



Refugial peatlands in the Northern Apennines. Vegetation-environment relationships and future perspectives

Lisa Brancaloni, Michele Carbognani, Renato Gerdol*, Marcello Tomaselli & Alessandro Petraglia

Abstract

Aims: We aimed to detect the environmental drivers conditioning plant diversity and to predict how modifications in habitat conditions and ongoing global warming could lead to vegetation changes or biodiversity losses in a region especially rich in peatlands despite its relatively low latitude. **Study area:** The study area was located in the Northern Apennines, Northern Italy (about 44°45' N; 10°20' E). The vegetation study was carried out at 12 peatland sites where 206 plots were set up. Species composition in the 206 plots were recorded in the field and classified with cluster analysis. Data on hydrology, water chemistry and peat chemistry were collected at a subset of 127 plots and statistically analysed by a multivariate ordination method. Species richness and evenness were calculated for all plots. Relationships between species composition and environmental variables were analysed by stepwise multiple regression. **Results:** The cluster analysis defined 17 vegetation units. Water table depth represented the major environmental factors accounting for vegetation patterns, with the vegetation units being grouped in four main blocks based on vegetation physiognomy and species composition: *Sphagnum* hummocks, *Sphagnum* lawns, fens and pools. Water chemistry and peat chemistry both presented moderate variations among the vegetation units with mean water pH ranging from 4.9 to 6.3. Concentrations of major cations in the pore water showed that all of the habitats investigated were influenced by telluric water, with no evidence of ombrotrophic conditions. Species richness and evenness both presented poor relations with the environment while responses of individual species to environmental factors were more informative on vegetation changes triggered by climate change. **Conclusions:** Prolonged drought events associated with high temperature in summer months are expected to exert a strong impact on peatland vegetation. The main effect of climate change on the vegetation of the peatlands investigated consists in the spreading of vascular plants at the expense of *Sphagnum* mosses.

Keywords: biodiversity; climate change; hydrology; indicator value index; mire ecology; peat chemistry; species richness; water chemistry; water table depth, water table range

Taxonomic references: Portal to the Flora of Italy (2021) for vascular plants; Aleffi et al. (2020) for bryophytes.

Abbreviations: CCA = canonical correspondence analysis; IndVal = Indicator Value; H = Shannon-Wiener diversity index; S = Species richness index.

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Introduction

Wetlands in general and peatlands in particular have a wide range of ecosystem functions, from storing carbon and water to providing food, medical supplies and building materials as well as offering wilderness areas for recreation (Bonn et al. 2016; Joosten et al. 2017). Moreover, a widely valued function of peatlands is the maintenance

of regional biodiversity, because peatlands provide specific habitats for flora and fauna and are home to specialized biota (Essl et al. 2012). Nutrient shortage and extreme hydrological conditions in these habitats act as strong limiting factors for many plant species (Bridgham et al. 1996). Hence, only the species capable to cope with such extreme environmental conditions can grow in peatlands, thus becoming part of their plant communities. In

*Corresponding author's address: Department of Environmental and Prevention Sciences, University of Ferrara, Corso Ercole I d'Este 32, 44121 Ferrara, Italy (grn@unife.it). Complete addresses of all authors can be found at the bottom of the paper.

the European Union, a number of these plant species are considered of community interest according to the Directive 92/43/EEC for being rare and endangered and, therefore, worthy to be preserved (Bragazza 2009). Peatlands represent vulnerable ecosystems, strongly depending on delicate equilibria among water input, nutrient loading, climate and major ecological processes, especially plant production and organic matter decomposition (Rydin & Jeglum 2006). In the last few decades, peatland cover declined because of changing habitat conditions proceeding at unprecedented rates as an effect of climate warming and human activities (Gerdol et al. 2008). Loss and degradation of peatlands led to a 70% decrease in their total surface in Europe (Raeymaekers 2000). As a result, this habitat is regarded as one of the most threatened in the European Union (Janssen et al. 2016). Therefore, peatland conservation and restoration is becoming a major priority on European and national agendas (Colomer et al. 2019).

Peatlands are particularly sensitive to human-driven environmental changes such as peat mining, water reservoir construction, irrigation diversions for agricultural water use, road construction, livestock grazing, housing and ski area development (Chimner et al. 2010) but are also highly vulnerable to water table drawdown and increased evapotranspiration induced by climatic changes such as decreasing precipitation and rising temperatures. They can be seen as adaptive systems that are resilient to some level of environmental change, but strong or persistent levels of disturbance can promote succession towards new states (Heijmans et al. 2008; Dise 2009; Page & Baird 2016). Peatland type has a strong impact on the response to water table drawdown. A recent experiment of water level drawdown over 17 years in three peatland types differing in fertility highlighted that minerotrophic fens underwent rapid species turnover, while bog vegetation was more resilient to change (Kokkonen et al. 2019). Anyway, understanding the response of peatland vegetation to changing hydroecological conditions is a key step in setting peatland management and conservation within a context of global climate change. In particular, periodic monitoring of vegetation patterns, hydrology, groundwater and peat chemistry in these ecosystems could be strategic for assessing the integrity of plant communities and for planning conservation and/or restoration measures (Schumann & Joosten 2008; Gerdol et al. 2011; Tomaselli et al. 2018).

In the light of the above considerations, we wondered whether it was possible to individuate a mountain area in Italy where peatlands: i) occurred with adequate frequency and habitat richness; ii) were poorly documented with respect to similar habitats of the Atlantic and boreal regions; iii) provided regionally important refugia for rare plant species. An area with such features seemed suitable for a study aiming at establishing a connection between vegetation ecology and conservation. We ex-

cluded the Alps where peatlands have been thoroughly studied in the last decades (see Gerdol 1990; Gerdol et al. 1994; Gerdol & Tomaselli 1997; Bragazza & Gerdol 1999, 2002; Lederbogen 2003; Miserere et al. 2003; Gerdol et al. 2011; Conradi & Friedmann 2013) and individuated the Northern Apennines as the mountain system which met the above requirements. In fact, peatlands in the Northern Apennines are both abundant and relatively diversified in species composition and habitat features (Gerdol & Tomaselli 1993; Raffaelli et al. 1997; Petraglia & Tomaselli 2003; Fogli et al. 2014). Moreover, the Northern Apennines are an area of phytogeographic and ecologic transition between the Alps and the central Apennines (Foggi 1990), representing an important refugium for boreal species, several of them attaining here their southernmost distribution border in Italy (Petraglia & Tomaselli 2003). Despite the high phytogeographic and conservation interest, peatlands in this area are overall poorly known. Peatland vegetation in the Northern Apennines has been the object of very few studies dating back to thirty or more years ago. These studies principally addressed species composition in peatland habitats, providing few if any data on environmental variables.

We undertook this study under the assumption that peatlands are presently undergoing losses of plant diversity (Jiménez-Alfaro et al. 2016; Sperle & Bruelheide 2021; Spitale 2021). Starting from this consideration, our study aimed to: i) individuate microhabitat patterns based on floristic composition; ii) detect the main environmental drivers conditioning plant diversity within the microhabitats; iii) predict how environmental modifications could lead to vegetation changes and biodiversity losses. In order to attain these goals, we examined species and vegetation patterns in relation to environmental variables that can potentially be responsible for such modifications (Hájek et al. 2022). Special focus was given to variables concerning hydrology, water chemistry and peat chemistry.

Materials and methods

The study area

The study area lies in the Northern Apennines, a 250 km long mountain range with NW-SE orientation at a latitude of about 44° N. The study sites were located in the Tuscan-Emilian district (provinces of Parma, Reggio Emilia and Lucca; Fig. 1), which represents the core of this mountain system whose highest peak is Monte Cimone (2165 m). The bedrock consists of sandstones of the Macigno Formation and medium- to coarse-grained sandstones alternating with fine-grained sandstones and siltstones of Monte Modino Formation (Bruni et al. 1994; Dinelli et al. 1999). The climate is temperate oceanic (Pesaresi et al. 2017) with average total annual precipita-

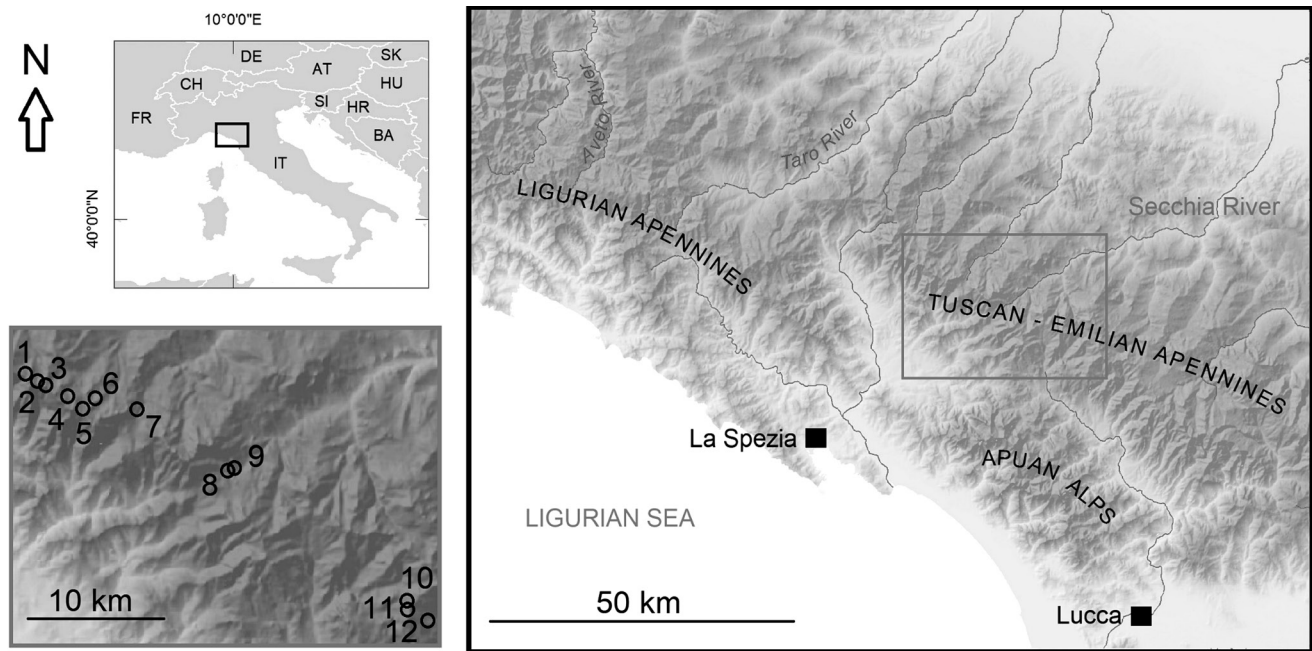


Fig. 1. Map of the study area with the locations of the peatlands.

1: Lago Scuro (LASC); 2: Pozza di Scala (POSC); 3: Sella di Rocca Pianaccia (SERP); 4: Lago Verde (LAVE); 5: Capanna Bianciani (CABI); 6: Pratospilla (PRSP); 7: Pradacci (PRAD); 8: Cerreto A (CERA); 9: Cerreto B (CERB); 10: Lamarossa Nord (LAMN); 11: Lamarossa (LAMA); 12: Campaiana (CAMP).

Table 1. List of the studied peatlands. Acronym, elevation, area, geographic coordinates and number of permanent plots are reported for each peatland site.

Peatland name	Acronym	Elevation (m)	Area (m ²)	Latitude N	Longitude E	No. of plots
Lago Scuro	LASC	1515	1950	44°22'50"	10°03'11"	22
Pozza di Scala	POSC	1680	1900	44°22'26"	10°03'34"	15
Sella di Rocca Pianaccia	SERP	1712	800	44°22'16"	10°04'05"	11
Lago Verde	LAVE	1543	2500	44°21'53"	10°05'16"	22
Capanna Bianciani	CABI	1552	4900	44°21'18"	10°05'50"	24
Pratospilla	PRSP	1349	4150	44°21'46"	10°06'31"	17
Pradacci	PRAD	1119	8500	44°21'30"	10°08'27"	18
Cerreto A	CERA	1285	1450	44°18'09"	10°14'03"	16
Cerreto B	CERB	1295	550	44°18'14"	10°14'23"	12
Lamarossa Nord	LAMN	1430	300	44°13'33"	10°22'52"	8
Lamarossa	LAMA	1450	11500	44°13'05"	10°22'52"	28
Campaiana	CAMP	1450	2800	44°12'30"	10°23'22"	13

tion exceeding 2000 mm on the south-western (Tuscan) slope of the Tuscan-Emilian Apennines lying closer to the Ligurian Sea. Along the north-eastern (Emilian) slope the climate is less humid with average total annual precipitation of about 1500 mm (Rapetti & Vittorini 1989).

The Tuscan-Emilian Apennine district of the Northern Apennines is asymmetric, with the Tuscan slope be-

ing rough and steep and almost entirely free from glacial and periglacial landforms. This is not surprising, since glacial activity took place only in the northern and eastern gentle slopes where glacial landforms are still apparent nowadays (Losacco 1982). Most of the peatlands in the Northern Apennines occur on these slopes where they represent more or less mature stages in the dynamic

process of filling up glacial lakes (Gerdol & Tomaselli 1993). Twelve peatlands were selected according to vegetation and environmental features in order to account for as much broad range of floristic and ecological diversity as possible at regional scale (Table 1). Most of the selected peatlands were located within the montane vegetation belt characterized by different types of beech forests (Ubaldi et al. 1993), with only two of them being located in the subalpine vegetation belt dominated by *Vaccinium* heaths (Ferrari & Piccoli 1997).

Field work

In spring 2014, we set up a total of 206 1 m × 1 m plots. These plots were randomly located in vegetation stands that covered the full range of habitats visually distinguished within each of the twelve peatland sites. Vegetation data was collected in summer 2014 by visual estimation of species cover (for both vascular plants and bryophytes) within each plot. Each plot had in its centre a pipe inserted into the peat for measuring water table depth. Measurements of water table depth were taken at least three times per growing season during the years 2014–2016. The mean values of water table depth and the range of water table depth calculated across all measurements were used in the subsequent analyses. Water and peat samples were taken in a subsample of 127 plots during summer 2016. On that occasion, 50 ml of water was collected from the pipes and immediately analysed for pH (XS Instruments; Carpi, MO, Italy) and electrical conductivity (Delta OHM, RS Components; Sesto San Giovanni, MI, Italy). In addition, two peat subsamples were collected by a cylindrical stainless steel corer (8 cm in diameter and 15 cm in depth) in each of the 127 plots. The peat subsamples were bulked and frozen. The water samples were also frozen and carried, together with the peat samples, to the Laboratory of Plant Ecology at Ferrara University for subsequent analyses.

Chemical analyses

Concentrations of major dissolved cations (Na^+ , K^+ , Ca^{2+} and Mg^{2+}) in the water samples were determined by atomic absorption spectrophotometry (Solaar 969; Unicam, Cambridge, UK) after adding lanthanum to reduce anionic interference.

Concentrations of extractable nutrients were determined in the peat samples. A 10-g subsample of peat was extracted in 100 mL of distilled water for analysing of extractable ammonium (N-NH_4) and nitrate (N-NO_3). A 2-g subsample of peat was extracted in 40 mL of NaHCO_3 buffered at 8.5 pH with NaOH , according to the Olsen method, for analysing extractable phosphate (P-PO_4). Nutrient concentrations in the peat extracts

were determined colorimetrically using a micro-flow automated continuous-flow analyser (Systema Flowsys; Anagni, FR, Italy). Ammonium concentrations were determined by the sodium salicylate method at 630 nm wavelength. Nitrate concentrations were determined by the cadmium reduction method at 525 nm wavelength. Phosphate concentrations were determined by the molybdenum blue method at 880 nm wavelength.

Data analyses

The 206 vegetation plots were classified with numerical procedures. The original cover values were transformed using the Hellinger distance (Legendre & Gallagher 2001). A cluster analysis was then performed with the Ward's minimum variance method on the transformed distance matrix. All computations concerning the numerical classification were performed in R version 4.0.1 (R Core Team 2020) with the 'vegan' and 'cluster' packages. The plot groups obtained by the classification corresponded to microhabitats within peatlands and represented the analysed vegetation units. For each vegetation unit we defined indicator species by calculating the Indicator Value (IndVal) index which measures the association between a species and a plot group (Duf rene & Legendre 1997). The IndVal index combines the mean relative abundance and the frequency of species occurrence in the target plot group. A high indicator value results from a combination of high mean abundance of a species within a group compared to the other groups (specificity) and its presence in most plots of that group (fidelity). We considered as significant indicator species those having an IndVal > 0.50 ($p < 0.001$). These indicator species were also used for naming the vegetation units. Some vegetation units more weakly characterized from the floristic viewpoint were named using indicator species significant at $p < 0.05$. The IndVal index was computed with the R package 'indicspecies'.

The species richness index (S ; as number of species m^{-2}) was calculated separately for vascular plants, bryophytes and all species occurring in each plot. The Shannon-Wiener diversity index (H) was calculated, as a measure of species evenness, for all plots with the following formula:

$$H = - \sum_{i=1}^n p_i \ln p_i$$

where p_i is the frequency of the i_{th} species and n the total number of species (both vascular plants and bryophytes) recorded in the plot.

A constrained ordination method (canonical correspondence analysis, CCA) was run on the 127 plots for which data on hydrology and water chemistry were available besides data on species composition. The CCA

was applied to the matrix of vegetation data containing the cover values, transformed with the Hellinger distance, of all significant and weakly significant indicator species (28 in total) and the matrix of eight hydrological and hydrochemical variables (water table depth, water table range, pH, electrical conductivity, Na^+ , K^+ , Ca^{2+} and Mg^{2+} concentrations). The CCA analysis was performed with the Software PAST (4.06, Hammer et al. 2001). The data on peat chemistry (N-NH_4 , N-NO_3 and P-PO_4 concentrations in the peat) were statistically analysed by univariate ANOVAs with vegetation unit as fixed factor. Significance of differences between mean values were assessed by the post-hoc LSD test.

Relationships between species richness and diversity, on one side, and the hydrological and hydrochemical variables, on the other side, were statistically analysed by linear regressions. Relationships between the frequencies of the indicator species and six variables related to hydrology, water chemistry and peat chemistry (water table depth, water table range, pH and electrical conductivity of the water, N-NH_4 , + N-NO_3 concentration in the peat and P-PO_4 concentration in the peat) were statistically analysed by multiple regressions. A stepwise procedure was used for the multiple regressions, with forward selection of the variables at a threshold of $F > 1$. All regressions were carried out using the package Statistica© (v. 13.5. TIBCO Software Inc., Palo Alto, CA, USA).

Results

Vegetation classification

Seventeen plot groups were recognized in the classification dendrogram at a dissimilarity value of about 2 (Fig. 2). These groups represented the main vegetation units. The frequency of the indicator species, as well as the fre-

quency of all other species in each group are shown in a synoptic table (Table 2) and the main features of the vegetation units are briefly described below. The detailed list of all plot samples of the vegetation units can be found in the Supplementary Material (Supplements S1-17). At higher hierarchical level in the dendrogram, the 17 groups were merged into two big clusters. The first cluster (SSU-SCA; Fig. 2) included all of the *Sphagnum*-dominated hummocks and lawns besides three fen grasslands. The second cluster included the remainder of the fen grasslands besides pools (CVE-CNI; Fig. 2).

1. *Sphagnum capillifolium* group (SCA; Table 2, Supplement S1)

Significant indicator species: *Sphagnum capillifolium*.

Constant species: *Sphagnum capillifolium*, *Potentilla erecta*.

Dominant species: no species dominating throughout. *Sphagnum capillifolium* was dominant in most plots, replaced in two of them by *Calluna vulgaris* or *Molinia caerulea*, respectively.

Physiognomy: species-poor elevated *Sphagnum* hummocks where *Sphagnum capillifolium* dominated, alternatively accompanied by *S. centrale*, *S. compactum* and *S. rubellum*. Vascular species played a subordinate role, with only *Calluna vulgaris* and *Molinia caerulea* being alternatively important and occasionally dominant.

2. *Sphagnum palustre* group (SPA; Table 2, Supplement S2)

Significant indicator species: *Sphagnum palustre*.

Constant species: *Sphagnum palustre*, *Carex nigra*, *Potentilla erecta*.

Dominant species: *Sphagnum palustre*.

Physiognomy: *Sphagnum* hummocks ranging from species-poor to moderately rich, with an extensive carpet of *Sphagnum palustre*. Vascular associates were relatively

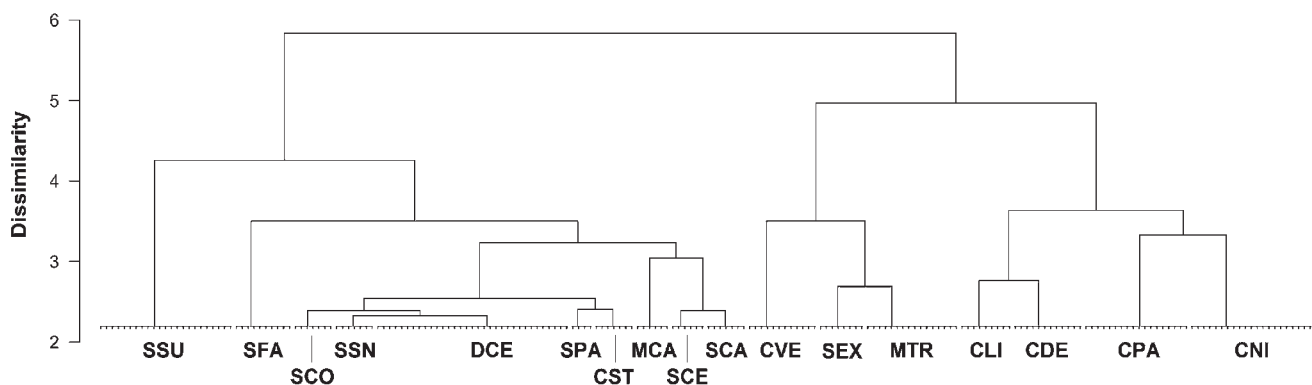


Fig. 2. Schematic classification dendrogram obtained by cluster analysis of 206 vegetation plots by the Ward's minimum variance method on the transformed Hellinger distance matrix. The branches at dissimilarity levels < 2 were omitted. Legend of acronyms as in Table 2.

Table 2. Species frequencies in the main vegetation units. The IndVal is shown for the significant indicator species ($p < 0.001$) and weakly significant indicator species ($p < 0.05$). The vegetation units are grouped based on physiognomy: *Sphagnum* hummocks (SCA-SCE); *Sphagnum* lawns (SCO-SSN); fens (MCA-CLI); pools (CVE-MTR). SCA: *Sphagnum capillifolium* group; SPA: *Sphagnum palustre* group; SCE: *Sphagnum centrale* group; SCO: *Sphagnum compactum* group; SSU: *Sphagnum subsecundum* group; SFA: *Sphagnum fallax* group; SSN: *Sphagnum subnitens* group; MCA: *Molinia caerulea* group; DCE: *Deschampsia cespitosa* group; CST: *Campyllum stellatum* group; CNI: *Carex nigra* group; CDE: *Carex demissa* group; CPA: *Caltha palustris* group; CLI: *Carex limosa* group; CVE: *Carex vesicaria* group; SEX: *Sarmentypnum exannulatum* group; MTR: *Menyanthes trifoliata* group.

Plot group	SCA	SPA	SCE	SCO	SSU	SFA	SSN	MCA	DCE	CST	CNI	CDE	CPA	CLI	CVE	SEX	MTR	IndVal
No. of plots	7	4	6	7	23	10	7	6	33	7	21	12	18	9	12	8	16	
No. of species	28	25	36	29	51	21	51	15	89	46	75	53	49	31	20	13	18	
INDICATOR SPECIES																		$p < 0.001$
<i>Sphagnum capillifolium</i>	100	.	17	57	0.85
<i>Sphagnum palustre</i>	.	100	.	14	.	20	.	.	3	.	5	8	0.98
<i>Sphagnum centrale</i>	57	.	100	.	4	10	.	.	42	57	5	8	0.84
<i>Sphagnum compactum</i>	29	.	.	100	13	.	.	67	6	13	19	0.84
<i>Sphagnum subsecundum</i>	29	.	.	100	100	.	.	50	48	.	10	8	.	.	8	38	25	0.76
<i>Sphagnum fallax</i>	29	25	.	14	4	100	.	33	12	8	.	.	0.93
<i>Sphagnum subnitens</i>	4	.	86	.	.	14	.	.	.	11	.	.	.	0.82
<i>Drosera rotundifolia</i>	57	0.57
<i>Molinia caerulea</i>	43	50	.	29	30	.	14	100	27	14	19	17	0.70
<i>Campyllum stellatum</i>	9	10	.	.	21	86	14	33	0.83
<i>Pinguicula christinae</i>	.	.	.	14	22	.	.	.	6	86	5	25	0.69
<i>Carex davalliana</i>	.	.	33	9	86	5	8	50	0.62
<i>Tomentypnum nitens</i>	.	.	17	.	4	.	.	.	3	71	10	0.58
<i>Carex demissa</i>	.	50	33	29	30	.	29	.	24	86	24	100	33	89	.	.	.	0.64
<i>Caltha palustris</i>	4	33	17	94	11	.	.	.	0.77
<i>Calliergonella cuspidata</i>	14	.	30	14	52	58	100	100	.	.	.	0.66
<i>Phragmites australis</i>	5	.	67	0.66
<i>Epilobium palustre</i>	.	.	17	.	.	.	14	.	12	14	38	17	94	100	8	.	.	0.56
<i>Carex limosa</i>	89	.	.	.	0.89
<i>Carex vesicaria</i>	83	.	.	0.83
<i>Veronica scutellata</i>	83	.	.	0.83
<i>Sphagnum inundatum</i>	14	83	.	.	0.83
<i>Galium palustre</i>	.	25	.	.	4	.	14	.	18	.	67	75	89	100	92	.	6	0.54
<i>Sarmentypnum exannulatum</i>	13	.	.	.	9	.	.	8	.	.	.	100	6	0.99
<i>Juncus filiformis</i>	29	.	.	29	48	30	14	.	15	.	19	.	.	.	33	100	31	0.54
<i>Menyanthes trifoliata</i>	14	.	.	.	9	20	50	0.39
<i>Carex nigra</i>	71	100	100	43	70	70	29	67	79	86	100	58	72	.	8	88	31	0.36
<i>Deschampsia cespitosa</i>	.	.	.	29	48	10	.	42	42	.	14	25	6	0.26

Plot group	SCA	SPA	SCE	SCO	SSU	SFA	SSN	MCA	DCE	CST	CNI	CDE	CPA	CLI	CVE	SEX	MTR	IndVal
No. of plots	7	4	6	7	23	10	7	6	33	7	21	12	18	9	12	8	16	
No. of species	28	25	36	29	51	21	51	15	89	46	75	53	49	31	20	13	18	
OTHER SPECIES																		
<i>Potentilla erecta</i>	100	100	100	100	100	80	100	83	94	100	48	67	17	100	8	25	6	
<i>Nardus stricta</i>	43	75	67	100	96	60	71	33	88	14	14	25	.	33	8	13	6	
<i>Carex rostrata</i>	14	25	.	43	96	100	86	33	42	14	43	75	.	100	83	100	100	
<i>Eriophorum angustifolium</i>	14	50	33	29	13	60	71	17	45	29	57	100	28	89	.	.	6	
<i>Carex echinata</i>	.	50	33	43	70	30	100	.	39	57	43	67	28	56	.	13	6	
<i>Agrostis stolonifera</i>	14	75	17	14	9	60	71	.	33	14	29	25	72	22	42	.	.	
<i>Festuca rubra commutata</i>	14	50	83	43	39	40	71	17	58	86	48	.	.	11	8	.	.	
<i>Equisetum palustre</i>	43	25	83	.	4	10	43	.	21	86	19	25	50	11	.	.	6	
<i>Dactylorhiza maculata fuchsii</i>	14	25	33	.	4	.	14	17	9	29	10	.	6	11	.	.	.	
<i>Parnassia palustris</i>	.	.	33	.	48	10	57	.	55	100	33	42	17	56	.	.	.	
<i>Crepis paludosa</i>	.	.	17	.	9	20	86	.	15	14	14	25	50	89	.	.	.	
<i>Calluna vulgaris</i>	57	25	100	.	4	.	71	.	9	43	10	8	
<i>Trichophorum alpinum</i>	14	.	17	43	52	10	.	50	18	71	.	8	
<i>Briza media</i>	14	25	50	.	.	.	14	.	15	71	24	8	56	
<i>Sanguisorba officinalis</i>	.	.	83	.	9	30	.	.	36	100	24	42	6	
<i>Eriophorum latifolium</i>	.	.	33	29	26	.	14	.	9	57	.	8	6	
<i>Danthonia decumbens</i>	.	50	67	.	.	.	71	.	121	57	10	8	
<i>Juncus alpinoarticulatus</i>	13	.	.	.	18	57	19	33	78	67	.	.	.	
<i>Carex pallescens</i>	.	.	.	29	9	.	57	33	.	29	5	.	.	11	.	.	.	
<i>Anthoxanthum nipponicum</i>	14	25	17	.	.	.	14	.	3	.	14	25	
<i>Lycopus europaeus</i>	3	.	33	33	17	78	58	.	.	
<i>Vaccinium uligin. microphyllum</i>	29	.	17	43	.	.	14	33	3	
<i>Fagus sylvatica</i>	.	.	17	.	17	.	57	.	27	.	.	8	.	.	8	.	.	
<i>Viola palustris</i>	.	.	17	.	.	.	14	.	6	29	10	.	39	
<i>Mentha aquatica</i>	.	25	14	.	.	.	43	42	.	56	.	.	.	
<i>Ranunculus repens</i>	14	.	.	.	48	.	56	.	50	.	6	
<i>Vaccinium myrtillus</i>	57	.	17	14	.	.	43	17	
<i>Luzula multiflora</i>	14	.	50	.	.	.	43	.	12	.	10	
<i>Angelica sylvestris</i>	13	.	29	.	3	38	.	42	
<i>Cirsium palustre</i>	.	25	29	.	9	.	5	33	
<i>Lathyrus pratensis</i>	14	.	33	9	.	24	.	11	
<i>Juncus effusus</i>	.	25	29	8	6	.	8	.	.	
<i>Eleocharis quinqueflora</i>	29	.	33	28	33	.	.	.	

Table 2. cont.

Plot group	SCA	SPA	SCE	SCO	SSU	SFA	SSN	MCA	DCE	CST	CNI	CDE	CPA	CLI	CVE	SEX	MTR	IndVal
No. of plots	7	4	6	7	23	10	7	6	33	7	21	12	18	9	12	8	16	
No. of species	28	25	36	29	51	21	51	15	89	46	75	53	49	31	20	13	18	
<i>Blysmus compressus</i>	14	.	.	.	10	42	50	
<i>Myosotis scorpioides</i>	33	8	17	11	.	.	.	
<i>Euphrasia stricta</i>	9	.	43	.	3	.	.	.	6	
<i>Viola reichenbachiana</i>	.	.	17	.	.	.	14	.	.	14	5	
<i>Cruciata glabra</i>	14	6	14	10	
<i>Brachypodium genuense</i>	4	.	14	.	6	.	5	
<i>Swertia perennis</i>	9	57	10	
<i>Juncus articulatus</i>	.	25	19	17	
<i>Trifolium pratense</i>	9	.	19	.	33	
<i>Trichophorum cespitosum</i>	13	.	.	.	9	
<i>Stellaria alsine</i>	14	.	.	.	5	.	28	
<i>Veronica beccabunga</i>	5	8	33	
<i>Ranunculus acris</i>	9	14	.	.	17	
<i>Plantago maritima serpentina</i>	.	.	.	14	6	14	
<i>Carex magellanica irrigua</i>	.	.	.	14	13	.	.	.	6	13	.	
<i>Genista tinctoria</i>	.	.	.	14	3	14	
<i>Alchemilla glaucescens</i>	4	14	10	
<i>Prunella vulgaris</i>	3	.	.	8	6	
<i>Ranunculus flammula</i>	29	25	
<i>Carex leporina</i>	10	.	.	.	33	.	.	
<i>Lathyrus vernus</i>	.	.	33	6	
<i>Lotus corniculatus</i>	.	25	6	
<i>Polygala alpestris</i>	.	.	17	.	.	.	14	
<i>Holcus lanatus</i>	.	25	5	
<i>Geum rivale</i>	14	10	
<i>Filipendula ulmaria</i>	3	11	.	.	.	
<i>Alchemilla alpina</i>	9	.	.	.	3	
<i>Veratrum album</i>	3	.	.	.	6	
<i>Scirpus sylvaticus</i>	3	.	5	
<i>Rhinanthus alectorolophus</i>	4	.	.	.	3	
<i>Cardamine asarifolia</i>	33	
<i>Poa pratensis</i>	28	
<i>Bistorta officinalis</i>	19	

Plot group	SCA	SPA	SCE	SCO	SSU	SFA	SSN	MCA	DCE	CST	CNI	CDE	CPA	CLI	CVE	SEX	MTR	IndVal
No. of plots	7	4	6	7	23	10	7	6	33	7	21	12	18	9	12	8	16	
No. of species	28	25	36	29	51	21	51	15	89	46	75	53	49	31	20	13	18	
<i>Cynosurus cristatus</i>	17	
<i>Carex canescens</i>	11	
<i>Ranunculus tuberosus</i>	11	
<i>Chaerophyllum hirsutum</i>	10	
<i>Gallium mollugo</i>	10	
<i>Aulacomnium palustre</i>	57	.	100	.	.	.	86	.	18	14	5	17	.	11	.	.	.	
<i>Aneura pinguis</i>	17	.	14	.	18	14	5	17	6	11	.	.	.	
<i>Ptilostomum pseudotriquetrum</i>	4	.	.	.	18	.	.	33	11	22	.	.	.	
<i>Scapania irrigua</i>	13	.	14	.	15	.	5	13	.	
<i>Chiloscyphus pallescens</i>	3	.	5	8	6	11	.	.	.	
<i>Plagiomnium elatum</i>	6	.	29	.	17	44	.	.	.	
<i>Polytrichum commune</i>	.	.	.	43	9	.	.	.	6	38	.	
<i>Sphagnum teres</i>	9	14	.	8	
<i>Scorpidium cossonii</i>	9	.	.	.	3	14	
<i>Sphagnum girghensonii</i>	.	.	.	14	4	.	.	.	6	
<i>Fissidens osmundoides</i>	14	.	3	.	5	
<i>Calliergon giganteum</i>	5	8	6	
<i>Calliergon cordifolium</i>	4	.	.	.	9	.	5	
<i>Sphagnum rubellum</i>	29	3	
<i>Ptilostomum schleicheri</i>	8	11	
<i>Palustrisella falcata</i>	8	6	
<i>Scorpidium scorpioides</i>	3	.	.	.	6	
<i>Philonotis fontana</i>	3	.	5	
<i>Climacium dendroides</i>	24	
<i>Sphagnum auriculatum</i>	17	.	.	
<i>Stramineogon stramineum</i>	9	

Species with low frequency

Sphagnum centrale group: *Juniperus communis* (17), *Vaccinium vitis-idaea* (17); **Sphagnum compactum group:** *Scapania paludicola* (14); **Sphagnum subsecundum group:** *Centaurea triumfetti* (4); **Sphagnum subnitens group:** *Euphorbia* sp. (14), *Geranium sylvaticum* (14), *Solidago virgaurea* (14), *Marsipella emarginata* (14); **Deschampsia cespitosa group:** *Allium schoenoprasum* (3), *Juncus conglomeratus* (3), *Ranunculus apenninus* (3), *Rubus idaeus* (3), *Sorbus aucuparia* (3), *Calypogeia fissa* (3), *Drepanocladus aduncus* (3), *Plagiocchia asplenoides* (3), *Racomitrium aquaticum* (3), *Sanionia uncinata* (3); **Campyllum stellatum group:** *Carex flacca* (14), *Tofieldia calyculata* (14); **Carex nigra group:** *Brachythecium rivulare* (5), *Rhizomnium punctatum* (5); **Carex demissa group:** *Carex paniculata* (8); **Caltha palustris group:** *Salix apennina* (6), *Fontinalis antipyretica* (6), *Palustrisella decipiens* (6).

frequent in some plots, but they generally occurred patchy with low cover.

3. *Sphagnum centrale* group (SCE; Table 2, Supplement S3)

Significant indicator species: *Sphagnum centrale*.

Constant species: *Sphagnum centrale*, *Calluna vulgaris*, *Potentilla erecta*, *Carex nigra*, *Aulacomnium palustre*.

Dominant species: *Sphagnum centrale*.

Physiognomy: moderately species-rich *Sphagnum* hummocks dominated by extensive carpets of *Sphagnum centrale*. Vascular species were numerous and frequent, but attained prominence in an only plot. The most frequent and abundant vascular species was the low shrub *Calluna vulgaris*.

4. *Sphagnum compactum* group (SCO; Table 2, Supplement S4)

Significant indicator species: *Sphagnum compactum*.

Constant species: *Sphagnum compactum*, *S. subsecundum*, *Nardus stricta*, *Potentilla erecta*.

Dominant species: no species dominating throughout; *Sphagnum compactum* was dominant in most plots.

Physiognomy: species-poor *Sphagnum* lawns with varying composition and physiognomy. The bryophyte layer was prevailing in the plots where *Sphagnum compactum* and *S. subsecundum* formed a virtually continuous carpet, occasionally accompanied by *S. capillifolium* and *S. girgensohnii*. Vascular species cover slightly exceeded bryophyte cover only where the *Sphagnum* carpet was less continuous; among them only *Potentilla erecta*, *Nardus stricta* and *Molinia caerulea* locally attained prominence.

5. *Sphagnum subsecundum* group (SSU; Table 2, Supplement S5)

Significant indicator species: *Sphagnum subsecundum*.

Constant species: *Sphagnum subsecundum*, *Potentilla erecta*.

Dominant species: *Sphagnum subsecundum* in the majority of the plots.

Physiognomy: species-poor to moderately rich *Sphagnum* lawns with varying composition and physiognomy. Bryophyte cover was prevailing in the plots having a luxuriant carpet of *Sphagnum subsecundum*. In other plots, where the cover of the dominant *Sphagnum* was lower, *Potentilla erecta* and *Nardus stricta* became prevalent.

6. *Sphagnum fallax* group (SFA; Table 2, Supplement S6)

Significant indicator species: *Sphagnum fallax*.

Constant species: *Sphagnum fallax*, *Carex rostrata*.

Dominant species: *Sphagnum fallax*.

Physiognomy: species-poor *Sphagnum* lawns dominated by extensive carpets of *Sphagnum fallax*. Vascular plants were relatively frequent, but generally with low cover,

except *Carex rostrata*, *C. nigra* and *Potentilla erecta* that locally attained prominence.

7. *Sphagnum subnitens* group (SSN; Table 2, Supplement S7)

Significant indicator species: *Sphagnum subnitens*, *Drosera rotundifolia*.

Constant species: *Carex echinata*, *Potentilla erecta*.

Dominant species: *Sphagnum subnitens* and *Potentilla erecta*, alternatively.

Physiognomy: moderately species-rich lawns with double-faced physiognomy determined by the alternating occurrence of the two dominant species. The total cover of vascular species was slightly prevailing on that of bryophytes also where *Sphagnum subnitens* was dominant and largely prevalent elsewhere. Nevertheless, all vascular species except *Potentilla erecta* exhibited low cover.

8. *Molinia caerulea* group (MCA; Table 2, Supplement S8)

Significant indicator species: *Molinia caerulea*.

Constant species: *Molinia caerulea*.

Dominant species: *Molinia caerulea*.

Physiognomy: extremely species-poor fen grasslands, characterized by the overwhelming abundance of *Molinia caerulea*. Under the extensive cover of the dominant grass, the other vascular plants and bryophytes often occurred as scattered individuals. Among these associates, only *Sphagnum compactum* and *Potentilla erecta* occurred with appreciable frequency and prominence.

9. *Deschampsia cespitosa* group (DCE; Table 2, Supplement S9)

Weakly significant indicator species: *Deschampsia cespitosa*.

Constant species: none; *Potentilla erecta* was the most frequent species.

Dominant species: no species dominating throughout. Several species attained dominance in different plots. *Potentilla erecta* and *Nardus stricta* tended to dominate in the herbaceous layer of many plots, locally replaced by *Scirpus sylvaticus*, *Trichophorum cespitosum*, *Deschampsia cespitosa* and *Sanguisorba officinalis*. Several *Sphagnum* species (*S. centrale*, *S. girgensohnii*, *S. teres*) were locally dominant in the moss layer.

Physiognomy: fen grasslands ranging from extremely poor to moderately species-rich, quite different in their floristic composition but overall characterized by the prevalence of vascular species on bryophytes and by the high frequency and overwhelming abundance of *Nardus stricta* and *Potentilla erecta*. The bryophyte cover became prevailing only in the few plots with extensive *Sphagnum* carpet.

10. *Campylium stellatum* group (CST; Table 2, Supplement S10)

Significant indicator species: *Campylium stellatum*, *Pinguicula christinae*, *Carex davalliana*, *Tomenthypnum nitens*.

Constant species: *Potentilla erecta*, *Sanguisorba officinalis*, *Parnassia palustris*.

Dominant species; no species dominating throughout; *Carex davalliana* was dominant or co-dominant in many plots, *Potentilla erecta* and *Campylium stellatum* in others.

Physiognomy: moderately species-rich to rich short-sedge fens with variable composition and physiognomy, alternatively characterized by the small sedge *Carex davalliana* and the forb *Potentilla erecta*. Another occasionally prominent species was *Swertia perennis*. The total cover of vascular species was largely prevalent also where the moss *Campylium stellatum* formed extensive carpets or smaller patches.

11. *Carex nigra* group (CNI; Table 2, Supplement S11)

Weakly significant indicator species: *Carex nigra*.

Constant species: *Carex nigra*.

Dominant species: no species dominating throughout. *Carex nigra* was dominant in most plots, replaced by *Mentha aquatica*, *Swertia perennis*, *Ranunculus repens* and *Calliergonella cuspidata* in the other plots.

Physiognomy: species-poor to rich short-sedge fens, whose distinctive physiognomy was due to the frequency and abundance of small sedges (namely *Carex nigra*). Bryophytes played a subordinate role and lacked at all in some plots. Among them only *Calliergonella cuspidata* locally attained prominence.

12. *Carex demissa* group (CDE; Table 2, Supplement S12)

Significant indicator species: *Carex demissa*.

Constant species: *Carex demissa*, *Eriophorum angustifolium*.

Dominant species: no species dominating throughout. *Carex demissa* was dominant or co-dominant in most plots, replaced by *Eriophorum angustifolium* and *Calliergonella cuspidata* in the others.

Physiognomy: moderately species-rich short-sedge fens with variable composition and physiognomy. Vascular species prevailed on bryophytes that occurred mostly as scattered individuals or lacked at all in some plots. Among bryophytes, only *Calliergonella cuspidata* occasionally achieved prominence.

13. *Caltha palustris* group (CPA; Table 2, Supplement S13)

Significant indicator species: *Caltha palustris*, *Calliergonella cuspidata*, *Phragmites australis*, *Epilobium palustre*.

Constant species: *Calliergonella cuspidata*, *Caltha palustris*, *Epilobium palustre*.

Dominant species: no species dominating throughout. *Calliergonella cuspidata* was dominant in most plots, replaced alternatively by *Eriophorum angustifolium*, *Caltha palustris* and *Carex nigra* in the other plots.

Physiognomy: moderately species-rich fen grasslands with variable composition and physiognomy. Vascular plants were dominant in about half of the plots. The most prominent and locally dominant vascular species were *Eriophorum angustifolium*, *Caltha palustris* and *Carex nigra*. Bryophytes were scarce in number, but attained dominance in the other half of the plots due to the extensive *Calliergonella cuspidata* carpet.

14. *Carex limosa* group (CLI; Table 2, Supplement S14)

Significant indicator species: *Carex limosa*.

Constant species: *Calliergonella cuspidata*, *Carex rostrata*, *Potentilla erecta*, *Galium palustre*, *Epilobium palustre*.

Dominant species: no species dominating throughout. *Carex limosa* was dominant in half of the plots and prominent in the others. *Calliergonella cuspidata* was dominant in three plots and *Carex rostrata* in an only plot.

Physiognomy: moderately species-rich short-sedge fens whose physiognomy was given by the dominant small sedges (namely *Carex limosa*). Bryophytes were few, but often formed a dense carpet under the vascular layer.

15. *Carex vesicaria* group (CVE; Table 2, Supplement S15)

Significant indicator species: *Carex vesicaria*, *Veronica scutellata*, *Sphagnum inundatum*, *Galium palustre*.

Constant species: none. *Carex vesicaria* and *Galium palustre* are the most frequent species.

Dominant species: no species dominating throughout. *Sphagnum inundatum* was dominant in the majority of the plots. *Carex vesicaria*, *Galium palustre*, *Juncus filiformis*, *Lycopus europaeus* and *Veronica scutellata* were alternatively prominent in several plots.

Physiognomy: species-poor pools with variable composition and physiognomy. The cover of vascular species was prevalent in most plots with *Carex vesicaria* overall frequent and largely dominant in two plots. In other plots the physiognomy was mainly given by a mixture of helophytes. Among bryophytes, *Sphagnum inundatum* formed extensive carpets in the majority of the plots.

16. *Sarmentypnum exannulatum* group (SEX; Table 2, Supplement S16)

Significant indicator species: *Sarmentypnum exannulatum*, *Juncus filiformis*.

Constant species: *Sarmentypnum exannulatum*, *Juncus filiformis*, *Carex rostrata*.

Dominant species: no species dominating throughout. *Sarmentypnum exannulatum* was dominant in the major-

ity of the plots and prominent also where *Juncus filiformis* or *Carex rostrata* achieved dominance.

Physiognomy: very species-poor pools with variable composition and physiognomy. The bryophyte cover prevailed where the moss *Sarmentypnum exannulatum* was dominant. In the other plots the physiognomy was given by the rush *Juncus filiformis* and the sedges *Carex rostrata* and *C. nigra*.

17. *Menyanthes trifoliata* group (MTR; Table 2, Supplement S17)

Weakly significant indicator species: *Menyanthes trifoliata*.

Constant species: *Carex rostrata*.

Dominant species: no species dominating throughout. *Carex rostrata* was the most frequently dominating species, replaced by *Menyanthes trifoliata* in some plots and by *Calliergon giganteum* and *Sphagnum subsecundum* in two other plots, respectively.

Physiognomy: very species-poor pools with double-faced physiognomy determined by the alternating dominance of *Carex rostrata* and *Menyanthes trifoliata*. Bryophytes occurred sporadically, largely overtaken by vascular plants except in two plots and lack at all in many plots.

Hydrology, water chemistry and peat chemistry

The first two axes of CCA accounted for 58% of the total variance. The plots of the vegetation units and environmental variables pointed to water table depth (WT depth) as the main environmental variable accounting for variations in the species composition of the 17 vegetation units (Fig. 3a). Indeed, water table depth presented the longest vector oriented almost parallel to the first CCA axis which defined a gradient in water table depth where the vegetation units characterized by deeper, i.e. more negative, mean water table (Table 3) were positioned in the left sector of the diagram. This applied to all of the *Sphagnum*-dominated hummocks (*Sphagnum capillifolium* group, *Sphagnum palustre* group and *Sphagnum centrale* group) and lawns (*Sphagnum compactum* group, *Sphagnum subsecundum* group, *Sphagnum fallax* group and *Sphagnum subnitens* group) as well as to the two less humid fen grasslands (*Molinia caerulea* group and *Deschampsia cespitosa* group). The other fens (*Carex nigra* group, *Carex demissa* group, *Caltha palustris* group and *Carex limosa* group), except the *Campylium stellatum* group, and all pools (*Carex vesicaria* group, *Sarmentypnum exannulatum* group and *Menyanthes trifoliata* group) were positioned in the right sector of the diagram with increasingly higher, i.e. less negative, mean water table from the centre to the right end of the diagram (Fig. 3a, Table 3). The vector of the water table range (WT range) was almost orthogonal to that of the water table depth which suggests that fluctuations in water table

were unrelated to the mean depth of the water table. Consistently, the water table range increased towards the upper right end of the diagram, with highest values in the *Sarmentypnum exannulatum* group, *Molinia caerulea* group and particularly in the *Carex vesicaria* group (Fig. 3a, Table 3).

The vectors of the variables related to water chemistry were mostly directed towards the lower end of the diagram. The vegetation units with negative scores of the second CCA axis were characterized by high mean Ca^{++} and Mg^{++} concentrations in the pore water. This applied particularly to the *Caltha palustris* group and the *Carex limosa* group and, to a lesser extent, to the *Deschampsia cespitosa* group, the *Campylium stellatum* group and the *Carex nigra* group. In contrast, the vegetation units with positive scores of the second CCA axis had low Ca^{++} and Mg^{++} concentrations and generally lower values of electrical conductivity (Fig. 3a, Table 3). This was especially the case of the *Molinia caerulea* group and of most of the *Sphagnum*-dominated hummocks and lawns with the exception of the *Sphagnum subnitens* group. The mean pH presented an overall rather modest range (from 4.9 in the *Molinia caerulea* group to 6.3 in the *Caltha palustris* group; Table 3). The vegetation units in the upper sector of the diagram had more acidic pH but in general there were modest differences among the vegetation units (Fig. 3a, Table 3). Na^+ and K^+ concentrations varied rather erratically. In particular, Na^+ concentration presented peak values in the *Sphagnum subnitens* group, the *Carex limosa* group and the *Carex vesicaria* group while K^+ concentration peaked in the *Sphagnum subnitens* group (Table 3). The ordination of species in the CCA diagram was consistent with their association with the vegetation units (Fig. 3b).

Peat chemistry did not exhibit consistent patterns among the vegetation units. Concentrations of both extractable N forms (NH_4 , $F_{1,16} = 7.61$; $p < 0.001$; NO_3 , $F_{1,16} = 9.44$; $p < 0.001$) presented a distinct peak in the *Carex vesicaria* group compared with all other vegetation units (Fig. 4a, b). Conversely, PO_4 concentration ($F_{1,16} = 2.86$; $p < 0.001$) was highest in the *Sphagnum subnitens* group and varied rather erratically among the other vegetation units (Fig. 4c).

Relationships of plant diversity with environmental variables

Patterns of species richness in relation to environmental variables were only conditioned by decreasing S index of vascular plants with increasing water table range and increasing S index of vascular plants with increasing pH, both paralleled by similar trends in the total species richness (Fig. 5). In contrast, there were no relationships of the S index with water table depth, electrical conductivity in the water or available N concentration in the peat (Fig.

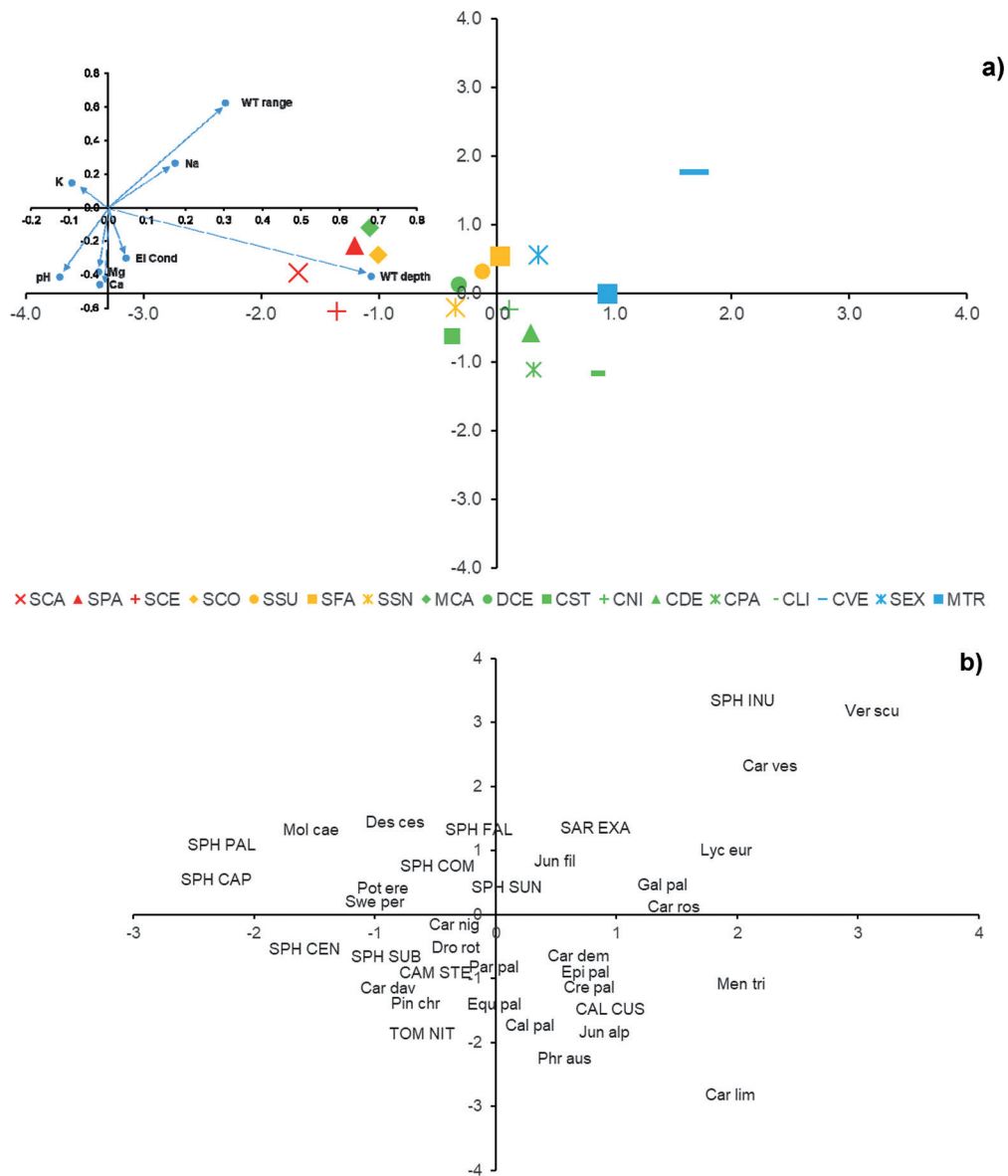


Fig. 3. Ordination of vegetation data with environmental variables in the small inner panel (a) and species (b). The symbols in panel a indicate the centroids of the vegetation units with different colours according to physiognomy (red: *Sphagnum hummocks*; orange *Sphagnum lawns*; green: fens; blue: pools).

Legend of species abbreviations: (vascular plants in small letters, bryophytes in capital letters).

Calliergonella cuspidata (CAL CUS), *Caltha palustris* (Cal pal), *Campylium stellatum* (CAM STE), *Carex davalliana* (Car dav), *Carex demissa* (Car dem), *Carex limosa* (Car lim), *Carex nigra* (Car nig), *Carex vesicaria* (Car ves), *Deschampsia cespitosa* (Des ces), *Drosera rotundifolia* (Dro rot), *Epilobium palustre* (Epi pal), *Galium palustre* (Gal pal), *Juncus filiformis* (Jun fil), *Menyanthes trifoliata* (Men tri), *Molinia caerulea* (Mol cae), *Phragmites australis* (Phr aus), *Pinguicula christinae* (Pin chr), *Sarmentypnum exannulatum* (SAR EXA), *Sphagnum capillifolium* (SPH CAP), *Sphagnum centrale* (SPH CEN), *Sphagnum compactum* (SPH COM), *Sphagnum fallax* (SPH FAL), *Sphagnum inundatum* (SPH INU), *Sphagnum palustre* (SPH PAL), *Sphagnum subnitens* (SPH SUN), *Sphagnum subsecundum* (SPH SUB), *Tomentypnum nitens* (TOM NIT), *Veronica scutellata* (Ver scu).

5). The *H* index was unrelated to any environmental variable (Fig. 6).

Half of the 28 indicator species had significant relationship with environment, as documented by the multiple regressions. Water table depth was the variable most strongly influencing the distribution of the species in the

peatlands investigated. Indeed, three of the species showed negative slopes and five species showed positive slopes across the gradient in water table depth (Table 4). Trends of species responses to water table depth were further defined by varying relationships of species frequencies with other variables related to environment. The frequency of

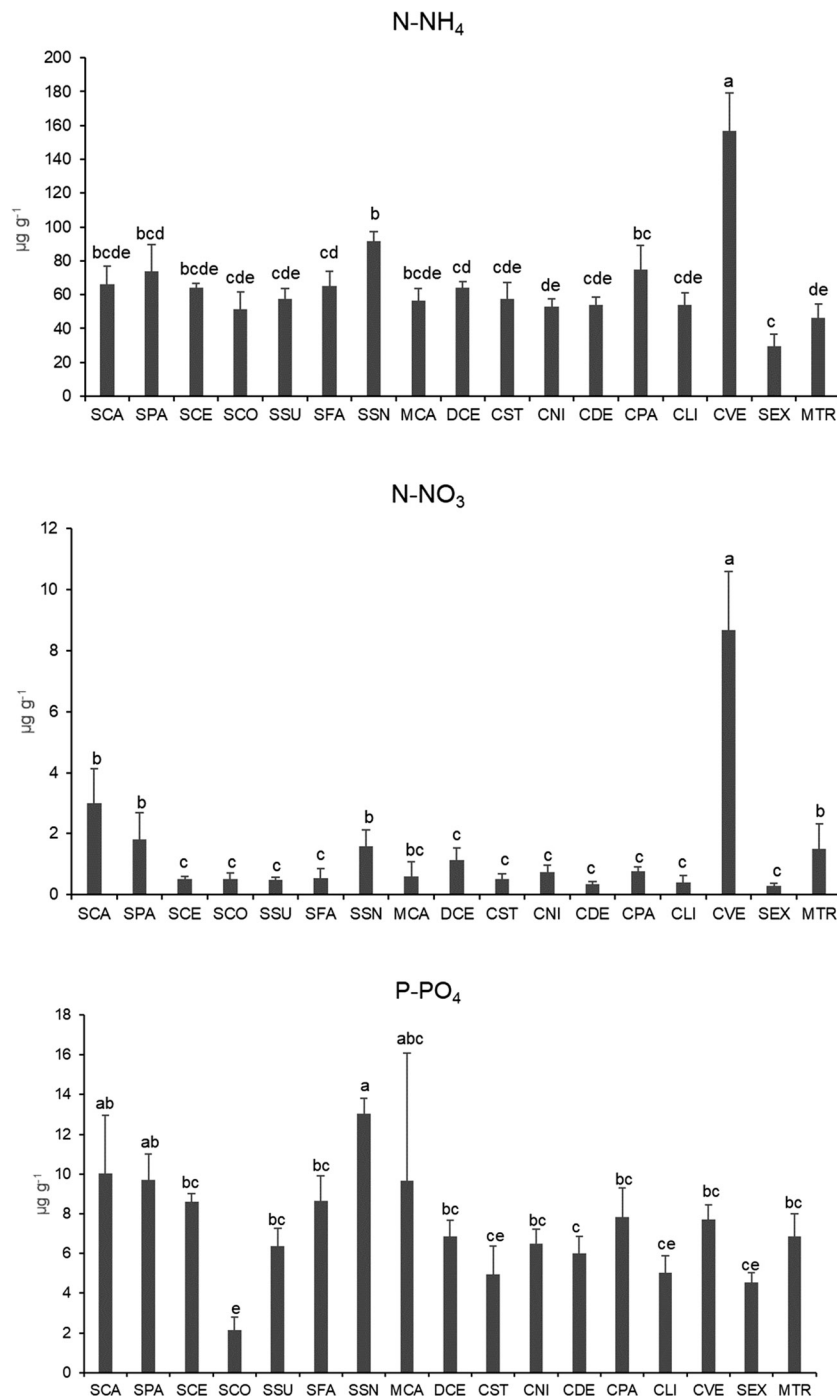


Fig. 4. Mean (+ 1 SE) concentrations of extractable nutrients in the peat of the vegetation units (legend of acronyms as in Table 2). In each panel the means with the same letter do not differ significantly ($p > 0.05$) based on Fisher's LSD post-hoc tests.

Molinia caerulea and *Deschampsia cespitosa* both increased in acidic habitats with deep water table. However, *Molinia caerulea* was enhanced by low N concentrations and high P concentrations in the peat while the reverse was true for *Deschampsia cespitosa*. *Epilobium palustre* also was enhanced when the water table was deep but this happened

where the water table fluctuated much and the peat presented high N concentrations (Table 4). The frequencies of the two lawn *Sphagnum* species *S. fallax* and *S. subnitens* was highest in habitats characterized by high water table with high P concentrations for *S. subnitens* (Table 4). The frequencies of *Veronica scutellata*, *Carex nigra* and *Cal-*

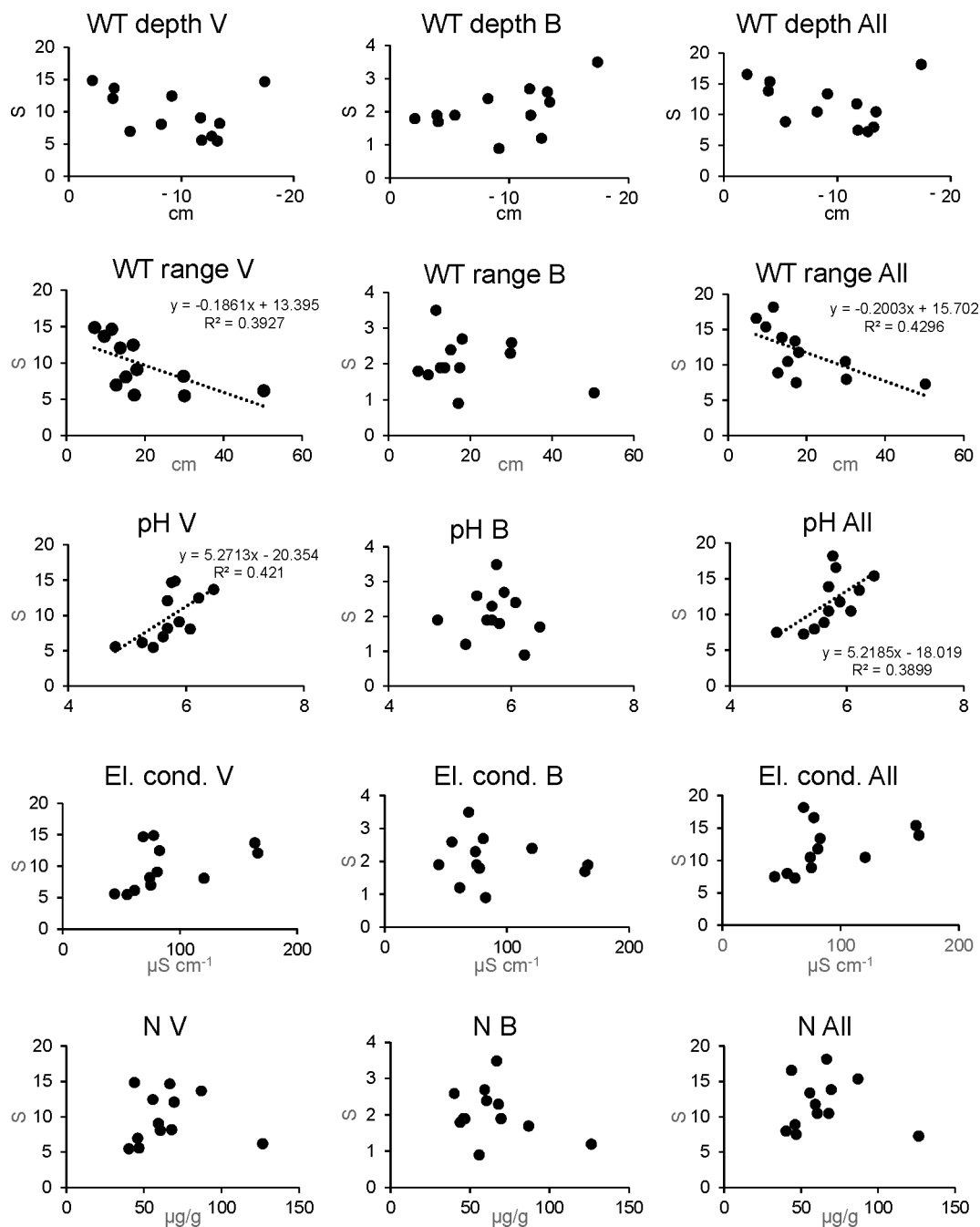


Fig. 5. Relationships between the species richness index (S) and selected environmental variables: water table depth (WT depth), water table range (WT range), pH and electrical conductivity (El. cond.) in the water, N-NH₄ + N-NO₃ concentration in the peat (N). The S index is shown for vascular plants (V), bryophytes (B) and all species grouped together (All). Equations and slopes are shown for significant ($p < 0.05$) regressions.

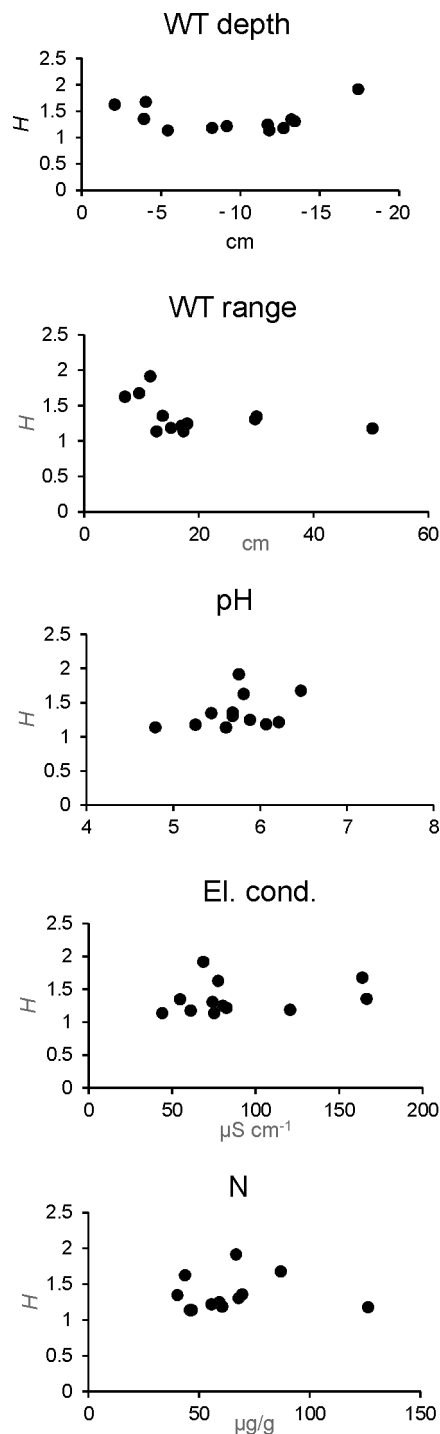


Fig. 6. Relationships between the Shannon-Wiener diversity index (H) and selected environmental variables: water table depth (WT depth), water table range (WT range), pH and electrical conductivity (El. cond.) in the water, N-NH_4 , + N-NO_3 concentration in the peat (N). There were no significant regressions.

liergonella cuspidata were highest in habitats with high water table and high cover of bryophytes (Table 4).

Discussion

Environment and vegetation

The vegetation in the peatlands investigated was comprised of a considerable variety of vegetation units occupying habitats that ranged from *Sphagnum*-dominated hummocks and lawns, to fens, wet hollows and pools. This supported the results of a previous study addressing wetland vegetation of the Northern Apennines across a large number of sites (Gerdol & Tomaselli 1993). However, as this study aimed at analysing vegetation patterns at the microhabitat scale we were able to detect the environmental drivers conditioning vegetation diversity at a higher detail than the previous phytosociological study. The canonical ordination of vegetation and environmental data pointed to water table depth as the main environmental driver of vegetation patterning. Water table depth has been recognized as a major factor in structuring peatland vegetation since the seminal works of Fennoscandian mire ecologists (see, for example, Sjors 1950; Malmer 1962). This principally depended on small-scale surface microtopography that influenced the water table level providing an important range of micro-environments (Moeslund et al. 2013). Consistently, the mean water table depth in our peatlands varied over short distances from about -30 cm in the highest hummocks to +7 cm in the wettest pools. The range of water table depth, indicating the degree of water table fluctuation, also played some role in differentiating the vegetation units. The water table showed little to moderate fluctuations (< 20 cm) in most of the vegetation units independent of mean water table depth, from *Sphagnum* hummocks and lawns, to short-sedge fens and pools. A similar pattern was observed in peatlands in the Alps (Conradi & Friedmann 2013). Conversely, the water table fluctuated more strongly in the vegetation units experiencing reduced groundwater inflow during dry periods (Asada 2002). This was the case of fen grasslands (*Molinia caerulea* group and *Deschampsia cespitosa* group) and pools (*Sarmentypnum exannulatum* group and, especially, *Carex vesicaria* group). Only in one case did *Sphagnum* hummocks experience some degree of desiccation (*Sphagnum palustre* group). Water table depth and, to a lesser extent, range of water table depth have been shown to be more important than water chemistry in structuring the vegetation of southern mountain peatlands both in Europe (Pérez-Haase & Ninot 2017; Colomer et al. 2019) and in North America (McIlroy & Allen-Diaz 2012).

Water chemistry generally was much more similar across vegetation units than water table depth. In particular, the overall range of pH values barely reached 1.5

Table 4. Summary of the stepwise multiple regressions of the frequencies of the indicator species against water table depth (WT depth), water table range (WT range), pH and electrical conductivity (El. cond.) of the water, N-NH₄, + N-NO₃ concentration in the peat (N) and P-PO₄ concentration in the peat (P).

The species with significant ($p < 0.05$) F values are in bold character. Significant ($p < 0.05$) regression slopes are indicated (+, positive slope; -, negative slope).

	No.	F (p level)	WT depth	WT range	pH	El. cond.	N	P
<i>Sphagnum capillifolium</i>	9	–						
<i>Sphagnum palustre</i>	9	17.20 (0.02)			+			
<i>Sphagnum centrale</i>	19	6.92 (0.02)						
<i>Sphagnum compactum</i>	9	–						
<i>Sphagnum subsecundum</i>	6	–						
<i>Sphagnum fallax</i>	15	12.87 (0.001)	+					
<i>Sphagnum subnitens</i>	32	8.17 (<0.001)	+					+
<i>Drosera rotundifolia</i>	4	–						
<i>Molinia caerulea</i>	23	4.36 (0.008)	–		–		–	+
<i>Campylium stellatum</i>	15	4.93 (0.02)				+		–
<i>Pinguicula christinae</i>	9	–						
<i>Carex davalliana</i>	10	–						
<i>Tomentypnum nitens</i>	4	–						
<i>Carex demissa</i>	35	3.59 (0.02)						+
<i>Caltha palustris</i>	17	–						
<i>Calliergonella cuspidata</i>	36	19.0 (<0.001)	+					
<i>Phragmites australis</i>	5	–						
<i>Epilobium palustre</i>	17	11.48 (<0.001)	–	+			+	
<i>Carex limosa</i>	4	–						
<i>Carex vesicaria</i>	5	–						
<i>Veronica scutellata</i>	6	25.95 (0.004)	+					
<i>Sphagnum inundatum</i>	6	–						
<i>Galium palustre</i>	47	–						
<i>Sarmentypnum exannulatum</i>	6	–						
<i>Juncus filiformis</i>	26	4.18 (0.02)			–			
<i>Menyanthes trifoliata</i>	8	9.80 (0.02)						+
<i>Carex nigra</i>	86	7.01 (<0.001)	+					
<i>Deschampsia cespitosa</i>	16	10.81 (0.002)	–	+	–		+	–

units. Concentrations of major cations in the water showed that all of the habitats investigated were influenced by telluric water. In particular, mean Ca²⁺ concentrations always were > 1 mg l⁻¹, i.e. the threshold that has since long been recognized to discriminate ombrotrophic from minerotrophic habitats in continental regions not influenced by dust-fall from cultivated grasslands (Gorham et al. 1985; Comeau & Bellamy 1986; Proctor 1994; Bragazza et al. 1998; Keimowitz et al. 2013; Rocchio et al.

2021). Furthermore, the Ca²⁺/Mg²⁺ ratio in the water always was > 1, a threshold separating ombrotrophic from minerotrophic conditions in peatlands (Proctor et al. 2009). This can explain the lack of species such as *Andromeda polifolia*, *Vaccinium microcarpum*, *Scheuchzeria palustris*, *Sphagnum fuscum*, *Sphagnum papillosum* and others, all of which characterizing the vegetation of bogs and/or extremely poor acidic fens in the Alps (see Gerdol & Tomaselli 1997 and several papers cited in the Intro-

duction). The absence of these species can also be due to chorological reasons. Indeed, they are circumboreal or arctic-alpine species with a distribution range located in northern regions so that most of them are lacking in European peatlands located at latitudes $< 45^\circ \text{N}$ (Joosten et al. 2017). *Carex limosa* was the only species recorded in our peatlands that is frequently found in poor acidic mire habitats in the Alps. This was likely due to the wide ecological amplitude of this species that occurs across a range of habitats from rich alkaline fens to ombrotrophic bogs (Krisai 1970). Based on water chemistry, the habitats in the peatlands investigated were weakly acidic ranging from moderately rich to rich in electrolytes. As typical of minerotrophic conditions, concentrations of telluric cations in the pore water largely reflected the chemistry of the underlying bedrock. Most of the peatlands investigated lie on the same type of bedrock, i.e. compact sandstone. However, the sandstone in two peatlands (CERA and CERB) was overlain by a debris layer enriched in sodium (Cartografia Geologica della Regione Emilia-Romagna 2015). This explains the high Na^+ concentrations observed in the *Carex limosa* group, that occurred only at CERA, in the *Carex vesicaria* group, that occurred only at CERB and to a lesser extent in the *Sphagnum subnitens* group, mostly occurring at both peatlands (Supplements S7, S14, S15).

Peat chemistry played an overall modest role in regulating vegetation composition. Indeed, nutrient concentrations in the peat was unrelated to hydrology and, especially, water chemistry as demonstrated by previous studies showing that nutrient content does not vary across the acidity-alkalinity gradient in peatlands (Griffiths et al. 2019). The only exception with this regard consists in the peak values of extractable N forms recorded in the *Carex vesicaria* group. High nutrient, especially N, levels in the peat are most often caused by eutrophication from surrounding pastures and/or crops. Increased N content in the peat can also be due to land-use abandonment (Rion et al. 2018). Either of the two mechanisms were unlikely to account for the high N levels in the *Carex vesicaria* group because CERB, the only peatland where the *Carex vesicaria* group was recorded (Supplement S15), lies in a forested area without managed grasslands or crops in the surroundings. Neither did this area experience recent changes in land use. So, we believe that high N availability in the *Carex vesicaria* group was caused by the accumulation of high amounts of litter by the dominant sedge *Carex vesicaria*. Sedge litter generally exhibits high decomposability (Palozzi & Lindo 2017), especially in wet habitats (Yajun et al. 2016).

Vegetation dynamics in relation to environmental changes

The water table in northern peatlands is predicted to decline in the next future by 14–22 cm as an effect of climate warming (Whittington & Price 2006). Our results suggest that water table drawdown of moderate magnitude will unlikely imply biodiversity losses in terms either of species richness or of evenness. On the other hand, if environmental changes associated with climate warming bring about stronger fluctuations of the water table this will decrease species richness because of loss of vascular species typical of this habitat. If higher frequency of drought periods leads to greater soil oxygenation with consequent acidification of the peat this will probably enhance a few acidophilous species at the expense of fen specialists, particularly vascular plants species, with consequent reduction of species richness (Heijmans et al. 2013; Hajek et al. 2022). Although eutrophication due to whatever cause can decrease species richness in peatlands (Rion et al. 2018), we did not observe any relationships between species richness and nutrient concentrations in the peat. Whatever the environmental changes triggered by global warming in the peatlands investigated, our data suggest that their impact on species richness will affect vascular plants to much a greater extent than bryophytes. Recent studies addressing peatland vegetation at the southern border of the distribution range of peatlands in Europe found total species richness to represent a poor indicator of how climatic changes will actually affect peatland vegetation in these regions. This principally depends on the fact that most environmental factors are poorly related to species richness and, most importantly, that plant specialists are much more sensitive to environmental changes in peatlands compared with plant generalists (Hájková et al. 2006; Jiménez-Alfaro et al. 2012), i.e. the so-called matrix species (Horsáková et al. 2018). Responses of individual species to environmental factors appeared to provide much more information on the effects of climate change on peatland vegetation compared with species richness or evenness.

So we assumed that, if the mean water table depth decreases as an effect of reduced precipitation and/or higher evapotranspiration, the species exhibiting a negative relationship with water table depth will expand and those exhibiting a positive relationship with water table depth will decline (Heijmans et al. 2008; Kooijman et al. 2016). Relationships with water table did not suggest hummock-forming peat mosses to experience significant changes in cover. This can be explained considering that the *Sphagnum* species typical of hummocks possess a high ability to raise water by capillarity although growing distant from the water table. They also recover faster than other *Sphagnum* species during rehydration (Hájek & Beckett 2008). However, if the water table declines

below about -40 cm, surface pore-water pressure becomes non-linearly related to the water level, which may strongly increase the probability of desiccation in *Sphagnum* tissues under future climate scenarios (Moore & Waddington 2015). Furthermore, hummock-forming peat mosses suffer if summer temperatures rise above a certain threshold (Norby et al. 2019), especially if high temperatures are coupled with insufficient precipitation (Nijp et al. 2014). For example, Bragazza (2008) observed dieback of *Sphagnum* species forming high hummocks after the 2003 heat wave with 2°C rise of mean monthly temperature combined with a drought spell in 2003 in the Italian Alps. Consistently, experimental manipulation of temperature and water table in peat monoliths demonstrated that a temperature increase of 4°C , which corresponds to the worst scenario of temperature increase foreseen by the end of this century (IPCC 2022), associated with water table drawdown triggers increasing cover of vascular plants at the expense of peat mosses (Weltzin et al. 2001). So, we expect a strong increase in the frequency of *Molinia caerulea* and *Deschampsia cespitosa* at sites where hummock-forming peat mosses are jeopardized by water table drawdown coupled with excessively high temperatures. *Molinia caerulea* is expected to expand especially in N-poor habitats, while *Deschampsia cespitosa* is expected to expand in N-rich habitats. In both cases vegetation dynamics may result in gradual invasion of species-poor fen grasslands at the expense of *Sphagnum* species as an effect of competition for light (Malmer et al. 2003). *Molinia caerulea* has been found to invade desiccated northern peatlands under differing level of N availability provided P is not limiting (Tomassen et al. 2004). This is in line with our data indicating a positive relationship of *Molinia caerulea* frequency with P concentration in the peat. On the other hand, we expect water table drawdown to negatively affect two of the lawn *Sphagnum* species, i.e. *S. fallax* and *S. subnitens*. In acidic to moderately acidic, nutrient-poor habitats *S. fallax* may be outcompeted by more drought-tolerant hummock-forming *Sphagnum* species such as *S. capillifolium*, *S. palustre* or *S. centrale*, all capable of suppressing hollow species under drought conditions by competing for water resources (Gąbka & Lamentowicz 2008; Bu et al. 2013). *Sphagnum subnitens*, a species tolerating rather high pH (Hájková & Hájek 2004) and high P levels (Kooijman & Kanne 1993), will presumably undergo competition with *Aulacomnium palustre*. This non-*Sphagnum* moss, representing a frequent component of the vegetation unit characterized by *S. subnitens* (*Sphagnum subnitens* group; Table 2), will probably expand at the expense of the indicator species *S. subnitens* because of its better tolerance to drier conditions (Hájek et al. 2020). Water table drawdown in wet subneutral fen grasslands (*Caltha palustris* group) will give rise to an expansion of vascular plants with concomitant contraction of the moss carpet prevalently formed

of the drought-intolerant species *Calliergonella cuspidata* (Kooijman & Paulissen 2006; Kooijman et al. 2016). Among the vascular indicator species of the *Caltha palustris* group, we expect the nitrophilous *Epilobium palustre* to expand most strongly especially if declining water table is accompanied by increased N mineralization (Gustafsson 1988; Sheppard et al. 2013). Conversely, water table drawdown in less wet, slightly acidic short-sedge fens with lower cover of the moss layer (*Carex nigra* group) may trigger some reduction of cover of the dominant species *Carex nigra* (van Bogedom et al. 2008). On the other hand, such possible declining trend may be partly offset by increasing water table range because *Carex nigra* tolerates even considerable water table fluctuations (Laitinen et al. 2008). Our results suggest that pool vegetation is less sensitive to changes triggered by water level drawdown, at least in terms of varying cover of indicator species. We only expect the cover of *Veronica scutellata* to decrease with declining water table in the most acidic stands of the *Carex vesicaria* group (Bruinsma 2007).

Overall, our results suggest that southern peatlands are resilient to drought up to a certain level of disturbance, but they may shift to new states when a critical point is reached (Heijmans et al. 2013). In particular, prolonged drought events associated with high temperature in summer months can exert a strong impact on peatland vegetation (Dieleman et al. 2015; Gerdol & Brancaleoni 2015; Colomer et al. 2019; Antala et al. 2022). In conclusion, the main effect of climate change on the vegetation of the peatlands investigated consists in the spreading of vascular plants at the expense of *Sphagnum* mosses.

Author contributions

A.P. and M.C. planned the research. A.P. and M.C. carried out the field sampling. L.B. and M.C. performed the statistical analyses. L.B., R.G. and M.T., wrote the first draft of the text. All authors contributed to the final version of the text.

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Authors addresses

Brancaleoni, L.¹, Carbognani, M.², Gerdol, R. (Corresponding author, grn@unife.it)¹, Tomaselli, M.², Petraglia, A.²

¹ Department of Environmental and Prevention Sciences, University of Ferrara, Corso Ercole I d'Este 32, 44121 Ferrara, Italy

² Department of Chemistry, Life Sciences and Environmental Sustainability, University of Parma, Parco Area delle Scienze, 11/A, 43124 Parma, Italy

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