Acta Societatis Botanicorum Poloniae

ORIGINAL RESEARCH PAPER Acta Soc Bot Pol 84(4):431–438 DOI: 10.5586/asbp.2015.035
Received: 2015-02-02 Accepted: 2015-10-09 Published electronically: 2015-12-03

Modeling the potential distribution of three lichens of the *Xanthoparmelia pulla* group (Parmeliaceae, Ascomycota) in Central Europe

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Abstract

The paper presents models of potential geographical distribution of *Xanthoparmelia delisei*, *X. loxodes*, and *X. verruculifera* in Central Europe. The models were developed with MaxEnt (maximum entropy algorithm) based on 224 collection localities and bioclimatic variables. The applied method enabled to identify the areas where climatic conditions are the most suitable for modeled species outside their known localities. According to obtained model, high potential distribution of the *X. delisei* and *X. loxodes* was found in the northern and northeastern Poland, when areas most suitable for *X. verruculifera* were placed in the south, especially in the Carpathians. Model also suggests that potential distribution of *X. delisei* could be wider than known data on its occurrence and extend to Lithuania, Belarus and the Czech Republic. MaxEnt modeling of *X. loxodes* showed the widest potential distribution for this species in Central Europe with the best regions in Lithuania. Potential distribution in all models was strongly influenced by precipitation-related variables. All the modelled species prefer areas where precipitation in the coldest quarter is very low.

Keywords: niche modeling; MaxEnt, biogeography; parmelioid lichens; *Xanthoparmelia delisei*; *X. loxodes*; *X. verruculifera*

Introduction

The genus *Xanthoparmelia* is one of the largest within the Parmeliaceae, including over 800 species of lichen-forming fungi [1,2]. Most of these grow on siliceous rocks in dry and well-sunlit places, including arid and semiarid Mediterranean climates. The genus is widespread throughout the world and considered to be cosmopolitan [3], although its representatives occur mainly in the southern hemisphere [4].

The *Xanthoparmelia pulla* group includes about 25 taxa of worldwide distribution, seven of which occur in Europe [5]. Due to the brown color of the thalli, and lack of atranorin, usnic and isousnic acids in the upper cortical layer, these species have been until recently classified as a separate genus *Neofuscelia* Essl. However, molecular studies have shown that *Neofuscelia* genus was polyphyletic, with the clades scattered within *Xanthoparmelia* [1]. Consequently, the species of *Neofuscelia* genus have been synonymized with *Xanthoparmelia*.

Till now, four taxa of *X. pulla* group have been recorded in Poland: *Xanthoparmelia delisei*, *X. loxodes*, *X. pulla*, and *X. verruculifera* [6]. However, as proved by recent taxonomic studies [6], their distribution in the country and ecology seem to be other than previously thought. In the light of these data, the aim of the study was modeling the potential geographical distributions of the mentioned species on the area of whole Poland as well as in neighboring countries in Central Europe. Species potential distribution modeling, also known as niche or habitat modeling [7], is a method that enables to identify the areas where ecological factors are the most favorable for the species outside their known localities. It is a tool which has been used for many years in such fields as biogeography, ecology, agriculture, horticulture, forestry and conservation biology [7,8]. One of the best performing distribution-modeling technique for analysis of the presence-only data is MaxEnt – maximum-likelihood modeling method based on the maximum entropy principle [9–13]. Developed MaxEnt models allow us to indicate the new areas where discussed species may probably occur. It is especially important for those taxa which are considered as a rare in Poland. Furthermore, modeling distribution of those species enables to better understand their climate requirements and to identify the factors that determine their occurrence in this area. Recognition of distribution of species and parameters affecting their distribution is also necessary for the estimation and protection of local and global biodiversity.

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Handling Editor: Joanna Zalewska-Gałosz

Material and methods

Study material

The study involved herbarium specimens representing three species of the *Xanthoparmelia pulla* group. Potential geographical distribution models were developed using 50 localities of *X. delisei*, 63 of *X. loxodes* and 111 of *X. verruculifera*. Potential distribution of *X. pulla* was not modeled due to the lack of sufficient number of specimens needed to perform the analyzes. The studied material originated from 13 Polish herbaria (BSG, GPN, KRA, KRAM-L, KRAP, KTC, LOD-L, OLTC-L, POZ-L, TRN, UGDA, WA, WRSL) and private collections (herb. M. Dimos-Zych, herb. P. Grochowski, herb. W. Gruszka, herb. M. Kossowska, herb. L. Lipnicki, herb. K. Pietrzykowska and herb. K. Szczepańska). In order to avoid the errors arising from incorrect identification of taxa, all specimens were subjected to a detailed analysis of their morphological and chemical properties. Thin-layer chromatography was employed according with the methods described by Orange et al. [14].

Climatic variables

Climatic data with a height resolution [30 arc-seconds (~1 km)] were used for the analysis of the current distribution of *Xanthoparmelia delisei*, *X. loxodes*, and *X. verruculifera* in Central Europe. We used 20 bioclimatic and topographic variables (Tab. 1) downloaded from World-Clim dataset: http://www.worldclim.org. The climatic conditions were interpolated on the basis of the monthly recorded data, from the years 1950–2000 [15].

Data preparation

Before modeling a correlation matrix calculated in ENMTools software version 1.3 was used to determine a multicolinearity between the environmental variables [16]. The variables with a cross-correlation coefficient value above 0.6, elimination of which did not result in a loss of information on climatic conditions in the study area, were excluded from the analysis. Based on the obtained results we decided to use only 6 environmental variables in MaxEnt modeling: precipitation in the coldest quarter (bio 19), precipitation in the warmest quarter (bio 18), precipitation seasonality (bio 15), mean temperature of the wettest quarter (bio 8), annual temperature range (bio 7) and altitude.

Model building

The modeling was carried out using MaxEnt software version 1.4.3 [9,10]. The analyzes were carried out for the logistic output format with maximum of 500 iterations and the maximum of background points 10 000 [17]. The area under the receiving operator curve (AUC) was used to evaluate the resulting models. The AUC values above 0.9 indicated high model accuracy, AUC values from 0.7 to 0.9 indicated moderate model accuracy and AUC values from 0.5 to 0.7 indicated low model accuracy [18–20]. Generated maps of potential distribution of the studied species were characterized by a range of values from 0 to 1, where the values >0.6 represented "high potential", 0.4–0.6 "good potential", 0.2–0.4 "moderate potential", and <0.2 "least potential" class [17]. The Jackknife test was used to estimate the importance of the climatic variables predicting the distribution of the studied species.

Tab. 1 Environmental variables used in a ENMTools and Maxent software.

Variable code	Variable type	Data source
Alt	Altitude	WorldClim
Bio 1	Annual mean temperature	WorldClim
Bio 2	Mean diurnal range: mean of monthly (max temp – min temp)	WorldClim
Bio 3	Isothermality: (Bio2/Bio7) × 100	WorldClim
Bio 4	Temperature seasonality (*SD* × 100)	WorldClim
Bio 5	Maximum temperature of warmest month	WorldClim
Bio 6	Minimum temperature of coldest month	WorldClim
Bio 7	Temperature annual range (Bio5 – Bio6)	WorldClim
Bio 8	Mean temperature of wettest quarter	WorldClim
Bio 9	Mean temperature of driest quarter	WorldClim
Bio 10	Mean temperature of warmest quarter	WorldClim
Bio 11	Mean temperature of coldest quarter	WorldClim
Bio 12	Annual precipitation	WorldClim
Bio 13	Precipitation of wettest month	WorldClim
Bio 14	Precipitation of driest month	WorldClim
Bio 15	Precipitation seasonality (coefficient of variation)	WorldClim
Bio 16	Precipitation of wettest quarter	WorldClim
Bio 17	Precipitation of driest quarter	WorldClim
Bio 18	Precipitation of warmest quarter	WorldClim
Bio 19	Precipitation of coldest quarter	WorldClim

Results

Xanthoparmelia delisei

The AUC value was 0.970, thus confirming high accuracy of the potential distribution model for *X. delisei*. High potential distribution of the studied species (>0.6) was found in the northeastern and central part of Poland, especially in the Greater Poland and Mazovian Lowlands, together with mezoregions of Tuchola Forest, Ciechanow Plateau, Suwalki Lakeland and Bialystok Plateau. In the western part of Belarus, the potential distribution of *X. delisei* included Vawkavysk Plateau and the region of Polesia. In the Ukraine, high potential distribution was found in the western parts of Polesia and Volhynian Upland. Optimal climatic conditions for *X. delisei* were also found in the Lusitan Mountains and the Central Bohemian Uplands (Czech Republic), and in the Thuringian Forest (Germany). Good (0.4–0.6) and moderate (0.2–0.4) potential distribution of *X. delisei* included majority of eastern and central parts of Poland, central part of Lithuania, western parts of Belarus and Ukraine and a central part of the Czech Republic. The regions found unsuitable for *X. delisei* included the western, north-western and northern part of Poland, that is the Pomeranian Lakeland together with the Slovincian Seashore and the north part of the Masurian Lakeland, and the south of the country, especially the Carpathian Mountains and their foothills. Outside Poland, unsuitable climatic conditions for *X. delisei* occurred in the central part of Volhynian Upland and the region of Podolia (Ukraine), southwestern part of the Czech Republic and within about 96% area of Slovakia (Fig. 1).

The Jackknife test showed that precipitation of the coldest quarter and precipitation seasonality were the most important factors affecting *X. delisei* distribution (Fig. 2).

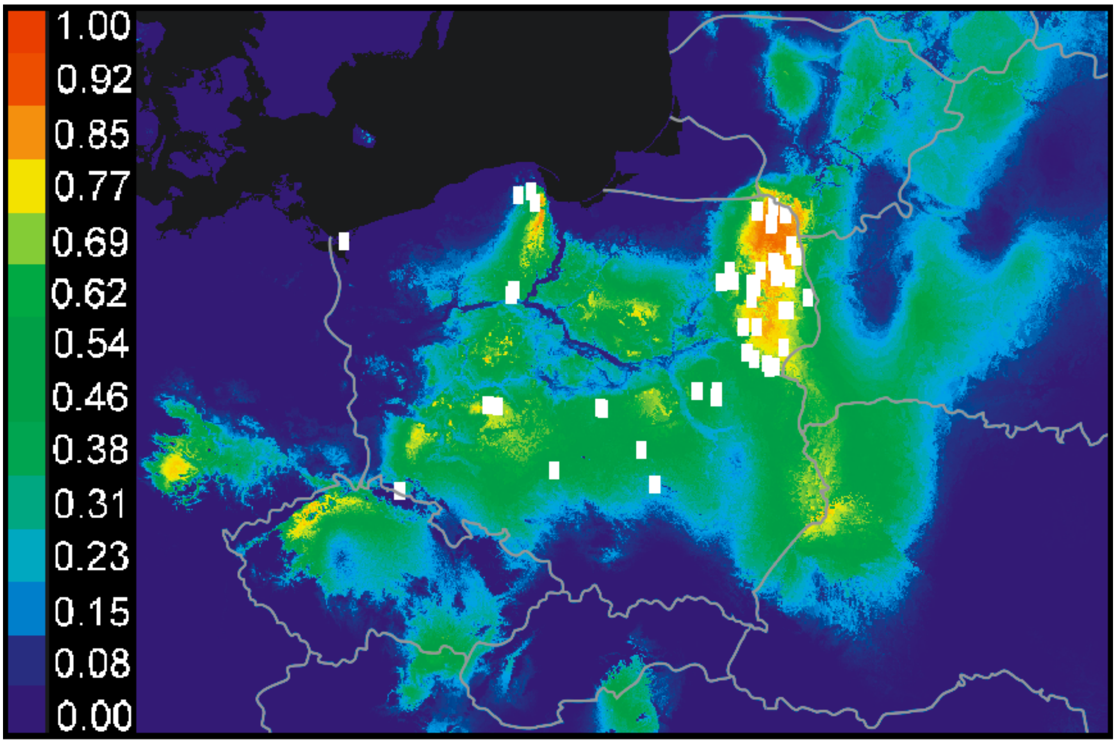

Fig. 1 The potential distribution of *Xanthoparmelia delisei* in the Central Europe.

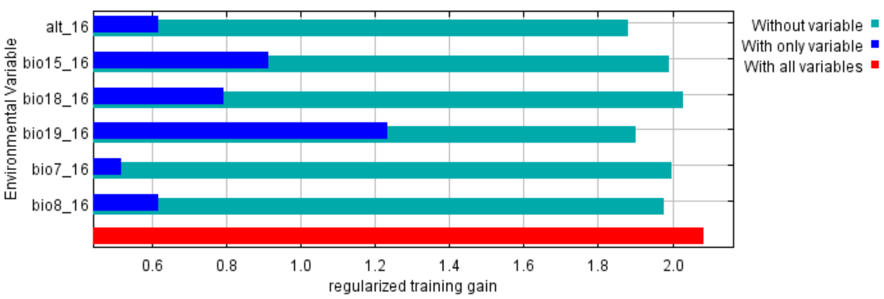

Fig. 2 The Jackknife test of the environmental variables used in the *Xanthoparmelia delisei* potential distribution modeling.

Xanthoparmelia loxodes

The model of potential distribution of *X. loxodes* exhibited high accuracy with 0.944 AUC value. High potential distribution (>0.6) of the studied species was found in Poland in the Silesian Lowlands and in the mezoregions of Tuchola Forest and Suwalki Lakeland. Outside Poland, high potential distribution was found in the Samogotian Lakeland (Lithuania), Volhynian Upland (Ukraine), Central Bohemian Uplands (Czech Republic) and in the Thuringian Forest (Germany). Good (0.4–0.6) and moderate (0.2–0.4) potential distribution of *X. loxodes* was found in the northern, central and southern part of Poland, the majority of Lithuania, western part of Belarus and Ukraine, and about 90% area of the Czech Republic. The regions with unsuitable climatic conditions for this species in Poland were: Szczecin Lowland, central part of the Slovincian Seashore, Mysliborz Lakeland, Lubusz Lakeland, Kutno Plain, Siedlce Plateau and the Carpathians with their foothills. The lowest potential was found in the Belarusian region of Zagorod'ye, in the central part of Volhynian Upland and Podolia in the Ukraine, and in 88% area of Slovakia (Fig. 3).

The Jackknife test showed that precipitation in the coldest quarter and precipitation seasonality were the factors influencing *X. loxodes* distribution (Fig. 4).

Xanthoparmelia verruculifera

The AUC value was 0.961, thus confirming high accuracy of the model of potential distribution of *X. verruculifera*. High potential distribution of the studied species (>0.6) was found in the southern part of Poland, especially in the Carpathian Mountains, and in the easternmost part of the country, namely in the mezoregion of Suwalki Lakeland and the Polish part of Roztocze region. Good (0.4–0.6) and moderate (0.2–0.4) potential distribution of *X. verruculifera*

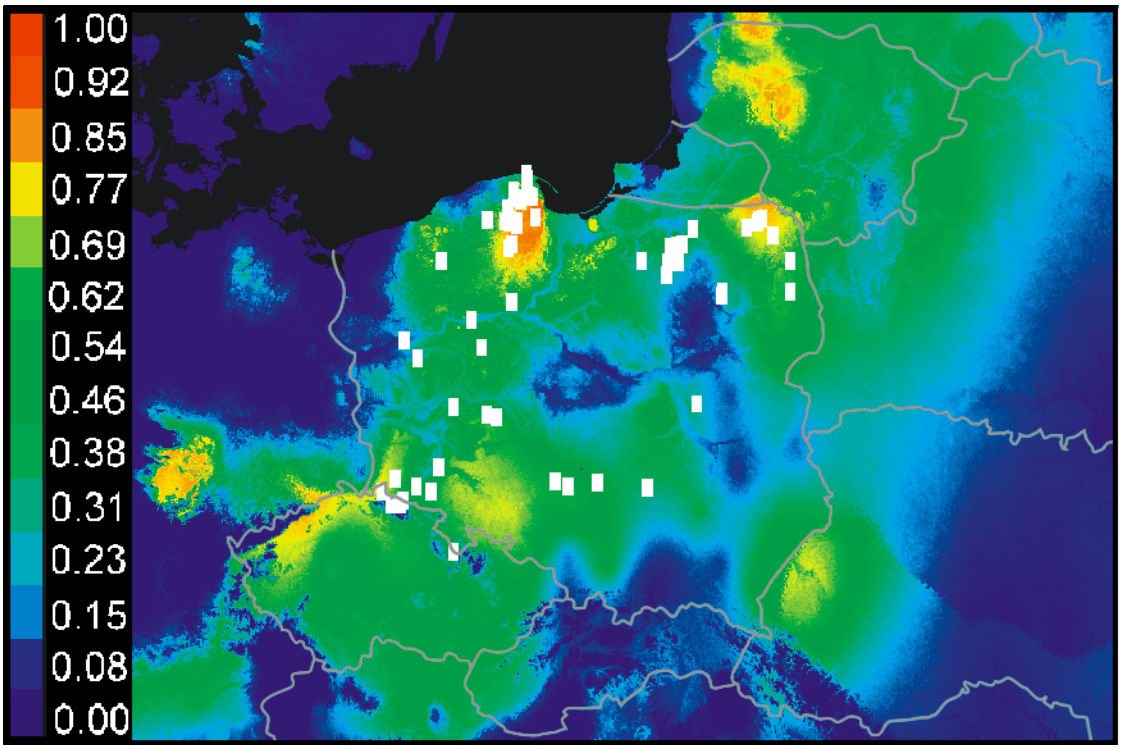

Fig. 3 The potential distribution of *Xanthoparmelia loxodes* in the Central Europe.

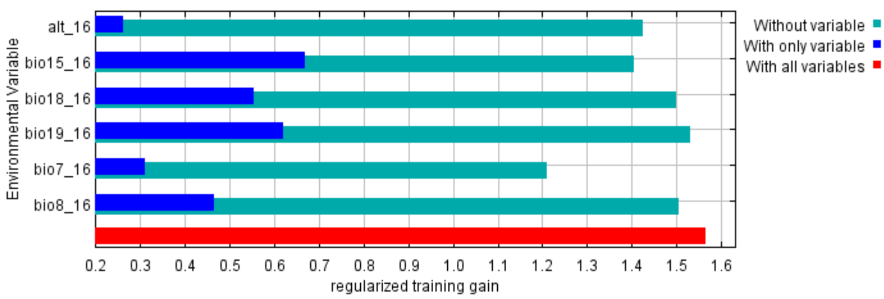

Fig. 4 The Jackknife test of the environmental variables used in the *Xanthoparmelia loxodes* potential distribution modeling.

was found in the central, southern and eastern part of Poland, the western part of Belarus and the western part of Ukraine, especially in the region of Roztocze and Podolia. In the Czech Republic, good and moderate potential distribution of the studied species was found in the Central Bohemian Uplands, the Lusitan Mountains, the Elbe Lowland, the Drahany Upland, and the westernmost part of the Carpathians (Hostyn Mts). The regions with unsuitable climatic conditions for *X. verruculifera* included the western part of Poland, especially the mezoregions of Szczecin Lowland and Lubusz Lakeland, and the Slovincian Seashore and part of the Masurian Lakeland in the north. Outside Poland, the lowest potential was found in the region of Zagorod'ye (Belarus), in the central part of Podolia and Volhynian Upland (Ukraine), in the western and eastern part of Slovakia, and the southwestern part of the Czech Republic (Fig. 5).

The Jackknife test showed that precipitation in the coldest quarter and precipitation seasonality were the factors influencing *X. verruculifera* distribution (Fig. 6).

Discussion

Most of the lichens belonging to the genus *Xanthoparmelia*, together with the species of *X. pulla* group, are considered cosmopolitan as they occur throughout the world, including most of the European countries [3,21,22]. However, in many regions, e.g., in the central and eastern parts of Europe, the data illustrating local ranges and habitat requirements of particular species are still scarce and incomplete. The models generated in this study using MaxEnt suggest much broader areas of potential distribution of the three *Xanthoparmelia*

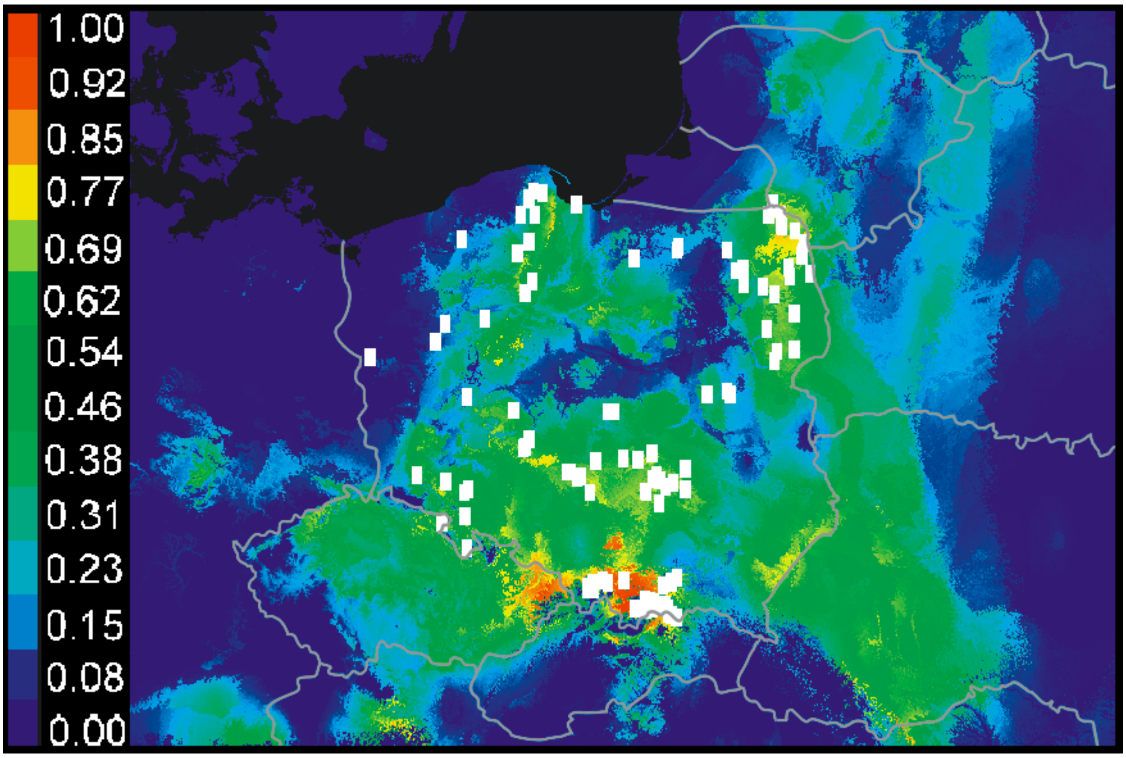

Fig. 5 The potential distribution of *Xanthoparmelia verruculifera* in the Central Europe.

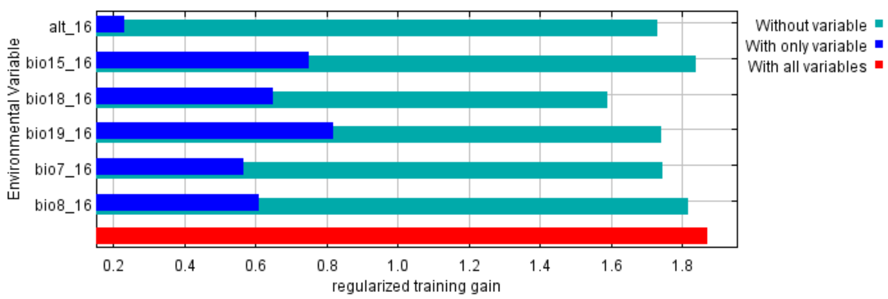

Fig. 6 The Jackknife test of the environmental variables used in the *Xanthoparmelia verruculifera* potential distribution modeling.

pulla group species investigated here, both on Polish territory and beyond, compared with their known records.

The first of the investigated species, *Xanthoparmelia delisei* is, as proved in the recent study [6], much more frequent in Poland than it was previously thought and occurs especially in the central and northeastern lowland regions of the country. According to the MaxEnt model, these areas represent the most suitable climatic conditions for *X. delisei*. However, there is some probability to find new localities of this species on the modeled area, for example in the southeastern part of the country (the Lublin Upland).

In the Central and Eastern Europe, *X. delisei* was reported from Germany, Russia and Ukraine [21,22] which is also confirmed by the obtained MaxEnt model. However, result of the model suggests that the potential distribution of this taxon could be wider and also extend to Lithuania, Belarus and the Czech Republic.

Another species belonging to this group, *Xanthoparmelia loxodes*, has a similar range in Poland as *X. delisei*, with distinct concentration of localities in the central and northeastern parts of the country [6]. This taxon also avoids higher altitudes, as confirmed in the literature [23,24], and has not been recorded in the Carpathians till now. MaxEnt modeling showed similar regions in Poland (e.g., the Tuchola Forest and the Suwalki Lakeland) with optimal climatic conditions for both *X. loxodes* and *X. delisei*. In addition, unsuitable regions for both species include the Slovincian Seashore, the Carpathian Foothills and the Carpathian Mountains, which are the areas with the highest annual precipitation in Poland [25]. These observations seem to confirm the hypothesis that these two species represent a small intergrading morphotypes of a single species, as suggested by some authors [26]. A similar situation was observed in Italy, where *X. delisei* and *X. loxodes* showed completely overlapping distributions and similar ecological requirements [24]. Both *X. delisei* and *X. loxodes* do not occur in mountainous areas. However, an important factor determining their occurrence in the generated models is not altitude, but air humidity. The absence of these taxa in mountainous area is probably connected with a clear preference of these two taxa for the areas of low annual precipitation. Thus, they avoid the regions of higher altitude, where the climate is generally more humid.

Xanthoparmelia loxodes seems to have the widest geographical range in Central and Eastern Europe, as compared with *X. delisei* and *X. verruculifera*. Currently, it has been recorded in the Czech Republic, Germany, Lithuania, Russia and Ukraine [21,22,27]. There are no known reports of this species from Belarus and Slovakia, although the MaxEnt modeling showed moderate probability of finding it in both countries.

The third of the studied species, *X. verruculifera*, was considered to be endangered in Poland [28]. However, the results of a recent study [6] proved that this taxon was widely dispersed from the lowlands to the lower mountain regions. At the same time, it is the only representative of *X. pulla* group that occurs in the Carpathian Mountains. These observations are consistent with the predicted distribution model, based on which it can be concluded that a significant part of Poland features climatic conditions suitable for *X. verruculifera*. However, some new localities of this species may be found, especially in south-eastern part of the country (the Lublin Upland). Moreover, the model suggests that, unlike in the case of *X. delisei* and *X. loxodes*, optimal conditions for *X. verruculifera* prevail in the southern part of Poland, although it was recorded with equal abundance in the central and northern regions of the country. This is probably due to the highest range of tolerated humidity, as compared to the other two species, so *X. verruculifera* can occur in areas with slightly higher annual precipitation, including low mountains.

The species has been found in many countries of Central and Eastern Europe, such as: Belarus, Czech Republic, Germany, Lithuania, Russia, Slovakia and Ukraine [21,22], which was also confirmed in the generated model.

Most species in *Xanthoparmelia* prefer habitats in arid and sub-arid regions [4,24]. However, an important parameter determining their potential distribution is the air humidity [24]. The variables most often represented in the models and holding the highest predictive power in the presented MaxEnt analyzes are those related to precipitation, while the variables related to temperature are less strongly represented. It may be explained by the fact that precipitation and air humidity are the primary sources of water for the lichens, which they absorb over the entire surface of the thallus. In turn, proper hydration allows for the regulation and appropriate course of physiological processes, such as gas exchange, nitrogen fixation and photosynthesis [29–31]. Therefore, all the environmental factors that affect the period of thallus hydration are crucial for the lichen growth, and they are also significant for modeling potential ecological niches. Many lichens have a relatively wide range of temperature tolerance [32]. Therefore, this factor may play a less important role in predicting ecological distributions. The results of our niche modeling analyzes suggest that the examined species of *Xanthoparmelia pulla* group prefer the driest areas in Europe during the coldest quarter. The most important variables that determine the distribution ranges of all three modeled species are precipitation seasonality and precipitation of the coldest quarter. Both variables are characterized by low values, which further confirms that the lichens of *Xanthoparmelia pulla* group thrive best in the areas with a dry climate.

Climate and habitat related variables are the most commonly used parameters in the distribution model studies and have been shown many times to correlate well with the species occurrence [33]. However, while drawing conclusions regarding the potential distribution of species, it should be taken into account that this distribution is influenced by many other factors, most of which could not be included in the analyzes. The factors limiting the species local ranges can be, among others, agriculture, urbanization, geographical barriers that reduce the dispersion, edafic factors, and, primarily in the case of lichens, the availability of suitable substrates [33,34]. In the obtained maps presenting the distribution of *Xanthoparmelia* species, some inaccuracy between recorded data and areas with optimal ecological conditions can be expected. Previously documented species occurrences were not always included in the 50–100% (>0.6) probability area estimated by MaxEnt. In such cases, the occurrence of the species was likely to be primarily determined by local microclimate conditions not included in the models, and the availability of silicate rocks that are the most suitable substrate for the lichens of *Xanthoparmelia pulla* group. In addition, it should be taken into account that the occurrence of widespread species is usually less well modeled than that of the species representing more restricted geographical ranges [34,35]. Perhaps the application of additional variables related to the substrate for modeling the lichen ranges would improve the relevance of the predicted models.

Potential distribution modeling based on the herbarium material is a very useful tool that can be applied in the research involving the biogeography of lichens. However, in order to obtain reliable MaxEnt models one needs to avoid errors stemming from incorrect identification of taxa and overfitting caused by including excessive number of environmental variables [33,36]. Therefore, in the case of *Xanthoparmelia* species, one of the primary goals of the study was the revision of the herbarium materials and a thorough selection of variables. However, herbarium data, even if they seem to be collected randomly, may be concentrated in areas that are of more interest to collectors. It is especially common for very attractive and easily accessible places, such as natural valuable and protected areas, tourist places and locations close to roads, large cities and universities, and collectors commonly focus on such places. This pattern can be also observed in the irregularly recorded data of modeled species of *Xanthoparmelia pulla* group that are distinctly concentrated in the well-studied north-eastern part of Poland. Consequently, the prediction model based on these data may be unreliable [13,33–35]. However, uneven distribution of the spatial data (spatial bias) may not have a negative impact on the model, if the specimens are collected equally in different types of environments, therefore avoiding the so-called environmental biases [33]. In the case of *Xanthoparmelia* species this rule was maintained, because the specimens originated from different ecosystems, both wooded and open, such as meadows, agricultural areas, roadsides, edges of woods, areas of quarry and cemeteries. Moreover, the use of a sufficiently large sets of data allows for an effective modeling of the species distribution, even if some climatic biases appeared during their collection [37]. Thus, it seems that the obtained models can suggest a real distribution of species of *Xanthoparmelia pulla* group in Central Europe. The next step towards a validation of the obtained models could be field studies that would confirm the presence of the investigated taxa in new areas that represent the most suitable climatic conditions.

To date, a number of studies using the MaxEnt have been carried out to model the geographical range of many types of organisms, especially vascular plants and bryophytes [38–41]. This method, however, has very rarely been used for predicting the ranges of macrofungi [34] and lichen-forming fungi [42–44]. However, obtained results indicate that this method can be a valuable tool supporting ecological and biogeographic research, as well as ordinary fieldwork concerning lichens. The interpretation of potential distribution models always requires particular caution. However, this method allows for estimating the size of species ranges and thus increases our knowledge on these ranges, as well as our understanding of the mechanisms affecting them. Distribution modeling also enables us to predict the risk of species extinction and is therefore a very valuable tool in the efforts to estimate and conserve the biological diversity of all organisms.

Acknowledgments

We are grateful to all Polish lichenologists and curators of Polish herbaria for making the specimens available for this study. The authors would like to also thank anonymous reviewers for their valuable remarks and corrections. The study was funded by Department of Botany and Plant Ecology, Wrocław University of Environmental and Life Sciences and Laboratory of Lichenology, Department of Botany, Institute of Environmental Biology, University of Wrocław.

Authors' contributions

The following declarations about authors' contributions to the research have been made: morphological analyses of the specimens: KS, MK; chemical analyses of the specimens: KS; MaxEnt models building: DP; MaxEnt analysis: DP, KS; writing of the manuscript: KS, DP, MK.

Competing interests

No competing interests have been declared.

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