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Testate amoebae as functionally significant bioindicators in forest-to-bog restoration

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ABSTRACT

In north-west Europe, large areas of open peatland have been drained and planted with spatially homogenous stands of non-native conifers. The detrimental impact of afforestation on peatland carbon and biodiversity have led to large-scale attempts to restore these landscapes back to their open, tree-less form. The responses of dominant microbial consumers – testate amoebae – to peatland forest-to-bog restoration are largely unexplored. We studied changes in testate amoebae with forest-to-bog restoration in the largest expanse of blanket bog in the UK and compared testate amoeba communities in relatively undisturbed open bog with forested and forest-to-bog restoration sites. Forested areas contained testate amoeba communities which were functionally different from open bog, characterised by a lack of mixotrophic taxa known to contribute to primary production. Seventeen years after restoration management, the microbial communities in the forest-to-bog sites remained more similar to forested areas than to the open bog community. Our results suggest that afforestation has reduced the trophic level of testate amoeba communities, which are only beginning to recover post-restoration in the wettest areas where *Sphagnum* has re-colonized. This study also highlights the need to consider a wide-range of reference sites to encompass the natural variability within ombrotrophic blanket bog. We conclude that testate amoebae have the potential to act as functionally-significant bio-indicators in peatlands undergoing forest-to-bog restoration.

1. Introduction

Afforestation is one of the most widespread vegetation changes currently occurring in peatlands worldwide (Lachance et al., 2005). While large areas of the world's peatlands are naturally forested, many areas of naturally tree-less peatlands are being drained for forestry. In north-west Europe much of this afforested peatland is blanket bog. Blanket bogs are predominantly tree-less peatland ecosystems mostly occurring in temperate, hyperoceanic regions (Gallego-Sala and Prentice, 2012; Lindsay et al., 1988; Moore, 2002). These geographically restricted ecosystems store globally-significant quantities of carbon (Gorham, 1991) and are important for biodiversity by providing habitat for unique assemblages of species adapted to the wet and acidic conditions (Bonn et al., 2016). Like many peatlands, blanket bogs have been widely exploited for fuel, agriculture and forestry, threatening biodiversity and carbon storage (IUCN, 2016).

The British Isles hold a significant proportion (~20%) of the global blanket bog resource (Tallis, 1998). Between the 1940s and 1980s up to 20% of UK blanket bogs were planted with non-native conifers (Stroud et al., 1987). Afforestation involved drainage by ploughing and ditch-cutting and planting with the conifers Lodgepole pine (*Pinus contorta)* and Sitka spruce (*Picea sitchenisis)* (Anderson et al., 2000). This afforestation of deep peat was essentially prohibited in the 1990s primarily due to concerns about impacts on birds (Stroud et al., 1987). For instance, losses of key conservation-priority species such as the European Golden Plover (*Pluvialis apricaria*) have been associated with edge effects surrounding forestry plantations (Wilson et al., 2014). More recently the impact of drainage on peatland carbon stock has also become an increasing concern. It is likely that water table drawdown following afforestation may promote peat mineralisation leading to carbon losses to the atmosphere and watercourses (Lindsay, 2010).

It is now widely recognised that peatlands in relatively good condition deliver a range of benefits to society, including: climate mitigation, flood prevention, provision of fresh water, support of biodiversity, as historic archives and for recreation opportunities (IUCN, 2016). Land use changes such as the afforestation of blanket bogs have the potential

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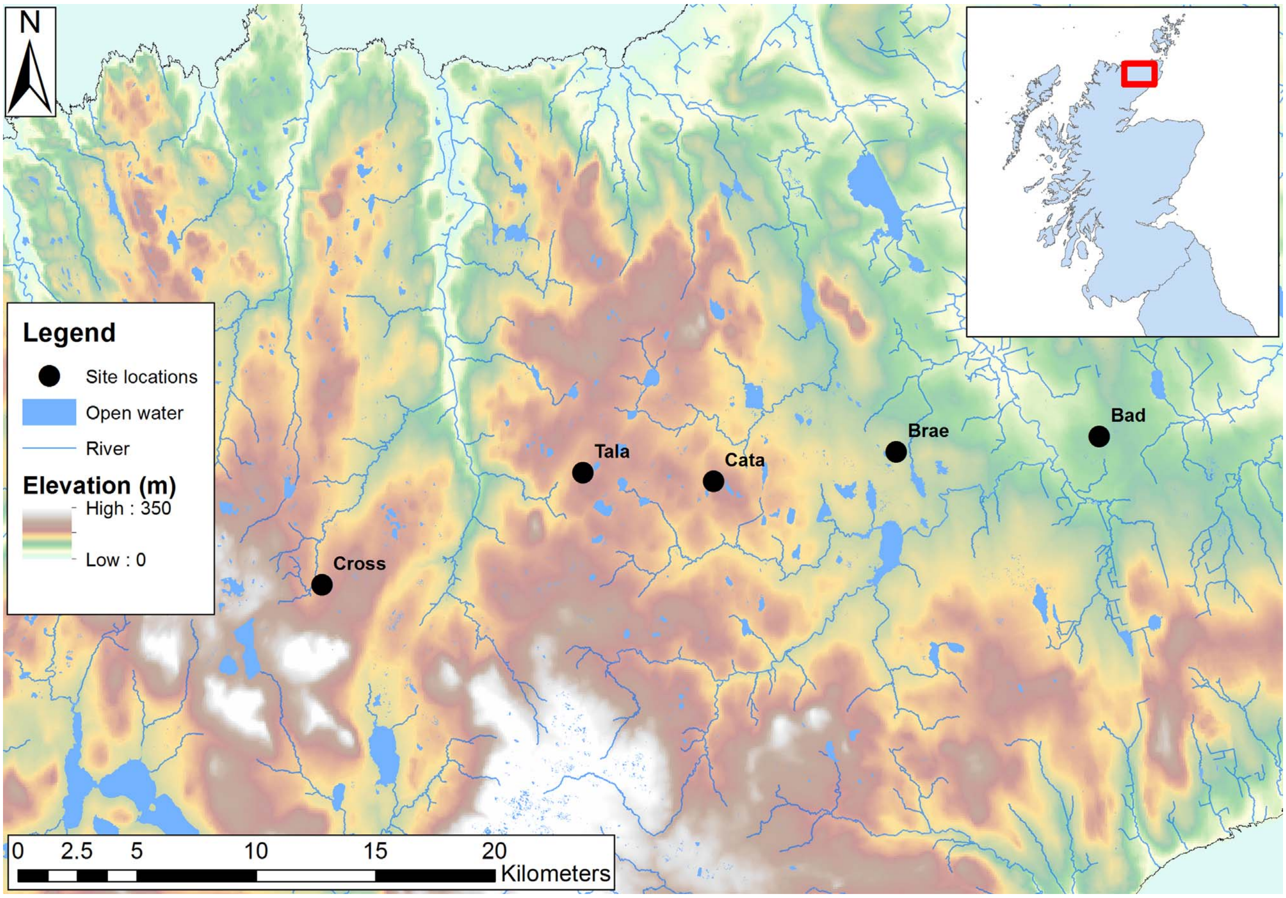

Fig. 1. Location of sampling sites in this study.

to erode these benefits, with significant costs to society (Bonn et al., 2014). Large investments are now being made in peatland restoration with some of the most intensive schemes focused on the restoration of afforested blanket bog back to a more natural tree-less state. Forest-to-bog restoration typically involves tree-felling and ditch-blocking to raise the water table, with more recent trials also including whole tree harvest and furrow blocking.

Impacts of peatland afforestation on macroscopic organisms are relatively well-known with birds and plants particularly well-studied (Stroud et al., 1997; 1998; Lachance et al., 2005; Wilson et al., 2014). However impacts below-ground have seldom been explored. Many studies emphasize the need to integrate microbial communities in the evaluation of restoration in peatlands yet, our understanding of responses to these often large and rapid land-use changes is still fragmentary (Andersen et al., 2013a; Andersen et al., 2013b; Elliott et al., 2015; Swindles et al., 2016; Nwaishi et al., 2015). This is surprising given that peatland restoration is often justified in terms of carbon storage and biodiversity. Microorganisms constitute both the vast majority of species in peatlands and play crucial roles in carbon and nutrient cycling. Reduction of carbon losses can only be achieved if the imbalance between higher net primary productivity (NPP) by plants and lower decomposition by microbial communities can be restored (Andersen et al., 2013a, 2013b, 2013c).

Testate amoebae form a polyphyletic group of unicellular eukaryotes exhibiting a shell (test), traditionally placed in the phylum Rhizopoda (Margulis and Chapman, 2009) and now split between three major unrelated groups (Kosakyan et al., 2016). As microbial consumers considered to feed on bacteria, fungi, microalgae, ciliates, rotifers and nematodes (Yeates and Foissner, 1995; Gilbert et al., 1998; Jassey et al., 2013a) they are a key element in the functioning of peatland ecosystems playing an important role in carbon and nutrient cycling (Wilkinson and Mitchell, 2010; Rydin and Jeglum, 2013; Jassey et al., 2013b). These protists are widely-used as sensitive indicators of peatland surface moisture conditions and have been the focus of contemporary (Koenig et al., 2015; Sullivan and Booth, 2011; Lamentowicz and Mitchell, 2005; Lamentowicz and Obremska, 2010) and palaeoenvironmental studies (Booth, 2002; Payne et al., 2006; Charman et al., 2007). While testate amoebae have been used as peatland restoration indicators in several previous studies (Buttler et al., 1996; Jauhiainen 2002; Davis and Wilkinson, 2004; Vickery 2006; Laggoun-Défarge et al., 2008; Valentine et al., 2012), we are aware of only one study which evaluates the use of testate amoebae as bio-indicators following blanket bog restoration (Swindles et al., 2016), and none which consider forest-to-bog restoration.

Functional traits (FT's) of testate amoebae have particular potential as restoration indicators (Fournier et al., 2012) and indicators of environmental change in peatlands (Fournier et al., 2015). Recently, traits such as mixotrophy and aperture position/size have been reported to be potentially useful proxies of disturbance in *Sphagnum* peatlands (Marcisz et al., 2016). Recent research investigating FT's in naturally forested peatlands suggests afforestation could lower the trophic level of testate amoeba communities and reduce the contribution of mixotrophic taxa to primary production (Payne et al., 2016). Jassey et al. (2015d) highlight the potential importance of such effects for peatland carbon dynamics. However the functional response of testate amoebae to afforestation is not known, nor whether these changes are reversible.

The aims of this study were 1) to evaluate how testate amoebae respond to forest-to-bog restoration and 2) to assess whether they could be used as microbial indicators of disturbance and recovery. We used a multi-site approach to encompass the natural variability in blanket bog at the landscape scale, and within the blanket bog between different micro-topographic features. The following hypotheses were tested: