



Successional change of testate amoeba assemblages along a space-for-time sequence of peatland development

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Received 8 June 2018; received in revised form 17 July 2018; accepted 18 July 2018
Available online 24 July 2018

Abstract

It is well established that in ombrotrophic bogs, water-table depth (WTD) is the primary environmental control on testate amoeba distribution. However, the environmental controls on testate amoebae in minerotrophic fens are less well known and successional change in their assemblages associated with fen-bog peatland development has been scarcely investigated. Here we investigate a peatland space-for-time sequence resulting from postglacial rebound on the west coast of Finland, to assess successional patterns in testate amoeba communities and their relationships with environmental variables during peatland development. Sample sites along a 10-km transect from coast to inland ranged from a recently emerged wet meadow to a mature bog. Environmental variables (e.g., peat thickness, carbon and nitrogen content, pH, WTD and vegetation) were measured alongside testate amoeba samples. Results showed that even though the distribution of testate amoebae was to some extent determined by the succession stage, many taxa had wide WTD and pH ranges. The primary environmental control for many taxa changed along the succession. In conclusion, the ecological constraints on testate amoebae in minerotrophic systems are more complex than in bogs. The detected patterns also complicate the use of testate amoebae as a primary proxy in palaeoecological reconstructions where fen-to-bog shifts occur.

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Keywords: Ecological constraints; Fen environment; Peatland succession; Testate amoebae

Introduction

Testate amoebae are widely used to (semi)quantitatively reconstruct past environmental changes and, in particular, changes in hydrological conditions (Amesbury et al. 2016;

Booth 2008; Charman et al. 1999; Lamarre et al. 2013; Zhang et al. 2017). Understanding their ecology is important in the development and application of these techniques. A new pan-European dataset (Amesbury et al. 2016) as well as many other previous studies on bogs from Eurasia (e.g. Bobrov et al. 1999; Qin et al. 2013; Väiliranta et al. 2012; Woodland et al. 1998), North America (e.g. Booth 2008; Charman and Warner 1992) and South America (e.g. Swindles et al. 2014; van Bellen et al. 2014) have indicated that peatland water-table depth is the most important

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factor determining testate amoeba community composition in ombrotrophic systems. The strong relationship between taxa composition and hydrology allows reconstructions of past changes in bog water-table depth conditions based on a transfer function approach where fossil assemblages are modelled against modern assemblages with known ecological constraints. To date, testate amoeba response to other environmental variables such as pH or trophic status has been less thoroughly investigated, with the exception of limited transfer function studies on pH (e.g., Lamentowicz and Mitchell 2005; Lamentowicz et al. 2008) or nutrient status (Dudová et al. 2013; Lamentowicz et al. 2013a), although many studies have referred to the likely importance of these factors (Booth et al. 2008; Jassey et al. 2014; Kroupalova et al. 2013; Mitchell et al. 2008; Tolonen et al. 1992; Woodland et al. 1998). An increasing number of studies infer that pH is an important determining factor for testate amoeba composition in many peatland systems (Lamentowicz et al. 2007, 2011; Opravilová and Hájek 2006; Payne 2011).

The fen-bog transition, one of the key landscape changes of the Holocene (Hughes and Barber 2003; Väiliranta et al. 2017), shows obvious pH and nutrient status succession and provides important opportunities to study the corresponding responses of various biological organisms. Successional changes in plant species composition over the fen-bog transition are well known based on palaeoecological as well as spatial chronosequence studies (Hughes and Barber 2003, 2004; Klínger and Short 1996; Ronkainen et al. 2014; Tuittila et al. 2013; Väiliranta et al. 2017). However, successional change in other organisms during mire development is much less well understood (see however Larmola et al. 2014; Merilä et al. 2006) with a relatively limited amount of data concerning the succession of testate amoeba communities (Galka et al. 2017; Jassey et al. 2011; Lamentowicz et al. 2010, 2013b; Opravilová and Hájek 2006; Payne 2011).

Here, we aim to define successional changes in testate amoeba assemblages during peatland development and link taxa distribution to different environmental variables. We hypothesise that testate amoebae show a clear successional pattern in their community structure during mire development. Unlike previous successional studies (e.g., Hughes and Barber 2003, 2004), which are based on downcore sediment analysis, in this study we use a space-for-time approach. The space-for-time approach is justified because the changes in site type which occur over our spatial transect relate closely to downcore changes in preserved vegetation remains seen over the fen to bog transition in previous studies (Hughes and Barber 2003; Väiliranta et al. 2017). By using this approach, we: i) avoid the loss of decomposition-prone taxa, and ii) can directly measure environmental variables. In addition, we aim to improve the level of understanding of ecological constraints of testate amoeba in fen environments.

Material and Methods

Study area

The study area is located on the western coast of Finland in Siikajoki (SJ) commune (64°45'N, 24°42'E) (Fig. 1). The region represents the middle boreal ecoclimate zone. The mean annual temperature and precipitation are 2.6 °C and 539 mm respectively and the length of the growing season is 150 days (observation period 1979–2009; Revonlahti, Siikajoki, 64°41'N, 25°05'E, 48 m a.s.l., Finnish Meteorological Institute). Primary paludification is an ongoing process in the area and postglacial land uplift has created a space-for-time sequence of peatlands.

Seven study sites (SJ0–SJ6; Table 1) form a 10-km long transect from the coast to inland. They have been selected to represent different stages of mire development, with SJ0 being a newly formed shoreline meadow (ca. 50 years) and SJ6 being a fully developed bog community with an estimated age of ca. 3000 years (Table 1). In between there are young minerotrophic meadows and fens a few kilometres from the shore.

The vegetation at site SJ0 was dominated by graminoids (e.g., *Festuca rubra*, *Calamagrostis stricta*, *Carex glareosa* and *Juncus gerardii*), with very few bryophytes present. Site SJ1 was a wet meadow with a patchy cover of brown mosses such as *Warnstorfia* spp. At SJ2, bryophytes were more extensive and *Sphagnum* mosses occurred as patches among brown mosses. Otherwise, both SJ1 and SJ2 were dominated by sedges and grasses such as *Carex nigra* and *Agrostis canina* while the forbs *Comarum palustre* and *Lysimachia thyrsoiflora* were also common. Sites SJ3 and SJ4 were featured by mesotrophic and oligotrophic fen vegetation, respectively. At both sites, the vegetation consisted mainly of sedges (e.g., *Carex chordorrhiza*, *Carex rostrata* and *Carex limosa*), but dominant forbs at SJ3 and SJ4 were *C. palustre* and *Menyanthes trifoliata* respectively. Hummock formation with very dense *Sphagnum* carpets was evident at the edges of both SJ3 and SJ4. Site SJ5 was at the fen-bog transition stage with a mosaic of clearly ombrotrophic hummock surfaces with *Rubus chamaemorus*, *Empetrum nigrum*, *Vaccinium oxycoccos* and *Sphagnum fuscum* and wetter surfaces dominated by *Scheuchzeria palustris*, *Carex livida*, *C. limosa* and *C. chordorrhiza*. *Sphagnum* species accustomed to different water-table depths formed a continuous moss layer. Site SJ6 was an ombrotrophic bog, characterised by *S. fuscum*, *Sphagnum angustifolium* and dwarf shrubs such as *E. nigrum* and *Rhododendron tomentosum* at the hummock surfaces and *Sphagnum balticum* and *Eriophorum vaginatum* in wetter depressions. The modern spatial mire succession series realistically mimics the historical (vertical) peatland development pattern where initial minerotrophic plant communities are, over the course of time, replaced by bog plant communities (Tuittila et al. 2013).

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