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 Notec rivers in the south. The region occupies an area of 52,000 km², 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

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Competing interests
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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: cc-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                         |
| Salsoila 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                          |
| ×Calamamphila 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                         |
| Corrus 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                         |
threshold-independent receiver operation characteristic (ROC) analysis and threshold-dependent binomial test of omission [15,23]. The analyses 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 ≥ 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.
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 Ammophilettea, 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. 1** Data transformation scheme.

**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 – Ammophilettea arenaria; Ast – Asteretea tripoli; Cak – Cakiletea maritima; Lit – Littorelletea uniflorae; M-A – Molinoio-Arrhenatheretea; N-C – Nardo-Callinetea; O-S – Oxyccoco-Sphaginetea; P – Potametereteea; Ph – Phragmitettea australis; Q-F – Querco-Fagetea; R-P – Rhamno-Prunetea; Rupp – Ruppiettea maritima; Sag – Saginettea maritima; S-C – Scheuchzerio-Caricetea nigrae; Th-Sal – Thero-Salicorniettea; Urt – Utriculariettea intermedio-minorit. (B) Explanations: AFA – Amphi-Atlantic subelement; Al-A – Altai-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.
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,
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 glabrioscida                        | 1,070            | 1.811                     | 1.875                       | 0.9167       | 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. litorale          | 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                  |

Fig. 4  Results of MaxEnt analyses: percentage (1 = 100%) of 57 species characterizing Pomerania for which the probability of occurrence ≥60%.
| Species                  | Training samples | Regularized training gain | Unregularized training gain | Training AUC | Test gain | Test samples | 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                  |
| Geaea 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                  |
| Honkenya 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 odor a           | 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 dortmannia      | 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                  |
| ×Calamophila 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.

| 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      | bio16| 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 glabriscula                        | 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 |
| Capitella 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 |
| Centaurea 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 | 47   | 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 |
| Honkenya 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 |
| Lathyra japonica 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 purpureostraulem               | bio15| 25   | bio04| 19   | bio09| 0.87 | bio04| 1.02 |
| Linaria odora                               | minh | 27   | bio09| 34   | bio01| 0.93 | bio09| 1.19 |
| Lithottella uniflora                        | bio07| 29   | bio07| 23   | bio09| 0.83 | bio07| 0.82 |
| Lobelia dortmannia                          | bio18| 25   | bio18| 26   | bio05| 0.80 | bio05| 0.68 |
| Lunaria 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 lachenii                           | bio04| 57   | bio04| 45   | bio04| 0.83 | bio04| 0.92 |
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 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: *Calamophila baltica*, *Rubus marssonianus*, *Baeothryon cespitosum*, *Gentianella baltica*, *Salix repens subsp. repens var. arenaria*, *Alopecurus calotheca*, and *Halimione pendunculata* (Fig. 4, Tab. 2).

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).
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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