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ORIGINAL RESEARCH

Ecological monitoring of disturbed mountain peatlands: an analysis based on desmids

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Abstract
Ombrogenous peat bogs at lower altitudes of the Bohemian Massif occur close to their natural climatic limits in the Northern Hemisphere. They have been significantly affected by peat extraction and severe acidification. Recently, climate change effects, such as decreased snow cover and summer heat waves, have resulted in frequent seasonal desiccation of these habitats, indicating their ongoing transition into a different ecological state. Biomonitoring may provide insight into these rapidly changing ecosystems and identify key habitats for biodiversity conservation. The present study focused on the community structure of desmids, one of the most frequent groups of peatland phytobenthos. In total, 207 sites were sampled from the Ore Mts. (Czech Republic) at the altitude range of 750–850 m a.s.l. A modification of the desmid-based nature conservation value (NCV) index was devised to account for the differences among the observed strongly acidic habitats. In the fragments of ombrogenous bogs, which currently cover less than 3% of the area, several ecologically sensitive taxa, such as *Cosmarium sphagnicolum* and *Staurastrum scabrum*, were recorded. These taxa did not occur in other habitat types. In addition, the NCV indices of the bog samples were consistently higher than those of the restored pools created in the disturbed bog areas. However, the highest species richness was recorded in several slightly acidic ponds and sinkholes, which were often located outside the existing protected areas. Thus, we concluded that future conservation strategies should consider the remaining bogs and anthropogenic sites as habitats with relatively high ecological values.

Keywords Desmidiales · NCV index · Peatlands · Phytobenthos · Zygnematophyceae

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Introduction

Peatlands are defined as ecosystems with long-term excess of net primary production over the decomposition of organic matter, which leads to the gradual accumulation of partially decomposed organic substances, i.e., peat (Wieder et al. 2006). More than 80% of global peatlands are found in the boreal regions, covering vast expanses of forested and non-forested habitats of Northern Hemisphere, which are largely distributed between 55° and 70° of northern latitude (Vitt 2006). Notably, most wetland areas distributed in this zone consist of *Sphagnum*-dominated acidic and oligotrophic peat bogs and acidic fens (Gignac and Vitt 1994).

However, significant areas of acidic wetlands are also distributed south of the boreal zone in the mountain orobiomes of temperate regions (Rybníček 1984). In Europe, these mountainous peatlands are frequent in the Alps, Carpathians, and Pyrenees. In addition, significant areas of acidic wetlands occur in the relatively lower mountainous parts of the Bohemian Massif in Central Europe (Tanneberger et al. 2017). Mountainous peatlands at the summit plateau of the Krušné Hory Mts. (Ore Mts., Erzgebirge) in the northwestern part of the Czech Republic are located at the altitude range of approximately 750–1050 m a.s.l. These peatlands are composed of an array of ombrogenous (ombrotrophic) bogs dependent on the water supply from precipitation, as well as geogenous (minerotrophic) fens fed by springs, streams, or developed at the margins of anthropogenic ponds (Vilímek and Raška 2016). From a climatic point of view, ombrogenous peat bogs represent marginal habitats distributed close to their natural limits within the temperate zone (Čížková et al. 2013).

The ongoing climate change caused by the rapid increase in atmospheric greenhouse gases will likely push the key climatic characteristics in many of these habitats beyond their limits, allowing the persistence of *Sphagnum*-dominated oligotrophic wetlands. Notably, according to the models of changes in the forested habitats of the Czech Republic under the climatic changes approximately corresponding to the RCP 4.5 scenario (IPCC 2019), the mean annual temperature is expected to rise for about 3.5–4.0 °C in the lower mountainous regions of the Bohemian Massif. The mean annual number of days with maximum temperatures exceeding 30 °C is projected to increase by approximately 400% after 2070. In addition, the number of rainless periods lasting for at least 10 days during the vegetative season at altitudes of 600–900 m a.s.l. is predicted to increase from approximately four to at least seven during the same period (Hlásny et al. 2011; Kalvová and Nemešová 1997). These changes will likely lead to considerable shifts in the water regime of peatland areas, such as a decrease in the water level in permanently flooded areas and pronounced seasonal desiccation of shallow pools and puddles, pointing to an ongoing transition of peatland ecosystems into a different ecological state (Yu 2006).

Moreover, these habitats, situated in the anthropogenic landscape of Central Europe, have also been affected by direct human activities, such as wetland drainage, peat extraction, pond construction, and recent restoration of excavated peatlands. Within the latter activity, artificial aquatic habitats have also been constructed. In addition, during the second half of the twentieth century, these mountainous areas were hit by an intense pulse of sulphur emissions from thermal power plants in the former country of

Czechoslovakia burning sulphur-rich lignite. This caused a significant increase in the concentration of sulphate anions in acrotelmic peat layers, largely replacing the organic anions of dissociated humic and fulvic acids (Hruška et al. 1996) and resulting in extensive acidification of aquatic sites in these poorly buffered peatland habitats. The consequences of these events largely persist to the present day (Garmo et al. 2014).

Microorganisms inhabiting wetland microhabitats respond rapidly to various environmental changes (Coesel et al. 1978; Łuców et al. 2022; van Dam and Meesters 2021a), and their reaction is usually considerably faster than that of macroorganisms such as macrophytes (Hájek et al. 2014; van Dam and Meesters 2021b). One of the most frequent protist groups in peatlands are desmids (Desmidiales, Zygnematophyceae), which, along with diatoms, usually form the dominant part of phytobenthos in dystrophic habitats (Brook 1981; Coesel 1982). Because of the well-defined ecological characteristics of individual species, these microalgae are used for biomonitoring the ecological status of aquatic habitats in peatlands. The basic framework for this biomonitoring is the index of nature conservation value (NCV), which is based on the species composition and richness of desmid taxa at individual sites (Coesel 2001). Thus, NCV belongs to a group of conservation value indices based solely on the biotic characteristics of habitats (Capmourteres and Anand 2016). In general, conservation value is inherently linked to the ability of a community in a given site to recover from environmental disturbances. From a conservation perspective, communities that can easily recover are typically more common and less significant than those that are highly sensitive to disturbances. The overall NCV score is based on three species-specific parameters. First, mature ecosystems are less easily replaced than those in early successive stages. Thus, species typically occuring in mature ecosystems contribute more to the NCV rating. In addition, the regional rarity of individual taxa and overall species richness are also used to compute the overall desmid-based index value.

It has been repeatedly shown that different types of disturbances in peatland habitats may lead to a reduction in their NCV (Coesel 2001; Neustupa et al. 2011; van Dam and Meesters 2021a). Similarly, relatively high NCV can indicate sites that provide refugia for the most valuable communities (Hansen et al. 2018; Paul et al. 2017). Therefore, the present study used the NCV framework to analyse desmid phytobenthos in a mosaic of peatland habitats in the Krušné hory Mts. (Ore Mts., Czech Republic), which is an area characterised by a long history of direct human activity in mountain landscapes and strong indirect anthropogenic impacts.

We conducted a detailed analysis of the species composition of desmid assemblages from virtually all available aquatic and wetland habitats in a selected mountain area of approximately 24 km^2. Using these data, we wanted to answer the following questions: (1) What is the conservation value of ombrogenous bog localities with a natural hydrological regime and minimal direct human influence compared to anthropically altered or disturbed sites in their vicinity? (2) What are the effects of the recent restoration efforts undertaken to revitalise the peatbogs that were severely disturbed by peat extraction in the second half of the twentieth century? (3) Which anthropogenic habitats in temperate mountainous landscapes can provide refugia for more sensitive taxa in terms of their desmid-based conservation value?

To answer these questions, we analysed the original NCV index and devised a modification of the NCV framework that might be more suitable to capture the observed differences among the strongly acidic sites predominating in the studied area.

Materials and methods

Sampling and identification

The study area is located at a relatively low altitude range (750–850 m a.s.l.), in the headwater area of a levelled mountainous plateau. The average annual precipitation for the period 1961–1990 is approximately 850 mm, and there is a continuous snow cover of 100–120 days per year (Tolasz 2007; Weisse 2023). The overall climatic conditions are close to the natural limit for the occurrence of ombrogenous peat bogs (Čížková et al. 2013). Thus, the remnants of ombrogenous peat bogs in the area are threatened by recent climatic extremes associated with ongoing climate change. In particular, these bogs were recently affected by two subsequent waves of extreme seasonal droughts, which occurred in 2018 and 2019, resulting in a reduction of approximately 25–30% of the total annual precipitation (ČHMÚ 2022). In the summer season, however, there was a reduction in precipitation of about 55% (Weisse 2023). On the other hand, parts of the study area were the subject of the transboundary Saxonian-Czech peatland restoration scheme, which involved the construction of numerous artificial pools in the excavated bog habitats (Moorevital 2018).

A total of 207 sites were analysed in the study area (24.18 km^2) between October 2021 and July 2022 (Online Resource 1, Fig. 1). At each site, a square of approximately 25 × 25

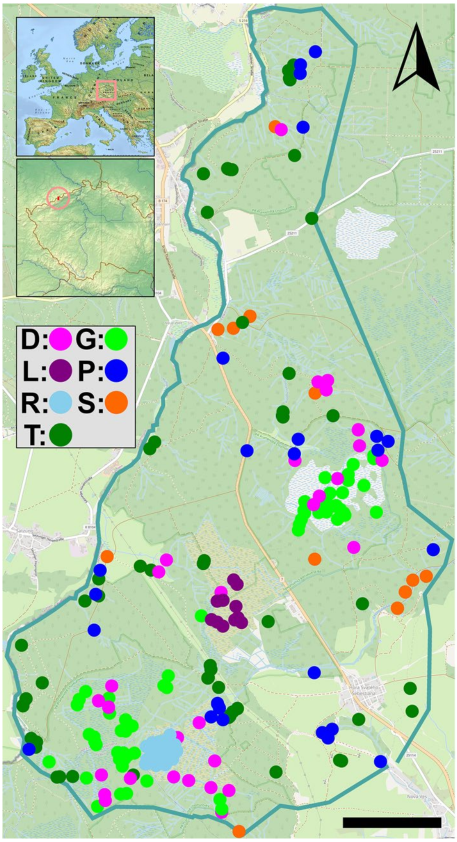


Fig. 1 Map of the study area in the context of Europe and the Czech Republic with the position of individual samples. Colors of circles correspond to the habitat types in the map. Scale bar = 1.5 km. D—old drainage channels, G—bog pools, L—recent drainage channels, P—dystrophic ponds, R—restored bog pools, S—streams, T—minerotrophic fen pools

cm was selected. The epipelon from each selected square was sampled from the uppermost 5 mm layer of sediment using a 50 ml plastic syringe. Metaphytic desmids were added by squeezing out mosses and submerged macrophytes. Water pH and conductivity were measured using a combined WTW 340i pH/conductivity meter (WTW GmbH, Weilheim, Germany) immediately before sampling in the field (Online Resource 1).

As a rule, the samples were processed on the day of sampling. For each sample, five microscopic slides (22 × 22 mm) were examined at ×200 magnification under bright-field illumination using a Leica DM2500 light microscope (Leica Microsystems, Wetzlar, Germany). Class-level abundances of individual taxa in the samples were estimated using a semi-quantitative scale as follows: 1 = less than 5 cells (scarce); 2 = 6–50 cells (rather abundant); and 3 = more than 51 cells (very abundant).

Under the term "desmids", many earlier studies included essentially all unicellular representatives of the class Zygnematophyceae, such as representatives of the traditional genera *Mesotaenium*, *Spirotaenia*, and *Cylindrocystis*. However, it is now clear that these taxa are non-monophyletic with core Desmidiales (Gontcharov 2008). Many of these traditional "saccoderm desmids" are actually more closely related to filamentous zygnematophycean genera such as *Zygnema* or *Spirogyra*. Therefore, in the present study, the focal group included taxa belonging to the families Desmidiaceae, Closteriaceae, Gonatozygaceae, and Peniaceae, as well as the genus *Roya*. Together, these taxa form a firmly supported monophyletic lineage within the class Zygnematophyceae and comprise the vast majority of traditionally defined desmids (Gontcharov 2008; Hall et al. 2008).

Habitat types

The samples were classified into seven distinct groups according to habitat type determined by their origin, ecological characteristics, and type of direct anthropogenic pressure. First, 51 samples were collected from pools of undisturbed ombrogenic bogs (Fig. 2a, b). These microhabitats are almost entirely fed by precipitation, either in the form of rainwater or snow. In recent years, however, these pools have been drying up regularly, probably because of the decreased snow cover, which led to long-term water deficits within bog ecosystems, as well as because of the more frequent extreme droughts in summer. In the study area, almost all bog pools dried up during the two subsequent extremely dry summer

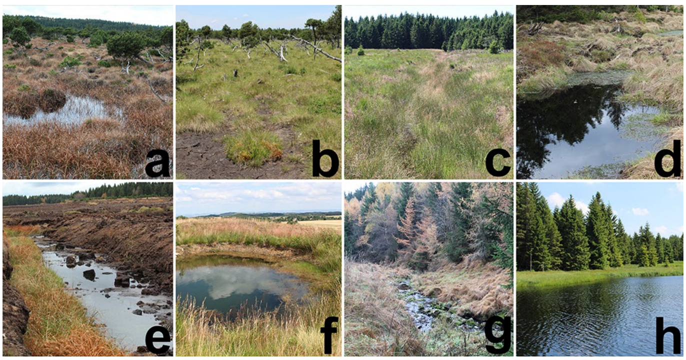


Fig. 2 Photographs of sites from different habitat types. **a** Natural bog pools, **b** a dried up bog site during the summer season, **c** old drainage channels, **d** restored bog pools, **e** recent drainage channels, **f** minerotrophic spring pools, **g** streams, **h** ponds

periods of 2018 and 2019 (Rothanzl, pers. comm.). In the course of the present study, in both the summer seasons of 2021 and 2022, these bog pools were also completely desiccated for several weeks between June and September.

Recently, a large-scale restoration project has been implemented in the study area (Moorevital 2018). Within the framework of the project, old drainage canals were dammed in an extracted peat bog area of 11.5 ha, levees were piled up to prevent water runoff, and pools about 100–150 cm deep were dug. These pools are now 5 years old and are characterised by strong acidity and *Sphagnum*-dominated littoral vegetation (Fig. 2c, d). In the present study, 26 samples were collected from these restored bog habitats for comparative analysis with other habitat types.

The third habitat type consisted of minerotrophic spring pools, which were part of acidic fens in the study area. The aquatic microhabitats of these sites are usually characterised by rich macrophyte vegetation dominated by *Sphagnum* spp. and *Utricularia* spp. In addition to the typical spring pools, this group also includes three unique anthropogenic pools formed by the collapse of the subterranean horizontal shafts of early modern ore mines (Fig. 2e, f). Nowadays, these pools are fed by groundwater and typically have a slightly acidic pH and relatively stable water regime.

The fourth group of sites consisted of smaller anthropogenic ponds constructed from the eighteenth century onwards, mainly to regulate water runoff from the area (Fig. 2g, h). The fifth group included the old drainage channels that have been built in extracted bogs since the nineteenth century. Today, these localities are mostly overgrown by bog vegetation (*Sphagnum* spp., *Eriophorum vaginatum*, *Empetrum nigrum*, etc.) and fed by adjacent bog pools. Furthermore, several samples were also collected from drainage channels in the area, where peat extraction continued until the 1990s. These sites, which were classified into a separate category within the studied habitats, were characterised by an almost complete absence of macrophyte vegetation on the exposed peat. The last group consisted of samples collected from the benthos of small streams that originated and flowed through the study area. As these streams are fed by water from the surrounding bogs and acidic fens, they have a dystrophic character with frequent occurrence of *Sphagnum*-dominated vegetation in the littoral zone.

Data analysis

Multivariate patterns in the community structures of individual sites were illustrated using principal component analysis (PCA). The eigenvalues and eigenvectors of the principal components (PCs) were computed based on the variance-covariance matrix of the sites. Species loadings were shown by projecting them onto the ordination plot of principal components.

To quantify the relationship between individual factors and desmid community structure, three linear models were fitted using permutational multivariate analysis of variance (PERMANOVA). For these analyses, species-in-site data were converted to principal components to ensure their normal distribution. First, variation in the matrix of Euclidean distances among the sites was evaluated by fitting multivariate linear models with pH and conductivity levels used as independent factors. Then, the effect of the categorical variable with the codes of individual habitat types on the differences in species structure of the sites was quantified by a separate linear model, too. The models yielded the sum of squares (SS) and the percentage proportion (η^2) of the total variation in the species structure of the sites, which may be attributed to each of the factors. In addition, the *p*-values evaluating the probabilities that the observed relation of independent factors with the community structure of the sites might have been yielded by random variation were quantified by comparing the original SS values with the distribution of random SS yielded by 999 permutations (Anderson 2017).

When the non-random relationships of habitat types with community structure were detected, we asked which species were the most responsible for the observed differences and which species were characteristic of particular habitats. This was assessed using similarity percentage (SIMPER) analysis, a technique that quantifies the taxa responsible for the observed differences between sample groups (Clarke 1993). The groups were pooled to compute an overall multi-group SIMPER, and the analysis identified which taxa were the most important for distinguishing groups by habitat types within the entire assemblage and which taxa had the highest abundances in individual habitat types.

The structure of variability among the habitat types was illustrated using between-group PCA (Culhane et al. 2002). This variant of PCA performs eigenanalysis on the means of a priori defined groups, and the individual objects are then projected onto these principal components. One of the convenient properties of between-group PCA is that the variability is usually concentrated in a few axes; therefore, it can be more easily illustrated using an ordination plot. As with the standard PCA, loadings of individual species were shown by projecting them onto the ordination plot.

PERMANOVA analyses were performed in R, ver. 4.0.5 (R Core Team 2021), using the function *adonis* implemented in the *vegan* package, ver. 2.6–2 (Oksanen et al. 2022). Then, permutation analyses to compare the original SS values with the distribution of 999 randomly created SS were conducted using the function *procD.lm* in the *geomorph* package, ver. 4.0.0 (Baken et al. 2021). Standard and between-group PCAs and linear bivariate regression were conducted in PAST, ver. 4.10 (Hammer et al. 2001).

NCV index

Calculation of the NCV index was based on tabulated species characteristics based on the extensive body of floristic and ecological data on desmids in European aquatic habitats. The original list of species characteristics was published by Coesel (1998), with an emphasis on data from the Netherlands and neighbouring countries. An updated list of Central European habitats, which we based the present study on, was published by Stastny (2010). For each species, values of regional rarity and ecological sensitivity in relation to habitat disturbance are in the range of 0–3. Furthermore, the total species richness of the analysed sites is included in the calculation. In the original Coesel's notation of the NCV index, the sum of the values for rarity and sensitivity of each species and their total richness are converted to integer scores for each of these three components, ranging from 1 to 3 (Table 1). The calculation is then carried out on a different scale for strongly acidic sites with a $pH < 5.0$, moderately acidic habitats with pH levels between 5.0 and 6.5, which usually contain the most species of desmids, and sites with a neutral $pH > 6.5$. The sum of the scores for each component (richness, rarity, and sensitivity) is the resulting integer value of the site, ranging from 1 to 10 (Coesel 2001).

Reduction in the actual values of species richness and sums for rarity and sensitivity of taxa to three integer levels necessarily leads to leaps in the index scores and, at the same time, a certain levelling of differences among sites. Note, for example, that two hypothetical assemblages consisting of 6 and 30 species in a strongly acidic environment would both

Table 1 Threshold values of species richness, and sums of points for species rarity and sensitivity at three different pH levels for the calculation of the original and modified NCV index of samples

ph < 5.0						5.0 ≥ pH ≤ 6.5						pH > 6.5					
Diversity (d)		Rarity (r)		Sensitivity (s)		Diversity (d)		Rarity (r)		Sensitivity (s)		Diversity (d)		Rarity (r)		Sensitivity (s)	
Original NCV (after Coesel and Meesters 2007)																	
1–5	1.0	1–2	1.0	1–5	1.0	1–10	1.0	1–5	1.0	1–10	1.0	1–5	1.0	1–2	1.0	1–5	1.0
6–30	2.0	3–30	2.0	6–20	2.0	11–50	2.0	6–40	2.0	11–40	2.0	6–30	2.0	3–10	2.0	6–20	2.0
> 30	3.0	> 30	3.0	21–40	3.0	> 50	3.0	> 40	3.0	41–80	3.0	> 30	3.0	> 10	3.0	21–40	3.0
				> 40	4.0					> 80	4.0					> 40	4.0
Modified NCV																	
1	1.0	1	1.0	1	1.0	1–2	1.0	1	1.0	1–2	1.0	1	1.0	1	1.0	1	1.0
2	1.2	2	1.5	2	1.2	3–4	1.2	2	1.2	3–4	1.2	2	1.2	2	1.5	2	1.2
3	1.4	3–7	2.0	3	1.4	5–6	1.4	3	1.4	5–6	1.4	3	1.4	3	2.0	3	1.4
4	1.6	8–13	2.2	4	1.6	7–8	1.6	4	1.6	7–8	1.6	4	1.6	4–5	2.2	4	1.6
5	1.8	14–19	2.4	5	1.8	9–10	1.8	5	1.8	9–10	1.8	5	1.8	6–7	2.4	5	1.8
6–10	2.0	20–25	2.6	6–8	2.0	11–18	2.0	6–12	2.0	11–16	2.0	6–10	2.0	8–9	2.6	6–8	2.0
11–15	2.2	26–30	2.8	9–11	2.2	19–26	2.2	13–19	2.2	17–22	2.2	11–15	2.2	10	2.8	9–11	2.2
16–20	2.4	> 30	3.0	12–14	2.4	27–34	2.4	20–26	2.4	23–28	2.4	16–20	2.4	> 10	3.0	12–14	2.4
21–25	2.6			15–17	2.6	35–42	2.6	27–33	2.6	29–34	2.6	21–25	2.6			15–17	2.6
26–30	2.8			18–20	2.8	43–50	2.8	34–40	2.8	35–40	2.8	26–30	2.8			18–20	2.8
> 30	3.0			21–24	3.0	> 50	3.0	> 40	3.0	41–48	3.0	> 30	3.0			21–24	3.0
				25–28	3.2					49–56	3.2					25–28	3.2
				29–32	3.4					57–64	3.4					29–32	3.4
				33–36	3.6					65–72	3.6					33–36	3.6
				37–40	3.8					73–80	3.8					37–40	3.8
				> 40	4.0					> 80	4.0					> 40	4.0

For each component the first column indicates the observed values, the second column indicates the corresponding score conversions that provide a basis for subsequent NCV calculation by summing the three integer scores for components of species richness, rarity, and sensitivity score two points for diversity, even though they clearly consisted of communities with very different complexities (Table 1).

For such habitats, it might therefore be useful to distinguish more finely among sites with relatively few species, which in some cases may belong to taxa with higher sensitivity to disturbance or less frequent regional distribution. Because of the large number of extremely acidic sites analysed in the present study, it was deemed sensible to introduce a slight modification to the original NCV procedure. Essentially, this was done by introducing a finer scale in the distribution of scores across the components of richness, sensitivity, and rarity, typically by 0.2 points between each level (Table 1). In our analyses, the index values obtained using the original procedure and this modified calculation were compared using a bivariate regression model. In addition to the linear bivariate regression, second- and third-order polynomials were fitted. Akaike Information Criterion (AIC) was used to evaluate the optimal polynomial function showing the relationship between the original and modified NCVs (Findley 2014).

Results

A total of 129 desmid species were found in the study area. The number of species found in the individual samples varied from 1 to 20 (Online Resource 1). The pH values of the sites were significantly related to their species structure. This was exemplified by the 10.3% of the total variation in species composition that the PERMANOVA model apportioned to the explanatory effect of pH (Table 2). In addition, pH was moderately related to species richness in the linear bivariate regression (Pearson's $r = 0.274$, $R^2 = 0.075$, $p = 0.0001$; slope $a = 1.04$, 95% CI [0.42, 1.55]). Conversely, electrical conductivity was not significantly related to the species-in-site data (Table 2).

Habitat types proved to be relatively strongly related to species data. The corresponding PERMANOVA model showed that 19.9% of the variation in community structure could be explained by of the classification of sites into different habitats (Table 2). This was also reflected in the differences in species richness among the habitats (Fig. 3a, Online Resource 2). In particular, the restored bog pools typically had very low desmid diversity, consisting of only 1–3 desmid taxa. Likewise, individual samples taken from peatbog drainage channels and streams typically included less than three desmid taxa. On the other hand, dystrophic ponds were the most diversified habitat, with a mean value of more than six desmid taxa in each sample. Habitat types also clearly differed in their typical pH levels

Table 2 Results of multivariate linear models evaluating the effects of three independent factors on desmid community structure of samples

Source of variation	df	SS	MS	η^2	p
pH	1	167.74	167.74	0.1025	**0.001**
Conductivity	1	8.66	8.66	0.0053	0.305
Habitat type	6	325.06	54.18	0.1986	**0.001**
Total	206	1636.48			

Total df and SS are identical for each of the three separate multivariate models. Significant Bonferroni-corrected p-values lower than 0.017 are depicted in bold

df degrees of freedom; *SS* sum of squares; *MS* mean squares; η^2 coefficient of determination; *p* probability of the null hypothesis

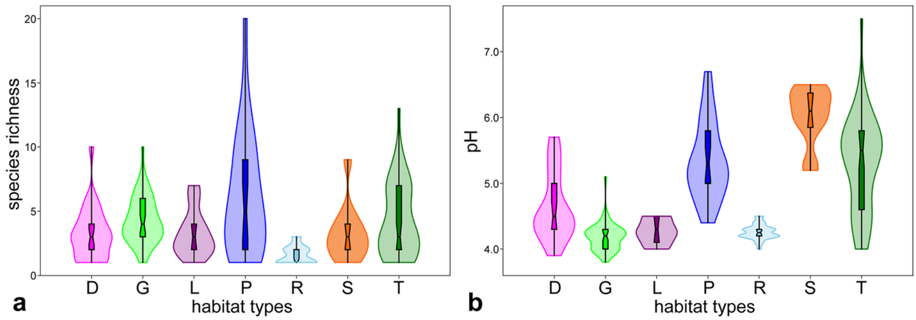


Fig. 3 Variation of **a** species richness and **b** pH values among the habitat types. The violin plots show the probability density of the observed data smoothed by a kernel density estimator at different values of the variables under study. D—old drainage channels, G—bog pools, L—recent drainage channels, P—dystrophic ponds, R—restored bog pools, S—streams, T—minerotrophic fen pools

(Fig. 3b, Online Resource 2). The natural and restored bog pools were typical for extremely acidic waters with mean pH values of 4.18 and 4.26, respectively. On the other hand, moderately acidic samples were mostly those obtained from dystrophic ponds (mean pH 5.34), minerotrophic pools (mean pH 5.3), and streams (mean pH 6.04).

The most important patterns of diversification in species composition of the studied sites largely reflected their classification into the seven habitat types. In the ordination plot of the first two axes yielded by standard PCA, PC1 largely differentiated between the samples taken from strongly acidic sites, such as those in natural peatbogs or in restored bog pools, and the samples taken from sites with typically higher pH values, namely dystrophic ponds, streams, and minerotrophic pools (Figs. 4, 5a).

A highly similar pattern was also illustrated along the first two axes of between-group PCA, which highlighted the differences among the habitat types (Fig. 6). However, this analysis also differentiated stream samples from other habitat types along the second principal component. In both PCAs, *Staurastrum margaritaceum* was the single most prominent species, typifying the strongly acidic sites, especially restored bog pools. This was also confirmed by the SIMPER analyses, which showed that this species was the single most important discriminating factor in the overall analysis, as well as the most abundant desmid taxon in all types of bog pools and drainage channels (Table 3).

On the other hand, this species was rarely recorded in the less acidic sites, such as ponds, streams, and minerotrophic pools. Natural bog pools were also typical for the frequent occurrence of *Actinotaenium silvae-nigrae*, *Tetmemorus flensburgii*, and *Euastrum neogutwinskii* (Fig. 4a, Table 3). Conversely, in restored bog pools and recently created drainage channels, *Staurastrum hirsutum* proved to be the second most frequent species (Table 3). In addition to these frequent taxa, several rather rare taxa, such as *Cosmarium obliquum*, *C. sphagnicolum*, and *Staurastrum scabrum*, were also recorded in some highly acidic pools in natural bog areas (Online Resource 1). These taxa were generally absent from other strongly acidic sites, such as the pools in restored bog areas. At these sites, the samples often included only *S. margaritaceum* as the sole desmid species. However, relatively rare species such as *Cosmarium decedens* or the more sensitive *T. flensburgii*, were also recorded in a few of these artificial pools. Samples with comparatively less acidic conditions were largely taken from ponds, minerotrophic pools, and streams (Figs. 4a, 6). In particular, *Closterium striolatum*, *Euastrum ansatum*, *E. humerosum*, and *Micrasterias*

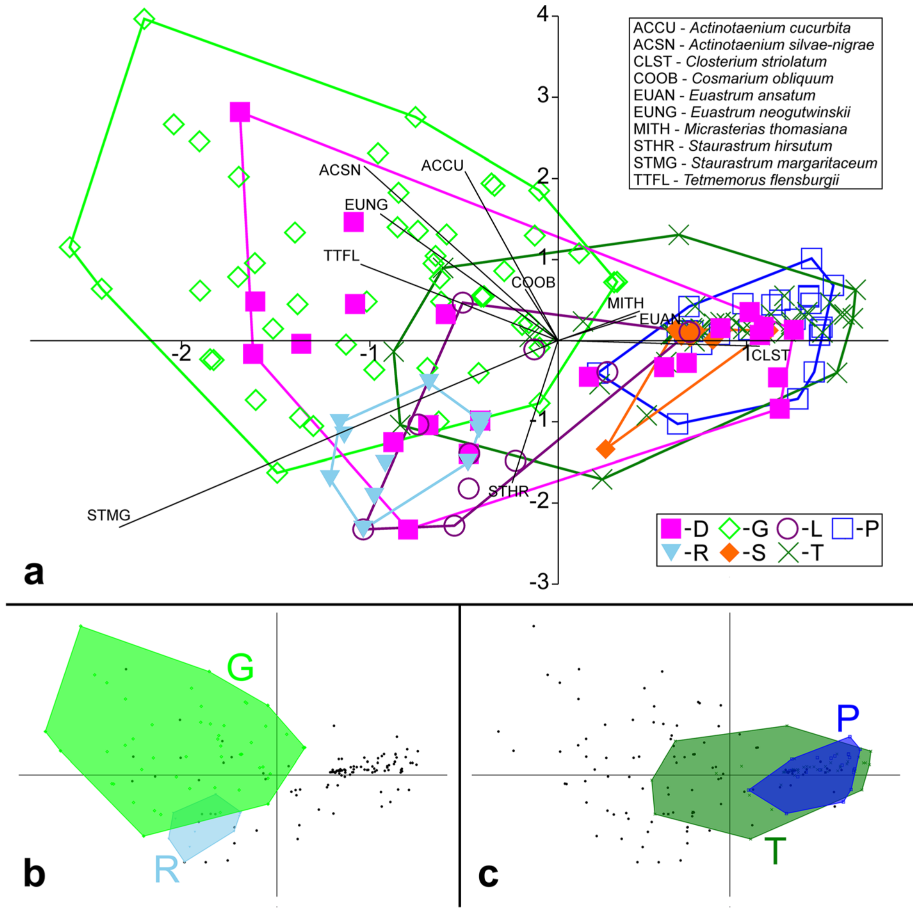


Fig. 4 PCA ordination plot of species composition in samples showing first two PCs spanning 15.4% (PC1) and 7.5% (PC2) of the variation, respectively. Samples representing seven habitat types are **a** distinguished by colours, symbol signs and polygons delimiting their position in the ordination space. Desmid species that are most responsible for the observed ordination structure are projected into the plot by vectors. The **b** natural (G) and restored (R) bog pools and **c** the minerotrophic fens (T) and ponds (P) are highlighted in the ordination space. Designation of the remaining habitat types is listed in the caption of Fig. 3

thomasiana were typical for these habitat types and did not occur in bog areas. Interestingly, the samples taken from several streams originating in the study area contained a peculiar desmid assemblage of *Roya obtusa*, *Closterium tumidulum*, *C. tumidum var. nylandicum*, and *Actinotaenium cruciferum*, which were not found at any other site (Fig. 6, Table 3).

The values of original and modified NCV showed a strong linear positive relationship, yielding Pearson's $r = 0.96$ and $R^2 = 0.92$. However, when comparing the results of the linear correlation analysis with the polynomial fits of higher orders, the lowest AIC was yielded by the 2nd order polynomial curve, indicating an optimal fit with $R^2 = 0.94$ (Fig. 7). In this graph, we can see that the modified NCV often yielded slightly higher values, especially for those samples where the original score was relatively low (i.e., 2.0 or 3.0). At higher values, the difference between the values of the two indices decreased. If

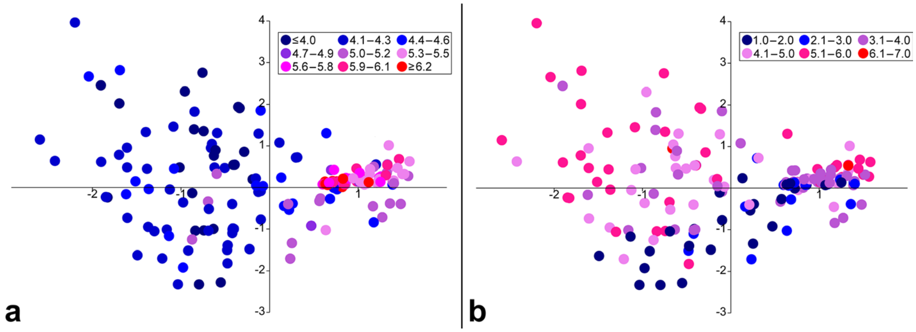


Fig. 5 PCA ordination plot of species composition in samples showing first two PCs (PC1 vs. PC2). Colour gradients illustrate **a** pH variation and **b** modified NCV scores within the ordination space

the maximum value for each component (richness, rarity, and sensitivity) was reached, the values of the modified and original NCV would obviously be identical.

The modified and original NCV of the samples ranged from 1.0 to 6.8 and from 1.0 to 6.0, respectively. However, almost a quarter of the samples (51 samples) had a modified NCV lower than 2.0. On the other hand, a total of 11 samples had a modified NCV of at least 6.0 (Online Resource 1). Among these, six samples were obtained from strongly acidic natural bog pools, three were obtained from dystrophic ponds, and two were obtained from smaller minerotrophic sites. Thus, we see that the most valuable sites did not occur within only one of the habitat types or at specific pH values. Nevertheless, significant differences in NCV scores were found among the habitat types (Fig. 8, Online Resource 2). In particular, the restored bog pools had very low NCV with a mean score of 1.7. Conversely, original bog pools had the highest mean NCV of 4.7, indicating the presence of relatively rarer and more sensitive taxa. Among the other habitat types, recently created drainage channels and streams had very low mean NCV of 2.7 and 2.6, respectively. Conversely, ponds and minerotrophic pools yielded somewhat higher NCV with mean values of 3.9 and 3.3, respectively (Fig. 8, Fig. 5b, Online Resource 2).

Discussion

The observed structure of the desmid assemblages among the 207 samples generally confirmed the well-known relationship between environmental acidity and species composition. Usually, this is also closely correlated with the ombro-minerotrophic gradient, differentiating strongly acidic and poorly buffered ombrotrophic bogs from minerotrophic sites typical for slightly acidic conditions (Garraza et al. 2019; Mataloni 1999; Neustupa et al. 2013). However, the present study was conducted in an area that was particularly strongly affected by acidic precipitation in the period from the 1970s to the 1990s (Evans et al. 2001). The overall strong acidity of the existing aquatic habitats, which has persisted ever since, was reflected in the pH levels below 5.0 measured not only in ombrogenous bog pools, but also in multiple minerotrophic sites, such as drainage channels and even several minerotrophic spring pools. In the ordination analyses, this was reflected by the positions of these sites in the left parts of the ordination space formed by the two most informative

Table 3 Results of the multi-group SIMPER analysis identifying desmid taxa distinguishing the habitat types and the taxa with the highest abundance in individual groups

Taxon	Average dissimilarity	% Contribution
Staurastrum margaritaceum	2.43	10.36
Closterium striolatum	1.40	5.98
Actinotaenium silvae-nigrae	1.21	5.16
Tetmemorus flensburgii	1.20	5.12
Staurastrum hirsutum	0.97	4.14
Euastrum neogutwinskii	0.96	4.08
Actinotaenium cucurbita	0.81	3.44
Bambusina borreri	0.69	2.98
Staurastrum simonyi	0.52	2.20
Closterium rostratum	0.46	1.97
Habitat type	Taxon	Mean abundance
D (old drainage channels)	*Staurastrum margaritaceum*	1.13
	Tetmemorus flensburgii	0.63
	Euastrum neogutwinskii	0.58
G (bog pools)	*Staurastrum margaritaceum*	1.40
	Actinotaenium silvae-nigrae	1.22
	Euastrum neogutwinskii	0.88
L (recent drainage channels)	*Staurastrum margaritaceum*	1.40
	Staurastrum hirsutum	1.30
	Euastrum neogutwinskii	0.60
P (dystrophic ponds)	*Closterium striolatum*	1.13
	Euastrum ansatum	0.50
	Micrasterias thomasiana	0.46
R (restored bog pools)	*Staurastrum margaritaceum*	2.41
	Staurastrum hirsutum	0.27
	Bambusina borreri	0.14
S (streams)	*Closterium tumidulum*	0.91
	Roya obtusa	0.73
	Closterium tumidum var. nylandicum	0.73
T (minerotrophic fen pools)	*Closterium striolatum*	0.64
	Closterium rostratum	0.30
	Staurastrum margaritaceum	0.30

PCs. Nevertheless, the samples from the strongly acidic minerotrophic sites still lacked characteristic taxa that were only present in the ombrogenous bogs.

In the study area, these sites with natural hydrological regimes are currently represented by only three isolated locations with a total extent of 0.75 km^2, i.e., approximately 3% of the total area, which is only a fraction of their original pre-industrial area. Nevertheless, these isolated sites clearly still represent unique habitats from the perspective of biodiversity conservation. Our ordination diagrams showed that natural bog samples were all concentrated in the part of the ecological space that included all kinds of strongly acidic sites. However, typical bog species, such as *C. obliquum*, *C. sphagnicolum*, and *C. pygmaeum*,

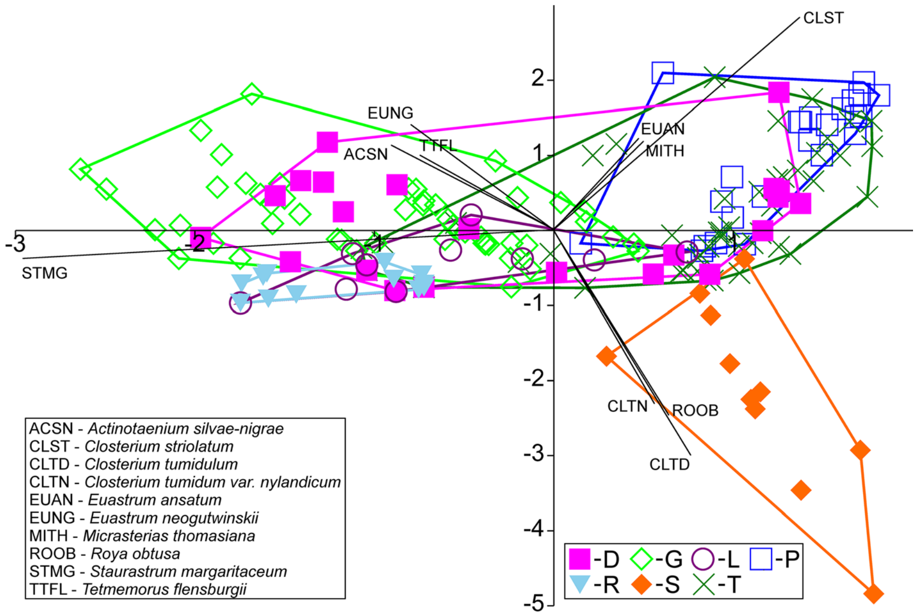
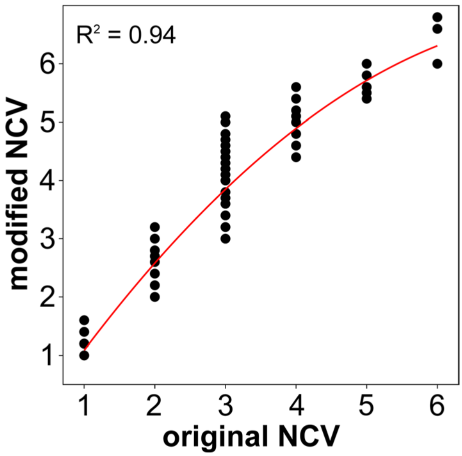


Fig. 6 Between-group PCA ordination plot of species composition in samples showing first two PCs spanning 48.4% (PC1) and 19.9% (PC2) of the variation, respectively. Samples representing individual habitat types are distinguished by colours, symbol signs and polygons delimiting their position in the ordination space. Taxa that are most responsible for the observed ordination structure are projected into the plot by vectors. Designation of the habitat types is listed in the caption of Fig. 3

Fig. 7 The 2nd order polynomial relationship between the original and modified NCV scores of samples



were not found in samples from any other habitat type, not even in sites in the immediate vicinity of natural ombrogenous bogs. Thus, these taxa can probably be considered as indicators of bog environments, at least in the studied region. Likewise, *A. silvae-nigrae*, a characteristic species of strongly acidic sites (Coesel 1998; Stastny 2010), occurred in 39 out of 51 bog samples. In addition, it was found in several samples taken from old overgrown drainage channels dug through bog areas as well as in other strongly acidic sites.

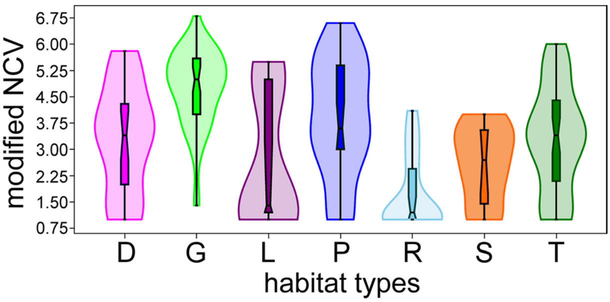


Fig. 8 Variation of the modified NCV scores among the habitat types. The violin plots show the probability density of the observed data smoothed by a kernel density estimator at different values of the variables under study. Designation of the habitat types is listed in the caption of Fig. 3

Furthermore, it has been shown that natural bog pools are among the most valuable habitats based on the desmid-based ecological monitoring. In the present study, the NCV index scores of samples obtained from bog pools were clearly higher than those for comparable strongly acidic anthropogenic habitats such as drainage channels and restored bog pools. Interestingly, in recent years, almost all surveyed bog sites have been completely desiccated for at least a few weeks during the summer season. In addition, peat desiccation during dry periods can locally enhance past acidification effects because deposited reduced sulphur and nitrogen compounds can be mineralised, which further acidifies the aquatic bog microhabitats (van Dam and Meesters 2021a). Sulphur deposition in the region decreased by at least 75% since the peak emissions in late 1980s. On the other hand, anthropogenic wet and dry deposition of nitrogen decreased relatively slowly to values corresponding to approximately 50% of the extreme levels of the second half of the twentieth century (Kopáček and Veselý 2005). However, a further decline of the anthropogenic nitrogen deposition no longer seems to occur in the 2000s (Fottová 2003). Thus, acidification caused by mineralized nitrogen deposits, which are facilitated by desiccation events, may continue to negatively affect natural communities of phytobenthos in the future.

This indicates that the desmid species detected in these samples repeatedly survived these conditions and were able to replicate from cells that survived in the desiccated peat substrate after the dry period has passed. The association of some species found in the studied bog pools with strongly acidic hydroterrestrial or subaerial microhabitats has been documented in the literature. This applies to *C. obliquum*, *A. silvae-nigrae*, *A. cucurbita*, and *Tetmemorus laevis* (Evans 1959; Stastny 2008; van Westen and Coesel 2010). Thus, it is likely that these taxa have specific adaptations, such as a relatively low cell surface-to-volume ratio, that allow them to survive in an environment without liquid water in the immediate vicinity (Coesel 1982; Neustupa et al. 2011).

On the other hand, it should be mentioned that some taxa that were also typically found in bog pools, such as *S. scabrum*, *C. sphagnicolum*, and *C. pygmaeum*, have rather been considered to be benthic organisms, generally not occurring in ephemeral habitats (Coesel and Meesters 2007). This raises a question about the prospects for such species in the changing environment of Central European mountainous peatbogs, where seasonal desiccation is becoming an annual phenomenon. In general, changes in the community structure of various eukaryotic microorganisms, such as testate amoebae, diatoms, and desmids, in aquatic microhabitats of peatlands have been repeatedly shown to be closely linked to the water table dynamics of individual sites (Hájek et al. 2011; Lamentowicz et al. 2010; Mataloni 1999). Therefore, increased desiccation frequency is expected to lead to significant shifts in the community structure and possibly to a further decrease in desmid diversity in the studied bog sites. In this respect, it should be noted that actual ecophysiological data on the differential resilience and adaptive mechanisms of desmids against desiccation stress are still lacking. Such data could provide a basis for estimating desmid resilience to changes in ombrogenous bog habitats, as these changes are an inevitable consequence of ongoing climate change. In addition, continuing nitrogen deposition from anthropogenic sources will further contribute to acidity driven by inorganic ions and eutrophication pressures on ombrogenous bogs in the region (Bragazza et al. 2005). Thus, the synchronous effects of these parallel environmental stress factors may accelerate shifts in community structure and diversity decrease of benthic microalgae in these habitats.

It should also be noted that the actual distribution of desmid taxa in extremely acidic habitats may be limited by the availability of free CO_2 as the dominant source of carbon for photosynthesis in aquatic environments (Spijkerman et al. 2005). In sites with pH exceeding 5.5, the HCO_3^- ion is prevalent, and most acidophilic desmid species are replaced by more diversified assemblages of slightly acidic habitats (Coesel and Meesters 2007). In the mountainous peatland landscape of the Bohemian Massif, such conditions are present in minerotrophic springs and various anthropogenic habitats, such as small ponds constructed in the vicinity of peatbogs or flooded mine sinkholes. Interestingly, in the present study, samples taken from anthropogenic ponds with a pH between 5.3 and 6.5 were among those with the highest species richness and NCV. These sites are often positioned outside the existing protected areas and are not under any explicit conservation strategy. For example, this was the case for sample no. 180 with the single highest species richness of 20 taxa in a standardised 25 × 25 cm square. Thus, these localities play a crucial role in maintaining desmid biodiversity in the anthropogenised mountain landscapes of Central Europe. Similar patterns of diversity and desmid-based NCV were also detected in the neighbouring Saxony, where the highest values were typically reported at sites with $pH > 5.5$ (Paul et al. 2017). It should also be emphasized that anthropogenic ponds, because of their higher resilience to desiccation, especially compared to that of smaller minerotrophic pools, may represent essential refugia for aquatic peatland biota in the changing climatic conditions of the region.

Our results showed that streams were the only habitat type with a higher average pH, which differed markedly in species composition from the others. Even though this microhabitat is not usually associated with the occurrence of desmids, they were present in all dystrophic stream samples. This assemblage was composed of species that, in most cases, did not occur in any other habitat, namely *R. obtusa*, *A. cruciferum*, *C. tumidulum*, and *C. tumidum* var. *nylandicum*. None of these species have been explicitly associated with stream phytobenthos in the literature, although Růžička (1977) stated that both of the above mentioned taxa of the genus *Closterium* have been observed several times in running waters. Thus, while the phytobenthos of dystrophic streams has rarely been studied in terms of desmids, our data suggested that it may represent a unique microhabitat suitable for relatively rare desmid taxa that are missing from other localities.

In general, desmid flora of the study area was similar and comparable to the species lists from other recent surveys of mountain peatlands in Central Europe. The total number of recorded species was higher than that in datasets from other areas of the Bohemian Massif, such as the western parts of the Krušné hory Mts. (41 species, Neustupa et al. 2013; 88 species, Stastny 2017), Jizerské hory Mts. (76 species, Štěpánková et al. 2008), Krkonoše Mts. (44 taxa, Nováková 2002), and Jeseníky Mts. (51 species, Štěpánková et al. 2012). However, these studies were based on a considerably smaller number of samples, which may explain most of the observed differences. On the other hand, floristic data from subalpine altitudes of Central and Eastern Alps indicated that the desmid diversity of these regions might be systematically higher than that in the mountain regions of the Bohemian Massif (Lenzenweger 1981, 2002).

Thus, it is interesting to ask which conspicuous species that might occur in the studied localities based on their ecological characteristics and are known to occur in other Central European mountain peatland localities were completely absent here. In this context, it may be useful to focus on distinctive "flagship" taxa, the occurrence of which is usually well documented in floristic and ecological studies. Within the Bohemian Massif, in the strongly acidic peatland habitats of Jizerské hory Mts., Štěpánková et al. (2008) recorded several conspicuous species, such as *Euastrum insigne*, *Micrasterias jenneri*, and *Xanthidium armatum*. These taxa are considered indicators of ecologically stable, highly acidic sites (Coesel 1998; Stastny 2010). Interestingly, Stastny (2017) recently recorded these taxa, together with *S. scabrum*, *T. flensburgii* and multiple other desmid taxa, in acidic bog and fen sites located in the western parts of the Krušné hory Mts. at the altitudes about 250 m higher than the studied localities. Likewise, *E. insigne* has recently been also recorded in the subalpine peatlands of the Jeseníky Mts. located in the north-eastern part of the Czech Republic and western Carpathians in Poland (Štěpánková et al. 2012; Lenarczyk et al. 2015). All these acidophilic taxa are also known from several of localities in the Alps (Lenzenweger 2000, 2002). Given the detailed screening of virtually all suitable sites conducted in the present study, it is likely that these distinctive and characteristic taxa are indeed absent from the study area. Their absence might be considered one of the key indicators of previous environmental disturbances that decreased the overall complexity of desmid communities. Conversely, the occurrence of these taxa in the natural acidic habitats of Central European mountain ecosystems should be considered a sign of the relatively high ecological status of individual sites.

Restoration efforts in the peatland areas of the Krušné Hory Mts. are still in their early stages, and their actual impacts on aquatic biota will only be comprehensively assessed in the long term. The pools dug in the mined bog approximately five years ago contained only a fraction of desmid diversity and cannot compensate for the existing bog microhabitats. Even in the long term, the original desmid communities may not fully recover in artificially restored sites (Goodyer 2014; van Dam and Meesters 2021b). Similar long-term patterns have also been observed for testate amoebae and diatoms (Łuców et al 2022). However, other studies have shown that successful restoration of aquatic peatland habitats can actually lead to the development of highly valuable and diversified desmid assemblages in artificially created localities (Coesel 2003).

At this point, the present study can only be considered as a relatively detailed database from which it will be possible to evaluate future changes in the composition of desmid assemblages in artificial pools created as a result of restoration projects, or in anthropogenic ponds, remaining natural peatbogs, and fen sites. In the mountain ecosystems of Central Europe, climate change will inevitably lead to a shift from the relatively stable climatic period of the Holocene (Kalvová and Nemešová 1997). It is possible that a number of aquatic peatland localities will not survive these changes and will disappear completely or become periodically flooded ephemeral wetlands. This would likely result in significant changes and an overall reduction in microphytobenthos biodiversity. However, it is possible that targeted restoration efforts to retain water in the environment of the mountain plateaus of the Bohemian Massif will provide refugia that will be able to sustain peatland biota in this landscape in the long term.

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Author contributions JN and JS conceived and designed the study design, JN and KW did the field sampling and measurements, JS and JN identified the taxa, JN analysed the data and wrote the manuscript. All authors reviewed and approved the manuscript.

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Data availability All primary data of this study are published as the electronic supplementary material (Online Resources 1 and 2) available at the publisher's site.

Declarations

Competing interests The authors declare that they have no competing financialor non-financial interests that could have influenced the work reported in this manuscript.

Ethical approval Not applicable.

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