

Scots pine bog woodlands in the Eastern Carpathians versus their northern, lowland counterparts: floristic dissimilarities and underlying ecological gradients

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SUMMARY

We investigated the floristic dissimilarities and their ecological drivers between three regional groups of Scots pine woodlands from mires dispersed along a latitudinal gradient in Eastern Europe. Phytosociological data regarding such woodland communities from the Eastern Carpathians (Romania) and lowlands of Poland and Latvia were collected from 47 published relevés. In spite of the small number of good discriminant species, the relative positions of the three regional groups of communities in the bi-dimensional ordination space roughly matched their geographical separation along latitude and longitude. When the spatial autocorrelation was filtered out, the three regional groups of communities appeared partly overlapping in the two-dimensional ordination space, whose axes correlated with the occurrences of some species that are typical of either open or wooded bogs and, respectively, either hummocks or hollows. The total herb cover was negatively and significantly correlated with both the first partial ordination axis and total shrub cover. We concluded that the observed, small floristic dissimilarities were mainly induced by weak, small-scale gradients of autogenic successional development and groundwater level/microtopography. Our results do not support the distinction of a montane, Eastern Carpathian vicariant of the syntaxon *Vaccinio uliginosi-Pinetum sylvestris* from the lowlands of Central and Baltic Europe.

KEY WORDS: Baltic pinewood mires, discriminant species, open–wooded bog gradient, *Vaccinio uliginosi-Pinetum sylvestris*

INTRODUCTION

Raised (ombrotrophic) bogs host azonal vegetation that is embedded in the nemoral, boreal and temperate biomes (Montanarella *et al.* 2006, Mucina 2013). In temperate Europe, most of the raised bogs have been formed due to colmation (terrestrialisation) of dystrophic lakes (Leuschner & Ellenberg 2017) or non-dystrophic lakes fed by mineral rich groundwater (Couwenberg *et al.* 2001). With the gradual accumulation of peat in a thick layer, the ecohydrological regime changes from groundwater to completely precipitation dependent, which favours the establishment of species that are intolerant of prolonged water stagnation (Gunnarsson *et al.* 2002, Hughes & Dumayne-Peaty 2002) but tolerating very nutrient-poor conditions (Joosten *et al.* 2017).

The distribution of wooded bogs dominated by either *Pinus sylvestris* or *Betula pubescens* in Europe is considered to be largely dependent on continentality (Leuschner & Ellenberg 2017). The pine bog woodlands occurring in central Europe, under a subcontinental temperate climate were assigned to the association *Vaccinio uliginosi* -

Pinetum sylvestris Kleist 1929 by Matuszkiewicz (2006). Several papers (e.g., Neuhausel 1972) reported the meridional and occidental limits of this plant association at the periphery of the southern Alps and, respectively, in the Rhine region. Its eastern distribution limit in Europe is probably somewhere in north-western Russia, based on currently available reports (Galanina 2006).

Depending on the depth of the water table, such pine-wooded bogs can differ physiognomically, mainly on the basis of stature and density of individual pines (Boşcaiu & Soran 1965), but also on the preferential occurrence of some indicator species of either open (raised) bogs or coniferous forest understorey (Freléchoux *et al.* 2003, Dyderski *et al.* 2016). Such spatio-temporal floristic variations were interpreted either as seral stages along primary successional pathways from shallow lake to marsh, bog and eventually forest (Neuhausel 1992, Freléchoux *et al.* 2000, Czerepko 2011, Dyderski *et al.* 2016, Jagodziński *et al.* 2018) or as toposequential communities expressing the spatial zonation of vegetation around infilling water bodies (Feldmeyer-Christe 1990, Klinger 1996).

It is known that the floristic composition of the bog pinewoods from the Eastern Carpathians is poorer in arctic/boreal species, compared to those described in northern and central Europe (Coldea & Plămadă 1989). For instance, *Vaccinium uliginosum* and some other boreal species (*Rhododendron tomentosum*, *Rubus chamaemorus*, *Chamaedaphne calyculata*) are missing in these communities from the easternmost part of the Carpathian range. Therefore, it is questionable whether the pine-wooded bog communities described in the Eastern Carpathians by Coldea & Kovács (1969), Pop *et al.* (1973) and Coldea & Plămadă (1989) could be assigned to *Vaccinio uliginosi* - *Pinetum sylvestris*.

In this article we address the following questions:

- i) are there regional differential species for the Scots pine communities distributed in mires at different latitudes (temperate to boreal) in eastern Europe?
- ii) if yes, are these floristic differences sufficient to justify the distinction of a new vicariant syntaxon in the Eastern Carpathians?
- iii) to what extent are these compositional differences driven by large-scale climatic factors and/or by local environmental conditions?

METHODS

Description of study areas

The Scots pine bog woodlands from the eastern part of the Romanian Carpathians occur at elevations of 900–1110 m a.s.l. on a more or less thick layer (1.5–4 m) of acidic oligotrophic peat. The annual rainfall is about 850–900 mm and the growing season lasts for 210–220 days (Schreiber 1994). These woodlands have been considered relict azonal communities, which have persisted in some isolated montane bogs since the pre-Boreal period (Pop 1960, Coldea & Plămadă 1989). The most representative wooded bogs, in terms of the presence of character species of the alliance *Vaccinio uliginosi* - *Pinion sylvestris*, are distributed in the bogs of Poiana Stampei, Mohoş and Luci (Figure 1). Within the former bog, a rare glacial relict moss - *Sphagnum wulfianum* - reaches its southernmost presence in the whole of Europe (Daniels & Eddy 1990). Also, an arctic shrub - *Betula nana* - occurs in the Luci bog, which is its southernmost locality in Europe (Pop 1960). These montane bogs are still active and in good status of conservation, being included in protected areas.

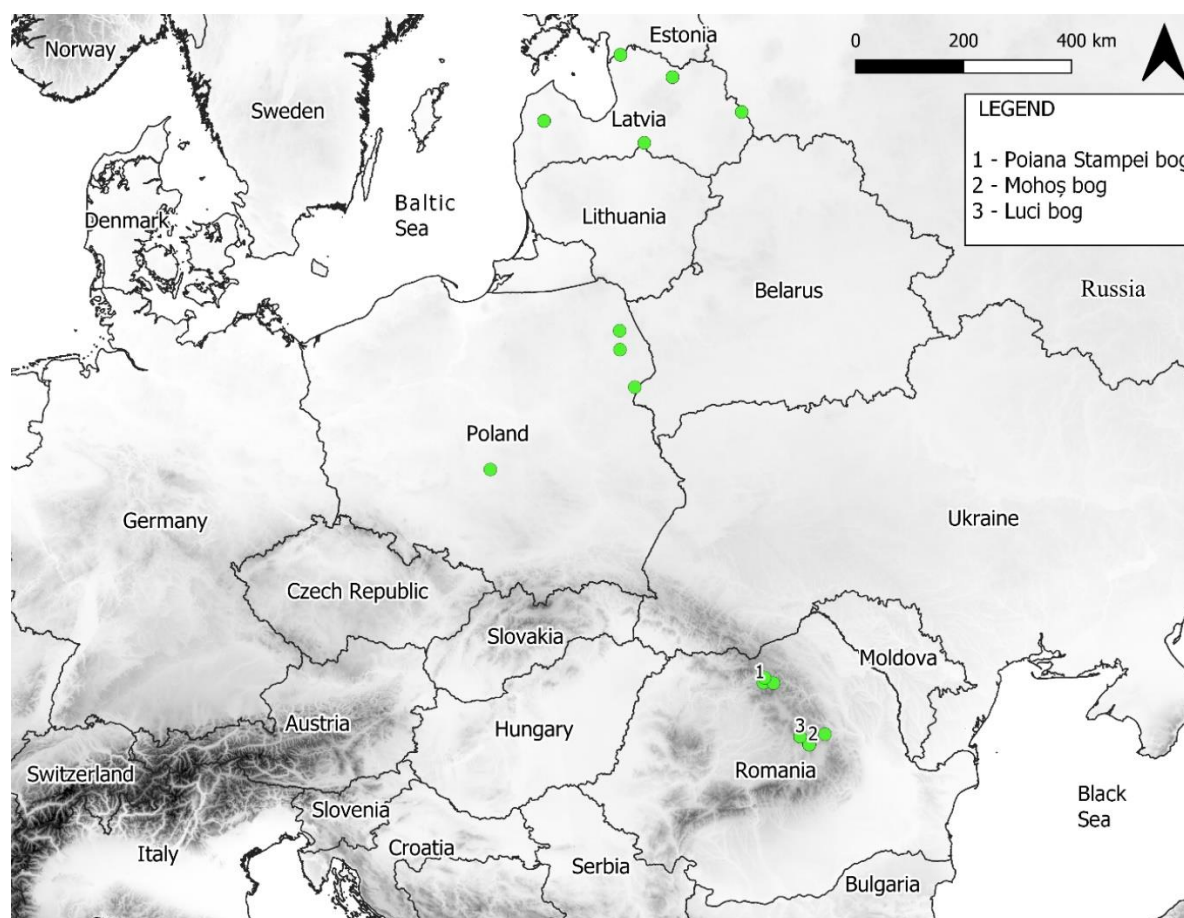


Figure 1. Approximate geographical distribution of the pine, bog woodland communities considered in the present study (green dots).

The study mire woodlands from Poland are distributed in the central Polish Plain and the Masurian Lake District (Figure 1), at elevations ranging from 120 to 170 m a.s.l. The average annual rainfall ranges between 550 and 600 mm, and the length of the vegetation period is about 210 days. All Polish study mires are well preserved in natural protected areas, although the one included in the Jodły Łaskie Reserve has been affected to some extent by the old drainage ditches (Woziwoda 1998).

The Latvian mires under study are distributed from about 50 m a.s.l., close to the sea coast, up to about 100 m of elevation in the Alūksne Upland (Figure 1). The average amount of precipitation is 600–650 mm annually and the period of active plant growth is approximately 190 days. The peat layer in these mires is usually 0.8–4 m thick (Prieditis 1993).

Following the mire regionalisation in Europe by Moen *et al.* (2017), the study areas are included in four eco-units: typical raised bog region (Latvia), continental fen and bog region (eastern Poland), nemoral-submeridional fen region (central Poland) and central-southern European mountain compound region (the Carpathians). Despite their distribution in different vegetation zones/belts, the Eastern Carpathian wooded mires are comparable with their lowland, subcontinental and Baltic counterparts from northern latitudes, given their edaphic, hydrological and physiognomic similarities. However, the lowland mires seem to have undergone stronger anthropogenic disturbance in the past (mainly through drainage ditches and peat cutting) than the montane ones (Sotek *et al.* 2015, Čugunovs *et al.* 2016, Dyderski *et al.* 2016, Jagodziński *et al.* 2018).

Data collection

Single phytosociological relevés assigned to *Vaccinio uliginosi* - *Pinetum sylvestris* were gathered from published literature with the constraint that the total relative cover of pines should be larger than 50 %. A total of 47 relevés were merged in a single table, out of which 25 were from Latvia (Prieditis 1993), 4 from Poland (Woziwoda 1998, Czerepko 2011) and 18 from Romania (Coldea & Kovács 1969, Coldea & Plămadă 1989). Some of the Latvian mires displayed a weak transition character because of the occurrence of few species (e.g., *Carex nigra* and *C. echinata*) that are typical for acidic, minerotrophic fens (*Sphagno-Caricion canescentis* Passarge (1964) 1978).

The areas in which the relevés considered in this study were recorded are geographically indicated in Figure 1. A synthetic table comprising the species frequencies in each of the three groups of relevés (Table A1 in the Appendix), as well as a list of the

geographic coordinates of the investigated sites (Table A2 in the Appendix), was prepared for reference. A series of subspecies and species were merged under the species name in order to achieve the same taxonomic resolution. The nomenclatural synonyms of vascular plant species were replaced by the current accepted names, according to Sârbu *et al.* (2013) for the Romanian flora and Euro+Med PlantBase (<https://www.emplantbase.org/home.html>) for the species that do not occur in Romania. The indicator values of plant species (Ellenberg *et al.* 2001, Hájek *et al.* 2020) were used as a reference for inferring the ecological gradients underlying the observed variation in species composition in the study mire communities.

Data analysis

All analyses were performed under R software environment (<https://www.r-project.org>) using the packages ‘indicspecies’ (De Cáceres *et al.* 2020), ‘vegan’ (Oksanen *et al.* 2020) and ‘lmodel2’ (Legendre 2018).

For the purpose of detecting possible discriminant species, the relevés performed in the Eastern Carpathians (RO) were involved in indicator species analysis along with the Baltic ones (LV). Because of their low number, the relevés from Poland (PL) were not involved in a similar analysis. The association between the presence of species and each of the regional groups of relevés was assessed using the group-equalised phi coefficient (De Cáceres & Legendre 2009). Its statistical significance was estimated through 9999 permutations.

The compositional distinction between the three regional groups of relevés (LV, PL and RO) was illustrated via local, non-metric multidimensional scaling (NMDS) by employing a dissimilarity matrix based on the complement of Sørensen index. The retained solution, with the lowest stress index, was selected from 5000 runs starting from a random configuration of relevés and subsequently from the best previous solution. The latitude and longitude of relevés were tested separately as dependent variables against both NMDS axes through linear trend surface fitting by employing 9999 permutations.

In order to partition out the spatial compositional autocorrelation between intra-regional relevés, the geographical distances were first involved in principal coordinates analysis of neighbourhood matrix (PCNM) with the aim of transforming distances to rectangular data (Borcard & Legendre 2002). Subsequently a partial, unconstrained, distance-based redundancy analysis (Legendre & Legendre 2012), which is equivalent to a partial principal coordinates analysis (p-PCoA), was

performed by using the following terms in the linear model: i) the above-mentioned matrix of floristic dissimilarities as response, and ii) the intercept and extracted PCNM vectors as main and, respectively, conditioned effects. The correlations between the species presence and each of the first two p-PCoA axes were calculated through the point biserial coefficient. The pairwise linear relationships between all variables estimated with error (ordination scores and cover of different plant growth-forms) were assessed through model II simple regressions (Legendre & Legendre 2012).

RESULTS

The Eastern Carpathian communities can be mainly distinguished through the higher frequency of *Polytrichum strictum*, *Aulacomnium palustre*, *Vaccinium microcarpum* and *V. myrtillus* (Table 1 and Appendix), but none of them has a limited regional distribution. On the other side, the Baltic communities feature - among others - *Rhododendron tomentosum* (syn. *Ledum palustre*) and *Vaccinium uliginosum* (Table 1 and Appendix), the former being a boreal species whose distribution does not extend south to the Romanian Carpathians and the latter being absent from the Scots pine bog woodlands in these mountains.

In spite of the small number of discriminant species, the overall specific composition is sharply distinctive between the three regional groups of communities (Figure 2). In fact, their relative positions in the bi-dimensional NMDS space shows a clear separation, which is explained to a large extent (80 %) by latitude and, independently, to a much lesser extent (28 %) by longitude (Table 2). This outcome suggests that the compositional dissimilarity between the three regional groups is mostly determined by their geographical separation. When the spatial autocorrelation is filtered out, the three regional groups of communities appear largely overlapped in the p-PCoA space, but the relevés displaying the largest scores along both dimensions are all from the Eastern Carpathians (Figure 3).

The first axis is negatively correlated with the presence of three woody late-successional species (*Picea abies*, *Betula pubescens* and *Vaccinium vitis-idaea*) and a boreal forest moss (*Pleurozium schreberi*), but positively correlated with some species that are typical of open raised bogs (*Empetrum nigrum*, *Sphagnum magellanicum* and *S. fuscum*) (Table 3). In addition, the herb cover sum increases steadily along the first p-PCoA axis, suggesting a weak gradient of light availability (Figure 4a). Instead, the second axis is negatively correlated with some species usually dwelling on

Table 1. Group-equalised phi coefficient (r.g.) of correlation between each species and the associated regional group of relevés (either Baltic or Eastern Carpathian). Only species displaying r.g. larger than 0.5 in the paired group analysis are reported.

Regional group distinguished	Species	r.g.	p-value
Baltic (LV)	<i>Vaccinium uliginosum</i>	0.886	0.0001
	<i>Rhododendron tomentosum</i>	0.851	0.0001
	<i>Vaccinium oxycoccos</i>	0.789	0.0001
	<i>Melampyrum pratense</i>	0.686	0.0001
	<i>Sphagnum rubellum</i>	0.686	0.0001
	<i>Betula pendula</i>	0.624	0.0002
	<i>Carex nigra</i>	0.593	0.0004
	<i>Sphagnum balticum</i>	0.593	0.0004
	<i>Calluna vulgaris</i>	0.531	0.0012
E Carpathian (RO)	<i>Polytrichum strictum</i>	0.946	0.0001
	<i>Aulacomnium palustre</i>	0.654	0.0001
	<i>Vaccinium microcarpum</i>	0.620	0.0001
	<i>Vaccinium myrtillus</i>	0.511	0.0020

peat moss hummocks (*Andromeda polifolia* and *Drosera rotundifolia*), but positively correlated with three *Sphagnum* taxa (*S. fallax*, *S. flexuosum* and *S. subsecundum*) of the niche-distinctive subgenera *Cuspidata* and *Subsecunda*.

The growth-form structure of the pine mire communities studied reveals a significant negative relationship between herb and shrub cover sums (Figure 4b). As an exception, the Polish mires do not follow this trend but that may be simply due to their very low number of relevés.

DISCUSSION

The regional specificity of Scots pine mire woodlands from central and northern Europe is

mostly determined by boreal and arctic-alpine species such as *Vaccinium uliginosum* and *Rhododendron tomentosum*. Their absence from the floristic composition of similar Eastern Carpathian communities is most likely related to climatic differences, especially those circumscribed by the growing season, which is on average slightly longer and warmer. On the other hand, no regional discriminant species are present in the Scots pine-wooded bogs of the Eastern Carpathians, which is the main reason for not distinguishing a different syntaxon from the classic *Vaccinio uliginosi-Pinetum sylvestris*. Interestingly, *Vaccinium uliginosum* is actually present in some ombrotrophic bogs in the northern Romanian Carpathians, but only within communities dominated by *Pinus mugo* (Coldea & Plămadă 1989). It is also worth noting that toward

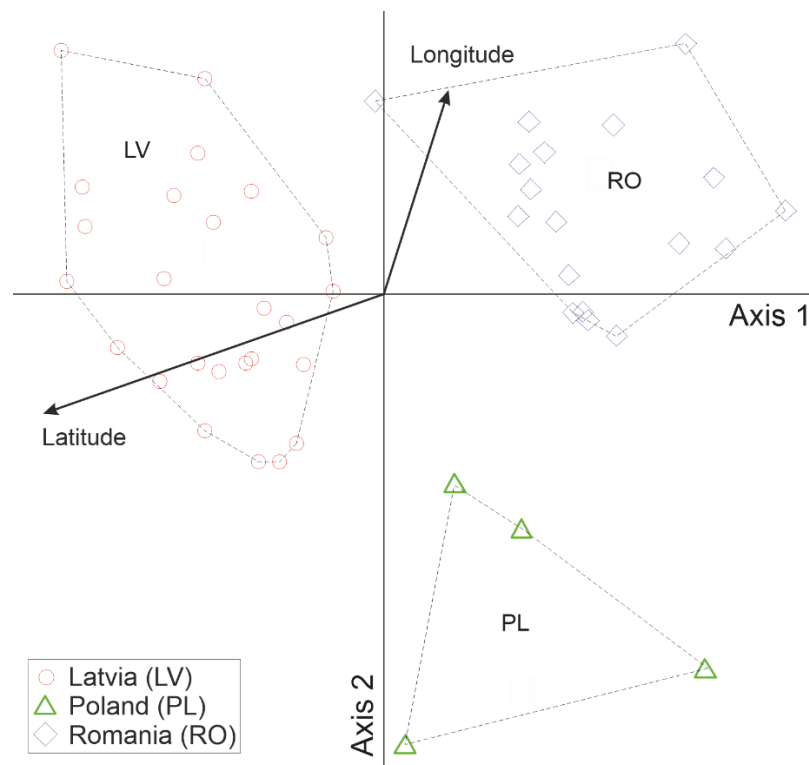


Figure 2. Non-metric multidimensional scaling of the 47 pine, bog woodland communities under study based on raw compositional dissimilarities. Convex hulls were used to group the communities by region (country).

Table 2. Independent linear fit of the geographical coordinates (latitude and longitude) of all relevés against their scores along the two axes extracted through non-metric multidimensional scaling (NMDS).

Response variable	NMDS 1	NMDS 2	R-square	Prob(>R-sq.)
Latitude	-0.943	-0.332	0.804	0.0001
Longitude	0.306	0.952	0.281	0.001

lower latitudes the distribution of Scots pine bog woodlands shifts upward in the lower montane belt. In the bogs from the upper montane and subalpine belts, *Pinus sylvestris* is replaced by *Pinus mugo*, as in the southern Alps (Pedrotti 1978) and Eastern Carpathians (Coldea & Plămadă 1989), or by *Pinus uncinata*, as in the Jura mountains (Freléchoux *et al.* 2000).

The removal of the spatial autocorrelation from compositional similarities allowed the inference of two weak gradients that are very likely related to autogenic successional processes (Neuhäusel 1992, Czerepko 2011, Leuschner & Ellenberg 2017) and, respectively, small-scale variations of water table level (Rydin & Jeglum 2013, Parish *et al.* 2008, Kolari *et al.* 2021).

Firstly, the species best related with the first p-PCoA axis are indicators of either wooded late-successional stages (e.g., *Picea abies*, *Vaccinium vitis-idaea*) or open (unwooded) mid-successional stages (i.e., *Sphagnum magellanicum*, *S. fuscum* and *Empetrum nigrum*) developing in ombrotrophic bogs throughout temperate and boreal Europe, irrespective of the dominant pine species i.e., either *P. sylvestris*

(Dyderski *et al.* 2016) or *P. uncinata* (Freléchoux *et al.* 2000). The two *Sphagnum* species mentioned previously were assigned the maximum rank (9) as indicator value for light availability (Ellenberg *et al.* 2001), whereas *Empetrum nigrum* is a half-light heather (rank 7) but mostly occurring at full light (Chytrý *et al.* 2021). On the other hand, the proliferation of spruce and downy birch contributes to bog drainage (Fay & Lavoie 2009, Talbot *et al.* 2010, Jagodziński *et al.* 2018) and, consequently, to increasing encroachment of other woody species and decreasing herb cover (Gunnarsson *et al.* 2002, Limpens *et al.* 2003, Czerepko 2011, Holmgren *et al.* 2015). This is in accordance with both negative relationships revealed between the herb cover sum on the one hand, and the first p-PCoA axis scores and shrub cover sum on the other. The observed shift in species composition along the first ordination axis may also be associated with a small segment of the mire expanse – mire margin gradient, also called the open mire – swamp forest gradient (Rydin *et al.* 1999, Økland *et al.* 2001).

Secondly, the species best related with the second p-PCoA axis can be grouped based on their optimal

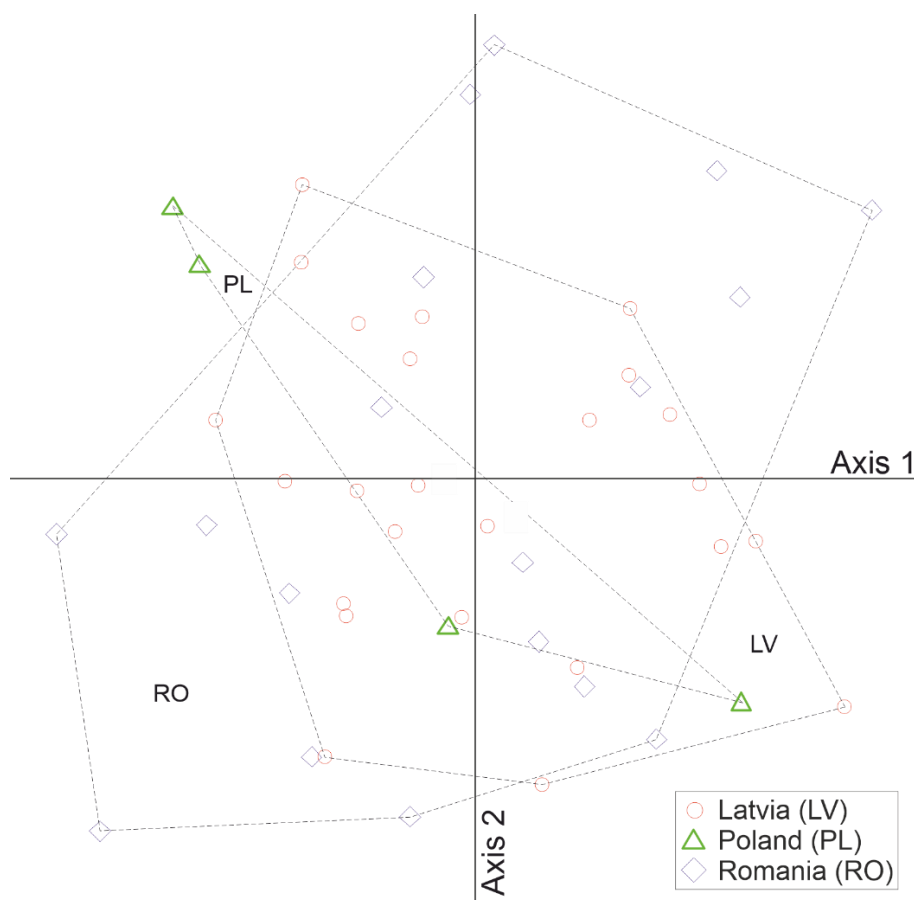


Figure 3. Ordination of the 47 pine, bog woodland communities under study after filtering out the spatial autocorrelation through unconstrained partial redundancy analysis. Community grouping as in Figure 2.

microhabitat with respect to microtopography and water-table depth. One group of species, including *Andromeda polifolia* and *Drosera rotundifolia*, usually occurs on bog hummocks (Nordbakken 1996, Jacquemart 1998, Rydin *et al.* 1999, Virtanen & Oksanen 1999, Freléchoux *et al.* 2000). The other group is composed of hollow species, for instance *S. fallax*, *S. flexuosum* and *S. subsecundum*, which tolerate long periods of flooding (Rydin *et al.* 1999, Wojtuń *et al.* 2013, Johnson *et al.* 2015, Hájek *et al.* 2020). A similar small-scale hydrological-topographic gradient was detected by Økland (1989, 1990), Bragazza & Gerdol (1999), Malhotra *et al.* (2016) and Kolari *et al.* (2021) in *Sphagnum* mires of SE Norway, SE Alps (Italy), western Canada and eastern Finland, respectively.

The observed disproportionality between herb and shrub cover very likely reflects the main gradient of light availability and successional development from open to wooded stages. A similar pattern was also observed in other mires from NW Poland (Dyderski *et al.* 2016, Jagodziński *et al.* 2018), NE Denmark (Kollmann & Rasmussen 2012) and Jura Mountains (Freléchoux *et al.* 2000, Freléchoux *et al.* 2003). Based on their spread along the ordination axes, the Eastern Carpathian bogs had the largest contribution to both gradients revealed. This could be the consequence of the higher environmental heterogeneity of the montane bogs, which - in our study - were fewer but probably better preserved than

lowland mires that are mostly affected by anthropogenic disturbance such as drainage (Czerepko 2011, Čugunovs *et al.* 2016).

In conclusion, the absence of a few boreal/arctic species from the *Pinus sylvestris*-dominated bog woodlands in the Eastern Carpathians does not justify their syntaxonomic separation from their central and north European counterparts. They all share many ombrotrophic species, while most of the observed floristic dissimilarity is determined by latitudinal separation. The spatial-independent ordination of the *Vaccinio uliginosi* - *Pinetum sylvestris* communities from the study areas is governed by weak, fine-scale gradients (successional, hydrological and microtopographical), and not by regional floristic differentiation. The Baltic pine mire woodlands appear floristically more homogeneous than their counterparts in the Eastern Carpathians. However, our results are based on a relatively low number of relevés and, therefore, may not be valid for less investigated regions (e.g., Ukraine, Belarus).

The bog communities with Scots pine from the Eastern Carpathians are of great conservation value because they host several other boreal/arctic species (e.g., *Betula nana*, *Betula humilis*, *Trientalis europaea*), which occur here at the southern limit of their European distribution. The current protection status of these habitats is well-deserved, but very likely not sufficient against the threat of global warming.

Table 3. Descending-ordered list of species best correlated with the first two partial PCoA axes. Only correlations over 0.4 in absolute values are reported.

Species	Axis 1		Axis 2	
	Correlation	<i>p</i> -value	Correlation	<i>p</i> -value
<i>Picea abies</i>	-0.690	<0.0001		
<i>Betula pubescens</i>	-0.479	0.0006		
<i>Pleurozium schreberi</i>	-0.477	0.0007		
<i>Vaccinium vitis-idaea</i>	-0.416	0.0028		
<i>Empetrum nigrum</i>	+0.466	0.0009		
<i>Sphagnum magellanicum</i>	+0.431	0.0024		
<i>Sphagnum fuscum</i>	+0.428	0.0025		
<i>Sphagnum fallax</i>			+0.627	<0.0001
<i>Andromeda polifolia</i>			-0.547	<0.0001
<i>Sphagnum flexuosum</i>			+0.527	0.0001
<i>Drosera rotundifolia</i>			-0.456	0.0012
<i>Sphagnum subsecundum</i>			+0.401	0.0052

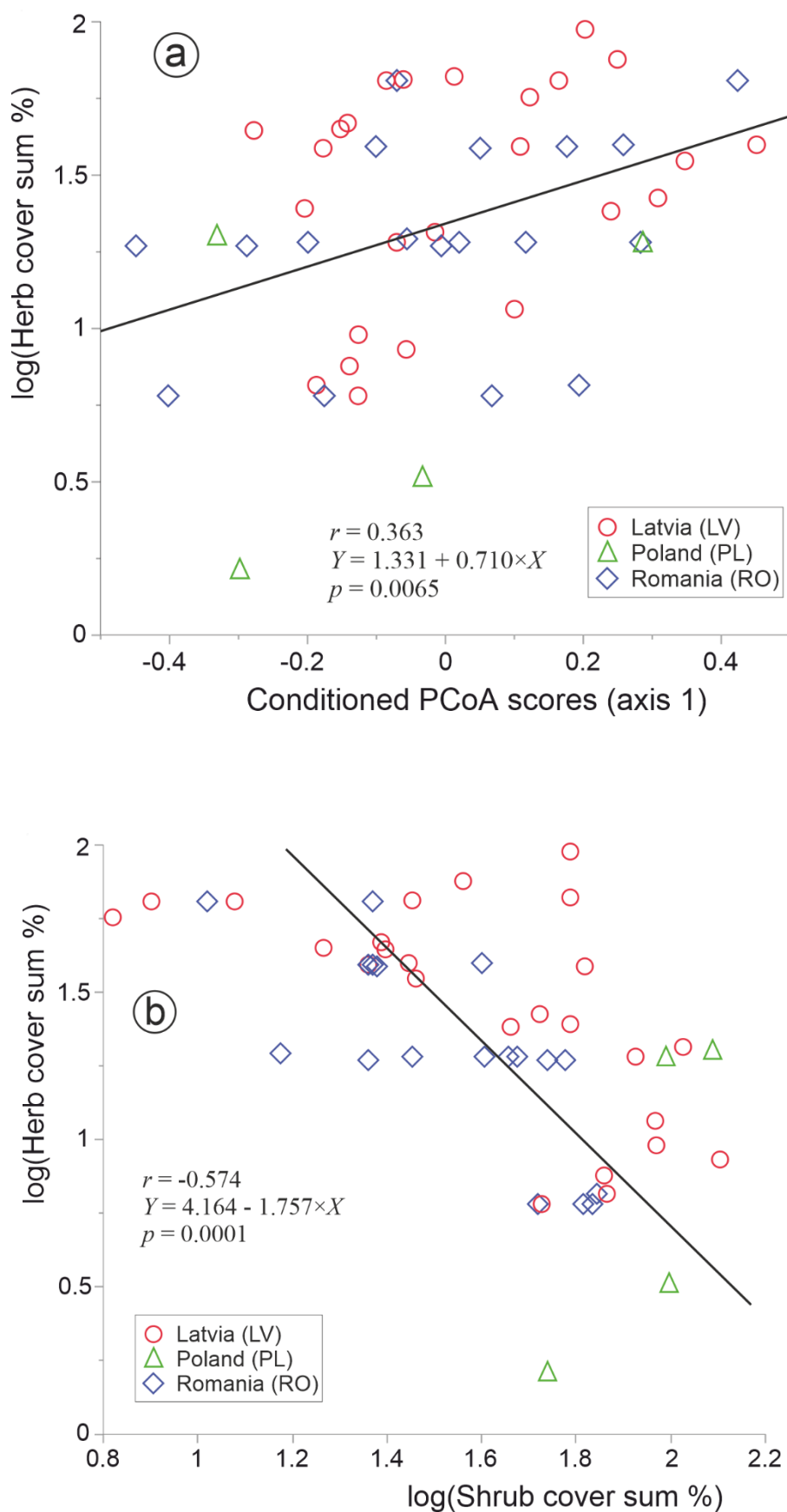


Figure 4. Model II linear regressions of the herb cover sum against (a) the relevé scores on the conditioned PCoA axis 1 and (b) the shrub cover sum, respectively.

AUTHOR CONTRIBUTIONS

AIS digitised the published relevés. DG analysed the data and wrote the initial draft. All authors crafted the objectives and participated in interpreting the results as well as in preparing the final manuscript.

REFERENCES

- Borcard, D., Legendre, P. (2002) All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecological Modelling*, 153, 51–68.
- Boşcaiu, N., Soran, V. (1965) Considérations sur la distribution structurale d'un peuplement de pin sylvestre d'un marais oligotrophe (Roumanie) (Considerations on the structural distribution of a Scots pine stand within an oligotrophic mire, Romania). *Vegetatio*, 13, 88–96 (in French).
- Bragazza, L., Gerdol, R. (1999) Ecological gradients in some *Sphagnum* mires in the south-eastern Alps (Italy). *Applied Vegetation Science*, 2, 55–60.
- Chytrý M., Danihelka J., Kaplan Z., Wild J. and 35 others (2021) Pladias database of the Czech flora and vegetation. *Preslia*, 93, 1–87.
- Coldea, G., Kovács, A. (1969) Cercetări fitosociologice în Munții Nemira (Phytosociological research in the Nemira Mountains). *Studii și Cercetări de Biologie*, 21, 95–104 (in Romanian).
- Coldea, G., Plămadă, E. (1989) Vegetația mlaștinilor oligotrofe din Carpații Românești (The vegetation of the oligotrophic mires from the Romanian Carpathians). *Contribuții Botanice*, 29, 37–43 (in Romanian).
- Couwenberg, J., De Klerk, P., Endtmann, E., Joosten, H., Michaelis, D. (2001) Hydrogenetische Moortypen in der Zeit - eine Zusammenschau (Hydrogenetic mire types in time - an overview). In: Succow, M., Joosten, H. (eds.) *Landschaftsökologische Moorkunde (Landscape Ecology of Peatlands)*, 2nd edition, E. Schweizerbart, Stuttgart, 399–403 (in German).
- Čugunovs, M., Nikodemus, O., Dauškane, I., Brūmelis, G. (2016) The colonization history of Scots pine (*Pinus sylvestris*) in pristine and drained raised bogs in Latvia. *Environmental and Experimental Biology*, 14, 97–106.
- Czerepko, J. (2011) Długookresowe zmiany roślinności w zespole sosnowego boru bagiennego *Vaccinio uliginosi* - *Pinetum* Kleist 1929 (Long-term vegetation change in marshy pine forest *Vaccinio uliginosi* - *Pinetum* Kleist 1929). *Forest Research Papers*, 72, 21–29 (in Polish).
- Daniels, R.E., Eddy, A. (1990) *Handbook of European Sphagna*. 2nd edition, Institute of Terrestrial Ecology, HMSO, London, 263 pp.
- De Cáceres, M., Legendre, P. (2009) Associations between species and groups of sites: indices and statistical inference. *Ecology*, 90, 3566–3574.
- De Cáceres, M., Jansen, F., Dell, N. (2020) 'indicspecies' (v1.7.9): Relationship between species and groups of sites. Online at: <https://cran.r-project.org/package=indicspecies>
- Dyderski, M.K., Czapiewska, N., Zajdler, M., Tyborski, J., Jagodziński, A.M. (2016) Functional diversity, succession, and human-mediated disturbances in raised bog vegetation. *Science of the Total Environment*, 562, 648–657.
- Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W., Paulißen, D. (2001) *Zeigerwerte von Pflanzen in Mitteleuropa (Indicator Values of Plants in Central Europe)*. 3rd edition, Scripta Geobotanica 18, Goltze-Verlag, Göttingen, 262 pp. (in German).
- Fay, E., Lavoie, C. (2009) The impact of birch seedlings on evapotranspiration from a mined peatland: an experimental study in southern Quebec, Canada. *Mires and Peat*, 5, 03, 7 pp.
- Feldmeyer-Christe, E. (1990) *Étude phytoécologique des tourbières des Franches-Montagnes (cantons du Jura et de Berne, Suisse) (Phytoecological Study of the Franches Mountains Bogs, Jura and Bern Cantons, Switzerland)*. Beitrage zur geobotanischen Landesaufnahme der Schweiz 66, F. Flück-Wirth, Teufen AR, 163 pp. (in French).
- Freléchoux, F., Buttler, A., Gillet, F. (2000) Dynamics of bog-pine-dominated mires in the Jura Mountains, Switzerland: a tentative scheme based on synusial phytosociology. *Folia Geobotanica*, 35, 273–288.
- Freléchoux, F., Buttler, A., Gillet, F., Gobat, J.M., Schweingruber, F.H. (2003) Succession from bog pine (*Pinus uncinata* var. *rotundata*) to Norway spruce (*Picea abies*) stands in relation to anthropic factors in Les Saignolis bog, Jura Mountains, Switzerland. *Annals of Forest Science*, 60, 347–356.
- Galanina, O. (2006) Comparative application of two vegetation classification approaches to large-scale mapping of bog vegetation. *Suo*, 57, 71–79.
- Gunnarsson, U., Malmer, N., Rydin, H. (2002) Dynamics or constancy in *Sphagnum* dominated mire ecosystems? A 40-year study. *Ecography*, 25, 685–704.
- Hájek, M., Dítě, D., Horsáková, V., Mikulášková, E., Peterka, T., Navrátilová, J., Jiménez-Alfaro, B., Hájková, P., Tichý, L., Horsák, M. (2020) Towards the pan-European bioindication system:

- assessing and testing updated hydrological indicator values for vascular plants and bryophytes in mires. *Ecological Indicators*, 116, 106527, 10 pp.
- Holmgren, M., Lin, C.-Y., Murillo, J.E., Nieuwenhuis, A., Penninkhof, J., Sanders, N., Bart, T., Veen, H., Vasander, H., Vollebregt, M.E., Limpens, J. (2015) Positive shrub-tree interactions facilitate woody encroachment in boreal peatlands. *Journal of Ecology*, 103, 58–66.
- Hughes, P.D.M., Dumayne-Peaty, L. (2002) Testing theories of mire development using multiple successions at Crymlyn Bog, West Glamorgan, South Wales, UK. *Journal of Ecology*, 90, 456–471.
- Jagodziński, A.M., Dyderski, M.K., Horodecki, P., Rawlik, K., Gdula, A.K. (2018). Succession of tree species on drained bogs in 'Brzozowe Bagno koło Czaplinka' nature reserve, NW Poland. *Polish Journal of Ecology*, 66, 352–368.
- Johnson, M.G., Granath, G., Tahvanainen, T., Pouliot, R., Stenøien, H.K., Rochefort, L., Rydin, H., Shaw, A.J. (2015) Evolution of niche preference in *Sphagnum* peat mosses. *Evolution*, 69, 90–103.
- Joosten, H., Moen, A., Couwenberg, J., Tanneberger, F. (2017) Mire diversity in Europe: mire and peatland types. In: Joosten, H., Tanneberger, F., Moen, A. (eds.) *Mires and Peatlands of Europe: Status, Distribution and Conservation*, Schweizerbart, Stuttgart, 5–64.
- Klinger, L.F. (1996) The myth of the classic hydrosere model of bog succession. *Arctic and Alpine Research*, 28, 1–9.
- Kolari, T.H.M., Korpelainen, P., Kumpula, T., Tahvanainen, T. (2021) Accelerated vegetation succession but no hydrological change in a boreal fen during 20 years of recent climate change. *Ecology and Evolution*, 11, 7602–7621.
- Kollmann, J.C., Rasmussen, K.K. (2012) Succession of a degraded bog in NE Denmark over 164 years – monitoring one of the earliest restoration experiments. *Tuexenia*, 32, 67–85.
- Legendre, P. (2018) 'lmodel2' (v1.7-3): Model II Regression. Online at: <https://cran.r-project.org/web/packages/lmodel2/index.html>
- Legendre, P., Legendre, L. (2012) *Numerical Ecology*. Elsevier Science, Amsterdam, 990 pp.
- Leuschner, C., Ellenberg, H. (2017) *Vegetation Ecology of Central Europe*. Volume 1, Springer, Cham, 779 pp.
- Limpens, J., Berendse, F., Klees, H. (2003) N deposition affects N availability in interstitial water, growth of *Sphagnum* and invasion of vascular plants in bog vegetation. *New Phytologist*, 157, 339–347.
- Malhotra, A., Roulet, N.T., Wilson, P., Giroux-Bougard, X., Harris, L.I. (2016) Ecohydrological feedbacks in peatlands: an empirical test of the relationship among vegetation, microtopography and water table. *Ecohydrology*, 9, 1346–1357.
- Matuszkiewicz, W. (2006) *Przewodnik do oznaczania zbiorowisk roślinnych Polski (Guide for the Identification of Polish Plant Communities)*. Wydawnictwo Naukowe PWN, Warszawa, 297 pp. (in Polish).
- Moen, A., Joosten, H., Tanneberger, F. (2017) Mire diversity in Europe: mire regionality. In: Joosten, H., Tanneberger, F., Moen, A. (eds.) *Mires and Peatlands of Europe. Status, Distribution and Conservation*. Schweizerbart, Stuttgart, 97–150.
- Montanarella, L., Jones, R.J., Hiederer, R. (2006) The distribution of peatland in Europe. *Mires and Peat*, 1, 01, 10 pp.
- Mucina, L. (2013) Ecosystems of Europe. In: Levin, S.A. (ed.) *Encyclopedia of Biodiversity*. Volume 3, Academic Press, Waltham, 333–346.
- Neuhäusel, R. (1972) Subkontinentale Hochmoore und ihre Vegetation (Subcontinental raised bogs and their vegetation). *Studie ČSAV*, 13, 1–144 (in German).
- Neuhäusel, R. (1992) Primary and secondary succession on wooded peat-bogs. *Acta Societatis Botanicorum Poloniae*, 61, 89–102.
- Nordbakken, J.F. (1996) Plant niches along the water-table gradient on an ombrotrophic mire expanse. *Ecography*, 19, 114–121.
- Økland, R.H. (1989) Hydromorphology and phytogeography of mires in inner Østfold and adjacent part of Akershus, SE Norway, in relation to SE Fennoscandian mires. *Opera Botanica*, 97, 1–122.
- Økland, R.H. (1990) A phytoecological study of the mire Northern Kisselbergmosen, SE Norway. II. Identification of gradients by detrended (canonical) correspondence analysis. *Nordic Journal of Botany*, 10, 79–108.
- Økland, R.H., Økland, T., Rydgren, K. (2001) A Scandinavian perspective on ecological gradients in north-west European mires: Reply to Wheeler and Proctor. *Journal of Ecology*, 89, 481–486.
- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H. (2020) 'vegan' (v2.5.7): *Community ecology package*. Online at: <https://cran.r-project.org/package=vegan>
- Parish, F., Sirin, A., Charman, D., Joosten, H., Minayeva, T., Silvius, M., Stringer, L. (eds.) (2008) *Assessment on Peatlands, Biodiversity and Climate Change: Main Report*. Global

- Environment Centre, Kuala Lumpur and Wetlands International, Wageningen, 179 pp.
- Pedrotti, F. (1978) La végétation de la tourbière du Vedes (Trento) (The vegetation of the Vedes bog, Trento). *Colloques Phytosociologiques*, 7, 231–250 (in French).
- Pop, E. (1960) *Mlaştinile de turbă din Republica Populară Română (The Bogs of the People's Republic of Romania)*. Editura Academiei Române, Bucharest, 511 pp. (in Romanian).
- Pop, E., Boşcaiu, N., Rădulescu, D. (1973) Eficienţa ecologică a măsurilor pentru protecţia tinovului de la Lucina (jud. Suceava) (The ecological efficiency of provisions for the protection of the Lucina bog, Suceava county). *Studii şi Comunicări de Ocrotirea Naturii* (Suceava), 3, 21–28 (in Romanian).
- Prieditis, N. (1993) Pine-birch forest communities on non-drained peatlands in Latvia. *Feddes Repertorium*, 104, 271–281.
- Rydin, H., Sjörs, H., Lofroth, M. (1999) Mires. In: Rydin, H., Snoeijs, P., Diekmann, M. (eds.) *Swedish Plant Geography*. Acta Phytogeographica Suecica 84, Opulus Press, Uppsala, 91–112.
- Rydin, H., Jeglum, J.K. (2013) *The Biology of Peatlands*. Oxford University Press, Oxford, 398 pp.
- Sârbu, I., Ştefan, N., Oprea, A. (2013) *Plante vasculare din România. Determinator ilustrat de teren (Vascular Plants of Romania. An Illustrated Field Guide)*. Editura Victor B Victor, Bucharest, 1320 pp. (in Romanian).
- Schreiber, W.E. (1994) *Munţii Harghita. Studiu geomorfologic (The Harghita Mountains. Geomorphologic Study)*. Editura Academiei Române, Bucharest, 134 pp. (in Romanian).
- Sotek, Z., Grzejszczak, G., Stasinska, M., Malinowski, R. (2015) Synanthropisation of the Baltic-type raised bog “Roby” (North West Poland). *Biodiversity Research and Conservation*, 38, 51–56.
- Talbot, J., Richard, P.J.H., Roulet, N.T., Booth, R.K. (2010) Assessing long-term hydrological and ecological responses to drainage in a raised bog using paleoecology and a hydrosequence. *Journal of Vegetation Science*, 21, 143–156.
- Virtanen, R., Oksanen, L. (1999) Topographic and regional patterns of tundra heath vegetation from northern Fennoscandia to the Taimyr Peninsula. *Acta Botanica Fennica*, 167, 29–70.
- Wojtuń, B., Sendyk, A., Martyniak, D. (2013) *Sphagnum* species along environmental gradients in mires of the Sudety Mountains (SW Poland). *Boreal Environment Research*, 18, 74–88.
- Woziwoda, B. (1998) Szata roślinna rezerwatu Jodły Łaskie (Plant cover of Jodły Łaskie Nature Reserve). *Acta Universitatis Lodzianae (Folia Botanica)*, 12, 3–45 (in Polish).

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Appendix

Table A1. Synthetic table displaying the species frequencies (%) of occurrence in the Scots pine woodland communities (*Vaccinio uliginosi-Pinetum sylvestris*) from ombrotrophic bogs of Latvia, Poland and the Eastern Carpathians (Romania). The values in bold (within grey-shaded cells) correspond to regional differential species.

Region (country)	Latvia	Poland	E Carpathians (Romania)
No. of relevés	25	4	18
Trees			
<i>Betula pendula</i>	56	75	0
<i>Betula pubescens</i>	44	75	67
<i>Picea abies</i>	64	75	56
<i>Pinus sylvestris</i>	100	100	100
<i>Quercus robur</i>	0	50	0
<i>Sorbus aucuparia</i>	0	25	0
Shrubs			
<i>Andromeda polifolia</i>	68	25	67
<i>Betula nana</i>	0	0	11
<i>Calluna vulgaris</i>	44	50	0
<i>Empetrum nigrum</i>	56	0	56
<i>Frangula alnus</i>	8	25	0
<i>Rhododendron tomentosum</i>	84	75	0
<i>Salix aurita</i>	8	0	0
<i>Salix cinerea</i>	12	25	0
<i>Vaccinium microcarpum</i>	0	0	56
<i>Vaccinium myrtillus</i>	40	100	89
<i>Vaccinium oxycoccos</i>	84	25	6
<i>Vaccinium uliginosum</i>	88	100	0
<i>Vaccinium vitis-idaea</i>	52	75	94
Herbs			
<i>Agrostis capillaris</i>	0	25	0
<i>Calamagrostis canescens</i>	4	0	0
<i>Carex chordorrhiza</i>	4	0	0
<i>Carex curta</i>	8	0	0
<i>Carex echinata</i>	28	0	0
<i>Carex globularis</i>	4	25	0
<i>Carex limosa</i>	8	0	0
<i>Carex nigra</i>	52	0	0

Region (country)	Latvia	Poland	E Carpathians (Romania)
No. of relevés	25	4	18
<i>Carex pauciflora</i>	16	0	0
<i>Carex rostrata</i>	4	0	6
<i>Dactylorhiza fuchsii</i>	4	0	0
<i>Dactylorhiza maculata</i>	4	0	0
<i>Deschampsia flexuosa</i>	0	0	22
<i>Drosera rotundifolia</i>	48	0	33
<i>Dryopteris carthusiana</i>	8	25	0
<i>Equisetum palustre</i>	8	0	0
<i>Eriophorum vaginatum</i>	100	50	100
<i>Goodyera repens</i>	4	0	0
<i>Juncus effusus</i>	4	0	0
<i>Juncus filiformis</i>	4	0	0
<i>Luzula sylvatica</i>	0	0	6
<i>Melampyrum pratense</i>	64	0	0
<i>Menyanthes trifoliata</i>	12	0	0
<i>Molinia caerulea</i>	4	75	6
<i>Potentilla palustris</i>	8	0	0
<i>Scheuchzeria palustris</i>	8	0	0
<i>Trientalis europaea</i>	8	0	0
Mosses and lichens			
<i>Aulacomnium palustre</i>	24	75	89
<i>Bazzania trilobata</i>	0	0	11
<i>Calliergon cordifolium</i>	0	0	11
<i>Cladonia chlorophaea</i>	0	25	0
<i>Dicranella heteromalla</i>	0	25	0
<i>Dicranum polysetum</i>	20	75	0
<i>Dicranum scoparium</i>	0	25	0
<i>Dicranum undulatum</i>	0	25	0
<i>Hylocomium splendens</i>	4	75	22
<i>Leucobryum glaucum</i>	0	50	0
<i>Lophocolea</i> sp.	0	0	6
<i>Lophocolea heterophylla</i>	0	25	0
<i>Pleurozium schreberi</i>	60	100	78
<i>Pohlia nutans</i>	0	25	0
<i>Polytrichum commune</i>	68	0	50

Region (country)	Latvia	Poland	E Carpathians (Romania)
No. of relevés	25	4	18
<i>Polytrichum formosum</i>	0	50	0
<i>Polytrichum stefureacii</i>	0	0	17
<i>Polytrichum strictum</i>	0	25	94
<i>Ptilium crista-castrensis</i>	0	25	28
<i>Sphagnum balticum</i>	52	0	0
<i>Sphagnum capillifolium</i>	88	75	100
<i>Sphagnum centrale</i>	16	0	33
<i>Sphagnum cuspidatum</i>	4	0	0
<i>Sphagnum fallax</i>	4	75	33
<i>Sphagnum flexuosum</i>	0	0	33
<i>Sphagnum fuscum</i>	12	0	28
<i>Sphagnum girgensohnii</i>	0	0	33
<i>Sphagnum magellanicum</i>	92	0	78
<i>Sphagnum palustre</i>	0	0	11
<i>Sphagnum recurvum</i>	0	0	28
<i>Sphagnum rubellum</i>	64	0	0
<i>Sphagnum russowii</i>	12	0	33
<i>Sphagnum squarrosum</i>	0	0	17
<i>Sphagnum subsecundum</i>	0	0	11
<i>Sphagnum warnstorffii</i>	4	0	0
<i>Tetraphis pellucida</i>	0	25	0

Table A2. Geographic coordinates (in decimal degrees) of the relevés by region (country). All coordinates were roughly determined based on the toponyms (locality names) declared in the original publications (Coldea & Kovács 1969, Coldea & Plămadă 1989, Woziwoda 1998, Czerepko 2011), except for those located in Latvia that were reported explicitly by the author (Prieditis 1993).

Region (country)	Relevé no.	Latitude (°N)	Longitude (°E)
Latvia	1	56.454	24.947
	2	56.454	24.947
	3	57.963	24.807
	4	57.963	24.807
	5	57.963	24.807
	6	57.963	24.807
	7	57.963	24.807
	8	56.582	28.020
	9	56.582	28.020
	10	56.582	28.020
	11	57.123	22.092
	12	57.123	22.092
	13	57.123	22.092
	14	57.123	22.092
	15	57.123	22.092
	16	57.123	22.092
	17	57.123	22.092
	18	57.123	22.092
	19	57.415	26.230
	20	57.415	26.230
	21	57.415	26.230
	22	57.415	26.230
	23	57.415	26.230
	24	57.415	26.230
	25	57.415	26.230
Poland	26	53.483	23.172
	27	52.482	23.543
	28	53.173	23.085
	29	51.536	19.104
Eastern Carpathians (Romania)	30	46.297	25.728
	31	46.297	25.728
	32	46.297	25.728
	33	46.297	25.728
	34	46.133	25.903
	35	46.133	25.903
	36	46.133	25.903
	37	46.133	25.903
	38	47.298	25.116
	39	47.298	25.116
	40	47.257	25.355
	41	47.257	25.355
	42	47.375	25.169
	43	46.133	25.903
	44	46.133	25.903
	45	46.297	25.728
	46	46.297	25.728
	47	46.248	26.325