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Sphagnum-dwelling Testate Amoebae in Subarctic Bogs are More Sensitive to Soil Warming in the Growing Season than in Winter: the Results of Eight-year Field Climate Manipulations

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***Sphagnum*-dwelling testate amoebae are widely used in paleoclimate reconstructions as a proxy for climate-induced changes in bogs. However, the sensitivity of proxies to seasonal climate components is an important issue when interpreting proxy records. Here, we studied the effects of summer warming, winter snow addition solely and winter snow addition together with spring warming on testate amoeba assemblages after eight years of experimental field climate manipulations. All manipulations were accomplished using open top chambers in a dry blanket bog located in the sub-Arctic (Abisko, Sweden). We estimated sensitivity of abundance, diversity and assemblage structure of living and empty shell assemblages of testate amoebae in the living and decaying layers of *Sphagnum*. Our results show that, in a sub-arctic climate, testate amoebae are more sensitive to climate changes in the growing season than in winter. Summer warming reduced species richness and shifted assemblage composition towards predominance of xerophilous species for the living and empty shell assemblages in both layers. The higher soil temperatures during the growing season also decreased abundance of empty shells in both layers hinting at a possible increase in their decomposition rates. Thus, although possible effects of climate changes on preservation of empty shells should always be taken into account, species diversity and structure of testate amoeba assemblages in dry subarctic bogs are sensitive proxies for climatic changes during the growing season.**

Key words: Bogs; climate; open top chambers; *Sphagnum*; subarctic; testate amoebae.

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Abbreviations: OTC, open top chambers.

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Introduction

Understanding of climate-ecosystem relationships is important for development of paleoclimate reconstruction techniques and estimation of possible effects of climate change. It has been shown that climate changes can considerably affect all levels of ecological organisation, including ranges of species distribution, community composition and ecosystem functioning (McCarty 2001; Norf et al. 2007; Traill et al. 2010; Walther et al. 2002). Ecosystem responses to climate change will greatly depend on the considered range on environmental conditions because the rates of many biological processes have unimodal relationships with physical parameters (Shaver et al. 2000). This means that effects of climate change will vary seasonally and spatially being positive when environmental parameters are shifted in the direction to the optimum and negative otherwise. Thus, providing the complexity of climate-ecosystem relationships, studies on seasonal and spatial variation of climatic effects are necessary for reliable estimation of climate impacts on ecosystems.

High-latitude bog ecosystems are known to be very sensitive to climate conditions because their functioning is primarily controlled by temperature and precipitation (Moore and Bellamy 1974). Climate models predict that, during this century, both average temperature and annual precipitation in the sub-Arctic will increase and the greatest increase in those factors will take place in winter (Christensen et al. 2007). These changes can affect all components of bog ecosystems including diverse and abundant assemblages of *Sphagnum*-dwelling testate amoebae. Testate amoebae are shelled protozoa which play an important role in food webs as decomposers of organic matter and as a trophic link between bacteria and invertebrates (Gilbert et al. 1998; Wilkinson and Mitchell 2010). They are valuable bioindicators and are widely used for paleoclimate reconstructions (Charman 2001; Mitchell et al. 2008; Tolonen 1986). *Sphagnum*-dwelling testate amoebae represent good model organisms for studying climate effects because of their small size and short-generation times which allow testing hypotheses in an experimental set-up. In addition, testate amoebae have specific distribution along *Sphagnum* stems in response to vertical gradients of light, temperature, moisture, oxygen, etc. (Mitchell and Gilbert 2004) so they can be used for estimation of spatial variation of climate effects. However, the relationships between testate amoeba assemblages in *Sphagnum* and climate remain poorly understood and usually are not differentiated among seasonal components of climate.

Changes in seasonal climate can affect both living and empty shell assemblages of *Sphagnum*-dwelling testate amoebae in the sub-Arctic. Increased temperatures during the growing season can either increase or reduce abundance of living organisms depending on whether the temperature shifts towards or away from the ecological optimum (Savage et al. 2004). Higher summer temperatures may have even stronger effects on abundance through changes in species diversity and assemblage structure (Beveridge et al. 2010; Ives 1995; Jiang and Morin 2004; Petchey et al. 1999). In addition, summer warming may affect testate amoebae via decreasing temperature-dependent moisture, especially in dry biotopes, because testate amoebae in *Sphagnum* are known to be strongly controlled by moisture availability in summer (Lamentowicz and Mitchell 2005; Mitchell et al. 1999). Increased winter precipitation can lead to a thicker snow cover and, as a consequence, more favourable temperatures for testate amoebae in *Sphagnum* possibly resulting in a greater abundance. Besides, a thicker snow cover can also affect environmental conditions at the beginning of the subsequent spring by delaying the onset of the growing season or changing soil moisture (Lamentowicz et al. 2010; Maxwell 1992). However, higher spring temperatures can counteract such a shortening of the growing season and increase soil moisture due to snow melt (Maxwell 1992). These changes can positively affect testate amoeba abundance and shift assemblage composition towards predominance of hydrophilous species as a result of favourable moisture and temperature regimes. The effects of both increased winter precipitation alone and in combination with spring warming can be long-lasting so that the effects can be detected during the subsequent growing season. Empty shell assemblages can be also affected by the changes in the climate parameters through shifts in the living testate amoeba assemblages and/or by altering biological decomposition (Wilkinson and Mitchell 2010).

So far, there has been a lack of in situ experimental studies on relationships between testate amoebae and climate. Most previous field climate manipulation experiments were aimed at studying responses of soil testate amoeba assemblages to warming or increased precipitation separately, were focused on changes in summer climate only and did not last longer than one growing season (Beyens et al. 2009; Lousier 1974a, b; Tsyganov et al. 2011). Although these experiments are important