



## Additive partitioning of testate amoeba species diversity across habitat hierarchy within the pristine southern taiga landscape (Pechora-Ilych Biosphere Reserve, Russia)

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### Abstract

In order to better understand the distribution patterns of terrestrial eukaryotic microbes and the factors governing them, we studied the diversity partitioning of soil testate amoebae across levels of spatially nested habitat hierarchy in the largest European old-growth dark coniferous forest (Pechora-Ilych Biosphere Reserve; Komi Republic, Russia). The variation in testate amoeba species richness and assemblage structure was analysed in 87 samples from six biotopes in six vegetation types using an additive partitioning procedure and principal component analyses. The 80 taxa recorded represent the highest value of species richness for soil testate amoebae reported for taiga soils so far. Our results indicate that testate amoeba assemblages were highly aggregated at all levels and were mostly controlled by environmental factors rather than dispersal processes. The variation in species diversity of testate amoebae increased from the lowest to the highest hierarchical level. We conclude that, similarly to macroscopic organisms, testate amoeba species richness and community structure are primarily controlled by environmental conditions within the landscape and suggest that metacommunity dynamics of free-living microorganisms are driven by species sorting and/or mass effect processes.

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### Introduction

What are the diversity patterns of different groups of living organisms? How is this diversity generated and maintained? Answering these questions is a prerequisite for effective biodiversity preservation and assessment and mitigation of the

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effects of natural and human-induced environmental perturbations on biodiversity. However, the diversity of many groups of organisms is poorly documented, and this is especially true for soil microorganisms (Decaens 2010). Extensive data sets on soil microorganisms documenting their diversity but also allowing to assessing the factors potentially controlling their diversity and community patterns remain rare; existing data are mostly patchy, making it difficult to test ecological theories and to develop sound management policies for a major component of Earth's biodiversity.

The theoretical framework of metacommunity ecology (Leibold et al. 2004) considers that local communities are linked by dispersal of multiple interacting species and that patterns in species diversity are regulated by dispersal processes as well as environmental factors. Depending on the relative importance of these processes, four types of metacommunity dynamics can be distinguished: species sorting, mass effects, patch dynamics and the neutral model (reviewed by Holyoak et al. 2005). The species sorting dynamics is mostly related to niche processes, which assume that variation in community composition should be more strongly associated with environmental factors in regional contexts with high environmental variation than in those with low environmental variation (Heino 2011). Mass effect occurs when increasing dispersal in heterogeneous environments results in local populations being quantitatively affected by dispersal through source-sink dynamics, independent of environmental gradients. Dispersal limitation is more important in patch dynamics and the neutral model. The patch metacommunity dynamics implies a trade-off between dispersal capacity and competitive strength among species, whereas species are ecologically equivalent in the neutral model. Thus, an estimation of the contribution of dispersal processes and environmental factors to the species diversity of a particular area or habitat is necessary to assess the drivers of species diversity, which ultimately has practical implications for biodiversity management.

One of the ways to quantify the contribution of dispersal and local environmental conditions to the general species diversity of an area (or a region, or a habitat) ( $\gamma$ ) is to compare components of diversity that occur within ( $\alpha$ ) and among sampling units ( $\beta$ ) at hierarchical sampling scales or at the levels of a habitat hierarchy (Crist et al. 2003; Wagner et al. 2000). If the  $\alpha$  component contributes most to species diversity then variations in broad-scale processes are more important than local process and the number of species in each fine-scale area is only a predictable fraction of the broad-scale diversity. On the contrary, in cases where the  $\beta$  component is more important, then local processes strongly regulate local diversity, which will vary considerably from one site to another. This approach has been successfully applied to describe species diversity patterns in agricultural landscapes (Wagner et al. 2000), tropical forests (DeVries et al. 1997), temperate forests (Gering et al. 2003) and aquatic ecosystems (Schmera and Podani 2013). However, it has rarely been used for describing diversity patterns

of protists and other microorganisms (Cadotte 2006; Mazei 2008).

Biogeographical and macroecological patterns of microorganisms might differ fundamentally from those of larger organisms because of the smaller size, the presence of resting stages and quick reproductive rates which can considerably increase dispersal and colonisation abilities of microorganisms (Foissner and Hawksworth 2009; Fontaneto and Hortal 2012). Earlier views considered that these features could allow many microscopic organisms to attain cosmopolitan and ubiquitous distribution (De Wit and Bouvier 2006; Finlay 2002). In contrast, recent studies indicated that biogeographical and macroecological patterns of microorganisms might be similar to those observed for macroorganisms (Azovsky and Mazei 2013; Foissner 2006; Fontaneto and Hortal 2012). Our focus here is on testate amoebae, a common group of free-living amoeboid protozoa, which are characterised by the presence of a shell. Testate amoebae have a worldwide distribution and inhabit soils, aquatic ecosystems, mosses, etc. In soils, testate amoebae constitute a considerable part of biota in terms of biomass and biodiversity (Schröter et al. 2003) and they are considered as reliable indicators of micro-environmental characteristics (soil type, moisture, pH, etc.) (Mitchell et al. 2008). They prey on a wide range of organisms, including bacteria, protozoa, microalgae, fungi, and micro-metazoa, and may also consume dead organic matter (Gilbert et al. 2003; Wilkinson and Mitchell 2010).

The diversity of testate amoebae has been intensively studied in many regions including the taiga (boreal dark coniferous forest) zone (Bobrov et al. 1994; Schönborn 1986; Schröter et al. 2003). They also have been used as model organisms for studying spatial patterns of diversity distribution (Finlay et al. 2001; Mazei 2008). Although these studies provide useful information on the diversity of testate amoebae and its spatial patterns, most were conducted in strongly disturbed areas (but see Mazei et al. 2012) where the species diversity patterns might be biased, e.g. as a result of reduced biotope diversity and introduced species. Our objective was therefore to characterise the diversity patterns of testate amoebae in a very pristine old-growth dark coniferous forest in the Pechora-Ilych Biosphere Reserve (Smirnov 2013; Smirnova et al. 2006) and to estimate how the diversity is distributed across nested levels of habitat hierarchy. To this purpose we collected samples to cover the entire diversity of terrestrial vegetation types and biotopes existing in the area, using a hierarchically nested sample design (Gering et al. 2003). We analysed the variation in species richness and species structure of testate amoeba assemblages using an additive partitioning procedure and principal component analyses. We hypothesised that (i) the pristine forest will be characterised by greater species richness of testate amoebae than similar but less pristine taiga regions due to higher habitat diversity; (ii) species richness of testate amoebae will be strongly regulated by local environmental conditions (vegetation and habitat type) within the studied taiga landscape.

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