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Testate Amoeba Communities of Epilithic Mosses and Lichens: New Data from Russia, Switzerland and Italy

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Abstract. The testate amoebae (TA) of many potential habitats around the world have been barely investigated but data on species presence and abundance is essential to answering big questions about microbial biogeography and the diversity of protist life. One such habitat lacking basic data is epilithic mosses and lichens with only a small number of samples analysed in previous studies and no systematic attempt to understand potential environmental controls. We use a large dataset (n = 81) from sites in Russia, Switzerland and Italy to demonstrate that testate amoebae in this habitat are both abundant and diverse. The community of our samples was dominated by ubiquitous taxa and differed between the northern (Russia) and southern (Switzerland and Italy) sites, perhaps due to differences in climate or air quality. Community composition, concentration and diversity were explained by moisture content but not by elevation above the ground surface and there were no significant differences between communities of mosses and lichens. Surprisingly our data showed a significant difference between communities of epiphytic and epilithic lichens in the same region sampled at the same time. Our study adds to the evidence that moisture availability is a critical factor in structuring testate amoeba communities across habitats and highlights the paucity of knowledge of TA in many environments.

Key words: Arcelllinida, Euglyphida, bryophytes, lichens, ecology, biogeography.

INTRODUCTION

Testate amoebae are a polyphyletic group of protists characterised by shells ('tests') which are often strikingly distinctive. Testate amoebae (TA) occur widely in freshwater and aquatic ecosystems (Mitchell *et al.* 2008; Qin *et al.* 2011), can constitute a large proportion

of microbial biomass (Gilbert *et al.* 1998) and are likely to perform important roles in biogeochemical cycling (Wilkinson and Mitchell 2010) but the communities of many habitats have been little studied (Foissner 1999). Testate amoebae are particularly abundant in habitats dominated by mosses but most mosses examined have been terricolous (e.g. Beyens *et al.* 1986; Mitchell *et al.* 2004) with the *Sphagnum* mosses of peatlands particularly well-studied (Mitchell *et al.* 2008). Here we consider the TA of epilithic mosses and lichens, which we take to mean growing on solid rock, typically elevated above the ground surface. The communities of

epilithic mosses and lichens are particularly interesting as with reduced opportunity for nutrient supply from the substrate there is likely to be a strong link between the TA community and the atmosphere. We are aware of only a few samples which have been analysed from this habitat, and these are primarily from high latitude environments with limited alternative sampling locations (e.g. Smith 1992, Todorov and Golemansky 1996). It is likely that this habitat may harbour novel communities of TA which have yet to receive systematic study. Here we consider the testate amoeba communities of a large number of epilithic moss and lichen samples from sites across Europe; assess their variability and provide an initial examination of some factors which may be important in structuring the community. Our study forms a companion to a recently-published study of testate amoeba communities of forest epiphytes (Payne *et al.* 2015). On the basis of that study, data from other moss-dominated habitats and what is known of TA ecology more generally we hypothesise that:

– Epilithic mosses will host diverse TA communities.
– TA diversity will decline with elevation above the ground surface.
– Variability in TA communities will be explained by moisture content.
– TA communities of lichens will be less diverse and abundant than those of mosses.
– TA communities of epilithic mosses will not differ from those of epiphytic mosses.

MATERIALS AND METHODS

81 samples were taken from the Karelia region of western Russia (66.5°N, 32.9°E; 26 samples), the Baikal region of Siberia (51.6°N, 103.6°E; 32 samples), the Swiss city of Neuchâtel (47.0°N, 6.9°E; 15 samples) and the Veneto region of Italy (45.5°N, 11.5°E; 8 samples). The dataset reported here has been developed incrementally and opportunistically as part of several research projects and as a consequence is somewhat heterogeneous including a diverse range of sites. The Swiss site is urban, the Italian site rural but ad-

Table 1. Relative abundance of most numerous testate amoeba taxa (> 1% total) by sampling region.

Taxon	Relative abundance (%)				
	Karelia	Neuchâtel	Veneto	Baikal	Overall
Arcella arenaria compressa	0.1	4.6	0.3	3.0	2.1
Assulina seminulum	8.0	0.2	0.1	3.3	3.9
Centropyxis aerophila	1.4	21.3	23.4	10.2	10.7
Centropyxis aerophila shagnicola	2.9	1.4	15.3	1.4	3.2
Corythion dubium	32.0	1.0	0.6	9.8	14.4
Euglypha ciliata glabra	1.7	5.9	3.6	3.0	3.2
Euglypha cristata	6.6	0.0	0.0	0.5	2.3
Euglypha laevis	3.1	0.0	0.0	0.5	1.2
Euglypha rotunda	4.4	6.0	2.5	1.7	3.4
Euglypha strigosa	0.5	1.2	0.4	1.8	1.1
Euglypha strigosa glabra	0.2	4.2	0.7	1.0	1.3
Heleopera sylvatica	0.0	6.9	5.6	1.1	2.3
Nebela parvula	4.6	0.0	0.0	0.1	1.5
Nebela tincta	0.0	0.0	0.0	3.9	1.6
Phryganella acropodia	2.3	10.0	8.0	22.4	12.2
Phryganella hemisphaerica	5.2	13.6	11.3	11.4	9.8
Tracheleuglypha dentata	0.4	0.0	0.0	3.7	1.6
Trinema complanatum	1.2	4.1	3.4	2.5	2.5
Trinema enchelys	11.7	1.3	7.7	5.4	6.9
Trinema lineare	5.5	0.4	3.1	1.8	2.8
Trinema penardi	0.3	6.4	1.7	0.2	1.5

jacent to the city of Vicenza and the Russian sites remote but some of the Karelia samples are exposed to marine influence. Geologies vary, the Swiss site is the only one in which the rock was quarried rather than natural, and the Karelia site the only one in which lichens as well as mosses were encountered in the sampling locations. There is a strong contrast between colder and less-polluted sampling regions in Russia and warmer and more-polluted sites in Italy and Switzerland (Supplementary Table 1).

In each region 3–11 sampling locations were identified and a frame (100 × 100 mm) placed over the rock and gently scraped to remove all epiphytes. The substrate type (moss/lichen) was recorded in the field and moisture content determined by drying at 110°C for six hours and re-weighing the samples. Mosses and lichens were not identified to species level; this is a limitation of our study given that different species may harbour distinct microbial associations with different food sources available for testate amoebae (e.g. Bay *et al.* 2013). In all regions other than Veneto multiple samples were taken at a variety of elevations above the ground surface (typically 50, 100 and 150 cm). Samples for TA analysis were prepared following the method described in Mazei *et al.* (2011). 1 cm^3 of sample was soaked in water, stirred, filtered at 500 μm and examined using a BIOMED-2 microscope with tests identified following Mazei and Tsyganov (2006). From the raw data we calculated test concentration, taxon richness and Simpson diversity.

To explore the overall structure in the dataset and compare between regions we used a non-metric multi-dimensional scaling (NMDS) ordination on Bray-Curtis dissimilarity (Bray and Curtis 1957). We used redundancy analysis (RDA) on Hellinger transformed species data to test for correlations with moisture and elevation (excluding the Veneto samples) while accounting for difference between the four sampling regions.

To test for differences in the univariate data between regions we used ANOVA with Levene's test for equality of variances and Tukey's test for post-hoc comparisons, or the non-parametric Kruskal-Wallis test for data which did not meet the requirements of ANOVA. To test for correlations with moisture content we used Spearman's Rs.

To determine whether there were differences between the TA communities of epilithic and epiphytic mosses and lichens we also considered a dataset composed of the Karelia samples from this study and the samples of epiphytes from the same region extracted at the same time considered by Payne *et al.* (2015; total n = 48). We used NMDS to examine this dataset and tested for differences using ANOSIM (9999 permutations; Clarke 1993). We tested for differences in univariate indices using t-tests.

To determine whether there were any differences between TA communities of epiphytic lichens and mosses we compared samples from the Karelia region where both mosses and lichens were sampled (n = 23). We excluded samples in which both mosses and lichens were present and compared the data using Mann-Whitney tests for richness, diversity and concentration data, and ANOSIM for compositional data.

RESULTS

51 taxa were identified in the 81 samples (Supplementary Table 1) with assemblages dominated by small euglyphids such as *Corythion dubium* (14.4% of all tests) and arcellinids such as *Centropyxis aerophila* (10.7%), *Phryganella hemisphaerica* (9.8%) and *Phryganella acropodia* (12.2%). The NMDS ordination (Fig. 1) suggests some differences between the assemblages of the sampling regions: Veneto and Neuchâtel show considerable similarity but Karelia is distinct with lower scores on axis one; Baikal overlaps both of these groups (Fig. 1). ANOSIM shows the difference between regions to be statistically significant (global test R_{ANOSIM} = 0.35, P < 0.001) with the difference between Karelia and other regions the only significant difference in pairwise comparisons (Bonferroni-corrected P < 0.001; other comparisons P > 0.05). The species abundance data (Table 1) suggests that an important factor in distinguishing Karelia from the other sites is the high abundance of *C. dubium* which is much rarer in Veneto and Neuchâtel in particular. Conversely, *C. aerophila* has much higher relative abundance in Italy and Switzerland than in Russia, and particularly Karelia. There was no significant difference in taxon richness and Simpson diversity amongst regions (ANOVA, P > 0.05). However, test concentration did vary (Kruskal-Wallis K = 24.8, P < 0.001) with significant difference between the Russian and more southern regions (Mann-Whitney pairwise comparisons P < 0.05; Fig. 2).
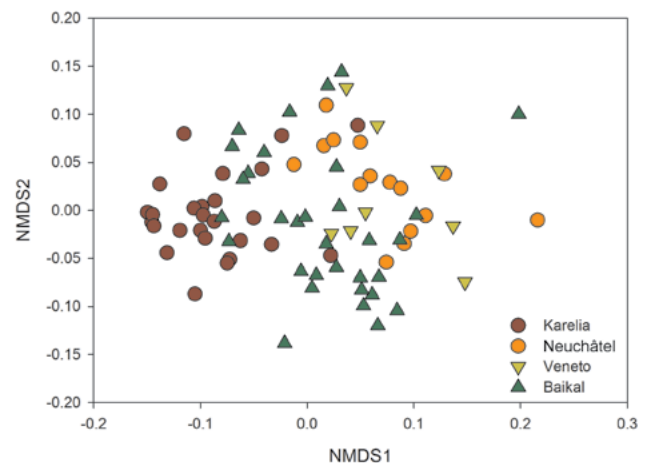

Fig. 1. NMDS ordination of testate amoeba relative abundance data from epilithic mosses and lichens (Bray-Curtis dissimilarity).
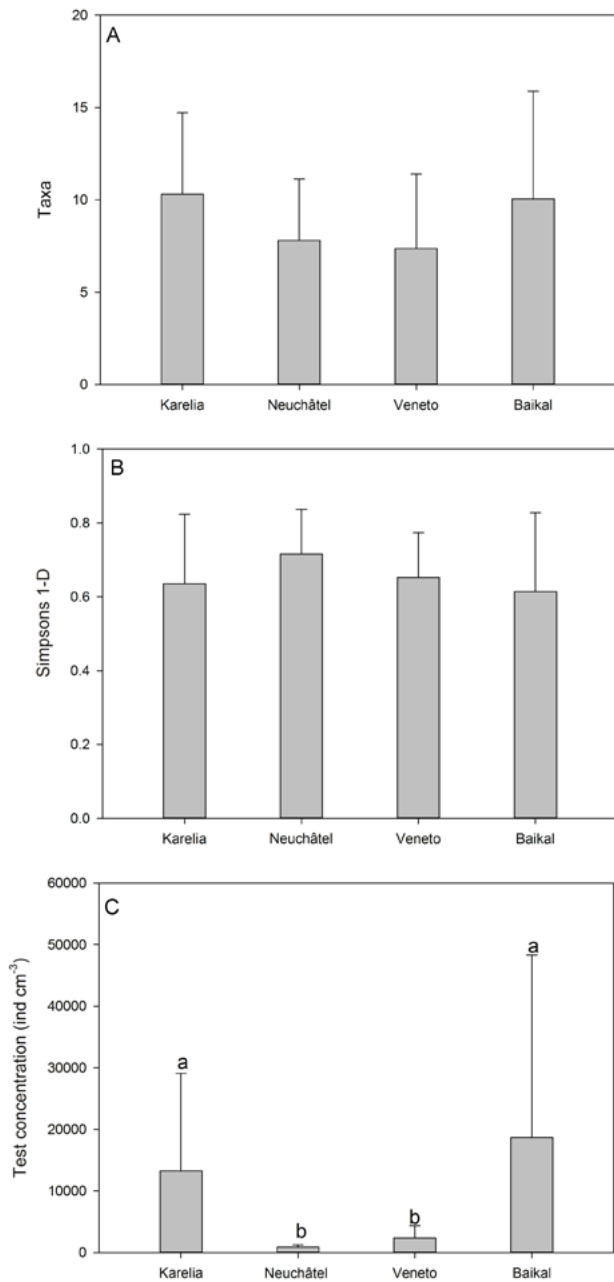
Fig. 2. Taxon richness (A), Simpson diversity (B) and test concentration (C) by region. Bars show mean and error bars the standard deviation. Letters denote significant differences (P < 0.05) where the global test is significant, see text for details.

Across all the sites with data there was no significant correlation between sample elevation on the rock and test concentration, taxon richness or Simpson diversity (Spearman's Rs P > 0.05, n = 73). This remained the case when breaking the dataset down by region, although for the Karelia data correlations with test concentration and Simpson diversity were only marginally non-significant (P = 0.06). Elevation did not explain significant variance in the compositional data (RDA; P > 0.05).

There were significant correlations between substrate moisture content and taxon richness (Rs = 0.40, P < 0.001) and test concentration (Rs = 0.57, P < 0.001) but not Simpson diversity. Broken-down by region there was a significant correlation with test concentration in Karelia (Rs = 0.4, P = 0.03) and with taxon richness (Rs = 0.62, P < 0.001) and test concentration (Rs = 0.63, P < 0.001) in Baikal but other correlations were non-significant (Fig. 3). In redundancy analysis moisture explained a significant (P = 0.001) but minor (3.5%) proportion of variance.

Comparing samples from lichens and mosses in the Karelia region we found no significant difference in taxon richness, Simpson diversity or test concentration (t-test P > 0.05) and also no difference in community structure (ANOSIM P > 0.05).

ANOSIM showed a modest but significant difference between the communities of epiphytic and epilithic mosses and lichens in Karelia (R_{ANOSIM} = 0.17, P = 0.001). An NMDS shows epiphytic samples typically having lower scores on axis two and a group of five epiphytic samples having notably low scores on axis one (Fig. 4). This difference was most sharply noted in the *Corythion* species which overall are more than twice as abundant in the epiphytic samples than the epilithic samples. In particular *Corythion orbicularis* averaged 19.5% of tests in the epiphytic samples and only 1.5% in the epilithic samples. Taxon richness (Mann-Whitney U = 72, P < 0.001), Simpson diversity (Mann-Whitney U = 110, P < 0.001) and concentration (Mann-Whitney U = 181, P < 0.001), were significantly higher in the epilithic samples (Fig. 5). One possible explanation for this result is difference in substrate so we repeated all analyses with only samples from lichens (n = 30). Results were generally weaker but remained significant for most tests (composition R_{ANOSIM} = 0.18, P = 0.01; richness Mann-Whitney U = 16, P < 0.001; Simpson diversity U = 36, P = 0.002) other than concentration for which there was no significant difference (Mann-Whitney U = 67, P = 0.08).
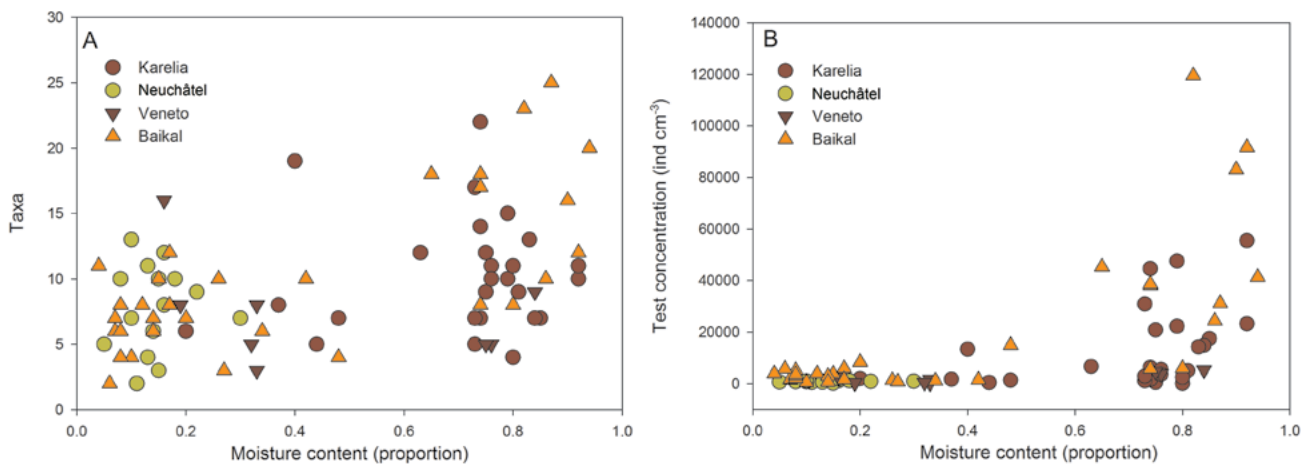
Fig. 3. Taxon richness (A) and test concentration (B) against moisture content expressed as a proportion.
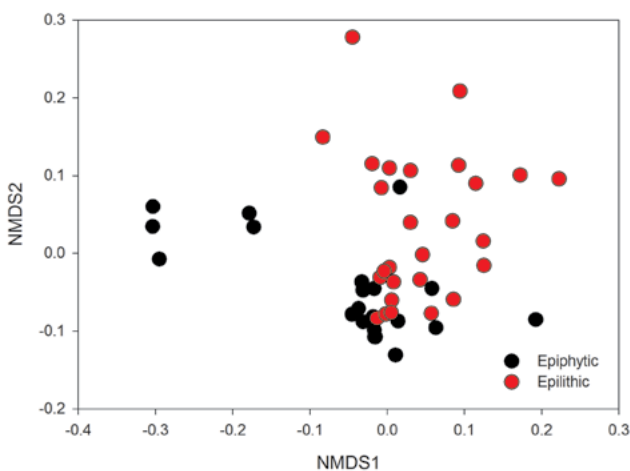

Fig. 4. NMDS ordination of testate amoeba relative abundance data from epilithic and epiphytic vegetation of the Karelia region (Bray-Curtis dissimilarity).

DISCUSSION

Our results show that epilithic mosses host diverse and abundant communities of testate amoebae. The community of this habitat is primarily composed of widely-dispersed/ubiquitous species although a few less-frequently reported taxa such as *Cyphoderia schonborni* are present (Supplementary Material 2). The community composition and test concentration differed between regions although the identity of the species present remained similar. The data suggest the most significant differences are between the two more southern regions (Veneto and Neuchâtel) and the two more northern regions (Karelia and Baikal). There are several possibilities for this result including differences in geology, climate and air quality. Testate amoebae have been shown to respond to several pollutants which differ between the northern and southern sites (Meyer *et al*. 2012; Nguyen-Viet *et al*. 2004; Payne *et al*. 2010, 2012a, b; Supplementary Table 1). There is also experimental evidence of testate amoeba sensitivity to temperature (e.g. Jassey *et al*. 2011) but our study does not include sufficient regional-scale replication to untangle these effects.

The data suggest links between substrate moisture content and test concentration, taxon richness (more weakly) and community composition (very weakly). The importance of moisture has not been previously demonstrated in this habitat. However, this is a relatively unsurprising result as studies across multiple habitats have shown strong correlations with moisture (Charman 2001) and similar results were found for epiphytic mosses by Payne *et al*. (2015). Our data do not suggest changes in TA community with elevation above the ground surface. This result defied our expectation that concentration and diversity would decline, as previously found by Payne *et al*. (2015). Our hypothesis was based primarily on an assumption substrate moisture would decline with elevation but our data do not show this to be the case – there is no significant correlation ($P > 0.05$).
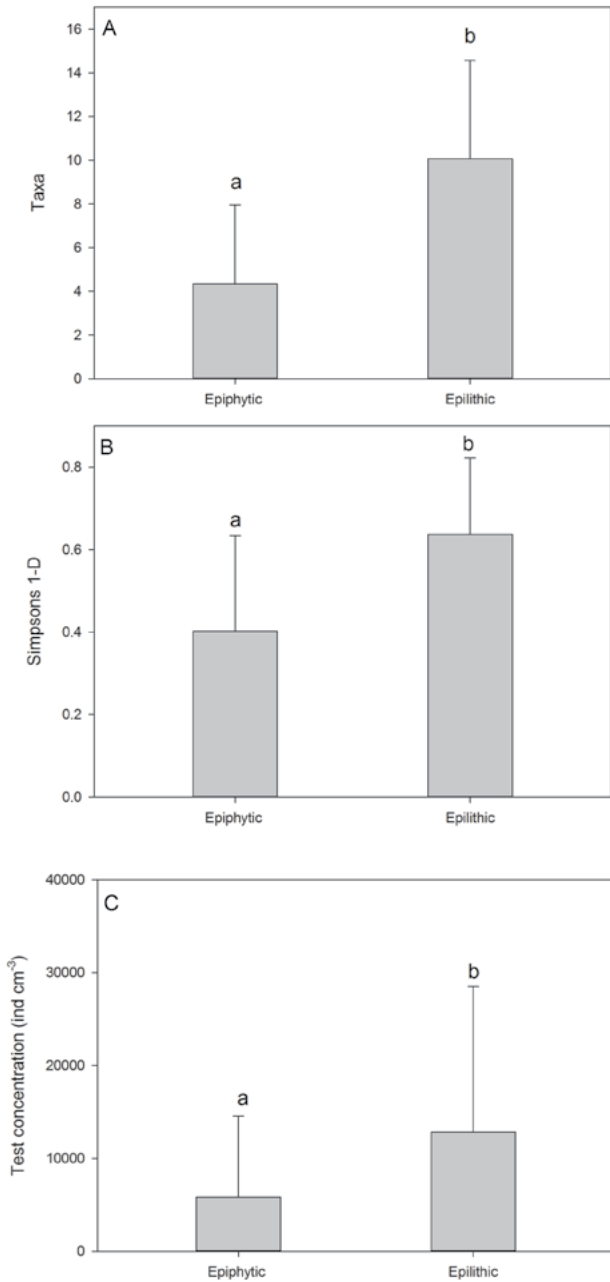
Fig. 5. Taxon richness (A), Simpson diversity (B) and test concentration (C) for epilithic and epiphytic samples from the Karelia regions. Bars show mean and error bars the standard deviation. Letters denote significant differences (P < 0.05), see text for details.

Our data do not show any difference between TA samples from lichens and mosses, contradicting our expectations based on epiphytic samples where there was a significant difference between these habitats. However, this dataset is much smaller with only ten samples from lichens and it would be desirable to repeat this analysis with more data before concluding that there is no difference.

Perhaps the most surprising finding of our study is a significant difference between the TA communities of epiphytic and epilithic vegetation based on samples from the Karelia region. Part of this difference is explained by differences in substrate (lichens or mosses) but results remain highly significant even when considering samples from lichens alone. Many factors were harmonised between these two datasets including sampling time, analyst and region, but some differences remained. Potential causes of the difference we observe include: 1) microclimate of the sampling locations, 2) greater shading of the epiphytic situations, 3) differences in lichen species, or 4) lichen weathering of the rock leading to differences in litter quality and the availability of environments buffered from environmental variability in the regolith. In researching this paper we found that many publications reporting the TA communities of mosses and lichens provided little or no information on the context to those mosses. Our results suggest that this is a potentially important factor and this information should be routinely presented. It is interesting to compare our results to those of Ragon *et al*. (2012) who examined the protist communities of epilithic biofilms at sites in France and the UK using a molecular approach based on SSU rDNA. Although the sampling context is somewhat different and no TA sequences were recorded these authors also found differences in protist assemblages between their sampling regions but no difference between different substrate types. By contrast, prokaryote communities did not differ between regions but did vary by substrate type.

Taken overall our results illustrate how little is known of TA in this habitat. Our study is the first to address the possible environmental controls on TA communities in epilithic mosses and suggests patterns which are both predictable, such as the link with moisture content, and more surprising, such as the difference between TA of epiphytic and epilithic mosses. Clearly much remains to be learnt.

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Supplementary material (for website)

Mazei Y., Belyakova O., Coppellotti O. and Payne R. J. (2016) Testate amoeba communities of epilithic mosses and lichens: new data from Russia, Switzerland and Italy. Acta Protozool. 55:

Supplementary Table 1. Indicative climate and air quality data for the sampling regions. Air quality data is from the EMEP trans-national pollution distribution model (EMEP 2014). Data are produced on a 50 km grid and therefore do not account for local emissions sources; real values for the Neuchâtel and Veneto sites are likely to be considerably greater than those indicated here due to vehicle emissions and other local sources. Note that EMEP predictions do not extend as far as the Baikal region; data listed in parentheses are from the most easterly point for which predictions are available, ca. 500 km west of the sampling location. Despite the considerable spatial offset there are few major emission sources and EMEP predictions are relatively constant across Siberia so these are probably reasonable estimates given the limitations discussed above. Precipitation data is from the EMEP dataset (for consistency) and therefore considers similarly large areas. EMEP does not include temperature data so these data are from the nearest station with available data included in the NOAA database (Karelia: Station Umba, period 1959–2008; Baikal: Station Slyudyanka, period 1948–2001; Veneto: Station Vicenza, period 1966–2008; Neuchâtel: Station Neuchâtel, period 1982–2008).

Region	Temperature (°C)	Precipitation (mm)	Pollutant concentrations			
			SO_2 (µgS m^{-3})	NO_2 (µgN m^{-3})	O_3 (ppb)	PM10 (µg m^{-3})
Karelia	0.44	713	0.075	0.310	29.7	2.32
Baikal	−0.36	[725]	[0.122]	[0.044]	[40.9]	[0.71]
Veneto	14.04	821	0.465	0.807	30.4	3.70
Neuchâtel	10.37	1686	0.252	1.353	39.0	5.77

Supplementary Table 2. Full list of testate amoeba taxa identified.

Arcella arenaria Greef, 1866

Arcella arenaria compressa Chardez, 1974

Arcella arenaria sphagnicola Deflandre, 1928

Arcella catinus Penard, 1890

Assulina muscorum Greef, 1888

Assulina seminulum (Ehrenberg, 1848) Leidy, 1879

Centropyxis aculeata (Ehrenberg, 1838) Stein, 1857

Centropyxis aerophila Deflandre, 1929

Centropyxis aerophila sphagnicola Deflandre, 1929

Centropyxis cassis (Wallich, 1864) Deflandre, 1929

Centropyxis constricta (Ehrenberg, 1841) Deflandre, 1929

Centropyxis orbicularis Deflandre, 1929

Centropyxis platystoma (Penard, 1890) Deflandre, 1929

Centropyxis sylvatica (Deflandre, 1929) Bonnet et Thomas, 1955

Corythion dubium Taránek, 1881

Corythion dubium minima Chardez, 1969

Corythion orbicularis (Penard, 1910) Iudina, 1996

Cryptodifflugia oviformis Penard, 1890

Cyclopyxis arcelloides (Penard, 1902) Deflandre, 1929

Cyclopyxis kahli Deflandre, 1928

Cyphoderia schonborni Laminger, 1973

Difflugia lucida Penard, 1890

Difflugia penardi Hopkinson, 1909

Euglypha acanthophora (Ehrenberg, 1841) Perty, 1849

Euglypha anodonta Bonnet, 1960

Euglypha capsiosa Coûteaux, 1978

Euglypha ciliata (Ehrenberg, 1848) Leidy, 1878

Euglypha ciliata glabra Wailes, 1915

Euglypha compressa Carter, 1864

Euglypha cristata Leidy, 1879

Euglypha cristata major Wailes, 1912

Euglypha denticulata Brown, 1912

Euglypha laevis (Ehrenberg, 1832) Perty, 1849

Euglypha marginata Van Oye, 1958

Euglypha rotunda Wailes, 1915

Euglypha scutigera Penard, 1911

Euglypha simplex Decloitre, 1965

Euglypha strigosa (Ehrenberg, 1871) Leidy, 1878

Euglypha strigosa glabra Wailes, 1898

Euglypha tuberculata Dujardin, 1841

Heleopera sphagni Leidy, 1874

Heleopera sylvatica Penard, 1890

Nebela collaris (Ehrenberg, 1848) Leidy, 1879

Nebela galeata Penard, 1902

Nebela militaris Penard, 1890

Nebela parvula Cash, 1909

Nebela tincta (Leidy, 1879), Awerintzew, 1906

Paraquadrula irregularis (Archer 1877) Deflandre, 1932

Phryganella acropodia (Hertwig et Lesser 1874) Hopkinson, 1909

Phryganella hemisphaerica Penard, 1902

Plagiopyxis declivis Thomas, 1958

Plagiopyxis penardi Thomas, 1958

Tracheleuglypha dentata Deflandre, 1938

Trigonopyxis arcula (Leidy, 1879) Penard, 1912

Trinema complanatum Penard, 1890

Trinema enchelys (Ehrenberg, 1838) Leidy, 1878

Trinema enchelys biconvexa Awerintzew, 1907

Trinema galeata (Penard, 1890) Jung, 1942

Trinema lineare Penard, 1890

Trinema penardi Thomas et Chardez, 1958