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Modeling the distribution of rare and interesting moss species of the family Orthotrichaceae (Bryophyta) in Tajikistan and Kyrgyzstan

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Abstract

Bryological research carried out from 2008 in Tajikistan and Kyrgyzstan brought interesting data on the occurrence of epiphytic bryophytes which have not been recorded yet there. One of the species was recently described as a new (*Orthotrichum pamiricum*) and some of the other newly recorded species are considered as rare or endangered in the region of Middle Asia. To make detailed field monitoring of the species with the aim of mapping their distribution in a wild and complex mountainous terrain, it was necessary in the first instance to identify the area with suitable conditions for the occurrence of these species. We present an innovative modeling program MaxEnt (maximum entropy modeling), which have not previously been used for modeling either epiphytic bryophytes or in the Middle Asia region. Using 205 samples (presence-only data), percent tree cover, and seven uncorrelated bioclimatic variables, regions suitable for the occurrence of the studied species were identified. Distribution models for eight most interesting species of *Orthotrichum* are presented here (*O. affine, O. anomalum, O. crenulatum, O. cupulatum, O. pallens, O. pamiricum, O. pumilum,* and *O. speciosum*). They indicated appropriate areas for the most probable occurrence of the species in western Tajikistan, and southwestern and northeastern Kyrgyzstan. These results could serve as guides for future survey expeditions, and aid in the conservation of target species and our understanding of their ecology. Different environmental variables for various species were selected as the most important for modeling. However, for most species higher minimum temperatures and higher precipitation in the wettest month and mean diurnal range were the variables with the greatest contribution to the models.

Keywords

Introduction

Detailed bryofloristic research focused on epiphytic mosses began in Middle Asia in 2008 by the senior author. Four species new to Tajikistan (*Orthotrichum crenulatum, O. moravicum, O. sordidum,* and *O. urnigerum*) and five species new to Kyrgyzstan (*Orthotrichum crenulatum, O. dagestanicum, O. revolutum, O. scanicum,* and *O. vladikavkanum*) were observed [1–9]. Moreover, *O. pamiricum*, a species new to science, was described from the Tajik-Afghan border [10].

Although many important floristic and ecological data from the countries were collected and analyzed, there still exist numerous "white spots" on the map, from which bryological data are missing, especially in mountainous areas. This fact led the authors to

create a predictive distribution model, primarily for the rare species recently discovered in this region. It was subsequently extended to common species, and as such, could be easily tested in the field. Predictions of the species' geographical distribution based on available information would be beneficial for future field research [11], and could accelerate the discovery of unknown populations and species [12,13].

For this purpose, species distribution models (SDMs) have become a fundamental tool, because one potentially significant contribution of these models is to identify areas of higher probability of occurrence where future survey expeditions or the conservation of target species could be planned [14]. Several alternative methods have been used to predict the geographical distributions of species; on a few occasions, these were also used to model the distribution of mosses [11,14–18] and in one case, to model *Orthotrichum* species (*Orthotrichum rogeri*) using multiple logistic regression [19].

The problem with species distribution modeling (SDM) is that, in many cases, methods require both presence and absence data, but reliable absence data are rarely available in poorly sampled regions or for species that are easily missed during surveys [20], as is the case for bryophytes. Modeling is also problematic for species that have few records of occurrence. For these cases, maximum entropy modeling (MaxEnt) was ranked among the most effective applications for SDM [21]. MaxEnt is a machine-learning method [22–24] that uses principles of Bayesian estimation [25], and it calculates a raw probability value for each pixel of a study region using the maximum likelihood estimation method [26–28]. These raw probabilities are scaled to sum to one, and do not represent probability of occurrence, but rather an index of relative suitability [29]. Furthermore, it would be inappropriate to interpret the modeled distributions as actual borders of a species range. Rather, the models identify regions that have similar environmental conditions to those where the species currently maintains its populations [20]. It requires only species presence data (not absence) and environmental variable (continuous or categorical) layers for the study area [30]. A detailed and accessible description of the approach was provided by Elith et al. [25].

Studied species

All moss species presented in this article belong to the family Orthotrichaceae. One of the largest genera within the family, *Orthotrichum*, composed of at least 162 species [31], has been updated according to a number of sources [10,32–40]. Conversely, the genus *Nyholmiella* includes only two taxa (*Nyholmiella gymnostoma* and *N. obtusifolia*) [41]. Most are epiphytic mosses, occasionally growing as epiliths [42]. The taxa of these genera are widespread throughout the world from the Arctic to the Antarctic, except in deserts and wet tropical forests [43].

Study area

Tajikistan and Kyrgyzstan are two countries in Middle Asia. Altogether, they cover an area of 341 600 km² (Tajikistan 143 100 km², Kyrgyzstan 198 500 km²). They are very diverse countries in terms of their topography, mountain relief, climatic conditions, and vegetation cover. Their environmental uniqueness includes a great variety of habitats suitable for moss species. According to a recently published classification of global bioclimates, which mainly took precipitation rates and temperature values into account, the study area can be classified as a Mediterranean macrobioclimate [44]. This type of climate is characterized by a period of summer drought lasting for at least 2 consecutive months, in which $P < 2T$. As is typical of a Mediterranean climate, the area generally receives high levels of solar radiation as well as a low percentage of cloud cover, high-amplitude annual temperatures, and low humidity and precipitation. These climatic and bioclimatic conditions determine the vegetation types and plant communities found in study areas where evergreen forests, xerothermophilous swards, and shrubs dominate the lowlands and the colline belt.

Tajikistan lies mostly between latitudes 36° and 41° N and longitudes 67° and 75° E. It is covered by the mountains of the Pamir range, and more than 50% of the country lies at altitudes over 3000 m. The highest summit is Ismoil Somoni Peak at 7495 m. The

only major areas of lower lands are in the region of Fergana Valley and in the valleys of the southern Kofarnihon and Vakhsh rivers.

Kyrgyzstan lies between latitudes 39° and 44° N, and longitudes 69° and 81° E. The mountainous region of the Tian Shan Mountains covers approximately 80% of the country, with the remainder made up of valleys and basins. In the northeastern Tian Shan Mountains lies Issyk-Kul Lake, the largest lake in Kyrgyzstan. The highest peak is Jengish Chokusu Mountain at 7439 m.

Material and methods

Sampling methods

Field research during which epiphytic mosses were collected began in 2008 in Middle Asia. Tajikistan was visited twice (2008, 2012). Excursions were always directed into different regions, to explore as much of the various biotopes of the country as possible. In 2013, two expeditions to Kyrgyzstan were conducted using the same approach.

The mosses were collected from sites of abundance on different trees (they grew solitary, in alleys, or in the wood plots along river valleys) distributed across almost the entire territory of the countries. For all samples, GPS positions were recorded. Altogether, 896 samples (*Orthotrichum* 819 and *Nyholmiella* 77) were collected and identified by the authors. The plant material collected during the field surveys was deposited in the Herbarium of the University of Ostrava, Czech Republic (OSTR).

Sampling bias

MaxEnt tends to produce overfitted predictions when using biased occurrence records [20] and overfit models are more complex than the true relationships between the species niche and the examined environmental variables [45]. However, the problem with modeling species distributions is not the spatial bias in itself, but a bias in how the available environmental conditions are sampled. Sampling bias causes biased estimation of environmental relationships, with suitability being overestimated for environments that have been sampled more intensively and underestimated for those surveyed less frequently [46]. The most straightforward resolution of this problem is to manipulate the occurrence data to remove the bias; for example, by discarding or down-weighting records in over-sampled regions [47]. This was also confirmed by Fourcade et al. [48] who found that such a systematic sampling (reducing the spatial aggregation of records) was the simplest and most obvious way to solve the geographic bias. For these reasons, we filtered occurrence records with a linear distance ≤10 km to neighboring records using QGIS [49]. This distance was not chosen to approximate the species dispersal capabilities, but rather to reduce the inherent geographic biases associated with collection data (see Boria et al. [50]). Specifically, we filtered the final dataset to obtain the maximum number of samples that were at least 10 km apart (see Anderson and Raza [51]). This radius was chosen because of the topographic and environmental heterogeneity of this system, following Boria et al. [50], who predicted that mountainous regions would require a spatial filter that is smaller than that for regions having more homogenous environments.

After filtering occurrence records to reduce the likely effects of spatial autocorrelation caused by biased sampling, we had 205 samples (196 samples of the genus *Orthotrichum* and nine samples of the genus *Nyholmiella*). We also removed all species for which the number of samples ≤5 because of their inapplicability in SDM because of the low number of occurrences (*O. alpestre* – four samples, *O. dagestanicum* – two samples, *O. scanicum* – one sample, *O. revolutum* – four samples, *O. rupestre* – one sample, *O. sordidum* – three samples, *O. stramineum* – two samples, and *O. vladikavkanum* – one sample). After removing these species, we could create SDMs for 10 species of the genus *Orthotrichum* (*O. affine*, *O. anomalum*, *O. crenulatum*, *O. cupulatum*, *O. pallens*, *O. pamiricum*, *O. pumilum*, *O. speciosum*, *O. striatum*, and *O. urnigerum*) and for one species of the genus *Nyholmiella* (*N. obtusifolia*).

Environmental variables

For all species, we considered an initial set of 20 environmental variables representing various candidate predictors that were potentially relevant to the distribution of epiphytic bryophytes. In total, 19 environmental variables (Bioclim) were downloaded from WorldClim (http://www.worldclim.org/) [52], which is a set of global climate layers generated through interpolation of climate data from weather stations. These data were available at the resolution of 30 arc-seconds (approximately 1-km² resolution). Because we modeled species that were mainly epiphytic, we also included percent tree coverage (PTC) global version data in our model, which indicated percent coverage of tree canopy (i.e., density of trees on the ground) (http://www.iscgm.org/; Geospatial Information Authority of Japan, Chiba University and collaborating organizations). These data were based on 2008 MODIS data (Terra and Aqua satellites) available in 15-arc-second resolutions. PTC data were slightly modified; values representing water surface were converted to "no data" values because water surface is uninhabitable for the studied species. Furthermore, for MaxEnt analysis, these data have to be clipped and resampled to the same extent and resolution as the Bioclim data. We choose the cubic resampling method, because it is preferred for continuous data [53]. All environmental data were acquired in the WGS84 geographical coordinate system (EPSG:4326). For preparing environmental layers, we used functions from the GDAL library [54].

To avoid problems with multicollinearity (highly correlated variables), we selected the most meaningful and uncorrelated bioclimatic variables using ENMTools [55,56] to calculate Pearson's correlation coefficients. We used only those bioclimatic variables whose correlation coefficient, Pearson's r, was >0.7 or <−0.7. If variables were correlated between annual and one or more limiting variables (extreme events), we chose limiting variables for SDMs because they have more biological meaning to the distribution of the species [57,58]. In this regard, "annual average" factors, such as average temperature and precipitation, may have little meaning [59]. This resulted in eight bioclimatic variables (Tab. 1).

Tab. 1 List of uncorrelated environmental variables used for SDMs*.

Ecological variables used in the analysis	
BIO2	Mean Diurnal Range (mean of monthly max temp. – min temp.)
BIO6	Min Temperature of the Coldest Month
BIO7	Temperature Annual Range (max temp. of warmest month – min temp. of coldest month)
BIO13	Precipitation of the Wettest Month
BIO14	Precipitation of the Driest Month
BIO15	Precipitation Seasonality (coefficient of variation)
BIO18	Precipitation of the Warmest Quarter
PTC	Percent Tree Coverage

* SDMs – species distribution models.

The remaining set of variables was used to compile MaxEnt models and variables with contribution scores <5% were removed. This process was repeated until a set of uncorrelated variables with a model contribution >5% remained.

We performed a jackknife analysis to measure the importance of each variable to the final distribution models. This analysis provided a heuristic estimate of the relative contribution of the environmental variables to the MaxEnt model and it is standard output of MaxEnt.

Background area

Appropriate selection of background locations is essential for presence-only SDM [60], and recent studies have shown that the extent of the study area has a strong effect on the parameterization and evaluation of the resulting models [61–63]. Studies have also highlighted several methods for selection of background points (see van der Wal et al. [64]). For our study, we based the extent of the geographic region in which background points were taken on dispersal capacity and history of the species (see Acevedo et al. [62]) using buffers around presence points.

Spore dispersal patterns of bryophytes show a leptokurtic distribution [65,66] and density of falling spores is higher near the source with decreasing density in scales ranging from several dozens of meters [67] to several hundreds of kilometers [68], with significant number of spores travelling longer distances [69–72]. However, the typical effective dispersal for most colonizing bryophytes is in the tens of kilometers [73–75], and approximately 1% of the spore rain at the regional scale is assumed to have trans- or intercontinental origin [68].

We also assumed, with high probability (because of the long evolutionary history of bryophytes), that the genus *Orthotrichum* has had a long-term presence in the studied area. This means that a single generation's maximum dispersal distance will underestimate its maximum dispersal "reach" in the sense that the species may have had the potential to move out several-fold more than the basic, individual dispersal distance [61].

Based on previous information and because when seeking to identify unsurveyed sites for new survey efforts, it is better to use background points that are more likely to be true absences (outside the suitable area of the species and not too close to a presence point) [63], we used 200-km buffers around presence points for SDMs. This area seemed reasonable for background selection because it did not include large regions that the species did not inhabit, or areas too close to presence points. Models were then reprojected on the area of Tajikistan and Kyrgyzstan using MaxEnt software for species habitat modeling version 3.3.3k (http://biodiversityinformatics.amnh.org/open_source/maxent/).

In cases of spatial or temporal transfer, it is necessary to examine maps that indicate the degree of clamping [76]. "Clamping" indicates where the prediction is most affected by variables outside of their training range, while projecting the model onto the environmental variables in a newly projected area [23] to determine the effect (if any) that it had on model predictions; we did this by inspection. For all species, the effect of clamping was negligible.

Background points

MaxEnt takes a sample of 10 000 pixels from the study region used in model calibration to characterize the "background" of environments available to the species [29] and estimate habitat preferences by comparing the environmental characteristics at sites where the species has been recorded with those throughout the region modeled [46]. For the MaxEnt technique, Phillips and Dudík [24] found that predictive accuracy was higher with approximately 10 000 background pseudo-absences. Accordingly, we included 10 000 random background points identified from a circular 200-km buffer area around each presence point.

Feature class and regularization

In MaxEnt, several settings affect model accuracy by determining the type and complexity of dependencies on the environment that MaxEnt tries to fit. The complexity of dependencies is controlled by the choice of feature types, and by settings called "regularization parameters" [24]. MaxEnt selects default settings for feature classes, called "auto features", which applies the appropriate class or classes estimated for the particular sample size of occurrence records, according to the extensive tuning experiment of Phillips and Dudík [24]. In our models, the selection of "features" was

conducted automatically and for regularization, multipliers (that affect how focused or closely fitted the output distribution will be) were selected from a range of β values from 0.5 to 6 in increments of 0.5.

Model evaluation

For species with ≤20 samples. Because some species had only a very few occurrence records, we followed Pearson et al. [20] and used the "$n − 1$ jackknife" or "leave-one-out-jackknife" approach suggested for model evaluation with few samples. To aid in model validation and interpretation, tests required the use of a threshold value above which model output would be considered a prediction of presence defined as "suitable" and "unsuitable" areas [20]. Choice of a decision threshold was influenced by the application of the model, which should guide future fieldwork toward identification of unknown distributional areas and undiscovered species. Because of this, we did not need excessively conservative predictions, and we used the "lowest presence threshold" (LPT; Pearson et al. [20]) to convert continuous models to binary predictions for calculating threshold-dependent omission rate (OR). LPT can be interpreted ecologically as identifying pixels predicted as being at least as suitable as those where a species' presence has been recorded [20]. High-quality models should have zero or low omission of evaluation localities and predict evaluation localities statistically better than a random prediction [29]. This approach may be useful for higher sample sizes (up to approximately 25 records) [21], but herein we employed it for species with ≤20 records.

For validation, we used the secondary criterion. The area under curve (AUC) was calculated from the receiver operating characteristics curve (ROC). The AUC calculated from background evaluation data represented a threshold-independent measure of a model's discriminatory ability [23]. An AUC with high values referred to good results that significantly differed from random predictions [77]. Categories of AUC scores were invalid (<0.6), poor (0.6–0.7), fair (0.7–0.8), good (0.8–0.9), and excellent (0.9–1.0) [78,79]. We extracted evaluation OR and AUC values from the MaxEnt output for each jackknife iteration and averaged them to determine the final score. The logistic output was used for all visualizations. For every species, we chose the model with the lowest OR score, similar to the first criterion, or with the highest AUC score, similar to the secondary criterion, with the latter becoming necessary because of the same OR score for multiple models.

For species with >20 samples. To test the performance of the model independent of the data used to build it, we divided the occurrence data into training data (75% of occurrence point data used for model prediction) and test data (25% of occurrence point data used for model validation). We evaluated the resulting model using the ROC to calculate the AUC. High-value AUCs referred to good results that significantly differed from random predictions [77]. This operation was repeated 50 times and the AUC value averaged. The logistic output was used for all visualizations. From all models for every species, we chose the model with the highest AUC score.

If the AUC score for modeled species (any number of samples) did not reach an AUC score of at least 0.7 (fair), we did not include the results in our study. This applied to the following species: *Nyholmiella obtusifolia* (AUC = 0.3877), *Orthotrichum striatum* (AUC = 0.5867), and *O. urnigerum* (AUC = 0.6691).

Results

For all species used for modeling with an AUC score ≥0.7, we provide the basic characteristics of the models in Tab. 2. We also provide geographic maps of the models identifying regions that have similar environmental conditions to where the species currently maintains populations in Fig. 1.

The environmental variable with the highest relative contribution to the MaxEnt model was BIO6, with total percent contribution to all final models being 22.5%, which

was also the highest contribution score for models for two species (*O. anomalum* and *O. crenulatum*) and second highest contribution score for models of another four species (*O. affine*, *O. cupulatum*, *O. pallens*, and *O. pumilum*). The second highest relative contribution score among all models was BIO13 with a total score of 18.8%, which also had the highest contribution score for models of two species (*O. affine* and *O. pallens*). Next, the variable with the highest relative contribution score among all models was BIO2 with a contribution score of 16.8%, which also had the highest contribution score for the models of two species (*O. pamiricum* and *O. speciosum*) and the second highest for another (*O. crenulatum*). The following is the order of variables in terms of relative contribution: PTC 11.9%, which was the second most important factor for *O. pamiricum*; BIO18 10.1%, which was the most important variable for *O. pumilum* and the second most important for *O. anomalum*; BIO7 with 9.7%, which was the second most important variable for *O. speciosum*; BIO14 8.9%, which was the most important variable for *O. cupulatum*; and BIO15 with 1%.

Based on the jackknife test of variable importance, the environmental variable with highest gain when used in isolation (had the most useful information by itself) was BIO6 (for *O. anomalum*, *O. crenulatum*, *O. pallens*, and *O pumilum*), BIO2 (*O. pamiricum* and *O. speciosum*), BIO13 (*O. affine*), and BIO14 (*O. cupulatum*). The environmental variable that decreased the gain the most when it was omitted (had the most information that was not present in other variables) was BIO18 (*O. anomalum*, *O. crenulatum*, *O. pumilum*, and *O. speciosum*), BIO13 (*O. affine*, *O. cupulatum*, and *O. pallens*), and BIO2 (*O. pamiricum*).

The best model from species with >20 samples was the model for *O. anomalum* with an AUC score of 0.9236. The best model from species with ≤20 samples was the model for *O. pallens* with OR = 0.0769 and AUC = 0.7928.

All models had the same basic characteristics, but we observed some differences among them. The model for *O. affine* had the highest values in the center of the western part of Tajikistan. The model for *O. anomalum* had the highest values in northeastern and southeastern areas of Issyk-Kull Lake, around the Toktogul Reservoir near Bishkek City, and near the confluence of the Vakhsh and Obikhingou rivers. The model for *O. crenulatum* clearly showed highest values in areas in the northeastern part of Kyrgyzstan and in the eastern parts of Issyk-Kull Lake. The model for *O. cupulatum* reached highest values in the center of the western part of Tajikistan. The model for *O. pamiricum* was influenced by the low number of samples, but we observed high values in the southwestern region of Tajikistan along its borders with Afghanistan and near Arslanbob town in Kyrgyzstan. The model for *O. pumilum* showed the highest values around the Toktogul Reservoir, in southwestern Kyrgyzstan near its borders with Uzbekistan, and in the areas northeast of Issyk-Kull Lake. The model for *O. speciosum* reached the highest values around Dushanbe City, in areas around the confluence of the Vakhsh and Obikhingou rivers, and east of Issyk-Kull Lake.

Discussion

Bryophytes are very sensitive to microclimatic changes [80,81], and ecological conditions needed for most mosses are likely to be microenvironmental [82], but on coarser spatial and temporal scales, other drivers are crucial to the composition of epiphytic communities, including macroclimatic conditions [82,83].

As we mentioned, similar research focused on species distribution modeling within the genus *Orthotrichum* was already realized [19]. However, in the case of *O. rogeri*, multiple logistic regression was used by the authors and both types of the data, presence and absence, were required. Because we had only presence data available, MaxEnt was used for all models. However, we also decided to use MaxEnt because (*i*) it appears preferable for its efficiency of prediction over wider geographical areas, (*ii*) it requires only presence data, (*iii*) it requires fewer, easily obtainable environmental variables, which has been confirmed by previous studies [84].

In our study, we used three variables connected with temperature (BIO2, BIO6, and BIO7) and four with precipitation (BIO13, BIO14, BIO15, and BIO18). We also used the PTC (percentage of tree coverage) as a factor. The reason was that some of these

Tab. 2 Summarization of results from SDMs for all species with a final AUC score >0.7.

	O. affine	O. anomalum	O. crenulatum	O. cupulatum	O. pallens	O. pamiricum	O. pumilum	O. speciosum
Sampl.	13	23	40	13	13	6	26	23
β	0.5	0.5	0.5	1.5	0.5	1	0.5	0.5
Contr. (BIO2)	-	14	18.2	-	9.9	52.6	17.6	22.8
Contr. (BIO6)	32.4	22.1	25.5	22.1	40	-	22.5	15.4
Contr. (BIO7)	-	18.8	15.4	-	-	-	22.2	21.6
Contr. (BIO13)	52.9	5.1	11.2	20.9	41.5	-	7.7	11
Contr. (BIO14)	-	7.7	-	56.9	-	-	6.8	-
Contr. (BIO15)	-	-	-	-	8.6	-	-	-
Contr. (BIO18)	-	21.3	15.6	-	-	-	23.2	20.7
Contr. (PTC)	14.7	10.9	14	-	-	47.4	-	8.6
JK1	13	6	6	14	6	2	6	2
JK2	13	18	18	13	13	2	18	18
OR	0.0769	-	-	0.0769	0.0769	0.1667	-	-
AUC	0.7821	0.9236	0.8568	0.7355	0.7928	0.7864	0.8633	0.8542

Sampl. – number of samples; β – regularization multiplier; contr. – relative percent contributions of the environmental variables; JK1 – environmental variable with highest gain when used in isolation; JK2 – environmental variable that decreases the gain the most when it is omitted; AUC – average area under the receiver operating characteristic curve; OR – average omission score.

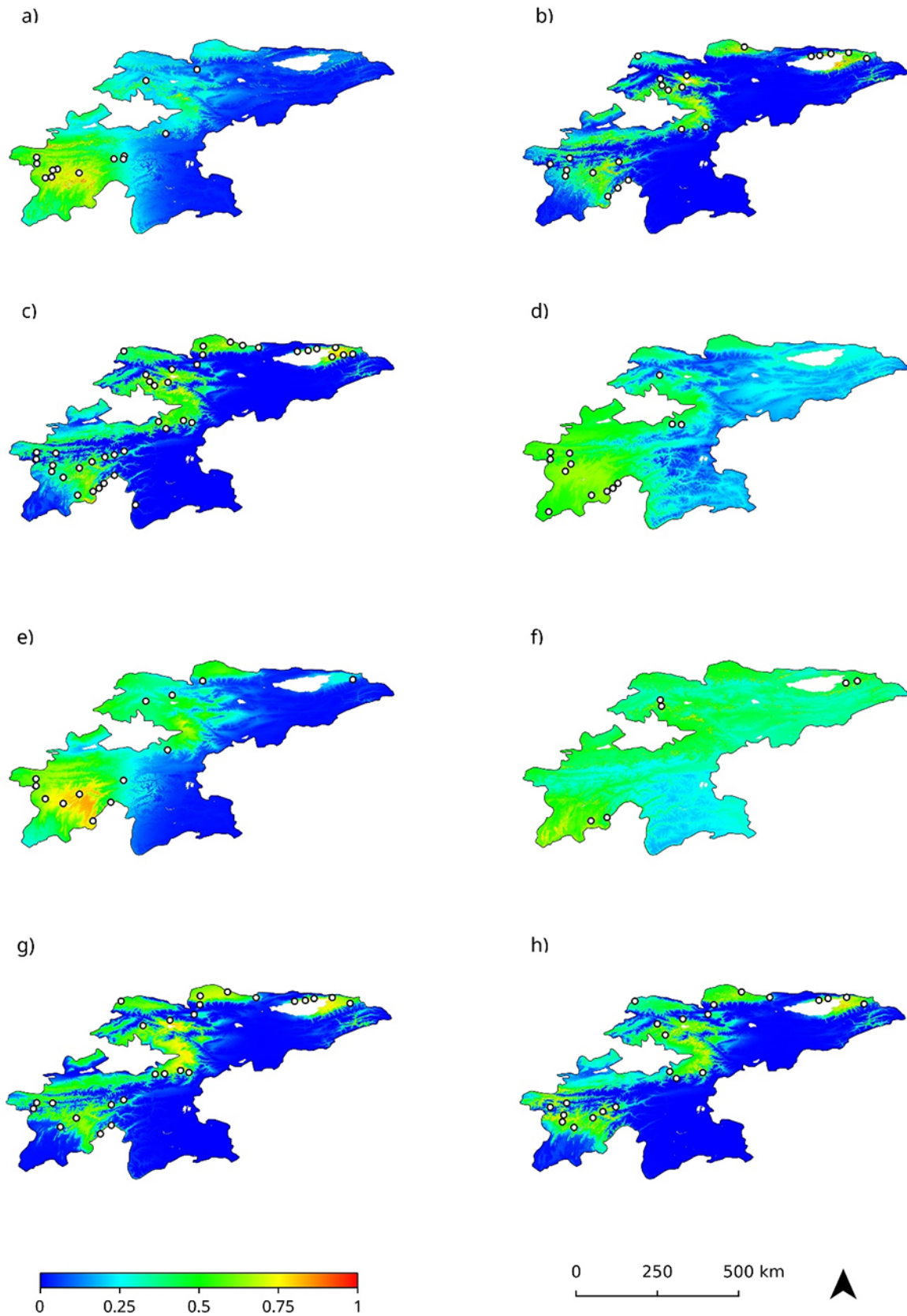**Fig. 1** Geographic map identifying regions that have similar environmental conditions to currently known populations visualized on a scale from 0 to 1 for the area of Tajikistan and Kyrgyzstan with displayed collection points. **a** *Orthotrichum affine*. **b** *O. anomalum*. **c** *O. crenulatum*. **d** *O. cupulatum*. **e** *O. pallens*. **f** *O. pamiricum*. **g** *O. pumilum*. **h** *O. speciosum*.

epiphytic species also grew saxicolously (less than 5% of all the recorded populations). That is why the samples were always biased between saxicolous and epiphytic data, and between presence and absence of trees. By analyzing data in this manner, we proved that "tree cover" is one of the most crucial factors influencing the occurrence of the studied species. It is important not only as a substrate, but also as a barrier to the spread of spores, source of shading, and creator of microclimate conditions, among other factors. Furthermore, this layer will also be important when we model the distribution of saxicolous or terrestrial species. It can also be interpreted as a factor marking the tree line in these mountainous countries. Because all species that exhibited correlations with higher values of the PTC factor had distributions below the tree line, we can assume that above this line their occurrence rapidly declines. Based on field research, we also know that epiphytic species within the *Orthotrichum* genus grow only sporadically above the tree line.

The most important factor for almost every species was minimum temperature in the coldest month. This variable acted as a limiting factor and in combination with other factors influenced the occurrence of almost every modeled species. Essentially, most of the species can be divided into two groups: the first group consists of species that are most influenced by a combination of minimal temperature of the coldest month and precipitation during the wettest month (*O. affine*, *O. pallens*), and the second group consists of species dependent on the combination of minimal temperature in the coldest month, mean diurnal range, annual temperature range, and precipitation during the warmest quarter (*O. anomalum*, *O. crenulatum*, *O. pumilum*, and *O. speciosum*). The species *O. cupulatum* did not fit in either of these groups, but had something in common with the first group (dependence on minimum temperature and precipitation during the wettest month). The last species, which did not fit into either group, was *O. pamiricum*, which exhibited dependence on mean diurnal range and tree cover. Species in the first group were dependent on higher values of precipitation in the wettest month, and only minimally dependent on other temperature variables (mean diurnal range and annual temperature range). This may be because the wettest month in the study area is during the spring, which means that precipitation is mostly snow. Snow can function as isolation from the surrounding environment, and thus makes these species more resistant to temperature ranges.

Species in the second group, which exhibited minimal dependence on snowfall, were more connected with variables associated with the range of temperatures. These two factors had opposite effects. Higher values for mean diurnal range reflected positively on the probability of occurrence, which could reflect their tolerance to short-term fluctuations. Higher values of annual temperature range over the year led to lower probabilities of occurrence. This could indicate a limitation because of the temperature range. Another interesting feature in the second group is the dependence on rainfall in the driest quarter of the year. The higher values are for rainfall, the higher is their probability of occurrence, which indicates a connection with drying and their dependence on water availability.

The most important factor for *O. cupulatum* was precipitation during the driest month. In this case, higher values of rainfall in the driest month were related with higher altitudes where rainfall occurs even during the driest periods of the year. The probability of occurrence decreased with higher values of this variable, and as such, this could indicate a greater adaptation to desiccation and ability to survive prolonged periods of drought. This may be explained by the fact that *O. cupulatum* is largely adapted to an epixylic life strategy and these extreme conditions.

The species *O. pamiricum* was the last of the studied species, and it showed a different dependence on factors than did the others. It was mainly dependent on the variance of monthly temperatures and higher percentage of tree cover, which points to continuous forest vegetation at lower elevations.

A total of 896 moss specimens from Tajikistan and Kyrgyzstan were collected, but only 205 samples could be used for the purposes of modeling because of sampling bias. The significant difference between collected samples and samples used for modeling resulted from the need to collect as much material as possible for later determination in the laboratory. Even if samples were biased because of higher collection effort, this collection effort occurred because of the impossibility of determination of species in the field and the need for enough material for later determination. In addition, although

we discovered 18 species of the genus *Orthotrichum* and one species of the genus *Nyholmiella*, we could use only 11 species for modeling and only eight final models were of sufficient quality to use in our study.

Final models can contribute to our understanding of the ecological requirements of species. All our models were based on percent tree cover and seven uncorrelated climatic factors, from which a set of variables that all had a model contribution >5% were chosen for the final models. Results showed different preferences among species, but for most species, their requirements reflected reliance on higher minimum temperatures and mean diurnal range, which are both higher in the lower-situated areas. As such, the models reached higher values in the lowlands and in western Tajikistan, where greater precipitation was observed in the wettest month. However, there were exceptions, for example, the model for *O. cupulatum* showed a greater dependence on precipitation during the driest month. At higher values of this variable, there were lower values in the model. This was probably connected with higher precipitation in the mountains in the dry month, which favored the areas with lower precipitation in the lower-lying areas.

As we can see, some species (usually with higher number of analyzed localities), have more exact maps (with stronger contrast) than those with fewer localities. This can be explained by the fact that with increasing numbers of the analyzed samples, the number of the degrees of freedom also increases. Therefore, the number of solutions also exhibit accretion and maps with more samples have greater contrast.

For bryologists, it is often not possible to examine the entire area of interest. Additionally, field research in unexplored areas of the world is usually associated with substantial financial costs, as well as substantial time consumption. In this regard, the SDMs could help to focus efforts in areas that could provide a larger number of suitable sites for studied species.

Based on our results and relatively high AUC and low OR scores, we can assume that our models reflect the real situation in the studied countries, but in the future, it would be appropriate to test the models directly in the field, because such research could improve the validity and precision of predicted distributions of the genus *Orthotrichum*. Until then, the models can serve as a guide to future survey expeditions, and an aid in the conservation of the target species and understanding of their ecology.

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