



Short-term response of testate amoebae to wildfire



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ABSTRACT

Many peatlands are exposed to intermittent burning but the implications of this burning for microbial communities have been little-studied. Here we consider the impacts of burning on the dominant protists of peatland ecosystems, the testate amoebae. To do this we used a 'natural experiment', a peatland exposed to wildfire where fire-fighting activity left a combination of unburned and heavily burned areas in close proximity. We assessed the change in testate amoebae three days after the end of the fire. We find that burning led to a large change in taxon composition, primarily noted by a shift from taxa with tests constructed of idiosomes to those constructed of xenosomes. The most likely explanation for this change is the direct destruction of mostly idiosome tests by extreme heat. Although we did not differentiate live individuals from empty tests it is probable that the fire led to a significant change in the testate amoeba community. This change may have interesting implications for the structure of microbial food webs, for biogenic silica cycling and for palaeoecological reconstruction in burned peatlands. This is clearly a topic which deserves more research attention.

1. Introduction

Natural fire is a complex process that plays an important role in terrestrial ecosystems as a driver of biodiversity (Williams et al., 2002; Andersen et al., 2005), soil carbon sequestration and stocks (Garnett et al., 2000; Turetsky et al., 2002), biogenic silica cycling (Unzué-Belmonte et al., 2016) and landscape heterogeneity (Turner et al., 1994). The impacts of fire on above-ground biodiversity are relatively well-understood (Gill, 1996), but impacts below ground have been much less studied (Ahlgren, 1974; Odion et al., 2004; Murphy et al., 2006). Palaeoecological records demonstrate that, despite high surface wetness, peatland ecosystems are exposed to wildfire with relative frequency (e.g. Kuhry, 1994) and in some regions peatlands are deliberately burned as a land management tool (Davies et al., 2008; Ward et al., 2007; Clifford and Booth, 2015).

A key group of soil protists in peatland ecosystems is the testate amoebae (TA) which constitute a large proportion of total microbial biomass and play an important functional role as microbial top predators (Gilbert et al., 1998; Wilkinson and Mitchell, 2010; Creevy et al., 2016). There are reasons to suppose that fire might have important impacts on peatland TA community compositions but there is currently very little direct evidence (Turner and Swindles, 2012;

Wanner, 2012).

It may be expected that burning would have an immediate negative effect on TA due to heat-induced mortality but long-term consequences may be more complex. In a New Zealand hill soil Stout (1961) found that the initial effect of wildfire was a partial sterilization of the soil but recovery in soil fauna was relatively rapid (> 3 months) and top-soil protist diversity was actually increased by nutrient inputs. The impacts of burning are likely to be highly dependent on the heat and depth of burning which differ between managed, burning and wildfire (Davies et al., 2008; Ward et al., 2007; Clifford and Booth, 2015). In the context of managed burning showed that transient fire had little impact on soil TA abundance (Wanner and Xylander, 2003; Wanner, 2012). Soil micro fauna was found alive in the upper soil layers immediately after burning and the community remained relatively constant over post-fire periods up to 9–12 months. However, in a northern English moorland, Turner and Swindles (2012) showed considerable spatial variability which was partially explained by burning. Fire may also have indirect impacts on TA through impacts on hydrology, as shown by palaeoecological data (Marcisz et al., 2015).

Here we took advantage of an unusual fire event in a Chinese peatland to conduct a controlled study of the immediate impact of wildfire on TA assemblages. We hypothesized that the heat of burning

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would produce detectable impacts on TA assemblage through direct destruction of tests.

2. Methods and materials

2.1. Sites, experiment design and sampling

The site for this study is a poor fen with a mean pH of 5.6, located near the middle reach of Nanwenghe River in northeastern China (Supplementary Fig. 1). The vegetation in the fen is dominated by vascular plants including *Carex* sp., *Sphagnum* sp. and *Phragmites australis*, while *Betula platyphylla* dominates in forest located about 200 m northwest from the fen.

It was extremely dry in northeast China from the end of spring to early summer 2012, which led to some intense wildfires. In June 2012 the site was subject to an intense fire which destroyed much of the surface vegetation. The fire was extinguished by a group from the Chinese army leaving the site divided between burned and unburned areas offering an ideal opportunity to study impacts on the soil biota. We sampled the site three days after the fire.

Our study consisted of two sub-components. In experiment 1 we considered the central area affected by the fire and extracted five samples in each of the burned and unburned areas ($n = 10$). The boundary of burning reflects the point at which firefighters were able to control the fire, rather than any intrinsic difference in flammability. There is nothing to suggest any differences between unburned and burned areas prior to burning. In experiment 2, we considered the margin of the peatland where the wildfire left a mosaic of burned and unburned areas. Here we conducted paired sampling by selecting ten points each with a burned and an adjacent unburned spot ($n = 20$).

In the field we collected about 50 g of the upper 2 cm of moss or peat which was sealed in plastic bags and refrigerated till analysis. A sub-sample of this sample (ca. 20 g) was used for testate amoeba analysis.

2.2. Laboratory analyses

Samples were prepared following a modified version of the method of Hendon and Charman (1997) involving i) disaggregation in boiling water; ii) sieving to remove coarse material using a 300 μm sieve; iii) centrifugation at 3000 rpm for 5 mins; iv) adding 1–2 drops of Safranin (red color) for staining, followed by further centrifugation; and v) storage in water. The back-sieving step advocated by Hendon and Charman (1997) was omitted (Avel and Pensa, 2013; Payne, 2009; Mazei et al., 2015). Samples were analyzed microscopically at 400x magnification and tests identified following a range of standard literature (Charman and Wanner, 1997, 1999, 2008; Booth, 2001; Mazei and Tsyganov, 2006; Swindles et al., 2009; Lamentowicz et al., 2010; Markel et al., 2010). At least 100 tests per sample were enumerated, following Payne and Mitchell (2009).

Taxonomy partly follows the conservative approach of Charman et al. (2000) with the exception of a few rarer taxa not included in that guide, and the *Cyclopyxis arcelloides* type which was split into two morphotypes representing larger and smaller taxa with broadly 'bowl-shaped' tests (Meisterfeld, 2002; Mazei and Tsyganov, 2006). We attempted to differentiate empty tests from those with cytoplasm, however the samples from the burned locations were difficult to observe under the microscope due to abundant fine degraded organic matter which meant that we could not always be confident of the accuracy of this differentiation. We ultimately decided to group all tests for data analysis. The remaining sample not used for TA analysis was split in two parts; one half was weighed and dried to determine moisture content and the other half suspended in deionized water for pH measurements using a Hanna EC-214 pH meter.

2.3. Numerical analyses

In analyzing the data we first addressed whether burning affected the TA diversity of the samples. We considered two widely-used measures of diversity: the total species (taxon) richness and the Shannon diversity index (H), which incorporates a measure of evenness. In experiment 1 we tested for differences using the non-parametric Mann-Whitney U test. In experiment 2 we tested for differences using Wilcoxon signed-rank tests to account for the paired sampling structure. The two experiments were conducted in different areas of the peatland but results show little evidence for differences in TA assemblage (see below); therefore, as our sample size is comparatively small (total $n = 30$), we also analyzed a combined dataset from both experiments using Mann-Whitney tests. We next considered the overall TA assemblage structure.

We first explored the overall structure of the data using a non-metric multi-dimensional scaling (NMDS) ordination based on Bray-Curtis dissimilarity (Beals, 1984; Bray and Curtis, 1957). We used redundancy analysis to test for differences between burned and unburned treatments while accounting for potentially co-varying factors (pH and moisture). Species data were Hellinger-transformed prior to analysis and significance tested using permutation tests (999 permutations). We tested for difference in assemblage based on each experiment individually and all experiments combined, with and without co-variates. As our experimental design does not include replication of treatment, our samples are arguably pseudo-replicates rather than true replicates; results should be interpreted in this light.

3. Results

3.1. Testate amoebae diversity

Across all analyzed samples the most abundant taxa were *Cyclopyxis cassis* type, *Cyclopyxis arcelloides* type (large) and *Euglypha strigosa* type. Most taxa in this study are widely distributed in peatlands and organic soils around the world (Charman and Warner, 1997; Booth, 2001; Mitchell et al., 1999; Payne et al., 2008; Swindles et al., 2009; Lamentowicz et al., 2010; Markel et al., 2010; Lamentowicz et al., 2015). Both the species present and the community composition are broadly consistent with other studies from Chinese peatlands (Table 1) (Li et al., 2010; Qin et al., 2012; Song et al., 2014). However, a few taxa like *Hyalosphenia papilio* and *Archerella (Amphitrema) flavum*, which are abundant in the present study and in other northern hemisphere peatlands, have been rarely reported in southern China (Qin et al., 2011, 2012). In addition, *Hyalosphenia papilio* and *Argygnia dentistoma* have been reported only recently from peatlands in China (Qin et al., 2013; Li et al., 2015).

3.2. Differences between burned and unburned areas

There were no significant differences in species richness with burning in either experiment individually or overall (Experiment 1: Mann-Whitney $U = 6.5$, $p = 0.24$, Experiment 2: Wilcoxon $W = 32$, $p = 0.25$, Overall: $U = 107$, $p = 0.83$) (Fig. 1a–c). Overall H was significantly lower in the burned points (Overall: Mann-Whitney $U = 48$, $p = 0.008$) (Fig. 1d). This difference was, however, relatively small with the H of burned points on average 0.43 lower. The same trend was evident in both experiments but the difference was not significant when analyzed separately (Experiment 1: Mann-Whitney $U = 3$, $p = 0.06$; Experiment 2: $W = 40$, $p = 0.22$, Fig. 1e–f). There was no significant difference in moisture content or pH between burned and unburned points in either experiment separately or both combined (Moisture overall: $U = 89$, $p = 0.34$; Moisture Experiment 1: $U = 10$, $p = 0.68$, Moisture Experiment 2: $W = 42$, $p = 0.14$, pH overall: $U = 76$, $p = 0.13$; pH experiment 1: $U = 7.5$, $p = 0.34$; pH experiment 2: $W = 36.5$, $p = 0.36$).

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