BOREAL ENVIRONMENT RESEARCH 27: 81–96
ISSN 1797-2469 (online) Helsinki 3 May 2022

Habitat preferences of *Hamatocaulis vernicosus* at the junction of continental and boreal phytogeographical regions (Lithuania)

Monika Kalvaitienė and Ilona Jukonienė

Nature Research Centre, Žaliųjų Ežerų Str., 49, 12200 Vilnius, Lithuania
*(*corresponding author's e-mail: monika.subkaite@gamtc.lt)*

Received 21 Oct. 2021, final version received 1 Mar. 2022, accepted 21 Mar. 2022

Kalvaitienė M. & Jukonienė I. 2022: Habitat preferences of *Hamatocaulis vernicosus* at the junction of continental and boreal phytogeographical regions (Lithuania). *Boreal Env. Res.* 27: 81–96.

Based on the Nature Conservation Act, the rare fen moss *Hamatocaulis vernicosus* (Bern Convention, EU habitat directive) is protected in more than 500 Natura 2000 territories of Europe. Knowledge on its ecology is required to ensure favourable conservation status, meanwhile data from specific regions is still insufficient. The aim of this study was to highlight habitat characteristics specific at the junction of boreal and continental biogeographical regions. The data of 63 study plots included cover and abundance of the plant species, water parameters (conductivity, pH, and concentrations of Ca^{2+}, Fe^{3+}, K^{+}, Mg^{2+}, NH_4^{+}, NO_3^{-}, and PO_4^{3-}), topography type and microrelief form. The specific features both in terms of water parameters and vegetation were ascertained. The habitats showed wide variation and high amounts of electrical conductivity, calcium, iron and magnesium. Most associated species were *Carex diandra*, *C. rostrata*, *Menyanthes trifoliata*, and *Calliergonella cuspidata*. The highest restriction with the most frequent plant communities showed *Marchantia polymorpha*, *Plagiomnium ellipticum*, and *Rumex acetosa*. Thus, the study confirms the general trends known for the habitat preferences of *H. vernicosus* and highlights the regionally based characteristics related to both water physical-chemical parameters and vegetation. To ensure favourable status of *H. vernicosus* throughout Europe, conservation measures that consider the particular features of the regional habitats should be applied.

Introduction

The rare fen moss *Hamatocaulis vernicosus* is a circumboreal species that is widespread in Europe (Hill *et al.* 1994). Usually, *H. vernicosus* grows in mineral-rich environments but avoids calcium-rich fens (Hedenäs 1989). Such specific habitats occur in different numbers and qualities throughout Europe. From the first half of the 20th century, when Europeans started to drain fens and convert arable land intensively, they experienced a severe decline (Lamers *et al.* 2015, Joosten *et al.* 2017). Apart from habitat destruction by drainage, fens are also permanently threatened by eutrophication and acidification (Lamers *et al.* 2015, Kooijman *et al.* 2020), factors which have resulted in a decline in *H. vernicosus* populations (Štechová and Kučera 2007).

Considering the general rarity of *H. vernicosus* and the threats to its habitats, this species was listed in the Convention on the Conservation of European Wildlife and Natural Habitats

Editor in charge of this article: Christina Biasi

(Bern Convention) (Council of Europe 1979). Later, similar to many species in the Convention, *H. vernicosus* was included in Annex 2 of the EU Habitats Directive (European Commission 1992). Under the Natura 2000 network, *H. vernicosus* is now protected in 522 territories in 21 countries of Europe. The largest number of NATURA territories where *H. vernicosus* is protected is in Finland (more than 90 territories) and Sweden (79) (boreal region) and in Germany (68) and Poland (60) (continental region) (EEA, 2019). Lithuania contains 33 Natura 2000 territories protecting populations of *H. vernicosus*, which is more than those in not only other Baltic countries (Latvia (26) and Estonia (13)) but also many other European countries (France (27), Czech Republic (22), Denmark (15), Ireland (9), Romania (9) and others). *Hamatocaulis vernicosus* is included in many national red lists. This species is further categorised as endangered or critically endangered, in Germany, the Netherlands, Slovakia, and Spain. In seven countries (Austria, Bulgaria, Czech Republic, Latvia, Norway, and Romania) including Lithuania, the species is treated as vulnerable; in Finland, Great Britain, Ireland, Northern Ireland, Slovakia, Sweden, and Switzerland *H. vernicosus* is considered a near-threatened species; and in Luxemburg, it is thought to be regionally extinct (Hodgetts and Lockhart 2020).

The special status of *H. vernicosus* in Europe in recent years has attracted particular attention for its ecology and the distribution pattern and abundance of its populations across different countries to ensure favourable conservation status of the species (Hodgetts *et al.* 2019b). The first information obtained on the habitat requirements of *H. vernicosus* was based on results from Northern Europe in Hedenäs (1989, 2003) and Hedenäs and Kooijman (1996). Recently, the most exhaustive data on the species have been from Central Europe, covering various aspects of its habitat conditions and statuses of its populations (Štechová and Kušera 2007, Štechová *et al.* 2008, 2010, 2012). In addition, some data on the habitat characteristics of the species (e.g., pH and vegetation) were included in national reports of Ireland (Campbell *et al.* 2013, 2015, 2019) and Spain (Heras and Infante 2000). Sometimes, *H. vernicosus* has also been included in various surveys of fens, specifically in terms of hydrology, surface water chemistry (Belland *et al.* 1995, Jabłońska *et al.* 2011, Cusell *et al.* 2013, 2015, Pawlikowski *et al.* 2013, Mettrop *et al.* 2014, 2015, 2018, Vicherová *et al.* 2015, Kooijman *et al.* 2020) and vegetation (*Navrátilová et al.* 2006, Dítě *et al.* 2007, Hájek *et al.* 2008, 2021, Peterka *et al.* 2014, 2017, Udd *et al.* 2015). Despite studies showing that habitats of this species differ among regions, the amount of data from specific regions, except Central Europe, is still insufficient, providing only very common and uneven characteristics of the habitats.

The high number of *H. vernicosus* localities occurring in Lithuania provides an opportunity to study the species in relatively defined areas in a wide range of habitats at the junction of boreal and continental biogeographical regions, where the highest number of *H. vernicosus* populations occur in Europe. With the task of identifying habitat preferences of *H. vernicosus* we aimed to highlight their characteristics specific to this particular region. In addition, we tested the following hypothesis: 1) *H. vernicosus* abundance would be lower in habitats with increasing Ca^{2+} concentrations, as mentioned by Hedenäs (1989, 2003); and 2) the concentration of PO_4^{3-} would be related to a higher cover of *H. vernicosus*, as established by Pawlikowski *et al.* (2013) and Mettrop *et al.* (2018).

Material and methods

Study area

Lithuania (65.3 x 10^3 km^2) is situated on the southeastern coast of the Baltic Sea. The main characteristics of its mild climate (between central latitude oceanic and continental climates) are as follows: the average annual precipitation is 675 mm, the hydrothermal coefficient (HTC) is 1.3–1.9 and the mean annual air temperature is 6.2°C (Bukantis *et al.* 2001). Lithuania occurs at the junction of two biogeographical regions: boreal (most of the country) and continental (southern and southwestern parts of the country) (Roekaerts 2002).

In Lithuania, lowlands cover 50% of the area, hilly uplands cover 21%, and plateaus cover

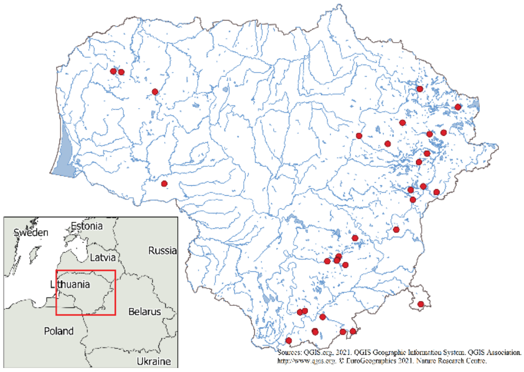

Fig 1. Distribution of the study plots.

29% (Kudaba 1983). Peatlands occupy approximately 9.9% of the territory of Lithuania. As a result of drainage and transformation of land to agriculture since the beginning of the 20th century, approximately 70% of the peatlands have been disturbed, or their natural processes have been interrupted. Therefore, relatively natural, not directly drained lands make up only one-third of the peatlands that have survived in their original forms. Fens are the most drained peatlands. Natural fens currently cover 346.76 km^2 (0.53% of the territory). In addition, transitional mires cover 73.42 km^2 (0.11% of the territory) (Povilaitis *et al.* 2011).

The most valuable fens and transitional mires, considered habitats of European importance, cover approximately 80 km^2: 7140 Transitional mires and quaking bogs cover 65.15 km^2, 7160 Fennoscandian mineral-rich springs and spring fens cover 3.96 km^2, 7210 Calcareous fens with *Cladium mariscus* cover 0.79 km^2, and 7230 Alkaline fens cover 9.61 km^2 (Gamtos tyrimų centras 2015).

Hamatocaulis vernicosus is known to occur in 180 mires in Lithuania and is mostly located in southern and eastern parts of the country (Jukonienė 2021). This species is protected in 33 Natura 2000 territories (approximately 1 territory/2000 km^2).

Vegetation and environmental sampling

The field study was performed in June–August of 2014–2019 at 32 study sites (Fig. 1), which represented almost 20% of all known (including recently destroyed) locations of *H. vernicosus* in Lithuania.

At each study site, depending on the habitat diversity and distribution of *H. vernicosus* in the mire, one to seven 4 m x 4 m study plots (Štechová and Kučera 2007) were established (63 study plots in total). For each study plot, the following parameters were recorded:

a) Percentage cover of tree and shrub, herb and bryophyte layers and cover of *H. vernicosus*.

b) Cover and abundance (by Braun-Blanquet (1964) scale) of all vascular plant and bryophyte species (in subsequent analyses, cover-abundance values of the Braun-Blanquet scale were transformed into percentage cover values following Maarel (1979)).

c) Water physical (pH, conductivity) and chemical parameters: concentrations of Ca^{2+}, NH_4^+, NO_3^- and Fe^{3+} from 56 study plots, 27 of them had additional parameters of K^+, Mg^{2+}, and PO_4^{3-}. Conductivity and pH were measured in situ using a portable instrument (Multi 350i, WTW, Germany). Water samples for chemical analyses were taken in autumn and frozen until chemical analysis. The analysis was performed in an accredited laboratory UAB "EKOMETRIJA". In the laboratory, spectrophotometrical methods were used for the measurements of Fe^{3+} (method: ISO 6332:1995), K^+ (ISO 9964-3:1998), NH_4^+ (ISO 7150-1:1998), NO_3 (ISO 7890-3:1998), and PO_4^{3-} (EN ISO 6878:2004), while titrimetric analysis was used for the measurements of Ca^{2+} (ISO 6058:2008) and Mg^{2+} (ISO 6059:2008).

d) Characteristics of topography: depending on the prevailing microrelief forms and water table level, we assigned the study plots to the following six types of topography (Table 1).

To ascertain the distribution of *H. vernicosus* under the various microsite conditions in every study plot (in its corners and in the middle), five subplots of 0.5 m x 0.5 m were arranged (315 subplots in total). For each of them, we recorded the percentage cover of trees and shrubs, herb and bryophyte layers and the percentage cover of each vascular plant and bryophyte species. Five forms of microrelief were distinguished (Table 2).

The subplot included one form of microrelief that was predominant. In the case when the subplot covered two different microrelief forms, the predominant form was taken into account.

The nomenclature of the bryophytes followed Hodgetts *et al.* (2020), and the nomenclature of the vascular plants followed the World Checklist of Vascular Plants (WCVP) (2021).

We treated *H. vernicosus* as one species here, though recent molecular evidence revealed that *H. vernicosus* is a complex of two cryptic species: clade 1 (southern cryptic species) and clade 2 (northern cryptic species) (Hedenäs and Eldenäs 2007, Hedenäs 2018). Different patterns of genetic variation in both cryptic species were assessed in the studies in the Czech Republic (Manukjanová *et al.* 2020). According to Hedenäs (2018a), cryptic species of *H. vernicosus* require special consideration in biodiversity conservation. Although genetically different, the species seem morphologically identical (Hedenäs and Eldenäs 2007, Manukjanová *et al.* 2019a). They are neither different in their sex expression nor sex ratio (Manukjanova *et al.* 2019b). In addition, no differences in their habitat preferences were found (Hedenäs and Eldenäs 2007, Manukjanová *et al.* 2019a). Consequently, in the species conservation, including redlists, action plans and monitoring, both at European and national levels, and in ecological and vegetation surveys (see references cited above), *H. vernicosus* as a complex of cryptic species is considered. This is the extent to which the species is treated in our paper.

Data analysis

Two data matrices were used to classify the study plots according to: a) water physical-chemical; and b) vegetation parameters. A matrix of six environmental variables (pH, conductivity, Ca^{2+}, Fe^{3+}, NH_4^+, and NO_3) from 56 studies was used for hierarchical cluster analysis (HCA). Concentrations of K^+, Mg^{2+} and PO_4^{3-} were excluded from hierarchical cluster analysis, due to the lack of data from 51% of study plots. These parameters (alongside with pH, conductivity, Ca^{2+}, Fe^{3+}, NH_4^+, and NO_3) were included into subsequent analyses to assess their variation among environmental groups. HCA was performed with PAST statistical software, ver. 3.20 (Hammer *et al.* 2001) to categorise the

Table 1. Topography types distinguished in the habitats of *H. vernicosus*.

Topography types	Characteristics
1	Pools or deep hollows occupy more than 50% of the plot
2	Lawns with negligible microtopography, where the water table on the peat surface par tially covers the moss layer and usually occurs on a logged flood plain adjacent to a river, stream or lake
3	Lawns with negligible microtopography, where the water table is below peat
4	Area with abundant hummocks and the hollows (depressions) are formed by water flows
5	Patches of mosses (mostly lawns and low hummocks) surrounded by water flows
6	High *Sphagnum* hummocks surrounded by fen vegetation

Table 2. Microrelief forms distinguished in subplots.

Microrelief forms	Characteristics
1	Deep hollows, including pools
2	Shallow hollows
3	Lawns (small elevations up to 5 cm were assigned to lawns)
4	Low hummocks (up to 20 cm)
5	High hummocks (higher than 20 cm)

study plots with similar water physical-chemical parameters. The UPGMA method was used, and Euclidean distance was chosen as a measure of this similarity. The species matrix contained information on 63 study plots, and abundance data for 159 species were used for the modified TWINSPAN classification (Hill 1979). TWINSPAN was implemented in JUICE software and used to compare plant communities and define the most characteristic species for vegetation groups. To evaluate the fidelity of diagnostic species to vegetation groups, the phi-coefficient was calculated.

The normality of the data distribution was evaluated using the Kolmogorov-Smirnov test. One-way ANOVA was used to examine the differences in the water physical-chemical parameters (pH, conductivity, Ca^{2+}, Fe^{3+}, K^{+}, Mg^{2+}, NH_4^{+}, NO_3^{-}, and PO_4^{3-}) between environmental groups (produced from hierarchical cluster analysis), as well as to identify significant differences in the cover of *H. vernicosus* among ecological and vegetation groups and between topography types and microrelief forms. The data that showed a non-normal distribution (cover of *H. vernicosus*, and concentrations of NH_4^{+}, NO_3^{-} and Fe^{3+}) were ln-transformed to reduce skewness and provide an approximate normal distribution to meet the assumptions of ANOVA. Tukey's HSD post hoc multiple comparison test was used to examine differences.

Differences in the frequency of vegetation and ecological groups and frequency of topography types between the ecological and vegetation groups were evaluated by Pearson's chi-squared (χ^2) test.

Since the distributions of most vegetation data sets (percentage cover of the bryophyte layer and cover of most plant and bryophyte species per study plot and subplot) were non-normally distributed, the non-parametric Spearman correlation was used to assess correlations between the cover of *H. vernicosus* and vegetation parameters ascertained in both the study plots and subplots. Calculations were performed using SPSS software (version 16). All p values of less than 0.05 were considered statistically significant.

Results

Characteristics of *Hamatocaulis vernicosus* habitats

Water physical-chemical parameters and topography

The characteristics of the physical-chemical parameters of the water of the habitats of *H. vernicosus* are summarised in Table 3. The mean water pH in the habitats of *H. vernicosus* was near a neutral pH of 6.9, ranging from acidic (pH 5.9) to slightly alkaline (pH 7.5). The total conductivity in the study plots ranged from 95.6 µS/cm to 542 µS/cm. Water chemical parameters across analysed habitats showed wide variation. Concentration values of Fe^{3+}, K^{+}, PO_4^{3-} and NH_4^{+} varied markedly between the study sites, and the values differed more than 10^2 times from the minimum to the maximum values. At the same time, the concentrations of Ca^{2+}, NO_3^{-} and Mg^{2+} did not show such a wide variation in values.

Hierarchical cluster analysis (HCA) categorised the study plots with similar water characteristics into several groups. First, the cluster analysis resulted in two groups: A (11 study

Table 3. Characteristics of water physical-chemical parameters.

Measurements	pH	Conductivity (µS/cm)	Ca^{2+} (mg/l)	Mg^{2+} (mg/l)	Fe^{3+} (mg/l)	K^{+} (mg/l)	PO_4^{3-} (mg/l)	NH_4^{+} (mg/l)	NO_3 (mg/l)
Min	5.9	95.6	15.2	5.4	0.07	0.8	0.02	0.02	0.01
Max	7.5	542.0	96.6	47.2	11.80	16.9	0.20	4.57	0.59
Mean	6.9	315.9	54.9	21.9	1.80	4.0	0.06	0.77	0.12
SD	0.3	112.4	19.9	9.2	2.90	3.8	0.06	1.00	0.11

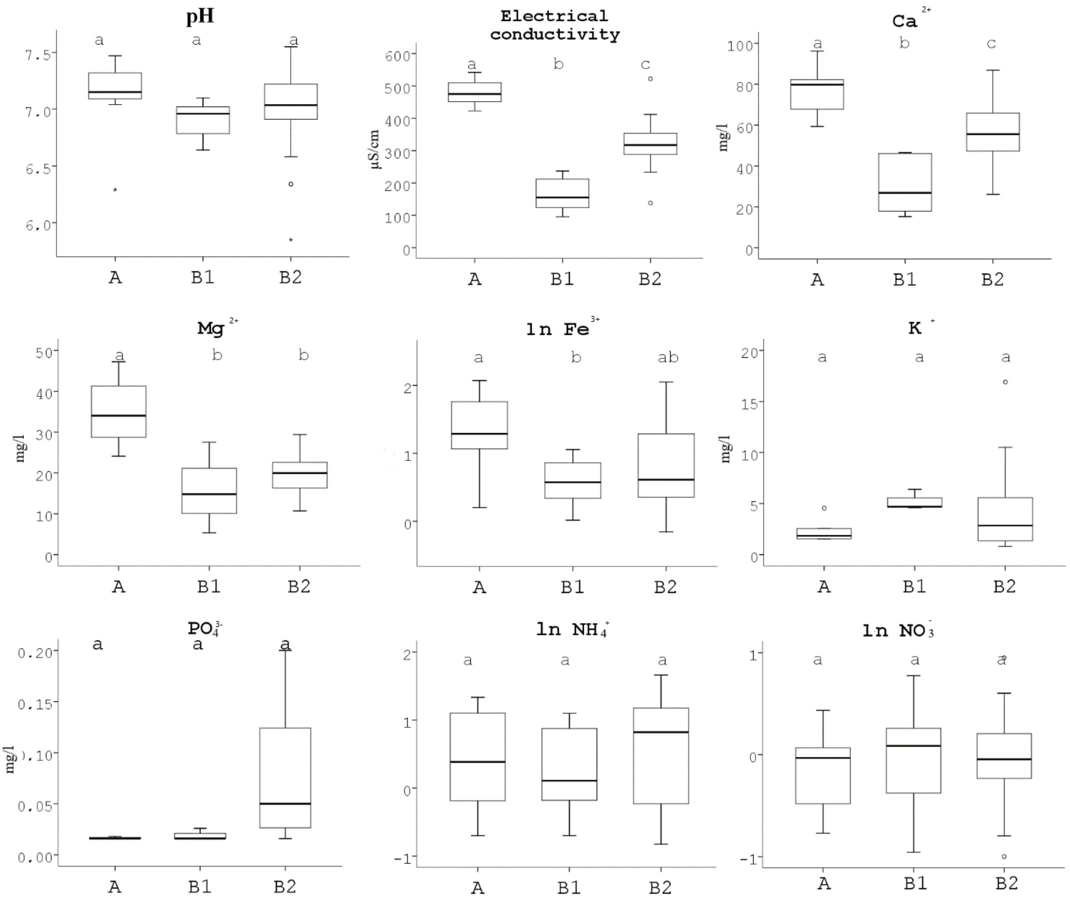

Fig 2. Values of water physical-chemical parameters across the ecological groups (A, B1, and B2). Different letters show significant differences (one-way ANOVA, Tukey's HSD test). The values of Fe^{3+}, NH_4^+, and NO_3^- were ln-transformed.

plots) and B (45), with similar physicochemical characteristics. For a detailed analysis, we selected two clusters with a lower hierarchical order of cluster B (namely, groups B1 and B2) and cluster A (group A). Values of the water parameters across the different groups are presented in Fig. 2. All three groups (A, B1, and B2) were significantly different in terms of electrical conductivity (one-way ANOVA, $F_{2,53} = 79.18$, $p = 0.000$) and concentration of Ca^{2+} (one-way ANOVA, $F_{2,53} = 20.17$, $p = 0.000$). No significant differences were revealed among the ecological groups in terms of pH or amounts of K^+, NH_4^+, NO_3^-, and PO_4^{3-}. Group A represented slightly alkaline, mineral-rich (Ca-rich, Mg-rich and Fe-rich) habitats. Habitats in group B1 were characterised by weakly acidic-neutral conditions and lower concentrations of Ca^{2+}, Mg^{2+} and Fe^{3+} and conductivity values. Group B2 mostly represented habitats with moderate values of the chemical parameters, and the habitats in this group had a wide range of most parameters (pH, Ca^{2+}, Fe^{3+}, K^+, and PO_4^{3-}) and were significantly different from those in group A in that they had lower concentrations of magnesium.

The most frequently recorded topography types in the *H. vernicosus* habitats were lawns with surface water and hummocky areas (46% and 21%, respectively). The other types of topography were reported in only one-third of all studied plots. *Hamatocaulis vernicosus* was rarely recorded in fens characterised by lawns with water levels beneath peat surfaces (11%) and in fens where moss patches were surrounded by water flushes (10%). The two types of topography that contained fens with prevailing pools and deep hollows (6%) and fens with abundant high hummocks (6%) were the least distributed among the study plots. The distribution of the topography types between the ecological groups did not show significant differences (χ^2 = 11.6, p = 0.3).

Vegetation characteristics

Habitats of *H. vernicosus* had well-developed bryophyte and herb layers, and tree and shrub layers were scarce (Table 4).

A total of 159 plant species were recorded across the 63 study plots. Species richness ranged from 18 to 43 species per study plot and from 6 to 21 species per subplot. The vascular plant species most associated *H. vernicosus* habitat were *Carex diandra* (registered in 85.4% of all study plots), *C. rostrata* (81.8%), *Menyanthes trifoliata* (81.8%), *Epilobium palustre* (78.2%), and *Cardamine pratensis* (74.5%), and the most associated bryophyte species included *Calliergonella cuspidata* (87.2%), *Marchantia polymorpha* (63.6%), and *Ptychostomum pseudotriquetrum* (60%).

The main differences in species composition in the three vegetation groups (Ia, Ib and II) resulting from TWINSPAN are presented in Table 5. In all study plots of the Ia group, *Campylium stellatum*, *Carex lepidocarpa, Scorpidium cossonii* and *Trichophorum alpinum* were recorded. The indicator species of group Ib in 16 study plots were *Calliergon giganteum, Peucedanum palustre*, *Salix aurita,* and *S. rosmarinifolia*. Common species for groups Ia and Ib that resulted in their differentiation from group II were *Carex lasiocarpa*, *C. limosa*, *Vaccinium oxycoccos* and *Peucedanum palustre*. Group II contained the largest number of study plots (41) and was characterised by *Cardamine pratensis*, *Comarum palustre*, *Epilobium palustre*, *Festuca rubra*, *Marchantia polymorpha*, *Myosotis scorpioides*, *Plagiomnium ellipticum*, and *Rumex acetosa.* The species *Carex rostrata*, *Caltha palustris*, and *Galium uliginosum* were recorded only in groups Ib and II, although they were initially assigned to different groups.

Vegetation groups were differently (χ^2 = 14.84, p = 0.05) distributed among the ecological groups (Fig. 3), some of them being in close relationship with water parameters. Vegetation group Ia was exceptionally associated with ecological group B2. The group Ib covered ecological groups B1 and B2. Study plots from vegetation group II contained all the ecological groups (A, B1, and B2).

Moreover, the vegetation groups were distributed differently (χ^2 = 49.23, p = 0.00) among the topography types. Vegetation group Ia occurred only in the lawns with a water table below the peat surface. Vegetation group Ib was more specific to the lawns with surface water and the most abundantly occurring vegetation was group II, which occurred in the study plots of almost all the topography types.

Abundance of *Hamatocaulis vernicosus*

The abundance (percentage cover) of *H. vernicosus* in the study plots varied from 0.5% to 62.5%; however, the maximum values were obtained only in four study plots. The percentage cover of

Table 4. Vegetation characteristics of the study plots/subplots.

Statistics	Cover of trees and shrubs (%)	Cover of herbs (%)	Cover of bryophytes (%)	Number of vascular plant species	Number of bryophyte species
				species	species
Min	0/0	40/8	40/3	12/3	4/1
Max	40/85	100/100	100/100	34/17	12/8
Mean	6.45/2.5	73.96/58.43	83.05/76.67	21.31/9.8	7.62/3.7
SD	1.48/0.53	1.76/1.21	1.90/1.32	0.69/0.16	0.28/0.07

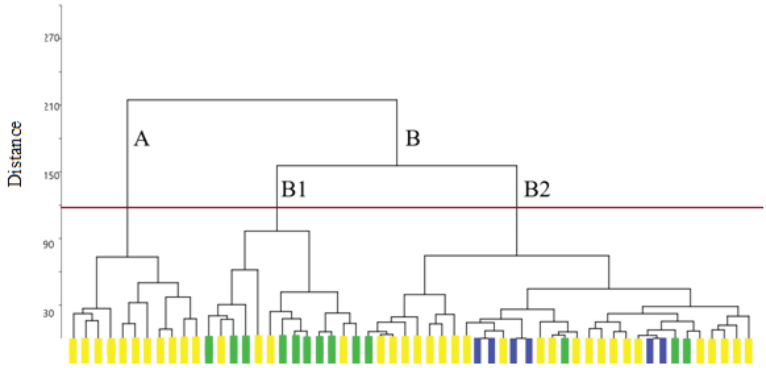

Fig 3. Distribution of vegetation groups (Ia — blue, Ib — green, II — yellow colour) among the ecological groups (A, B1, and B2).

Table 5. Synoptic table (after TWINSPAN classification) of percentage frequency (constancy) and fidelity (phi coefficient × 100, upper indices). Only diagnostic species for specific vegetation groups with phi coefficients ≥ 0.30 are shown in the table.

Vegetation groups Number of relves	Ia 6	Ib 15	II 42
Campylium stellatum	100 $^{95.8}$	31	2.4
Carex lepidocarpa	100 $^{65.7}$	50	12.19
Scorpidium cossonii	100 $^{48.4}$	25	4.8
Trichophorum alpinum	100 $^{76.7}$	43.8	2.4
Calliergon giganteum	25	87.5 $^{45.2}$	41
Comarum palustre	—	87.5 $^{82.4}$	9.7
Peucedanum palustre	33	75 $^{67.1}$	14.6
Salix aurita	—	62.5 $^{69.4}$	9.7
Salix rosmarinifolia	16.6	87.5 $^{85.3}$	4.8
Agrostis stolonifera	16.6	56.25	80.4 $^{34.2}$
Cardamine pratensis	16.6	50	90 $^{51.5}$
Epilobium palustre	33.3	73.3	85 $^{42.6}$
Festuca rubra	—	6.25	52.5 $^{45.7}$
Helodium blandowii	—	—	70 $^{30.7}$
Marchantia polymorpha	—	37.5	87.5 $^{60.6}$
Myosotis scorpioides	—	6.25	78 $^{52.9}$
Plagiomnium ellipticum	16.6	37.5	50 ^{61}
Rumex acetosa	16.6	6.25	75 ^{57}
Others most frequent species in study plots			
Carex diandra	100	80	88
Carex rostrata	—	80	92.8
Caltha palustris	—	62.5	87.8
Epipactis palustris	66.6	53.3	85.7
Galium palustre	66.6	80	78.5
Galium uliginosum	—	33.3	71
Menyanthes trifoliata	100	93.3	80.9
Aulacomnium palustre	66.6	40	57.1
Calliergonella cuspidata	66.6	93.3	90.4
Ptychostomum pseudotriquetrum	50	66.6	52.3

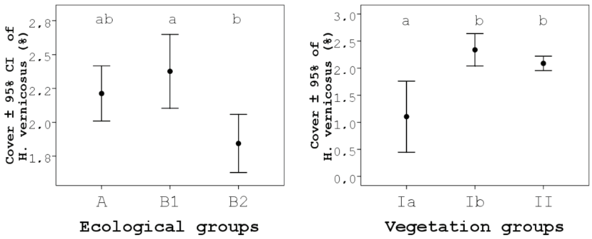

Fig 4. Cover of *H. vernicosus* among the ecological groups (left) and the vegetation groups (right). Different letters indicate significant differences (one-way ANOVA, Tukey's HSD test).

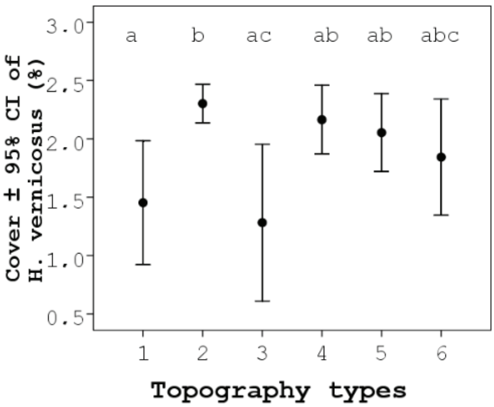

Fig 5. Cover of *H. vernicosus* in plots with different topography types (see Material and methods for definitions). Different letters indicate significant differences (one-way ANOVA, Tukey's HSD test). The cover of *H. vernicosus* was ln-transformed.

H. vernicosus in the subplots varied more widely from 0% to 95%, and the mean cover of *H. vernicosus* in the subplots was 28.4% (± 1.8 SD).

The analysis of the relationship between *H. vernicosus* abundance and environmental and vegetation properties showed similar correlations in the study plots and subplots. In the study plots and subplots, the cover of *H. vernicosus* was positively correlated with the development of the bryophyte layer (r_s = 0.36, n = 63) and negatively correlated with that of herbs (r_s = –0.4, n = 63). The same trend with weaker correlations was determined to occur in the subplots. The only species that showed a correlation with the abundance of *H. vernicosus* was *Menyanthes trifoliata* (r_s = –0.4, n = 63), while in the subplots, *H. vernicosus* positively correlated with *Carex diandra* (r_s = 0.3, n = 116). Negative correlations were found at the subplot level for cover of *H. vernicosus* and bryophyte species *Marchantia polymorpha* (r_s = –0.18, n = 124) and *Calliergonella cuspidata* (r_s = –0.20, n = 287), but this correlation was very weak.

One-way ANOVA revealed significant differences in *H. vernicosus* abundance among the different groups of the study plots as distinguished by environmental (one-way ANOVA, $F_{2,55}$ = 5.139, p = 0.009) and vegetation parameters (one-way ANOVA, $F_{2,60}$ = 14.811, p = 0.000) (Fig. 4).

The analysis of the distribution of *H. vernicosus* showed significant differences in the mean abundance of the species among the topography types (one-way ANOVA, $F_{5,57}$ = 7.103, p = 0.000) (Fig. 5). The species was most abundant in the study plots with lawns with surface water and in fens with abundant low hummocks.

Analysis of subplot data revealed that *H. vernicosus* most frequently occurred in shallow hollows and lawns and was very rare or undetectable in the deep hollows and on high hummocks (Fig. 6).

Discussion

Our survey of *H. vernicosus* habitats, in addition to confirming the general trends identified in previous studies, highlights the regionally based characteristics related to both water physical-chemical parameters and vegetation.

Water physical-chemical parameters and topography

Research conducted in Central Europe has generally shown that areas of *H. vernicosus* habitats are slightly acidic to weakly alkaline (Štechová and Kučera 2007, Štechová *et al.* 2008, 2010, 2012, Pawlikowski *et al.* 2013). A wide range of pH values was recorded in Ireland (pH 5.1–7.5 (Campbell *et al.* 2013, 2015, 2019)) and in Sweden (pH 5.4–7.8 (Hedenäs 2003)). The range

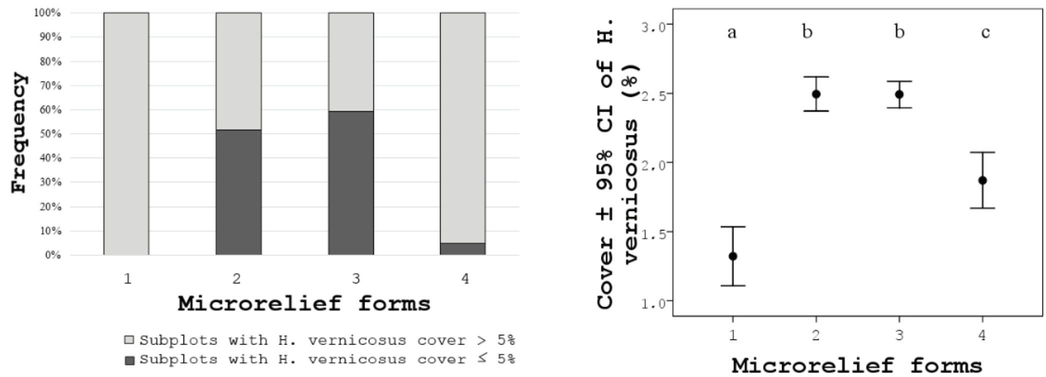

Fig 6. Frequency (left) and abundance (right) of *H. vernicosus* in subplots with different microrelief forms (1 — deep hollows; 2 — shallow hollows; 3 — lawns; 4 — low hummocks). Different letters indicate significant differences (one-way ANOVA, Tukey's HSD test). The cover of *H. vernicosus* was ln-transformed.

of pH in this study (pH 5.9 –7.5) was within the limits recorded in different regions of Europe. However, we determined that *H. vernicosus* to be most frequent (≤ 85% of all study plots) in fens with a water pH of 6.5–7.3 and the mean pH value (6.9) was slightly higher than that mentioned for most of the regions, and the value in this study is more in line with the results obtained by Pawlikowski *et al.* (2013) in Poland. Moreover, the habitats from Lithuania like those from Poland (Pawlikowski *et al.* 2013) show a wide range and high values of electrical conductivity. On the other hand, the recordings of electrical conductivity from other European *H. vernicosus* habitats were lower (Hedenäs 2003, Hedenäs and Kooijman 1996, Štechová and Kučera 2007, Štechová *et al.* 2012).

It is a complicated process to compare water chemistry with data published from other European regions because the data are either very minimal or vary greatly (Hedenäs 1989, 2003, Hedenäs and Kooijman 1996, Heras and Infante 2000, Štechová and Kučera 2007, Štechová *et al.* 2008, 2010, 2012, Campbell *et al.* 2013, 2015, 2019, Pawlikowski *et al.* 2013, Mettrop *et al.* 2018). In the habitats in this study, the amount of minerals was generally high. The total calcium content in the habitats of *H. vernicosus* in Lithuania ranged between 15.2 and 96.6 mg/l. In other regions of Europe, the amounts of calcium were lower: Sweden at 2.5–56.8 mg/l (Hedenäs and Kooijman 1996) and especially the Czech Republic at 3–22.61 mg/l (Štechová and Kučera 2007, Štechová *et al.* 2008, 2010, 2012). High amounts of calcium were found in the fens with *H. vernicosus* close to the border of Lithuania, in the northeastern part of Poland (Pawlikowski *et al.* 2013).

The other major cations in the surface water, magnesium (5.4–47.2 mg/l) and potassium (0.8–16.9 mg/l), recorded in this study occurred at wider ranges and higher values than those in previous studies in Europe (Hedenäs and Kooijman 1996, Štechová et al 2010, Pawlikowski *et al.* 2013). High concentrations of cations are probably the result of a high influence of spring feeding (Tahvanainen *et al.* 2002). A wide variation in iron was one more parameter (following pH, electrical conductivity and amount of calcium) that was similar to fens in Poland (Pawlikowski *et al.* 2013), indicating the distribution of such *H. vernicosus* habitats in a wider region of neighbouring territories. In other European regions, concentrations were significantly lower with a narrower range of values (Hedenäs and Kooijman, 1996, Štechová and Kučera 2007, Štechová *et al.* 2010, 2012).

The other group of elements analysed in our study were nutrients: NH_4^+, NO_3^-, and PO_4^{3-}. Of available studies, Pawlikowski *et al.* (2013) found the widest and highest mean values of PO_4^{3-} (≤ ~0.8 mg/l, mean approximately 0.4 mg/l), while in other regions (Hedenäs and Kooijman 1996, Štechová *et al.* 2010, 2012) also studied by us, values were four or more times lower. Concerning the ammonium concentration our results did not show any exceptional values compared with those obtained by Hedenäs and Kooijman (1996), Štechová and Kučera (2007), Štechová *et al.* (2012), Campbell *et al.* (2013, 2015, 2019) and Pawlikowski *et al.* (2013). Investigations of nitrate content in habitats of *H. vernicosus* have slightly wider values than those recorded in the studies mentioned above.

A wide variation in surface water chemistry allowed us to distinguish three groups of *H. vernicosus* habitats that differ significantly in values according to various environmental parameters. We focused on differences in ecological factors through the ecological groups to investigate their impact on the distribution and abundance of *H. vernicosus* in the region. The hypothesis (see Introduction, hypothesis 1) concerning calcium amount was partially confirmed. Our results showed a high abundance of *H. vernicosus* in the habitats with the lowest amount of calcium. At the same time, the species occurs no less abundantly in habitats with the highest amount of Ca^{2+}. On the other hand, the most frequent habitats of *H. vernicosus* are in the fens with moderate values of calcium. The ecological group with a high content of calcium is also characterised by a high concentration of magnesium, which, as was mentioned above, shows the influence of springs. We cannot confirm the relationship between the abundance of *H. vernicosus* and the amount of phosphorus, as stated by Pawlikowski *et al.* (2013) and Mettrop *et al.* (2018) (see Introduction, hypothesis 2). Our results are in accordance with those of Štechová *et al.* (2012), who showed no differences in the abundance of *H. vernicosus* in habitats with different amounts of phosphorus.

There are few data on the influence of iron on the abundance of *H. vernicosus,* and the available data are contrasting (Hedenäs and Kooijman, 1996, Štechová and Kučera 2007, Štechová *et al.* 2012). Although our data indicate that *H. vernicosus* occurs in areas with wide ranges of iron values, the effect of iron amount on species abundance was not ascertained, which agrees with the results of Štechová and Kučera (2007), although these authors obtained the species in habitats with a narrower range of amounts of iron.

Many studies indicate that a poor-rich gradient in water chemistry is an important factor that determines the composition of fen vegetation (Wheeler and Proctor 2000, Økland *et al.* 2001, Kooijman and Hedenäs 2009), meanwhile some have emphasised hydrological conditions as the most important factor for vegetation and even habitat biogeochemistry (Bragazza *et al.* 2005, Jabłońska *et al.* 2011, Cusell *et al.* 2013, Pawlikowski *et al.* 2013, Kooijman *et al.* 2020). To date, only a few detailed studies analysing the influence of water level on habitat biogeochemistry variation and the distribution of *H. vernicosus* have been conducted (Cussel *et al.* 2013, Mettrop *et al.* 2018). We did not perform direct water level measurements, but the impact of this factor on the distribution and abundance of *H. vernicosus* was evaluated indirectly by analysing its distribution in fens of various topography types and in microhabitats (subplot level). Lawns with negligible microtopography and surface water prevail among *H. vernicosus* habitats. This result was also supported by the distribution of *H. vernicosus* in various microhabitats, showing that this species most frequently and abundantly occurs in lawns. Cussel *et al.* (2013) found that under conditions of low water levels, the photosynthetic power of *H. vernicosus* decreases. *Hamatoculis vernicosus* was also often recorded in hummocky areas with depressions; the analyses of microhabitats show that suitable habitats for the species mostly provide lawns and shallow hollows. According to Štechová and Kučera (2007), this fen species does not develop submersed forms, so despite the preference for wet microsites, it does not occupy completely inundated microhabitats. This explains why we find the species growing in fen areas with prevailing pools very rarely. The occurrence of the species on hummocks is determined by essential changes in habitat characteristics — the higher hummocks are, the more bryophytes are distant or isolated from mineral fen water due to the specific physical and chemical characteristics (Hájkova *et al.* 2004, Udd *et al.* 2015).

Vegetation in the habitats of *H. vernicosus*

The most exhaustive data on vegetation in *H. vernicosus* habitats have been provided to date from Central Europe (Navrátilová *et al.* 2006, Štechová and Kučera 2007, Štechová *et al.* 2008, 2012); thus, the data in this study are primarily compared with that data. The vascular plant species most associated *H. vernicosus* habitat in Central European and Lithuanian fens are the specialists of waterlogged mires *Carex diandra, Menyanthes trifoliata* and *Equisetum fluviatile*. We find the positive interrelationship between the abundance of *H. vernicosus* and the most frequent *Carex diandra* at the microhabitat scale, showing that they can grow together under the same ecological conditions without competing with each other. Otherwise, the most negative interrelationship occurs with *Menyanthes trifoliata*. This confirms the results of Štechová *et al.* (2012) that *H. vernicosus* thrives best in habitats with sparse herbs and abundant brown moss cover.

Our vegetation survey shows that *Carex rostrata* (species of waterlogged mires), the calcicolous species *Epipactis palustris* and the spring species *Cardamine pratensis* and *Epilobium palustre,* indicating considerable water movement among the habitats (Koczur and Nicia 2013), are no less associated with the habitat of *H. vernicosus* than the species mentioned above. In terms of bryophyte cover, the *Calliergonella cuspidata* and *Ptychostomum pseudotriquetrum* co-occurred the most with *H. vernicosus* in both regions. However, *Campylium stellatum,* which is highly associated with the habitats of *H. vernicosus* in Central Europe, was recorded in only 15% of the plots in this study. Instead, *Marchantia polymorpha* was one of the most frequent species. Notably, this hepatic is also not mentioned among the most associated bryophytes with *H. vernicosus* in Europe (Hodgetts *et al.* 2019a).

However, a different species composition from that in both from Central Europe and Lithuania was observed in the habitats of *H. vernicosus* from Ireland (Campbell *et al.* 2013, 2015, 2019), the territory, which, based on Roekaerts (2002), is attributed to the Atlantic biogeographical region. The vascular plants most associated with *H. vernicosus* in this region are *Agrostis stolonifera*, *Carex echinata*, *C. panicea*, *Juncus acutiflorus* and *Ranunculus flammula*. However, only *Agrostis stolonifera* relatively frequently occurs in *H. vernicosus* habitats in Lithuania. In terms of bryophyte cover, in addition to *Calliergonella cuspidata* and *Ptychostomum pseudotriquetrum*, *Sarmentypnum exannulatum*, which, according to Štechová *et al.* (2008), prefers slightly acidic conditions, relatively frequently occurs in the fens of Ireland. Whereas *H. vernicosus* and *S. exannulatum* are separated along a pH gradient in the boreal region (Hedenäs and Kooijman 1996).

Regional differences in the species composition of habitats lead to differences in plant communities. In Lithuania, the most rarely presented in *H. vernicosus* habitats are plant communities with a high fidelity of the bryophytes S*corpidium cossonii* and *Campylium stellatumu* as well as *Carex lepidocarpa* (group Ia). In addition, important components of this group are calcium-tolerant sphagnum species (*Sphagnum teres* and *S. warnstorfii*) and boreal sedges *(Carex limosa*, *C. lasiocarpa* and *Trichophorum alpinum*) occurring within a wide range of base richness (Diersen 1996). It seems likely that such rich fens in Lithuania, following Peterka *et al.* (2017), are attributable to the *Sphagno warnstorfii-Tomentypnion nitentis* (Dahl 1956) alliance, in which *H. vernicosus* is distributed in Central Europe (Hájek *et al.* 2006, 2021). The plots of this clearly differentiated vegetation group accounted for less than 10% of all studied plots. Assessing the rarity of such communities, our results are in accordance with those from Northern Europe (Hedenäs 1989) stating that *H. vernicosus* grows with *Scorpidium cossonni* very rarely. Moreover, in such rare cases, its abundance is lower than that of other plant communities.

Indicator species of the most frequent plant communities, occurring in a wide range of ecological conditions, are the bryophytes *Marchantia polymorpha* and *Plagiomnium ellipticum* and the herbaceous species *Cardamine pratensis*, *Myosotis scorpioides* and *Rumex acetosa*, which are not among those indicated for the habitats of *H. vernicosus* in Central Europe. At the same time, fen communities with similar species composition were described in Poland (Pawlikowski *et al.* 2013). Following diagnostic species noted in Peterka *et al.* (2017), such communities can be assigned to *Saxifrago-Tomentypnion*, which are scattered across the northeastern European lowlands, so they are not known in Central Europe. We found that the communities with species characteristic to *Saxifrago-Tomentypnion* were distributed in habitats with a wide range of calcium concentrations; in addition to habitats that are calcium rich, which correspond to Peterka *et al.* (2017), we found them to be distributed in calcium-poor fens. May be part of the communities, described by us, can be assigned to *Caricion fuscae alliance* of calcium-poor fens, also characterised by frequent fen species *Carex diandra* and *Menyanthes trifoliata* (Peterka *et al.* 2017). Taking into consideration the low amounts of phosphorus in all habitats in this study, we cannot confirm the statements of Pawlikowski *et al.* (2013) and Peterka *et al.* (2017) that namely these communities show better phosphorus availability than that of other communities.

It seems likely that a specific microtopography — the presence of permanently waterlogged depressions is the main driver of the group, the indicators of which are species of very wet habitats *Calliergon giganteum* and *Comarum palustre*. Here, we found tree and shrub species and bryophyte *Plagiomnium elatum* settling on drier sites. In addition to species characterising specific topography, this group combines species from the two other vegetation groups.

Conclusions

In comparison to that in other specific regions of Europe, *H. vernicosus* in Lithuania, at the junctions of continental and boreal biogeographical regions, occurs under a wide range of habitat conditions that, according to water parameters, contains broader range and higher amounts of minerals. Topography with a specific hydrological regime that ensures lawns with surface water and shallow hollows is of high importance throughout fens covering a wide range of water parameters. The prevailing plant communities in habitats with *H. vernicosus* in terms of species composition can be assigned to *Saxifrago-Tomentypnion* distributed in the lowlands of the boreal region of northeastern Europe). In *Sphagno warnstorfii-Tomentypnion nitentis* communities, characteristic of the *H. vernicosus* habitats in Central Europe (continental region), in Lithuania, *H. vernicosus* occurs very rarely and not abundantly. It has to be noted that *H. vernicosus* likely consists of two separate lineages (clade 1, clade 2), and ecological behaviour may differ between these two lineages, distinguished by molecular analysis. Future research in Lithuania and adjacent regions needs to assess distribution of these two lineages and ascertain habitat preferences of them.

The comparison of environmental variables and plant species diversity in the habitats of different regions of Europe provides evidence that although *H. vernicosus* is protected at the European level, suitable conservation measures that consider the particular features of the regional habitats should be applied to ensure favourable conditions.

Acknowledgements: We are grateful to Zofija Sinkevičienė, Dalytė Matulevičiūtė, Zigmantas Gudžinskas and Lukas Petrulaitis for the identification of vascular plant species. We want to thank Domas Uogintas for the help in map preparation, also Birutė Paršonytė and Viktoras Subka for their kind assistance during fieldwork. This research was financed by Environmental Protection Agency, Lithuania (agreement no. 28TP-2014-90-ES) and support programme of the Nature Research Centre for PhD students.

References

Belland R.J. & Vitt D.H. 1995. Bryophyte vegetation patterns along environmental gradients in continental bogs. *Écoscience* 2(4): 395–407.

Bragazza L., Rydin H. & Gerdol R. 2005. Multiple gradients in mire vegetation: a comparison of a Swedish and an Italian bog. Plant Ecology 177(2): 223–236.

Braun-Blanquet J. 1964. Pflanzensoziologie. Grundzüge der Vegetationskunde. Springer, Wien.

Bukantis A. (ed.), Gulbinas Z., Kazakevičius S., Kilkus K., Mikelinskienė A., Morkūnaitė R., Rimkus E., Samuila M., Stankūnavičius G., Valiuškevičius G., Žaromskis R. 2001. Klimato svyravimų poveikis fiziniams geografiniams procesams Lietuvoje. Geografijos institutas, Vilniaus universitetas, Vilnius.

Campbell C., Hodd R. & O'Neill F. 2019. The monitoring and assessment of *Hamatocaulis vernicosus* (Slender Green Feather-moss) in the Republic of Ireland 2015–2017. Irish Wildlife Manuals, No. 110. National Parks and Wildlife Service, Dublin.

Campbell C., Hodgetts N. & Lockhart N. 2013. *Hamatocaulis vernicosus* (Mitt.) Hedenäs (Slender Green feather-moss) in the Republic of Ireland. Article 17

Report Backing Document. National Parks and Wildlife Service, Dublin.

Campbell C., Hodgetts N. & Lockhart N. 2015. Monitoring methods for *Hamatocaulis vernicosus* Mitt. Hedenäs (Slender Green feather-moss) in the Republic of Ireland. Irish Wildlife Manuals, No. 91. National Parks and Wildlife Service, Dublin.

Council of Europe (ed.). 1979. Convention on the conservation of European wildlife and natural habitats. Appendix I. European Treaty Series 104.

Cusell C., Lamers L.P.M., van Wirdum G. & Kooijman A.M. 2013. Impacts of water level fluctuation on mesotrophic rich fens: acidification versus eutrophication. *Journal of Applied Ecology* 50: 998–1009.

Cusell C., Mettrop I.S., Loon E.E.van., Lamers L.P.M., M. Vorenhout. & Kooijman A.M. 2015. Impacts of short-term droughts and inundations in species-rich fens during summer and winter: Large-scale field manipulation experiments. *Ecological Engineering* 77: 127–138.

Dierssen K. 1996. Vegetation Nordeuropas. Ulmer, Stuttgart.

Dítě D., Hájek M. & Hájková P. 2007. Formal definitions of Slovakian mire plant associations and their application in regional research. *Biologia* 62: 400–408. Available at: https://eunis.eea.europa.eu/species/14002.

European Commission. 1992. Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. *Official Journal of the European Union* 206: 7–50.

Gamtos tyrimų centras. 2015. EB svarbos natūralių buveinių palankios apsaugos būklės kriterijų nustatymas ir monitoringo sistemos metodinių pagrindų sukūrimas. Ataskaita I dalis. Vilnius, available at: https://am.lrv.lt/uploads/am/documents/files/saugom_teritorijos_kra%C5%A1tov/natura_2000/EB_buveiniu_inventorizavimo_duomenu_analize_palankios_bukles_kriteriju_nustatymas_ataskaita_I%20dalis%20Final.pdf.

Hájek M., Hájková P. & Apostolova I. 2008. New plant associations from Bulgarian mires. *Phytologia Balcanica* 14: 377–399.

Hájek M., Hájková P., Apostolova I., Sapotlieva D., Goia I & Dítě D. 2021. The vegetation of rich fens (Sphagno warnstorfii-Tomentypniom nitentis) at the southeastern margins of their European range. *Vegetation classification and survey* 2: 177—190.

Hájkova P. & Hájek M. 2004. Bryophyte and vascular plants responses to base-richness and water level gradients in Western Carpathian *Sphagnum*-rich mires. *Folia Geobotanica* 39(4): 335–351.

Hammer Ø., Harper D.A.T. & Ryan P.D. 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontologia Electronica* 4(1): 9.

Hedenäs L. 1989. The genera *Scorpidium* and *Hamatocaulis* gen. nov. in northern Europe. *Lindbergia* 15: 8–36.

Hedenäs, L. 2003. The European species of the *Calliergon-Scorpidium-Drepanocladus* complex, including some related or similar species. *Meylania* 28: 1–116.

Hedenäs L. 2018. Conservation status of the two cryptic species of *Hamatocaulis vernicosus* (Bryophyta) in Sweden. *Journal of Bryology*: 40: 307–315.

Hedenäs L & Eldenäs P. 2007. Cryptic speciation, habitat differentiation, and geography in *Hamatocaulis vernicosus* (Calliergonaceae, Bryophyta). *Plant Systematics and Evolution*. 268: 131–145.

Hedenäs L. & Kooijman A.M. 1996. Phylogeny and habitat adaptations within a monophyletic group of wetland moss genera (Amblystegiaceae). *Plant Systematics and Evolution* 199: 33–52.

Heras P. & Infante M. 2000. On the presence of *Hamatocaulis vernicosus* (Mitt.) Hedenäs (Amblystegiaceae) in Spain. *Journal of Bryology* 22(4): 297–298.

Heras P. & Infante M. 2012. *Hamatocaulis vernicosus* (Mitt.) Hedenäs. In: Garilleti R. & Albertos B. (eds). Atlas de los briófitos amenazados de España. Universitat de València, Valencia.

Hill M.O. 1979. TWINSPAN: a FORTRAN program for arranging multivariate data in an ordered two-way table by the classification of the individuals and attributes. Ecology and Systematics, Cornell University, Ithaca, New York.

Hill M.O., Preston C.D. & Smith A.J.E. (eds). 1994. Atlas of the bryophytes of Britain and Ireland. Volume 3, Mosses (Diplolepideae). Harley Books, Colchester.

Hodgetts N., Blockeel T., Konstantinova N., Lönnell N., Papp B., Schnyder N., Schröck C., Sergio C. & Untereiner A. 2019a. *Hamatocaulis vernicosus*. *The IUCN Red List of Threatened Species* 2019: eT86484012A87793257, available at: https://www.iucnredlist.org/species/86484012/87793257.

Hodgetts N. & Lockhart N. 2020. Checklist and country status of European bryophytes – update 2020. *Irish Wildlife Manuals*, no. 123. National Parks and Wildlife Service, Department of Culture, Heritage and the Gaeltacht, Ireland.

Hodgetts N.G., Cálix M., Englefield E., Fettes N., García Criado M., Patin L., Nieto A., Bergamini A., Bisang I., Baisheva E., Campisi P., Cogoni A., Hallingbäck T.,Konstantinova N., Lockhart N., Sabovljevic M., Schnyder N., Schröck C., Sérgio C., Sim Sim M., Vrba J., Ferreira C.C., Afonina O., Blockeel T., Blom H., Caspari S., Gabriel R., Garcia C., Garilleti R., González Mancebo J., Goldberg I., Hedenäs L., Holyoak D., Hugonnot V., Huttunen S., Ignatov M., Ignatova E., Infante M., Juutinen R., Kiebacher T., Köckinger H., Kučera J., Lönnell N., Lüth M., Martins A., Maslovsky O., Papp B., Porley R., Rothero G., Söderström L., Ştefănuţ S., Syrjänen K., Untereiner A., Váňa J., Vanderpoorten A., Vellak K., Aleffi M., Bates J., Bell N., Brugués M., Cronberg N., Denyer J., Duckett J., During H.J., Enroth J., Fedosov V., Flatberg K.-I., Ganeva A., Gorski P., Gunnarsson U., Hassel K., Hespanhol H., Hill M., Hodd R., Hylander K., Ingerpuu N., Laaka-Lindberg S., Lara F., Mazimpaka V., Mežaka A., Müller F., Orgaz J.D., Patiño J., Pilkington S., Puche F., Ros R.M., Rumsey F., Segarra-Moragues J.G., Seneca A., Stebel A., Virtanen R., Weibull H., Wilbraham J. & Żarnowiec J. 2019b. A miniature world in decline: European Red List of Mosses, Liverworts and Hornworts. IUCN, Brussels.

Hodgetts N.G., Söderström L., Blockeel T.L. Caspari S., Ignatov S., Ignatov M.S., Konstantinova N.A., Lockhart

N., Papp B., Schröck C., Sim-Sim M., Bell D., Blom H., Bruggeman-Nannenga M.A., Bruges M., Garilleti J.E.R., Flatberg K.I., Hedenäs L., Holyoak D.T., Hugonnot V., Kariyawasam I., Köckinger H., Kučera J., Lara F., Porley R.D. 2020. An annotated checklist of bryophytes of Europe, Macaronesia and Cyprus. *Journal of Bryology* 42(1): 1–116.

Jabłońska E., Pawlikowski P., Jarzombkowski F., Chormański J., OkruszkoT. & Kłosowski S. 2011. Importance of water level dynamics for vegetation patterns in a natural percolation mire (Rospuda fen, NE Poland). *Hydrobiologia* 674(1):105–117.

Joosten H., Tanneberger F. & Moen, A. (eds). 2017. Mires and Peatlands of Europe: Status, Distribution and Conservation. Schweizerbart Science Publishers, Stuttgart.

Jukonienė I. 2021. Žvilgančioji riestūnė. *Hamatocaulis vernicosus* (Mitt.) Hedenäs. In: Rašomavičius V. (ed.) Red Data Book of Lithuania. Animals, plants, fungi: 364. Lututė, Vilnius.

Koczur A. & Nicia P. 2013. Spring fen Scheuchzerio-Caricetea nigrae in the Polish Western Carpathians –- vegetation diversity in relation to soil and feeding waters. *Acta Societatis Botanicorum Poloniae* 82(2) 117–124.

Kooijman A.M., Cusell C., Hedenäs L., Lamers L., Mettrop I.S. & Neijmeijer T. 2020. Re-assessment of phosphorus availability in fens with varying contents of iron and calcium. *Plant and Soil* 447: 219–239.

Kooijman A. & Hedenäs L. 2009. Changes in nutrient availability from calcareous to acid wetland habitats with closely related brown moss species: increase instead of decrease in N and P. *Plant and Soil* 324: 267–278.

Kudaba Č. 1983. Lietuvos aukštumos. Mokslas, Vilnius.

Lamers L.P.M., Vile M.A., Grootjans A.P., Acreman M.C., Diggelen R. Van, Evans M.G., Richardson C.J., Rochefort L., Kooijman A.M., Roelofs J.G.M., Smolders A.J.P. 2015. Ecological restoration of rich fens in Europe and North America: from trial and error to an evidence-based approach. *Biological Reviews* 90: 182–203.

Maarel E. van der. 1980. Transformation of Cover-Abundance Values in Phytosociology and its Effects on Community Similarity. In: Maarel E. van der., Orlóci L & Pignatti S. (eds). Data-prrocessing in phytosociology. Advances in vegetation science I, vol 1. Springer, Dordrecht.

Manukjanová A., Štechová T. & Kučera J. 2014. Drought survival test of eight fen moss species. *Cryptogamie, Bryologie* 35: 397–403.

Manukjanová A., Košnar J. & Kučera J. 2020. Genetic variation in two cryptic species of the rare fen moss *Hamatocaulis vernicosus* in the Czech Republic. *Preslia*, 92: 57–72.

Manukjanová A, Koutecký P, Štechová T & Kučera J. 2019a. Insights into the distribution patterns, habitat and morphologic differentiation of cryptic species of the moss *Hamatocaulis vernicosus* in the Czech Republic. *Herzogia* 32: 183–199.

Manukjanová A., Štechová T. & Kučera J. 2019b. Expressed sex ratio in populations of the moss *Hamatocaulis vernicosus* (Mitt.) Hedenäs (Scorpidiaceae) in the Czech Republic with consideration of its cryptic species. *Cryptogamie, Bryologie* 40:41–58.

Mettrop I.S., Cusell C., Kooijman A.M. & Lamers L.P.M. 2014. Nutrient and carbon dynamics in peat from rich fens and Sphagnum-fens during different gradations of drought. *Soil Biology and Biochemistry* 68: 317–328.

Mettrop I.S., Cusell C., Kooijman A.M. & Lamers L.P.M. 2015. Short-term summer inundation as a measure to counteract acidification in rich fens. *PLoS ONE* 10(12): e0144006.

Mettrop I.S., Neijmeijer T., Cusell C., Lamers L.P.M., Hedenäs L. & Kooijman A.M. 2018. Calcium and iron as key drivers of brown moss composition through differential effects on phosphorus availability. *Journal of Bryology* 40: 350–357.

Navrátilová J., Navrátil J. & Hájek M. 2006. Relationships between Environmental Factors and Vegetation in Nutrient-Enriched Fens at Fishpond Margins. *Folia Geobotanica* 41(4) 353–376.

Pawlikowski P., Abramczyk K., Szczepaniuk A. & Kozub Ł. 2013. Nitrogen: phosphorus ratio as the main ecological determinant of the differences in the species composition of brown-moss rich fens in north-eastern Poland. *Preslia* 85: 349–367.

Peterka T., Plesková Z., Jiroušek M., Hájek M. 2014. Testing floristic and environmental differentiation of rich fens on the Bohemian Massif. *Preslia* 86: 337–366.

Peterka T., Hájek M., Jiroušek M., Jiménez-Alfaro B., Aunina L., Bergamini A., Dítě D., Felbaba-Klushyna L., Graf U., Hájková P., Hettenbergerová E., Ivchenko T.G., Jansen F., Koroleva N.E., Lapshina E.D.E., Lazarević P.M., Moen A., Napreenko M.G., Pawlikowski P., Plesková Z., Sekulová L., Smagin V.A., Tahvanainen T., Thiele A., Biţă-Nicolae C., Biurrun I., Brisse H., ćušterevska R., De Bie E., Ewald J., Fitz-Patrick Ú., Font X., Jandt U., Kącki Z., Kuzemko A., Landucci F., Moeslund J.E., Pèrez-Haase A., Rašomavičius V., Rodwell J.S., Schaminée J.H.J., Šilc U., Stančić Z. & Chytrý M. 2017. Formalized classification of European fen vegetation at the alliance level. *Applied Vegetation Science* 20(1): 124–142.

Povilaitis A., Taminskas J., Gulbinas Z., Linkevičienė R. & Pileckas M. 2011. Lietuvos šlapynės ir jų vandensauginė reikšmė. Apyaušris, Vilnius.

Økland R.H., Akland T. & Rydgren K. 2001. A Scandinavian perspective on ecological gradients in north-west European mires: reply to Wheeler and Proctor. *Journal of Ecology* 89(3): 481–486.

Roekaerts M. 2002. The biogeographical regions map of Europe. Basic principles of its creation and overview of its development. European Environment Agency, Copenhagen.

Štechová T. & Kučera J. 2007. The requirements of the rare moss, *Hamatocaulis vernicosus* (Calliergonaceae, Musci), in the Czech Republic in relation to vegetation, water chemistry and management. *Biological Conservation* 135: 443–449.

Štechová T., Hájek M., Hájková P. & Navrátilová J. 2008. Comparison of habitat requirements of the mosses *Hamatocaulis vernicosus*, *Scorpidium cossonii* and *Warnstorfia exannulata* in different parts of temperate Europe.

Preslia 80: 399–410.

Štechová T., Holá E., Manukjanová A. & Mikulášková E. 2010. Distribution and habitat requirements of the moss *Hamatocaulis vernicosus* (Mitt.) Hedenäs in the Bohemian Forest. *Silva Gabreta* 16: 1–11.

Štechová T., Kučera J. & Šmilauer P. 2012. Factors affecting population size and vitality of *Hamatocaulis vernicosus* (Mitt.) Hedenäs (Calliergonaceae, Musci). *Wetlands Ecology and Management* 20: 329–339.

Štechová T., Štech M. & Kučera J. 2012. The distribution of *Hamatocaulis vernicosus* (Mitt.) Hedenäs (Calliergonaceae) in the Czech Republic. *Bryonora* 49: 5–16.

Tahvanainen T., Sallantaus T., Heikkilä R. & Tolonen K. 2002. Spatial variation of mire surface water chemistry and vegetation in northeastern Finland. *Annales botanici fennici* 39: 235–251.

Udd D., Mälson K., Sundberg S. & Rydin, H. 2015. Explaining species distributions by traits in bryophytes and vascular plants in a patchy landscape. *Folia Geobotanica* 50(2): 161–174.

Vicherová E., Hájek M. & Hájek, T. 2015. Calcium intolerance of fen mosses: Physiological evidence, effects of nutrient availability and successional drivers. *Perspectives in Plant Ecology, Evolution and Systematics* 17: 347–359.

World Checklist of Vascular Plants (WCVP). 2021. World Checklist of Vascular Plants. Version 2.0. Facilitated by the Royal Botanic Gardens, Kew, available at http://wcvp.science.kew.org.

Wheeler B.D. & Proctor M.C.F. 2000. Ecological Gradients, Subdivisions and Terminology of North-West European Mires. *Journal of Ecology* 88(2): 187–203.