2015) sequence-based analyses have been applied to study natural protist communities in soils.

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From before the full development of the current systems approach to global ecology it was known that life was sustained by the cycling of energy and chemical elements (e.g. Hutchinson, 1970), however a systems approach can be seen as putting particular emphasis on the merging of organismal and ecological physiology (Wilkinson, 2003, 2006). To understand such processes we need to be able to quantify microbial diversity, population sizes and biomass. Given that, as Nee (2004, p. 804) emphasised, 'the contribution of visible life to biodiversity is very small indeed' this is no small task—much of the life we need to quantify to understand the world is microscopic. This vast expanse of microscopic biological diversity forms part of what has been called 'cryptic diversity' and is not included in most conservation surveys (Esteban and Finlay, 2010). Indeed the microbial aspect of this cryptic diversity is seldom assessed in biodiversity surveys—it's unusual to have good data on even the small metazoan fauna and fungi (e.g. Corbet, 2011). One substantial and understudied aspect of this cryptic diversity in soils is composed of protists (Geisen et al., 2015). A number of papers from the 1950's to the 1970's provided some limited estimates of Testate amoebae production in soils—especially the work by Bonnet and Thomas (1955); Lousier and Parkinson (1984) and Schönborn (1965, 1978, 1983), this work is extensively summarised and evaluated by Wilkinson and Mitchell (2010). As Heger et al. (2014) have argued, there needs to be a resurgence in field research on microbial eukaryotes because this area of study is currently limited by the shortage of data on natural protist communities—especially heterotrophic protists.

In this study we constrain the problem to manageable proportions by considering just two functional groups of protists—testate amoebae (TA) and diatoms, and use the silicon (Si) cycle as an example of the potential importance of soil protists. Various pro- and eukaryotes are evolutionarily adapted to synthesise siliceous structures (biosilicification). These organisms use monomeric silicic acid (H_4SiO_4) for synthesis of biogenic silica, i.e. hydrated amorphous silica ($SiO_2 \cdot nH_2O$) (e.g. Ehrlich et al., 2010). In terrestrial ecosystems the accumulation of biogenic silica of microbial (bacteria, fungi), phytogenic (plants), protophytic (diatoms), protozoic (TA) and zoogenic (sponges) origin results in formation of corresponding biogenic Si (BSi) pools (Puppe et al., 2015; Sommer et al., 2006). TA form a polyphyletic group traditionally placed in the phylum Rhizopoda (Margulis and Chapman, 2009) but now split between two Eukaryote supergroups, the Amoebozoa (for the Arcellinida) and SAR (for the Euglyphida and other taxa with filose pseudopodia) (Adl et al., 2012). The members of the Euglyphida make self-secreted siliceous plates (idiosomes) (Ogden and Headley, 1980). The diatoms also form part of the SAR eukaryotic supergroup forming the Diatomea (classically the Bacillariophyta) in the classification of Adl et al. (2012). These are predominately marine or freshwater photosynthetic microbes with tests (frustules) formed from amorphous silica and so require dissolved Si for growth (Margulis and Chapman, 2009). Although primarily aquatic, in some situations they may be important for retaining BSi in soils and peats (Kokfelt et al., 2009; Alfredsson et al., 2015). Accumulation and recycling of BSi in terrestrial ecosystems influence fluxes of dissolved Si from the continents to the oceans, thus act as a filter in the global Si cycle (Dürr et al., 2011; Struyf and Conley, 2012). Although this biogenic control mechanism has been generally recognized for decades (e.g. Bartoli, 1983; Meunier et al., 1999; Struyf and Conley, 2012) quantitative information on particular terrestrial BSi pools are surprisingly rare (Sommer et al., 2006). We hypothesise that diversity of TA and diatoms differs within spatially heterogenic terrestrial ecosystems (i.e. various habitats within a single nature reserve) and this, in turn, leads to corresponding patterns in the protophytic and protozoic Si pools.

The aims of our work were: (1) to quantify soil protist diversity and population sizes in various habitats and (2) to investigate relationships between soil protist diversity and corresponding protophytic and protozoic Si pools.

2. Methods

2.1. Study site and sampling procedure

Mere Sands Wood (MSW) Nature Reserve (53°63'55" N, 2°83'71" W) is an artificial, post sand- mined catchment situated in the county of Lancashire in North West England. The soils of MSW have an interesting geological history and provide the best sections available for understanding the deposition of the Shirdley Hill Sands of Lancashire laid down during the late glacial and early post glacial periods (Chiverall et al., 2004). Sand extractors recognised the commercial value in the glass making industry and between 1974 and 1982 the site was quarried. Extracted areas were then landscaped into shallow-edged lakes. This spatially heterogeneous site is now managed as a nature reserve and is characterised by a series of artificially created lakes surrounded by deciduous and coniferous woodland with smaller patches of grassland, heathland and scrub. This is the first study investigating soil protists on the nature reserve. Field sampling was undertaken over two consecutive days in September 2011 and directed toward capturing the range of environmental variability within terrestrial habitats on the 42 ha reserve. Four broad habitat types were identified: (DW) early successional deciduous woodland comprised open Silver birch (*Betula pendula*) canopy with a ground cover of grasses (Poaceae spp.) and bryophytes on a sandy substrate, (CW) artificially planted mature Scots pine (*Pinus sylvestris*) woodland with ground cover comprised of male fern (*Dryopteris* spp.) and bramble (*Rubus fruticosus* agg.), (G) Mesotrophic grassland mainly comprised of grasses (Poaceae spp.) and Rushes (*Juncus* spp.) periodically grazed by sheep and (B) low silt island in the centre of a shallow lake used by roosting waterfowl and covered by bryophytes and Poaceae spp. A randomly placed quadrat (1 × 1 m) was placed within each habitat type and three replicate subsamples were taken at random from within it. Each sample comprised about 20 g of leaf litter (0–2.5 cm) and an equivalent amount from the soil horizon directly below the leaf litter horizon (2.5–5 cm). All samples were frozen prior to laboratory analysis.

2.2. Slide preparation and protist counting

2.2.1. Diatoms

A known weight of sample was oven-dried at 105 °C for 48 h. The range of sample used varied between 0.1 g for leaf litter to 1 g for samples with high mineral content. Diatom samples require digestion to remove organic matter. In this study diatom frustules were treated with 50 ml of 30% hydrogen peroxide (H_2O_2) to remove organic matter. Hydrochloric acid (10% HCL) was added to remove calcium carbonates and the supernatant was removed after >12 h of sedimentation. Samples were re-suspended and cleaned in 30 ml de-ionised water and a 0.3 ml aliquot of the diatom suspension was dried on a glass cover slip and the clean diatom valves were mounted in Naphrax. Diatoms were identified to species level and abundance was measured as the number of individuals per unit dry matter. Diatom frustules were counted under oil immersion at 1000× magnification using a Meiji Techno microscope. Where possible, a minimum of 400 frustules were counted and identified when more than half the valve was intact. As a result of the differences between aquatic and soil diatoms (Schuttler 1986; Lund 1946), the taxonomy of soil diatoms mainly followed that of Lund (1946). Micrographs illustrating how we

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