Classification of European bog vegetation of the Oxycocco-Sphagnetea class

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Article type : Vegetation Survey
Jörg Ewald

Manuscript category: Vegetation Survey

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Funding information

The research was funded by the Czech Science Foundation (grant no. 19-28491X). The contribution of VP is a part of research projects of the EU structural funding Operational Programme Research and Development for Innovation (project no. CZ.1.05/2.1.00/19.0388), and the Ministry of Education, Youth and Sports of the Czech Republic in the 'National Feasibility Program I' (project no. LO1208 'TEWEP'). IB was supported by the Basque Government (grant no. IT936-16), TGI by the grant of RFBR (no. 19-05-00830-a), IAL and OVL by the Russian Science Foundation (no. 20-17-00160), OLK by project IB KarRS RAS (FMEN-2022-0008) and PH by the long-term developmental project of the Czech Academy of Sciences (RVO 67985939).

Abstract

Aims: Classification of European bog vegetation (*Oxycocco-Sphagnetea* class); identification of diagnostic species for the class and vegetation subgroups (orders and alliances) development of an expert system for automatic classification of vegetation plots; and production of distribution maps of the *Oxycocco-Sphagnetea* class and its alliances.

Location: Europe

Methods: A dataset of vegetation-plot records was compiled to cover most of the European continent by various bog types. An unsupervised classification (beta-flexible linkage method, Sørensen distance measure) and DCA ordination were applied. Formal definitions of syntaxa based on species presence and covers, and respecting the results of the unsupervised classification, were developed and included in a classification expert system.

Results: The *Oxycocco-Sphagnetea* class, its two orders (*Sphagno-Ericetalia tetralicis* and *Sphagnetalia medii*) and seven compositionally distinct alliances were formally defined. In addition to the syntaxa included in EuroVegChecklist, three new alliances were distinguished: *Rubo chamaemori-Dicranion elongati* (subarctic polygon and palsa mires); *Erico mackaianae-Sphagnion papillosi* (blanket bogs of the northwestern Iberian Peninsula); and *Sphagno baltici-Trichophorion cespitosi* (boreal bog lawns). The latter alliance was newly described in this article.

Conclusions: This first pan-European formalized classification of European bog vegetation partially followed the system presented in EuroVegChecklist, but suggested three additional alliances. One covers palsa and polygon mires, one covers Iberian bogs with endemics and one fills the syntaxonomical gap for lawn microhabitats in boreal bogs. A classification expert system has been developed, which allows assignment of vegetation plots to the types described.

Key words

Blanket mires, Braun-Blanquet approach, expert system, ombrotrophic mire, palsa mire, polygon mire, raised bog, vegetation classification, vegetation-plot database

Introduction

The vegetation of mires (peat-forming wetlands) is traditionally divided into bogs and fens (Du Rietz, 1949; Moore, 1984; Wheeler & Proctor, 2000; Hájek et al., 2006; Joosten et al., 2017). Bogs are ombrotrophic (rainwater-fed), extremely acidic and nutrient-poor habitats, whereas fens are mainly minerotrophic mires saturated by groundwater. Nutrient availability and surface water chemistry on fens depend largely on bedrock and catchment hydrology. The ecological difference between bogs and fens in terms of water supply, chemistry and water-level depth is reflected in their plant species composition. The vegetation of European bogs has been mainly classified in the phytosociological class *Oxycocco-Sphagnetea*, while fens have been classified in the phytosociological class *Scheuchzerio palustris-Caricetea nigrae*. However, the vegetation of both classes may co-occur in the same mire complexes due to differences in micro-topography. The vegetation of the *Oxycocco-Sphagnetea* class then occupies hummocks that are permanently above the water level. The vegetation of dystrophic hollows (waterlogged depressions or pools) is usually assigned to the *Scheuchzerion palustris* alliance within the

Scheuchzerio palustris-Caricetea nigrae class (e.g., Dierssen, 1982, 1996; Lapshina, 2010; Mucina et al., 2016; but see e.g. Succow, 1974; Timmermann, 2004), based on physiognomy, species composition and frequent occurrence also outside ombrotrophic mire complexes in the boreal zone of Europe (Peterka et al., 2017). Plant species that distinguish *Oxycocco-Sphagnetea* from *Scheuchzerio palustris-Caricetea nigrae* are dwarf shrubs (*Chamaedaphne calyculata*, *Empetrum hermaphroditum*, *Erica tetralix*) together with *Sphagnum* species that preferably grow on hummocks elevated above the water level (*S. capillifolium*, *S. compactum*, *S. fuscum*, *S. medium*). Characteristic species of *Scheuchzerio palustris-Caricetea nigrae* are *Carex limosa*, *Scheuchzeria palustris*, *Sphagnum majus* or *Warnstorfia fluitans* (Peterka et al., 2017). Westhoff and Den Held (1969) described the separate class *Scheuchzerietea palustris* for bog hollow vegetation, but this solution cannot be accepted in formal syntaxonomy, as the *Scheuchzerio palustris-Caricetea nigrae* class is typified by the vegetation of dystrophic bog hollows (Tüxen, 1937).

There is, however, an obvious syntaxonomic gap for lawns, micro-topographically intermediate habitats between hummocks and hollows. They are classified either in the *Oxycocco-Sphagnetea* class or the *Scheuchzerio palustris-Caricetea nigrae* class. The former approach had been used primarily in Atlantic areas of western, central and northern Europe (Dierssen, 1982, 1996), where the *Oxycocco-Sphagnetea* class also comprise lawns. The latter approach was adopted largely in eastern Europe and Siberia (Kuznetsov, 1991; Lapshina, 2010; Zeliankevich et al., 2016), where lawns are more floristically distinct from high hummocks than from waterlogged hollows (Lapshina, 2010), but no specific alliance has yet been described for boreal lawn vegetation.

The gradient from relatively dry hummocks through flat lawns close to the water level to waterlogged hollows generally explains most of the vegetation variation in a single mire or small area (Du Rietz & Nannfeldt, 1925; Sottocornola et al., 2009; Jiroušek et al., 2013; Malhotra et al., 2016). The gradient from mire margin to mire expanse is another source of compositional variation in bogs, which is also evident at a much larger spatial scale (Malmer, 1986; Bragazza et al., 2005). This complex gradient coincides with differences in: (i) the depth of the water level; (ii) water chemistry; (iii) peat sediment thickness; and (iv) tall-shrub and tree cover between the central parts of a bog and mire-margin habitats such as fens, mire forests, wet mat-grass swards or dwarf-shrub heaths. Base saturation, a key factor for the variability of fen vegetation (Malmer, 1986; Heikkilä, 1987; Økland et al., 2001; Tahvanainen, 2004; Peterka et al., 2014; Peterka et al., 2017), has little influence on bog vegetation because of the ombrotrophic conditions, i.e. lack of base cations and nutrients. It can only influence bog margins and harvested or young bogs with

a shallow peat layer (Bourbonniere, 2009; Howie & van Meerveld, 2013; Mežaka et al., 2018). Precipitation chemistry also varies with distance of bogs to oceans (Aletsee, 1967; Damman, 1995)

Biogeographical gradients affect the species composition of bogs as well. The gradient between Atlantic and continental bogs is well known (Aletsee, 1967; Robroek et al., 2017) and reflected the existing vegetation classification, which clearly distinguishes between Atlantic and boreal-continental bogs (Mucina et al., 2016). Nevertheless, the newest European checklist of alliance and higher-rank syntaxa (Mucina et al., 2016) does not stress the occurrence of narrow-range endemic species, such as *Erica mackaiana* or *Carex durieui* in Iberian bogs. This checklist also does not cover palsa bogs, the habitat clearly delineated in the EUNIS classification (Chytrý et al., 2020) and the European Red List of Habitats (Janssen et al., 2016).

As bog vegetation is strongly dependent on the regular supply of rainwater, its occurrence in Europe is limited to regions with sufficiently high amount and low seasonal fluctuations of precipitation, i.e. Atlantic Europe, or with low evapotranspiration, i.e. northern Europe and Central and Eastern European mountains (Montanarella et al., 2006). A southwest-northeast gradient of continentality is reflected in compositional variation, but also in the topography of bog habitats and their hydrology. Flat oceanic bogs, valley bogs, blanket bogs and moist peat heaths occur in Western Europe, while raised bogs occur in the temperate and boreal zones of Central, Northern and Eastern Europe. Bog vegetation also occurs as distinct zones or patterns in aapa mires, palsa and polygon mires in the boreal and subarctic zones of Northern Europe (Janssen et al., 2016; Joosten et al., 2017; Chytrý et al., 2020).

The classification of mire vegetation dates back to early phytosociology (Cajander, 1913). Already before World War II, local studies were carried out to document the vegetation of bogs in various parts of Europe, including classical studies by: Osvald (1923), Warén (1926), Nordhagen (1928) and Paasio (1933) in Northern Europe; Katz (1926) and Bogdanovskaya-Guihéneuf (1928) in Eastern Europe; and Zlatník (1928), Kästner and Flössner (1933) and Schwickerath (1933) in Central Europe. To our knowledge, the first attempts to produce a pan-European overview of bog vegetation were made by Osvald (1925), Schwickerath (1940) and Duvigneaud (1949). A pan-European vegetation synthesis based on a large vegetation dataset (more than 3000 relevés) was first carried out by Moore (1964), who prepared a synoptic table of the *Oxycocco-Sphagnetea* class and presented a classification scheme with 2 orders, 4 alliances and 25 associations and sub-associations. In contrast to previous studies, he widened the class to include the compositionally similar vegetation of subarctic palsa mires and Atlantic moist peat heaths. For the latter vegetation type, he proposed a separate order *Ericetalia tetralicis* in contrast to the core bog

vegetation of the *Sphagnetalia medii* order. Later on, Aletsee (1967), Neuhäusl (1972) and Dierssen (1982) summarized the current knowledge about bog vegetation at supra-national to European scales.

Recent national vegetation checklists generally accept the concept of two orders, *Sphagno-Ericetalia tetralicis* (*Erico-Ledetalia* in EuroVegChecklist) and *Sphagnetalia medii*. The order *Sphagno-Ericetalia tetralicis* is further divided into *Ericion tetralicis* and *Oxycocco-Ericion tetralicis* alliances, while the order *Sphagnetalia medii* comprises *Sphagnion medii* and *Oxycocco microcarpi-Empetrion hermaphroditi* alliances (e.g., Pott, 1992; Dierssen, 1996; Valachovič, 2001; Smagin, 2007; Hájková et al., 2011; Thébaud, 2011; Zeliankevich et al., 2016; Dubyna et al., 2019). This concept has also been accepted in EuroVegChecklist (Mucina et al., 2016), which represents the current consensus of dozens of vegetation scientists and acts as an authoritative platform for international communication in vegetation science, ecology and nature conservation, but also serves as a baseline for subsequent classification studies that can build on the large pan-European datasets (Chytrý et al., 2016) and update current knowledge. Besides the scheme of high-rank syntaxa presented in EuroVegChecklist, some alternative approaches to the classification of the *Oxycocco-Sphagnetea* class have been presented in the regional literature (Smagin, 2000, 2012a; Timmermann, 2004; Lavrinenko & Lavrinenko, 2015; Molina, 2017).

The recent development of large electronic vegetation-plot (or co-occurrence based) databases (Chytrý et al., 2016; Bruelheide et al., 2019) as well as advances in classification methods, tools and software, provide unique opportunities to process vegetation data on a pan-European scale according to well-defined and consistent criteria (De Cáceres et al., 2015). In this study, we gathered vegetation-plot records from bog hummocks, lawns and Atlantic moist peat heaths (vegetation associated to *Oxycocco-Sphagnetea* following Mucina et al., 2016) across Europe with the aim of: (i) identifying the main vegetation types within the *Oxycocco-Sphagnetea* class; (ii) developing an expert system for the automatic assignment of vegetation plots to the *Oxycocco-Sphagnetea* class and its alliances; (iii) identifying diagnostic species and map distribution ranges for the formally defined alliances; (iv) validating or updating the classification scheme of the *Oxycocco-Sphagnetea* class in EuroVegChecklist.

Methods

Data compilation and filtering

The phytosociological databases stored in the European Vegetation Archive (EVA; Chytrý et al., 2016) served as a basic data source covering most of the European territory. Vegetation plots from EVA were

supplemented with unpublished private data sampled by the authors of this study (Appendix S1). Vegetation plots for the initial ("working") dataset were selected if at least two species from the preliminary list of bog specialist species occurred in the plot (Appendix S1). All the vegetation-plot records from these sources were merged into one large dataset using the TURBOVEG 3 software (Hennekens, 2015) and imported into the JUICE 7.0 program (Tichý, 2002). Taxonomic concepts and nomenclature were unified according to: the Euro+Med PlantBase (2006–2018; ww2.bgbm.org/EuroPlusMed) for vascular plants; Laine et al. (2018) for *Sphagnum* species; Hill et al. (2006) for other mosses; Söderström et al. (2016) for liverworts; Ahti and Stenroos (2013) for *Cladoniaceae*; and Wirth et al. (2013) and Stenroos et al. (2016) for other macrolichens. Some taxonomically problematic species were merged into aggregates (Appendix S2). Records of algae, non-lichenicolous fungi and higher taxonomic levels such as "hepatics" were deleted. The names of syntaxa were unified according to EuroVegChecklist (Mucina et al., 2016) or referenced to the publication in which they were originally published. For the class *Scheuchzerio palustris-Caricetea fuscae*, we used the corrected name *Scheuchzerio palustris-Caricetea nigrae*. Furthermore, since the name *Erico-Ledetalia* Tx. 1937 was considered invalid according to Art. 3f of the International Code of Phytosociological Nomenclature (ICPN; Theurillat et al., 2021), we accepted *Erico-Sphagnetalia* Schwickerath 1941 (*Sphagno-Ericetalia tetralicis nom. invers.*) as the oldest valid name of the order.

We removed duplicate plots, non-georeferenced plots and plots with only presence/absence data. To define the *Oxycocco-Sphagnetea* class and to select plots that belong to it, we developed the formal definition for an expert system (for details see the next section and Landucci et al., 2015; Chytrý & Tichý, 2018; Tichý et al., 2019; Chytrý et al., 2020). The *Oxycocco-Sphagnetea* class shows some peculiarities that make a formalized definition difficult, such as: (i) a small species pool and a low number of diagnostic species of the class; (ii) a low number of species per plot; (iii) a broad ecological niche of several dominant species, which are often diagnostic also for other classes; and (iv) a high ecological importance of bryophytes. Therefore, in our formal definition, we emphasized the proportion of species indicative of bogs over the proportion of species indicative of other habitats rather than absolute numbers of indicator species. Such an expert system can deal with plots of different sizes including mosaics, as the result of the classification depends on the ratio of species in the plot. To achieve this, the following species groups were defined (Appendix S3):

(i) 'Bog species' - indicators of bogs;

(ii) 'Neutral species' - ecological generalists that might occur in bogs but are also common in other habitats;

(iii) 'Negative species' - all other species that occur in the rest of the European flora (adopted from the species list used by Chytrý et al., 2020).

The initial lists of 'Bog species' and 'Neutral species' were compiled from diagnostic species of the class *Oxycocco-Sphagnetea* in EuroVegChecklist (Mucina et al., 2016: their Appendix S6), critically evaluated by the authors of this study and modified based on several classification trials with successive versions of the expert system, followed by an expert-based assessment of the results.

The class was finally defined using the ratio between the sum of square-root transformed percentage covers of 'Bog species' and the sum of square-root transformed percentage covers of 'Negative species'. The presence of 'Neutral species' does not affect the result. To be classified in the *Oxycocco-Sphagnetea* class, the plot must reach a ratio > 1, separately for the herb and bryophyte layers. Alternatively, the plot must reach a ratio > 1 in the herb layer and the total cover of the 'Negative species' group in the bryophyte layer must not exceed 5%, so that plots with a poorly developed or no bryophyte layer can be classified. The 'Bog species' and 'Negative species' groups serve as so-called discriminating species groups (for details see Willner, 2011; Chytrý et al., 2020). Applying the ratio between the summed covers of the species groups gives species-poor and species-rich plots an equal chance to match the definition. Plots with tree cover above 25% are also excluded during the expert system classification. Because some databases lack information on vegetation layers, we did not filter the vegetation plots by tree or tall shrub cover, but only by cover resulting from merged covers of all layers in the plot.

Sample-size correction (only plots equal or larger than 1 m^2 and equal or smaller than 100 m^2 were kept; Peterka et al., 2020). Further, for unsupervised classification and counting fidelity and frequency in synoptic table, the vegetation plots without bryophytes were removed and geographical stratification (Knollová et al., 2005) was applied. The geographical stratification was performed in order to achieve a more balanced dataset by removing some plots from oversampled areas. A maximum of 10 plots was randomly selected during the stratification process from each cell of a geographical grid of 0.75 minutes of longitude and 1.25 minutes of latitude.

Unsupervised classifications

Since our aim was not to merely reproduce existing classification systems, we started with the unsupervised numerical classifications of the geographically stratified dataset of plots identified as the vegetation of the *Oxycocco-Sphagnetea* class. The aim of this step was to test not only the extent to which the existing data fit the current classification scheme of bogs, but also whether other specific vegetation types not covered by the existing classification form well-separated clusters in the unsupervised classification. Non-hierarchical k-means clustering or divisive methods such as Twinspan emphasize compositional differences along the major gradients such as macroclimate or water level (i.e., they may separate also lawns or polygon and palsa bogs). In contrast, agglomerative methods may capture ecologically or biogeographically exceptional features that may lead to distinctive species composition, such as in narrow-range Iberian blanket bogs. Since the results of each classification method were quite consistent at the highest levels, we selected only one of them, which is presented in this paper. We present the results of agglomerative beta-flexible clustering, with beta parameter of -0.25, based on the Sørensen distance measure (Tichý, 2002), and using pseudospecies cut levels (0, 5 and 25%) to account for species covers. After preliminary testing various clustering solutions, the number of resulting clusters was arbitrarily set at eight. With fewer clusters, some of the resulting groups would be too heterogeneous (Atlantic bogs). In contrast, accepting more clusters would result in unnecessarily much too narrowly defined clusters (mainly according to the single dominant *Sphagnum* species), especially when considering classification at the alliance level.

Supervised classification and formal definitions of syntaxa

A classification approach based on the ratios between discriminating species groups was also used in the formal definitions of orders and alliances. As mentioned earlier, the expert system uses the ratios between the sum of square-root transformed percentage covers of one species group over another group(s). The discriminating species groups (Appendix S3) for individual orders (first decision step) and alliances (further decision steps) included sociological groups determined by the previous unsupervised analysis. However, they were adjusted for the higher classification precision of the expert system by prioritizing ecologically and geographically more distinct species. The criterion for assigning the plot to the class had to be met simultaneously. For a plot to be classified in one of the bog alliances, there had to be: (i) a greater proportion of 'Bog species' than of 'Negative species' (class-level classification); (ii) higher proportion of group of Atlantic species or Continental species (order-level classification); and (iii) higher proportion of a discriminating species group of one alliance than discriminating species groups of the other alliances of the same order (alliance-level classification). The traditionally used system of two orders was retained after the preliminary results of the unsupervised classifications had clearly separated the

Atlantic bogs (*Sphagno-Ericetalia tetralicis*) and the continental bogs (*Sphagnetalia medii*) in the division. The use of discriminating species groups eliminates the possibility of classifying a vegetation-plot record into more than one alliance. Likewise, it minimizes the likelihood that the vegetation plot will remain unclassified. Only vegetation plots with equal proportions of two or more discriminating species groups of alliances and plots completely lacking species from discriminating groups of alliances left unclassified and are classified in the next step into the *Sphagnion medii* alliance (if the species of the 'Atlantic species' group are missing) or the *Oxycocco-Ericion tetralicis* alliance (if 'Atlantic species' are present; Appendix S3). Since these two alliances have the diagnostic species of the next higher unit but are largely negatively differentiated from the next similar units of the same rank, they correspond to the concept of central alliances (Willner, 2020) within the *Sphagnetalia medii* and *Sphagno-Ericetalia tetralicis* orders, respectively. The final step of the expert system distinguishes the core plots of the alliances with a minimal number of diagnostic species of the particular alliance and/or their cover (another restrictive condition; Appendix S3) from the plots classified only on the basis of the proportion of species of the discriminating species groups (non-core plots). The logical formulas in the expert system were defined for seven alliances. This decision was based primarily on the results of the unsupervised analysis and the presence of absolute diagnostic species (Willner, 2020). The expert system file can be run in JUICE (Tichý, 2002), TURBOVEG 3 (Hennekens, 2015) or R (Bruelheide et al., 2021).

Diagnostic and constant species (Chytrý & Tichý, 2003) of the defined alliances are sorted in the form of a synoptic table showing percentage species frequency and fidelity measure. The phi coefficient was used as a fidelity measure (Chytrý et al., 2002). The sizes of all groups were virtually standardized to equal size, and the significance of fidelity was tested using Fisher's exact test ($P < 0.05$; Tichý & Chytrý, 2006). In addition, the table lists the species that were identified as diagnostic for the two or more alliances, the orders or the class. The diagnostic species of the orders were determined in a synoptic table resulting from the classification of the plots at the order level only by the expert system. Diagnostic species of the class were identified by applying the expert system to the dataset of all European habitats that was analyzed by Chytrý et al. (2020); the fidelity of the group of plots classified as *Oxycocco-Sphagnetea* class was analyzed in comparison with unclassified plots of other vegetation types.

Plots classified at the alliance level were subjected to a detrended correspondence analysis (DCA) in CANOCO 5 (Šmilauer & Lepš, 2014) to visualize the relationships among the alliances and identify the main gradients in species composition. The same method was applied to the clusters produced by unsupervised classification to identify the similarities between these two approaches.

The maps showing the distribution class, orders and alliances in Europe defined by the expert system were processed using the ArcGIS 10 software (ESRI, 2011). To map the distribution of the alliances, the expert system was applied to the original (i.e., geographically unstratified) dataset.

Results

Distribution of the *Oxycocco-Sphagnetea* class and its orders and alliances in Europe

A new expert system (see the 'OXY_SPH_ESY_2022_file.txt' in Zenodo repository, version 2022/2; https://doi.org/10.5281/zenodo.5851129) was developed for the automatic classification of vegetation plots into the *Oxycocco-Sphagnetea* class, its two orders and finally seven compositionally distinct alliances. A total of 8089 vegetation-plot records were classified by the expert system into the *Oxycocco-Sphagnetea* class. The plots identified as *Oxycocco-Sphagnetea* class are concentrated in the Atlantic and Boreal zones, and their occurrence continually decreases towards the temperate-continental Central and Eastern Europe. This class is missing in southern and south-eastern Europe (Figure 1).

Unsupervised classification

The first division separated Atlantic bogs (*Sphagno-Ericetalia tetralicis* order) from continental bogs (*Sphagnetalia medii* order; Figure 2). The formation of 3–8 final clusters was found sufficient to show the gradual division of our dataset into clusters corresponding to the four bog alliances listed in EuroVegChecklist, as well as other clusters differing in species composition and geographic distribution. When only four final clusters were used (the same number as in EuroVegChecklist), a cluster corresponding to the bog lawns of boreal Europe and high mountains of temperate-subcontinental Europe emerged (cluster 6 in Figure 2) while the Atlantic-bog alliances remained undivided. Vegetation plots corresponding to *Sphagnion medii* formed the largest group and were further divided into open mires with heliophilous species (cluster 4) and a group of bogs with species characteristic of small mountain bogs surrounded by forest or krummholz or bog margins with occurrences of *Vaccinium* spp., *Sphagnum russowii* or *Melampyrum pratense* (cluster 5). The cluster of subarctic bogs on polygon mires and palsas with *Dicranum elongatum* and lichens prevailing over sphagna was separated as cluster 8. Blanket bogs with *Erica mackaiana* from northwestern Spain (cluster 3) were recognized as the first cluster within the Atlantic branch of bogs. In the case of eight final clusters, partitions corresponding to *Ericion tetralicis* and *Oxycocco-Ericion tetralicis* alliances (clusters 1 and 2) were finally separated.

Alliances: synoptic table, ordination, syntaxonomic synopsis and short descriptions

Almost 81% of the plots identified as *Oxycocco-Sphagnetea* class were classified as core plots of alliances (Table 1, Figure 3). The ordination of vegetation-plot groups (clusters) produced by the unsupervised classification (Figure 2) gave analogous results to the ordination of alliances identified by the expert system (Figure 3). The main pattern in ordination diagrams (DCA1 axis in Figure 2 and 3) reflects a longitudinal gradient extending from the southwest and west to the east and northeast of the study extent. Individual alliances are clearly separated, with overlaps between ecologically and geographically related alliances. The extremes of the main gradient are formed by *Erico mackaianae-Sphagnion papillosi* plus *Ericion tetralicis* (bogs and peat heaths in Atlantic Europe) and *Rubo chamaemori-Dicranion elongati* (subarctic polygonal peatlands and palsas). Two alliances of the *Sphagnetalia medii* order, i.e., *Sphagnion medii* and *Sphagno baltici-Trichophorion cespitosi*, are differentiated along the second axis (DCA2, Figure 3). Bog vegetation with the presence of trees did not form a single separate cluster in any classification. In both the supervised and unsupervised classifications presented in this article, bogs with *Picea abies*, *Betula pubescens* and *Pinus mugo* agg. were included in the *Sphagnion medii* alliance, while bog vegetation with *Pinus sylvestris* was included in the *Sphagnion medii* alliance or *Oxycocco microcarpi-Empetrion hermaphroditi* alliance (see Table 1). Differentiation of bog vegetation by trees or forest species occurred in partitions with a higher number of clusters, allowing for possible classification at the association level within both focal alliances. Frequency of trees or forest species in Atlantic bogs, palsas or boreal continental lawns is small. Based on the critically assessed results of the unsupervised classification and comparison with the available literature, a hierarchical system of European hummock and lawn bog vegetation is proposed as follows:

Cl. *Oxycocco-Sphagnetea* Br.-Bl. et Tüxen ex Westhoff et al. 1946

O. *Sphagno-Ericetalia tetralicis* Schwickerath 1941 *nom. invers.*

All. *Erico mackaianae-Sphagnion papillosi* (Fernández Prieto et al. 1987) Rivas-Martínez et al. 1999

All. *Ericion tetralicis* Schwickerath 1933

All. *Oxycocco-Ericion tetralicis* Nordhagen ex Tüxen 1937

O. *Sphagnetalia medii* Kästner et Flössner 1933

All. *Sphagno baltici-Trichophorion cespitosi* Jiroušek et al. 2022 all. nova

All. *Sphagnion medii* Kästner et Flössner 1933

All. *Oxycocco microcarpi-Empetrion hermaphroditi* Nordhagen ex Du Rietz 1954

All. *Rubo chamaemori-Dicranion elongati* Lavrinenko et Lavrinenko 2015

Erico mackaianae-Sphagnion papillosi

This alliance includes hyperoceanic peat heath vegetation with *Erica mackaiana* and the rarer *E. ciliaris*, while *E. tetralix* is nearly absent. *Carex durieui*, an endemic sedge to the Northwestern Iberian Peninsula (Luceño Garcés, 1994), also has high diagnostic value for this alliance. Typical components of this vegetation are mire generalists such as *Eriophorum angustifolium* or *Narthecium ossifragum*, growing together with species of Atlantic heaths and grasslands (e.g., *Agrostis curtisii*, *Avenella flexuosa*, *Molinia caerulea* agg., *Potentilla erecta* and the endemic *Arnica montana* subsp. *atlantica* or *Serratula tinctoria* var. *seoanei*). Common dominant species of the bryophyte layer are the acidophilous peat-mosses *Sphagnum papillosum*, *S. subnitens* and, less commonly the endangered *S. pylaesii*. The bryophyte layer is further characterized by the frequent occurrence of liverworts (*Kurzia trichoclados*, *Odontoschisma sphagni*) and the absence of lichens. This alliance is geographically restricted to the north of Galicia and Asturias (Atlantic humid zone of the Iberian Peninsula). The non-core vegetation of this alliance is distributed also in Western Ireland in case of *Erica mackaiana* presence (Figure 4a).

Ericion tetralicis

The species composition of the Atlantic moist peat heath vegetation is characterized by the dominance of the dwarf shrub *Erica tetralix*, accompanied by mire generalists that also occur in fens (e.g., *Carex panicea*, *Drosera intermedia*, *Rhynchospora fusca*, *Trichophorum cespitosum*) and species common in Atlantic heaths or mat-grass swards (e.g., *Calluna vulgaris*, *Juncus squarrosus*). *Sphagnum compactum* is a common and dominant species of the bryophyte layer and also has the highest diagnostic value for the alliance. The bryophyte layer is further composed of *S. tenellum*, non-sphagnaceous mosses (*Hypnum cupressiforme* agg.), liverworts (*Gymnocolea inflata*) or fruticose lichens (*Cladonia portentosa*). The alliance is widespread in Atlantic Europe from the northern Iberian Peninsula through France, Ireland, the United Kingdom, Belgium, the Netherlands, northern Germany and Norway to the Baltic coast of Poland. The non-core vegetation of this alliance is also found more to the east (Figure 4b; in Kaliningrad Oblast of Russia and the Czech Republic were the plots recorded only on bogs affected by drainage or fires).

Oxycocco-Ericion tetralicis

The herb layer of these true Atlantic bogs is formed mostly by the dwarf shrubs *Erica tetralix* and *Calluna vulgaris*, accompanied by *Eriophorum angustifolium*, *E. vaginatum*, *Narthecium ossifragum* and *Trichophorum cespitosum*. Diagnostic or frequent bryophytes are peat mosses *Sphagnum magellanicum* agg., *S. papillosum* or *S. rubellum* but liverworts such as *Fuscocephaloziopsis connivens*, *Odontoschisma sphagni* and *Kurzia pauciflora* are also common. In contrast to the previous alliances, minerotrophic species (e.g. *Carex panicea*, *Juncus squarrosus*) are rare or absent. This alliance occurs in Atlantic Europe from the northern Iberian Peninsula through the United Kingdom, Ireland, France, Belgium, the Netherlands and Germany to the Czech Republic and southern Baltic coast. In Scandinavia, *Oxycocco-Ericion tetralicis* is much more widespread than *Ericion tetralicis* (Figure 4c).

***Sphagno baltici-Trichophorion cespitosi* Jiroušek et al. all. nova**

Nomenclatural type: *Trichophoro cespitosi-Sphagnetum compacti* Warén 1926 (orig. *Scirpus caespitosus-Sphagnum compactum*-Ass.); holotypus.

Name-giving taxa: *Sphagnum balticum* (Russow) C.E.O. Jensen and *Trichophorum cespitosum* (L.) Hartm. The name of the new alliance refers to *S. balticum*, an absolute (exclusive) diagnostic species with highest frequency and fidelity to the alliance within the *Oxycocco-Sphagnetea* class, and frequently dominating *T. cespitosum*, vascular plant with highest frequency and fidelity to the alliance within the *Sphagnetalia medii* order.

Diagnostic species (species with the highest fidelity to the alliance within the *Oxycocco-Sphagnetea* class) include: *Andromeda polifolia*; *Carex limosa*; *C. pauciflora*; *Drosera longifolia*; *Eriophorum vaginatum*; *Scheuchzeria palustris*; *Sphagnum balticum*; *S. rubellum*; and *Trichophorum cespitosum*.

Other species differentiating the alliance mainly within the *Sphagnetalia medii* order and contrary to the *Scheuchzerion palustris* alliance are: *Gymnocolea inflata*; *Sphagnum compactum*; *S. papillosum*; and *S. tenellum*.

Constant species (species with the highest frequency) are: *Andromeda polifolia*; *Carex pauciflora*; *Drosera rotundifolia*; *Eriophorum vaginatum*; *Sphagnum balticum*; *S. compactum*; *S. papillosum*; *S. rubellum*; *S. tenellum*; *Trichophorum cespitosum*; and *Vaccinium oxycoccos* agg.

Associations: *Sphagno tenelli-Trichophoretum cespitosi* Osvald 1925; *Trichophoro cespitosi-Sphagnetum baltici* Warén 1926; *Trichophoro cespitosi-Sphagnetum compacti* Warén 1926; *Andromedo polifoliae-Sphagnetum baltici* Bogdanovskaya-Guihéneuf 1928; *Trichophoretum cespitosi* Zlatník 1928

The unsupervised classification confirmed that although the boreal bog lawns have not yet been assigned to any distinct alliance, they have a distinct species composition and the sharpness of their delimitation is similar to other accepted alliances. *Sphagnum balticum* and *Drosera longifolia* were found to be the best diagnostic species of boreal bog lawns, while other frequent or diagnostic species (*Andromeda polifolia*, *Carex pauciflora*, *Eriophorum vaginatum*, *Drosera rotundifolia*, *Sphagnum rubellum*) also occur frequently in other types of bog vegetation. Therefore, the presence of species of dystrophic hollows (*Carex limosa*, *Scheuchzeria palustris*) or Atlantic bog species (*Sphagnum compactum*, *S. tenellum*, *Trichophorum cespitosum*) is crucial to distinguish the *Sphagno baltici-Trichophorion cespitosi* alliance from the *Sphagnion medii* and *Oxycocco-Empetrion hermaphoditi* alliance. The main area of occurrence is the Baltic region, Scandinavia, Finland, Belarus and western part of European Russia. Extrazonally, this vegetation occurs in Central-European mountains (Figure 4d).

Sphagnion medii

The (boreo)temperate bog lawns and low hummocks are characterized by *Sphagnum magellanicum* agg. (*S. medium*), *S. recurvum* agg. (*S. angustifolium*, *S. fallax*), *S. rubellum*, *S. russowii* and *Polytrichum strictum*, as part of the bryophyte layer. In the herb layer, *Eriophorum vaginatum* and various dwarf shrubs such as *Andromeda polifolia*, *Calluna vulgaris*, *Vaccinium oxycoccos* agg. (mainly *V. oxycoccos* s.s.) and *V. uliginosum* are typical dominant species. Many *Sphagnion medii* sites are encroached by scattered trees or occur in contact with bog woodlands or as a mosaic with them. Therefore, seedlings or adult individuals of *Picea abies*, *Pinus mugo* agg. or *Betula pubescens* can be found in this alliance. Acidophilous forest species (*Melampyrum pratense, Vaccinium myrtillus*, *V. vitis-idaea*) are also common and diagnostic species for this alliance. The *Sphagnion medii* alliance is widespread in the mountains of temperate Europe (Pyrenees, Massif Central, Jura, Alps, Vosges, Ardennes, Rhön, Harz, Bohemian Massif, Carpathians, Southern Urals; marginally also in the United Kingdom and Ireland) and further north also in the lowlands of northern Germany, Poland, northern Ukraine, Belarus, Lithuania, Latvia, Estonia, Russia, Scandinavia and Finland (Figure 4e).

Oxycocco microcarpi-Empetrion hermaphroditi

The boreal type of bog-hummock vegetation is characterized by dwarf shrubs such as *Andromeda polifolia*, *Betula nana*, *Chamaedaphne calyculata*, *Empetrum nigrum* agg., *Rhododendron tomentosum*, *Rubus chamaemorus* and *Vaccinium oxycoccos* agg. (mainly *V. microcarpum* in this alliance), together with *Carex pauciflora* and *Eriophorum vaginatum* in the herb layer. *Sphagnum fuscum* frequently dominates among bryophytes. Other common bryophytes include *Polytrichum strictum*, *Mylia anomala* and *Sphagnum recurvum* agg. (mainly *S. angustifolium*). Other mosses (e.g., *Pleurozium schreberi* and *Dicranum undulatum*) and lichens (mainly species of the genus *Cladonia* such as *C. arbuscula* agg., *C. mediterranea*, *C. rangiferina*, and *C. stygia*), as well as pines (*P. sylvestris*), are typical of the driest hummocks. The continuous range of the alliance extends from the Baltic region, northern Belarus and central part of European Russia to Fennoscandia and northern Russia. On the European mainland, the alliance occurs at higher elevations in contrast to the *Sphagnion medii* alliance (Massif Central, Vosges, Alps, Bohemian Massif, Carpathians, Southern Urals). Non-core plots also occur in the mountain systems of the United Kingdom (Figure 4f).

Rubo chamaemori-Dicranion elongati

Subarctic bog vegetation on polygon mires and palsas consists of boreo-arctic low shrubs (*Rhododendron tomentosum*, *Empetrum nigrum* agg.), *Rubus chamaemorus* and graminoids (*Luzula wahlenbergii*, *Carex rariflora*). Typical species of the bryophyte layer are non-sphagnaceous mosses (*Dicranum elongatum*, *Polytrichum hyperboreum* and *P. strictum*) and lichens (*Alectoria nigricans*, *Cetraria islandica*, *Cladonia amaurocraea*, *C. arbuscula* agg., *C. gracilis*, *Flavocetratraria nivalis*, *Ochrolechia frigida*, *Sphaerophorus globosus* and others; see Appendix S4). *Sphagnum* species (*S. fuscum*, *S. russowii*) occur regularly but have low cover. The alliance is widespread in northernmost Fennoscandia, Nenets Autonomous Okrug of Russia and the isolated area of palsas in the Rondane Massif (Figure 4g).

DISCUSSION

Distribution of *Oxycocco-Sphagnetea* class in Europe

We show that the vegetation of the *Oxycocco-Sphagnetea* class is distributed throughout the entire European continent except for its southern (especially south-eastern) part and the northernmost Arctic areas. In Northern Europe, bog vegetation reaches the subarctic zone, which is consistent with the observations of Dierssen (1996), Koroleva (2014) and Lavrinenko and Lavrinenko (2015). The southern

limit of the distribution of the *Oxycocco-Sphagnetea* class extends from northern Portugal through northern Spain, the Pyrenees, France, the southern Alps, Hungary, the Southern Carpathians, northern Ukraine and central parts of European Russia up to the southern Urals. This limit corresponds well with the bog occurrences reported in local studies and national phytosociological checklists (Coldea, 1997; Borhidi et al., 1999; Yamalov et al., 2012; Biondi et al., 2014; Molina, 2017). Hájek et al. (2008) also reported the presence of a pine bog woodland of the *Oxycocco-Sphagnetea* class in the Rhodope Mountains in Bulgaria. However, their plot records were not classified in this class by the expert system because of the relatively high abundance of fen and woodland species in the tree, shrub and herb layers, even though the dominant bryophyte species correspond to the *Sphagnion medii* alliance. *Sphagnum* hummocks scattered in fens and affected by the species spread from nearby habitats (mass effect; Shmida & Ellner, 1984) are a common feature towards the southern distribution limit of bogs (see also Pérez-Haase & Ninot, 2017).

Despite the large amount of phytosociological data we have compiled, there is still an unsufficient cover of large with abundant presence of bog vegetation (large areas in Scandinavia, Ukraine, Belarus, and especially in Russia; Figure 1). Although there has been considerable progress in the development of vegetation-plot databases in recent decades, stimulated especially by the establishment of the Global Index of Vegetation Databases (Dengler et al., 2011) and the integration of European databases into the European Vegetation Archive (Chytrý et al., 2016), uneven coverage of Europe by vegetation-plot data with significant gaps still persists (Sporbert et al., 2019). Therefore, further efforts are needed in vegetation sampling and data digitizing in areas with poor representation in vegetation-plot databases.

Vegetation analogous to the *Oxycocco-Sphagnetea* class has also been documented or is known to occur in regions adjacent to Europe, such as the Azores, the Black Sea coast of Georgia, northeastern Turkey and Western Siberia (Parolly, 2004; Kaffke, 2008; Lapshina, 2010; Lapshina & Filippov, 2012; Mendes & Dias, 2013; Joosten et al., 2017). In particular, the syntaxonomical position of Colchic percolation mires remains unclear. Although Kaffke (2008) characterizes them as clearly ombrotrophic, only a few species characteristic of bogs occur in these mires (e.g., *Polytrichum strictum* and *Sphagnum austinii*). This fact, together with a high abundance of minerotrophic species and local relict species (Kaffke, 2008), suggests that the Colchic bog vegetation does not correspond to the *Oxycocco-Sphagnetea* class concept as defined in the expert system developed here. Further research is needed to assess possible occurrences of the class beyond the geographical scope of this study.

Update of the EuroVegChecklist

EuroVegChecklist (Mucina et al., 2016) includes four alliances within the *Oxycocco-Sphagnetea* class: *Ericion tetralicis*; *Oxycocco-Ericion tetralicis*; *Sphagnion medii*; and *Oxycocco microcarpi-Empetrion hermaphroditi*. Our analyses support their validity but also show that three other distinct alliances of bog vegetation can be distinguished as well as the four alliances included in EuroVegChecklist. We suggest that these types should be recognized as separate alliances, namely *Erico mackaianae-Sphagnion papillosi*, *Rubo chamaemori-Dicranion elongati* and *Sphagno baltici-Trichophorion cespitosi* (alliancia nova). We also discuss the reason for using a different order name *Sphagno-Ericetalia tetralicis* as opposed to EuroVegChecklist (here *Erico-Ledetalia*).

Sphagno-Ericetalia tetralicis

The name *Erico-Ledetalia* Tüxen 1937 used in EuroVegChecklist (Mucina et al., 2016) should be considered invalid according to Art. 3f of the International Code of Phytosociological Nomenclature (ICPN; Theurillat et al. 2021). *Ledum palustre* (syn. *Rhododendron tomentosum*) does not occur in any description of the associations assigned to alliances mentioned by Tüxen (1937): neither (*Ulicio*)-*Ericion*; *Oxycocco-Ericion*; nor *Oxycocco-Empetrion*. Also in former work of Nordhagen (1937; referenced by Tüxen, 1937) *Oxycocco-Empetrion* prov., the alliance lacks *Ledum palustre* (in contrast to the *Oxycocco-Ledion* alliance). Schwickerath (1941) considered the name *Erico-Sphagnetalia* (orig. *Ericeto-Sphagnetalia*) superior to the alliance names *Ericion tetralicis* (Glockenheidegesellschaften) and *Sphagnion europaeum* (Hochmoorgesellschaften). He assigned at least one validly described alliance (*Ericion tetralicis*; described by Schwickerath, 1933) to the order. Furthermore, the order of name-giving taxa were inverted (see Art. 10b and Art. 42 of ICPN) and the name of the syntaxon was completed by adding the specific epithet of the second taxon - *Erica tetralix* (Rec. 10C of ICPN; Theurillat et al., 2021), the specific epithet for *Sphagnum* is not specified and cannot be selected with certainty (Schwickerath, 1941).

Erico mackaianae-Sphagnion papillosi

The *Erico mackaianae-Sphagnion papillosi* alliance was described by Rivas-Martínez et al. (1999) based on data of Fernández Prieto et al. (1987) from Galicia and Asturias. Mucina et al. (2016) synonymized this alliance with *Ericion tetralicis*, while the alliance was included in the recent vegetation checklist of Iberian wetlands (Molina, 2017). The traditional acceptance of the *Erico mackaianae-Sphagnion papillosi* alliance in national vegetation checklists is supported by its unique diagnostic species and distinct distribution range, which is restricted to the north-western part of the Iberian Peninsula. The alliance is characterized by the dominance of *Erica mackaiana*, a high abundance of *E. ciliaris* and the occurrence of taxa with

narrow distribution ranges (*Arnica montana* subsp. *atlantica*, *Carex durieui, Serratula tinctoria* var. *seoanei*). Although *Erica mackaiana* also occurs in western Ireland (Webb, 1955; Sheehy Skeffington, 2015) and Cantabrian wet heaths, the geographically restricted distribution of other diagnostic and endemic species allows the alliance to be easily defined using the expert system (the Irish vegetation plots with *Erica mackaiana* were not grouped with the *Erico mackaianae-Sphagnion papillosi* alliance in the unsupervised classification analysis). The specific Quaternary history of the north-western Iberian blanket bogs (Muñoz Sobrino et al., 2005) also supports the concept of separate alliance. Recent studies (Gómez-Orellana et al., 2013; Janská et al., 2017) even consider the north-western Iberian Peninsula as one of the most important refugia for bog ecosystems during the Last Glacial Maximum. The high regional stability and continuity of bogs probably resulted in specific and endemic bog vegetation (Rodríguez-Guitián et al., 2009; Romero Pedreira, 2015), but today this vegetation has relictual distribution.

Rubo chamaemori-Dicranion elongati

Lavrinenko and Lavrinenko (2015) suggested to classify the bog vegetation on polygon and palsa mires in subarctic Russia into a separate alliance named *Rubo chamaemori-Dicranion elongati*. This is the first phytosociological unit that closely matches the palsa and polygon mire hummock vegetation, which is high-rank habitat types in the EUNIS classification (Chytrý et al., 2020). The *Rubo chamaemori-Dicranion elongati* alliance occurs in the hummock surfaces in mire margins and most characteristically on the permafrost mounds of palsa mires and on the ridges of polygon mires in subarctic northern and north-eastern Europe. Similar vegetation with a high proportion of lichens and non-sphagnaceous mosses (*Dicranum elongatum*, *Polytrichum* spp.) instead of sphagna was previously distinguished only at the association level within the *Oxycocco microcarpi-Empetrion hermaphroditi* alliance (Paasio, 1933; Nordhagen, 1937; Vorren, 1979; Dierssen, 1996; Koroleva, 2006; 2014). The alliance *Rubo chamaemori-Dicranion elongati* was neither accepted nor synonymized in EuroVegChecklist, as it was only described recently, but it was included in the checklist of European Arctic syntaxa (Koroleva et al., 2016). The subarctic bog vegetation of the *Rubo chamaemori-Dicranion elongati* alliance is also clearly delimited from the other recognized European alliances and may be accepted as a new alliance in EuroVegChecklist. All the analytical methods used in this study supported the separation of this alliance based on a specific combination of species of boreal bogs with boreo-arctic elements and a significant proportion of lichens (Table 1).

Sphagno baltici-Trichophorion cespitosi

Boreal and subalpine bog lawns are ambiguously classified in national phytosociological systems (Kuznetsov, 1991; Pott, 1992; Boch & Smagin, 1993; Dierssen, 1996; Valachovič, 2001; Hájková et al., 2011; Smagin, 2000, 2012a, 2012b; Timmermann, 2004; Lapshina, 2010; Zeliankevich et al., 2016), where they are assigned to several different alliances. Such inconsistencies may have resulted from the helplessness of individual authors because the alliance corresponding to the boreal lawns did not exist. The support for establishing a new alliance was found in the analysis of vegetation-plot data across different regions of Europe. In terms of the alliance concept as outlined by Willner (2020), *Sphagnum balticum*, *S. rubellum* and *Carex pauciflora* may be considered as so-called absolute diagnostic species of the *Sphagno baltici-Trichophorion cespitosi* alliance. The latter two species also occur in other bog alliances, but show the highest fidelity to *Sphagno baltici-Trichophorion cespitosi*.

If *Sphagno baltici-Trichophorion cespitosi* was not described, the boreal lawns could be classified to *Sphagnion medii*, but this solution refutes the concept of *Sphagnion medii* being of mostly temperate nature. Similarly to *Sphagnion medii*, vegetation of *Sphagno baltici-Trichophorion cespitosi* is situated above the water level, but never overgrown by tall shrubs or trees, staying out of the intermittently wet shrubby or woody patches (*Pinus mugo*, *P. sylvestris*, *P. uncinata* subsp. *uliginosa*). These alliances can be distinguished also according to the dominant *Sphagnum* species, where *S. balticum*, *S. compactum*, *S. tenellum* are characteristic for *Sphagno baltici-Trichophorion cespitosi*, whereas *S. magellanicum* agg., *S. recurvum* agg. and *S. russowii* for *Sphagnion medii*.

Presence of *Trichophorum cespitosum* and *Sphagnum compactum*, *S. papillosum*, *S. tenellum* resemble both boreal *Sphagno baltici-Trichophorion cespitosi* and Atlantic *Oxycocco-Ericion tetralicis*. However, this view would ignore the most important vegetation gradient in bogs, namely the gradient from Atlantic and subatlantic to boreal-continental bogs. Indeed, the total absence of Atlantic species was an important feature that characterized the cluster of boreal lawns in the unsupervised classification. Another alternative would be to classify boreal lawns into the boreal alliance *Oxycocco microcarpi-Empetrion hermaphroditi* (e.g., Dierssen, 1996; Hájková et al., 2011). However, *Oxycocco microcarpi-Empetrion hermaphroditi* comprises high hummocks, typically with *Sphagnum fuscum*, while *Sphagno baltici-Trichophorion cespitosi* comprises lawns, sometimes even at the transition to hollows.

A completely different view of the boreal-continental lawns is to classify them as hollow vegetation, to the *Scheuchzerio palustris-Caricetea nigrae* class. *Sphagnion baltici* was validated by Lapshina (2010) for vegetation of *Sphagnum* lawns and hollows on ombrotrophic raised bogs and transitional mires with domination of oligotrophic *Sphagnum* species in continental boreal Holarctic. Lapshina proposed as

character species *Rhynchospora alba*, *Trichophorum cespitosum*, *Eriophorum russeolum*, *Sphagnum balticum*, *S. lindbergii*, *S. papillosum*, but the alliance *Sphagnion baltici* actually does not differ formally from the *Scheuchzerion palustris* as the alliance was determined by Mucina et al (2016). Lavrinenko et al. (2016) expanded the *Sphagnion baltici* area to the European north. They included into *Sphagnion baltici* alliance the vegetation of hollows within the palsa mires.

Boreal lawns were assigned based on the presence of bog hummock species above bog hollow species and therefore clearly belonged to the *Oxycocco-Sphagnetea* class (hollow species contained only subordinately). Based on this result and the clear micro-topographic position in the bogs, we prefer the classification of boreal lawns in the *Oxycocco-Sphagnetea* class. However, we acknowledge that the clear differentiation between bog lawns and hollows we observe in most of Europe may gradually disappear towards eastern Europe and Siberia, where *Sphagnum balticum* often dominates in bog hollows (Bogdanovskaya-Guihéneuf, 1928; Lapshina, 2010). Fluctuating water levels in more eastern continental areas may cause hollows to resemble lawns and differ from hollows in Western or Central Europe. Despite the risk of confusion between the European boreal lawns and Eurasian continental hollows in more eastern areas, we believe it is reasonable to distinguish the *Sphagno baltici-Trichophorion cespitosi* alliance within the bog vegetation of the *Oxycocco-Sphagnetea* class. From this perspective, however, there could be room for another alliance, but this alliance would belong to the *Scheuchzerio palustris-Caricetea nigrae* class.

The vegetation of the *Sphagno baltici-Trichophorion cespitosi* alliance is characteristic for bogs of Scandinavia, whole Baltic region, Belarus, Finland and westernmost Russia, and is also a characteristic feature of bog vegetation in mixed mire complexes of aapa mires and eccentric bogs (Tolonen, 1967). In the Finnish mire site type system (Eurola et al., 1984), 'ombrotrophic short-sedge bog' encompasses all bog lawns and is separated from 'ombrotrophic hollow bog' in line with the separation of *Sphagno baltici-Trichophorion cespitosi* from *Scheuchzerion palustris* alliances. Because the expert system works only with species data, not with the position of plots with respect to the water level, uncertainty about the position of vegetation relative to water levels is increasing significantly to the east of Finland and the Baltics. In a westward direction, *Sphagno baltici-Trichophorion cespitosi* changes into *Oxycocco-Ericion tetralicis* with an increasing number of Atlantic species. Occurrence of this vegetation in Central-European mountains is represented therein mainly by *Sphagnum compactum*, *S. tenellum* or *S. papillosum* lawns, in which Atlantic species are absent

The identification of the new alliance within north-eastern European mires, which is well-defined in terms of microhabitat and distribution but has few absolute diagnostic species, highlights the need for further research into the variability of bog lawns and hollows in north-eastern Europe. The inclusion of additional vegetation plots from north-eastern Europe, ideally with data from smaller plot sizes (1–25 m2), to avoid mixing ecologically contrasting species in aapa mires with distinct micro-topographic heterogeneity, as well as the analysis of a large dataset containing both the *Scheuchzerietalia palustris* and the *Sphagnetalia medii* orders, could provide a more convincing insight into the delimitation of *Oxycocco-Sphagnetea* and *Scheuchzerio palustris-Caricetea nigrae*, and ecological characterization of *Sphagno baltici-Trichophorion cespitosi* in the future.

Acknowledgements

The vegetation-plot data for this study were provided, besides the authors, by the custodians of the databases stored in the European Vegetation Archive (EVA; Henry Brisse, Els De Bie, Úna FitzPatrick, Zygmunt Kącki, Asbjørn Moen, Joop H. J. Schaminée, Urban Šilc, Annett Thiele, Milan Valachovič, Wolfgang Willner, Thomas Wohlgemuth). Ilona Knollová and Stephan Hennekens helped with data management in EVA and Lubomír Tichý helped with expert system functionality in JUICE.

Author contributions

M.J., M.C., M.H. and T.P. conceived the research idea; M.J. developed the expert system; M.J. and T.P. analyzed the data; M.J. wrote the paper with contributions from T.P. and M.H.; V.P. and A.K. identified problematic specimens of bryophytes and lichens from vegetation plots and helped with unifying the names of bryophytes and lichens; all other authors provided vegetation-plot data for the analyses; all authors commented on the manuscript.

Data availability statement

The vegetation-plot data used in this study are available in the European Vegetation Archive under project no. 12. The current version of the expert system is available from the Zenodo repository ('OXY_SPH_ESY_2022_file'; https://doi.org/10.5281/zenodo.5851129).

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Figures

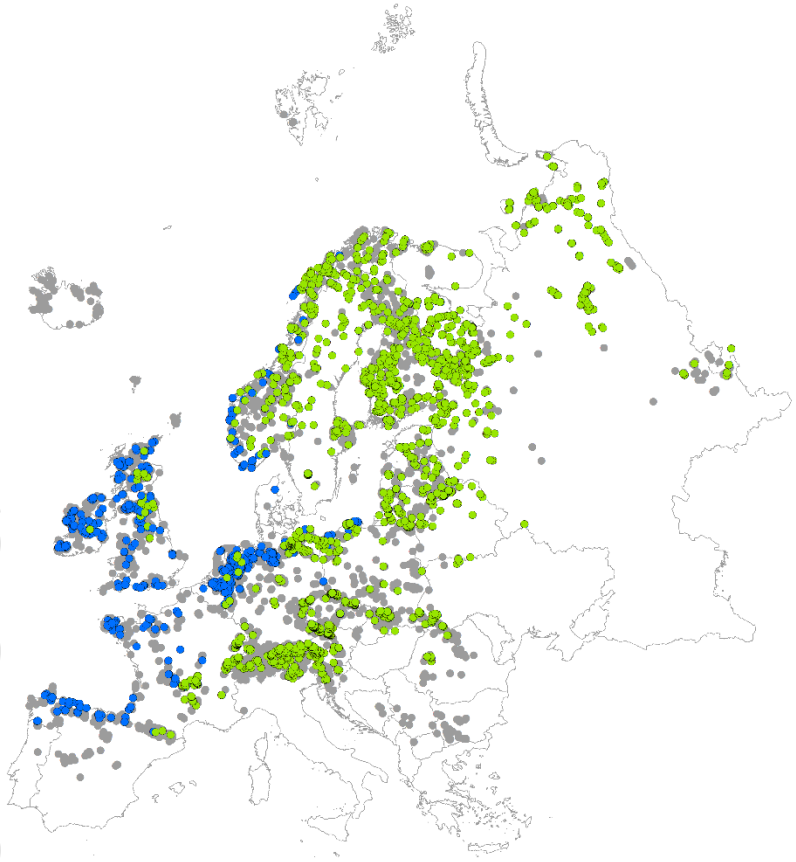


Figure 1. Distribution of the *Oxycocco-Sphagnetea* class and its two orders in Europe. *Sphagno-Ericetalia tetralicis* (blue circles) and *Sphagnetalia medii* (green circles) orders are differentiated by colors. Grey circles in the background show the unclassified plots of the initial “working” dataset. Note that the gaps in Belarus, Ukraine, Russia and Sweden are due to missing data in our database, not the absence of this vegetation.

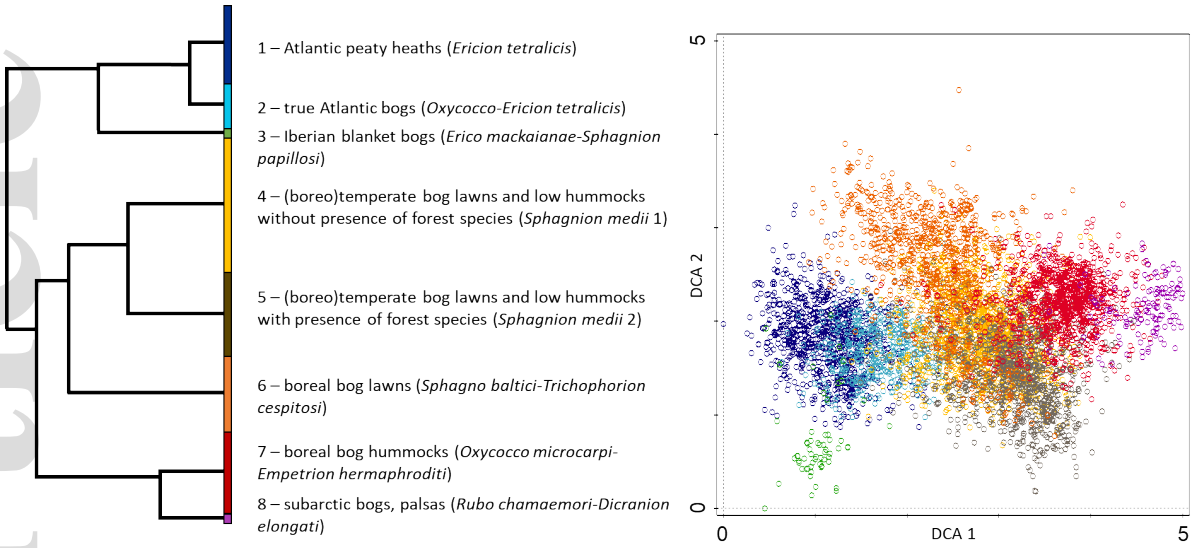


Figure 2. Result of unsupervised hierarchical cluster analysis (Sørensen distance measure, group-linkage method: beta-flexible = -0.5) at the level of eight resulting clusters. Further, vegetation plots coloured according to the clusters are displayed by ordination diagram (DCA).

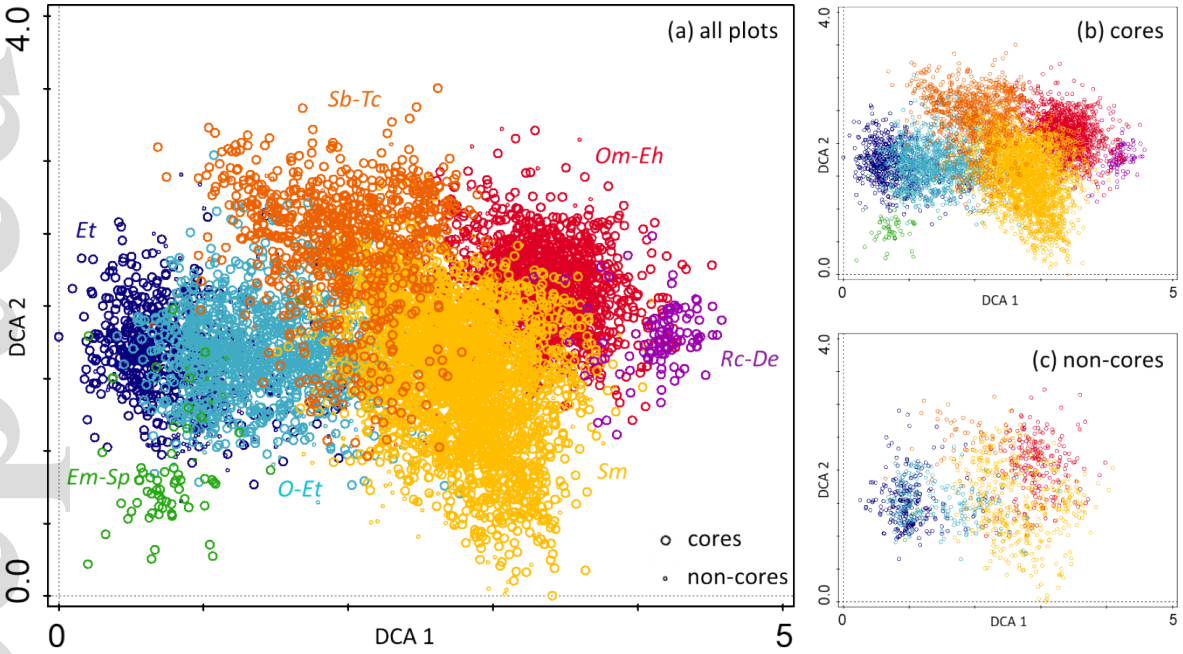
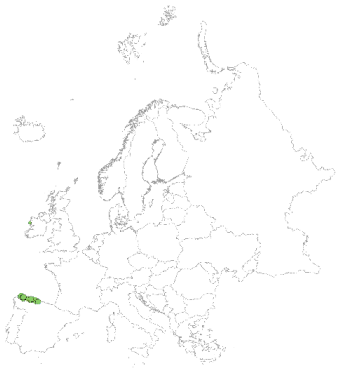


Figure 3. Ordination diagram of DCA analysis with plot colours according to the expert system classification (abbreviations of alliance names (see Table 1 for full names) are added to the clusters). The alliance cores and non-cores are indicated by different symbols in the diagram with all plots (a). Moreover, they are displayed in separate diagrams (b, c).

(a)

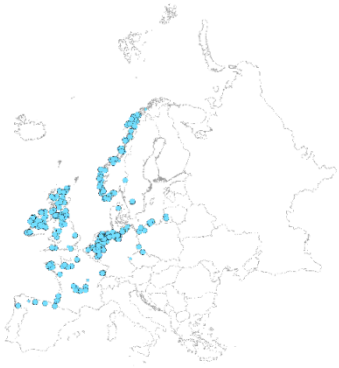


Erico mackaianae-Sphagnion papillosi

(b)

Ericion tetralicis

(c)



Oxycocco-Ericion tetralicis

(d)

Sphagno baltici-Trichophorion cespitosi

(e)

Sphagnion medii

(f)

Oxycocco microcarpi-Empetrion hermaphroditi

(g)

Rubo chamaemori-Dicranion elongati

Figure 4. Distribution of bog alliances in Europe based on the vegetation plots classified by the expert system.

Tables

Table 1. Synoptic table of bog alliances of the *Oxycocco-Sphagnetea* class as classified by the expert system presented in this paper (only plots classified as cores of alliances). The values of percentage frequency are shown. Species are sorted by decreasing fidelity within alliances (determined based on the phi coefficient calculation together with Fisher's exact test significance at $P < 0.05$). The gray shading indicates diagnostic species of alliances (species with phi > 20). The list of diagnostic species for the *Rubo chamaemori-Dicranion elongati* alliance was shortened due to a long list of lichens (for lichens with fidelity < 40 see Appendix S4). Diagnostic species of the orders are indicated by superscript letters ([A]*Sphagno-Ericetalia tetralicis*; [B]*Sphagnetalia medii*) and diagnostic species of the class are shown in bold (also here, phi > 20 and Fisher's exact test significance at $P < 0.05$). If the diagnostic species of the class or orders are not listed as diagnostic species of the alliances, they are placed at the end of the table. For the diagnostic, constant and dominant species of class and orders see Supplementary Information (Appendix S5) as well as for the full synoptic table (see Appendix S4). Abbreviations of column names (names of alliances): Em-Sp = *Erico mackaianae-Sphagnion papillosi*, Et = *Ericion tetralicis*, O-Et = *Oxycocco-Ericion tetralicis*, Sb-Tc = *Sphagno baltici-Trichophorion cespitosi*, Sm = *Sphagnion medii*, Om-Eh = *Oxycocco microcarpi-Empetrion hermaphroditi*, Rc-De = *Rubo chamaemori-Dicranion elongati*.

Alliance	**Em-Sp**	**Et**	**O-Et**	**Sb-Tc**	**Sm**	**Om-Eh**	**Rc-De**
Number of plots	53	491	1070	756	2646	1204	103
Erico mackaianae-Sphagnion papillosi							
Erica mackaiana	100	1	1	.	.	.	.
Carex durieui	92	.	.	.	.	.	.
Avenella flexuosa	62	1	1	1	3	1	1
Potentilla erecta [A]	60	23	16	3	6	1	.
Serratula tinctoria	25	.	.	.	.	.	.

Agrostis curtisii	25	1	.	.	.	.	.
Scilla verna	21	1	.	.	.	.	.
Leucobryum glaucum agg.	34	11	5	2	1	.	.
Erica ciliaris	23	3	1	.	.	.	.
Narcissus bulbocodium	17	.	.	.	.	.	.
Kurzia trichoclados	17	.	1	.	.	.	.
Gentiana pneumonanthe	32	20	1	.	.	.	.
Carex binervis	15	1	1	.	.	.	.
Arnica montana	13	.	1	.	1	.	.
Scorzonera humilis	13	1	1	.	.	.	.
Sphagnum subnitens [A]	25	5	12	1	1	.	.
Agrostis stolonifera agg.	9	1	.	.	.	.	.
Campylopus introflexus	13	4	2	.	.	.	.
Polygala serpyllifolia	19	12	7	.	1	.	.
Calypogeia sphagnicola	13	1	5	1	2	3	.
Danthonia decumbens	6	1	.	.	.	.	.
Ericion tetralicis							
Sphagnum compactum [A]	19	78	9	26	1	1	.
Drosera intermedia	.	32	5	1	1	.	.
Carex panicea	9	31	4	1	1	1	.
Juncus squarrosus	11	28	4	2	1	.	.
Rhynchospora fusca	.	14	1	1	.	.	.
Salix repens	.	12	1	1	1	.	.
Gymnocolea inflata	.	28	8	17	3	1	.
Sphagnum tenellum [A]	19	47	34	40	4	1	.
Lycopodiella inundata	.	8	1	1	1	.	.
Rhynchospora alba [A]	2	34	26	24	7	2	.
Oxycocco-Ericion tetralicis							
Narthecium ossifragum [A]	34	33	48	.	1	1	.
Odontoschisma sphagni [A]	26	22	41	.	1	1	.
Sphagnum papillosum [A]	30	12	51	38	9	3	.
Racomitrium lanuginosum [A]	.	7	17	.	1	1	1
Pleurozia purpurea	.	5	12	.	.	.	.

Myrica gale [A]	2	15	19	2	3	1	.
Fuscocephaloziopsis connivens [A]	.	7	11	1	1	1	.
Kurzia pauciflora [A]	.	12	17	4	1	5	.
Sphagno baltici-Trichophorion cespitosi							
Sphagnum balticum [B]	.	1	1	42	4	11	11
Drosera longifolia	.	2	6	17	2	2	.
Scheuchzeria palustris	.	1	1	15	6	2	.
Carex pauciflora [B]	.	1	3	28	22	19	.
Sphagnum rubellum	2	4	27	40	29	25	1
Carex limosa	.	.	1	9	3	1	.
Sphagnion medii							
***Sphagnum magellanicum* agg.** [B]	.	2	52	38	79	37	.
Pinus mugo agg. [B]	.	.	1	2	14	1	.
Vaccinium myrtillus [B]	.	1	3	4	25	15	7
Melampyrum pratense	.	1	1	1	10	3	.
Oxycocco microcarpi-Empetrion hermaphroditi							
Sphagnum fuscum [B]	.	.	2	8	18	95	29
Mylia anomala	.	7	17	22	11	46	8
Pinus sylvestris	.	14	11	8	26	44	.
Cladonia mediterranea	.	.	1	1	1	14	2
Chamaedaphne calyculata [B]	.	.	.	8	12	23	1
Dicranum undulatum	.	1	1	5	5	18	.
Cladonia stygia	.	1	.	1	1	8	.
Rubo chamaemori-Dicranion elongati							
Dicranum elongatum	.	.	1	.	1	3	100
Flavocetraria nivalis	.	1	1	.	1	5	82
Cladonia amaurocraea	.	.	.	.	.	2	74
Cladonia gracilis	.	3	1	.	1	5	78
Ochrolechia frigida	.	.	1	3	.	2	67
Sphaerophorus globosus	.	.	.	.	.	1	62
Cetraria islandica	.	1	1	3	2	8	74

Vaccinium vitis-idaea [B]	.	2	1	2	21	15	85
***Cladonia arbuscula* agg.**	9	6	7	6	4	40	97
Alectoria nigricans	.	.	.	.	.	1	52
Cladonia coccifera	.	2	1	1	.	2	56
Cladonia subfurcata	.	.	1	1	1	1	51
Coelocaulon divergens	.	.	.	.	.	.	50
Sphenolobus minutus	.	.	.	.	.	1	50
Cladonia bellidiflora	.	.	1	1	1	1	49
Thamnolia vermicularis	.	.	.	.	1	1	48
Flavocetraria cucullata	.	.	.	.	.	2	45
Ochrolechia inaequatula	.	.	.	.	.	1	41
Polytrichum hyperboreum	.	.	.	.	.	1	36
Carex rariflora	.	.	.	2	1	2	27
Luzula wahlenbergii	.	.	.	.	.	.	13
Ptilidium ciliare	.	1	1	3	1	3	17
Dicranum fuscescens	.	.	.	.	1	2	12
Aulacomnium turgidum	.	.	.	.	.	.	9
Orthocaulis binsteadii	.	.	1	1	1	1	8
Carex globularis	.	.	.	.	1	3	9
Loiseleuria procumbens	.	.	1	1	.	1	6
Sphagno-Ericetalia tetralicis							
Molinia caerulea agg. [A]	100	89	60	14	18	1	.
Eriophorum angustifolium [A]	75	58	76	10	11	5	1
Erica tetralix [A]	.	98	92	.	2	1	.
Trichophorum cespitosum [A]	2	62	33	61	12	11	1
Hypnum cupressiforme agg. [A]	15	31	26	1	1	1	.
Cladonia portentosa [A]	.	24	21	1	1	1	.
Calluna vulgaris [A]	58	76	74	47	53	58	5
Sphagnetalia medii							
Andromeda polifolia [B]	.	6	46	81	64	88	58
Eriophorum vaginatum [B]	.	23	58	85	92	90	35
***Sphagnum recurvum* agg.** [B]	8	2	29	15	73	52	1
***Vaccinium oxycoccos* agg.** [B]	.	4	51	68	84	91	17

Polytrichum strictum [B]	.	1	7	18	53	47	72
Rubus chamaemorus [B]	.	1	3	18	15	85	99
***Empetrum nigrum* agg.** [B]	.	2	10	12	23	84	98
Betula nana [B]	.	1	1	14	9	55	75
Rhododendron tomentosum [B]	.	1	1	4	22	45	49
Vaccinium uliginosum [B]	.	2	3	16	44	53	68
Cladonia rangiferina [B]	2	1	2	5	5	40	85
Pleurozium schreberi	.	7	10	4	20	35	34
Sphagnum russowii [B]	6	1	1	3	14	8	13
Oxycocco-Sphagnetea							
Drosera rotundifolia	17	52	58	50	42	60	.
Aulacomnium palustre	17	5	22	6	29	16	2
Sphagnum capillifolium	26	12	27	10	19	19	2

Supplementary Materials

Appendix S1. Sources of vegetation plots classified as *Oxycocco-Sphagnetea* class.

Appendix S2. List of species aggregates used in this article.

Appendix S3. Discriminating species groups and sociological species groups used for formal classification of the *Oxycocco-Sphagnetea* class and its alliances in the expert system.

Appendix S4. Synoptic table (Table 1) with a complete list of species.

Appendix S5. Diagnostic, constant and dominant species of the *Oxycocco-Sphagnetea* class and its orders (*Sphagno-Ericetalia tetralicis* and *Sphagnetalia medii*).