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ORIGINAL RESEARCH PAPER

Geobotanical distinction using the floristic method: example of the Polish Pomerania

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Abstract

In the geobotanical division of Poland, Pomerania was treated as a separate subdivision, divided into "coastal plains" and the "Pomeranian uplands" or, in the newest regionalization, the "Pomeranian division". The goal of this paper is to determine how well the distinctiveness of Pomerania is floristically justified. A total of 1,467 native species occur within the area of Pomerania, representing 57.5% of the native flora of Poland. Fifty-seven species distinguishing Pomerania were selected and their phytogeographic features were discussed and compared to the Polish vascular flora. The distribution of 32 species (56.1%) is characterized as (sub)Atlantic/oceanic. Of the taxa that characterize Pomerania, 47.45% represent the northern element of the Polish flora and 7.01% the western element; species of the eastern element do not exist in Pomerania. The maximum entropy (MaxEnt) method was used for collective distribution analysis of the 57 selected taxa. The analyzes were performed using 41 environmental variables. All the species analyzed are strictly linked to the western and the North Atlantic part of Europe. Statistical evaluation of the MaxEnt model yielded an AUC value of 0.75 for both training and test. The most important environmental variables are minimum high (min_h), temperature annual range (bio07), and mean temperature of driest quarter (bio09). The results of the MaxEnt analysis allowed us also to verify the boundaries of the region and suggest new criteria for them. The southern limit of Pomerania should run along the northern boundary of the terminal moraine belt. Also, the area east of the Vistula does not contain abundant representatives of the flora characteristic for Pomerania. The results of the present study may be used for a broader discussion on the revision of the geobotanical division of Poland, at least in its northern part.

Keywords

bioinformatics; GIS; MaxEnt model; geobotany; species distribution; regionalization; Central Europe

Introduction

Poland contains some areas specifically distinguished by their geological and climatic history both in the context of the country and in comparison with the rest of the continent. Such an area is Pomerania, a historical land in Poland and Germany situated at the mouths of the Reknica, Odra, and Vistula rivers where they flow into the Baltic Sea. The greater part of Pomerania is located within the borders of Poland. Pomerania here covers the area delimited by the Odra River in the west, the Baltic Sea coast in the north, the Vistula River in the east, and the Warta and Noteć rivers in the south. The region occupies an area of 52,000 km^2, more than one-eighth of Poland's territory. The morphology and surface geology of Pomerania were generated by the direct action of the late Pleistocene glaciation. Periods of cessation and withdrawal of glaciers are reflected in the morphology of the terrain, particularly in the area of the Pomeranian phase, which crosses the central part of the region. The area is characterized by a well-developed network of rivers, a large number of lakes and peat bogs, and by a great diversity of climatic conditions, caused mainly by overlapping masses of humid air from the Atlantic and of dry continental air, and the surface morphology [1,2].

Two geobotanical regionalizations have been developed for Poland. The first [3] was developed on the basis of data on the distribution of the most important trees and shrubs in the country and knowledge of the vegetation of the area. Both then and today, knowledge of the Polish flora and vegetation was not equal for different regions; hence, the boundaries of some regions have been intuitively determined. The second regionalization [4] was based on the recognition and scaling of the potential natural vegetation of Poland [5]. This scheme also used analysis of the abiotic environment as well as landscape and syntaxonomy; in addition, for higher regions, biogeographic criteria were taken into account.

In this work, we have attempted to analyze the geobotanical distinctiveness of Pomerania on the floristic basis. The aim of this work is to answer two questions:

- Which species or groups of species distinguish the native flora of Pomerania?
- Is their presence in the studied area a sufficient basis for distinguishing a separate phytogeographic region?

Material and methods

The flora of Poland contains 2,549 native species of vascular plant. A value of 2,490 taxa was given in 2003 [6]; since then, 35 additional native species have been discovered in Poland. In current research, occurrences of all these species in Poland were analyzed on the basis of all data in the databases: the Distribution Atlas of Vascular Plants in Poland ATPOL [7], and the West Pomeranian Distribution Atlas of Plants and Fungi (ZARRiG) [8]. These databases include published, unpublished, and herbarium information on occurrences of vascular plants since the beginning of the nineteenth century. In total, 6,796,834 records were analyzed. Taxa of ranges limited to the area of Pomerania or having a clear optimum in this area, were selected: in all 57 species (2,470 data points) were further analyzed (Tab. 1). The geographical and directional elements of the species studied were distinguished according to [9–11] and the nomenclature used was after [12–14].

The maximum entropy method was used [15–19] for collective distribution analysis of 57 selected taxa.

Plant ranges in Europe were analyzed on the basis of all data in the databases: Global Biodiversity Information Facility (GBIF) [20], the Distribution Atlas of Vascular Plants in Poland (ATPOL) [7], and the West Pomeranian Distribution Atlas of Plants and Fungi (ZARRiG) [8]. In total, 57 species and 1,314,729 occurrences were analyzed. Due to the fact that the majority of data for Poland was identified by the 10 × 10-km grid (the ATPOL method, see [21]), this required us to generalize the implementation of calculations and maps in relation to Europe using this method. Therefore, a cartogram grid of 10 × 10 km was used for the entire research area (Europe) using the projection proposed by Verey [22]. Then, in Poland, the data was assigned to specific cartograms using their codes, and for areas outside Poland, based on exact geographic coordinates. The occurrence of each species in the cartogram grid was treated as one locality, for which the geographical coordinates of the center of the cartogram grid in the coordinate system ATPOL were determined. In total, 138,084 points were created in this way. The analyzes were performed using 41 environmental variables. All variables in the asc standard format were prepared on the basis of a 10 × 10-km cartogram, averaging data from the resolution of 1 × 1 km.

These works were performed in the PostgreSQL database ver. 11, using vector geometry, which was then transformed into a grid in the ATPOL coordinate system using the SAGAGIS ver. 6.3.0 software (Fig. 1). The visualization of the results was performed in the QGIS 3.4 software. Statistical analyzes were carried out in MaxEnt ver. 3.4.1.

The jackknife analysis was used to indicate the most informative variables. The accuracy and performance of species distribution models were evaluated using

Tab. 1 Vascular plant species characterizing Pomerania – geographical and directional element and syntaxonomical affiliation.

Taxon	Geographical element*	Directional element in Poland**	Syntaxonomical affiliation***
A. Species connected with salt communities mainly in Baltic coast			
Atriplex calotheca (Rafn) Fr.	CE(n)	N	Cak
Atriplex glabriuscula Edmonston	AFA		Cak
Atriplex littoralis L.	sa-ES(s)-M	N	Cak
Batrachium baudotii (Godr.) Bosch	sa-CE(d)-M(d)	N	P
Cakile maritima Scop.	CE: sat-M	N	Cak
Carex extensa Gooden.	CE: at-w-M		Ast
Carex punctata Gaudin	CE(w)-M		Ast
Centaurium littorale (Turner) Gilmour subsp. *littorale*	CE: ce-n	N	Sag
Eleocharis parvula (Roem. & Schult.) Link ex Bluff, Nees & Schauer	CB(d): c-b-o		Ast
Halimione pedunculata (L.) Aellen	CE: at-w-PAN-PONT		Ast
Honckenya peploides (L.) Ehrh.	CB: c-b-o	N	Cak
Juncus balticus Willd.	CE: ce-n	N	N-C
Myrica gale L.	CB: c-b-o	N	Al
Oenanthe lachenalii C. C. Gmel.	CE: at-w-M(w)	W	Ast
Plantago coronopus L.	CE: sat-M-IR(?)		Sag
Plantago maritima L.	sa-ES(s)	N	Ast
Puccinellia capillaris (Lilj.) Jansen	CE(n)		Ast
Puccinellia maritima (Huds.) Parl.	AFA		Ast
Sagina maritima Don	CE: at-w-M		Sag
Salsola kali L. subsp. *kali*	sa-ES(s)-M-(n)	N	Cak
Suaeda maritima (L.) Dumort.	CE: at-w-M-IR		Th-Sal
Zostera marina L.	CB: c-b-o		P
Zostera noltii Hornem.	cosmop		P
B. Species occurring in Baltic coast connected with dune communities			
Ammophila arenaria (L.) Link	CE: sat-M	N	Am
×*Calammophila baltica* (Flüggé ex Schrad.) Brand	CE: sat		Am
Elymus farctus (Viv.) Runemark ex Melderis	CE: sat-M		Am
Eryngium maritimum L.	CE: at-w-M		Am
Hippophaë rhamnoides L.	Al-A	N	R-P
Lathyrus japonicus Willd. subsp. *maritimus* (L.) P. W. Ball	CB: c-b-o	N	Am
Linaria odora (M. Bieb.) Fisch.	CE-PAN-PONT	N	Am
Salix repens L. subsp. *repens* var. *arenaria* (L.) Ser.	ES		N-C
C. Species occurring in Poland in the Pomerania only in various plant communities			
Arum maculatum L.	sa-CE(w)-M(n)	W	Q-F
Cornus suecica L.	CB: c-b-o		
Inula germanica L.	CE-PAN-PONT		Q-F
Isoëtes echinospora Durieu	CB: c-b-o	N	Lit
Isoëtes lacustris L.	ES(d)	N	Lit

Tab. 1 Continued

Taxon	Geographical element*	Directional element in Poland**	Syntaxonomical affiliation***
Lithospermum *purpurocaeruleum* L.	SM-IR		Q-F
Littorella uniflora (L.) Asch.	CE: sat	N	Lit
Lobelia dortmanna L.	CB: c-b-o	N	Lit
Myriophyllum alterniflorum DC.	CE: at-w	N	Lit
Rubus marssonianus H. E. Weber	CE		R-P
Sparganium angustifolium F. Michx.	CB(d): c-b-o		Urt
D. Species of predominantly stands in Poland occurring in Pomerania			
Aster tripolium L.	sa-ES(s)-M(n)-IR		Ast
Ajuga pyramidalis L.	CE	N, S	N-C
Alopecurus arundinaceus Poir. in Lam.	ES-IR		Ast
Angelica archangelica L. subsp. *litoralis* (Fr.) Thell.	CE(n)	N	Ph
Baeothryon cespitosum (L.) A. Dietr.	CB(d)	N, S	O-S
Blysmus rufus (Huds.) Link	AFA	N	Ast
Corydalis pumila (Host) Rchb.	CE: ce-b	W	Q-F
Gagea spathacea (Hayne) Salisb.	CE	N	Q-F
Gentianella baltica (Murb.) Börner	CE(n)		M-A
Juncus gerardi Loisel.	CB	N, W	Ast
Juncus subnodulosus Schrank	sa-CE(w): ce-b-M(n)		S-C
Lathyrus montanus Bernh.	sa-CE:-M(n)		Q-F
Luronium natans (L.) Raf.	CE: sat	N, W	Lit
Ruppia maritima L.	cosmop.	N	Rupp
Senecio aquaticus Hill	sa-CE(w)		S-C, M-A

* Explanations: AFA – Amphi-Atlantic subelement; Al-A – Altaic-Alpic subelement; CB – Circumboreal subelement; c-b-o – Circumboreal-oceanic group; CE – European-temperate subelement; at-w – Atlantic proper distributional type; ce-b – European-temperate Balkan distributional type; ce-n – European-temperate-lowland group; sat – sub-Atlantic distributional type; cosmop. – cosmopolitan element; ES – Euro-Siberian subelement; IR – Irano-Turanian element; M – Mediterranean element; PAN-PONT – Pontic-Pannonian subelement; Sa – extension in the beginning of diagnosis to the Atlantic region of Europe; SM – sub-Mediterranean subelement; (d) – disjunctive range, (n) – northern, (s) – southern, (w) – western.
** Explanations: N – northern directional element; W – western directional element.
*** Explanations: Al – *Alnetea glutinosae*; Am – *Ammophiletea arenarie*; Ast – *Asteretea tripoli*; Cak – *Cakiletea maritimae*; Lit – *Littorelletea uniflorae*; M-A – *Molinio-Arrhenatheretea*; N-C – *Nardo-Callunetea*; O-S – *Oxycocco-Sphagnetea*; P – *Potametea*; Ph – *Phragmitetea australis*; Q-F – *Querco-Fagetea*; R-P – *Rhamno-Prunetea*; Rupp – *Ruppietea maritimae*; Sag – *Saginetea maritimae*; S-C – *Scheuchzerio-Caricetea nigrae*; Th-Sal – *Thero-Salicornietea*; Urt – *Utricularietea intermedio-minoris*.

threshold-independent receiver operation characteristic (ROC) analysis and threshold dependent binomial test of omission [15,23]. The analyzes were performed in 100 replicates for MaxEnt model and five replication for jackknife analysis for each of 57 species. The 25% random points were used for testing in relation to all sites of the analyzed species. The results are presented on a scale under the ROC curve (AUC) ranging between 0 and 1. Models with an AUC value greater than 0.75 were considered acceptable models [24].

Omission rates in optimal models were less than 0.05 [25]. A map of the range distribution of the 57 species was prepared in two class value $0 < 0.6$ and $1 \geq 0.6$ as value of cloglog output which estimates the probability of presence by 10 × 10-km quadrat. At the end of the analysis, the results were added to each asc result and prepared as the sum of the distribution as asc grid with all separated species normalized to a range of 0–1.

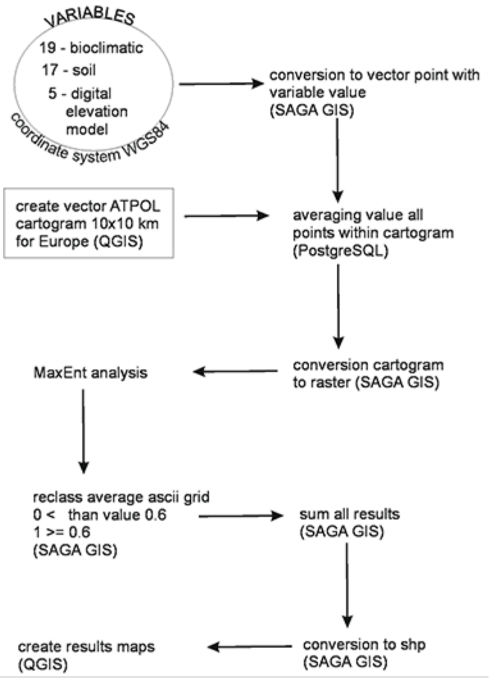

Fig. 1 Data transformation scheme.

Results

Species characterizing Pomerania

There are 57 species of plants characterizing Pomerania. They are mainly associated with the *Asteretea tripoli* vegetation class (21.0%), as well as the *Ammophiletea*, *Cakiletea*, *Littorelletea*, and *Querco-Fagetea* classes (10.5% each). The taxa analyzed represent 13 geographic elements or subelements, within which the Central-European, Circumboreal, and Central-European – Mediterranean elements dominate, and nearly half of the taxa (45.6%) represent the connective geographic element. The distributions of 32 species (56.1%) are characterized as (sub) Atlantic/oceanic (Fig. 2, Tab. 1). Of the taxa characterizing Pomerania, 47.45% represent the northern element of the Polish flora and 7.01% the western element; species of the eastern element are not present in Pomerania (Tab. 1).

Within the taxa characterizing Pomerania, four groups can be distinguished in terms of ecology and distribution patterns:

Group A contains 23 taxa associated with different vegetation in saline habitats along the Baltic coast (Fig. 3A, Tab. 1), which have a wide distribution and mainly (52.1%) belong to the connective element, where taxa occurring in the Mediterranean area are dominant (43.7%). These taxa are mostly species that live on the shores of all of Europe in salty

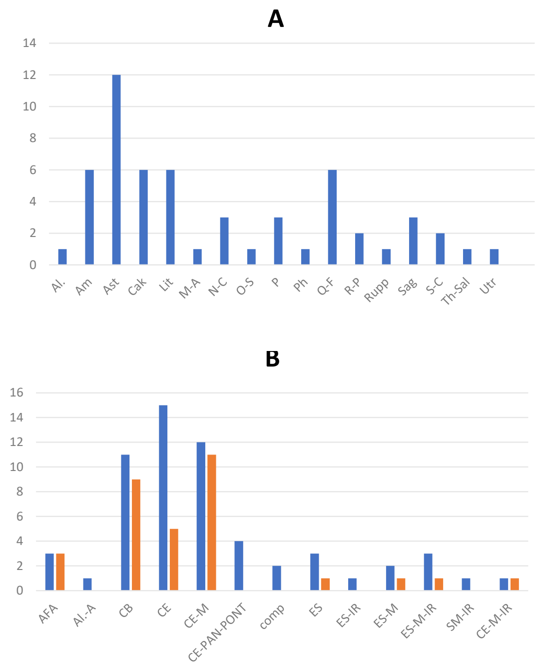

Fig. 2 Species characterized Pomerania. (**A**) Syntaxonomical affiliation. (**B**) Geographical element: general classification (blue), ranges extended to the Atlantic region of Europe (red). (**A**) Explanations: Al – *Alnetea glutinosae*; Am – *Ammophiletea arenarie*; Ast – *Asteretea tripoli*; Cak – *Cakiletea maritimae*; Lit – *Littorelletea uniflorae*; M-A – *Molinio-Arrhenatheretea*; N-C – *Nardo-Callunetea*; O-S – *Oxycocco-Sphagnetea*; P – *Potametea*; Ph – *Phragmitetea australis*; Q-F – *Querco-Fagetea*; R-P – *Rhamno-Prunetea*; Rupp – *Ruppietea maritimae*; Sag – *Saginetea maritimae*; S-C – *Scheuchzerio-Caricetea nigrae*; Th-Sal – *Thero-Salicornietea*; Urt – *Utricularietea intermedio-minoris*. (**B**) Explanations: AFA – Amphi-Atlantic subelement; Al-A – Altaic-Alpic subelement; CB – Circumboreal subelement; CE – European-temperate subelement; cosmop. – cosmopolitan element; ES – Euro-Siberian subelement; IR – Irano-Turanian element; M – Mediterranean element; PAN-PONT – Pontic-Pannonian subelement; SM – sub-Mediterranean subelement.

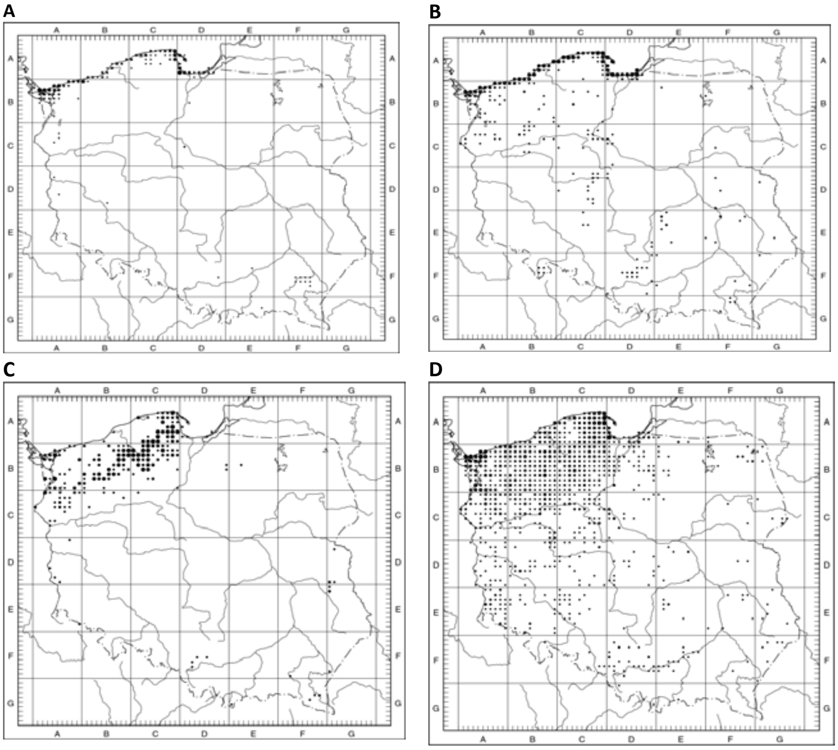

Fig. 3 Concentration of 57 species characterizing Pomerania. (**A**) Taxa associated with different vegetation on saline habitats along the Baltic coast (23 species). (**B**) Dune habitat species (eight species). (**C**) Species entirely located in Pomerania, but do not limit their occurrence only to the coastal strip (11 species). (**D**) Species that have the most numerous localities in Pomerania, but also occur in other phytogeographic parts of Poland (15 species). Data are located in a 10 × 10-km ATPOL square cartogram according to [21].

coastal habitats and also occur on the Baltic coast, despite the low salinity in that area. The largest proportion (60.9%) are associated with vegetation of salt meadows of the *Asteretea tripoli* class and dune salt communities of the *Cakiletea maritime* class.

Group B contains eight dune species that have a collective distribution along the seashore (Fig. 3B, Tab. 1). Six species are associated with the dune communities of the *Ammophiletea arenariae* class, and two with the bush communities of the *Betulo-Franguletea* class and the *Salicion arenariae* alliance. In terms of geography, most species (62.5%) show links with the oceanic/Atlantic habitats.

The next group (C) constitutes 11 species located in Poland only in Pomerania but are not limited only to the coastal strip in their occurrence (Fig. 3C, Tab. 1). They are mainly associated with the vegetation of oligotrophic lakes of the *Littorelletea* class, and forest and shrub vegetation of *Querco-Fagetea* and *Rhamno-Prunetea* classes.

The last group (D) contains 15 species that occur in large numbers of localities within Pomerania, but also occur in other phytogeographic parts of Poland (Fig. 3D, Tab. 1). They represent 10 phytosociological classes in which taxa of salt habitats of the classes *Asteretea tripoli* and *Ruppietea maritimae* (33.63%) prevail. These are taxa that, unlike the species of Group A, occur in single, inland sites; however, they occur very frequently in Pomerania.

Analysis of species distribution by MaxEnt model

From the results of the maximum entropy analysis, all the species analyzed are strictly linked to the western and the North Atlantic part of Europe (Fig. 4). Statistical evaluation of the MaxEnt model yielded an AUC value of 0.75 for both training and test (Tab. 2). The highest test AUC values (≥0.97) characterize *Calammophila baltica*, *Rubus marssonianus*, *Baeothryon cespitosum*, *Gentianella baltica*, *Salix repens* subsp. *repens* var. *arenaria*, *Alopecurus calotheca*, and *Halimione pendunculata*. In contrast,

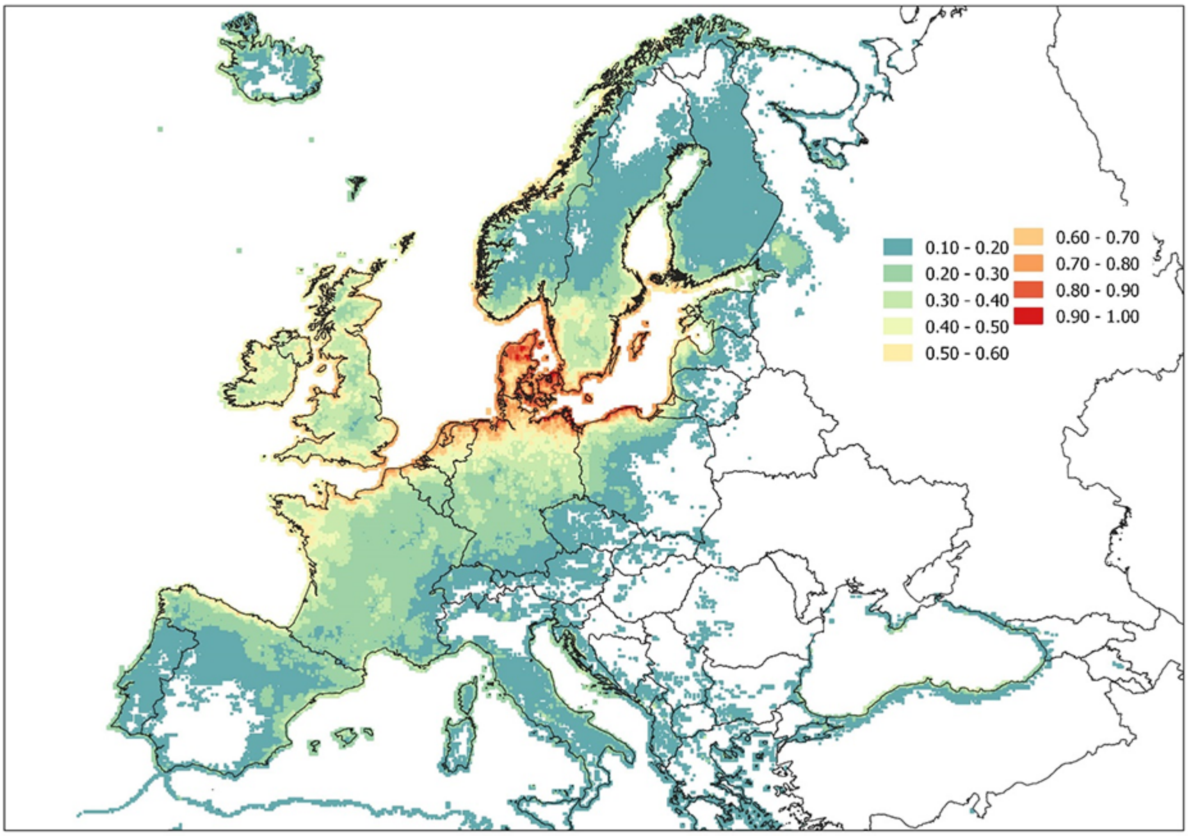

Fig. 4 Results of MaxEnt analyses: percentage (1 = 100%) of 57 species characterizing Pomerania for which the probability of occurrence ≥60%.

Tab. 2 Vascular plant species characterizing Pomerania: statistical evaluation of MaxEnt model (AUC – area under ROC curve).

Species	Training samples	Regularized training gain	Unregularized training gain	Training AUC	Test samples	Test gain	Test AUC	AUC Standard Deviation
Ajuga pyramidalis	3,657	0.848	0.906	0.8398	1,218	0.899	0.838	0.004
Alopecurus arundinaceus	825	1.404	1.611	0.9263	275	1.522	0.918	0.007
Ammophila arenaria	1,607	1.411	1.475	0.9098	535	1.453	0.908	0.004
Angelica archangelica subsp. *litoralis*	1,058	1.811	1.882	0.9406	352	1.853	0.939	0.003
Arum maculatum	6,411	0.690	0.721	0.7852	2,137	0.716	0.784	0.004
Aster tripolium	477	1.998	2.183	0.9594	159	2.069	0.953	0.005
Atriplex calotheca	240	2.762	2.956	0.9806	79	2.801	0.975	0.005
Atriplex glabriuscula	1,070	1.811	1.875	0.938	356	1.846	0.936	0.003
Atriplex littoralis	1,520	1.490	1.545	0.9167	506	1.524	0.915	0.004
Batrachium baudotii	517	1.786	1.961	0.9491	172	1.837	0.941	0.005
Baeothryon cespitosum	58	3.923	4.320	0.9953	19	4.019	0.993	0.003
Blysmus rufus	772	2.004	2.104	0.9527	257	2.054	0.950	0.003
Cakile maritima	1,911	1.237	1.293	0.8912	637	1.273	0.889	0.004
Carex extensa	1,154	1.542	1.633	0.9261	384	1.586	0.922	0.004
Carex punctata	397	1.969	2.150	0.9579	132	1.973	0.949	0.006
Centaurium litorale subsp. *littorale*	964	1.748	1.839	0.9395	321	1.797	0.937	0.004
Cornus suecica	4,617	0.829	0.882	0.82	1,538	0.878	0.819	0.004

Tab. 2 Continued

Species	Training samples	Regularized training gain	Unregularized training gain	Training AUC	Test samples	Test gain	Test AUC	AUC Standard Deviation
Corydalis pumila	450	2.366	2.524	0.9705	150	2.441	0.968	0.003
Eleocharis parvula	414	2.263	2.459	0.9688	137	2.349	0.964	0.004
Elymus farctus	395	2.073	2.273	0.963	131	2.164	0.958	0.004
Eryngium maritimum	1,183	1.573	1.653	0.9266	394	1.618	0.924	0.003
Gagea spathacea	950	2.007	2.088	0.9506	316	2.069	0.950	0.003
Gentianella baltica	32	3.624	4.344	0.995	10	3.779	0.989	0.005
Halimione pedunculata	30	2.866	3.714	0.9893	10	2.857	0.970	0.013
Hippophaë rhamnoides	2,795	0.848	0.925	0.8492	931	0.909	0.846	0.005
Honckenya peploides	2,028	1.334	1.388	0.8959	676	1.371	0.893	0.003
Inula germanica	162	2.339	2.752	0.9702	53	2.327	0.943	0.015
Isoëtes echinospora	1,968	1.137	1.212	0.8847	655	1.188	0.881	0.004
Isoëtes lacustris	2,402	1.053	1.126	0.8733	800	1.106	0.870	0.004
Juncus balticus	748	1.804	1.938	0.9472	249	1.863	0.943	0.004
Juncus gerardii	3,345	0.850	0.910	0.8432	1,115	0.901	0.842	0.004
Juncus subnodulosus	2,775	0.941	1.013	0.8533	924	0.998	0.850	0.004
Lathyrus japonicus subsp. *maritimus*	458	2.248	2.407	0.9666	152	2.295	0.962	0.003
Lathyrus montanus	698	1.909	2.101	0.9559	232	2.019	0.951	0.003
Linaria odora	29	3.514	4.419	0.9905	9	3.514	0.966	0.022
Lithospermum purpurocaeruleum	591	1.883	2.044	0.9529	196	1.926	0.946	0.005
Littorella uniflora	1,385	1.235	1.338	0.9028	461	1.294	0.898	0.004
Lobelia dortmanna	2,607	1.103	1.176	0.8753	868	1.161	0.873	0.004
Luronium natans	1,179	1.573	1.670	0.9281	392	1.632	0.925	0.003
Myrica gale	4,157	0.821	0.877	0.828	1,385	0.871	0.827	0.004
Myriophyllum alterniflorum	5,361	0.546	0.599	0.7758	1,786	0.592	0.774	0.004
Oenanthe lachenalii	1,492	1.261	1.362	0.9009	497	1.335	0.897	0.004
Plantago coronopus	5,717	0.634	0.673	0.7808	1,905	0.667	0.778	0.004
Plantago maritima	4,832	0.641	0.686	0.7987	1,610	0.680	0.797	0.004
Puccinellia capillaris	902	1.980	2.064	0.9494	300	2.020	0.947	0.003
Puccinellia maritima	1,668	1.479	1.537	0.9128	555	1.521	0.911	0.003
Rubus marssonianus	76	4.118	4.464	0.9958	25	4.345	0.995	0.001
Ruppia maritima	1,184	1.412	1.509	0.9174	394	1.460	0.913	0.004
Sagina maritima	1,484	1.410	1.484	0.9117	494	1.448	0.908	0.004
Salix repens subsp. *repens* var. *arenaria*	89	3.186	3.742	0.9916	29	3.437	0.987	0.004
Salsola kali subsp. *kali*	1,721	1.153	1.252	0.8934	573	1.220	0.889	0.004
Senecio aquaticus	3,155	1.058	1.110	0.86	1,051	1.103	0.858	0.004
Sparganium angustifolium	3,521	0.826	0.880	0.833	1,173	0.868	0.830	0.004
Sueda maritima	1,356	1.400	1.497	0.9155	452	1.455	0.912	0.004
×*Calammophila baltica*	11	4.637	5.477	0.998	3	5.219	0.997	0.002
Zostera marina	1,405	1.542	1.607	0.9207	468	1.581	0.918	0.004
Zostera noltii	445	2.160	2.323	0.9643	148	2.198	0.959	0.003

Tab. 3 Vascular plant species characterizing Pomerania: results AUC and jackknife test with high value of importance variable. For description of variables see Appendix S1.

	AUC – percent importance variable		AUC – importance variable		AUC – with only variable		"Jackknife" test of variable importance	
Species	Var.	Val.	Var.	Val.	Var.	Val.	Var.	Val.
Ajuga pyramidalis	bio04	30	bio04	36	bio05	0.74	bio05	0.44
Alopecurus arundinaceus	bio04	11	bio18	12	bio04	0.78	bio04	0.47
Ammophila arenaria	minh	52	bio07	46	bio07	0.86	bio07	1.07
Angelica archangelica subsp. *litoralis*	minh	48	bio07	24	bio02	0.87	bio02	1.02
Arum maculatum	bio14	42	bio04	34	bio14	0.75	bio07	0.54
Aster tripolium	minh	32	bio09	22	bio07	0.88	bio07	1.12
Atriplex calotheca	minh	36	bio05	40	bio05	0.91	bio09	1.45
Atriplex glabriuscula	minh	49	bio05	23	bio07	0.91	bio07	1.39
Atriplex littoralis	minh	56	minh	30	bio07	0.86	bio07	0.95
Baeothryon cespitosum	bio07	27	bio05	42	bio03	0.94	bio09	1.41
Batrachium baudotii	bio04	33	bio04	27	bio07	0.89	bio07	1.19
Blysmus rufus	minh	50	bio09	27	bio02	0.90	bio02	1.24
Cakile maritima	minh	64	minh	38	bio07	0.84	bio07	0.91
Carex extensa	minh	52	bio04	58	bio07	0.87	bio07	1.07
Carex punctata	bio04	37	bio04	39	bio04	0.88	bio04	1.18
Centaurium litorale subsp. *litorale*	minh	45	bio07	48	bio09	0.86	bio09	0.93
Cornus suecica	bio05	49	bio05	36	bio05	0.78	bio05	0.67
Corydalis pumila	bio04	28	bio04	60	bio04	0.88	bio04	1.17
Eleocharis parvula	minh	46	bio10	27	minh	0.88	minh	1.16
Elymus farctus	minh	33	bio04	27	bio06	0.90	bio06	1.36
Eryngium maritimum	minh	55	bio07	27	bio07	0.87	bio07	1.10
Gagea spathacea	bio04	22	bio04	29	bio09	0.92	bio09	1.45
Gentianella baltica	bio07	19	bio11	56	bio09	0.93	bio11	1.32
Halimione pedunculata	minh	37	bio14	25	bio18	0.91	bio18	1.24
Hippophaë rhamnoides	bio07	47	bio07	36	bio09	0.78	bio07	0.52
Honckenya peploides	minh	59	minh	35	bio02	0.86	bio02	1.03
Inula germanica	bio01	17	bio04	17	bio11	0.85	bio06	1.03
Isoëtes echinospora	s silt	22	bio01	19	bio05	0.80	bio05	0.73
Isoëtes lacustris	bio18	24	bio18	14	bio05	0.80	bio05	0.70
Juncus balticus	minh	44	bio05	35	bio02	0.87	bio02	1.12
Juncus gerardii	minh	47	bio07	31	bio07	0.78	bio07	0.58
Juncus subnodulosus	bio04	66	bio04	47	bio04	0.78	bio04	0.69
Lathyrus japonicus subsp. *maritimus*	minh	48	bio05	54	bio02	0.90	bio02	1.37
Lathyrus montanus	bio07	30	bio10	15	bio09	0.85	bio09	0.90
Lithospermum purpurocaeruleum	bio15	25	bio04	19	bio09	0.87	bio04	1.02
Linaria odora	minh	27	bio09	34	bio01	0.93	bio09	1.19
Littorella uniflora	bio07	29	bio07	23	bio09	0.83	bio07	0.82
Lobelia dortmanna	bio18	25	bio18	26	bio05	0.80	bio05	0.68
Luronium natans	bio14	26	bio07	32	bio09	0.88	bio09	1.04
Myrica gale	bio14	24	bio05	27	bio05	0.74	bio05	0.44
Myriophyllum alterniflorum	t silt	15	bio07	11	bio05	0.70	bio05	0.27
Oenanthe lachenalii	bio04	57	bio04	45	bio04	0.83	bio04	0.92

Tab. 3 Continued

Species	AUC – percent importance variable		AUC – importance variable		AUC – with only variable		"Jackknife" test of variable importance	
	Var.	Val.	Var.	Val.	Var.	Val.	Var.	Val.
Plantago coronopus	bio04	56	bio04	37	bio04	0.75	bio04	0.53
Plantago maritima	bio07	35	bio07	15	bio07	0.75	bio07	0.46
Puccinellia capillaris	min h	48	bio05	26	bio02	0.90	bio02	1.32
Puccinellia maritima	minh	55	bio07	61	bio07	0.88	bio07	1.21
Rubus marssonianus	bio08	21	bio04	33	bio09	0.98	bio09	2.44
Ruppia maritima	minh	59	bio07	26	bio07	0.84	bio07	0.91
Sagina maritima	minh	48	bio07	51	bio07	0.88	bio07	1.17
Salix repens subsp. *repens* var. *arenaria*	minh	26	bio10	14	bio10	0.91	bio02	1.16
Salsola kali subsp. *kali*	bio04	33	bio09	30	bio04	0.80	bio04	0.69
Senecio aquaticus	bio14	43	bio04	43	bio09	0.81	bio09	0.77
Sparganium angustifolium	s silt	25	bio10	14	bio05	0.78	bio05	0.62
Sueda maritima	minh	47	bio04	49	bio07	0.86	bio07	1.00
×*Calammophila baltica*	bio11	32	bio11	43	bio06	0.98	bio11	1.79
Zostera marina	minh	64	minh	34	bio07	0.87	minh	1.09
Zostera noltii	minh	44	bio07	36	bio07	0.91	bio07	1.56

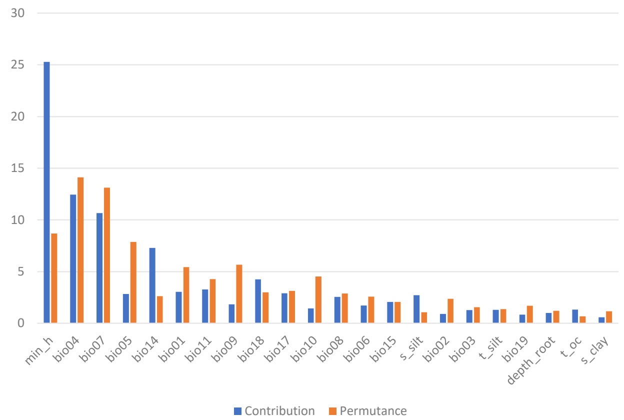

Fig. 5 Average contribution and permutation value of the variable in MaxEnt model (only variable where value ≥1).

the lowest AUC values (<0.8) characterize *Myriophyllum alterniflorum*, *Plantago coronopus*, *Arum maculatum*, and *Plantago maritima*.

Variables with the highest training and test values when considered separately are temperature annual range (bio07) and the mean temperature of driest quarter (bio09) (Tab. 3). Variables with highest average contributions are minimum high (min_h), temperature seasonality (bio04), and temperature annual range (bio07). The highest average permutation values are for bio04 and bio07 (Fig. 5).

Discussion

The vascular flora of Pomerania contains 57.5% of the native flora of Poland (1,467 species). Taking into account that new floristic studies have not been conducted for many regions of Pomerania and that only the more interesting species (e.g., rare or invasive taxa) are listed for other areas, it should be assumed that this percentage will increase in the future. In addition, research on critical groups such as *Taraxacum* or *Rubus* can add many new taxa to the flora of Pomerania. Compared to the data from Poland, the flora of Pomeranian dandelions is quite rich (more than 30%) [7]. New discoveries can also be expected in the genus *Hieracium*, and for this it is necessary to intensify the collection of herbarium materials, which have currently been very poor.

The geobotanical research of Czubiński [26] gave a partial answer to the question of whether geographical or edaphic groups of species characterize Pomerania in relation to other areas of Poland. These data were mainly used by Szafer [3] to assess the phytogeographic characteristics of Pomerania, and determined that this region is distinguished by a few ecological groups of taxa, such as lobelia species, species associated with the moraine belt, forest species of the sea coast, and, finally, mountain species. A different division from that of Szafer [3] was suggested by Matuszkiewicz [4] based mainly on potential vegetation and geographic criteria. Both studies indicated areas located east of the Vistula River belonged to the Baltic [3] and Pomeranian division [4] and indicate the area located to the south of the frontal moraine belt as the southernmost border of the region.

Our approach coincides with that presented by Szafer [3], but species were chosen slightly differently. We only considered taxa with ranges limited to the area of Pomerania or having a clear optimum in this area. For this reason, we did not use mountain species, as their ranges are not limited solely or predominantly to Pomerania. It should be emphasized that our research was based on far more complete data compared with Szafer [3]. Our analysis showed that there are 57 such species. Compared to Poland [10], analysis of the geographical element of the species discussed show very similar patterns, mainly domination by Central-European, Circumboreal, and connective elements; in the latter, Mediterranean elements prevail. Of the taxa analyzed, 56.1% of species have an oceanic/Atlantic distribution, which seems to be characteristic for the region studied. The species characterizing Pomerania principally represent vegetation classes connected to salty and dune habitats, as well as lobelia lake and deciduous forest habitats. These are distinguishing features against the background of Poland (see [14]). Another source for assessing the legitimacy of distinguishing Pomerania as a high-ranking phytogeographic unit is research on the directional elements of Poland's flora [9–11]. The vast majority of the Polish flora are transitional species that do not have range limits in Poland (about 56%), and southern taxa that have their northern limits in Poland (about 23%). In contrast, close to half of species currently used for distinguishing Pomerania represent the northern element (47.45%), with 3.2% of the Polish flora belonging to this element. Of the species analyzed, 10.5% are assigned to the western element, and most have the southeastern limit of their distribution in Pomerania. Species of the eastern element serve to distinguish Pomerania by their absence.

Maximum entropy analysis is often used to estimate the actual or potential distribution of species as a function of environmental variables by quantifying the relationship between plant distribution and these variables. This method is used, e.g., in modeling historical ranges, to indicate a possible Pleistocene refuge, as well as to research possible variations in ranges due to climate change (e.g., [27–29]). Maximum entropy analysis has also been used in biogeographic regionalization [30–32] and in our opinion is useful to distinguish the Pomerania region floristically. The MaxEnt analysis showed that the most important environmental variables are minimum high (min_h), temperature annual range (bio07), and mean temperature of driest quarter (bio09) (Tab. 3). All selected species clearly distinguish Pomerania against the background of Poland (Fig. 6). Against the background of Europe, this area is mainly distinguished by species with ranges limited to the western part of the Baltic Sea basin: *Calammophila baltica*, *Rubus marssonianus*, *Baeothryon cespitosum*, *Gentianella baltica*, *Salix repens* subsp. *repens* var. *arenaria*, *Alopecurus calotheca*, and *Halimione pendunculata* (Fig. 4, Tab. 2).

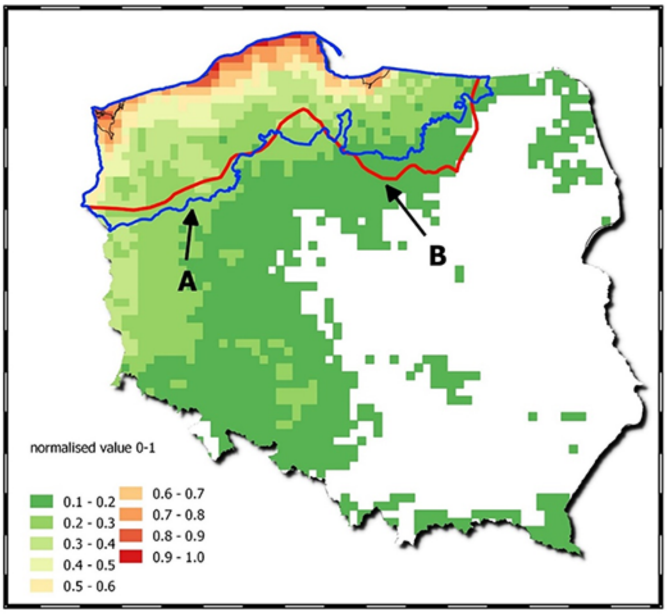

Fig. 6 Results of the MaxEnt analyses of the normalized sum averaged by 100 outputs grids where the bootstrap model is equal or higher than 0.6. (**A**) Southern border of geobotanical distinction of Pomerania according to Matuszkiewicz [4]. (**B**) Southern border of geobotanical distinction of Pomerania according to Szafer [3].

This method allowed us also to verify the boundaries of the region and suggest new criteria for their definition (Fig. 7). According to our results, the limits proposed by Szafer [3] and Matuszkiewicz [4] are thought to be too wide. Both authors accepted the belt of glacial outwashes as the southern border of the Pomerania geobotanical region. Moreover, the area of the Iława and Olsztyn districts lying to the east of the Vistula also included in Pomerania by these authors. Our results indicate that, if we assume the possibility of occurrence of species ≥40%, then the southern limit of the discussed area should run on the northern boundary of the terminal moraine belt and along the Pradolina Pomorska (Fig. 7). Also, the

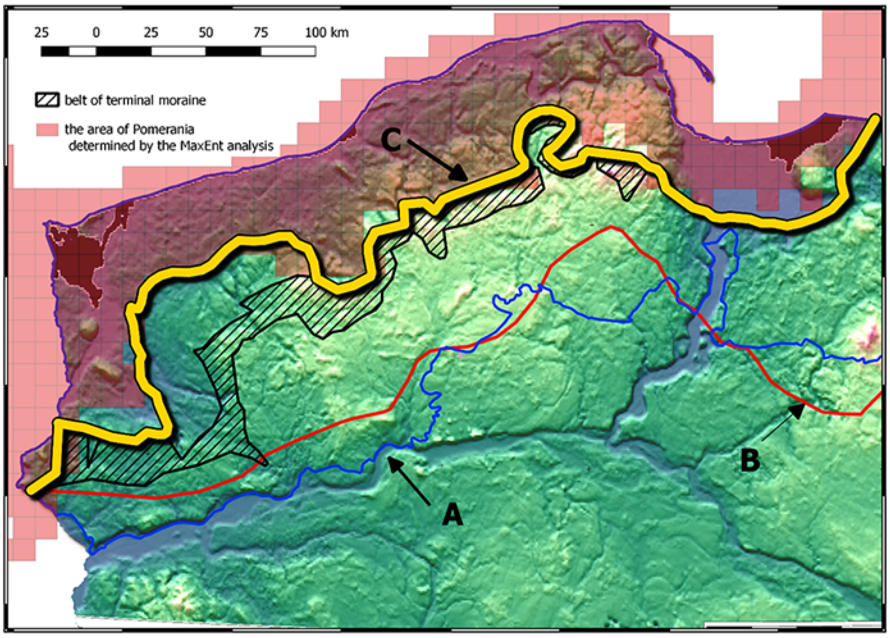

Fig. 7 Results of the MaxEnt analyses of the normalized sum averaged by 100 outputs grids where the bootstrap model is equal or higher than 0.6. (**A**) Southern border of geobotanical distinction of Pomerania according to Matuszkiewicz [4]. (**B**) Southern border of geobotanical distinction of Pomerania according to Szafer [3]. (**C**) Southern border of geobotanical distinction of Pomerania according to current research.

area east of the Vistula (except the Żuławy Wiślane region) does not contain abundant representatives of the flora characteristic of Pomerania. In the same way, Popiela [33] took the Vistula River as the eastern boundary of Pomerania when discussing forest species, as well as Sotek [34] and Sotek et al. [35]. It should also be emphasized that the western element of vascular flora has a clear border at the Vistula [9]. The area of Pomerania in Poland in geobotanical terms may be rather broadly connected with the areas of the North Sea basin and the western part of the Baltic Sea basin (Fig. 4). The results of the present study may be used for a broader discussion on the revision of the geobotanical division of Poland, at least in its northern part.

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Supplementary material

The following supplementary material for this article is available at http://pbsociety.org.pl/journals/index.php/asbp/rt/suppFiles/asbp.3619/0:

Appendix S1 Environmental factors used in entropy implemented analysis.

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