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Re-assessing the vertical distribution of testate amoeba communities in surface peats: Implications for palaeohydrological studies

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Abstract

Testate amoeba-derived transfer functions are frequently used in peatland palaeohydrological studies and involve the development of training sets from surficial peats. However, within acrotelmic peats, considerable vertical variation in assemblage composition can occur, particularly along *Sphagnum* stems, which may limit the representation of the associated 'contemporary' testate amoeba samples as analogues for the peatland surface. This paper presents contiguous testate amoeba assemblage data from nine monoliths collected from different peatland microforms (hummock, hollow, lawn) in three *Sphagnum* dominated ombrotrophic peatlands in Ontario and Quebec, eastern Canada. The aim is to: (i) gain a greater understanding of the vertical distribution of xerophilous/hygrophilous taxa along *Sphagnum* stems; (ii) determine the vertical extent of live/encysted taxa along this gradient; and (iii) assess the significance of this distribution on surface sampling protocols. The results show that testate amoeba communities in the uppermost acrotelmic peat layers display considerable variability. This may reflect a complex interplay of abiotic and biotic controls, including moisture, temperature, light and other characteristics, food availability, and mineral particle availability for test construction. These findings underline the complexity of testate amoeba community structure and highlight the importance of analysing both living and dead *Sphagnum* stem sections when developing calibration sets.

Keywords: Encystment; Live taxa; Microforms; *Sphagnum* peatlands; Testate amoebae; Vertical zonation

Introduction

Testate amoebae have been widely used as proxies for hydrological change and for inferring palaeoenvironmental conditions in peatlands (e.g. Hendon et al. 2001; Lamentowicz et al. 2015; Loisel and Garneau 2010; Payne et al. 2011; Swindles et al. 2009). Surface wetness reconstructions are commonly inferred from transfer functions, which aim to model the relationship between contemporary testate amoeba assemblages and depth to water table (Charman et al. 2007; Hendon and Charman 2004; Woodland et al. 1998). These are in turn applied to down core assemblages in contemporary peatland sites. However, it has long been known that considerable variability exists within testate amoeba communities in surficial peat layers (Buttler et al. 1996; Heal 1962; Mitchell et al. 2008). The ecology of testate amoebae inhabiting *Sphagnum* stems and in surficial peats has been shown to be controlled by a number of physi-

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cal parameters, for example, moisture, light, food resources, temperature and the availability of mineral material for test construction (Booth 2002; Charman et al. 2000; Heal 1962; Meisterfeld 1977; Mieczan 2010).

Below the surface, the acrotelm represents the aerobic uppermost layer of peatlands and varies in depth from between 5–50 cm, whereas the underlying catotelm has a lower rate of residual peat decay (Belyea and Clymo 2001; Clymo 1984). The vertical depth of the acrotelm is dependent upon surface microtopography (e.g. hummock, hollow and lawn microforms), the interaction between water tables and processes of peat accumulation (Belyea and Clymo 2001; Quinty and Rochefort 2003; Rydin and Jeglum 2006). However, the concept of two distinctive layers is arguably too simplistic, as the acrotelm contains anaerobic sections and aerobic channels that can extend into the catotelm via vascular plant roots (Hayward and Clymo 1983; Morris et al. 2011). Notwithstanding this, the boundary between the acrotelm and catotelm has been considered to occur at the minimum water table in summer (Clymo 1984). Other criteria that have been used to distinguish the boundary include changes in humification (Charman et al. 1999) and bulk density of the peat (Yu et al. 2003). The acrotelmic layer also shows considerable internal variation. The organic material here may be fibrous or pseudofibrous (with plant remains such as stems, rhizomes and root matter recognisable), or may be lost but the peat may still retain integral structure. As mosses and other plant communities die, fibrous material is added to the peat, providing physical structure for the new upwards growth of mosses (Malmer et al. 1994). Decomposing litter content also varies within the oxic, acrotelmic peat layers, and changes with depth, eventually becoming covered in the catotelm by rising water tables (Rydin et al. 2006).

In order to quantify hydrological changes within peatlands through transfer function models, modern analogues of testate amoeba assemblages must be sampled from these surficial peats. A number of methodological approaches have been employed to achieve this. In many European studies, for example, the uppermost 1 cm of surficial peat has been used to process testate amoeba samples after the removal of the *Sphagnum* capitulum (e.g. Swindles et al. 2009; Woodland et al. 1998). This narrow vertical interval has been selected to ensure that a sample representing only the very recent period is obtained. A slightly modified approach was applied by Swindles et al. (2015) in which the entirety of the green (living) moss fraction and 1 cm of the underlying brown *Sphagnum* were sampled. In other studies, assemblages have been characterised by identifying an ‘upper’ surficial peat section, which comprised living, vertical *Sphagnum* stems, and a ‘lower’ section, comprising brown, humified *Sphagnum* with collapsed stems (e.g. Booth 2002; Schönborn 1963). Such studies have aimed to explore vertical variations in assemblage composition in regions where there is considerable thickness of living *Sphagnum* present. The study of Booth (2002), for example, which was undertaken in Michigan, USA, involved sampling the entire green *Sphagnum* layer and a ~10 cm^3 lower sample from immediately below the green stems. In this case only the lower samples were included in the training set used for calibration model development (Booth 2002).

In spite of the large number of studies that have examined surficial peat samples, the vertical distribution of *living* testate amoeba communities in surficial *Sphagnum* stems remains largely unexplored, but is critical for understanding species–environment relationships. Environmental gradients (e.g. moisture) have been shown to control the vertical variation of ‘live’ and ‘dead’ assemblages, which can be distinguished through the staining of living protoplasm with Rose Bengal (Meisterfeld 1977, 1978; Scott and Medioli 1980; Schönborn 1963). Light appears to be a particularly important factor influencing the distribution of species containing symbiotic zoochlorellae, such as *Archerella flavum* (Gilbert and Mitchell 2006; Mazei and Bubnova 2007; Schönborn 1963). Similar symbiotic species include *Hyalosphenia papilio* and *Heleopera sphagni*, which live in the chlorophyllous upper few centimetres of peatlands (i.e. living green stems) to enable photosynthesis of algae to occur. Taxa that use xenosomes to build tests such as *Difflugia* spp., *Trigonopyxis arcula* and *Centropyxis* spp. have been observed in lower stem positions (Payne and Pates 2009) than idiosomic taxa such as *Euglypha* spp. (Heal 1962; Schönborn 1962).

Testate amoebae also have the ability to encyst for long periods of time (Foissner 1987; Ogden and Hedley 1980). However, there is a limited understanding of the vertical distribution of encysted testate amoebae and the potential factors controlling this state, as encysted species have typically not been distinguished from live or dead individuals in most modern (i.e. surficial peat) and palaeoecological studies (Jassey et al. 2011; Vincke et al. 2004). Encystment is nevertheless considered to be a response to unfavourable environmental conditions such as desiccation (Booth and Zygmunt, 2005; Lousier 1974; Woodland et al. 1998), frost (Mitchell et al. 2000; Warner et al. 2007) or decreases in food availability (Laminger and Sturn 1984). One challenge in understanding how testate amoeba communities respond to such unfavourable conditions relates to a lack of seasonal monitoring of species–environment relationships. A notable exception was a study by Sullivan and Booth (2011) who employed data loggers to measure relative humidity within the upper few centimetres of *Sphagnum* stems in 11 peatlands in Pennsylvania and Wisconsin, USA. The results were used to determine the influence of short-term environmental variability on testate amoeba communities. This study has highlighted the role of surface vegetation, as well as changes in precipitation and evapotranspiration in controlling sub-annual variation in testate amoeba community composition.

Many other studies have examined testate amoeba assemblages from short (<50 cm) cores collected from acotelmic peats to reconstruct recent hydrological change. Testate amoeba-inferred water table fluctuations from dated cores