



Comparative ecology of vascular plant, bryophyte and testate amoeba communities in four *Sphagnum* peatlands along an altitudinal gradient in Switzerland



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ABSTRACT

Monitoring tools are needed to assess changes in peatland biotic communities and ecosystem functions in response to on-going climate and other environmental changes. Although the responses of soil organisms and plants to ecological gradients and perturbations do not always correlate, peatland monitoring is mainly based on vegetation surveys. Testate amoebae, a group of protists, are important contributors to carbon and nitrogen cycling in organic soils and are useful bioindicators in peatland ecology and paleoecology. There is however little comparative data on the value of testate amoebae, vascular plants and bryophytes as bioindicators of micro-environmental gradients in peatlands.

We compared the relationships of testate amoebae, bryophytes, and vascular plants with soil temperature, water table depth, micro-habitats and the carbon and nitrogen content of *Sphagnum* mosses in four peatlands along a 1300 m altitudinal gradient in Switzerland. We used the full diversity of vascular plants and bryophyte but only a selection of ten easily identifiable testate amoeba morpho-taxa (i.e. species or species-complexes).

Indirect and direct gradient ordinations, multiple factor analysis (MFA) and transfer function models for inferring water table depth showed that a selection of ten testate amoeba taxa are more powerful (% variance explained in RDA) and accurate (discrimination among habitats) indicators of local conditions (micro-habitat type, water table depth and *Sphagnum* C/N ratio) than the vegetation (vascular plants and bryophytes either individually or combined and considering the full diversity).

Our study showed that a limited list of ten easily identifiable testate amoeba taxa have higher bioindication value than the full bryophytes and vascular plants. Furthermore, testate amoebae can be analyzed on samples collected at any season (accessibility allowing and if precise sampling sites are well marked) – a clear advantage for biomonitoring and can be used to infer past changes from the peat record at the same taxonomic resolution. This simple approach could therefore be very useful for biomonitoring of peatlands.

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1. Introduction

On-going rapid climate change, largely attributed to the increase in greenhouse gas emissions (IPCC, 2013) has stimulated a considerable research effort on how biotic communities and related processes respond to these changes especially with respect to carbon (C) dynamics. Peatlands stock approximately the equivalent of 75% of total atmospheric C (Gorham, 1991). If actively growing they represent a significant C sink, but, when mineralization surpasses

accumulation (e.g. owing to drainage or climate-related drought) they become a C source (Moore and Knowles, 1989). Climate warming or precipitation decrease may reduce C sequestration even of pristine peatlands and limit the regeneration potential of damaged peatlands (de Jong et al., 2010; Samaritani et al., 2011), thus feeding back positively on warming (Arneeth et al., 2010; Belyea and Malmer, 2004). It is therefore important to assess how peatlands respond to environmental change both in their structure (e.g. communities) and function (e.g. hydrology, C-balance) (Davidson and Janssens, 2006).

A powerful approach to understanding the effects of environmental perturbation is to use bioindicators. As it is clearly not possible to study all living organisms in detail the question

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then is to determine which group of organism should be studied and what information they can provide. To answer this question comparative studies of different functional and taxonomic groups are required. Research on peatland ecology has historically focused primarily on vegetation and many assumptions on ecological gradients or functioning are made on the basis of vegetation patterns.

Some groups of peatland soil micro-organisms have been quite well studied in the last few decades (Gilbert and Mitchell, 2006), and especially the testate amoebae, a group of protists building a shell (called test). The shell allows relatively easy identification and is preserved in peat and in lake sediments thus making it possible to use them for paleoenvironmental reconstruction. Testate amoebae are well correlated to the main ecological gradients in *Sphagnum* peatlands, especially soil moisture (generally measured as water table depth), pH and nutrients (Booth and Zygmunt, 2005; Mieczan, 2009; Swindles et al., 2009). This has led to their use in the study of primary (e.g. palaeoecological records, Chambers et al., 2012; Charman, 2001; McMullen et al., 2004) and secondary succession (Talbot et al., 2010). Testate amoebae are increasingly considered as a useful tool for peatland bio-monitoring and management (Davis and Wilkinson, 2004; Mitchell et al., 2008; Turner and Swindles, 2012). Although the taxonomy of these organisms is not fully satisfactory, recent studies have also shown that they could provide valuable ecological information even at low taxonomic resolution (Mitchell et al., 2014).

Few studies have compared the community patterns of testate amoebae (or other soil microbes) and plants or their respective potential as bioindicators (see for example Hajek et al., 2011; Hajkova et al., 2011). The existing ones (in peatlands and pro-glacial succession) show some discrepancy between the community–environment relationships (Carlson et al., 2010; Lamentowicz et al., 2010) and transfer function model performance (Mitchell et al., 2013) of testate amoebae vs. bryophytes and/or vascular plants. In *Sphagnum*-peatlands, higher species–environment correlations were found for testate amoebae than for bryophytes, vascular plants or both combined (Lamentowicz et al., 2010), while transfer function performance (on raw data) was higher for bryophytes for DWT but not for pH (Mitchell et al., 2013). Here we address this question in four *Sphagnum* peatlands located along elevation gradient from the Swiss lowlands (ca. 600 m a.s.l.) to the subalpine–alpine limit (ca. 1900 m a.s.l.).

To our knowledge, there are only three published studies of testate amoeba communities along altitudinal gradients. In forests soils and mosses, between 400 m and 2500 m a.s.l. in Bulgaria Todorov (1998) showed that species richness decreased with altitude and that there was a significant difference among the biotopes. Mitchell et al. (2004) studied testate amoeba communities in a single moss species (*Hylocomium splendens* (Hedw.) W.P. Schimp.) in the northern Italian Alps between 1000 and 2000 m a.s.l. Community structure was found to be more strongly correlated to soil chemical composition (silica vs. calcareous) than to altitude and no significant decrease in species richness was found with altitude. Krashevskaya et al. (2007) studied the testate amoeba communities in litter and upper soil horizons of three sites in a tropical mountain forest at 1000, 2000 and 3000 m a.s.l. in Equator. Testate amoeba density was lowest at the mid altitude and highest at 3000 m a.s.l., with an opposite pattern for specific richness. However part of these differences may be due to soil type, which varied with altitude (aluminic Acrisol, gley Cambisol and Podzol, respectively from the lowest to the highest site) as well as vegetation. Indeed, testate amoeba diversity and community structure were shown to vary in relation to factors such as plant functional richness (Ledeganck et al., 2003) and soil type (Bonnet, 1964). These factors should therefore either be accounted for in numerical analyses, or excluded using appropriate sampling design.

Our goal here was not to specifically address diversity or ecological patterns along this elevation gradient but by studying an altitudinal gradient we aimed to simulate a change in temperature (synchronic approach) while focusing on the same specific micro-habitats of *Sphagnum*-dominated peatlands. We covered a broader range of habitats at each elevation than Mitchell et al. (2004) while still remaining in comparable biotopes at each study site, unlike other two cited elevation gradient studies. We aimed to answer two main questions: (1) How do the relationships between testate amoebae, bryophytes and vascular plants and the main micro- and macro-ecological gradients compare and thus what are their respective predictive power for these variables? (2) How powerful are these three groups for discriminating among different micro-habitats along the whole humidity gradient (pool to hummock) within sites? As developing taxonomy expertise represents a true limitation for the use of protists in biomonitoring, rather than using the full community we addressed these questions using a selection of 10 morpho-taxa that can easily be identified by untrained analysts after a short learning period.

2. Methods

2.1. Study sites

We selected four sites in the same meso-climatic region (transition from Swiss Plateau to pre-Alps), in the northern Swiss Alps (canton Bern, Fig. 1). All sites are legally protected at least since 1987 and are categorized as open bogs in the Swiss Federal bogs and mires inventory (Ecker et al., 2008). The four study sites are located along an altitudinal gradient from 580 m a.s.l. to 1890 m a.s.l. The regional climate is temperate continental; only the lowest site (Lörmoos, Table 1) is slightly drier and warmer than the other three, being less influenced by higher rainfall associated to mountains. General climatic data was obtained from MeteoSwiss, the Swiss Federal Office of Meteorology and Climatology. The two lower sites have been impacted by peat harvesting and/or cattle grazing, but the upper two are considered to be relatively pristine (i.e. as close as can be in Switzerland).

2.2. Sampling design and fieldwork

Plots were selected in autumn 2010 in the main micro-habitats within each study site: pool, pool edge, dry hollow, lawn, hummock, and dry hummock, with five replicates per micro-habitat in most cases and three at the minimum (total: 19–25 plots per site and 84 overall). Pools were missing in Lörmoos owing to the general dryness of the site. As Lörmoos was particularly dry in autumn 2010 and no pools with standing water existed, we selected the lowest microtopography habitats and called them “hollows” to differentiate them with the pools with standing water that existed in the other sites. These hollows were indeed the wettest microsites in Lörmoos. In Rotmoos the “pool edge” micro-habitat was clearly defined, with specific vegetation, owing to the steeper slope between the lawns and the pools. Percentage cover of vascular plants and bryophytes were estimated according to the Londo scale (Londo, 1976). Nomenclature follows Lauber et al. (2007) for vascular plants and Jahns (2007) for bryophytes. *Sphagnum* species were identified, first in the field and identifications were confirmed by microscopy following Daniels and Eddy (1990).

An iron bar was inserted in each plot to obtain a time-integrated measurement of the depth of water table (DWT). The bars were left for ten to twelve months (September to November 2010–August 2011). The DWT was estimated as the vertical distance between the top of the moss carpet and the limit between the rusted and

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