Formalized classification of European fen vegetation at the alliance level

Tomáš Peterka, Michal Hájek, Martin Jiroušek, Borja Jiménez-Alfaro, Liene Aunina, Ariel Bergamini, Daniel Dítě, Ljuba Felbaba-Klushyna, Ulrich Graf, Petra Hájková, Eva Hettenbergerová, Tatiana G. Ivchenko, Florian Jansen, Natalia E. Koroleva, Elena D. Lapshina, Predrag M. Lazarević, Asbjørn Moen, Maxim G. Napreenko, Paweł Pawlikowski, Zuzana Plesková, Lucia Sekulová, Viktor A. Smagin, Teemu Tahvanainen, Annett Thiele, Claudia Biță-Nicolae, Idoia Biurrun, Henry Brisse, Renata Ćušterevska, Els De Bie, Jörg Ewald, Úna FitzPatrick, Xavier Font, Ute Jandt, Zygmunt Kącki, Anna Kuzemko, Flavia Landucci, Jesper E. Moeslund, Aaron Pérez-Haase, Valerijus Rašomavičius, John S. Rodwell, Joop H.J. Schaminée, Urban Šilc, Zvjezdana Stančić & Milan Chytrý

Peterka, T. (corresponding author, peterkatomasek@seznam.cz)[1],
Hájek, M. (hajek@sci.muni.cz)[1],
Jiroušek, M. (machozrut@mail.muni.cz)[1,2],
Jiménez-Alfaro, B. (borja@sci.muni.cz)[1],
Aunina, L. (lsalmina@latnet.lv)[3],
Bergamini, A. (ariel.bergamini@wsl.ch)[4],
Dítě, D. (daniel.dite@savba.sk)[5],
Felbaba-Klushyna, L. (kunik35@yandex.ru)[6],
Graf, U. (ulrich.graf@wsl.ch)[4],
Hájková, P. (buriana@sci.muni.cz)[1,7],
Hettenbergerová, E. (evka.hette@gmail.com)[1],
Ivchenko, T.G. (ivchenkotat@mail.ru)[8],
Jansen, F. (jansen@uni-greifswald.de)[9],
Koroleva, N.E. (flora012011@yandex.ru)[10],
Lapshina, E.D. (e_lapshina@ugrasu.ru)[11],
Lazarević, P.M. (predrag.m.lazarevic@gmail.com)[12],
Moen, A. (asbjorn.moen@ntnu.no)[13],
Napreenko, M.G. (maxnapr@gmail.com)[14],

Abstract

Aims: Phytosociological classification of fen vegetation (*Scheuchzerio palustris-Caricetea fuscae* class) differs among European countries. Here we propose a unified vegetation classification of European fens at the alliance level, provide unequivocal assignment rules for individual vegetation plots, identify diagnostic species of fen alliances, and map their distribution.

Location: Europe, western Siberia and SE Greenland.

Methods: 29 049 vegetation-plot records of fens were selected from databases using a list of specialist fen species. Formal definitions of alliances were created using the presence, absence and abundance of Cocktail-based species groups and indicator species. DCA visualized the similarities among the alliances in an ordination space. The ISOPAM classification algorithm was applied to regional subsets with homogeneous plot size to check whether the classification based on formal definitions matches the results of unsupervised classifications.

Results: The following alliances were defined: *Caricion viridulo-trinervis* (sub-halophytic Atlantic dune-slack fens), *Caricion davallianae* (temperate calcareous fens), *Caricion atrofusco-saxatilis* (arcto-alpine calcareous fens), *Stygio-Caricion limosae* (boreal topogenic brown-moss fens), *Sphagno warnstorfii-Tomentypnion nitentis* (*Sphagnum*-brown-moss rich fens), *Saxifrago-Tomentypnion* (continental to boreo-continental nitrogen-limited brown-moss rich fens), *Narthecion scardici* (alpine fens with Balkan endemics), *Caricion stantis* (arctic brown-moss rich fens), *Anagallido tenellae-Juncion bulbosi* (Ibero-Atlantic moderately rich fens), *Drepanocladion exannulati* (arcto-boreal-alpine non-calcareous fens), *Caricion fuscae* (temperate moderately rich fens), *Sphagno-Caricion canescentis* (poor fens) and *Scheuchzerion palustris* (dystrophic hollows). The main variation in the species composition of European fens reflected site chemistry (pH, mineral richness) and sorted the plots from calcareous and extremely rich fens, through rich and moderately rich fens, to poor fens and dystrophic hollows. ISOPAM classified regional subsets according to this gradient, supporting the ecological meaningfulness of this classification concept on both the regional and continental scale. Geographic/macroclimatic variation was reflected in the second most important gradient.

Conclusions: The pan-European classification of fen vegetation was proposed and supported by the data for the first time. Formal definitions developed here allow consistent and unequivocal assignment of individual vegetation plots to fen alliances at the continental scale.

Pawlikowski, P. (p.pawlikowski@uw.edu.pl)[15],
Plesková, Z. (pleskovicova@gmail.com)[1],
Sekulová, L. (sekulova.lucia@gmail.com)[1],
Smagin, V.A. (amgalan@list.ru)[8],
Tahvanainen, T.
(teemu.tahvanainen@uef.fi)[16],
Thiele, A. (annettthiele@gmail.com)[9],
Biţă-Nicolae, C. (bclaud_ro@yahoo.com)[17],
Biurrun, I. (idoia.biurrun@ehu.es)[18],
Brisse, H. (brisse.henry@orange.fr)[19],
Ćušterevska, R. (renatapmf@yahoo.com)[20],
De Bie, E. (els.debie@inbo.be)[21],
Ewald, J. (joerg.ewald@hswt.de)[22],
FitzPatrick, Ú.
(ufitzpatrick@biodiversityireland.ie)[23],
Font, X. (xfont@ub.edu)[24],
Jandt, U. (ute.jandt@botanik.uni-halle.de)[25,26],
Kącki, Z. (zygmunt.kacki@uni.wroc.pl)[27],
Kuzemko, A. (anya_meadow@mail.ru)[28],
Landucci, F. (flavia.landucci@gmail.com)[1],
Moeslund, J.E.
(jesper.moeslund@bios.au.dk)[29],
Pérez-Haase, A. (aaronperez@ub.edu)[24],
Rašomavičius, V.
(valerijus.rasomavicius@botanika.lt)[30],
Rodwell, J.S. (johnrodwell@tiscali.co.uk)[31],
Schaminée, J.H.J.
(Joop.Schaminee@wur.nl)[32],
Šilc, U. (urban@zrc-sazu.si)[33],
Stančić, Z. (zvjezdana.stancic@gfv.hr)[34],
Chytrý, M. (chytry@sci.muni.cz)[1]

[1]Department of Botany and Zoology, Masaryk
University, Kotlářská 2, 61137 Brno, Czech
Republic;
[2]Department of Plant Biology, Faculty of
Agronomy, Mendel University in Brno,
Zemĕdĕlská 1, 61300 Brno, Czech Republic;
[3]Laboratory of Geobotany, Institute of Biology,
University of Latvia, 3 Miera Street, 2169
Salaspils, Latvia;
[4]WSL Swiss Federal Institute for Forest, Snow
and Landscape Research, Zürcherstr. 111,
8903 Birmensdorf, Switzerland;
[5]Institute of Botany, Slovak Academy of
Sciences, Dúbravská cesta 9, 84523 Bratislava,
Slovakia;

[6]Uzhhorod National University, Tolstoy Str. 44,
88018 Uzhhorod, Ukraine;
[7]Department of Vegetation Ecology,
Institute of Botany, The Czech Academy of
Sciences, Lidická 25/27, 60200 Brno, Czech
Republic;
[8]Komarov Botanical Institute, Russian
Academy of Sciences, Prof. Popova 2, 197376
Sankt-Petersburg, Russia;
[9]Institute of Botany and Landscape Ecology,
University of Greifswald, Soldmannstr. 15,
17489 Greifswald, Germany;
[10]Polar-Alpine Botanical Garden-Institute, Kola
Science Center, Russian Academy of Sciences,
Kirovsk 6, Murmansk Province, 184256 Russia;
[11]Yugra State University, 628012 Khanty-
Mansiysk, Khanty-Mansiysk Autonomous
District, Russia;
[12]Institute for Nature Conservation of Serbia,
Dr. Ivana Ribara 91, 11070 Belgrade, Serbia;
[13]Museum of Natural History and Archaeology,
Norwegian University of Science and
Technology, 7491 Trondheim, Norway;
[14]Institute of Chemistry and Biology, Immanuel
Kant Baltic Federal University, Universitetskaya
2, 236040 Kaliningrad, Russia;
[15]Department of Plant Ecology and
Environmental Conservation, Biological and
Chemical Research Centre, Faculty of Biology,
University of Warsaw, Żwirki i Wigury 101,
02096 Warsaw, Poland;
[16]Department of Environmental and Biological
Sciences, University of Eastern Finland,
Yliopistokatu 7, 80101 Joensuu, Finland;
[17]Institute of Biology Bucharest, Romanian
Academy, 296 Spl. Independentei, 060031
Bucharest, Romania;
[18]Department of Plant Biology and Ecology,
University of the Basque Country UPV/EHU,
P.O. Box 644, 48080 Bilbao, Spain;
[19]36 rue Henri Dunant, 13700 Marignane,
France;
[20]Institute of Biology, Faculty of Natural
Sciences and Mathematics, University of Ss.
Cyril and Methodius, Arhimedova 3, 1000,
Skopje, Republic of Macedonia;

[21]Research Institute for Nature and Forest
(INBO), Kliniekstraat 25, 1070 Brussels,
Belgium;
[22]Faculty of Forestry, University of Applied
Sciences Weihenstephan-Triesdorf, Hans-Carl-
von-Carlowitz-Platz 3, D-85354 Freising,
Germany;
[23]National Biodiversity Data Centre,
Carriganore WIT West Campus, Carriganore,
County Waterford, Ireland;
[24]Facultat de Biologia, Universitat de
Barcelona, Av. Diagonal 643, 08028 Barcelona,
Spain;
[25]Geobotany and Botanical Garden, Institute
for Biology, Martin-Luther University Halle-
Wittenberg, Am Kirchtor 1, 06108 Halle,
Germany;
[26]German Centre for Integrative Biodiversity
Research (iDiv) Halle-Jena-Leipzig, Deutscher
Platz 5e, 04103 Leipzig, Germany;
[27]Department of Vegetation Ecology,
University of Wroclaw, Kanonia 6/8, 50-328
Wroclaw, Poland;
[28]National Dendrological Park 'Sofievka',
National Academy of Sciences of Ukraine, 12a
Kyivska St., 20300 Uman, Ukraine;
[29]Department of Bioscience, Aarhus
University, Grenåvej 14, 8410 Rønde, Denmark;
[30]Institute of Botany, Nature Research Centre,
Žaliųjų Ežerų 49, 08406 Vilnius, Lithuania;
[31]7 Derwent Road, Lancaster LA1 3ES, UK;
[32]Alterra Wageningen UR, P.O. Box 47, 6700
AA Wageningen, The Netherlands;
[33]Institute of Biology, ZRC SAZU, Novi trg 2,
1000 Ljubljana, Slovenia;
[34]Faculty of Geotechnical Engineering,
University of Zagreb, Hallerova aleja 7, 42000
Varaždin, Croatia

Introduction

Fens (minerotrophic mires) are natural or semi-natural
ecosystems with a unique species composition. They can
be defined as groundwater-fed wetlands poor in available
macronutrients whose herb layer is mostly dominated by
Cyperaceae species and whose bryophyte layer is usually
well developed and consists of *Sphagnum* species or so
called 'brown mosses' (i.e. non-sphagnaceous weft-
forming mosses; Udd et al. 2015) or both. From a syntaxo-
nomic point of view, Eurosiberian fens are traditionally
assigned to the class *Scheuchzerio palustris-Caricetea fuscae*
Tüxen 1937.

In many parts of Europe, fens are currently endangered
habitats with great importance for biodiversity protection.
A large number of fens were destroyed by fertilizer applica-
tion, drainage, abandonment of traditional uses and conse-
quent successional changes in the second half of the 20th

century (Topić & Stančić 2006; Mälson et al. 2008; Bergamini et al. 2009; Koch & Jurasinski 2014; Grootjans et al. 2015; Hájek et al. 2015). Therefore, selected types of fens have recently also been protected by the European Community (Habitats Directive, 92/43/EEC, from 1992) as Natural Habitat Types of Community Interest: depressions on peat substrates of the *Rhynchosporion* (code 7150), Fennoscandian mineral-rich springs and spring fens (7160), and several types of Calcareous fens (7210, 7230, 7240) and Boreal mires (7310). However, the effective protection of individual habitats and corresponding vegetation types at the continental scale is only possible on the basis of a harmonized classification system with clearly defined units that would enable unequivocal assignment of plant communities to higher syntaxa such as alliances and classes. Therefore, it is necessary to establish a consistent vegetation classification system useful for communication among scientists from different countries and for supporting conservation management (De Cáceres et al. 2015).

Classification of fen vegetation in various European countries is different due to diverse classification concepts. Despite some regional differences, two main approaches to fen vegetation classification are generally applied. The systems defining particular alliances on the basis of hydrological conditions and vegetation physiognomy were introduced by Vanden Berghen (in Lebrun et al. 1949), Vanden Berghen (1952), Oberdorfer (1957), Pop (1960) and Dierssen (1982), and more or less accepted in some other vegetation surveys (e.g. Steiner 1992; Martinčič 1995; Coldea et al. 1997; Gerdol & Tomaselli 1997; Lájer 1998; Oberdorfer 1998; Jermacāne & Laiviņš 2001; Lawesson 2004; Matuszkiewicz 2007; Graf et al. 2010). In these classification systems, topogenic waterlogged fens (usually called *Caricion lasiocarpae* and *Rhynchosporion albae*) are generally distinguished as opposed to spring fens and fen meadows (*Caricion davallianae* and *Caricion fuscae*). The dominance of different species of vascular plants (e.g. *Carex davalliana*, *C. lasiocarpa*, *C. limosa*, *C. nigra* and *Rhynchospora alba*) is usually used as the chief alliance-delimiting criterion. This concept results in broadly defined alliances spanning a range of habitats of different, or even contrasting, ecological features and entails the subsequent delimitation of numerous associations, subassociations and varieties.

The second classification approach distinguishes individual vegetation types along the main compositional and environmental gradient within fens that generally coincides with pH and calcium concentration (the poor–rich gradient; Du Rietz 1949; Sjörs 1952; Malmer 1986; Sjörs & Gunnarsson 2002; Tahvanainen 2004; Hájek et al. 2006). The vegetation classification based on the poor–rich gradient, as introduced by Fennoscandian botanists (Dahl 1956;

Ruuhijärvi 1960; Persson 1961; Heikkilä 1987), gives bryophytes and vascular plants equal importance. It was followed, with various modifications, by several national or regional vegetation surveys from outside Fennoscandia (e.g. Succow 1974; Rybníček et al. 1984; Sanda et al. 2001; Kuznetsov 2003; Dítě et al. 2007; Tzonev et al. 2009; Lapshina 2010; Hájek & Hájková 2011).

Furthermore, some transitional classification systems were introduced, reflecting ecologically delimited units but keeping some broadly defined alliances frequently characterized by selected vascular plant species (e.g. Kojić et al. 1998; Koska & Timmermann 2004; Felbaba-Klushyna 2010a,b; Rivas-Martínez 2011; Ermakov 2012). The discrepancies among classification systems for fen communities have resulted in different perception and delimitation of alliances in individual European countries, leading to confusion. The most problematic issues concern the *Rhynchosporion albae* and *Caricion lasiocarpae* alliances, which were originally delimited narrowly (Koch 1926; Lebrun et al. 1949), but thereafter interpreted in different ways (cf. Dierssen 1982; Rybníček et al. 1984).

The need for a consistent classification system in Europe has recently driven vegetation scientists to elaborate broad-scale syntheses integrating national classification systems (De Cáceres et al. 2015). One of the first steps is a synopsis of nomenclaturally valid high-rank syntaxa in Europe (EuroVegChecklist; Mucina et al. 2016). Simultaneously with the construction of EuroVegChecklist, which shares several authors with our study, we gathered available vegetation-plot records of fen vegetation in Europe, aiming to test the quality of delimitation of the major fen alliances reported from Europe in terms of their floristic composition and reproducibility using formal definitions (i.e. supervised classification; De Cáceres & Wiser 2012). Because some syntaxonomic aspects of our study have already been reflected in the final version of EuroVegChecklist, this study does not therefore concentrate on nomenclature, but deepens the classification scheme of EuroVegChecklist by (1) formally delimiting individual alliances using a large set of primary data, i.e. individual vegetation-plot records, (2) identifying diagnostic species and distribution patterns of individual alliances, and (3) testing the robustness of the presented supervised pan-European classification by comparing it with regional unsupervised classifications and unconstrained gradient analysis.

Methods

Data collection and filtering

The data sources were vegetation plots (phytosociological relevés) stored within national or regional vegetation databases, mostly registered in the Global Index of Vegetation-

Plot Databases (GIVD; Dengler et al. 2011) and available through the European Vegetation Archive (EVA; Chytrý et al. 2016), and also private data of European mire researchers (Appendix S1). For comparative purposes, the data set was enlarged with vegetation plots of E. Lapshina from western Siberia, the *locus classicus* of the *Saxifrago-Tomentypnion* alliance (Lapshina 2010), although there was a certain geographic gap between the European and Siberian data (Fig. 1). All the vegetation plots were combined into a single file using the TURBOVEG 3 software and thereafter imported to the JUICE 7.0 program (Tichý 2002), in which the subsequent analyses, apart from DCA, were performed.

As in our previous study of European fens (Jiménez-Alfaro et al. 2014), we had to deal with data collected using different sampling designs (see also Michalcová et al. 2011). Therefore, several steps had to be carried out to homogenize and balance the data set. First, only geo-referenced plots of a size of 1–100 m^2 were selected for analyses. Although Chytrý & Otýpková (2003) recommended 16 m^2 as a standard plot size for sampling fens, restriction to a narrower plot size range would have resulted in a large loss of important data from several regions. The possible effect of different plot sizes was assessed through applying unsupervised classification to subsets of plots of equal sizes (see the section Unsupervised classification). As suggested by Dengler et al. (2009), means and variation in plot sizes within individual clusters were presented.

The nomenclature was harmonized following Tutin et al. (1968–1993) for vascular plants and Frey et al. (2006) for bryophytes. Algae, fungi, lichens and hybrids

were omitted as well as taxa determined only to the genus level. Subspecies records were merged to the level of species. Taxa of problematic, unstable or ambiguous status (usually not equally differentiated in all the data sources) were merged to aggregates or species *sensu lato* (Appendix S2) to minimize the taxonomic bias (Jansen & Dengler 2010).

Since the original assignment of plots to the *Scheuchzerio palustris-Caricetea fuscae* class was inconsistent among data sets and was even absent in some data sets, we had to eliminate plots of vegetation types other than fens on the basis of habitat specialists (further referred to as 'typical fen species'; Appendix S3). First, plots containing at least four typical fen species were selected. However, plots of very species-poor communities, such as high-mountain fens dominated by *Drepanocladus exannulatus* or dystrophic hollows with *Sphagnum cuspidatum* or *S. lindbergii* did not match this simple criterion. Therefore, plots with at least one typical fen species reaching cover values over 25% or 50% (for details see Appendix S3) were added.

Since bryophytes are extremely important organisms in mires (Jones et al. 1994; Bergamini et al. 2001; Udd et al. 2015), all plots with no or insufficiently identified bryophytes (e.g. with non-identified species of sphagna) were excluded. Nevertheless, the data set still contained some plots of other vegetation types harbouring some fen species (mostly wet meadows of the *Calthion palustris* or *Molinion caeruleae* alliances). The following criteria were used to exclude these non-fen plots: (1) total cover of non-fen species exceeding 25% for plots in which covers of individual species were indicated, and (2) the presence of at least six non-fen species in plots with species presences/absences only. The list of non-fen species (Appendix S3) was partially adopted from Jiménez-Alfaro et al. (2014) and extended according to the authors' experience. Covers of individual species were merged following the protocol of the JUICE software, recently formally described by Fischer (2015). Moreover, plots with a cover of 25% or more of selected woody species (Appendix S3) were excluded to avoid forests and scrub with fen species in the herb layer.

As there was an overlap between some databases, duplicates were searched for and eliminated. Finally, it was necessary to stratify the data set geographically to reduce oversampling of some countries (Knollová et al. 2005), especially those of Western and Central Europe where thousands of digitized plots were available in contrast to other regions (see Schaminée et al. 2009; Peterka et al. 2015; Chytrý et al. 2016). Therefore, we geographically stratified the data from Western and Central Europe using a maximum of ten plots randomly selected from each grid cell of 1.25 min longitude × 0.75 min latitude (approximately 1.5 × 1.4 km).
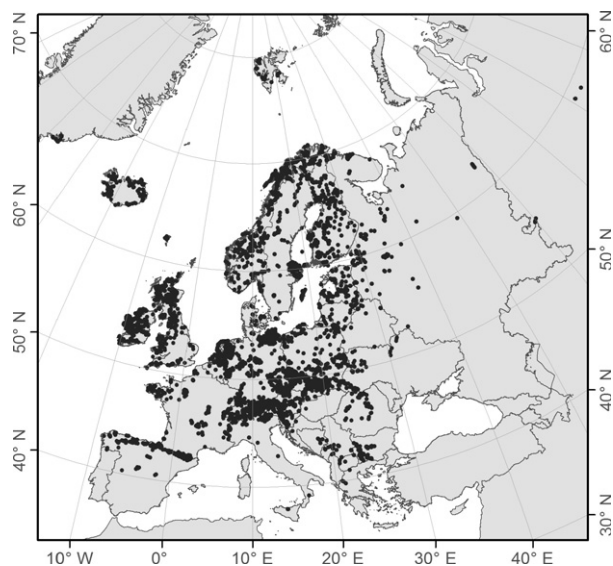

Fig. 1. Distribution of fen vegetation plots compiled in the initial data set.

Supervised classification

To identify the core set of plots representing particular alliances, we created formal definitions consisting of *a priori* defined species groups based on the geographically stratified data set. The sociological groups (Appendix S4), i.e. groups of species with a statistical tendency of co-occurrence in vegetation plots (Kočí et al. 2003), were developed using the Cocktail method (Bruelheide 1995, 2000) with the *phi* coefficient as a measure of interspecific association (Chytrý et al. 2002). The resulting sociological groups, supplemented by covers of selected species or total covers of some sociological groups ('functional groups with selection based on the total cover' in Landucci et al. 2015), were combined using the logical operators AND, OR and NOT (Bruelheide 1997). The formal definitions (Appendix S5) were applied to the entire data set except the plots containing presence–absence data only. A sociological group was considered as being present in a plot if at least half of its member species occurred within this plot. The groups of selected plots were considered cores of individual alliances after exclusion of a few transitional plots matching two definitions at the same time.

Using this method, we defined 13 alliances. In addition, we tried to define the *Caricion lasiocarpae* and *Rhynchosporion albae* alliances in their narrower 'ecological' concepts, i.e. to delimit groups of plots corresponding compositionally to the nomenclature type relevés of *Caricetum lasiocarpae* Koch 1926 and *Rhynchosporetum albae* Koch 1926 (see Dengler et al. 2004). Two oromediterranean alliances with a narrow geographic range (*Caricion intricatae* Quézel 1953, *Festucion frigidae* Rivas-Martínez et al. 2002), which are also listed in EuroVegChecklist, could not be distinguished due to the absence of plots with identified bryophytes.

To assess the distributional ranges of the alliances (including their non-core plots), the remaining plots, which were not ranked to any alliance or met the conditions of two formal definitions, were assigned to the most similar alliance based on the Frequency-Positive Fidelity Index (FPFI; Tichý 2005). This index expresses the similarity of species composition of individual vegetation plots to the predefined groups of plots assigned to given vegetation types, in our case to cores of particular alliances. This step also enabled the classification of plots with presences/absences. The minimum FPFI value for assignment was arbitrarily set to 0.15 for widespread fen vegetation types and 0.30 for more local types with a small number of core plots (*Anagallido tenellae-Juncion bulbosi*, *Caricion viridulo-trinervis*, *Caricion stantis*, *Narthecion scardici*, *Saxifrago-Tomentypnion*). Preliminary results suggested that such a two-level threshold made sense, since the value of the similarity index could be biased due to the higher constancy of

generalists in less numerous plot groups. Plots that reached lower index values remained unclassified.

The diagnostic species of particular plot groups (alliances) were calculated using the *phi* coefficient of association (Tichý & Chytrý 2006) for the equalized size of all groups. Species with a fidelity to a particular alliance of $\phi > 0.3$ were considered as diagnostic (Table 1). The significance of fidelity was tested using Fisher's exact test ($P < 0.001$). Diagnostic species were calculated twice, first for core plots only (Table 1, Appendix S6) and then for core plots plus plots assigned on the basis of FPFI (Appendix S7).

The data set of core plots of alliances was subjected to DCA with three pseudo-species cut levels for species cover (0%, 5% and 25%). Centroids were calculated for each alliance that was successfully reproduced by the formal definition. This analysis was performed in R software (v 2.9.0; www.r-project.org, package *vegan*). The original material of *Rhynchosporetum albae* Koch 1926 (valid nomenclature type of *Rhynchosporion albae* Koch 1926) consisting of two vegetation plots was also shown in the ordination space in order to demonstrate the original meaning of this alliance.

Unsupervised classification

To assess whether the classification based on formal definitions mirrors the main vegetation gradients, and to check for possible effects of different plot sizes on the classification results, we performed several unsupervised classifications using subsets of plots of different sizes from different regions. Ten plot subsets were chosen from six regions: (1) SE Greenland and arctic Europe (plots of 1 m^2); (2) southern and central Scandinavia (plots of 1 and 16 m^2); (3) NE Europe (plots of 1 and 100 m^2); (4) Eastern-Central Europe (plots of 1, 15–16 and 50–100 m^2); (5) the Alps (plots of 10–20 m^2); (6) southern and central Balkans (plots of 15–16 m^2). All these subsets were selected from the geographically non-stratified data set and then stratified in the same way as the main data set used for the supervised classification (i.e. taking a maximum of ten plots from each grid cell of 1.25 × 0.75 min). We applied the unsupervised non-hierarchical classification algorithm ISOPAM (Schmidtlein et al. 2010) at the level of six clusters with the Jaccard coefficient as the dissimilarity measure. ISOPAM is based on the classification of ordination scores from isometric feature mapping. Ordination and classification are repeated in a search for groups rich in diagnostic species and high overall fidelities of species to particular clusters. The number of clusters was arbitrarily set to six, which corresponds to the number of major ecological types of fens usually recognized in Europe (Hájek et al. 2006). In the case of southern and central Scandinavia, the first run

Table 1. Shortened synoptic table of fen alliances in Europe based on core plots (i.e. plots formally assigned to alliances).

Alliance	CvT	Cd	CaS	SCl	SwT	SaT	Ns	Cs	AJ	De	Cf	SCc	Sp
Group no.	1	2	3	4	5	6	7	8	9	10	11	12	13
Number of plots	138	2456	213	604	1059	101	37	17	97	449	1594	2001	542
Plot size range (m^2)	1–100	1–100	1–16	1–100	1–100	1–100	2–80	1–25	1–100	1–100	1–100	1–100	1–100
Mean plot size (m^2)	15	18.4	2.5	2.8	18.8	21.4	18.3	4.0	13.2	4.4	20.2	18.8	23.8
Caricion viridulo-trinervis													
Salix repens	**99**	4	.	1	5	4	.	.	1	.	5	1	.
Carex trinervis	**64**	.	.	.	.	.	.	.	.	.	1	.	.
Juncus anceps	**60**	.	.	.	.	.	.	.	.	.	.	.	.
Hydrocotyle vulgaris	**87**	2	.	1	2	.	.	.	24	.	17	3	1
Schoenus nigricans	**54**	3	.	1	1	.	.	.	13	.	1	.	.
Juncus articulatus	72	32	1	1	22	.	19	.	15	1	18	1	.
Campylium polygamum	28	1	.	1	1	1	.	.	.	.	1	.	1
Ranunculus flammula	59	2	.	2	4	.	.	.	40	.	24	1	1
Calliergonella cuspidata	74	48	.	3	27	11	.	.	13	1	34	1	2
Dactylorhiza incarnata	41	9	.	3	6	28	.	.	.	1	2	1	.
Liparis loeselii	26	3	.	2	2	14	.	.	.	.	1	1	.
Caricion davallianae													
Carex davalliana	.	**61**	8	1	18	.	.	.	.	.	2	1	.
Carex hostiana	.	34	1	1	4	.	.	.	2	.	2	.	.
Valeriana dioica s. l.	1	50	.	1	35	1	.	.	3	1	25	2	.
Schoenus ferrugineus	.	21	1	2	2	.	.	.	.	.	1	.	.
Carex panicea	29	78	7	21	53	.	3	.	45	1	44	6	1
Tofieldia calyculata	.	26	8	.	7	.	.	.	.	1	1	1	.
Succisa pratensis	.	41	.	1	21	.	.	.	20	1	17	2	.
Palustriella commutata s. l.	.	27	19	1	1	.	5	.	.	1	1	.	.
Caricion atrofusco-saxatilis													
Carex capillaris	.	2	**69**	1	3	.	.	.	.	.	.	.	.
Juncus triglumis	.	2	**71**	1	1	.	5	.	.	1	1	.	.
Salix reticulata	.	1	**63**	1	1	.	.	.	.	.	.	.	.
Polygonum viviparum	.	4	**85**	1	12	.	.	6	.	6	1	1	.
Carex atrofusca	.	1	**62**	1	1	.	.	.	.	.	.	.	.
Saxifraga aizoides	.	3	**62**	1	1	.	.	.	.	1	.	.	.
Equisetum variegatum	5	9	**70**	1	7	.	.	.	.	1	1	.	.
Thalictrum alpinum	.	1	**49**	2	8	.	.	.	.	1	1	.	.
Catoscopium nigritum	.	1	**40**	1	1	.	.	.	.	.	.	.	.
Tofieldia pusilla	.	1	**48**	1	11	.	.	.	.	.	1	.	.
Meesia uliginosa	.	1	**34**	1	1	.	.	.	.	1	.	.	.
Carex vaginata	.	1	**36**	1	8	.	.	.	.	1	1	1	.
Carex parallela	.	1	**27**	.	1	.	.	.	.	.	.	.	.
Carex microglochin	.	1	**27**	1	1	.	.	.	.	.	.	.	.
Saussurea alpina	.	1	**35**	1	11	.	.	.	.	.	.	.	.
Carex bicolor	.	1	**20**	.	.	.	.	.	.	.	.	.	.
Pinguicula alpina	.	3	**25**	1	1	.	.	.	.	1	1	.	.
Oncophorus virens	.	1	**23**	1	1	.	.	.	.	1	1	.	.
Selaginella selaginoides	.	9	46	3	18	.	19	.	1	1	3	1	.
Carex saxatilis	.	1	**23**	1	1	.	.	.	.	6	1	.	.
Drepanocladus revolvens agg.	4	52	72	33	41	.	5	65	.	18	3	1	.
Pinguicula vulgaris	.	34	**37**	3	17	.	.	.	1	1	3	1	1
Stygio-Caricion limosae													
Scorpidium scorpioides	4	4	2	**92**	8	.	.	6	5	11	1	1	1
Calliergon trifarium	.	1	8	36	3	.	.	.	.	1	1	.	1
Cinclidium stygium	.	1	12	32	11	.	.	6	.	8	1	1	.
Utricularia minor agg.	.	3	.	27	4	3	8	.	4	1	1	1	2
Sphagno warnstorfii-Tomentypnion nitentis													
Sphagnum warnstorfii	.	.	.	1	**85**	2	11	.	.	3	3	2	1
Tomentypnum nitens	.	19	19	1	66	41	.	29	.	1	4	1	.

Table 1. *(Continued).*

Alliance	CvT	Cd	CaS	SCl	SwT	SaT	Ns	Cs	AJ	De	Cf	SCc	Sp
Group no.	1	2	3	4	5	6	7	8	9	10	11	12	13
Number of plots	138	2456	213	604	1059	101	37	17	97	449	1594	2001	542
Plot size range (m²)	1–100	1–100	1–16	1–100	1–100	1–100	2–80	1–25	1–100	1–100	1–100	1–100	1–100
Mean plot size (m²)	15	18.4	2.5	2.8	18.8	21.4	18.3	4.0	13.2	4.4	20.2	18.8	23.8
Aulacomnium palustre	1	10	1	2	73	35	41	6	7	2	32	20	2
Sphagnum contortum	.	.	.	6	29	.	3	.	5	2	3	1	.
Paludella squarrosa	.	1	5	3	34	6	.	6	.	13	1	1	1
Sphagnum teres	.	.	.	2	36	2	8	.	.	7	17	5	1
Saxifrago-Tomentypnion													
Hamatocaulis vernicosus	.	4	1	6	10	**86**	.	.	.	.	4	1	1
Brachythecium mildeanum	1	2	1	.	2	**69**	.	.	.	.	1	1	.
Stellaria crassifolia	.	.	.	1	1	**62**	.	.	.	.	.	.	.
Drepanocladus aduncus agg.	14	1	.	1	1	**77**	.	.	.	.	2	1	1
Saxifraga hirculus	.	1	.	.	4	**69**	.	6	.	.	.	1	.
Carex diandra	.	3	.	12	10	**85**	.	.	.	1	11	3	1
Cicuta virosa	.	1	.	1	1	**55**	.	.	.	1	1	1	1
Triglochin maritima	1	2	.	.	1	**53**	.	.	.	.	.	.	.
Epilobium palustre	4	4	1	6	17	**82**	.	.	4	10	24	8	1
Eriophorum gracile	.	1	.	3	2	**38**	.	.	5	1	1	1	1
Lysimachia thyrsiflora	.	1	.	3	4	42	.	.	.	2	8	6	1
Carex appropinquata	.	2	.	1	7	32	.	.	.	.	2	1	1
Helodium blandowii	.	1	1	1	7	24	.	.	.	1	1	1	.
Bryum pseudotriquetrum agg.	4	43	37	16	35	69	32	.	6	7	13	1	1
Narthecion scardici													
Pinguicula balcanica	.	1	.	.	1	.	**100**	.	.	1	3	.	.
Plantago gentianoides	.	1	.	.	1	.	**68**	.	.	.	1	.	.
Pseudorchis frivaldii	.	1	.	.	1	.	**62**	.	.	1	1	1	.
Gentiana pyrenaica	.	1	.	.	.	.	**51**	.	.	.	1	.	.
Scapania irrigua	.	1	1	1	2	.	**49**	.	.	9	2	1	.
Primula deorum	.	.	.	.	.	.	**32**	.	.	.	1	.	.
Philonotis seriata	.	1	1	.	1	.	**41**	.	2	5	2	1	.
Sphagnum platyphyllum	.	.	.	1	1	.	30	.	.	2	2	.	1
Saxifraga stellaris	.	1	1	.	1	.	24	.	.	4	2	1	.
Juncus filiformis	.	1	.	.	1	.	27	.	.	7	12	7	1
Sphagnum subsecundum	.	.	.	4	10	.	35	.	10	3	28	2	1
Calliergon stramineum	.	1	1	6	31	4	57	24	2	25	28	42	2
Caricion stantis													
Dupontia fisheri	.	.	.	.	.	.	.	**94**	.	1	.	.	.
Calliergon turgescens	.	.	1	.	.	.	.	**35**	.	1	.	.	.
Ranunculus hyperboreus	.	.	.	.	1	.	.	29	.	3	.	.	.
Calliergon richardsoni	.	.	.	1	1	1	.	29	.	1	1	1	.
Eriophorum scheuchzeri	.	1	1	.	1	.	.	35	.	13	1	.	1
Aulacomnium turgidum	.	.	5	.	.	.	.	24	.	1	.	.	.
Sphagnum squarrosum	.	.	.	1	3	1	.	24	1	1	6	3	1
Anagallido tenellae-Juncion bulbosi													
Anagallis tenella	12	1	.	2	1	.	.	.	**90**	.	1	1	.
Juncus bulbosus	1	1	.	1	5	.	.	.	**89**	1	7	1	4
Hypericum elodes	.	.	.	1	.	.	.	.	**61**	.	1	.	1
Carum verticillatum	.	.	.	.	.	.	.	.	**60**	.	2	1	.
Sphagnum denticulatum agg.	.	.	.	1	2	.	.	.	**64**	1	14	1	3
Potamogeton polygonifolius	1	1	.	1	1	.	.	.	**41**	.	2	1	.
Narthecium ossifragum	.	1	.	1	1	.	.	.	**37**	.	1	1	1
Eleocharis multicaulis	1	1	.	1	1	.	.	.	**36**	.	1	1	1
Scutellaria minor	.	.	.	.	.	.	.	.	**32**	.	1	1	.
Wahlenbergia hederacea	.	.	.	.	.	.	.	.	24	.	1	1	.
Juncus acutiflorus	.	2	.	1	1	.	.	.	31	.	7	1	.
Erica tetralix	9	1	.	1	1	.	.	.	31	.	1	5	3

Table 1. *(Continued).*

Alliance	CvT	Cd	CaS	SCl	SwT	SaT	Ns	Cs	AJ	De	Cf	SCc	Sp
Group no.	1	2	3	4	5	6	7	8	9	10	11	12	13
Number of plots	138	2456	213	604	1059	101	37	17	97	449	1594	2001	542
Plot size range (m²)	1–100	1–100	1–16	1–100	1–100	1–100	2–80	1–25	1–100	1–100	1–100	1–100	1–100
Mean plot size (m²)	15	18.4	2.5	2.8	18.8	21.4	18.3	4.0	13.2	4.4	20.2	18.8	23.8
Drepanocladion exannulati													
Drepanocladus exannulatus	.	1	2	7	7	.	43	29	.	**89**	16	2	2
Calliergon sarmentosum	.	1	5	5	3	.	19	35	.	46	2	1	.
Caricion fuscae													
Viola palustris	.	4	.	2	30	.	.	.	19	2	60	18	1
Agrostis canina	12	7	.	1	27	2	46	.	13	1	61	23	4
Sphagno-Caricion canescentis													
Sphagnum recurvum agg.	.	.	.	1	28	.	.	.	2	1	22	**100**	1
Vaccinium oxycoccos agg.	.	2	.	24	40	35	.	.	.	2	8	67	38
Polytrichum commune	.	1	.	.	2	.	16	12	3	5	14	34	1
Scheuchzerion palustris													
Sphagnum cuspidatum	.	.	.	.	1	.	.	.	8	1	4	4	**64**
Scheuchzeria palustris	.	1	.	5	1	1	.	.	.	2	1	14	**67**
Sphagnum majus	.	.	.	.	1	.	.	.	.	3	1	1	**41**
Drepanocladus fluitans	4	1	.	1	1	.	.	18	2	1	3	5	42
Rhynchospora alba	.	1	.	9	6	.	.	.	11	1	4	10	31
Diagnotis species for two or more alliances													
Epipactis palustris	63	34	.	2	17	48	.	.	.	1	2	1	.
Eriophorum latifolium	.	59	2	4	34	6	51	.	1	1	3	1	.
Primula farinosa s. l.	.	42	14	1	8	.	**68**	.	.	1	1	1	.
Carex limosa	.	2	.	90	13	69	.	.	9	15	6	24	52
Carex chordorrhiza	.	1	.	57	14	**76**	.	.	.	13	2	7	1
Carex lasiocarpa	.	5	.	58	25	50	.	.	3	6	13	13	7
Menyanthes trifoliata	1	18	1	77	38	83	.	.	25	6	26	27	9
Carex dioica	.	11	22	7	47	50	.	.	.	1	3	1	1
Carex nigra	38	39	15	12	47	2	95	.	9	23	65	29	2
Carex echinata	.	12	.	1	31	1	70	.	66	5	67	15	1
Other species reaching a frequency higher than 25% in at least one cluster													
Eriophorum angustifolium	12	34	29	41	51	46	11	6	33	64	60	46	22
Carex rostrata	.	18	1	45	50	51	.	.	3	32	35	52	22
Campylium stellatum s. l.	27	68	69	31	57	14	16	24	14	2	5	1	.
Carex flava agg.	64	59	5	20	45	1	22	.	48	1	20	2	1
Parnassia palustris	55	59	27	4	39	29	22	.	12	2	13	1	.
Drosera rotundifolia	1	4	.	13	42	12	.	.	39	1	19	39	31
Potentilla palustris	12	2	.	21	25	36	.	.	8	23	37	23	5
Equisetum fluviatile	.	13	.	42	35	19	.	.	2	6	26	13	2
Andromeda polifolia	.	1	8	26	25	8	.	.	.	7	3	20	32
Carex curta	.	1	.	1	5	.	3	.	2	26	25	21	4
Eriophorum vaginatum	.	1	6	1	7	5	14	.	.	6	5	29	27
Fissidens adianthoides	12	28	6	1	15	.	.	.	3	1	3	1	.
Aneura pinguis	4	13	27	24	23	4	8	.	7	2	5	1	1
Eleocharis quinqueflora	33	22	16	6	7	.	3	.	3	1	1	1	.
Peucedanum palustre	.	4	.	9	7	30	.	.	.	1	14	11	1
Utricularia intermedia agg.	.	1	.	29	3	24	.	.	9	1	2	1	1

The percentage occurrence frequency values are shown. Species are sorted by decreasing fidelity within alliances. The background shading indicates diagnostic species of alliances in cases when $\phi > 0.3$, bold numbers indicate diagnostic species when $\phi > 0.5$. Species with a clear optimum outside fen vegetation and species reaching a frequency lower than 20% within any cluster are shown only in the full version of the table (Appendix S6).

of ISOPAM classification led to clusters that did not correspond to the clusters resulting from other regional classifications. Because the ISOPAM algorithm is non-hierarchical and because we expected a higher number of

alliances in Scandinavia as compared to other regions, this result may have been caused by an insufficient number of clusters. We therefore ran ISOPAM again, with seven resulting clusters. Diagnostic species of each cluster were

calculated in the same way as for the pan-European data set. The species with fidelity to a particular cluster of $\phi > 0.3$ were considered diagnostic (Appendix S8) and the significance of fidelity was tested using Fisher's exact test ($P < 0.01$).

Results

Vegetation units (supervised classification)

A total number of 29 049 vegetation plots were identified as representing fen vegetation (Fig. 1), of which 24 091 plots remained in the data set after geographic stratification that removed some plots from oversampled regions. In total, 9308 plots (38.6% of the geographically stratified data set) were assigned unequivocally to alliances (i.e. they met the assumption of exactly one formal definition). They are referred to as 'core plots'. Only 71 plots matched two definitions and were therefore moved to the unclassified subset. In the next step, 7629 plots (31.7%) were associated with groups of the core plots of particular alliances on the basis of the similarity expressed by the FPFI values; we refer to these as 'non-core plots'. The remaining 7154 plots (29.7%) were unclassified (see Appendix S9 for their characterization). Fen alliances were formally defined (Appendix S5) and their diagnostic species were identified (Table 1, Appendix S6). The effort to delimit *Caricion lasiocarpae* and *Rhynchosporion albae* was not successful due to the overlap with other alliances (Appendix S10). As a result, 13 alliances were defined formally. According to the ecological classification of fens (Hájek et al. 2006), they can be interpreted as follows: *calcareous fens* and *extremely rich fens* (groups 1–3), *rich fens* (groups 4–6), *moderately rich fens* (groups 9–11), *poor fens* (group 12) and *dystrophic* (*bog*) *hollows* (group 13). Groups 7 and 8 represent geographically restricted types of rich fens transitional to moderately rich fens. A generalized classification scheme with distinguishing features of the fen alliances is given in Appendix S11 and the geographic distribution of these alliances is presented in Fig. 2.

Caricion viridulo-trinervis Julve ex Hájek et Mucina in Theurillat et al. 2015 (group 1) includes the vegetation of the dune-slacks of the Atlantic coast of W Europe. Typical taxa are *Carex trinervis*, *Juncus anceps* and *Salix repens*. The alliance is further characterized by a peculiar combination of alkaline fen specialists (*Dactylorhiza incarnata*, *Eleocharis quinqueflora*, *Epipactis palustris*), sub-halophytic and halophytic species (*Centaurium littorale* s. l., *Glaux maritima*, *Samolus valerandi*) and species of disturbed wetlands or generalist taxa (*Agrostis stolonifera* agg., *Calamagrostis epigejos*, *Mentha aquatica*). Most plots occur in the Netherlands, with further occurrences in France, Ireland and Denmark.

Caricion davallianae Klika 1934 (group 2) comprises mineral-rich fen vegetation on both calcareous tufa-forming springs and peat substrates developed on limestone, calcareous sedimentary or metamorphic rocks and ultrabasic crystalline rocks. The herb layer consists mainly of calcicole graminoids (e.g. *Carex davalliana*, *C. hostiana*, *Eleocharis quinqueflora*, *Eriophorum latifolium*, *Schoenus ferrugineus*) and herbs such as *Parnassia palustris*, *Pinguicula vulgaris*, *Primula farinosa* subsp. *farinosa* and *Tofieldia calyculata*. The bryophyte layer is composed of brown mosses such as *Campylium stellatum* s. l., *Drepanocladus revolvens* agg. (*D. cossonii* in this case), *Palustriella commutata* s. l. and *Philonotis calcarea*. Plots are scattered throughout almost the whole of Europe, though concentrated in the Alps and the Carpathians. In Iceland and northern Scandinavia, the alliance is represented by stands dominated by *Eleocharis quinqueflora* only.

Caricion atrofusco-saxatilis Nordhagen 1943 (group 3) includes low-productive communities of calcareous mineral substrates, with initial successional stages occurring even on gravel, in arctic or alpine climates. The alliance shares some typical species with the previous alliances of extremely rich fens, but is differentiated by the presence of the arcto-alpine species (e.g. *Carex atrofusca*, *C. microglochin*, *Juncus triglumis*, *Kobresia simpliciuscula*, *Salix reticulata*, *Saxifraga aizoides*, *Thalictrum alpinum*) that also frequently occur in contact habitats such as snow-beds or alpine grasslands. It occurs in the Alps (mostly above 2000 m a.s.l.), the Scandinavian mountains, Iceland and Greenland.

Stygio-Caricion limosae Nordhagen 1943 (group 4) represents fens with sedges and brown mosses occurring mostly in topogenic, strongly waterlogged wetlands with peat accumulation. The vegetation is composed of boreal sedges (*Carex chordorrhiza*, *C. lasiocarpa*, *C. limosa* and occasionally *C. livida*) and weft-forming bryophytes (*Calliergon trifarium*, *Scorpidium scorpioides*) with sporadic occurrence of *Sphagnum* species such as *S. contortum* and *S. platyphyllum*. The alliance is widespread in N Europe, extending southwards to Britain, Ireland, the Baltic states, the Alps and, rarely, the Carpathians and the Balkans.

Sphagno warnstorfii-Tomentypnion nitentis Dahl 1956 (group 5) is characterized by calcium-tolerant sphagna, i.e. *Sphagnum contortum*, *S. subnitens*, *S. teres*, *S. warnstorfii* and *S. subfulvum* (the last in N Europe only), which are accompanied by other mosses depending on microtopography (e.g. *Aulacomnium palustre*, *Paludella squarrosa* and *Tomentypnum nitens*). Typical bryophytes of extremely rich fens (*Campylium stellatum* s. l., *Drepanocladus revolvens* agg.) or calcicole vascular plants (*Carex davalliana*, *Eleocharis quinqueflora*, *Eriophorum latifolium*, *Parnassia palustris*) still occur frequently. Some Central European vegetation types dominated by *Carex davalliana* in the herb layer and sphagna in the bryophyte layer, formerly often classified to *Caricion davallianae*, have also been included in this alliance. *Aulacomnium palustre*, *Sphagnum*
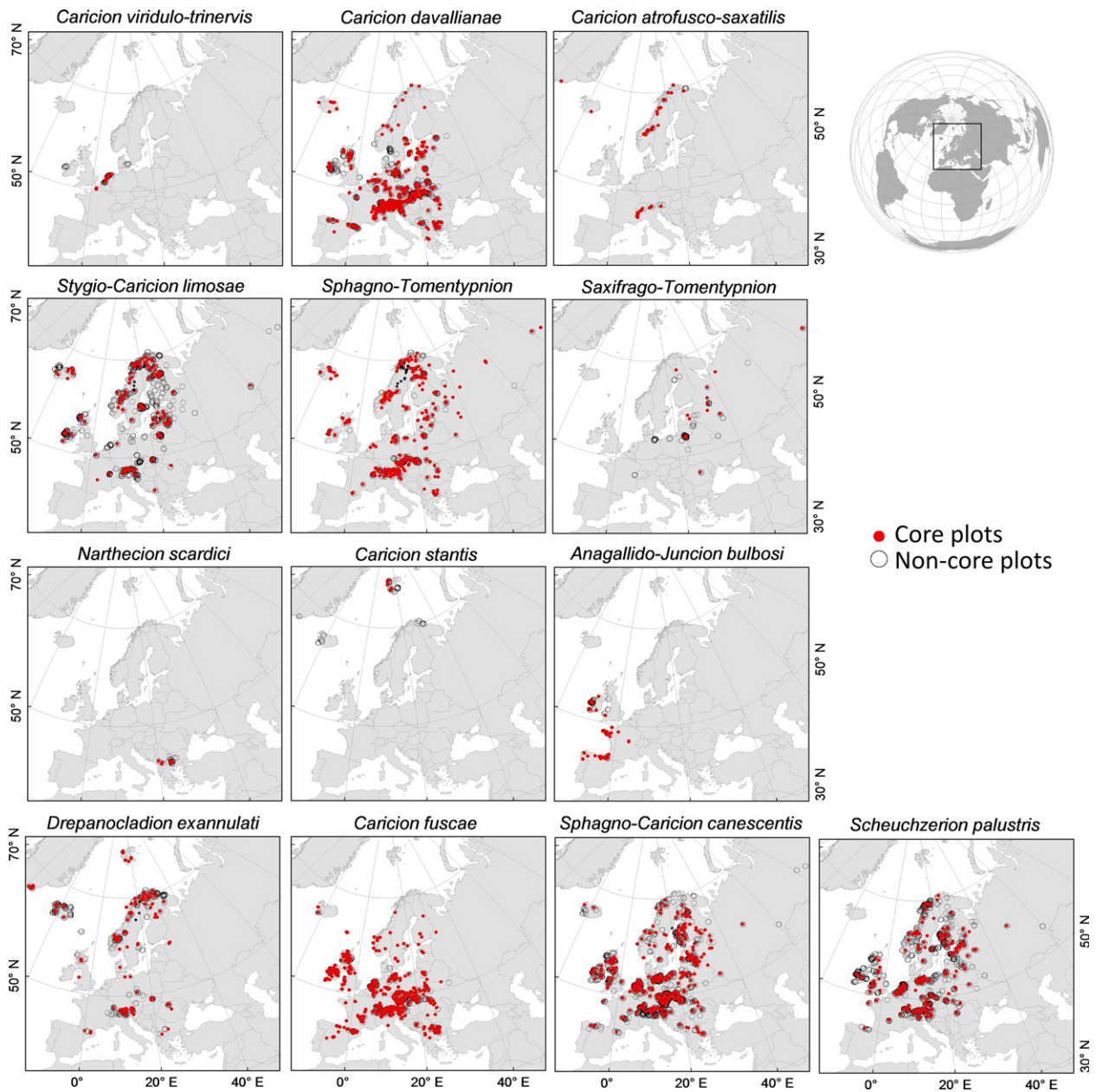
Fig. 2. Distribution of core and non-core plots of individual alliances within the non-stratified data set.

teres, *S. warnstorfii* and *Tomentypnum nitens* form small hummocks on which shallow-rooting acidophytes (*Drosera rotundifolia*) or species preferring drier (i.e. oxic) conditions can grow. Due to the superficial structure and water chemistry representing the niche margins of both calcicole and calcifuge plants, this vegetation type belongs to the most species-rich fen communities. The alliance is distributed across Europe, being concentrated in mountain or highland areas.

Saxifrago-Tomentypnion Lapshina 2010 (group 6) includes calcium-rich (but not tufa-forming) fens sharing some typical species with the previous rich-fen alliances. It further contains nutrient-demanding bryophytes of aquatic and semi-aquatic habitats, either generalists (*Brachythecium mildeanum*, *Drepanocladus aduncus* agg., *Marchantia polymorpha*) or fen specialists with higher phosphorus demands (*Hamatocaulis vernicosus*; compare Hájek et al. 2014). The co-existence of nutrient-demanding wetland generalists and reed-bed species (*Cicuta virosa*, *Ranunculus lingua*, *Thelypteris palustris*), phosphorus-demanding grassland species (*Poa pratensis* agg., *Rumex acetosa* s. l.) and species of low-productive boreo-continental habitats

(*Saxifraga hirculus, Stellaria crassifolia*, subhalophytic *Triglochin maritima*) is characteristic of the herb layer. The group of nutrient-demanding grassland and reed-bed species delimits this alliance against other fen types. *Sphagnum* species are usually absent. In addition to W Siberia, where it was first described (Lapshina 2010), the alliance has a scattered distribution across the NE European lowlands with an isolated occurrence in the Romanian Carpathians. Non-core plots are also distributed in NE Germany and the Jura Mountains. In contrast to the previous alliance, *Saxifrago-Tomentypnion* more frequently occupies topogenic habitats or waterlogged springs.

Narthecion scardici Horvat ex Lakušić 1968 (group 7) is a low-productive, rich to moderately rich fen community sharply differentiated from other fen alliances by the presence of Balkan endemics such as *Narthecium scardicum, Pinguicula balcanica, Primula deorum, P. farinosa* subsp. *exigua* and *Pseudorchis frivaldii*. Spring species of the *Montio-Cardaminetea* class (*Epilobium nutans, Saxifraga stellaris, Soldanella pindicola* agg.) and mountain grassland species (*Ligusticum mutellina, Nardus stricta*) are also typical for this alliance. The bryophyte layer is mostly formed by *Drepanocladus exannulatus, Philonotis seriata* and *Sphagnum subsecundum*. The alliance is restricted to the high mountains of the southern Balkan Peninsula (Bulgaria, Kosovo, Macedonia, Montenegro and probably also Albania and Greece) and is developed near streams and springs, usually above the timberline.

Caricion stantis Matveyeva 1994 (group 8) comprises brown-moss-sedge vegetation of high-arctic areas. The herb layer is typically formed of *Carex aquatilis* subsp. *stans* or *Dupontia fisheri*, accompanied by other species with Holarctic distribution in the arctic or sub-arctic zones (*Eriophorum scheuchzeri, Juncus biglumis, Ranunculus hyperboreus, Salix polaris, Saxifraga foliolosa*). The bryophyte layer contains, for example, *Aulacomnium turgidum, Calliergon giganteum, C. sarmentosum, C. turgescens* and *Campylium stellatum* s. l. All core plots come from Svalbard, none-core plots were recorded in Greenland, Iceland and the arctic coast of northern Norway. The community occupies the wettest habitats within the arctic tundra, e.g. stream valleys inundated by flowing water after snowmelt or permanently waterlogged depressions (Matveyeva 1994).

Anagallido tenellae-Juncion bulbosi Br.-Bl. 1967 (group 9) represents Ibero-Atlantic moderately rich fens characterized by diagnostic species with Atlantic or sub-Atlantic distribution ranges (*Anagallis tenella, Eleocharis multicaulis, Juncus acutiflorus, J. bulbosus, Hydrocotyle vulgaris, Hypericum elodes, Narthecium ossifragum, Potamogeton polygonifolius, Scutellaria minor*) which make its differentiation from other fen types rather pronounced. The moss layer is most frequently formed of *Sphagnum denticulatum* agg. or other bryophytes such as *Calliergonella cuspidata* and *Campylium*

stellatum s. l. The alliance had been previously reported only from the Iberian Peninsula, but we also detected occurrences in France, Britain and Ireland.

Drepanocladion exannulati Krajina 1933 (group 10) comprises species-poor low-productive communities dominated by the pleurocarpous mosses *Drepanocladus exannulatus* and *Calliergon sarmentosum*. The sparse herb layer consists of cotton grasses (*Eriophorum angustifolium, E. scheuchzeri*) accompanied by sedges (*Carex curta, C. lachenalii, C. rariflora*). In contrast to the following alliance, *Drepanocladion exannulati* usually lacks grasses (*Agrostis canina, Anthoxanthum odoratum* agg., *Festuca rubra* agg.) and moderately nutrient-demanding dicots of mire meadows (e.g. *Cirsium palustre, Lysimachia vulgaris, Ranunculus flammula*). The vegetation develops on waterlogged non-calcareous sites in boreal-arctic regions and in high mountains in Central and S Europe.

Caricion fuscae Koch 1926 (group 11) includes slightly acidic sedge-moss fens with intermediate to low calcium supply. The alliance comprises mesotrophic fens of waterlogged sites characterized by *Carex diandra, Menyanthes trifoliata* and *Potentilla palustris*, young mire meadows as well as initial stages of mire succession on shallow peat layers. Calcicole species are mostly absent. The bryophyte layer frequently contains nutrient-demanding peat-mosses (*Sphagnum denticulatum* agg., *S. subsecundum, S. teres*) and other bryophytes such as *Aulacomnium palustre, Bryum pseudotriquetrum* agg., *Drepanocladus exannulatus* and *Philonotis fontana* agg. In contrast to the following alliance, *Sphagnum* species of the *Cuspidata* section do not prevail. The alliance is not sharply differentiated in terms of species composition because of a high proportion of pH generalists. It occurs throughout Europe, but only a few plots were recorded in the boreal and arctic zones.

Sphagno-Caricion canescentis Passarge (1964) 1978 (group 12) represents vegetation of acidic minerotrophic mires that are poor with respect to both species richness and mineral supply. Frequent dominants of the bryophyte layer are *Sphagnum recurvum* agg., *S.* sect. *Sphagnum* (*S. palustre* s. l., *S. papillosum*) and *Polytrichum commune*. There are frequent transitions to initial stages of ombrotrophic mires (bogs) characterized by the presence of *Carex pauciflora, Eriophorum vaginatum* or *Sphagnum magellanicum*. Nevertheless, a minerotrophic water regime is still indicated by species that do not enter pristine bogs, e.g. *Agrostis canina, Carex echinata, C. nigra, Menyanthes trifoliata, Potentilla palustris* or *Viola palustris*. The community is distributed throughout Europe, especially in the temperate and boreal zones.

Scheuchzerion palustris Nordhagen ex Tx. 1937 (group 13) involves vegetation of dystrophic, extremely acidic and species-poor hollows. The bryophyte layer is usually formed of *Drepanocladus fluitans, Sphagnum cuspidatum*,

S. majus or *S. lindbergii* (the latter only in the boreal and arctic zones). The herb layer consists of few species such as *Carex limosa*, *Rhynchospora alba* and *Scheuchzeria palustris*. The alliance is traditionally included to the *Scheuchzerio palustris-Caricetea fuscae* class, although bog elements (*Carex pauciflora*, *Eriophorum vaginatum*) occur frequently. In Central Europe, this vegetation is restricted to small patches in bog hollows, having a limited extent, whereas in N Europe it can cover larger areas, especially in flat landscapes.

Ordination

The first axis of DCA based on the data set of core plots of particular alliances (Fig. 3) runs from calcareous and sub-halophytic fens (*Caricion atrofusco-saxatilis*, *Caricion davallianae*, *Caricion viridulo-trinervis*), through rich and moderately rich fens (*Anagallido tenellae-Juncion bulbosi*, *Caricion fuscae*, *Caricion stantis*, *Drepanocladion exannulati*, *Narthecion scardici*, *Sphagno warnstorfii-Tomentypnion nitentis*, *Saxifrago-Tomentypnion*), to poor fens (*Sphagno-Caricion canescentis*) and dystrophic hollows (*Scheuchzerion palustris*). The second axis reflects the geographic–macroclimatic gradient from the Atlantic alliances (*Anagallido tenellae-Juncion bulbosi*, *Caricion viridulo-trinervis*) through the widespread alliances, to arcto-alpine and arcto-boreo-alpine alliances (*Caricion atrofusco-saxatilis*, *Caricion stantis*, *Drepanocladion exannulati*). *Narthecion scardici* and *Stygio-Caricion limosae*

were shifted to the arcto-alpine end of the second gradient. The gradient of the third axis cannot be easily defined ecologically, but it delimits *Caricion stantis* from both *Stygio-Caricion limosae* and *Caricion atrofusco-saxatilis* and *Narthecion scardici* from *Sphagno warnstorfii-Tomentypnion nitentis*. The plots from the original diagnosis of *Rhynchosporetum albae* Koch 1926 were close to the core of *Caricion fuscae*.

Unsupervised classification

The ISOPAM classification into six or seven clusters could be interpreted analogously to the supervised classification presented above (Appendix S8), reflecting the main ecological types (i.e. calcareous and extremely rich fens, rich fens, moderately rich fens, poor fens and dystrophic hollows). Although there were some differences in diagnostic species and in the representation of plant communities among particular areas, the main vegetation pattern and units were generally consistent across regions and plot sizes. The high consistency in main diagnostic species among the study areas was observed for clusters related to *Sphagno warnstorfii-Tomentypnion nitentis* (*Sphagnum warnstorfii*, *Tomentypnum nitens*), *Sphagno-Caricion canescentis* (*Sphagnum recurvum* agg.), *Scheuchzerion palustris* (*Drepanocladus fluitans*, *Scheuchzeria palustris*, *Sphagnum cuspidatum*, *S. majus*) and *Stygio-Caricion limosae* (*Calliergon trifarium*, *Carex limosa*, *Scorpidium scorpioides*, *Utricularia*
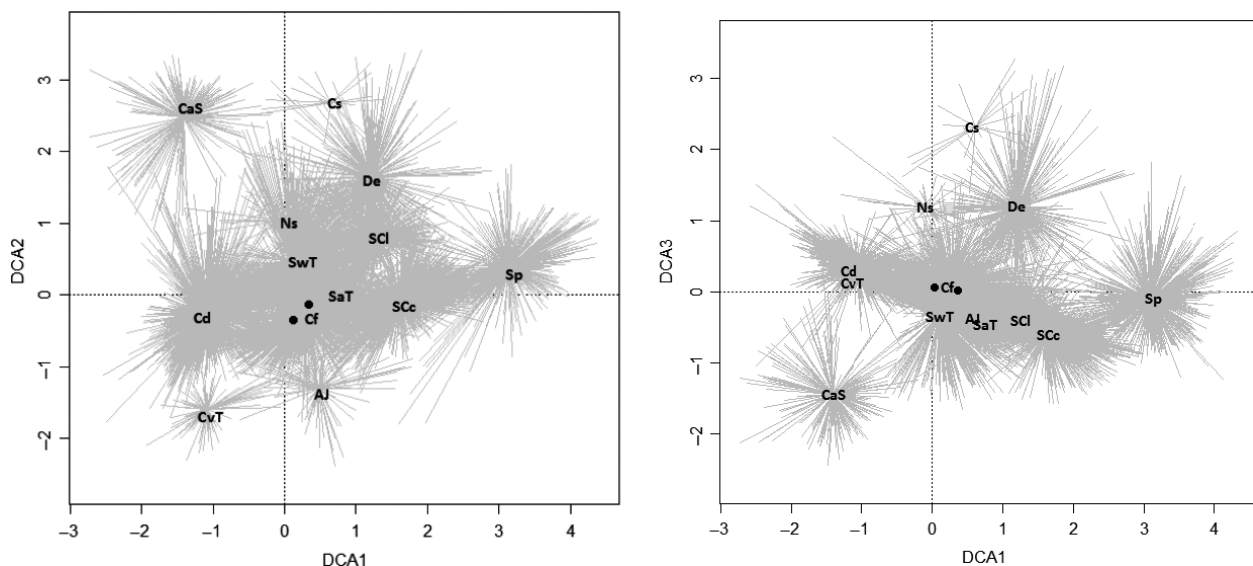
Fig. 3. DCA of core plots (i.e. plots formally assigned to alliances) with centroids of particular clusters (alliances) along the first three ordination axes. Eigenvalues: 1st axis (DCA1) 0.595, 2nd axis (DCA2) 0.430, 3rd axis (DCA 3) 0.378. CvT = *Caricion viridulo-trinervis*, Cd = *Caricion davallianae*, CaS = *Caricion atrofusco-saxatilis*, SCl = *Stygio-Caricion limosae*, SwT = *Sphagno warnstorfii-Tomentypnion nitentis*, SaT = *Saxifrago-Tomentypnion*, Ns = *Narthecion scardici*, Cs = *Caricion stantis*, AJ = *Anagallido tenellae-Juncion bulbosi*, De = *Drepanocladion exannulati*, Cf = *Caricion fuscae*, SCc = *Sphagno-Caricion canescentis*, Sp = *Scheuchzerion palustris*. Black points refer to plots from the original diagnosis of the association *Rhynchosporetum albae* Koch 1926 (valid nomenclature type of *Rhynchosporion albae* Koch 1926).

intermedia agg., *U. minor* agg.), the latter in boreal and arctic regions. On the Balkan Peninsula, the *Sphagno warnstorfii-Tomentypnion nitentis* alliance was mostly characterized by meadow species, though the typical peat moss of this community (*Sphagnum contortum*) also displayed high fidelity to the corresponding cluster. In the NE European subset, *Sphagno warnstorfii-Tomentypnion nitentis* was separated from *Saxifrago-Tomentypnion*, though only in the data set of plots of 1 m^2. For the 100-m^2 plot data set, two rich-fen clusters each containing plots of both alliances emerged.

Likewise, *Caricion davallianae* was repeatedly identified as a separate type and characterized, for example, by *Carex davalliana*, *Drepanocladus revolvens* agg., *Eleocharis quinqueflora*, *Palustriella commutata* s. l. and the absence of sphagna, though more clusters were established in the Alps, the Balkans and Central Europe (for the plot size of 16 m^2). In both Scandinavian subsets, *Caricion davallianae* was well delimited against *Caricion atrofusco-saxatilis*. Higher variability in sets of diagnostic species was apparent for moderately rich fens of the *Caricion fuscae* alliance, which are characterized by either species of mire meadows (*Epilobium palustre*, *Galium uliginosum*, *Ranunculus flammula*) or specialists of waterlogged mires (*Carex diandra*, *Drosera intermedia*, *Rhynchospora fusca*) in Central and NE Europe subsets. In the Balkan subset, the *Caricion fuscae*-related cluster is characterized by *Sphagnum subsecundum* and *Carex nigra*. Separate clusters corresponding to the *Drepanocladion exannulati* alliance appeared in the Scandinavian and high-arctic subsets, while in the Alps *Caricion fuscae* and *Drepanocladion exannulati* formed a joint cluster. As a geographically constrained vegetation type, a cluster corresponding to *Narthecion scardici* appeared in the Balkan subset.

Discussion

Methodological aspects and constraints of a broad-scale fen classification

The most prominent purpose of vegetation classification is defining distinct objects for habitat conservation, monitoring and ecological research. From this perspective, distinguished units are useful only if they reflect different habitat conditions, vegetation history or geographic distribution (Willner 2006). This fact advocates, in our opinion, application of supervised methods and prevents the application of fully automated procedures and the classification of all available plots over large geographic extents. This study is the first attempt to synthesize phytosociological data and to create a unified classification of the *Scheuchzerio palustris-Caricetea fuscae* class at the continental scale based on individual vegetation plots. It could therefore serve as a state-of-the-art baseline for further development of the pan-European fen typology on various hierarchical levels.

The large set of vegetation plots used in this study comprised primary data from different sources, regions and time periods, which maximized its representativeness. The pre-selection of fen data allowed us to create relatively straightforward Cocktail groups that adequately reflected internal variation within the class *Scheuchzerio palustris-Caricetea fuscae* and enabled the development of definitions of biogeographically or ecologically unique alliances within fens. Finally, 38.6% of plots met the criteria of the formal definitions, 33.7% were assigned using a similarity index, and 27.7% remained unclassified. These figures correspond to analogous studies across different vegetation types (Kočí et al. 2003; Roleček 2007; Rodríguez-Rojo et al. 2014; Douda et al. 2016). It is important to note that several alliances were defined by simple and therefore easily comprehensible and robust definitions. This holds true for both widespread alliances (*Sphagno-Caricion canescentis*, *Sphagno warnstorfii-Tomentypnion nitentis*) and regional alliances (*Anagallido tenellae-Juncion bulbosi*, *Narthecion scardici*). Construction of more complicated definitions could result in more classified plots, but such definitions might be too complex and hard to comprehend (Roleček 2007). In some cases, more complex definitions were however necessary, most apparently in the case of *Caricion fuscae*, which is a traditionally recognized, widely distributed alliance unequivocally understood as vegetation of moderately rich fens. In these terms, it corresponds to the 'central syntaxon' which has no diagnostic species (Willner 2006) or perhaps very few diagnostic species with a weak diagnostic value. *Caricion fuscae* is characterized by the occurrence of moderately rich-fen species with a broad ecological niche and the scarcity of species indicating extreme pH values. In contrast to *Anagallido tenellae-Juncion bulbosi* and *Narthecion scardici*, it also lacks geographically restricted species. This fact results in indistinct differentiation from other alliances (Table 1) and variable diagnostic species in the *Caricion fuscae*-related clusters in unsupervised regional classifications (Appendix S8).

An important issue related to broad-scale vegetation analyses is variation in plot size (Chytrý & Otýpková 2003; Dengler et al. 2009). As demonstrated in a previous study on European fens (Jiménez-Alfaro et al. 2014), a restriction to a narrow range of plot sizes would lead to a loss of a vast majority of data from important regions. Following a suggestion from Dengler et al. (2009), we made *a posteriori* assessment of the potential influence of different plot sizes via presentation of their means and ranges for particular clusters. The ranges of plot sizes among all alliances (Table 1) were almost equal, with the exception of *Caricion atrofusco-saxatilis* and *Caricion stantis*, which, however, occupy naturally small areas. *Drepanocladion exannulati* and *Stygio-Caricion limosae* were also sampled using smaller sizes in their centre of distribution in Scandinavia than in other

regions due to the regional sampling tradition. Generally, our formal definitions were able to classify plots across different sizes. Unsupervised classification (Appendix S8) reproduced identical vegetation types, largely corresponding to alliances, even when different plot sizes were used. These findings indicate that the quality of individual vegetation-plot records (i.e. precision in plant identification or degree of plot homogeneity) might have a greater potential to confound classification than plot size, at least for wetland vegetation.

Vegetation units and classification criteria

There has been a long-standing debate about the 'ideal' fen classification without reaching any general consensus (Rybníček 1981, 1985; Dierssen 1982; Dierssen & Dierssen 1985; Malmer 1985; Hájek et al. 2002; Dengler et al. 2004; Lapshina 2010; Peterka et al. 2014). The system as proposed here is similar to the classification established by Fennoscandian authors (Sjörs 1948; Dahl 1956; Ruuhijärvi 1960; Fransson 1972; Elveland 1976; Moen et al. 2012) and deepened further by Czech and Slovak (Rybníček et al. 1984; Dítě et al. 2007; Hájek & Hájková 2011) and some German (Passarge 1964; Succow 1974), Polish (Pałczyński 1975), Russian (Koroleva 2001), Bulgarian (Tzonev et al. 2009) and, to a certain extent, Irish (Críodáin & Doyle 1994) authors. In these classification systems, major vegetation units differ in particular in their position on the poor-rich gradient. Our pan-European study has confirmed that this gradient is the principal one even at the continental scale. An alternative approach uses the dominance of selected vascular plants along with hydrological characteristics (i.e. water table depth) as the main alliance-delimiting criteria (e.g. Oberdorfer 1957; Dierssen 1982; Steiner 1992; Matuszkiewicz 2007). A main disadvantage of this approach is that vascular plants whose dominance was used as the chief classification criterion (*Carex lasiocarpa*, *C. limosa*, *C. nigra*, *C. rostrata* or *Rhynchospora alba*) occur across a broad range of base richness (Gerdol 1995; Martinčič 1997), for which reason the resulting classification fails to mirror the major compositional gradient within fens. Furthermore, this approach does not consider bryophytes in the delimitation of alliances, thus ignoring the general knowledge that bryophytes precisely indicate habitat conditions (Malmer et al. 1994; Peterka et al. 2014) and have a crucial importance for the functioning of mire habitats (Jones et al. 1994). The classification proposed here refutes the concepts of the extremely wide *Caricion lasiocarpae* and *Rhynchosporion albae* alliances and accepts the *Stygio-Caricion limosae* and *Sphagno warnstorfii-Tomentypnion nitentis* alliances. This solution was also supported by the results of a set of regional unsupervised classifications.

The gradient of water table depth was not evident in the pan-European DCA, although it has been repeatedly reported to be important locally (Bragazza & Gerdol 1996; Jabłońska et al. 2011; Moeslund et al. 2013) or regionally (Schenková et al. 2014; Horsáková et al. 2015; Pérez-Haase 2015). This fact suggests that the variation in species composition related to water table should not be used as the main classification criterion within fens on a broad scale without also taking into account shifts in species composition driven by site chemistry. The second most important gradient in the species composition of European fens followed macroclimatic and biogeographic differences, advocating acceptance of geographically constrained alliances.

Since base richness and biogeographic influences were identified as the most important determinants of species composition, they should be used as the key criteria to define fen alliances. The reproduced alliances show ecologically and biogeographically meaningful diagnostic species, underlying the applicability of the presented classification.

Less well-known alliances

Some less well-known alliances described from specific parts of Eurasia proved to be clearly defined compositionally on the European scale, which was supported by DCA. Some geographically constrained fen alliances delimited in this study also show distinct environmental conditions or a specific history.

The *Caricion viridulo-trinervis* alliance represents sub-halophytic fens with a shallow peat layer occurring in coastal dune slacks. This well-defined habitat was a subject of ecological studies in W Europe (Grootjans et al. 1991; Lammerts et al. 1999) and served as a postglacial refugium of some continental wetland species such as *Blysmus rufus* (Hájková et al. 2015).

The *Caricion atrofusco-saxatilis* alliance comprises arctic and high-mountain calcareous fens delimited from the widespread *Caricion davallianae* by species with an arcto-alpine distribution. We confirmed the occurrence of this alliance in the Alps and in N Europe, though it has also been reported in Scotland (Rodwell 1991), Spain (Rivas-Martínez 2011) and the Romanian Carpathians (Coldea et al. 2008). Further research is therefore needed to compare communities in these regions with those from the Alps, Scandinavia and the European Arctic.

The *Narthecion scardici* alliance is an alpine relict alliance of the Balkans similar to rich and moderately rich fens of *Sphagno warnstorfii-Tomentypnion nitentis* and *Caricion fuscae*, though virtually lacking boreal species of fens and harbouring specific ecotypes of temperate fen plants instead (Hájková et al. 2008). Lakušić (1968) originally considered this alliance to be restricted to Kosovo and Macedonia.

Probably due to the absence of *Narthecium scardicum*, the corresponding communities in Bulgaria were previously assigned to *Caricion fuscae* (Roussakova 2000; Tzonev et al. 2009). However, the community is well defined by Balkan endemics and relicts (Lakušić & Grgić 1971; Lakušić 1973; Roussakova 2000) and displays sympatric distribution with *Caricion fuscae* on the Balkan Peninsula (Kojić et al. 1998), the latter occurring below the timberline in managed fen grasslands (Hájek et al. 2008).

The *Anagallido tenellae-Juncion bulbosi* alliance is confined to a strongly oceanic climate without significant boreal or continental influences, together with intermediate levels of pH and mineral richness. Nevertheless, classification of fens in Atlantic Europe deserves further research, since fen communities in this region frequently share some species with the *Oxycocco-Sphagnetea* and *Littoreletea uniflorae* classes (Fernández Prieto et al. 1987; Rodwell 1991; Heras et al. 2011).

The *Caricion stantis* alliance occurs in Europe as part of its broader circumpolar distribution range. It was described in northern Siberia (Matveyeva 1994) as vegetation of sedge-brown-moss fens with scattered sphagna dominated mostly by *Carex aquatilis* subsp. *stans* or *Dupontia fisheri*. Analogous communities were documented throughout the circumpolar arctic zone (Thannheiser 1976; Hadač 1989; Lavrinenko et al. 2016). We consider this alliance as the high-arctic vicariant of the rich to moderately rich fens found in the south. However, the internal variability of the alliance and the relationships to other syntaxa deserve further research.

The *Saxifrago-Tomentypnion* alliance was described in western Siberia (Lapshina 2010) and has been distinguished for Europe on the basis of data from NE Europe and Poland. An analogous vegetation type is included in the Finnish mire site type classification (Eurola et al. 2015) as 'Eutrophic diandra-hirculus birch fen'. Its species composition is similar to *Caricion davallianae*, *Sphagno warnstorfii-Tomentypnion nitentis* and tall-sedge vegetation, but it includes mostly brown-moss vegetation (as opposed to *Sphagno warnstorfii-Tomentypnion nitentis*) and contains true fen species (as opposed to tall-sedge vegetation). Although overall macronutrient availability is very low in all fens, the nutrient ratios account for the compositional uniqueness of *Saxifrago-Tomentypnion*. The species composition of most calcium-rich fens is shaped by a shortage of phosphorus caused by its immobilization during carbonate precipitation (Boyer & Wheeler 1989). In contrast, *Saxifrago-Tomentypnion* fens show better phosphorus availability, and therefore a lower N:P ratio in the biomass, and their productivity seems to be N-limited rather than P-limited (Pawlikowski et al. 2013). Consequently, most of the *Caricion davallianae* species are rare, while nutrient-demanding species occur quite frequently. The geographic restriction

of *Saxifrago-Tomentypnion* to the boreal-continental regions is probably shaped by improved phosphorus availability that would lead to the development of grassland or reed vegetation in warmer regions with a longer growing season. In Finland, occurrence of this vegetation has been connected to high phosphorus availability and vivianite deposits (Kotilainen 1944), although this pattern has not been studied in detail. The combination of a boreal-continental climate and good phosphorus availability leads to unique species combinations, such as the co-existence of *Saxifraga hirculus* with species of productive grasslands in pristine, undisturbed fens.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Data sources.

Appendix S2. List of aggregates, species complexes and problematic taxa merged at the species level.

Appendix S3. Lists of fen specialists ('typical fen species') and non-fen species.

Appendix S4. List of species groups based on the Cocktail method.

Appendix S5. Formal definitions of alliances.

Appendix S6. Full version of the synoptic table with core plots assigned to alliances on the basis of formal definitions.

Appendix S7. Synoptic table with all plots assigned to the alliances on the basis of both formal definitions and similarity in species composition established using the Frequency-Positive Fidelity Index (FPFI).

Appendix S8. Results of the ISOPAM analyses.

Appendix S9. Description of unclassified group of plots.

Appendix S10. Reasons for the abandonment of the *Rhynchosporion albae* and *Caricion lasiocarpae* alliances.

Appendix S11. Generalized classification scheme with distinguishing features of fen alliances.