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Response of *Sphagnum* Testate Amoebae to Drainage, Subsequent Re-wetting and Associated Changes in the Moss Carpet – Results from a Three Year Mesocosm Experiment

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Abstract. *Sphagnum* peatlands represent a globally significant pool and sink of carbon but these functions are threatened by ongoing climate change. Testate amoebae are useful bioindicators of hydrological changes, but little experimental work has been done on the impact of water table changes on communities.

Using a mesocosm experimental setting that was previously used to assess the impact of drought disturbance on communities and ecosystem processes with three contrasted water table positions: wet (–4 cm), intermediate (–15 cm) and dry (–25 cm), we studied the capacity of testate amoeba communities to recover when the water table was kept at –10 cm for all plots. The overall experiment lasted three years. We assessed the taxonomic and functional trait responses of testate amoeba communities. The selected traits were hypothesised to be correlated to moisture content (response traits: shell size, aperture position) or trophic role (effect traits: mixotrophy, aperture size controlling prey range).

During the disturbance phase, the mixotrophic species *Hyalosphenia papilio* dominated the wet and intermediate plots, while the community shifted to a dominance of "dry indicators" (*Corythion dubium*, *Nebela tincta*, *Cryptodifflugia oviformis*) and corresponding traits (loss of mixotrophy, and dominance of smaller taxa with ventral or ventral-central aperture) in dry plots. During the recovery phase we observed two contrasted trends in the previously wet and intermediate plots: communities remained similar where the *Sphagnum* carpet remained intact but species and traits indicators of drier conditions increased in plots where it had degraded. In the former dry plots, indicators and traits of wet conditions increased by the end of the experiment.

This is one of the first experiment simulating a disturbance and subsequent recovery in ex-situ mesocosms of *Sphagnum* peatland focusing on the response of testate amoebae community structure as well as functional traits to water table manipulation. The results generally confirmed that testate amoebae respond within a few months to hydrological changes and thus represent useful bioindicators for assessing current and past hydrological changes in *Sphagnum* peatlands.

Keywords: Mesocosm experiment, Testate amoebae, Functional traits, Recovery, Disturbance, *Sphagnum* peatlands, bio-indicators, water table depth.

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INTRODUCTION

The increasing influence of human activities on the biosphere makes it necessary to assess how direct and indirect impacts are affecting ecosystems (MEA 2005). Biomonitoring is an efficient approach for evaluating environmental condition in general and specifically the impact of perturbation but also ecosystem restoration and recovery (MEA 2005; Bonnett *et al.* 2011; Norris *et al.* 2011; Church *et al.* 2014; Bonn *et al.* 2016). Bioindicator taxa must be sensitive enough to rapidly response to environmental changes, and have measurable characteristics (e.g. community composition, morphology, or function) that are correlated to relevant processes (e.g. C sequestration, Niemi and McDonald 2004; Payne 2013). Protists play essential functional roles and are useful bioindicators in aquatic as well as terrestrial ecosystems (Caron *et al.* 2009; Norris *et al.* 2011; Pinto *et al.* 2014). Our focus here is on the use of testate amoebae living in *Sphagnum* peatlands as indicators of hydrological changes.

Testate amoebae are a polyphyletic group of unicellular protists which build a shell, termed a test. Although they are generally studied as a homogeneous ecological and functional group, they belong to three phylogenetic groups, each of which has specific morphological traits: 1) Arcellinida (Kosakyan *et al.* 2016), with "lobose" (wide) pseudopods, 2) Euglyphida (Cavalier-Smith and Chao 2003), with "filose" (narrow) pseudopods and (for most of the group) a test produced of self-secreted silica scales (idiosomes), both groups with a single pseudostome (aperture) to the test and 3) Amphitremidae (Gomaa *et al.* 2013), with "filose" pseudopods and two pseudostomes. Some taxa (in all three groups) possess photosynthetic endosymbionts (i.e. they are mixotrophic). Identification is based on test characteristics, thus allowing the use of this group in palaeoecological studies (Charman 2001). Tests are made of self-secreted protein, self-secreted silica plates (idiosomes) or an agglutination (xenosomes) of either prey (diatom frustules, euglyphid plates, i.e. kleptoplastidy – Lahr *et al.* 2015) or mineral particles present locally (Ogden and Hedley 1980; Delaine *et al.* 2017). Testate amoebae are a dominant group of micro-organisms in wet and humid environments (Gilbert *et al.* 1998; Gilbert and Mitchell 2006) and play a central role in soil microbial food webs and C cycling in *Sphagnum* peatlands (Wilkinson and Mitchell 2010; Jassey *et al.* 2015). Their community structure is correlated with key environmental gradient such as humidity (generally measured as water table depth), pH, or nutrient richness (Mitchell *et al.* 2008).

In addition to classical taxonomy-based approaches, changes in communities may be studied within the functional diversity framework. This approach aims at understanding the links between well selected morphological / behavioural traits and environmental constraint (Lavorel and Garnier 2002; Violle *et al.* 2007). The functional diversity framework was developed initially for plants, macro-invertebrates and fish and was more recently been applied to micro-eukaryotes and especially testate amoebae (Fournier *et al.* 2012, 2015; Arrieira *et al.* 2015; Kajukało *et al.* 2016; Marcisz *et al.* 2016). Selected morphological and physiological traits have been shown to be linked to hydrological gradients (Fournier *et al.* 2012). As functional traits are directly linked to ongoing processes, they could be used to monitor ecosystem functioning and give information on ecological niche dimensions (Mouillot *et al.* 2007; Holt 2009; Kearney *et al.* 2010).

To be useful, functional traits must be 1) related to known ecological processes and 2) measurable at the species level (Violle *et al.* 2007; Mlambo 2014). In practice, traits are most often selected based on correlations identified in observational ecological studies. Such correlations should ideally be further tested using controlled experiments to link traits to specific environmental changes. Mesocosm experiments provide the necessary level of control to assess how selected traits respond to manipulation, while other variables are kept (approximately) constant in the different treatments (Benton *et al.* 2007).

This study is the follow-up of a twenty months mesocosm experimental study in which we assessed the responses of testate amoeba communities to manipulated water levels (–4 cm, –15 cm, –25 cm, Koenig *et al.* 2018). At the end of the experiment, the mesocosms were kept in operation, providing the opportunity for further experimentation. We adjusted the water level to –10 cm in all mesocosms to assess how the testate amoeba communities may recover post-stress and to compare the taxonomic and functional trait responses over the two phases of the overall experiment. We hypothesised that the strongest changes during the recovery experiment would be observed in the previously driest plots (–25 cm) as these experienced the highest contrast in both the first and second phase of the experiment.

MATERIAL AND METHODS

Experimental design

We set up a mesocosm experiment to simulate the effect of water table changes on *Sphagnum*-peatlands. Mesocosms consisted of tanks filled with water (Fig. 1). In each tank a pierced PVC tube (45 cm high, 12 cm diameter) was filled with a peat core topped with a carpet of *Sphagnum fallax* (Mulot *et al.* 2015). The system allowed the manipulation of the water level independently in each mesocosm. The *Sphagnum* carpets were collected simultaneously on the same *Sphagnum* patch, in the Creux de l'Epral peatland, Canton du Jura (47°12'18.3"N; 006°56'05.83"E; elevation: 990 m a.s.l.). At the beginning of the experiment (T0 – 02/08/2012), all plots were seeded with a water extract from pool, hummock and lawn to provide the full community potential as describe in Mulot *et al.* (2015). The water table was set at –4 cm (wet treatment – W), –15 cm (intermediate treatment – I) and –25 cm (dry treatment – D), with five replicates of each treatment. On 27/03/2015 the water level was set at –10 cm in all mesocosms (i.e. beginning of recovery phase). To assess the impact of water table changes, samples were extracted on 27/03/2014 (D1, 18 month after the beginning of the experiment), then on 18/05/2015 (R1, two months after equalisation of water table) and on 24/09/2015 (R2, six month after equalisation, Fig. 1). At each sampling date, we collected the top three centimetres of *Sphagnum* stems. The samples were refrigerated on the same day at 4°C, fixed with Glutaraldehyde 5% ($C_5H_8O_2$) on the same or the day after, and stored at 4°C in the dark until the extraction. Sample codes indicate treatment, replicate and sampling date, e.g. D4_R2 corresponds dry treatment, replicate 4 sampled on 24/09/2015.

Testate amoeba isolation and characterization

Testate amoebae were extracted by sieving and back-sieving through mesh filters (15–200 µm, Booth *et al.* 2010; Jassey *et al.* 2011). We aimed for minimum counts of 100 individuals per sample with living and empty tests pooled together. In some plots, especially where the structure of the moss carpet had been degraded by the experimental conditions, testate amoeba density was very low and less than 50 individuals were counted (D2_D1: 47 ind.; D4_D1: 29 ind.; W2_D1: 28 ind.; W2_R1: 17 ind.). Identification was based on the keys of Charman *et al.* (2000) and Mitchell (2003) at the species or species complex level. Some taxa were grouped into broader morphological groups, in particular taxa from the *Nebela tincta* group (Kosakyan *et al.* 2013). *Cyclopyxis arcelloides* includes *Cyclopyxis kahli* (found only in one sample at R2) and *C. eurystoma*. *Heleopera sylvatica* includes *H. petricola.* To reduce the impact of rare species, taxa that did not exceed a mean of 3% in one treatment at one sampling time (n = 5) were not included in the analyses (*Argynnia dentistoma*, *Assulina seminulum*, *Bullinularia indica*, *Cryptodifflugia sacculus*, *Heleopera sphagni*, *Hyalosphenia elegans*, *Plagiopyxis labiata*, *Sphenoderia lenta*, *Trigonopyxis arcula*, *Trinema complanatum* and *Wailesella eboracencis*).

Functional traits

To be truly functional, traits should be directly or indirectly related to known processes or at least strongly expected to follow change in niche dimension (Lavorel and Garnier 2002; Messier *et al.* 2010; Mlambo 2014). We selected traits expected to indicated adaptations to water stress (response traits) and traits which are known to impact on food web structure (effect traits, Table 1). Test compression, an aperture in a ventral position and small biovolume allow amoebae to stay active in thin water films (Laggoun-Defarge *et al.* 2008; Fournier *et al.* 2012; Tsyganov *et al.* 2012). Mixotrophy is believed to be an adaptation to low nutrient availability (Fournier *et al.* 2012; Jassey *et al.* 2013a) while test material informs on the abundance of mineral particles or prey incorporated in test construction (Gilbert *et al.* 2003; Gilbert and Mitchell 2006; Jassey *et al.* 2011; Schwind *et al.* 2016). Finally, aperture size has been demonstrated to be correlated to prey size and thus the trophic level, small apertures corresponding to microbial feeder and large apertures to predator of micro-eukaryotes and micro-metazoan (Jassey *et al.* 2013a; Gomaa *et al.* 2014). Morphological dimensions were measured directly at 400× magnification, on a subset of ten randomly chosen individuals, using an inverted IX-81 Olympus microscope, and the Olympus *cellSens dimension* software. Biovolume was calculated according to the general shape of the shell, applying the formulas of Fournier *et al.* (2015).

Numerical analyses

Gradient analyses

The structure and temporal changes of the testate amoeba communities in the three treatments was first assessed based on the relative abundance of species over time. To illustrate the change in each community structure in response to the treatment, species were classified according to their optimal water table depth. These optima were calculated with a transfer function (weighted averaging regression) based on an independent dataset (Mitchell *et al.* 1999), in which the Creux de l'Epral bog was included.

We then computed the community weighted mean (CWM) of selected traits (biovolume, aperture position, test compression, test composition, mixotrophy and aperture size) in each sample. CWM represented the average of each trait value weighted by the relative abundance of each species (Dray and Legendre 2008; Ricotta and Moretti 2011).

We analysed the temporal patterns of community structure and community weighted mean of functional traits using principal component analyses (PCA) in which we passively projected treatment and time. Prior to PCA, the species dataset was Hellinger transformed according to Legendre and Gallagher (2001) and the CWM of traits dataset was standardised. Permutational multivariate analysis of variance (PERMANOVA) was used to assess the difference in testate amoeba community structure between sampling times for each treatment separately. This analysis partitions dissimilarities between groups and tests the significance of those partitioning (Anderson 2001; Oksanen 2015). We used a Bray-Curtis distance matrix of relative abundance of species with 999 permutations. The significance of any difference between sampling occasions for community weighted mean of traits was tested by analyses of variance with random effect and Tukey multiple comparisons of mean (Bonferroni correction), for each treatment separately.

Null models for functional diversity

Two main processes may drive community assembly processes (and hence explain community structure): change in niche dimension (habitat selection) and competition between species (biotic in-

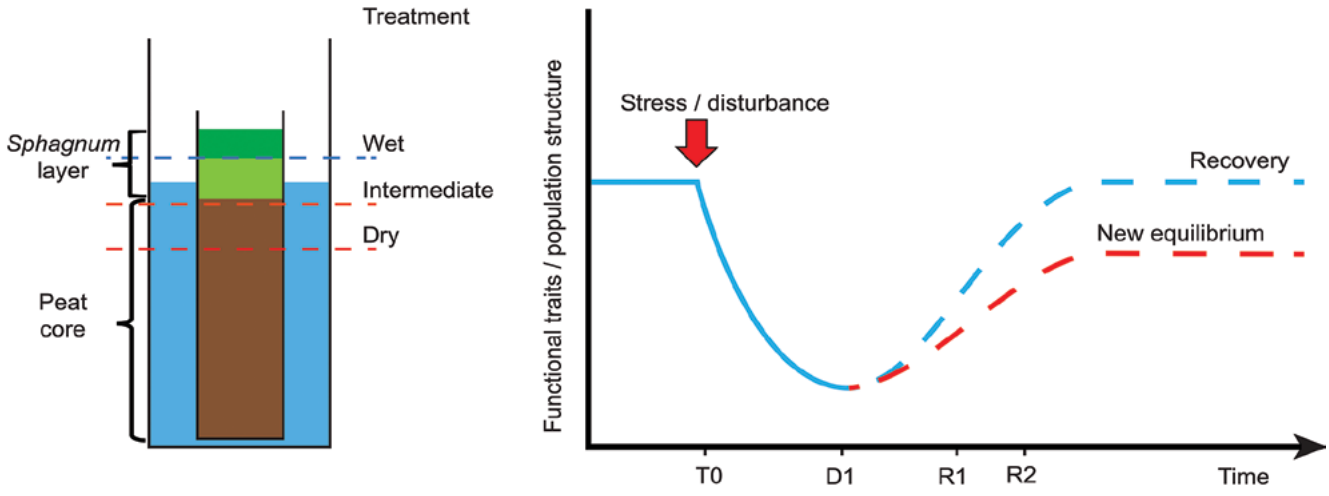


Fig. 1. Left: schematic cross-section through a mesocosm showing the peat and *Sphagnum* layer. Right: expected evolution of community structure or traits over the stress and recovery phases. At the onset of the experiment (T0) the community included the whole range of species living in pool, lawn and hummock, taken in a natural *Sphagnum* peatland. D1 is the point of maximum disturbance effect and R1 and R2 are sampling points during the recovery phase. Dotted lines represented the possible evolution of both species community structure and community weighted mean of functional traits in response to disturbance. Full recovery depended on the survival potential of species. The new equilibrium represents the situation when the local conditions or present species pool do not allow a fully recovery of original state. In our case this is due to the fact that some species are likely to be lost during the disturbance phase.

teraction). To disentangle these two processes, recent studies have suggested using null models (Webb *et al.* 2006; Mason *et al.* 2008; Cavender-Bares *et al.* 2009; Chase *et al.* 2011). As the niche dimension could be inferred from the community weighted mean of traits (Kearney *et al.* 2010), measuring the distance between the CWM calculated with the real dataset and a CWM constructed with a random community should indicate if the ongoing processes are related to habitat selection or to biotic interaction. The standardized effect size of mean pairwise distance (ses.mpd) compares the observed distance separating samples based on species community structure in relation with the pool of functional traits, and the same distance based on a random community matrix with respect to the species richness of the original community and the original traits matrix (Kembel *et al.* 2010). The standardized effect size is calculated by:

$$ses.mpd = \frac{mean(M_{null}) - M_{observed}}{sd(M_{null})} \quad (1)$$

where M_{null} = randomized mean pairwise distance, $M_{observed}$ = observed pairwise distance, $sd(M_{null})$ = standard deviation of randomized pairwise distance (Kembel *et al.* 2010). When ses.mpd is significantly lower than expected by chance, the main drivers of community structure are related to habitat filtering; when it is significantly higher, biotic factors are more likely to be the driver. As the trait matrix included binary variables, semi-quantitative factors and quantitative traits, the Gower distance was applied, using the method of Podani (1999) for ordinal variables (Gower 1971).

All analyses were carried out with the R statistical software (R Core Team 2016). Ordinations were computed using the package vegan (Oksanen 2015). The community weighted mean of functional traits was calculated using the package FD (Laliberté *et al.* 2014). Standardized effect size and null models were computed with package Picante (Kembel *et al.* 2010) and optima and tolerance of species were calculated with the package rioja (Juggins 2015).

RESULTS

Testate amoeba community composition and treatment effects on community structure

We identified a total of 26 testate amoeba morphotaxa in the 60 analysed samples (Table 2). *Hyalosphenia papilio* was the only taxon found in all samples and the most abundant overall, accounting for over half for the community on average and with a median abundance of 72.9%. *Corythion dubium*, *Nebela tincta* s.l., *Assulina muscorum*, *Phryganella acropodia*, *Centropyxis aculeata, Arcella catinus, Heleopera rosea,* and *Euglypha ciliata* each contributed > 2% of the overall community and occurred in > 45% of all samples (Table 2). Eighteen other morphotaxa were less abundant and frequent (Table 2).

The three treatments had contrasted effects on the species richness, relative abundance of individual taxa

Table 1. Description, ecological meaning and references for the six functional traits selected for testate amoebae.

	Unit	Description	Type of trait	Ecological meaning	References
Biovolume	μm^3	Volume of shell (90% occupied by the living amoeba)	Response	Related to the metabolic rate and the capacity of the food web to process energy.	Fournier *et al.* 2012 Laggoun-Défarge *et al.* 2008 Makarieva *et al.* 2008
Aperture position	Factor	From a terminal aperture to the completely central one.	Response	Represents the ability to survive in thin water film and thus the ability to remain active and contribute to the food web in dry conditions.	Fournier *et al.* 2012 Lamentowicz *et al.* 2015
Test material	Factor	Protein made, Idiosomes (secreted bio-siliceous plates), Xenosomes (built with particles collected in environment: organic debris, diatom frustules, mineral particles)	Response	Availability of material and / or prey to construct the test. Source of material appear to be a major regulator of abundance and repartition of testate amoeba along *Sphagnum* parts.	Gilbert and Mitchell 2006
Test compression	Binary	0: not compressed 1: compressed	Response	Survival potential in drier situations and thus potential contribution to the food web in dry conditions.	Fournier *et al.* 2012
Mixotrophy	Binary	Presence (1) or not (0) of photosynthetic endosymbionts	Effect	Mixotrophy is a key factor in oligotrophic conditions and plays a role in peatland C cycling.	Fournier *et al.* 2015 Jassey *et al.* 2011, 2015
Aperture size	µm	Width of the shell aperture	Effect	Related to prey size and food web functioning	Jassey and Meyer, *et al.* 2013

(Table 3) and community structure (Fig. 2a). At T0 communities were strongly dominated by *H. papilio*, and did not significantly differ among treatments (Fig. 2a). Within each treatment, the community structure changed significantly over the duration of the whole experiment (multivariate analyse of variance, dry plots R^2: 58.5%, p-value 0.001; intermediate plots R^2: 40.1%, p-value 0.001; wet plots R^2:36.8%, p-value 0.016, Table 4).

In dry plots, the species richness increased significantly from 5.2 taxa at T0 to 10.2 taxa at R1 (ANOVA p-adjusted T0-R1: 0.002) and 10.6 taxa at R2 (ANOVA p-adjusted T0-R2: 0.002) and the community structure diverged from the wet and intermediate plots (Fig. 2a, left of the diagram). At D1, the community was dominated by *N. tincta*, *H. rosea*, and *C. dubium.* By R1 *H. papilio* declined sharply (to 6.7% on average) and the community was dominated by *C. dubium*, *N. tincta*, and *Cryptodifflugia oviformis*. By R2, community structure was again similar to that of D1: *H. papilio* was again more abundant (23.6%) and the community was co-dominated by *N. tincta* (15.2%), *H. rosea* (12.2%), *Physochila griseola*, *Cyclopyxis arcelloides*, *C. aculeata* and *A. muscorum* (7.8–8.6%). This was the most balanced community in the entire experiment.

Species richness did not change significantly between wet and intermediate treatments. The community structure in these two treatments shifted from T0 to D1 with increasing representation of *P. acropodia* and *A. muscorum* (Fig. 2a, bottom right quadrat of the ordination diagram). At the start of the recovery period, the community structure diverged between two groups of samples. The communities of six samples (I1, I2, I4, I5, W1, W3) were still dominated by *H. papilio,* but to a less extent, together with *A. muscorum* and *P. acropodia* still abundant during the recovery period. The last four samples (I3, W2, W4, W5, labelled on the PCA) diverged towards a dominance of *A. muscorum* and *C. dubium* and an almost complete desappearance of *H. papilio* (centre of the diagram); the communities in these plots were more similar to those of dry plots at D1 and R1. W2 should be interpreted very carefully at R1 as only 18 individuals were counted; total count was higher at R2 (117 individuals) but with a different community structure, very close to that of the dry plots.

Treatment effects on testate amoeba functional traits

The first two axes of the PCA based on the community weighted mean (CWM) of functional traits (Fig. 2b) explained over 80% of the variance in the data (axis 1 =

59.6%, axis 2 = 20.7%). As axis 2 was significant based on the Kaiser-Guttmann rule (Kaiser 1991) but just not significant according to the broken stick model (MacArthur 1957), we decided to interpret both axes, as broken stick models often underestimate the significance (Cangelosi and Goriely 2007). The three treatments showed contrasting temporal patterns in the CWM ordination space. At T0 all treatments were represented by a high proportion of mixotrophic species (left of the diagram), a compressed, proteinaceous test, with a terminal aperture and a large biovolume, reflecting the dominance of *H. papilio*. In the Intermediate treatment, no strong change was observed. In the wet plots, a shift was observed towards taxa with smaller biovolume and aperture size, tests constructed of xenosomes and idiosomes and a ventral position of the aperture (axis 2). As for the community biplot (Fig. 2a), samples from the wet plots diverged in the recovery phase (R1 and R2). Two plots (W2 and W3) were correlated to a ventral-central aperture, with non-compressed, idiosomes tests. Two others (W4 and W5) were correlated to small taxa with a small ventral aperture and a test built from xenosomes, while the last one (W1) remained at the centre of the plot. In dry plots, the CWM of traits shifted towards small species, with small, ventral pseudostomes and compressed tests made with xenosomes at D1, corresponding to the maximal effect of the treatment. After restoring the hydrological conditions, the CWM of traits shifted back towards larger species, with a central-ventral aperture and idiosomes tests.

Changes in the standardised effect size of mean pairwise distance (ses.mpd) based on species traits are shown for each plot (Fig. 3). In dry plots, the trend was negative from D1 onwards: all replicates and sampling dates but one showed negative values as compared to the null model, two of these plots being significantly different from the null model. In wet plots, the trend was towards a positive distance from the null model but two samples (W2 and W5) showed the opposite at R2, again illustrating the high dispersion of responses in this treatment. In intermediate plots, no clear trend was visible.

DISCUSSION

Our aim was to assess the resilience capacity of the *Sphagnum* testate amoeba community following an experimental hydrological perturbation which included three treatments. The duration of the disturbance period was long enough (almost three years) to induce a deep change in mesocosm functioning. In dry samples, the mineralisation of peat was obvious and *Sphagnum fallax* was replaced by other bryophytes, or vascular plants (especially ferns), similar to most drained peatlands in Switzerland (Grosvernier *et al.* 1997; Graf *et al.* 2007).

Our results showed that the duration of the perturbation (i.e. thirty-two months) was clearly sufficient to allow both the *S. fallax* moss (i.e. amoeba habitat) and their associated microbial communities (among which testate amoebae) to respond first to the experimental hydrological perturbation and second to the experimental "restoration". Both the testate amoeba community structure and community weighted mean of functional traits reacted within one growing season to conditions comparable to restoration. The response patterns we observed are generally in line with known ecological preferences of species derived from observational and experimental studies (Marcisz *et al.* 2014).

Community structure and response to water table changes

At the beginning of the experiment, the community was dominated by *Hyalosphenia papilio*, a frequently dominant taxon in oligotrophic *Sphagnum* peatlands and especially *S. fallax* poor-fens (Lamentowicz and Mitchell 2005; Opravilova and Hajek 2006; Jassey *et al.* 2013b).

In the dry treatment, the community structure shifted by D1, as expected, towards a dominance of taxa characteristic for drier conditions: *Nebela tincta* s.l., *Corythion dubium*, *Assulina seminulum*, *Centropyxis aculeate* (Mitchell *et al.* 1999; Bobrov *et al.* 1999; Lamentowicz and Mitchell 2005; Qin *et al.* 2013; Amesbury *et al.* 2016), which is similar to the community structure observed in early stages of spontaneous cutover bog regeneration (Buttler *et al.* 1996; Laggoun-Defarge *et al.* 2008). Simultaneously, *Archerella flavum*, a mixotrophic taxa characteristic for moderately wet micro-habitats (Mazei *et al.* 2009), disappeared completely in the dry plots. This effect remained until R1 and some recovery became clear by R2 (Mitchell *et al.* 1999, Mazei *et al.* 2009). The increase in species richness at R1 and R2 suggests that some taxa were not detected at T0, possibly due to the strong dominance of *H. papilio*, but were recorded at R1 and R2 when this species decreased.

Unlike dry plots, neither the intermediate nor the wet treatments showed a clear change in community

Table 2. List of testate amoeba taxa, number and relative frequency of occurrence, mean, standard error (se), median, minimum and maximum relative abundance. Taxa are ordered by mean relative abundance over the four sampling times and within all treatment (n = 60). Rare taxa (i.e. maximum abundance in any single treatment and time < 3%) are indicated in grey and were excluded from numerical analyses.

Morphotaxa	N	n/N	mean	se	median	min	max
Hyalosphenia papilio Leidy, 1874	60	100.0%	56.6%	4.1%	72.9%	0.6%	94.7%
Corythion dubium Taranek, 1871	29	48.3%	7.1%	2.1%	0.0%	0.0%	83.4%
Nebela tincta s.l. (Leidy) sensu Kosadyan and Lara, 2012	41	68.3%	7.0%	1.3%	2.2%	0.0%	41.7%
Assulina muscorum Greeff, 1888	39	65.0%	6.7%	1.7%	1.2%	0.0%	70.0%
Phryganella acropodia (Hertwig & Lesser, 1874) Hopkinson, 1909	28	46.7%	4.1%	1.0%	0.0%	0.0%	33.3%
Centropyxis aculeata (Ehrenberg, 1838)	36	60.0%	3.0%	0.8%	0.6%	0.0%	30.8%
Arcella catinus Penard, 1890	44	73.3%	2.9%	0.4%	1.7%	0.0%	10.9%
Heleopera rosea Penard, 1890	32	53.3%	2.7%	0.7%	0.6%	0.0%	25.2%
Euglypha ciliata type	37	61.7%	2.0%	0.4%	0.7%	0.0%	13.7%
Cryptodifflugia oviformis Penard, 1902	5	8.3%	1.4%	0.7%	0.0%	0.0%	31.6%
Physochila griseola (Wailes & Penard, 1911)	13	21.7%	1.2%	0.4%	0.0%	0.0%	17.6%
Cyclopyxis arcelloides (Deflandre, 1929)	13	21.7%	1.0%	0.6%	0.0%	0.0%	37.7%
Archerella flavum (Archer, 1877) Loeblich and Tappan, 1961	10	16.7%	0.9%	0.4%	0.0%	0.0%	16.4%
Amphitrema wrightianum Archer, 1869	11	18.3%	0.8%	0.3%	0.0%	0.0%	11.1%
Heleopera sylvatica Penard, 1890	14	23.3%	0.6%	0.2%	0.0%	0.0%	8.9%
Pseudodifflugia gracilis Schlumberger, 1845	12	20.0%	0.5%	0.2%	0.0%	0.0%	5.9%
Hyalosphenia elegans Leidy, 1874	22	36.7%	0.5%	0.1%	0.0%	0.0%	5.1%
Heleopera sphagni Leidy, 1874	11	18.3%	0.5%	0.2%	0.0%	0.0%	9.6%
Trinema complanatum Penard, 1890	5	8.3%	0.2%	0.1%	0.0%	0.0%	7.4%
Assulina seminulum (Ehrenberg, 1848)	8	13.3%	0.1%	0.0%	0.0%	0.0%	0.9%
Sphenoderia lenta Schlumberger, 1845	3	5.0%	0.1%	0.0%	0.0%	0.0%	1.8%
Bullinularia indica (Penard, 1907)	3	5.0%	0.1%	0.0%	0.0%	0.0%	2.1%
Plagiopyxis labiata Penard, 1910	2	3.3%	0.0%	0.0%	0.0%	0.0%	1.6%
Wailesella eboracencis (Wailes & Penard, 1911)	1	1.7%	0.0%	0.0%	0.0%	0.0%	2.4%
Cryptodifflugia sacculus Penard, 1902	1	1.7%	0.0%	0.0%	0.0%	0.0%	1.3%
Argynnia dentistoma (Penard, 1890)	1	1.7%	0.0%	0.0%	0.0%	0.0%	0.6%

composition during the disturbance period (T0-D1). It seems that the water level contrast between the intermediate and wet treatments was not high enough to affect the population dynamics of *H. papilio* and the community structure thus remained similar in both treatments until D1. This lack of contrasted response of *H. papilio* between these two treatments is in line with the relatively wide tolerance of these taxon to water level (Table 3) (Lamentowicz *et al.* 2008; Booth and Meyers 2010; Turner *et al.* 2013). Previous studies have shown that although *H. papilio* is most frequent in *Sphagnum*-dominated poor fens it could also be found in relatively dry habitats (Heal 1964; Payne *et al.* 2008). This could be explained by the presence of cryptic species inside the *H. papilio* morphological taxon (Heger *et al.* 2013; Mulot *et al.* 2017) with different ecological preferences.

During the recovery phase, with a mean water table position at –10 cm, the relative abundance of *H. papilio* declined and that of several taxa related to drier conditions (i.e. *Assulina muscorum*, *Phryganella acropodia*, Mitchell *et al.* 1999; Bobrov *et al.* 1999) increased (Fig. 4). However, two patterns were observed (Fig 2a): the community structure of some wet and intermediate plots changed and became similar to that of the dry treatment, while the other wet and intermediate plots remained relatively stable during this phase, despite

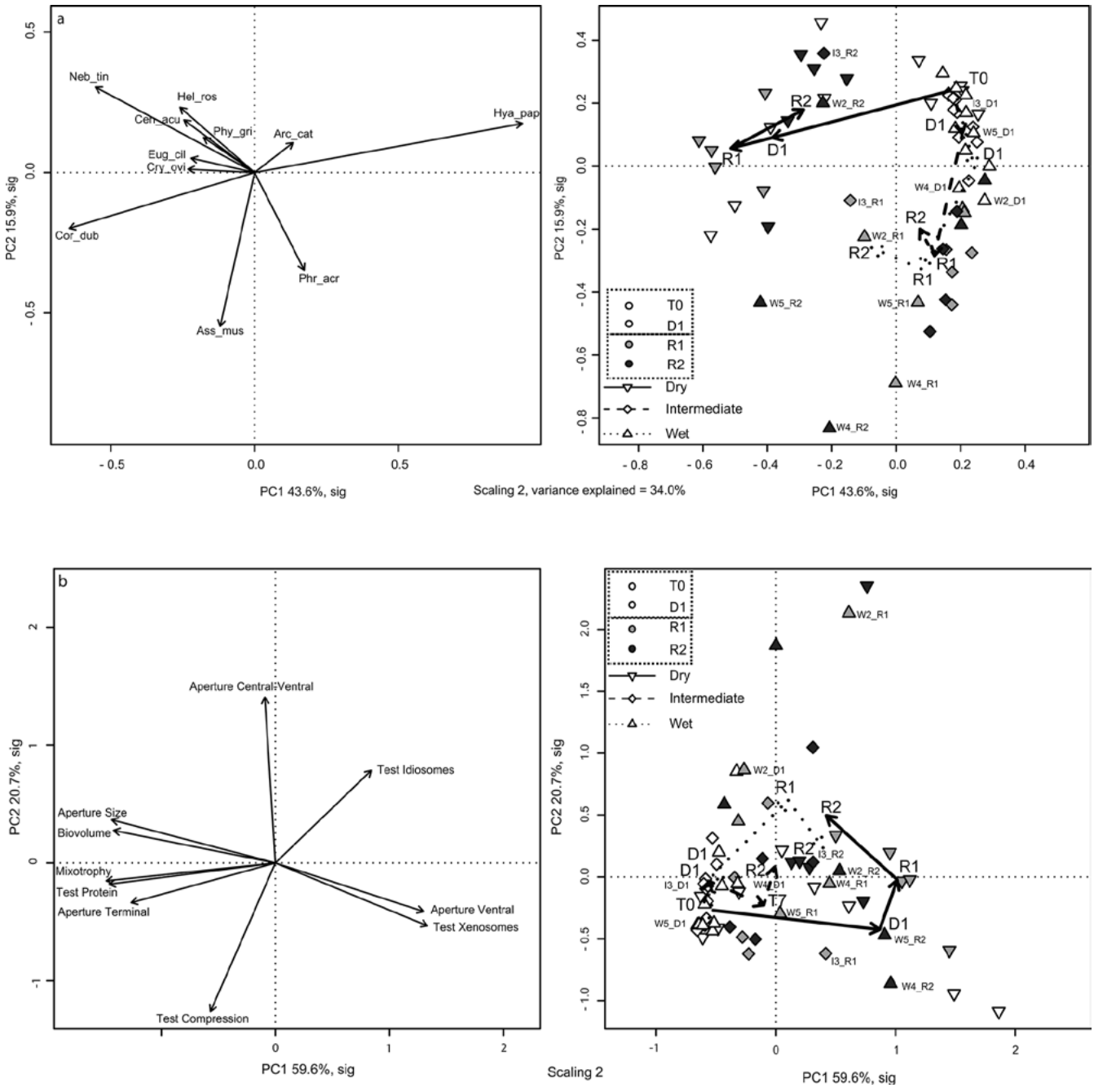


Fig. 2. Principal component analyses (PCA) of **a**) testate amoeba species and **b**) community weighted mean (CWM) of functional traits in *Sphagnum fallax* from a mesocosm experiment simulating water table changes. The species dataset was Hellinger transformed and the CWM data were scaled. Projection of descriptors (left) and samples (right), scaling 2. On the right plots, arrows represent the time line for each treatment (mean coordinates of the five sampling plots of each treatment and time). In both PCAs, axes 1 and 2 were the only significant axes and accounted respectively for 60.4% (species based) and 80.2% (CWM based) of the variance. Characteristic plots for wet and intermediate treatments were labelled. Taxa abbreviations: Amp_wri: *Amphitrema wrightianum*, Pse_gra: *Pseudodifflugia gracilis*, Arc_fla: *Archerella flavum*, Cyc_arc: *Cyclopyxis arcelloides*, Phy_gri: *Physochila griseola*, Hya_pap: *Hyalosphenia papilio*, Cen_acu: *Centropyxis aculeata*, Hel_syl: *Heleopera sylvatica*, Cry_ovi: *Cryptodifflugia oviformis*, Eug_cil: *Euglypha ciliata*, Phr_acr: *Phryganella acropodia*, Hel_ros: *Heleopera rosea*, Cor_dub: *Corythion dubium*, Neb_tin: *Nebela tincta* s.l., Arc_cat: *Arcella catinus*, Ass_mus: *Assulina muscorum*.

Table 3. Mean relative abundance and standard error (se, n = 5) and species richness of testate amoeba taxa in *Sphagnum fallax* from a mesocosm experiment at four sampling time, detail for the three treatments (dry, intermediate, and wet). T0: onset of the experiment, D1: after eight months of treatment, R1 and R2: after three, and six months maintaining the water level –10 cm. Taxa are listed in increasing water table depth optimum (Opt). The difference in mean species richness was only significant in the dry treatment between T0-R1 and T0-R2 (ANOVA and Tukey HSD test, in bold).

				T0		D1		R1		R2	
Morphotaxa	Opt.	Tol.	Treat.	Mean	se	Mean	se	Mean	se	Mean	se
Amphitrema wrightianum	9.4	4.1	Wet	0.0%	0.0%	3.1%	0.4%	6.1%	2.4%	0.5%	0.5%
Pseudodifflugia gracilis	9.4	7.5	Wet	0.0%	0.0%	0.0%	0.0%	0.4%	0.4%	1.0%	0.7%
Archerella flavum	10.9	8.5	Wet	4.7%	2.2%	0.0%	0.0%	0.0%	0.0%	0.1%	0.1%
Cyclopyxis arcelloides	11.1	9.2	Wet	0.6%	0.3%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
Physochila griseola	15.2	7.1	Wet	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	1.2%	0.9%
Hyalosphenia papilio	16.1	10.1	Wet	85.0%	3.9%	84.4%	3.5%	55.5%	11.2%	36.1%	14.6%
Centropyxis aculeata	17.0	7.0	Wet	0.8%	0.5%	1.7%	1.5%	1.3%	1.2%	7.1%	6.4%
Cryptodifflugia oviformis	19.5	13.2	Wet	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
Euglypha ciliata	19.6	11.8	Wet	1.7%	0.5%	0.4%	0.4%	0.5%	0.4%	5.7%	2.5%
Phryganella acropodia	21.6	11.5	Wet	0.0%	0.0%	7.4%	3.0%	17.0%	5.2%	11.1%	6.0%
Heleopera rosea	22.3	6.9	Wet	1.2%	0.8%	1.0%	0.6%	0.0%	0.0%	1.9%	1.3%
Heleopera sylvatica	23.0	11.9	Wet	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	2.0%	0.7%
Corythion dubium	23.7	11.0	Wet	0.0%	0.0%	0.0%	0.0%	6.4%	1.8%	4.2%	2.4%
Nebela tincta s.l.	23.8	12.7	Wet	1.8%	0.6%	0.3%	0.3%	1.2%	1.2%	4.4%	3.0%
Arcella catinus	24.7	8.7	Wet	3.5%	1.4%	1.1%	0.7%	1.4%	1.1%	1.8%	0.8%
Assulina muscorum	25.5	11.4	Wet	0.7%	0.5%	0.6%	0.4%	10.2%	7.3%	22.9%	14.3%
Specific richness				6.6	0.7	4.8	0.6	5.8	0.6	8.2	1.5
Amphitrema wrightianum	9.4	4.1	Inter	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.1%	0.1%
Pseudodifflugia gracilis	9.4	7.5	Inter	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.7%	0.7%
Archerella flavum	10.9	8.5	Inter	0.0%	0.0%	0.0%	0.0%	0.3%	0.3%	1.8%	1.2%
Cyclopyxis arcelloides	11.1	9.2	Inter	0.2%	0.1%	0.0%	0.0%	0.2%	0.2%	1.4%	1.2%
Physochila griseola	15.2	7.1	Inter	0.0%	0.0%	0.2%	0.2%	0.0%	0.0%	0.9%	0.9%
Hyalosphenia papilio	16.1	10.1	Inter	87.2%	2.7%	84.2%	1.1%	68.2%	4.8%	56.2%	8.0%
Centropyxis aculeata	17.0	7.0	Inter	0.9%	0.2%	0.5%	0.2%	0.6%	0.5%	4.3%	4.3%
Cryptodifflugia oviformis	19.5	13.2	Inter	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
Euglypha ciliata	19.6	11.8	Inter	0.1%	0.1%	0.5%	0.2%	0.3%	0.2%	0.4%	0.3%
Phryganella acropodia	21.6	11.5	Inter	0.0%	0.0%	2.6%	1.6%	5.3%	3.1%	6.1%	3.7%
Heleopera rosea	22.3	6.9	Inter	0.5%	0.5%	1.1%	0.6%	0.3%	0.3%	1.3%	1.2%
Heleopera sylvatica	23.0	11.9	Inter	0.0%	0.0%	0.0%	0.0%	0.2%	0.2%	0.9%	0.5%
Corythion dubium	23.7	11.0	Inter	0.2%	0.2%	0.0%	0.0%	6.6%	6.0%	1.3%	0.8%
Nebela tincta s.l.	23.8	12.7	Inter	3.6%	0.6%	2.0%	0.7%	1.4%	1.4%	4.0%	3.5%
Arcella catinus	24.7	8.7	Inter	6.6%	2.0%	7.1%	1.1%	1.4%	0.5%	3.0%	0.8%
Assulina muscorum	25.5	11.4	Inter	0.8%	0.2%	1.8%	0.7%	15.2%	3.3%	17.4%	4.9%
Specific richness				5.8	0.5	6.0	0.3	6.6	0.5	7.6	1.5
Amphitrema wrightianum	9.4	4.1	Dry	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
Pseudodifflugia gracilis	9.4	7.5	Dry	0.0%	0.0%	0.0%	0.0%	1.1%	0.6%	3.4%	0.8%
Archerella flavum	10.9	8.5	Dry	4.6%	3.2%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
Cyclopyxis arcelloides	11.1	9.2	Dry	0.4%	0.4%	0.0%	0.0%	1.1%	1.1%	8.4%	7.6%
Physochila griseola	15.2	7.1	Dry	0.0%	0.0%	1.1%	0.9%	2.9%	1.7%	8.6%	3.5%
Hyalosphenia papilio	16.1	10.1	Dry	81.7%	5.7%	17.1%	6.1%	6.7%	2.6%	23.6%	6.6%
Centropyxis aculeata	17.0	7.0	Dry	0.5%	0.4%	7.7%	5.1%	2.8%	1.1%	8.2%	1.9%
Cryptodifflugia oviformis	19.5	13.2	Dry	0.0%	0.0%	0.0%	0.0%	18.3%	5.9%	0.0%	0.0%
Euglypha ciliata	19.6	11.8	Dry	1.8%	0.8%	4.5%	2.1%	4.2%	1.7%	5.0%	1.2%

				T0		D1		R1		R2	
Morphotaxa	Opt.	Tol.	Treat.	Mean	se	Mean	se	Mean	se	Mean	se
Phryganella acropodia	21.6	11.5	Dry	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.7%	0.3%
Heleopera rosea	22.3	6.9	Dry	0.7%	0.3%	9.2%	5.3%	3.7%	0.8%	12.2%	2.6%
Heleopera sylvatica	23.0	11.9	Dry	0.0%	0.0%	0.0%	0.0%	1.3%	1.0%	3.1%	1.7%
Corythion dubium	23.7	11.0	Dry	0.7%	0.7%	33.9%	16.5%	30.1%	9.4%	3.5%	1.7%
Nebela tincta s.l.	23.8	12.7	Dry	4.3%	1.9%	22.2%	5.9%	24.8%	6.6%	15.2%	1.8%
Arcella catinus	24.7	8.7	Dry	5.3%	2.0%	1.9%	0.8%	1.2%	0.8%	0.4%	0.2%
Assulina muscorum	25.5	11.4	Dry	0.0%	0.0%	2.3%	0.7%	1.9%	0.9%	7.8%	5.3%
Specific richness				5.2	0.9	7.4	0.4	**10.2**	0.7	**10.6**	0.5

Table 4. Permutational multivariate analysis of variance of testate amoeba community dataset from *Sphagnum fallax* mesocosm experiment simulating water table level changes by treatment and between sampling time. Sampling time was significantly different in all treatments.

Treatment		Df	SumsOfSqs	MeanSqs	F-value	R^2	p-value
Dry	Time	3	2.34	0.78	7.52	0.585	0.001
	Residuals	16	1.66	0.10		0.415	
	Total	19	4.00			1	
Intermediate	Time	3	0.37	0.12	3.56	0.401	0.001
	Residuals	16	0.55	0.03		0.599	
	Total	19	0.92			1	
Wet	Time	3	0.88	0.29	3.11	0.368	0.016
	Residuals	16	1.51	0.09		0.632	
	Total	19	2.39			1	

Df – degree of freedom, SumOfSqs – sequencial sum of square, MeanSqs – mean square.

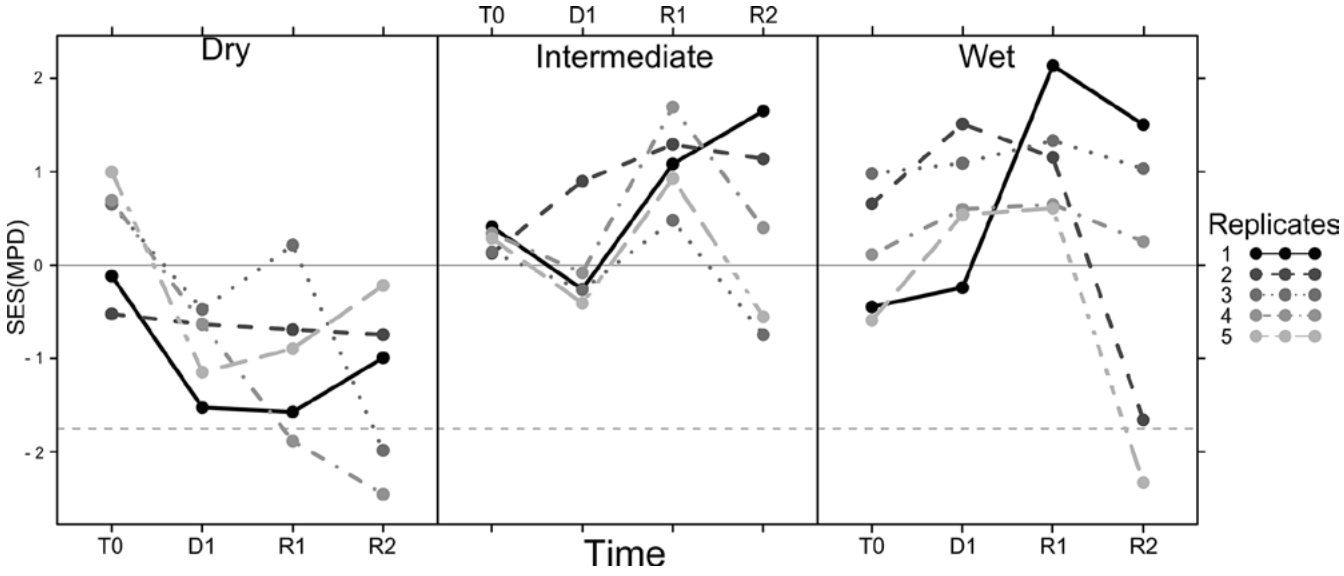


Fig. 3. Evolution of standardized effect size of mean pairwise distance between sampling plots relatively to a null model (random species matrix with respect to observed species richness, see text for details) of testate amoeba community weighted mean (CWM) of functional trait data from a *Sphagnum fallax* mesocosm experiment simulating water table changes. The mean pairwise distance represents the distance separating communities based on the pool of functional traits. Horizontal grey dotted line represents p-value of 0.05, points below the line are significantly different from the null model. Each replicate was represented separately, with a grey scale.

a decrease of *H. papilio.* This unexpected trend is however coherent with the contrasted evolution of the mesocosms (Suppl. Fig. 1–3). Indeed, when the water level was moved to –10 cm in all plots, we observed that the structure and vitality of the moss carpet had considerably changed in some mesocosms. This was most clear in dry treatments where the *S. fallax* carpet was almost completely dead and partly replaced by other bryophytes and ferns (Suppl. Fig. 2), but a similar situation was also observed in some wet and intermediate plots. At the end of the experiment, *S. fallax* recovered in most of the plots (Suppl. Fig. 3).

Treatment effects on testate amoeba functional traits

The clear community shift in the dry treatment corresponded to a shift in traits with an increased representation of smaller taxa, of shells with small ventral pseudostomes, a loss of mixotrophy, and an increase in idiosome and xenosome tests. These changes are in line with the drier conditions and probable thinner water films (Fournier *et al.* 2015; Payne *et al.* 2016; Marcisz *et al.* 2016). The clear decrease in mixotrophy (related to the diminution of *H. papilio* which was not replaced by another mixotrophic taxa) indicates that mixotrophy does not represent an advantage in drier conditions, even when light availability remains constant. Mixotrophy has been shown to be related to nutrient content and C cycling: a higher proportion of mixotrophs in the community being associated with higher C fixation (Jassey *et al.* 2013a, 2015). The reduction of mixotrophy thus indicates a potentially important functional change in the testate amoeba community in the dry plots during the disturbance phase. The shift in traits also indicates a shift from eukaryvory (*sensu* Lahr *et al.* 2015, i.e. feeding on Eukaryotes such as protists, micro-metazoa, fungi and eukaryotic microalgae) towards bacterivory, corresponding lowering of the trophic level the community and suggesting a faster turnover of carbon and nutrients (Jassey *et al.* 2013b, 2015; Fournier *et al.* 2015). During the recovery phase (R1–R2) in the dry treatment, the shifts of both community structure and traits towards the situation of T0 are in line with the increased moisture.

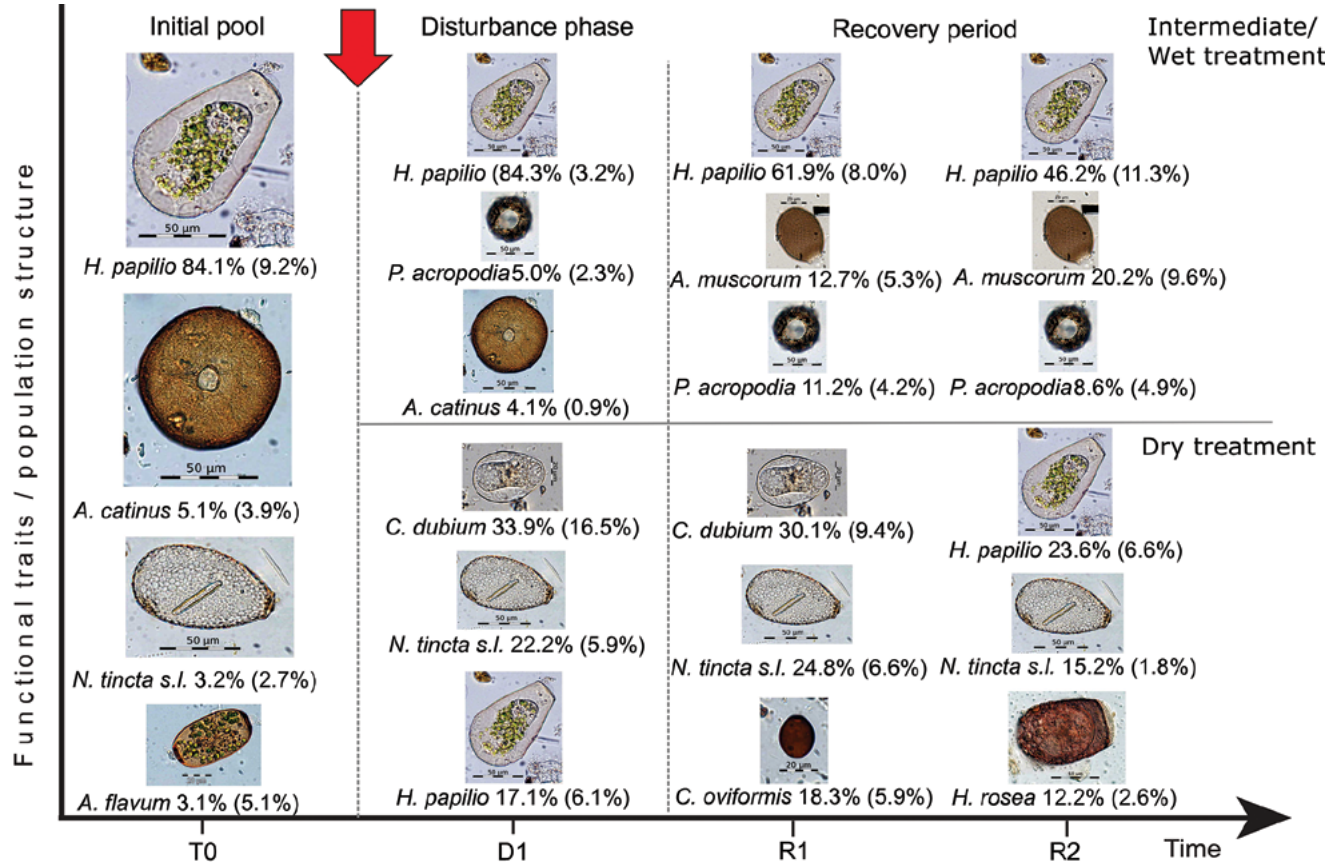
The CWMs did not differ significantly between the wet and intermediate treatments. In these two treatments, changes occurred only after D1, with a slow transition towards traits indicating drier conditions, at least in some plots. CWMs of traits further suggest that the vitality status of the *Sphagnum* layer was the main driver in wet & intermediate plots (Suppl. Fig. 1) while water table depth more strongly affected the testate amoeba community structure in the dry plots. This is in line with previous observations on the strong role of moisture conditions along the *Sphagnum* stem in shaping testate amoeba communities: Actual moisture conditions is a more likely driver of community structure than water level (Buttler *et al.* 1996; Mitchell *et al.* 1999; Booth 2001, 2002; Jassey *et al.* 2011; Payne *et al.* 2016), which also explains why transfer functions typically fail to predict very low water tables (e.g. lower than 30 cm depth, Mitchell *et al.* 1999).

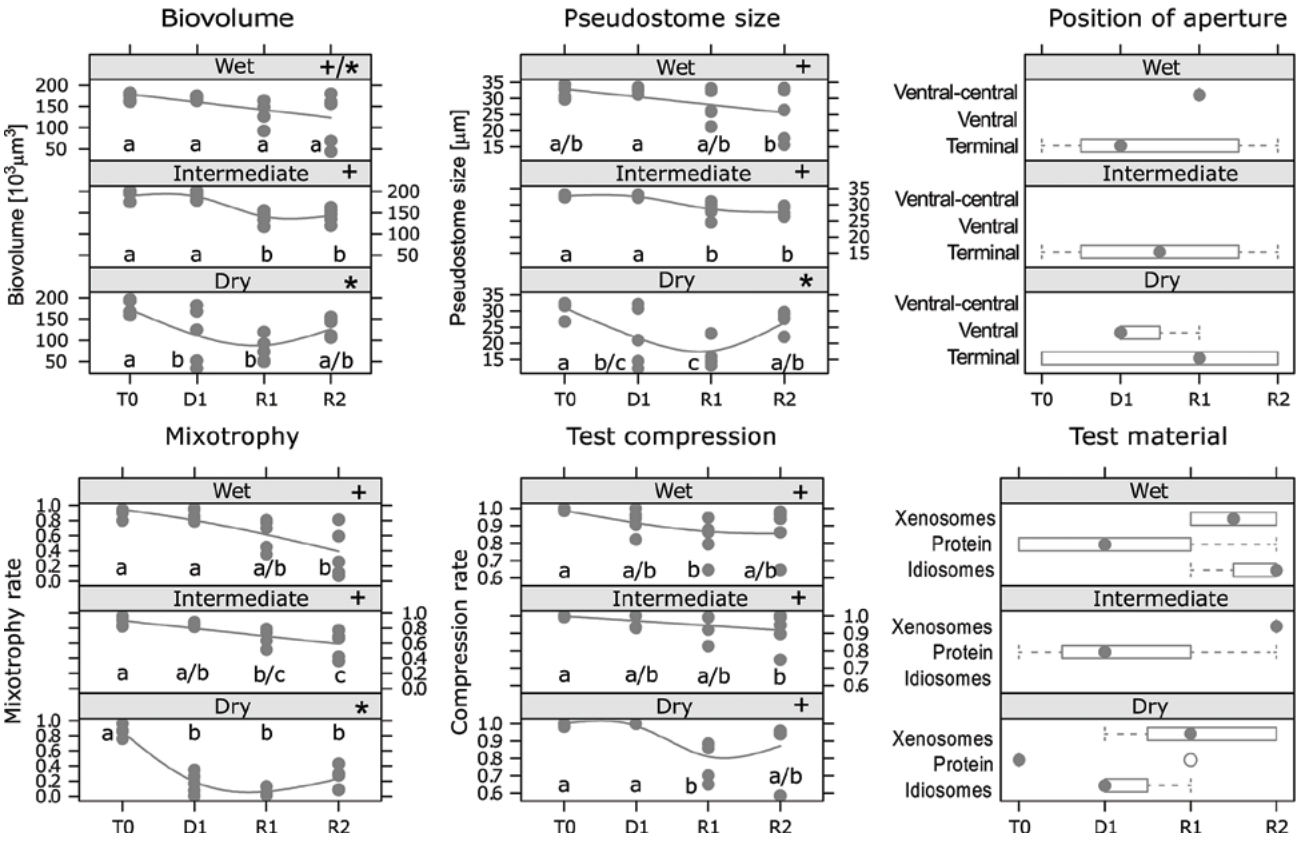
Community assembly: habitat filtering vs. biotic factors

We used the null model approach to disentangle biotic from abiotic drivers of community assembly. Changes in ecological niche should impact on testate amoeba community structure and this will be reflected by the CWM of traits. The distance between sampling plots (mean pairwise distance) should be significantly lower than the random distance in plots where abiotic drivers are more important than competition (Chase *et al.* 2011; Fournier *et al.* 2012; Arrieira *et al.* 2015). In our experiment, the trend in dry plots was negative (significantly in two replicates, Fig. 3) and, indicated that the community structure of testate amoeba was mainly driven by environmental filters (Villéger *et al.* 2008). The same pattern occurred in two replicates of the wet treatment (W2 and W5), in line with the state of the *Sphagnum* carpet in these plots. The shift toward reduced water saturation (related to dryness) imply an important constraint for the microbial communities living in *Sphagnum* and, as one of the most important groups, testate amoeba respond strongly to the change. The loss of mixotrophy and the increase of smaller, mainly bacterivorous taxa indicate a drastic change in ecosystem functioning with deep impact on nutrient and carbon cycling (Jassey *et al.* 2013a, 2013b; Fournier *et al.* 2015). Thus, by using CWM of well selected traits, we are able to highlight ongoing processes without prior knowledge on species ecology.

CONCLUSION AND SUGGESTIONS FOR FUTURE WORK

Our goal was to monitor the response of the testate amoeba community to a water level that had been "restored" to a level comparable to natural *Sphagnum*


Initial pool
Disturbance phase
Recovery period
Intermediate/
Wet treatment
Dry treatment
Functional traits / population structure
H. papilio 84.1% (9.2%)
A. catinus 5.1% (3.9%)
N. tincta s.l. 3.2% (2.7%)
A. flavum 3.1% (5.1%)
H. papilio (84.3% (3.2%)
P. acropodia5.0% (2.3%)
A. catinus 4.1% (0.9%)
C. dubium 33.9% (16.5%)
N. tincta s.l. 22.2% (5.9%)
H. papilio 17.1% (6.1%)
H. papilio 61.9% (8.0%)
A. muscorum 12.7% (5.3%)
P. acropodia 11.2% (4.2%)
C. dubium 30.1% (9.4%)
N. tincta s.l. 24.8% (6.6%)
C. oviformis 18.3% (5.9%)
H. papilio 46.2% (11.3%)
A. muscorum 20.2% (9.6%)
P. acropodia8.6% (4.9%)
H. papilio 23.6% (6.6%)
N. tincta s.l. 15.2% (1.8%)
H. rosea 12.2% (2.6%)
T0
D1
R1
R2
Time


Biovolume
Biovolume [10³µm³]
Wet
Intermediate
Dry
Pseudostome size
Pseudostome size [µm]
Position of aperture
Ventral-central
Ventral
Terminal
Mixotrophy
Mixotrophy rate
Test compression
Compression rate
Test material
Xenosomes
Protein
Idiosomes
T0
D1
R1
R2

peatlands using a mesocosm experiment. Due to the relatively small diameter of the mesocosms used in our experiment (12 cm) the survival of *Sphagnum* mosses cannot be guaranteed. Larger mesocosms would be useful to conduct longer-term experiments, but at a higher cost. The choice of the size is clearly a trade-off. Furthermore, over the course of our experiment, the differential growth of the mosses and mineralization of the underlying peat caused the surface of the moss carpet to strongly diverge among treatments (ca. 20 cm height difference by the end of the experiment), thus creating additional microclimatic effects (shading). Nevertheless, the survival of testate amoeba communities throughout the experiment, allowed us, for the first time experimentally, to assess community recovery in response to a raise in water level comparable with what is aimed for in peatland restoration projects in open areas. Our study also illustrates the importance of taking into consideration the changes in vegetation and especially the changes in *Sphagnum* cover. *Sphagnum* is a well-known keystone genus in peatland ecology. To this date few studies of peatland testate amoebae have explored specifically the difference of testate amoeba communities between *Sphagnum* and other mosses (e.g. Opravilova and Hajek 2006; Lamentowicz *et al.* 2011; Lizoňová and Horsák 2017). Our study suggests that where *Sphagnum* is absent the relationship between testate amoeba communities and water table depth is not the same as in *Sphagnum* carpet. This question deserves to be studied further.

The response patterns of the community weighted means of functional traits were similar to those of testate amoeba community structure and both were well correlated to ecological constraints. Through the link between the selected traits and the underlying processes, the CWM approach give information on local processes which complemented and sometimes explained the shift in community structure, as noted for the diverging response of some wet/intermediate plots in the recovery phase. In addition, the functional diversity approach circumvents to some extent the need for high taxonomic resolution, which may not be easily achieved for non-specialists and can lead to erroneous interpretation in some cases (Heger *et al.* 2009; Mitchell *et al.* 2014). Testate amoeba taxonomy is constantly changing and molecular based studies are revealing cryptic diversity (Lara *et al.* 2007; Heger *et al.* 2009; Kosakyan *et al.* 2013, 2016; Oliverio *et al.* 2014; Singer *et al.* 2015). Until a better taxonomy is available, the functional diversity approach, based on easily-measurable morphological traits represents a powerful approach to infer ecological processes (de Bello *et al.* 2010; Fournier *et al.* 2012, 2015; Mitchell *et al.* 2014). Measuring the proportion of mixotrophs, the size and position of the pseudostome or the size category of testate amoebae is thus a promising approach to monitor the impact of perturbations or restoration on *Sphagnum* peatlands (Fournier *et al.* 2015; Payne *et al.* 2016; Marcisz *et al.* 2016). To our knowledge these tools have not yet been used in environmental consulting or by managers, and it is worth developing them.

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Fig. 4. Top: summary representation of the evolution testate amoeba communities from a *Sphagnum fallax* mesocosm experiment simulating water table changes. The size of illustrated species is approximately to their relative body size. As communities in the intermediate and wet treatments were not significantly different, they are pooled together for the species based evolution (upper part). The three most abundant taxa (mean abundance) at each sampling time are represented (four at T0). Present at the beginning of the experiment, *A. flavum* recovered only slightly in intermediate plots at R2 (not shown). Small taxa (*P. acropodia*, *A. muscorum*, *C. oviformis*, *C. dubium*) increased after the disturbance (arrow) and in dry plots *H. papilio* almost disappeared at R1 and recovered at R2. Bottom: Evolution of testate amoeba functional traits. Different signs (+, *) or letters indicate significant differences. The lines show the cubic spline interpolation of the CWM of trait at each sampling points (n = 5). As shown in the upper graph based on taxonomic community structure, in the wet and intermediate treatments the disturbance effect remained in the recovery phase in some plots, which is indicated by the increasing spread of points and constantly decreasing spline line. By contrast, in dry plots, the maximum stress response was observed at D1 and R1 followed by a partial recovery at R2. In the dry treatment, the dominant positions of the pseudostome was ventral at D1 and terminal at R1.

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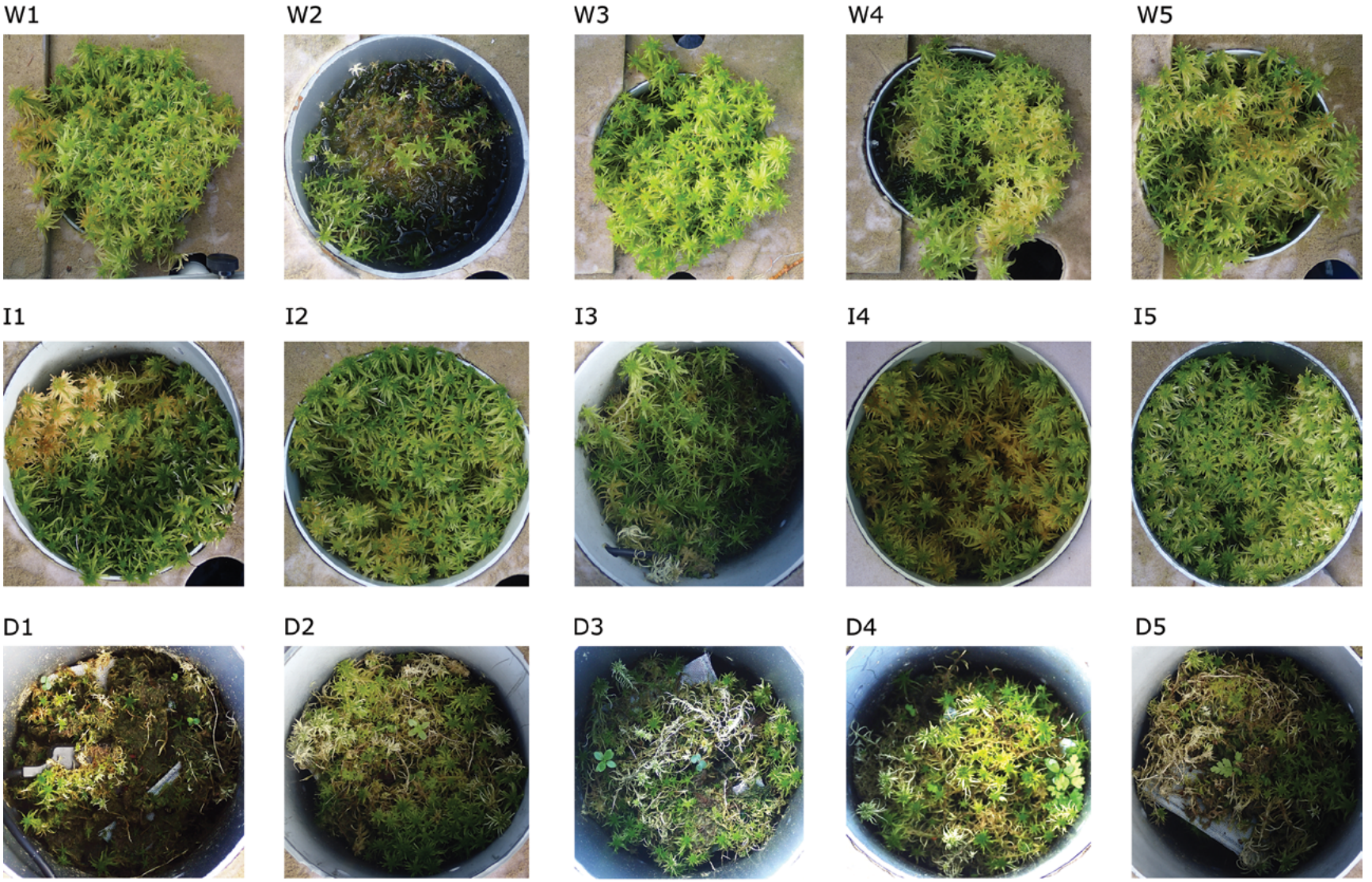
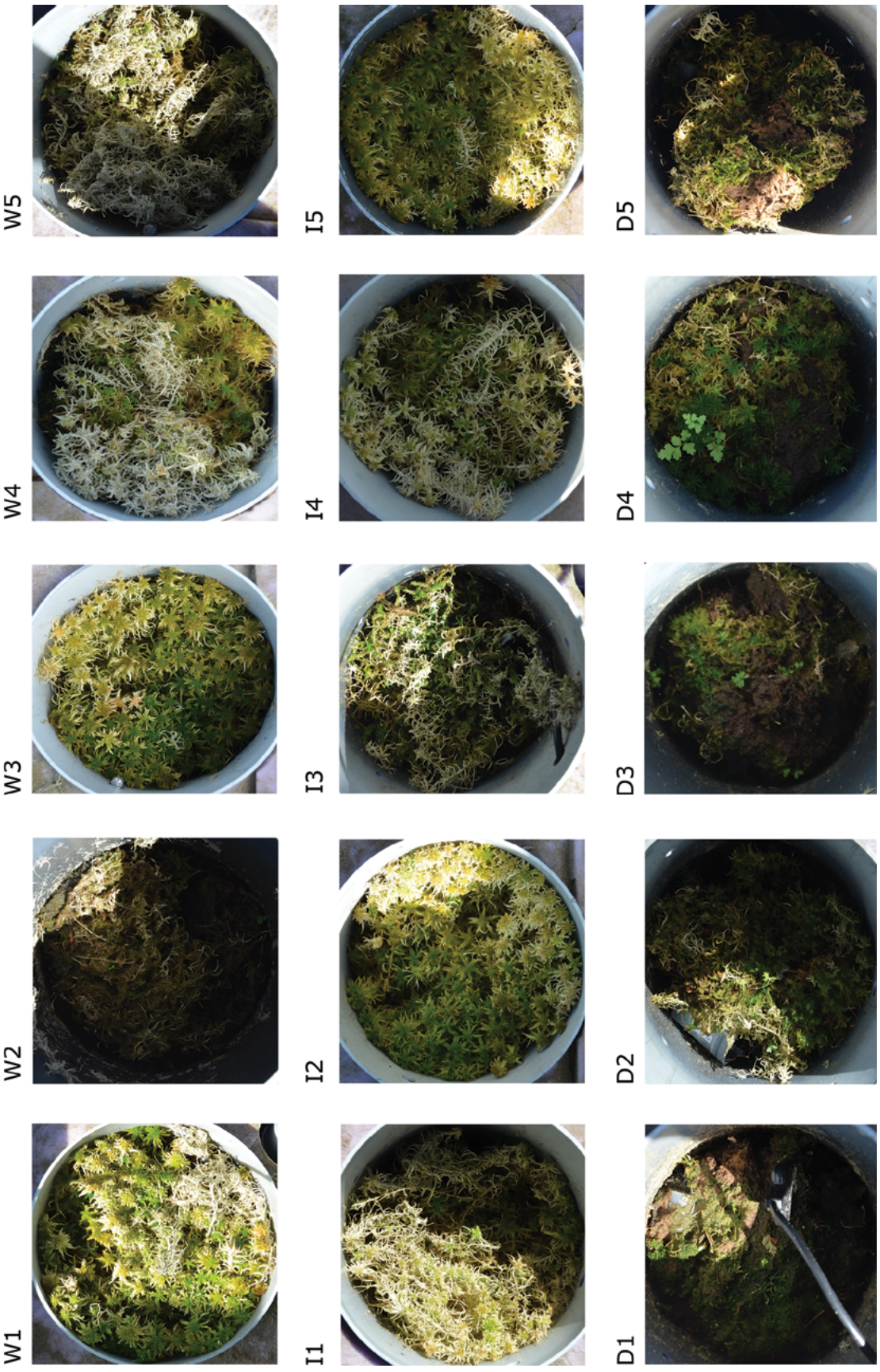
Supp. Table 1. Whole dataset of testate amoeba.

Site	Date	Time	Treatment	Amp_wri	Arc_cat	Arc_fla	Ass_mus	Cen_acu	Cor_dub	Cry_ovi	Cyc_eur	Eug_cil	Hel_ros	Hel_sph	Hya_pap	Neb_tin	Phr_acr	Phy_gri	Total Ind.
D1	2012-08-02	T0	Dry	0,0%	8,4%	0,8%	0,0%	0,0%	0,0%	0,0%	0,0%	2,3%	0,8%	0,0%	85,5%	2,3%	0,0%	0,0%	131
D2	2012-08-02	T0	Dry	0,0%	0,0%	5,6%	0,0%	0,8%	0,0%	0,0%	0,0%	0,0%	1,6%	0,0%	90,4%	1,6%	0,0%	0,0%	125
D3	2012-08-02	T0	Dry	0,0%	7,4%	16,7%	0,0%	1,9%	0,0%	0,0%	1,9%	3,7%	0,9%	0,0%	59,3%	8,3%	0,0%	0,0%	108
D4	2012-08-02	T0	Dry	0,0%	9,5%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	3,2%	0,0%	0,0%	87,3%	0,0%	0,0%	0,0%	63
D5	2012-08-02	T0	Dry	0,0%	1,2%	0,0%	0,0%	0,0%	3,5%	0,0%	0,0%	0,0%	0,0%	0,0%	85,9%	9,4%	0,0%	0,0%	85
I1	2012-08-02	T0	Intermediate	0,0%	9,8%	0,0%	0,0%	0,5%	1,0%	0,0%	0,0%	0,0%	0,0%	0,0%	84,0%	4,6%	0,0%	0,0%	194
I2	2012-08-02	T0	Intermediate	0,0%	1,6%	0,0%	1,0%	0,3%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	95,9%	1,3%	0,0%	0,0%	315
I3	2012-08-02	T0	Intermediate	0,0%	1,8%	0,0%	1,2%	1,2%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	90,9%	4,8%	0,0%	0,0%	165
I4	2012-08-02	T0	Intermediate	0,0%	11,1%	0,0%	0,5%	1,0%	0,0%	0,0%	0,5%	0,5%	0,0%	0,0%	82,9%	3,5%	0,0%	0,0%	199
I5	2012-08-02	T0	Intermediate	0,0%	8,5%	0,0%	1,2%	1,2%	0,0%	0,0%	0,6%	0,0%	2,4%	0,0%	82,3%	3,7%	0,0%	0,0%	164
W1	2012-08-02	T0	Wet	0,0%	2,7%	6,1%	2,7%	0,7%	0,0%	0,0%	0,0%	2,0%	0,7%	0,0%	83,8%	1,4%	0,0%	0,0%	148
W2	2012-08-02	T0	Wet	0,0%	3,6%	11,5%	0,0%	0,6%	0,0%	0,0%	0,6%	2,4%	0,6%	0,0%	79,4%	1,2%	0,0%	0,0%	165
W3	2012-08-02	T0	Wet	0,0%	8,6%	5,7%	0,0%	2,9%	0,0%	0,0%	1,4%	2,9%	0,0%	0,0%	74,3%	4,3%	0,0%	0,0%	70
W4	2012-08-02	T0	Wet	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,7%	0,0%	4,4%	0,0%	94,2%	0,7%	0,0%	0,0%	137
W5	2012-08-02	T0	Wet	0,0%	2,8%	0,0%	0,6%	0,0%	0,0%	0,0%	0,0%	1,1%	0,6%	0,0%	93,3%	1,7%	0,0%	0,0%	180
D1	2014-03-27	D1	Dry	0,0%	3,4%	0,0%	1,3%	7,4%	0,0%	0,0%	0,0%	2,7%	26,2%	0,0%	26,2%	28,2%	0,0%	4,7%	149
D2	2014-03-27	D1	Dry	0,0%	4,3%	0,0%	4,3%	2,1%	17,0%	0,0%	0,0%	10,6%	2,1%	0,0%	17,0%	42,6%	0,0%	0,0%	47
D3	2014-03-27	D1	Dry	0,0%	1,1%	0,0%	0,6%	0,0%	83,9%	0,0%	0,0%	0,6%	0,6%	0,0%	0,6%	12,6%	0,0%	0,0%	174
D4	2014-03-27	D1	Dry	0,0%	0,0%	0,0%	3,4%	27,6%	6,9%	0,0%	0,0%	0,0%	17,2%	0,0%	34,5%	10,3%	0,0%	0,0%	29
D5	2014-03-27	D1	Dry	0,0%	0,5%	0,0%	2,0%	1,5%	61,9%	0,0%	0,0%	8,4%	0,0%	0,0%	7,4%	17,3%	0,0%	1,0%	202
I1	2014-03-27	D1	Intermediate	0,0%	5,3%	0,0%	2,6%	0,0%	0,0%	0,0%	0,0%	0,9%	0,0%	0,0%	83,3%	0,9%	6,1%	0,9%	114
I2	2014-03-27	D1	Intermediate	0,0%	8,7%	0,0%	0,0%	0,6%	0,0%	0,0%	0,0%	0,6%	1,2%	0,0%	82,1%	0,0%	6,9%	0,0%	173
I3	2014-03-27	D1	Intermediate	0,0%	10,2%	0,0%	1,1%	0,5%	0,0%	0,0%	0,0%	0,0%	3,2%	0,0%	82,4%	2,7%	0,0%	0,0%	187
I4	2014-03-27	D1	Intermediate	0,0%	4,1%	0,0%	4,1%	0,0%	0,0%	0,0%	0,0%	0,0%	1,4%	0,0%	87,8%	2,7%	0,0%	0,0%	74
I5	2014-03-27	D1	Intermediate	0,0%	7,4%	0,0%	1,2%	1,2%	0,0%	0,0%	0,0%	1,2%	0,0%	0,0%	85,2%	3,7%	0,0%	0,0%	81
W1	2014-03-27	D1	Wet	1,6%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	3,2%	0,0%	84,1%	1,6%	9,5%	0,0%	63
W2	2014-03-27	D1	Wet	3,6%	3,6%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	75,0%	0,0%	17,9%	0,0%	28
W3	2014-03-27	D1	Wet	2,6%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	93,4%	0,0%	3,9%	0,0%	76
W4	2014-03-27	D1	Wet	3,9%	0,0%	0,0%	2,0%	7,8%	0,0%	0,0%	0,0%	2,0%	0,0%	0,0%	78,4%	0,0%	5,9%	0,0%	51
W5	2014-03-27	D1	Wet	3,6%	1,8%	0,0%	0,9%	0,9%	0,0%	0,0%	0,0%	0,0%	1,8%	0,0%	91,1%	0,0%	0,0%	0,0%	112
D1	2015-05-18	R1	Dry	0,0%	0,9%	0,0%	1,8%	1,8%	32,9%	34,7%	0,0%	5,0%	1,8%	0,9%	12,6%	2,3%	0,0%	5,4%	222
D2	2015-05-18	R1	Dry	0,0%	4,6%	0,0%	1,3%	6,6%	34,9%	11,8%	0,0%	2,0%	2,0%	0,0%	1,3%	34,9%	0,0%	0,7%	152
D3	2015-05-18	R1	Dry	0,0%	0,6%	0,0%	1,3%	0,0%	23,7%	29,5%	0,0%	2,6%	5,1%	0,0%	1,9%	35,3%	0,0%	0,0%	156
D4	2015-05-18	R1	Dry	0,0%	0,0%	0,0%	5,7%	4,1%	0,8%	4,1%	5,7%	11,5%	6,6%	0,0%	13,9%	38,5%	0,0%	9,0%	122
D5	2015-05-18	R1	Dry	0,0%	0,0%	0,0%	0,0%	1,8%	59,6%	11,9%	0,0%	0,9%	3,7%	0,0%	4,6%	17,4%	0,0%	0,0%	109
I1	2015-05-18	R1	Intermediate	0,0%	1,3%	0,0%	11,1%	0,0%	0,0%	0,0%	0,0%	0,7%	0,0%	0,7%	78,4%	0,0%	7,8%	0,0%	153
I2	2015-05-18	R1	Intermediate	0,0%	1,1%	0,0%	16,6%	0,0%	0,5%	0,0%	1,1%	0,0%	0,0%	0,0%	64,2%	0,0%	16,6%	0,0%	187
I3	2015-05-18	R1	Intermediate	0,0%	0,8%	0,0%	5,0%	2,5%	30,3%	0,0%	0,0%	0,0%	1,7%	0,8%	51,3%	6,7%	0,8%	0,0%	119
I4	2015-05-18	R1	Intermediate	0,0%	0,7%	1,3%	24,2%	0,0%	0,7%	0,0%	0,0%	0,0%	0,0%	0,0%	72,5%	0,0%	0,7%	0,0%	153
I5	2015-05-18	R1	Intermediate	0,0%	3,2%	0,0%	19,2%	0,6%	1,3%	0,0%	0,0%	0,6%	0,0%	0,0%	74,4%	0,0%	0,6%	0,0%	156
W1	2015-05-18	R1	Wet	0,4%	1,3%	0,0%	0,0%	0,0%	4,4%	0,0%	0,0%	0,0%	0,0%	1,3%	78,8%	0,0%	13,7%	0,0%	226
W2	2015-05-18	R1	Wet	11,1%	5,6%	0,0%	0,0%	5,6%	11,1%	0,0%	0,0%	0,0%	0,0%	5,6%	22,2%	5,6%	33,3%	0,0%	18
W3	2015-05-18	R1	Wet	0,0%	0,0%	0,0%	0,0%	0,5%	2,0%	0,0%	0,0%	0,0%	0,0%	0,0%	77,1%	0,0%	20,5%	0,0%	205
W4	2015-05-18	R1	Wet	9,6%	0,0%	0,0%	38,4%	0,0%	4,8%	0,0%	0,0%	0,7%	0,0%	0,0%	36,3%	0,0%	10,3%	0,0%	146
W5	2015-05-18	R1	Wet	8,7%	0,0%	0,0%	13,3%	0,0%	9,3%	0,0%	0,0%	2,0%	0,0%	0,0%	61,3%	0,0%	5,3%	0,0%	150
D1	2015-09-24	R2	Dry	0,0%	0,0%	0,0%	0,8%	11,8%	1,7%	0,0%	2,5%	4,2%	8,4%	1,7%	42,9%	9,2%	1,7%	15,1%	119
D2	2015-09-24	R2	Dry	0,0%	0,0%	0,0%	0,0%	10,5%	9,6%	0,0%	0,0%	0,9%	21,1%	0,0%	30,7%	21,1%	0,9%	5,3%	114
D3	2015-09-24	R2	Dry	0,0%	1,1%	0,0%	2,3%	3,4%	1,1%	0,0%	0,0%	6,8%	18,2%	0,0%	30,7%	15,9%	0,0%	20,5%	88
D4	2015-09-24	R2	Dry	0,0%	0,0%	0,0%	8,1%	4,4%	0,0%	0,0%	40,7%	6,7%	8,9%	0,0%	8,9%	17,8%	0,0%	4,4%	135
D5	2015-09-24	R2	Dry	0,0%	0,9%	0,0%	31,9%	12,9%	6,0%	0,0%	0,9%	8,6%	8,6%	1,7%	10,3%	17,2%	0,9%	0,0%	116
I1	2015-09-24	R2	Intermediate	0,0%	2,9%	0,0%	17,6%	0,0%	2,9%	0,0%	0,0%	0,0%	0,0%	0,0%	66,2%	0,0%	10,3%	0,0%	136
I2	2015-09-24	R2	Intermediate	0,0%	2,1%	2,8%	26,2%	0,0%	0,0%	0,0%	5,5%	0,0%	0,7%	9,7%	35,9%	0,0%	17,2%	0,0%	145
I3	2015-09-24	R2	Intermediate	0,8%	0,8%	0,0%	0,0%	23,0%	4,0%	0,0%	0,8%	1,6%	6,3%	0,0%	38,1%	19,0%	0,8%	4,8%	126
I4	2015-09-24	R2	Intermediate	0,0%	3,6%	5,8%	23,9%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	2,9%	61,6%	1,4%	0,7%	0,0%	138
I5	2015-09-24	R2	Intermediate	0,0%	5,6%	0,0%	16,2%	0,0%	0,0%	0,0%	0,0%	0,6%	0,0%	0,0%	77,1%	0,6%	0,0%	0,0%	179
W1	2015-09-24	R2	Wet	0,0%	4,2%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,7%	0,0%	2,8%	78,9%	0,0%	13,4%	0,0%	142
W2	2015-09-24	R2	Wet	2,8%	2,8%	0,0%	1,9%	33,6%	0,9%	0,0%	0,0%	15,0%	6,5%	0,0%	23,4%	6,5%	1,9%	4,7%	107
W3	2015-09-24	R2	Wet	0,0%	1,9%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	2,8%	0,0%	0,9%	60,2%	0,0%	34,3%	0,0%	108
W4	2015-09-24	R2	Wet	0,0%	0,0%	0,7%	71,5%	0,7%	9,5%	0,0%	0,0%	2,9%	0,0%	0,0%	10,9%	0,0%	3,6%	0,0%	137
W5	2015-09-24	R2	Wet	0,0%	0,0%	0,0%	46,0%	2,2%	11,7%	0,0%	0,0%	8,0%	3,6%	0,0%	7,3%	16,8%	2,9%	1,5%	137

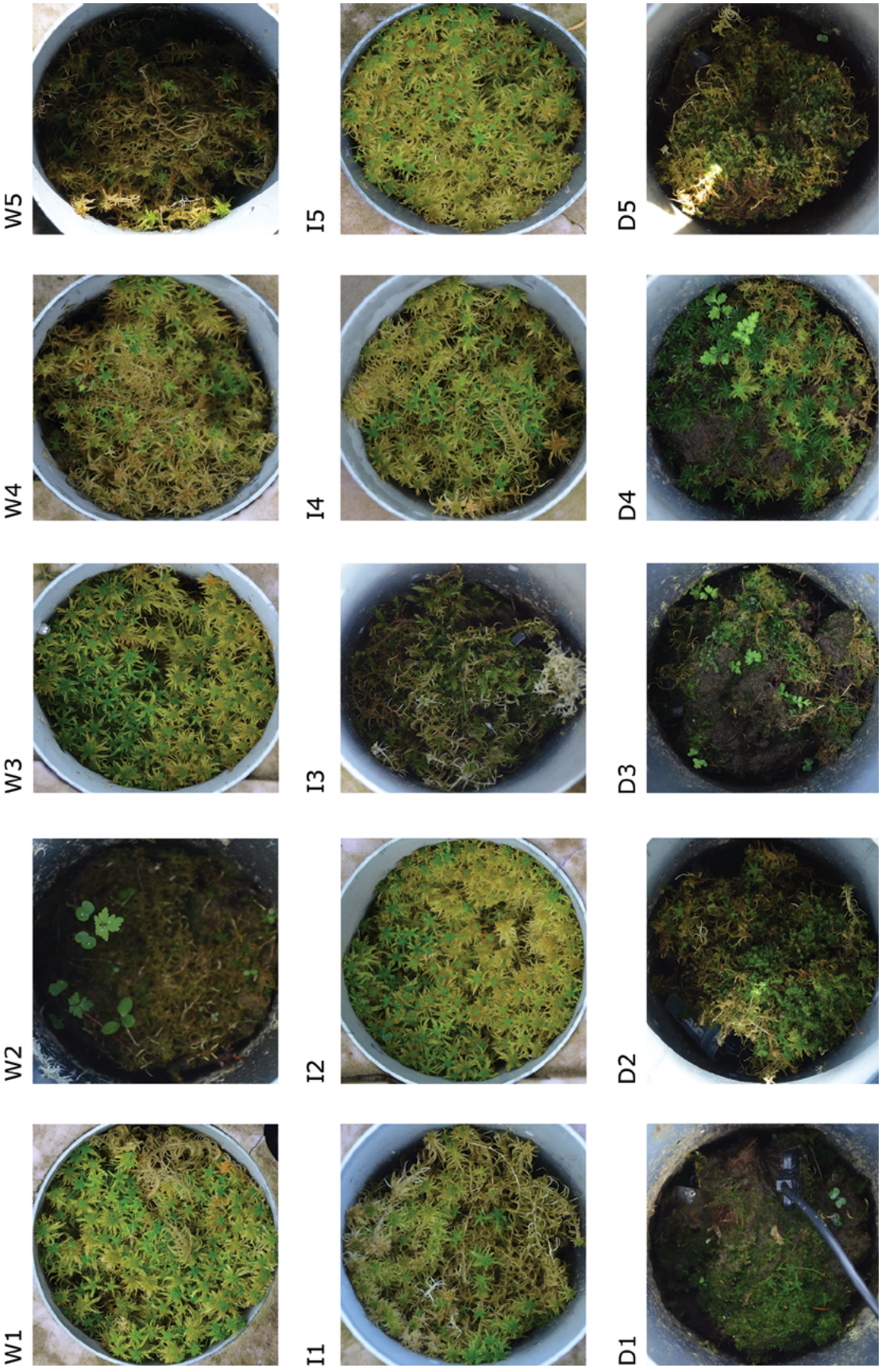
Supp. Figures 1–3. Orthogonal picture of each mesocosm with the *Sphagnum* carpets, W: wet treatment, I: Intermediate treatment, D: dry treatment:



1) D1, on the 05/08/2014



2) One year later, between R1 and R2: 28/08/2015



3) R2: on the 23/09/2015